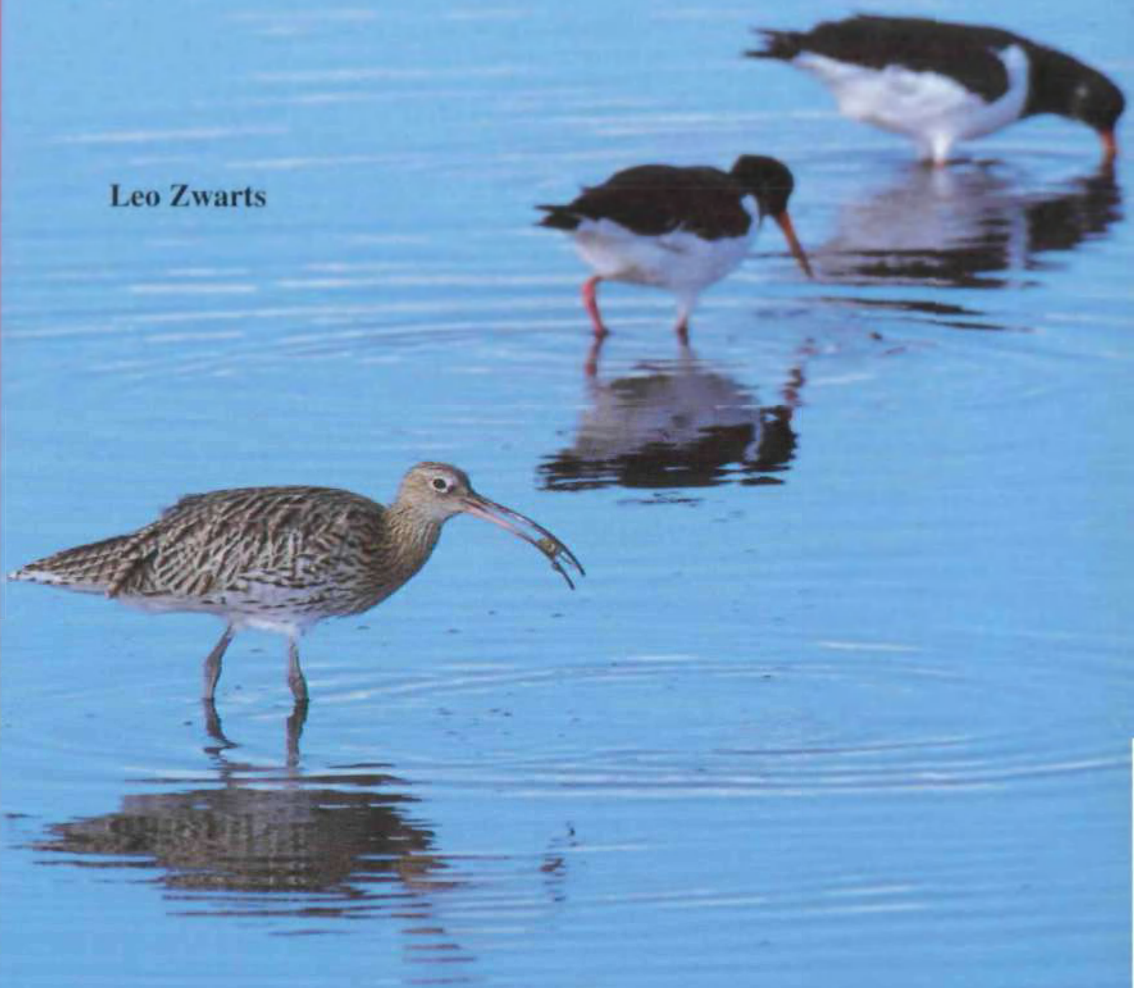
van zee tot land

WADERS AND THEIR ESTUARINE FOOD SUPPLIES Leo Zwarts

60

van zee tot land

WADERS AND THEIR ESTUARINE FOOD SUPPLIES



Leo Zwarts

Ministerie van Verkeer en Waterstaat

Directoraat-Generaal Rijkswaterstaat

Directie IJsselmeergebied

STELLINGEN

behorende bij het proefschrift
Waders and their estuarine food supplies
van Leo Zwarts

1. Schol helpt scholekster.

2. Aangezien de variatie in het daadwerkelijke voedselaanbod veelal meer wordt bepaald door de enorme variatie in de oogstbare fractie van het voedsel dan door de variatie in het totale hoeveelheid voedsel, is het altijd lonend om bij onderzoek naar predator-prooi-relaties de bereikbaarheid van het voedsel en de prooiselectie van de predator nauwkeurig te kwantificeren.

3. Als dominante vogels minder lichaamsreserves aanleggen dan subdominante vogels, is dit niet omdat het dominant zijn zoveel energie kost, maar omdat vogels die hoog in de pikorde staan kennelijk met een kleinere energetische noodvoorraad denken te kunnen volstaan (contra J.M. Bowler (1994) Ardea 82: 241-248).

4. De sterfte die optreedt bij het vangen van vogels met behulp van netten ten behoeve van wetenschappelijk onderzoek wordt ten onrechte nooit onderworpen aan een kritische evaluatie. Zeker wanneer het onderzoek afhankelijk is van de terugvangst van individuele vogels moet deze mortaliteit worden geschat.

Marita Cals

WADERS AND THEIR ESTUARINE FOOD SUPPLIES

UITNODIGING

tot het bijwonen van de verdediging van het proefschrift
en de daarbij behorende stellingen op
vrijdag 10 januari 1997 om vier uur precies
in het Academie-gebouw, Broerstraat 5, Groningen

Na afloop receptie in het Academie-gebouw

Leo Zwarts

huidig adres:
werk: RIZA
Postbus 17
8200 AA Lelystad

of privé:
Compagnonsweg 45/47
8427 RH Ravenswoud
tel. 0516-433905

5. Aangezien vele van de weide- en moerasvogels die hier te lande broeden, het grootste deel van het jaar geconcentreerd zijn in Afrikaanse moerasgebieden, is de toekomst van deze vogels in sterke mate afhankelijk van de gang van zaken in deze overwinteringsgebieden.

6. Jacht heeft een negatieve effect op de omvang van een dierpopulatie omdat, als gevolg van de toename in de schuwheid van de bejaagde dieren, het gebruik van hun leefgebied wordt beperkt. Dit indirecte effect is waarschijnlijk van veel groter belang dan het direct meetbare effect van de verhoogde mortaliteit als gevolg van het afschot.

7. Mensen die in de tropen leven, ervaren de natuur veelal als een bron van gevaren en zelden als een plek waar het aangenaam verpozen is. Dit bemoeilijkt de export van de natuurbeschermingsgedachte vanuit de gematigde streken naar de tropen.

8. Het feit dat de meeste, zelfs duur uitgevoerde, rapporten worden uitgebracht zonder dat titel en auteur op de rug worden vermeld, doet vermoeden dat het de bedoeling is ze te bewaren in een bureaula en niet in een boekenkast.

Waders and their estuarine food supplies

Ministerie van Verkeer en Waterstaat
Directoraat-Generaal Rijkswaterstaat
Directie IJsselmeergebied

Van Zee tot Land 60

Lelystad 1996

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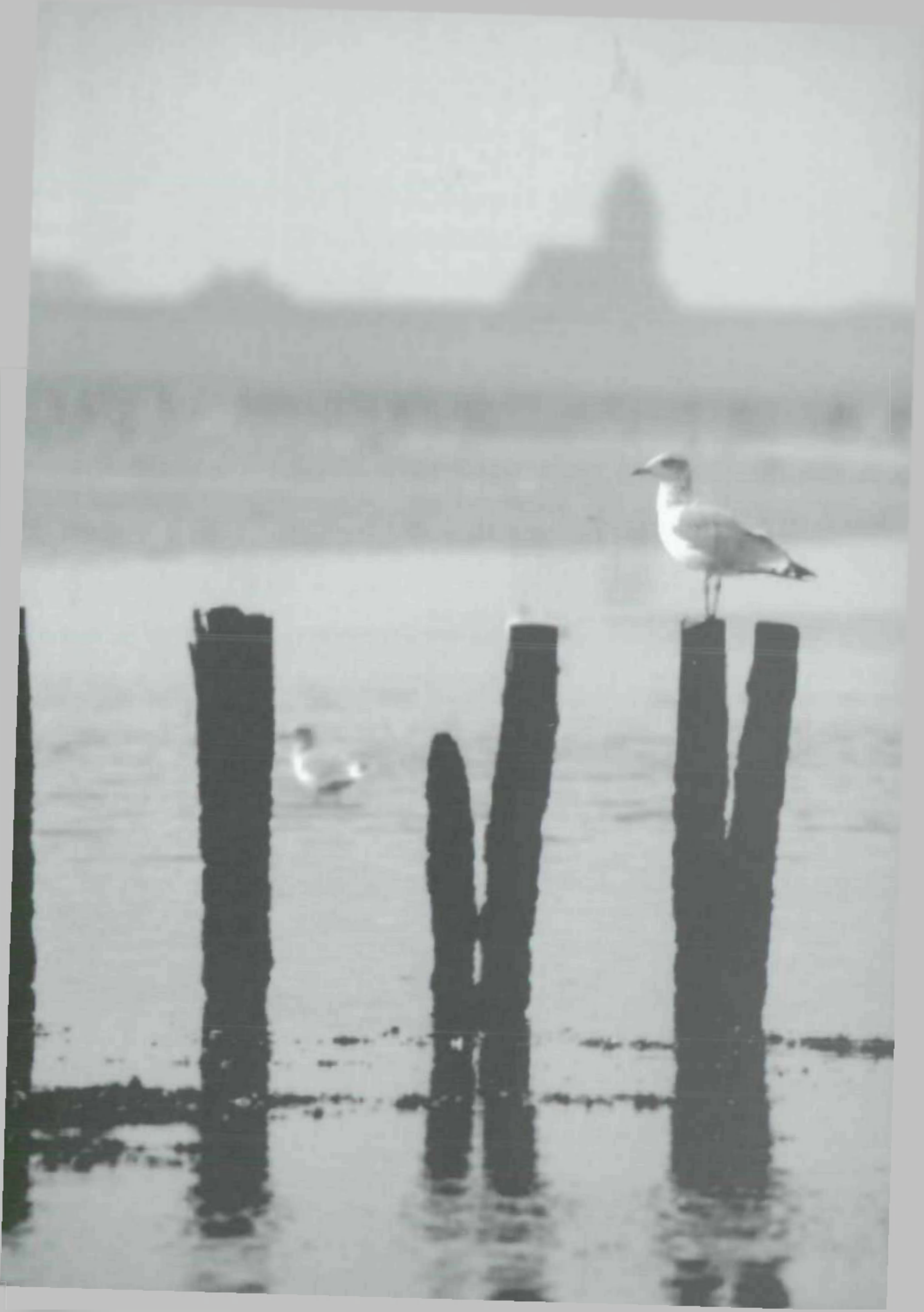
WADERS AND THEIR ESTUARINE FOOD SUPPLIES

Leo Zwarts

Van Zee tot Land 60

Dit rapport vormde tevens het proefschrift waarop de auteur op 10 januari 1997 promoveerde aan de Rijksuniversiteit te Groningen.
Als promotor trad op prof. dr. R.H. Drent.



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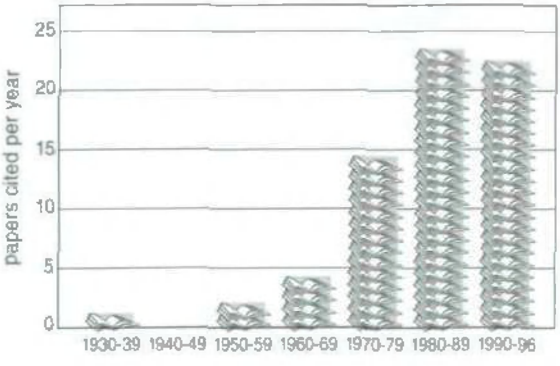
CONTENTS

INTRODUCTION

INTRODUCTION

That science is making progress, may clearly be illustrated with the growth of our knowledge about waders, or shorebirds, and their food supply, the macrozoobenthos living in the intertidal mud and sandflats. Forty years ago, the exciting phenomenon of the massive wader flocks passing through the Wadden Sea was appreciated but not quantified, nor were the migratory pathways known in detail. Now we know where the waders breed, where they winter and how many millions stage in the Wadden Sea, thanks to the many people who have been catching and counting birds the last decades. Also the year-to-year variation in their food supply is known, as well as the factors causing these fluctuations, thanks to the NIOZ, in particular the perseverance of Jan Beukema who started in 1964 a biannual sampling programme of the macrozoobenthos in the western part of the Wadden Sea. The annual number of scientific papers reflects this explosion of our knowledge in this field of research, as visualised with the frequency distribution of cited papers in the list of references.

Do we not know enough about the Wadden Sea? For scientists, this is an illogical question, because there is no limit to the sky. The most profitable research strategy must be a comparison between the well-studied Wadden Sea and less-studied estuarine systems elsewhere and, indeed, expeditions to West Africa and elsewhere during the last 15 years, in which many workers from the Wadden Sea took part, resulted in the most interesting papers. Clearly, these papers would not have been written without the knowledge built up during many years of research in the Wadden Sea. Yet it remains of importance to continue research in the Wadden Sea, and not only to monitor the annual fluctuations in animal life, because several fundamental questions have still not been answered. The question whether the population of birds using the intertidal flats is limited by their food supply, has been a leading question in most of the bird research in the Wadden Sea. The tendency of 'waderologists' in the Wadden Sea, but also elsewhere, to focus on the problem of the carrying capacity is not surprising, because the bird species depending on the tidal zone, have recently lost a substantial part of their feeding area in Europe and Asia. Does the loss of refuelling stations during migration and the decreasing surface area of their overwintering grounds negatively affect the size of the bird populations? The question is simple, but appears to be extremely difficult to answer. Therefore, the best strategy is to break down the main question into many small, more or less answerable, questions. Most of the papers collected in this thesis deal with these derived questions. To what extent the solution of the isolated questions contributes to the overall problem will help to define the research needs of the coming years.



Frequency distribution of cited papers in list of references.

Our research has focused in detail on the relationships between three waders, Oystercatcher, Curlew and Knot, and their food supply. On the tidal flats along the Frisian coast, we built hides on towers from which the feeding birds could be observed at short distance.

Thousands of Oystercatchers and hundreds of Curlews were individually marked with colour rings, so we were able to watch the same individuals for days or months and, some birds, even for years. Around these towers many thousands of pegs were placed to be able to describe in detail the searching path of individual birds and the feeding time spent per plot. For the same plots we determined the average density in which the different bird species foraged, the density in which the different prey species occurred in the substrate, but also the clay content of the substrate and the elevation. The burying depth of the bivalves and the burrow depth of the worms were measured in some selected plots.

This thesis collects sixteen papers that have already been published as separate papers in six journals or as chapters in two books. Apart from some corrections of small errors, they were printed without changes. The first two papers describe the seasonal and annual variations in the food supply of the waders. The next four papers deal with the burying depth of bivalves. Five papers are about Oystercatchers, two about Knot, one about Curlews and one about Oystercatchers and Curlews. All these papers have in common that they deal with the feeding decisions of waders and the anti-predator behaviour of their prey. As shown below, some matters are raised in more than one paper.

Sampling of the prey

Chapter 1 describes the procedures to sample the macrozoobenthos and the way in which the biomass (g ash-free dry weight m^{-2}) of the bivalves was determined. The samples in one of the study areas were taken once a month during nearly ten years. The lengths and weights of all collected prey were measured. This allowed to estimate the monthly growth for the different year classes (Ch. 11, 13 & 16), the mortality (Ch. 11, 16) and the somatic production (Ch. 11). Information about the temporal and spatial variation in biomass is given in chapter 2, 11 & 13.

Burying depth of the prey

The majority of the macrozoobenthos live buried safely beneath the surface, hence only a fraction of these prey are accessible to waders. To measure the fraction living within reach of the wader's bill, during seven years we determined the burying depth of bivalves and worms each fortnight (Ch. 2, 4, 8, 12, 14 & 16). In most species, the seasonal and annual variation in the accessible fraction was much larger than the variation in the numerical density. Consequently, the fluctuation in the prey density was much larger, if restricted to the prey actually accessible to waders.

Burying depth and feeding mode

There is no seasonal variation in the burying depth of Cockles *Cerastoderma edule* and Soft-shell Clams *Mya arenaria*, but two other clams, *Macoma balthica* and *Scrobicularia plana*, which use their siphon to graze at the substrate, live close to the surface in summer and deeply buried in winter (Ch. 2, 3). The latter two species bury in winter so deeply that they can just reach with their siphon the surface, whereas in summer they use a part of the siphon to graze at the surface (Ch. 5). Since Cockles and Soft-shell Clam are suspension feeders, they use their siphon to reach the surface and thus show no seasonal variation in burying depth.

Burying depth and prey risk

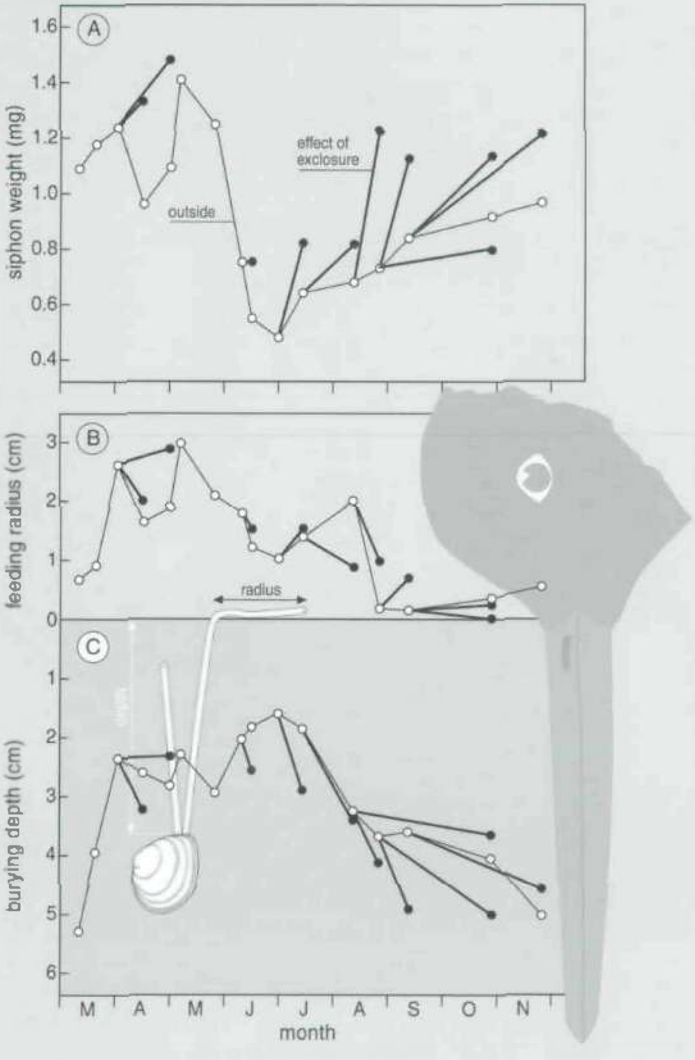
Deep-living prey have a much lower risk to be taken by a predator than shallow ones. Why do some bivalves risk their lives to be close to the surface? Burying depth increases with size, because the larger bivalves invest relatively more in their siphon weight, although above a certain size burying depth and siphon investment levels off (Ch. 3). There is a huge variation in burying depth for bivalves of similar size. This may be attributed in part to variation in siphon weight (Ch. 3 & 4). Bivalves with a light siphon live nearer to the surface, especially when their body reserves are low. For deposit-feeding bivalves, the selected burying depth is the compromise between two opposite tendencies: to minimize predation risk by using the siphon to live as deeply as possible, and to maximize the intake rate by using the same siphon to extend the feeding radius around their burrow on the mud surface. Apparently, bivalves in a poor condition take more risks.

Burying depth and siphon cropping

Siphon cropping experiments (Ch. 4 & 5) revealed that bivalves move to the surface after they have lost a part of the siphon. Still unpublished experiments showed that juvenile flatfish, Common Shrimps *Crangon vulgaris* and juvenile Shore Crabs *Carcinus maenas* exert

The remnants of brushwood groynes demarcated 53 areas on the tidal flats along the Frisian coast. From the high sea wall, we could easily count the feeding birds in all these areas.

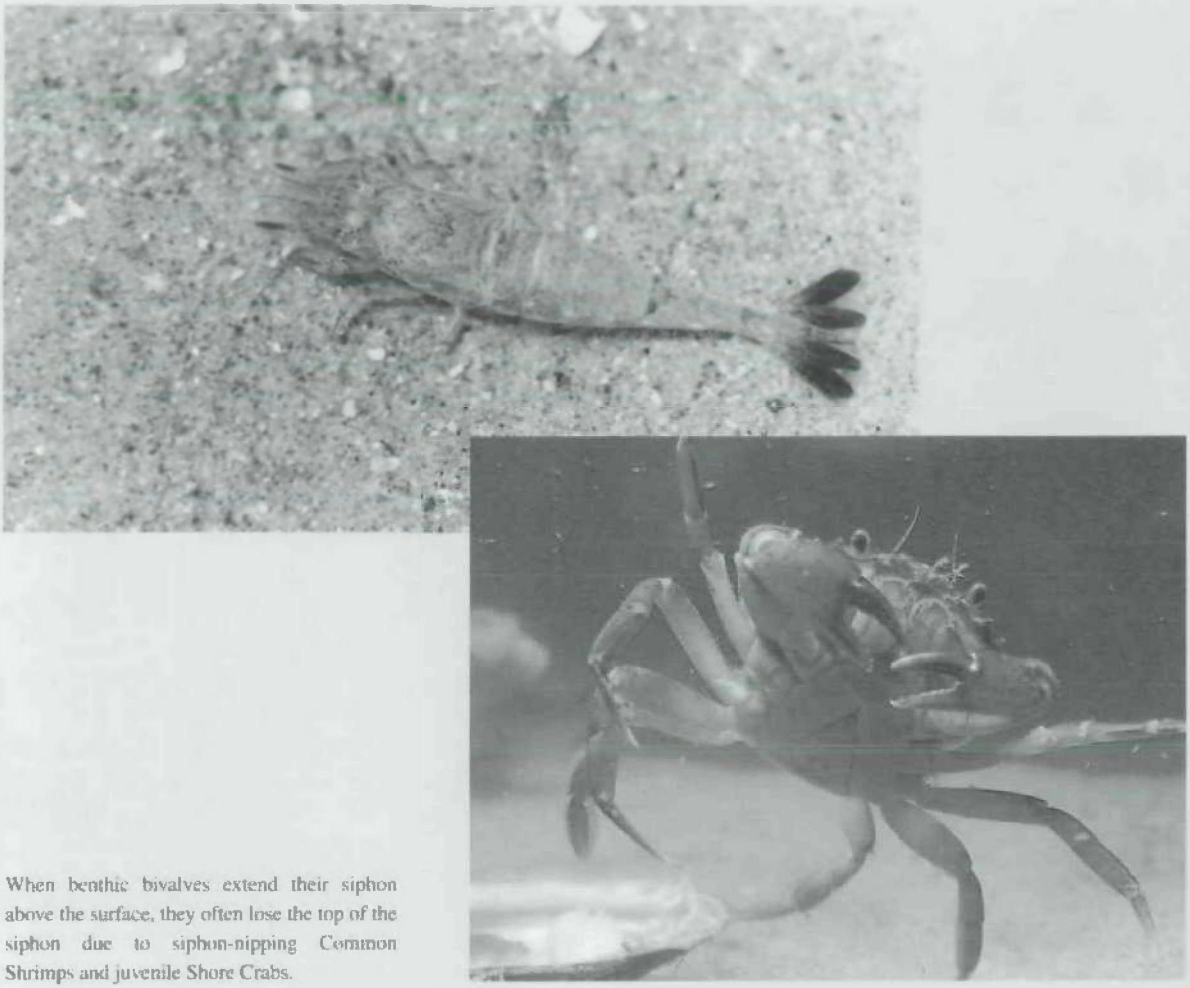
WHY FISH, SHRIMPS AND CRABS FACILITATE BIRD PREDATION ON BENTHIC BIVALVES



Siphon nipping reduces burying depth of bivalves. **A** The siphon weight, **B** feeding radius and **C** burying depth of *Macoma* 15 mm long between March and November 1986. The solid line connects the average values outside the exclosure; the thin lines indicate the effect of the exclosure which kept out siphon-nipping fish, shrimps and crabs.

Baltic Tellinids *Macoma balthica* can live safely hidden in the substrate because they are able to acquire oxygen and food by pushing their inhalant siphon through the mud to the surface. The siphon may even be stretched more, and bent horizontally, to graze at the surface. Especially in the latter case, the protruded siphon is an easy bite for predators. What happens if these siphon-nipping predators remove the tip of the siphon very often? Does the siphon become shorter, and if so, does the clam reduce its feeding radius on the surface and/or does it reduce its burying depth?

To answer these questions, we used cages of 1 × 1 m and 30 cm high. The top and sides were covered by fine netting with a mesh width of 1-2 mm, which was fine enough to exclude juvenile Shore Crabs, Common Shrimps and fish. After a fortnight, but sometimes longer, we compared the burying depth and siphon weights of *Macoma* within the cage and in the surroundings. Even within a fortnight, the siphons became heavier, which enabled the bivalves to increase their burying depth. The feeding radius on the surface was not measured directly, but could be estimated, after subtraction of the burying depth, from the quantified relationship between siphon weight and siphon length. As shown, also the potential feeding radius increased after the siphon-nipping predators were experimentally removed. Siphon nipping also affected (not shown) the body condition of *Macoma*. Apparently, the continuous regrowth of the siphon took place at the expense of the total body weight.



When benthic bivalves extend their siphon above the surface, they often lose the top of the siphon due to siphon-nipping Common Shrimps and juvenile Shore Crabs.

Does siphon nipping also affect the predation risk of *Macoma*? The exclusion of the siphon nippers caused an increase of the burying depth; in some cases *Macoma* even reached the winter depth of 5 cm. The main predator of large *Macoma* is the Oystercatcher. The bill of this species is 7 to 8 cm long and since the bird may thrust its bill entirely into the mud, one may ask whether the observed small increase of the burying depth is sufficient to reduce the risk to be taken by Oystercatchers. Detailed observations on the depth selection of Oystercatchers feeding on *Macoma* are still lacking. However, there is enough indirect evidence that Oystercatchers ignore *Macoma* living at 4 to 6 cm, because these prey, although still accessible, are unprofitable, due to the increase of handling time with burying depth. Therefore, *Macoma* are already safe from bird predation when they live 4 or 5 cm beneath the surface of the mud. For the same reason, *Macoma* are only a summer prey for Oystercatchers, because their increased winter depth makes them too unattractive to feed upon. Hence, the subtle reduction of the burying depth due to siphon grazing may increase its value as prey and, thus, the risk to be predated. Concluding, siphon nipping by fish, shrimps and crabs facilitates bird predation, or as Rudi Drent said immediately when I first showed him the graph: "Schol helpt Scholekster" (fish helps bird).

The macrozoobenthos sampled by a corer with a surface area of 178 cm^2 and 40 cm deep The core was sieved through a 1-mm mesh screen.

so heavy a grazing pressure on the siphons in spring and early summer that the bivalves not only end up with short siphon, but also a poor body condition (see pag. 14-15). The prey are thus forced to live near the surface and expose themselves to a higher risk to be taken by birds.

Only lean prey may be accessible

Bivalves and worms living close to the surface are in a poor condition compared to congeners of the same size living more deeply. Since waders can only feed upon bivalves that are within reach of the bill, the intake rate during feeding is overestimated when this is not taken into account (Ch. 6). The degree of overestimation can be calculated when the depth selection is known, as well as the relationship between prey condition and burying depth.

Surface activity of worms

Worms usually live out of reach of the bill, but they are extremely vulnerable to predation when they come to the surface to defecate (e.g. Lugworms *Arenicola marina*) or to make feeding excursions at the surface (e.g. Ragworms *Nereis diversicolor*). The tidal variation in the feeding activity of Ragworms is described in chapter 14 and the response of Curlews in chapter 15. Curlews use two strategies when they feed on Ragworms. When the worms live in shallow burrows, Curlews walk slowly, carefully searching for burrow entrances, after which the worms are extracted from the burrows, but when the burrow depths exceed the bill length, by which worms can safely retreat out of reach of the bird, Curlews walk fast to increase the encounter rate with worms emerging from their burrows. In practice, Curlews mix both strategies depending on the burrow depths and on the fraction of worms being actively feeding.

Prey size selection by waders

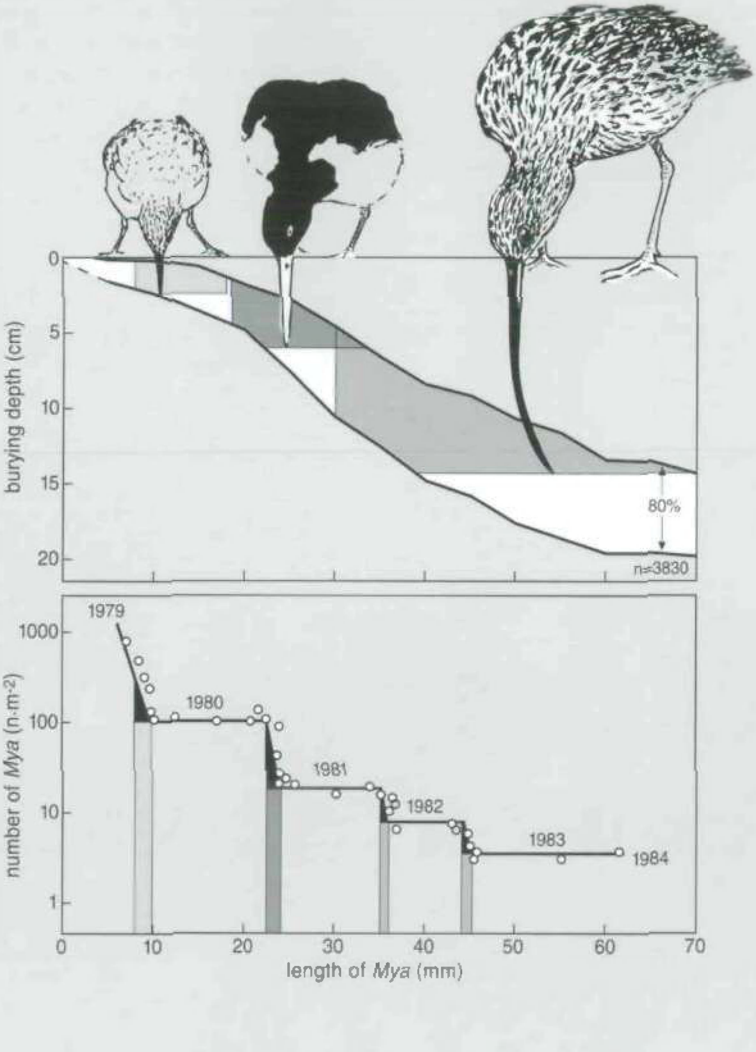
The prey size selection of a bird may be predicted, assuming that birds probe to a certain depth and do this at random, as shown for Oystercatcher (Ch. 8) and Knot (Ch.12). Comparison of the size frequency distribution of the prey taken with those of the size classes on offer, reveals that birds ignore the small size classes. These small prey are unprofitable, i.e. the intake rate during handling the prey is below the average intake rate during handling and searching combined. By ignoring these prey, the birds enhance their intake rate.

Ignoring prey to maximize intake rate

An experiment was set up to test whether an Oystercatcher feeding on bivalves buried at different depths maximized its intake rate (Ch. 7). Shallow prey could be handled very fast and were thus highly profitable. In contrast, it took much time to eat prey from greater depths. The prediction was that the decision to include these prey in the diet, or to ignore them, would depend on the intake rate. It was found that the bird, conforming the prediction, took all prey within reach of the bill at low prey densities, but only prey from the upper few cm when the prey occurred at high densities. However, the bird was able to eat more prey than the model predicted for the high prey densities. The explanation was that the bird selectively took only the prey that could

The observation towers on the tidal flats were strong enough to resist winds with hurricane force and storm tides, but the force of drifting ice was too much. Hence we had to rebuilt the towers after every severe winter.

WHY KNOT, OYSTERCATCHER AND CURLEW FEEDING ON SOFT-SHELL CLAMS TAKE DIFFERENT SIZE CLASSES



A The burying depth of *Mya* as a function of shell size; the range of depths within which 80% of the clams are found is indicated. The size selection of the accessible prey are shown for Knot, Oystercatcher and Curlew. **B** Decline and growth of the year class 1979. The step-wise decrease in the population is due to the successive predation of Shore Crabs (and not Knot) in late summer 1979, Oystercatchers in autumn 1980 and Curlews in the winters of 1981/1982 and 1982/1983.

The life history of the Soft-shell Clam *Mya arenaria* may be summarized in two simple graphs. After an initially high density, there is not a gradual, but a step-wise, decrease in the population size. These abrupt decreases are due to specific predators that exert a heavy predation pressure on the population during a short time. Spat of some months old are about five mm long and an easy prey for Shore Crabs and Common Shrimps. Also Knot may feed on them and continue to do so during the first winter. After the next growing season, Oystercatchers remove a high fraction of the population, after which Curlews exert a high predation pressure on the remaining specimens during the next two winters.

Shore Crabs, Common Shrimps and Knot only feed on first year *Mya*, because the next year the clams are too large to be swallowed and/or have increased their burying depth too much to be accessible. Due to a further increase of the burying depth, Oystercatchers cannot take *Mya* older than two years, and Curlews clams older than four years. Hence, the increase of burying depth with shell size explains why each predator

Mya invest 40% of their soft body in their siphon. This allows them to filter food from the water and nonetheless live deeply buried.

does not take specimens larger than observed.

Why do Oystercatchers and Curlews ignore the smaller specimens? The optimal diet model gives the explanation. Assuming that Oystercatchers maximize their intake rate during feeding, they have to ignore *Mya* smaller than 17 mm. For the Curlews, the lower acceptance level was calculated to be 25 mm. Both bird species would only lower their intake rate were these small prey included in their diet. Birds appear to obey this profitability rule.

Concluding, the profitable, ingestible and accessible fractions of *Mya* may be defined for each predator. These fractions differ between predators. This explains the timing of predation pressure by the three bird species and the resource partitioning among these predators. The clams have to traverse several windows of predation during the first four years of their life, but every time they can only survive when they bury deeply and, thus, have a long siphon.

Feeding waders have still to make many decisions after they have decided where to feed, e.g. how fast to walk, how deep to probe their bill into the substrate and which of the encountered prey to take.

be handled extremely fast, presumably prey with slightly opened valves. This shows that waders are versatile. They continuously make decisions how to search for prey, which of the encountered prey to take and how to handle them. All these decisions are made to maximize their intake rate during feeding.

Available + profitable = harvestable

Waders feeding on tidal flats encounter prey that may be too large to be ingested or too strong to be attacked successfully. Besides, variable fractions of the prey are not encountered because they live out of reach of the bill, whereas in visually hunting predators prey must also be detected. These constraints can be used to define which prey are actually available. However, as explained above, waders may voluntarily ignore available prey that are unprofitable. Since the acceptance threshold of prey depends on the intake rate (Ch. 8 & 11), this constraint is not fixed. However, by using the average intake rate the profitable fraction of the available prey may be delineated. The fractions of available prey that are profitable are called harvestable. By definition, the risk of a prey to be taken by a predator is zero when it is not harvestable. Moreover, due to the highly variable prey fraction being inaccessible and unprofitable, it makes more sense to relate prey choice and intake rate of the predator to the harvestable prey biomass (Ch. 2, 7 & 11-16; see also pag. 18-19).

Intake rate and processing rate

The intake rate during feeding was measured in Oystercatchers (Ch. 8-10, 16), Knot (Ch. 12) and Curlews (Ch. 15-16). Prey switching was described as a strategy to maximize their intake rate (Ch. 11). The intake rate depends on the density of the harvestable prey, but also on average profitability of the prey taken. Because large prey are more profitable than small ones, the intake rate increases with prey size (Ch. 9). The optimal prey choice model assumes that the intake rate is maximized, but the question may be raised why Oystercatchers would do so, because the intake rate usually exceeds the rate at which food can be processed. Hence Oystercatchers are forced to slow down their intake rate and/or to make more digestive pauses. This is the reason why Oystercatchers cannot maintain their daily energy requirements when their feeding time would be restricted to one low water period of six hours per day (Ch. 10).

Prey depletion

Each wader species selects certain prey species and size classes. In no case can the diet be restricted to one single species over a period of years. Hence, all wader species have to take different prey species in the long run. Is the harvestable food supply always large enough? Waders indeed sometimes deplete their food resources. Oystercatchers removed 80% of second year Soft-shell Clams within some months, after which Curlews took a high proportion of the remaining clams after the next growing season (Ch. 16). Such a high predation pressure on a year class of prey seems to be an exception (Ch. 11), although waders will often deplete highly profitable prey types such as thin-shelled, shallow or large size classes.

Enhanced bird mortality at low intake rates

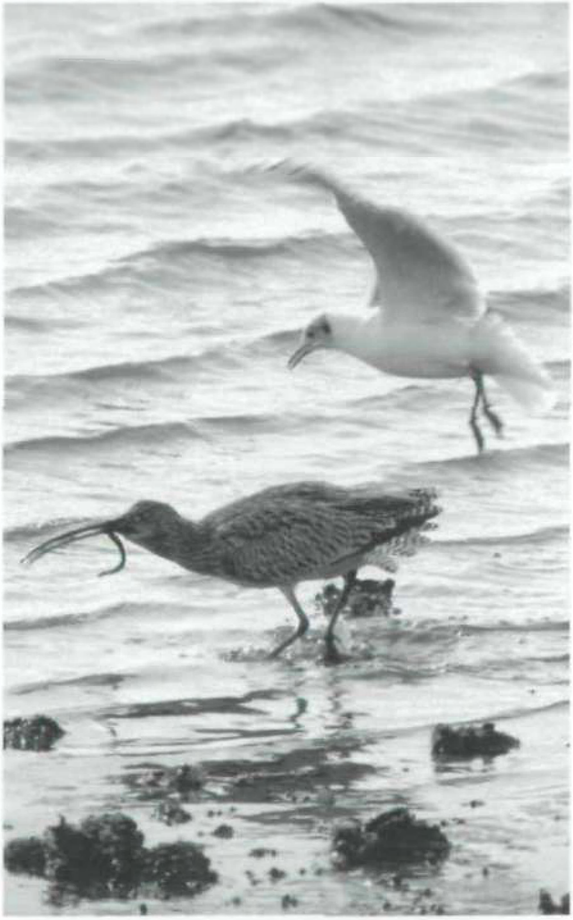
A local depletion of the highly profitable prey does not affect the survival of the waders, as long as they are able to switch to other prey which guarantee an intake rate high enough to get the necessary amount of food within the restricted time the tidal feeding areas are exposed. Generally speaking, the Wadden Sea offers the waders a rich food supply. They can easily meet their daily energy requirements by switching between prey species and by roaming over a large area. The winter remains, however, a difficult period for waders in the Wadden Sea because of the enhanced costs of living and the lower intake rate (Ch. 2, 9, 11). That is why most wader species leave the Wadden Sea in late summer or autumn to winter further south, but large numbers of Oystercatchers remain to winter in the Wadden Sea. Many birds die in severe winters, but even in mild winters the mortality increases when their intake rate is low (Ch. 11).

What do we need to know about carrying capacity?

Has our research contributed to answer the question about the carrying capacity? First, models developed in the laboratory to predict the intake rate during feeding as a function of prey density, appear to be much too simple to describe the natural situation. Predators do not feed in a mechanistic way, because they are versatile and continuously make decisions. The optimal prey choice model, based on the assumption that predators maximize their intake rate, appears to be a helpful tool to predict these decisions.

Second, the aggregation and functional responses of predators have always been described in terms of bird density and intake rate, respectively, in relation to prey density. The implicit assumption is that the harvestable fraction is invariable, or at least not related to prey density. This is a misleading simplification, rarely met in nature. We were able to define which prey will not be encountered by waders and which of the encountered prey will be ignored due to their low yield. Due to these constraints, the actual food supply is much less than the total food supply. The feeding density and intake rate of waders are not simply related to the total food supply, due to the large variation in the fraction of prey actually harvestable. Hence the bird responses are more closely related to the harvestable food supply. By carrying out measurements on an Oystercatcher in a rather simple experimental condition, we were able to predict encounter rate with prey, intake rate and prey choice on the basis of prey characteristics. When extrapolated to the field situation, results were encouraging and allow predictions of periods of shortage and therefore enhanced risks (Ch. 11). Indeed, winters during which Oystercatchers would suffer due to a predicted low intake rate, agreed with periods with an enhanced mortality.

Third, our research was based on the study of individuals. When we became acquainted with them, we became more and more aware how different they were. Individuals feeding on the same spot could take differ-



Black-headed Gull attempting to surprise a Curlew just after it found a Ragworm, this time probably without succes. The risk that a prey is stolen increases when waders eat large prey with long handling times. The kleptoparasites may be congeners or other species, usually gulls.

Worms appearing at the surface are always highly profitable prey for waders due to the short handling time. Grey Plovers can eat large Ragworms in about 15 seconds.

ent prey species, and if they took the same prey they could handle them in a different way. These individual differences could often be attributed to the variation in the bill length (Ch. 11, 15, 16), but the social behaviour of individuals also differed. Curlews in the non-breeding season subdivided the tidal flats into vigorously defended feeding territories, but there were sectors of 'no mans land' where other Curlews fed in loose flocks. This clearly shows that to solve the problem of carrying capacity, it is not sufficient to measure the feeding decisions of the individual waders and the anti-predator behaviour of the prey. In addition, we need detailed measurements on the social dominance, intraspecific kleptoparasitism and interference during feeding. All of us involved in the wader project devoted a great deal of effort to unravel the social behaviour of the birds, but so far this work has not emerged from the unpublished student reports. To complete the story I hope to have the opportunity to analyse this unique material together with my companion observers.

Acknowledgements

Long-term, broadly-based research can, of course, only be done when many people work together, and this is certainly also true for this research project. I hope I have already personally expressed my gratitude to all of them. Here, I only mention the people being essential to the prosperity of the undertaking.

First of all, I thank all my superiors in the former 'Rijksdienst voor de IJsselmeerpolders', later 'Regionale Directie Flevoland van Rijkswaterstaat', still later 'Regionale Directie IJsselmeergebied van Rijkswaterstaat' and now a department within RIZA, for their support, tolerance and patience. In its original set up, the research programme dealt with the ecological effect of the land reclamation works along the mainland coast of the Wadden Sea. I still highly appreciate the encouragement of Kees Berger and J.H. van Kampen to extend the research programme to answer also more fundamental questions. I am deeply convinced this has been a wise decision.

One of the aims was to measure the seasonal variation in food supply throughout the years. Hence, it was decided to measure the food density each month and the burying depth of the bivalves and worms even each fortnight. Such a series of measurements can only be built up if the field work continues during severe winter conditions and foul weather. It was thanks to the dedication of all members of the team that these data could be collected with only a few missing data during a long series of years. Most of the samples of the macozoobenthos were taken by Jan Bronkema, Justinus van Dijk, Sytse van de Meer and the late Lou Terpstra. The same team, together with Harm Hoekstra, built the towers, plotted the hundreds of study sites, measured the altitude of these sites and collected the mud samples. The burying depths of tens of thousands of bivalves and worms were determined for many years by Tonny van Dellen and Bert Toxopeus and later also by Justinus van Dijk and Lou Terpstra. The macrofauna samples were sorted out in the laboratory by Tonny van Dellen and Bert Toxopeus. In total, they must have determined the lengths and weights of hundreds of thousands of prey, whereas they also analysed many hundreds of pellets, droppings and gizzard contents. The ash fraction and the energy density were determined by J.L. Straat, who also did much of the first calculations. Willem Huizingh kept up the administration of all these data.

Jan Wanink became involved in the research project as conscientious objector. I highly appreciated that he spent so much time in checking the huge data bases, and I am glad we have promised each other now to finish off the several joint papers still in progress.

I am especially grateful to Piet Zegers who worked day and night during several years to catch and count birds. It was mainly due to his perseverance that the bird work could be based on marked individuals.

Many students were involved in the project: Joke Bloksma, Anne-Marie Blomert, Henrich Bruggemann, Jenny Cremer, Meinte Engelmoer, Bruno Ens, Peter Esselink, Roelof Hupkes, Dolf Logemann, Rick Looijen, Bertrin Roukema, Piet Spaak, Bauke de Vries, Marja de Vries and Renske de Vries, all from the University of Groningen. Besides, Nienke Bloksma from the Van Hall Institute, Renée Slooff from the University of Leiden, Tjarda de Koe and Jan Komdeur from the University of Wageningen, Kees Hulsman from the University of Brisbane, and Carol Cumming from the University of Edinburgh. I have many cherished memories of the hours we spent together in the hide or discussed the first results.

I am extremely grateful to Rudi Drent. He was not only the supervisor of this project, but also my guide during nearly a quarter century of research. During all this time, he made me feel at home at his institute, the Zoological Laboratory of the University of Groningen. I admire his sharp mind, but possibly still more his capacity to criticize work in an always constructive, friendly way.

It was Rudi who taught me how to do research and how to present the results in a talk, but it was John Goss-Custard who taught me how to write it up in clear English. His detailed comments on nearly all my papers greatly improved the text. I know he can read and edit manuscripts amazingly fast but, summed over all the years, reading my drafts must have taken a lot of time. I also like to thank several other colleagues who commented on drafts of the following chapters: Jan Beukema (Ch. 2), Anne-Marie Blomert (Ch. 2, 9, 10, 11) Bart Ebbinge (Ch. 11), Bruno Ens (Ch. 3, 4, 5, 6, 7, 8, 14, 15, 16), Karel Essink (Ch. 14), Peter Evans (Ch. 16), Jan Hulscher (Ch. 7), Victor de Jonge (Ch. 14), Mardik Leopold (Ch. 11), Theunis Piersma (Ch. 2, 3, 4, 12 & 13), Bill Sutherland (Ch. 7) and Joost Tinbergen (Ch. 7).

Anne-Marie Blomert, Rudi van Diggelen, Sjoerd Dirksen, Klaus-Michael Exo, Lenze Hofstee, Jan Hulscher, Marion Nieuwenhuis, Cor Smit and Harry Smit kindly permitted us to quote from their unpublished work. I am also grateful to Rinse Wassenaar (Ned. Ringcentrale) who sent immediately the Oystercatcher ringing data I asked for.

I am extremely glad that it was Dick Visser (Zoological Laboratory, Groningen) who made the many graphs. It was always a great moment to see for the first time how Dick had turned my sloppy draft figures into clear, beautiful figures. More than once, I realized he understood the figures better than I did, exactly as Herbert Prins recently wrote in the 'Acknowledgements' of his Buffalo book.

Jan van de Kam was extremely co-operative when I asked him for photographs; I still remember the delightful evening when we together made a first selection of the photos. I am also grateful to my brother Jos Zwarts who always sent bird sketches by return of post when I asked him to do this.

It was a pleasure to enter the phase of writing up not completely as a solist, but to work together with the co-authors Anne-Marie Blomert, Bruno Ens, Peter Esselink, John Goss-Custard, Jan Hulscher, Marcel Kersten and Jan Wanink. Anne-Marie was also a great help at the very last stage when there was hardly time left to correct the proofs. She, and Rob Bijlsma, also carefully read the Dutch summary.

Finally, I thank Peter Evans, Peter de Wilde and Wim Wolff who were prepared to be members of the reading committee.

Chapter 1

SEASONAL VARIATION IN BODY WEIGHT OF THE BIVALVES *MACOMA BALTHICA, SCROBICULARIA PLANA, MYA ARENARIA* AND *CERASTODERMA EDULE* IN THE DUTCH WADDEN SEA

Leo Zwarts

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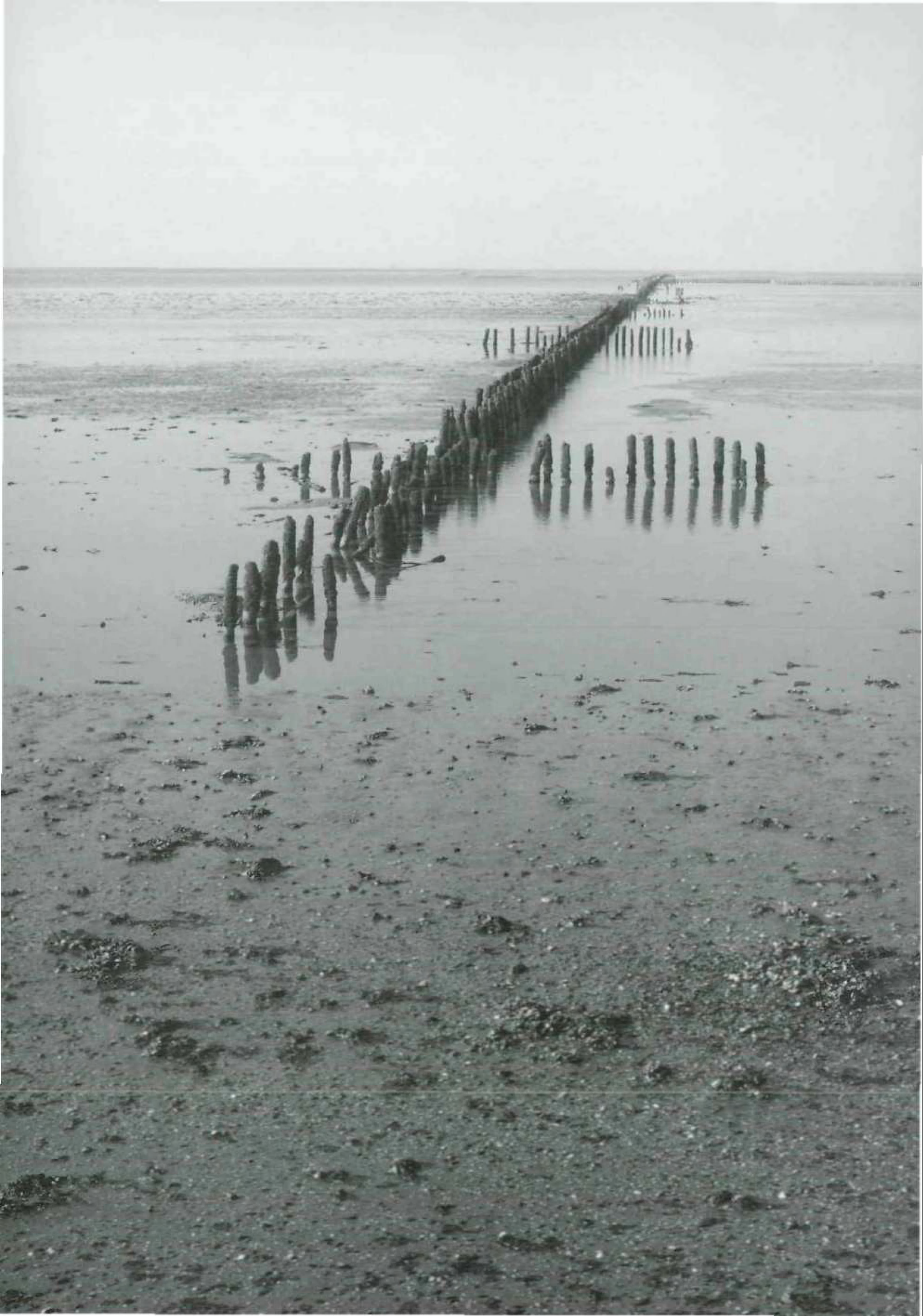


SEASONAL VARIATION IN BODY WEIGHT OF THE BIVALVES *MACOMA BALTHICA, SCROBICULARIA PLANA, MYA ARENARIA* AND *CERASTODERMA EDULE* IN THE DUTCH WADDEN SEA

The paper deals with the seasonal and annual variations in the weight of the soft parts of four bivalve species, *Macoma balthica, Scrobicularia plana, Mya arenaria* and *Cerastoderma edule* from tidal flats of the Dutch Wadden Sea. The paper reviews methodology and points to error sources. The variation in ash-free dry weight (AFDW) between individuals of the same size collected at the same time and place could be attributed to age, parasitic infestation, gametogenesis, burying depth and siphon size. The allometric relations between weight of soft parts and size are given in equations, averaged per month.

The body weight of all four bivalve species peaks in May and June at a level approximately twice the lowest value, which occurs in November to March. The extent of this seasonal fluctuation varies, however, from year to year. The presence of gametes explains a part of the peak weight in summer. The winter loss of body weight is less at low temperatures, due to reduced energy expenditure when the animals are inactive. No large differences were found between the seasonal change in body weight in the Wadden Sea and elsewhere in the temperate zone.

Introduction

Large seasonal variations occur in the biomass of macrozoobenthic animals living on intertidal flats in the temperate zone. Taking all species together, their biomass in the Wadden Sea is twice as high in summer as in winter (Beukema 1974). As has been well documented in the tellinid bivalve *Macoma balthica* (L.), this difference is partly due to summer recruitment, but predominantly results from somatic growth in late spring and early summer and loss of weight later in the season (Lammens 1967, Beukema 1982b, Beukema & Desprez 1986, Beukema *et al.* 1985, Essink & Bos 1985).

Somatic growth of bivalves can be considered in two components: an increase in shell size and an improvement in body condition, i.e. a change in flesh weight at constant shell size. The seasonal variation in body condition has important implications for predators, such as wading birds Charadrii, which depend on the macrozoobenthos. For them, a reduction in flesh content must be compensated by a corresponding increase in the number of prey captured if the same food consumption is to be maintained.

As part of a study on the interaction between waders and their food supply, this paper describes the seasonal and annual fluctuations in the flesh content of four bivalve species, *Macoma balthica, Scrobicularia plana* (Da Costa), *Mya arenaria* (L.) and *Cerastoderma edule* (L.). It is shown that the magnitude in the seasonal variation differs between these species and from year to year. The four species contribute a major share to the total biomass of the macrozoobenthos in the Wadden Sea, with exception of *Scrobicularia* (Beukema 1976). *Scrobicularia* was locally, however, an important species, contributing one quarter to the total benthic biomass (Zwarts 1988b).

Methods

Area

Animals were sampled over 11 years, 1976 to 1986, in the Dutch Wadden Sea along the mainland coasts of the provinces Groningen (53°25′ N, 6°20′ E) and Friesland (53°22′ to 53°25′ N, 5°46′ to 6°04′ E) (Fig. 1). The nine study sites were between 35 cm below and 1 cm above mean sea level, corresponding to an

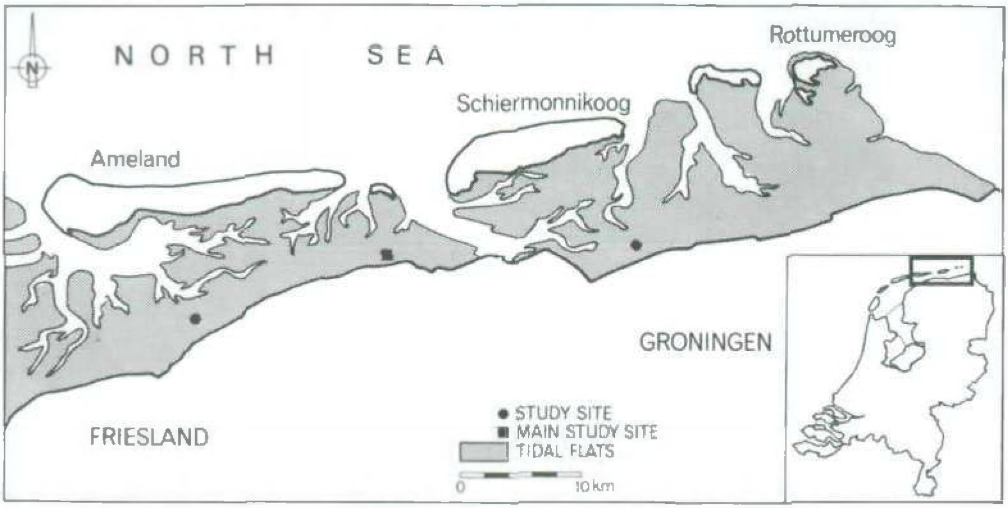


Fig. 1. Study sites along the mainland coast of the Dutch Wadden Sea. Seven of the nine study sites were situated in, or close to, the main study site.

average emersion time of 35 and 46%, respectively (Zwarts 1988b). The clay content (particles < 2 µm) varied between 2% and 11% and the median grain size (excluding the fraction < 16 µm) varied between 70 and 110 µm. Most samples were taken at sites just below mean sea level with a clay content of 4 to 6% and a median grain size of 95 µm. The data for the different study sites were pooled, since, in contrast to other studies (Sutherland 1982a, Cain & Luoma 1986, Bonsdorff & Wenne 1989, Harvey & Vincent 1989, 1990), no systematic differences in body weight were detected between the sites (Zwarts 1983), despite pronounced site-dependent differences in the species growth rates (Zwarts 1988b).

Concentrations of chlorophyll *a* in the water of nearby gullies, given in yearbooks of Rijkswaterstaat ('Kwaliteitsonderzoek in de Rijkswateren') were used as a measure of food supply. The sea water temperature and the frequency of ice days were both measured daily at the nearby station Holwerd (source: 'Jaarboeken der waterhoogten'; Rijkswaterstaat); ice days are defined as days during which ice was present in the Wadden Sea near the sampling station.

Procedures

Core samples were sieved with a 1-mm mesh sieve. Animals were put in sea water and transported to the laboratory within a few hours. Samples were stored at 2 to 4 °C for up to 36 hour or deep-frozen at -20 °C, if not handled within that period.

Bivalve length was measured to the nearest mm with vernier callipers along the anterior-posterior axis. Shell height and width were also measured in a subsample of the collected bivalves. Height was defined as the greatest distance between the dorsal and ventral margins of the clam. Width was taken as the greatest distance between the two valves when the clam was closed. Age class was determined from winter rings. Any infestation of *Macoma* by the parasitic trematode *Parvatrema affinis* (Swennen & Ching 1974) was noted. The reproductive condition was subjectively scored by macroscopic examination of the visceral mass according to criteria given by Caddy (1967): (1) 1/4 or less, (2) 1/2, (3) 3/4 or (4) >3/4 of the digestive gland covered by gonad tissues, or (5) absent after spawning.

Either all individuals, or samples of animals within 10 to 20 mm-classes, were selected for weight determination. Specimens > 11 mm long were immersed briefly in boiling water to extract the flesh. Any flesh remaining (e.g. the adductor and sometimes the mantle edge) was cut out. The flesh was dried at 70 °C

Table 1. Weight loss (% ± SE) in *Macoma* (12 to 21 mm, n = 960 specimens) stored in sea water at 4 °C for 0, 1, 2 or 3 days after collection. Average weight of each mm-class on day 0 is set to 100. Subsequent changes are expressed as relative deviation on day 1 to 3. The differences are weakly significant according to a one-way analysis of variance ($R^2 = 0.23$, $p = 0.05$, $n = 26$). The percentage ash (± SE) differs significantly ($R^2 = 0.61$, $p < 0.001$, $n = 36$).

storage period	*AFDW, %*	*ash, %*
0 hour	100	17.5 ± 0.5
24 hour	103.0 ± 1.7	15.5 ± 0.5
48 hour	91.0 ± 3.2	13.0 ± 0.5
72 hour	96.7 ± 3.8	13.6 ± 0.5

for 2 to 3 days, to obtain the dry weight (DW), and then ignited for 2 h at 550 °C to determine the ash-free dry weight (AFDW). DW was measured either separately in each specimen, or in grouped samples of animals from particular mm-classes. AFDW was usually determined in grouped size samples. Flesh and shell were not separated in specimens ≤ 11 mm long, so that DW and AFDW here refer to the soft as well as hard parts (but see next section).

Errors

Several errors may have occurred in the laboratory work.

(1) Animals may have lost weight during storage. However, a test (Table 1) showed the effect on the AFDW to be very small and probably a consequence of stomach emptying, since about a quarter of the ash disappeared. Therefore no correction was made for the duration of the storage.

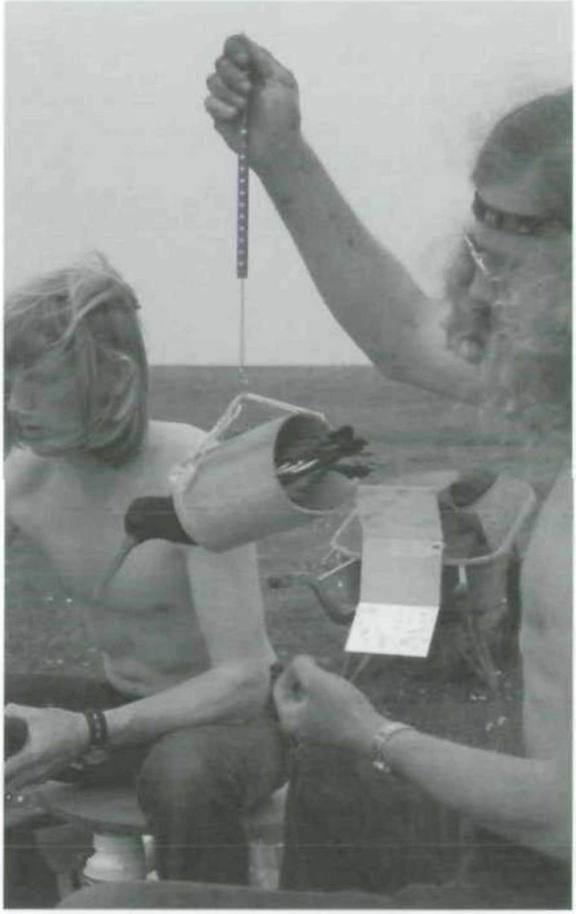
Table 2. Relative difference in AFDW and average percentage ash of *Macoma* (n = 188) and *Scrobicularia* (n = 379) if (1) the flesh was cut from the shell or (2) the flesh was taken out the shell after being immersed for 15 s in boiling water. The data were pooled for four mm-classes in *Macoma* and 15 mm-classes in *Scrobicularia*; the mean ± SE is given.

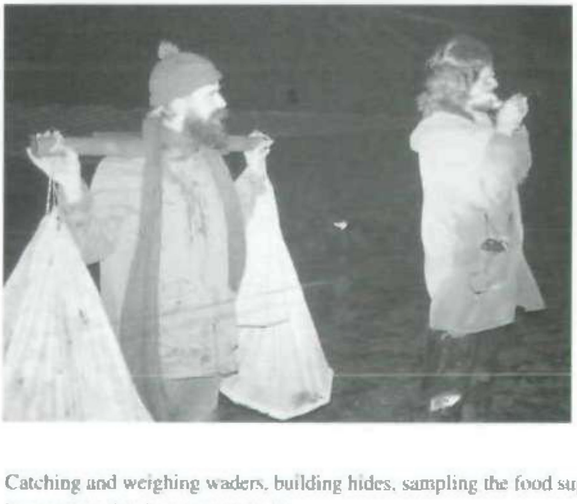
immersion	*Macoma*		*Scrobicularia*	
	AFDW, %	*ash, %*	*AFDW, %*	*ash, %*
no	100	21.2 ± 0.9	100	30.0 ± 1.2
yes	101.8 ± 3.3	12.8 ± 1.0	94.1 ± 2.6	17.6 ± 0.7

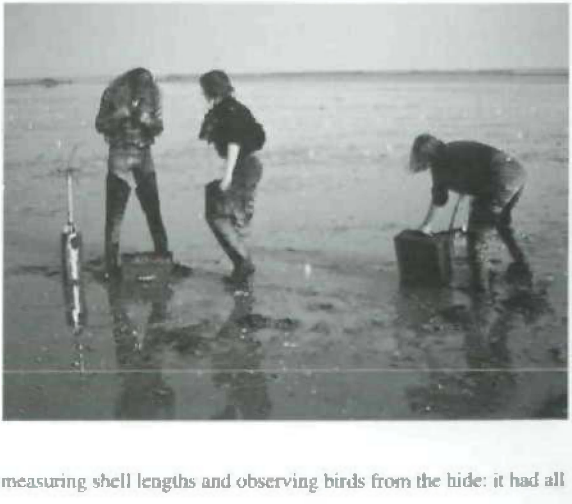
(2) Immersion in boiling water may have dissolved flesh. This effect also appeared to be negligibly small, even when the immersion time was 15 s (Table 2). Immersion halved the percentage ash, partly because salt dissolved but mainly because of the loss of sand particles. The immersion time was kept as short as possible and the flesh removed as soon as the shells started to gape. No correction was made for this, possibly very small, loss of AFDW.

(3) The AFDW of bivalves ≤ 11 mm long could not be compared directly with that of the larger bivalves. When the shells of small bivalves are ignited, organic material in the hard parts (viz. conchine) disappears along with water tightly bound in the shell. To determine how large an error this introduced, samples of shells were cleaned by placing them in a solution of collagenase at 37 °C for 24 h, so that all the flesh could be easily removed. The AFDW of the shells, bound water inclusive, was low (Fig. 2); 2.6% of the DW of the shell in *Macoma*, 1.9% in *Scrobicularia* (no spat), 2.9% in *Mya* and 2.2% in *Cerastoderma*. These values are in agreement with data of Hibbert (1976), Beukema (1980, 1982a), Kleef *et al.* (1982), and Goulletquer & Wolowicz (1989). Nonetheless, the contribution of the shell itself to the total AFDW of the shell and flesh together varied between 15% and 40%. It was greatest in *Cerastoderma* in winter, when the DW of the shell was 14 to 15 times that of the flesh. It was least in *Macoma* in summer when the DW of the shell was still 5 times that of the flesh. In view of this large contribution made by the AFDW of the shell, Fig. 2 was used to estimate how much should be subtracted from the total AFDW on those occasions when soft and hard parts of bivalves had not been separated, this being usually the bivalves ≤ 11 mm long.

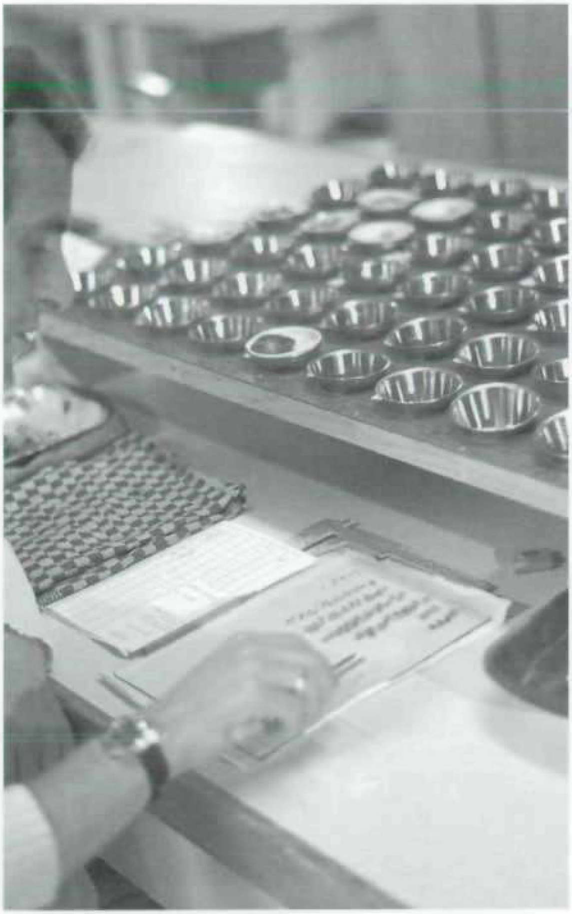
(4) The DW was determined for all size classes, but sometimes the ash content was not measured. The percentage ash appeared independent of size but varied seasonally (Figs. 3 and 4). The average percentage ash content per month was used to convert DW into AFDW on those occasions when samples had not been ignited. A similar seasonal variation in ash content was found in *Macoma* by Beukema & de Bruin (1977), but it occurred at a lower level, probably

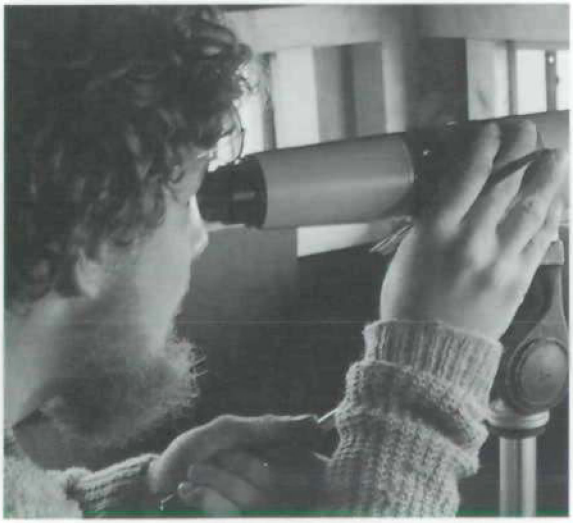






Catching and weighing waders, building hides, sampling the food supply, measuring shell lengths and observing birds from the hide: it had all in common that it was team work.





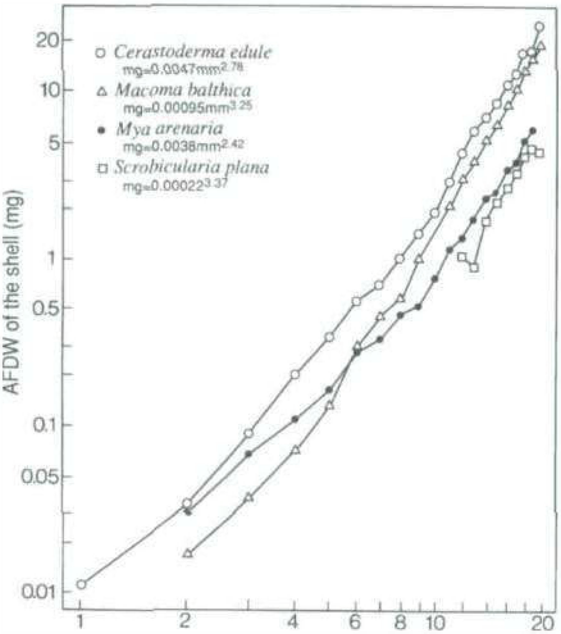


Fig. 2. AFDW of the shell as a function of size in *Cerastoderma* (n = 1351), *Macoma* (n = 703), *Mya* (n = 308) and *Scrobicularia* (n = 158). The allometric functions refer to bivalves < 20 mm. The correlations are high: $r > 0.99$, except for *Scrobicularia* ($r = 0.98$). Despite this, the relationships appear to deviate from linearity since they are concave.

because they stored the animals in running sea water at a temperature of 5 to 10 °C.

Analysis

The mean AFDW was determined for each mm size class on each sampling date. The regressions of ln(weight) on ln(size) were calculated for each sampling date (Table 3). The average number of animals sampled per size class varied between 5 in *Mya* and 43 in *Macoma*.

The variation in AFDW within each mm-class determined the number of specimens needed to reach a 95% probability that the standard error lay within 5% of the mean (Table 4). This variation was very small in *Cerastoderma*, so only 3 specimens were needed. But in the more variable *Scrobicularia*, the sample size must be six times larger, which is one of the reasons of the relatively poor correlation in the allometric equations in this species (Table 3).

Table 3. Overview of the data collected on the relation between ln(AFDW) and ln(length): number of regression analyses performed (formulae), the average correlation (r), the average number of mm-classes used (n), the average number of specimens weighed (x) and the average range (mm) over which the regressions were calculated.

species	*formulae*	*r*	*n*	*x*	*range*
Macoma	262	.9915	12.7	549	7-21
Scrobicularia	185	.9464	8.1	137	28-42
Mya	228	.9900	14.9	68	17-67
Cerastoderma	139	.9846	10.7	224	9-29

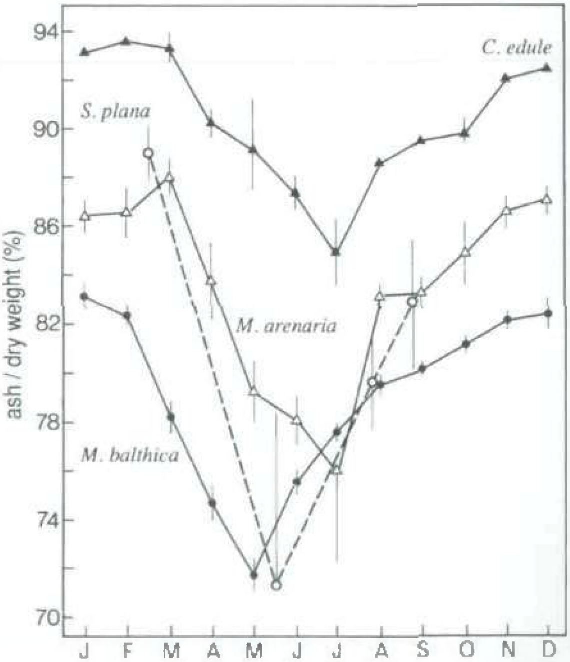


Fig. 3. Seasonal variation in ash content (± SE) of bivalves ≤ 11 mm, including the shell. One-way analyses of variance show that season has a highly significant effect on the ash content: *Macoma* ($R^2 = 0.28$, $p < 0.001$, $n = 1205$), *Scrobicularia* ($R^2 = 0.74$, $p < 0.02$, $n = 18$), *Mya* ($R^2 = 0.07$, $p < 0.001$, $n = 170$) and *Cerastoderma* ($R^2 = 0.26$, $p < 0.001$, $n = 421$).

Table 4. Variation in AFDW of three bivalve species when all specimens were weighed and separately cremated: month: month of sampling; *n: number of mm-classes; x: number of specimens;* RSD: *standard deviation as percentage of the average weight ± SE; x needed: sample size* in order to reach a SE which is 5% of the mean.

species	*month*	*n*	*x*	*RSD*	*x needed*
Macoma	1-11	33	188	15.80 ± 0.84	11.38 ± 1.36
Scrobicularia	1-11	139	996	15.00 ± 1.23	18.56 ± 1.49
Cerastoderma	8	30	228	8.78 ± 0.45	3.32 ± 1.74

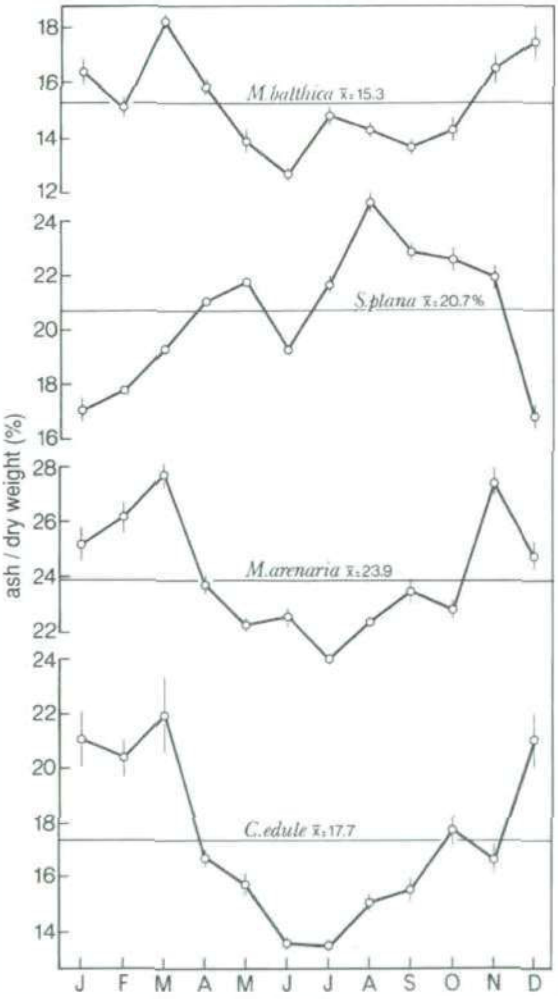


Fig. 4. Seasonal variation in ash content (± SE) of the soft parts of bivalves > 11 mm. One-way analyses of variance show that season has a highly significant effect on the ash content: *Macoma* ($R^2 = 0.05$, $p < 0.001$, $n = 4460$), *Scrobicularia* ($R^2 = 0.12$, $p < 0.001$, $n = 6970$), *Mya* ($R^2 = 0.07$, $p < 0.001$, $n = 5891$) and *Cerastoderma* ($R^2 = 0.20$, $p < 0.001$, $n = 1359$).

Results

Variation in body weight within a size class

Six factors were examined to explain the variation between individuals, collected from the same spot, at the same time and belonging to the same size class: (1) shell dimensions, (2) age, (3) stage of gametogenesis and spawning, (4) burying depth, (5) incidence of parasites and (6) siphon weight.

(1) The correlations between shell length and both height and width were very high (Table 5), and the data agreed closely with other studies on *Macoma* (Lammens 1967, Bachelet 1980, Beukema & Meehan 1985), on *Mya* (Munch-Petersen 1973, Newell & Hidu 1982) and *Cerastoderma* (Kristensen 1957, Hancock 1967, Chambers & Milne 1979). The variability in the ratio of shell length to height or shell length to width, expressed as relative standard deviation (RSD) was very small (Table 5). When species were compared, the RSD was not related to the variation in body weight (Table 4). Furthermore, in a stepwise multiple regression, neither height nor width added significantly to the variation in AFDW already explained by length, because of the high correlations between the three shell dimensions. Therefore, variations in shell dimensions do not account for variation in body weight.

(2) When animals of the same size but different age were compared, the younger year classes were lighter as already described for *Cerastoderma* by Hibbert (1976). The difference is best illustrated by *Macoma*, where size and year classes overlapped (Fig. 5).

(3) The presence of gametes in summer added about 20% to the body weight in *Macoma* (de Wilde & Berghuis 1978, Beukema *et al.* 1985) and *Scrobicularia* (this paper).

(4) Bivalves living at greater depths in the substrate

Table 5. The length of the shell as a function of the height and width; a is intercept (± SE), b is slope (± SE), RSD is the standard deviation as a percentage of the mean and calculated as follows: RSD was determined for the ratio height/length and width/length, separately per size class and then averaged because the ratio depended on the size. All specimens were collected alive in the main study site.

species	*b*	*a*	*r*	*n*	*RSD, %*
Macoma - height	1.265 ± 0.005	-0.134 ± 0.059	0.995	621	3.09
Scrobicularia - height	1.188 ± 0.008	1.746 ± 0.185	0.993	347	2.80
Mya - height	1.632 ± 0.007	0.077 ± 0.139	0.997	348	3.74
Cerastoderma - height	1.209 ± 0.004	-0.640 ± 0.085	0.998	425	2.74
Macoma - width	1.895 ± 0.015	2.574 ± 0.101	0.980	621	6.87
Scrobicularia - width	2.870 ± 0.027	3.180 ± 0.254	0.985	347	4.26
Mya - width	2.617 ± 0.016	1.622 ± 0.182	0.995	348	5.46
Cerastoderma - width	1.274 ± 0.123	1.457 ± 0.008	0.994	425	4.77

were in better condition than those shallowly buried (Zwarts 1986). This difference was substantial in *Scrobicularia* and *Macoma*, but small in *Mya* and *Cerastoderma* (Zwarts & Wanink 1991).

(5) *Macoma* infested by *Parvatrema* were, on average, including the additional weight of the parasites, 15% heavier than uninfested specimens, though the difference was greater in spring and summer than in autumn (Fig. 6).

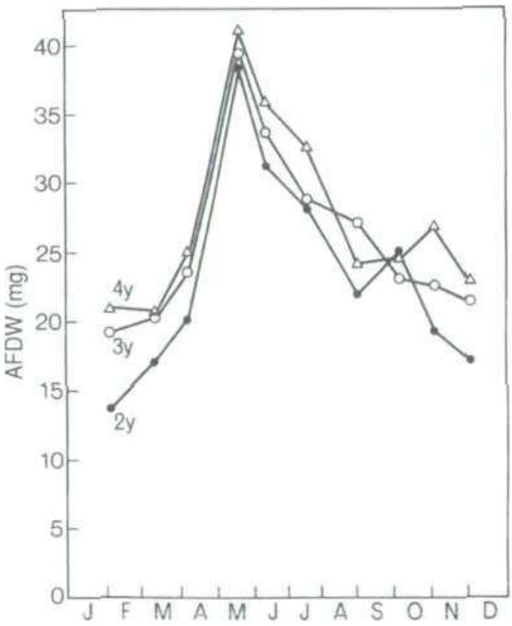


Fig. 5. AFDW of the soft parts of *Macoma* 13 mm long during 1986, divided into three year classes (n = 294). The average weights of third- and fourth-year animals are, respectively, 1.12 and 1.16 times the weight of second year specimens.

(6) Body weight appeared to be related to siphon weight (Zwarts 1986, Zwarts & Wanink 1989). Siphon weight depends on the frequency with which the shellfish are cropped (de Vlas 1985) and this affects the weight the animal (Trevallion 1971, Hodgson 1982a, Zwarts 1986). Cropping by flatfish, crabs and shrimps is highest in summer (de Vlas 1985) and so may explain why body weight in *Scrobicularia* varied more in late summer than in winter (Fig. 7). The greater summer variation may also be attributed to variable rates of gametogenesis and spawning, neither of which was completely synchronised. The expectation was that the same factors would cause a larger variation during the summer in the body weight of *Macoma*, but no significant seasonal trends in the variation of body weight were found.

Allometric relations

The slope of the regression of ln(weight) on ln(length) should remain constant if the relative variation in body weight is equal in all size classes. In such cases, the intercept can be used as a condition index to describe the common fluctuations in all size classes. The slopes, however, differed significantly between months (Tables 6 to 8), except in *Scrobicularia*, in which only a small range of size classes was available anyway (Table 3). The overall regression for *Scrobicu-*

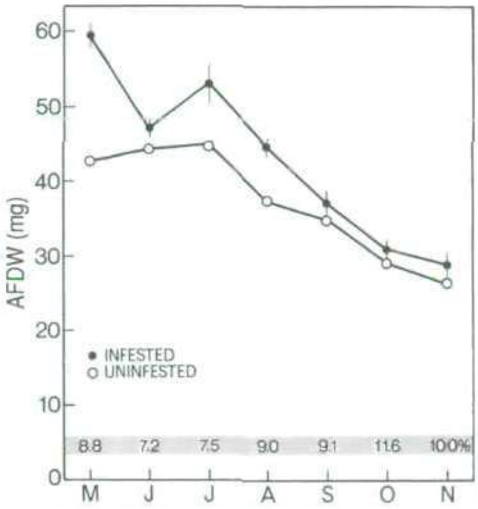


Fig. 6. AFDW (± SE) of the soft parts of *Macoma* 15 mm long during 1986, with a distinction made between uninfested and those that were infested by the trematode *Parvatrema affinis*. The SE of the uninfested individuals was always less than 0.5 mg and so could not be indicated. The percentages along the lower border indicate the degree of infestation of the population. A two-way analysis of variance reveals that month and infestion explain a significant part of the variance (R^2 = 0.32 and 0.04, respectively). Since the interaction term is also significant, the differences in weight between the infested and uninfested animals are not equal for each month; n = 2726.

laria calculated from 45 equations for which $r > 0.99$, with slope and intercept ± SE, is:

$$\ln(\text{mg}) = 2.900 \pm 0.089 \ln(\text{mm}) - 5.044 \pm 0.322.$$

Both the slopes and the intercepts for *Macoma* reached a minimum in early spring and a maximum in late summer. The slopes and intercepts for *Mya* and *Cerastoderma* were low in May-June and remained high in autumn and winter. Essink (1978) found differences in the value of the slope of *Cerastoderma* between the years, but no seasonal variation.

The body weight of all species was low in February and March and high in May and June (Fig. 8). The seasonal variation in body weight of *Mya* and *Cerastoderma* was 1.5 times larger in the smaller size classes than in the larger ones. This large difference did not occur in *Macoma*, in which the small animals

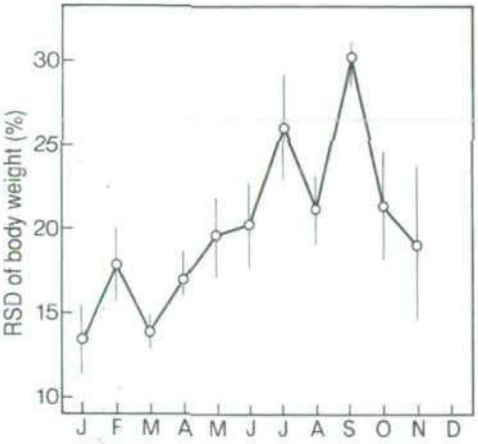


Fig. 7. The relative standard deviation (RSD; standard deviation as percentage of the mean ± SE) of the AFDW of the soft parts of *Scrobicularia* during the course of the year. The one-way analysis of variance shows that the RSD differs per month (R^2 = 0.30, $p < 0.001$, n = 139). The RSD was calculated over 139 size classes for which the AFDW was known in at least 5 individual specimens which were collected on the same date and the same spot.

Table 6. *Macoma*. Average slope (b ± SE) and average intercept (a ± SE) per month of the regression ln(mg AFDW of the soft parts) against ln (mm length). Regressions are selected for which $r > 0.99$. The slopes differ significantly per month (R^2 = 0.28, $p < 0.0001$), as well as the intercepts (R^2 = 0.27, $p < 0.0001$).

month	*b*	*a*	*n*
1	2.702 ± 0.095	-3.984 ± 0.167	3
2	2.673 ± 0.092	-3.830 ± 0.220	8
3	2.510 ± 0.044	-3.421 ± 0.109	9
4	2.593 ± 0.060	-3.490 ± 0.167	16
5	2.765 ± 0.068	-3.672 ± 0.186	26
6	3.120 ± 0.091	-4.667 ± 0.255	15
7	3.098 ± 0.087	-4.706 ± 0.218	18
8	3.063 ± 0.054	-4.759 ± 0.143	36
9	3.104 ± 0.079	-4.839 ± 0.218	18
10	2.914 ± 0.074	-4.373 ± 0.183	10
11	2.992 ± 0.096	-4.740 ± 0.276	19
12	2.836 ± 0.127	-4.297 ± 0.294	8
average	2.919 ± 0.027	-4.335 ± 0.073	187

were in a relatively good condition in January to May, compared to the larger ones. The reverse applied in June to October.

Seasonal and annual weight variation

The seasonal weight variations during the last eight years of the study period of the size class at the midpoint of the regressions (Table 3) are shown in Fig. 9.

Table 7. *Mya*. Average slope (b ± SE) and average intercept (a ± SE) per month of the regression ln(mg AFDW of the soft parts) against ln(mm length). Regressions are selected for which $r > 0.99$. The slopes differ significantly per month ($R^2 = 0.22$, $p < 0.0001$), as well as the intercepts ($R^2 = 0.31$, $p < 0.0001$).

month	*b*	*a*	*n*
1	3.351 ± 0.073	-6.610 ± 0.324	4
2	3.382 ± 0.061	-6.825 ± 0.215	10
3	3.270 ± 0.058	-6.342 ± 0.228	11
4	3.056 ± 0.086	-5.514 ± 0.244	17
5	2.996 ± 0.039	-4.955 ± 0.148	18
6	3.110 ± 0.085	-5.358 ± 0.345	13
7	3.258 ± 0.043	-5.988 ± 0.131	17
8	3.153 ± 0.041	-5.793 ± 0.122	31
9	3.344 ± 0.048	-6.439 ± 0.195	24
10	3.224 ± 0.050	-6.046 ± 0.214	9
11	3.192 ± 0.033	-6.058 ± 0.109	15
12	3.330 ± 0.060	-6.539 ± 0.231	7
average	3.199 ± 0.019	-5.932 ± 0.069	176

Table 8. *Cerastoderma*. Average slope (b ± SE) and average intercept (a ± SE) per month of the regression ln(mg AFDW of the soft parts) against ln(mm length). Regressions are selected for which $r > 0.99$. The slopes differ significantly per month ($R^2 = 0.32$, $p = 0.002$), as well as the intercepts ($R^2 = 0.40$, $p < 0.0001$).

month	*b*	*a*	*n*
1	3.014 ± 0.228	-4.747 ± 0.627	3
2	3.390 ± 0.057	-5.943 ± 0.181	3
3	3.480 ± 0.235	-6.263 ± 0.768	4
4	3.137 ± 0.160	-4.933 ± 0.576	4
5	2.886 ± 0.122	-3.957 ± 0.449	8
6	2.969 ± 0.027	-4.004 ± 0.046	3
7	3.128 ± 0.098	-4.644 ± 0.334	4
8	2.974 ± 0.094	-4.429 ± 0.252	21
9	3.063 ± 0.085	-4.620 ± 0.224	13
10	3.259 ± 0.173	-4.276 ± 0.527	6
11	3.414 ± 0.140	-5.804 ± 0.435	7
12	3.659 ± 0.147	-6.699 ± 0.436	8
average	3.157 ± 0.046	-4.977 ± 0.145	84

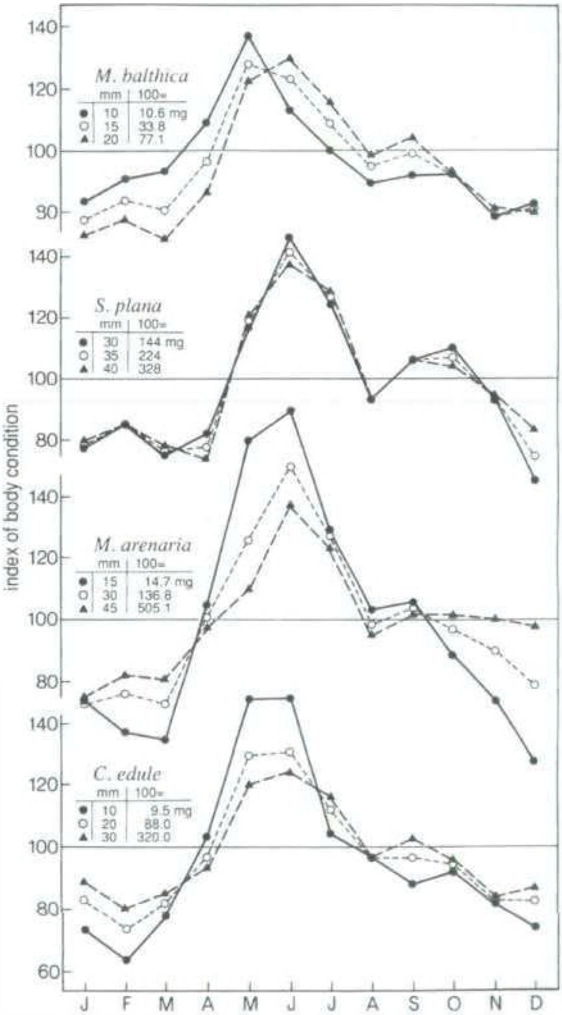


Fig. 8. Seasonal variation of AFDW of the soft parts in three size classes of *Macoma*, *Scrobicularia*, *Mya* and *Cerastoderma*. The average annual weight has been set to 100 and the monthly weights are given as percentage deviation; the inset displays the absolute values. See Tables 6 to 8 for the numbers of cases per month.

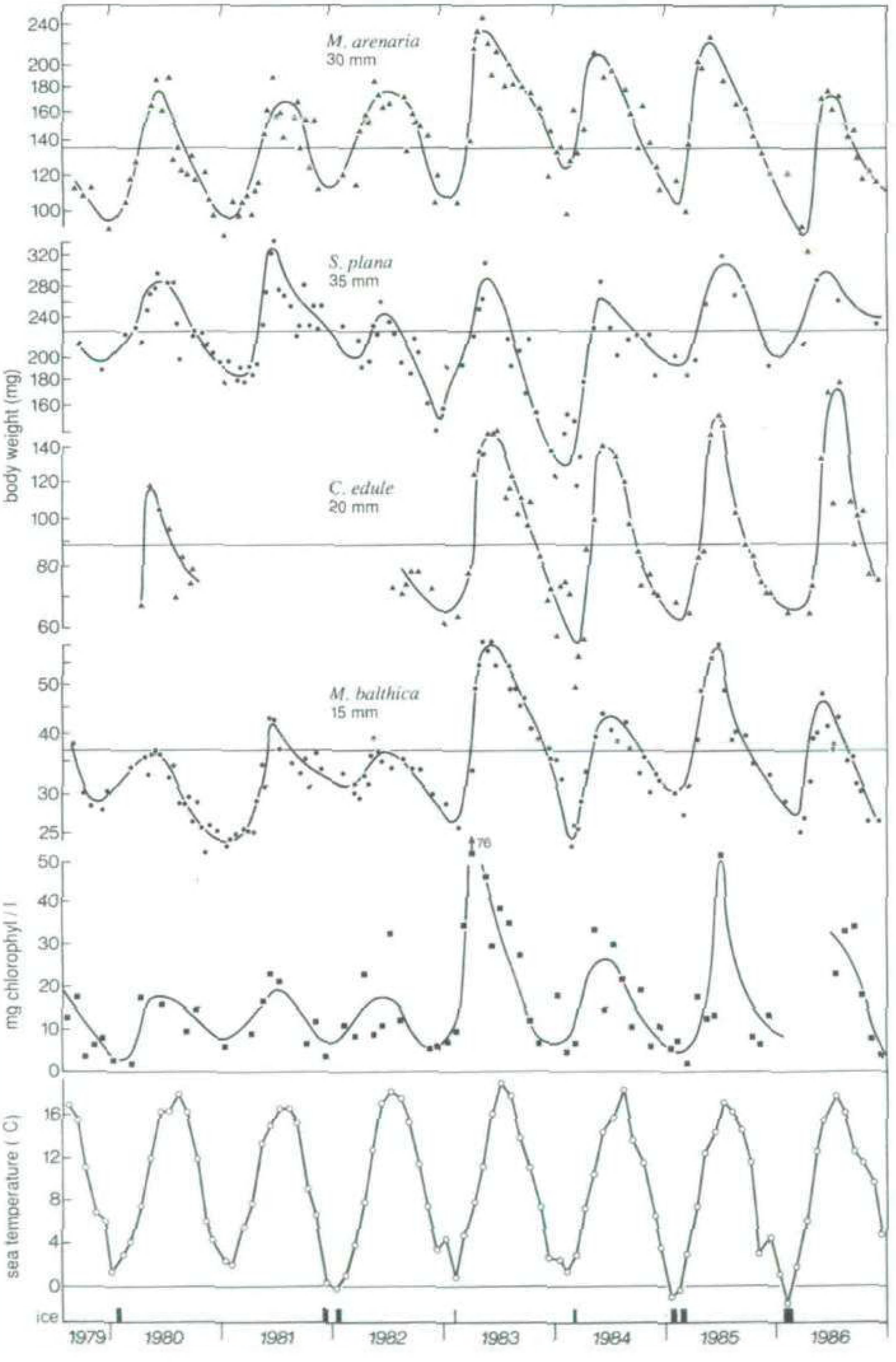


Fig. 9. Fluctuation in AFDW of the soft parts of *Macoma* (15 mm), *Scrobicularia* (35 mm), *Mya* (30 mm) and *Cerastoderma* (20 mm) during a period of 7.5 years. For more than one sampling date per month, the average weight is given. The lower panels show the variation in *chlorophyll a* concentration (mg dm^{-3}) in nearby gullies, the average sea water temperature (°C) and the frequency of ice days. All lines, except sea water temperature, are drawn by eye.

Table 9. Correlations between body condition of four bivalve species sea water temperature and chlorophyll *a* concentrations; same data as given in Fig. 9. All correlations are highly significant ($p < 0.001$); n is given between brackets.

	Scrobicularia	*Mya*	*Cerastoderma*	*temperature*	*chlorophylla*
Macoma	0.59 (78)	0.74 (90)	0.69 (66)	0.48 (91)	0.47 (68)
Scrobicularia		0.59 (78)	0.56 (54)	0.59 (79)	0.39 (59)
Mya			0.65 (65)	0.48 (91)	0.48 (69)
Cerastoderma				0.54 (67)	0.52 (50)
temperature					0.44 (70)

This figure also shows the concentration of chlorophyll *a* in the surface water in the gullies -a measure of the available food supply- and monthly mean sea water temperatures. With all data pooled, significantly positive correlations between the body weight of the four species and both sea water temperatures and chlorophyll *a* concentrations were found (Table 9).

Weight variation in winter

Body weights were low in mild winters but remained relatively high when winter temperatures were low (Fig. 9). To investigate this further, a selection was made of measurements of body weights taken during adjacent months in the period November to February. The changes in body weight, relative to the preceding month, appeared to be independent of food supply, but higher sea water temperature had a significant negative effect on body weight in three of the four species (Fig. 10). The slopes did not change when food supply was entered into the multiple regressions. The relationships shown in Fig. 10, suggest that winter is a starving period during which the decrease of body weight depends on the temperature-related cost of living.

Weight variation and gametogenesis

Seasonal variations in body weight during summer have been attributed to the development and spawning of gametes (e.g. Hughes 1970b). The contribution of gonads to total body weight can be estimated from the individual weights of animals at different reproductive stages. Figure 11 shows that *Scrobicularia* 35 mm long with few or no gametes -either before the start of the gametogenesis or after spawning- weighed about 200 mg, whereas individuals with gametes had a body weight of about 250 mg. On this basis the increment in body mass due to seasonal development of the gonads works out at about 20%, similar to the figure mentioned earlier for *Macoma*. However, the presence of gametes did not explain the whole variation in body weight between May and August. There was still a significant seasonal variation in body weight for specimens with equal gamete scores. Thus the decrease of body weight after June appears to have been independent of the development or loss of the gametes.

The effects of season and gamete development were similar over two years (Fig. 11). Nonetheless, there was a remarkable difference between the summers of 1981 and 1982 (Fig. 9). The relatively high body weight in 1981 can be attributed to gametogenesis. In June and July 1981, 98% of the individuals reached gamete stage 3 or 4, whereas in 1982 this was only true for 45%.

In conclusion, reproductive tissue explains only a part of the enhanced summer weight of *Scrobicularia*, whereas the differences between summers can be attributed to the variation in the amount of gametes produced.

Discussion

Weight change, growth and spawning

The body weight in *Macoma* in the Wadden Sea is at its highest in May and June (Beukema & de Bruin 1977, Beukema *et al.* 1985, Beukema & Desprez 1986, this paper: Figs. 5, 8, 9) and *Cerastoderma*, *Scrobicularia* and *Mya* reach maximum condition in the same months (Figs. 7, 8). In NW. Europe, this is

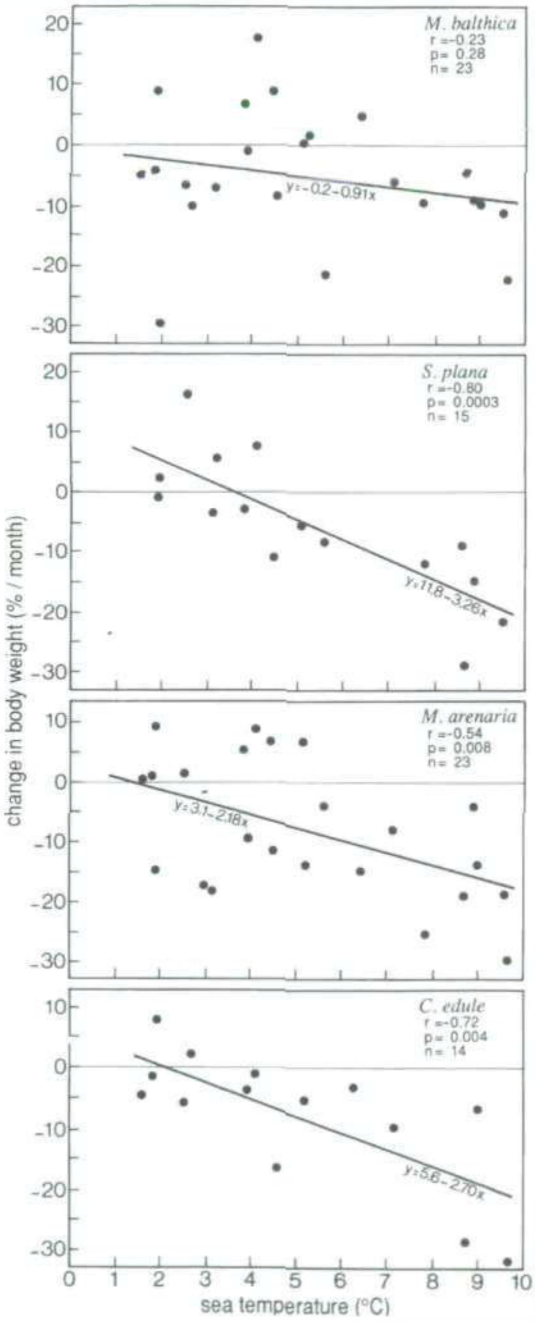


Fig. 10. Relative monthly changes in AFDW (%) as a function of the average sea water temperature during that same month in (top to bottom) *Macoma* (15 mm), *Scrobicularia* (35 mm), *Mya* (30 mm) and *Cerastoderma* (20 mm). These data are also given in Fig. 9 and refer to the winter period (November-February).

the period during which shell growth is also greatest in *Macoma* (Beukema & de Bruin 1977, Beukema *et al.* 1985, Beukema & Desprez 1986, Desprez *et al.* 1986), in *Scrobicularia* (Wanink & Zwarts unpubl.), *Mya* (Essink & Bos 1985) and *Cerastoderma* (Kristensen 1957, Hancock & Franklin 1972, Ankar 1980, Essink & Bos 1985, Desprez *et al.* 1986). All species thus appear to be in a good condition during the main growing season. Indeed, in a comparison between years, length increment and body weight at the end of the growing season in *Macoma* were found to be closely correlated (Beukema *et al.* 1985).

The weight of the gametes relative to the total body weight in *Macoma* was estimated at 24% in the laboratory (de Wilde & Berghuis 1978), at 15 and 30% in the field in different years in the same place (Beukema *et al.* 1985) and at 7 and 27% in two different sites in the same year (Harvey & Vincent 1989). It would be expected that spawning should produce a clear-cut reduction in body weight, but this weight loss is difficult to detect because it occurs around 1 May, when the growth rate is also at its maximum (Beukema *et al.* 1985).

In *Scrobicularia*, spawning takes place in early

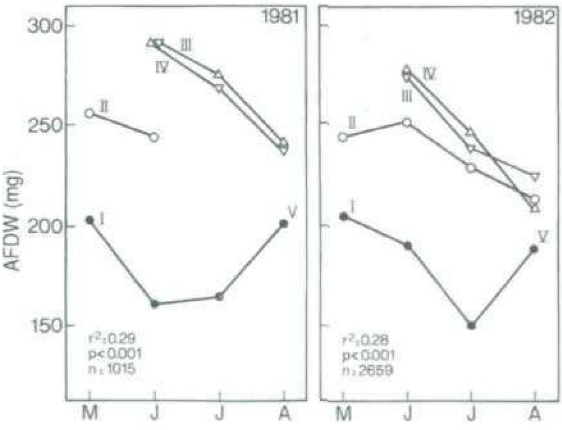


Fig. 11. Variation in AFDW of *Scrobicularia* (35 mm) in May-August 1981 (left) and 1982 (right), given separately for individuals at a different stage of development of the gametes: in (I) < 1/4 and in (IV) > 3/4 of the digestive gland was covered by gonad tissues, while II and III are intermediate classes; (V) refers to individuals after spawning. The results of two-way analyses of variance are given: the effect of the factors (month and gonad) is highly significant, as well as the interaction between both factors.

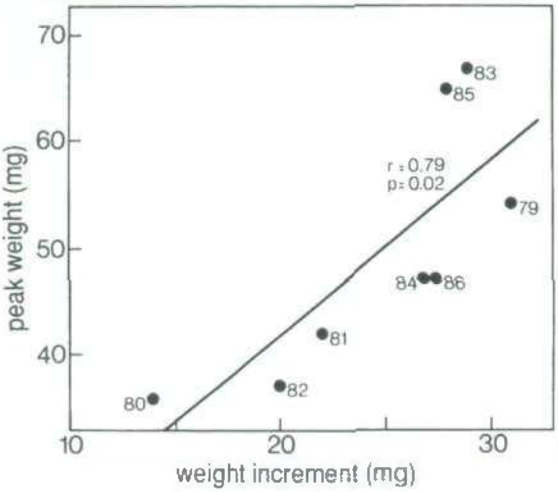


Fig. 12. Relation between highest annual body weight of *Macoma* in the eastern part of the Dutch Wadden Sea (Fig. 9) and the annual weight increment of a 7-mm specimen in the western Wadden Sea (data from Beukema & Cadée 1991). The years concerned are indicated.

August (Fig. 11). There are two cohorts each year in southern areas (Hughes 1972, Bachelet 1981, Worrall *et al.* 1983, Essink *et al* 1991). Spawning causes a 20% reduction of body weight and occurs in a period during which animals lose weight (Fig. 11). The species improves its body condition during September and even October (Fig. 8).

In contrast, a seasonal decrease in body weight as a consequence of spawning was not found in either *Mya* or *Cerastoderma* (Fig. 8). The reason is that, just like *Macoma*, but not in *Scrobicularia*, spawning occurs during the growing season: in June for *Mya* (Munch-Petersen 1973) and in May-June for *Cerastoderma* (Baggerman 1953, Boyden 1971, Kingston 1974, Newell & Bayne 1980, Yankson 1986).

Annual differences

Beukema & Cadée (1991) showed that the year-to-year variability in weight gain, and other parameters of growth rate, in *Macoma* depend on the food supply, i.e. the abundance of diatoms during the spring months. The annual weight gain measured in the western part of the Dutch Wadden Sea (Beukema & Cadée 1991) and the annual variation in the peak condition, measured 100 km to the east (Fig. 9), appear to be highly correlated (Fig. 12). This suggests that there is a similar common pattern of annual fluctuations in the feeding conditions for the macrozoobenthos over vast areas (see Figs. 4, 7 and 9 in de Jonge & Essink 1991).

Regional differences

Figures 13-16 summarize the available measurement on body weight of the four species from elsewhere, and compares them with the data from the study sites in the eastern part of the Dutch Wadden Sea. Since the seasonal trends and annual variations in *Macoma* on Balgzand, 100 km to the west, closely resemble those from our study sites (Beukema & de Bruin 1977, Beukema *et al.* 1985, Beukema & Desprez 1986), they are not presented to avoid cluttering Fig. 13. Several conversions had to be done in order to make the different data sets comparable: see legends to Figs. 13-16. In general, the seasonal variations in the Wadden Sea and elsewhere did not differ (very) much: the summer peak was about as high, and the winter weight was about 40 to 50% below the summer weight. There were, however, some interesting differences.

The summer peak in *Macoma*, reached in May and June in the Wadden Sea (Fig. 13), occurred a month later in the Baltic Sea, (Pekkarinen 1983, Bonsdorff & Wenne 1989) and Nova Scotia, Canada (Cranford *et al.* 1985), but a month or two earlier in S. France (Bachelet 1980). The low weight in the French population during the summer, and the subsequent increase in body weight in September, has been attributed to the occurrence of two spawning periods (Bachelet 1980, see Harvey & Vincent 1989 for a review). A detailed analysis of the regional variation in the improvement of the condition in spring has been given by Beukema & Desprez (1986).

The seasonal variation in body weight of *Scrobicularia* in S. England (Bryan & Hummerstone 1978, Boates & Goss-Custard 1989) and the Wadden Sea is similar (Fig. 14), though *Scrobicularia* retain a remarkable high winter weight in N. Wales (Hughes 1970b). The great variation in the body weight in SW. France can partly be attributed to systematic differences in sites studied (Bachelet 1979, 1981).

The seasonal variation of *Mya* in the Wadden Sea was similar to that recorded elsewhere (Munch-

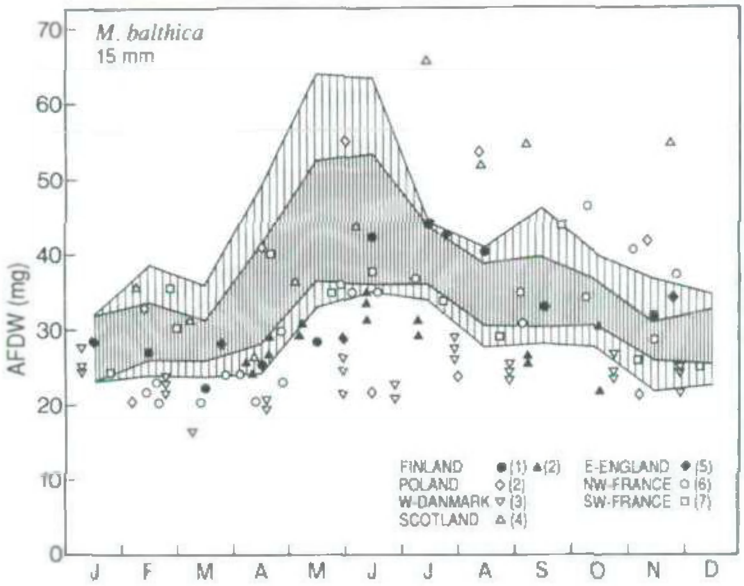


Fig. 13. Seasonal variation in the AFDW of the soft parts of *Macoma* (15 mm) in seven studies compared with the results obtained at the study sites in the eastern part of the Dutch Wadden Sea (dark: monthly range between 25 and 75 percentiles; light: ranges between 10-25 en 75-90 percentiles). Other studies: (1) Bonsdorff & Wenne (1989)*; they give DW for* specimens 13 mm long; percentages ash from Fig. 4 are used to estimate AFDW; these values are multiplied by 1.52 to obtain AFDW of individuals 15 mm long (Table 6). (2) Pekkarinen (1983); condition index of DW is given; these are converted to weights, after which the percentage ash given in her paper are used to estimate AFDW. (3) Madsen & Jensen (1987); they present the condition index of AFDW, which is transformed into the weight of an animal of 15 mm. (4) Chambers & Milne (1975a); they relate DW to shell height; their relation between shell height and length is used to calculate DW of bivalves 15 mm long; percentage ash, given in Fig. 4, is used to estimate AFDW. (5) Goss-Custard *et al.* (1977a). (6) Bachelet (1980). (7) Beukema & Desprez (1986).

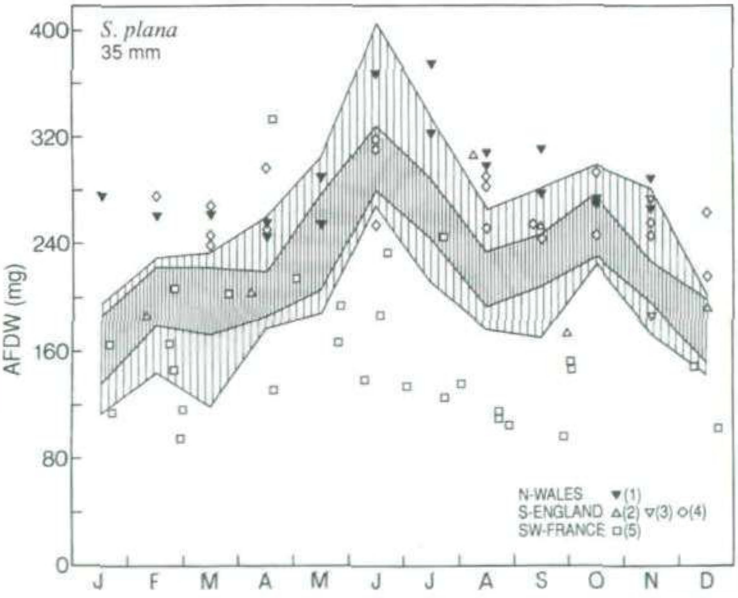


Fig. 14. Seasonal variation in the AFDW of the soft parts of *Scrobicularia* (35 mm) in five studies, compared with the eastern part of the Dutch Wadden Sea (dark: monthly range between 25 and 75 percentiles; light: ranges between 10-25 and 75-90 percentiles). Other studies: (1) Hughes (1970b); he presents DW as a function of size; percentage ash, given in his Table 2, is used to calculate AFDW. (2) Bryan & Hummerstone (1978). (3) Worrall *et al.* (1983); weights of a standard animal 30 mm long are multiplied by 1.57 to obtain AFDW of individuals 35 mm long (this paper). (4) Boates & Goss-Custard (1989). (5) Bachelet (1979, 1981).

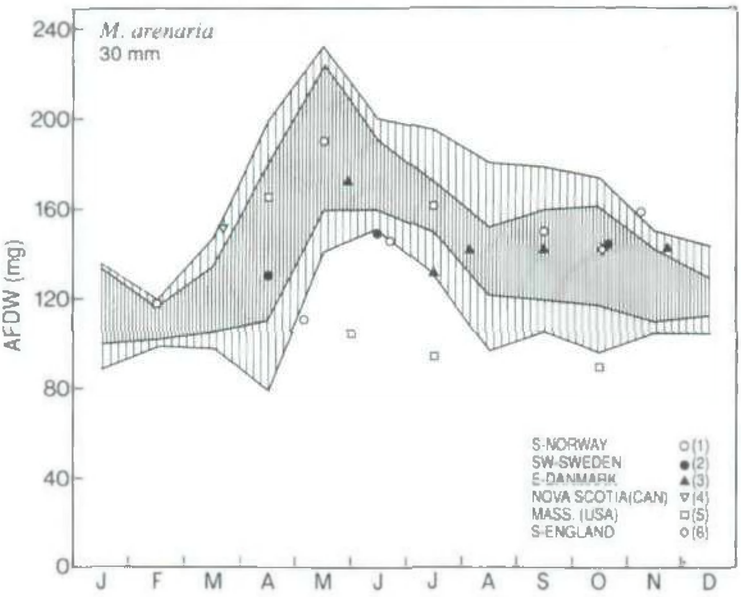


Fig. 15. Seasonal variation in the AFDW of the soft parts of *Mya* (30 mm) in six studies, compared with the eastern part of the Dutch Wadden Sea (dark: monthly range between 25 and 75 percentiles; light: ranges between 10-25 en 75-90 percentiles). Other studies: (1) Winther & Gray (1985) present DW; percentage ash from Fig. 4 is used to estimate AFDW. (2) Möller & Rosenberg (1983) determined AFDW for specimens shell inclusive; 18 mg is subtracted to allow for the AFDW of the shell (Fig. 2). (3) Munch-Peterson (1973) gives fresh weight; AFDW is assumed to be 17.6% of fresh weight (own data). (4) Emerson *et al.* (1988); they present DW; percentage ash from Fig. 4 is used to estimate AFDW. (5) Edwards & Huebner (1977). (6) Warwick & Price (1975).

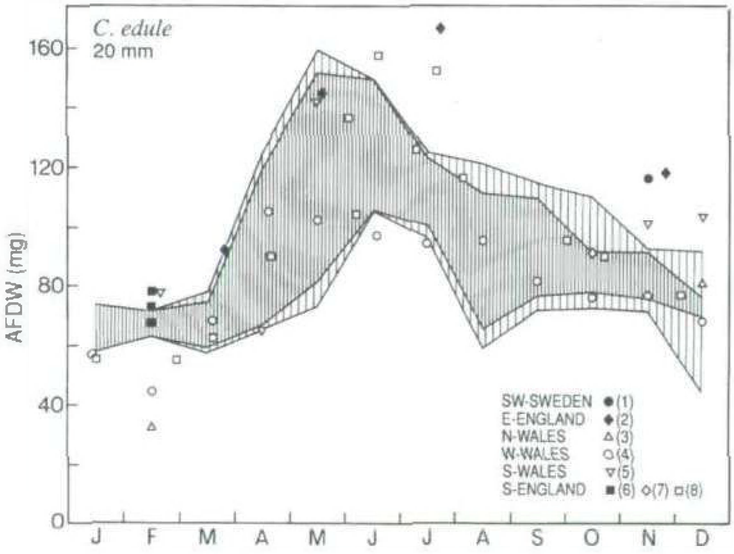
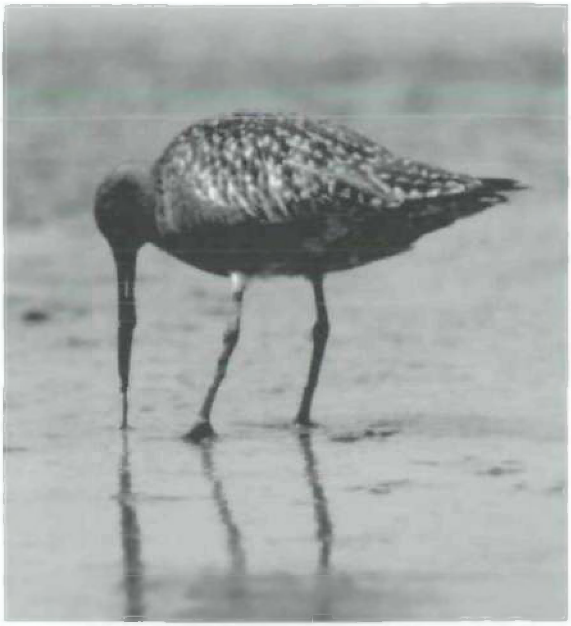
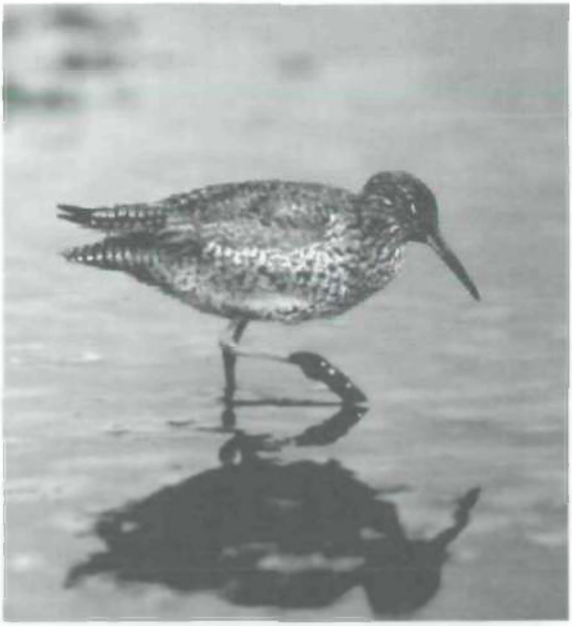


Fig. 16. Seasonal variation in the AFDW of the soft parts of *Cerastoderma* (20 mm) in eight studies, compared with the eastern part of the Dutch Wadden Sea (dark: monthly range between 25 and 75 percentiles; light: ranges between 10-25 en 75-90 percentiles). Other studies: (1) Möller & Rosenberg (1983); they determined AFDW for specimens including the shell; 27 mg is subtracted to allow for the AFDW of the shell (Fig. 2). (2) Goss-Custard *et al.* (1977a). (3) Sutherland (1982a, 1982c). (4) Jones (1979); DW is given for specimens 25 mm long; these are divided by two to obtain DW of individuals 20 mm long, after which percentages ash from Fig. 4 are used to estimate AFDW. (5) Newell & Bayne (1980) give DW; percentages ash from Fig. 4 are used to estimate AFDW; since they relate AFDW to shell height, Table 5 is used to convert this to shell length. (6) Warwick & Price (1975); (7) Hibbert (1976). (8) Hancock & Franklin (1972); they give DW; percentages ash from Fig. 4 are used to estimate AFDW.





In winter, all wader species have to eat more prey to compensate for the poor condition of their prey: Bar-tailed Godwit (left), Redshank (right), *Grey Plover (bottom)*.

Petersen 1973, Warwick & Price 1975, Möller & Rosenberg 1983, Winther & Gray 1985, Emerson *et al.* 1988), although the summer weights in Massachusetts (Edward & Huebner 1977) were lower (Fig. 15). There was also a reasonable similarity in the seasonal variations in the body weight of *Cerastoderma* in Sweden (Möller & Rosenberg 1983), E. England (Goss-Custard *et al.* 1977a), S. England and Wales (Hancock & Franklin 1972, Warwick & Price 1975, Hibbert 1976, Jones 1979, Sutherland 1982a, 1982c) and the Wadden Sea (Fig. 16).

Weight change and scope for growth

If the negative relation between winter temperature and change in body weight (Fig. 10) is a general phenomenon, very low body weights are to be expected in southern areas during winter. The average winter sea water temperature is close to 0 °C in SW. Sweden (Möller & Rosenberg 1983), 2-4 °C in the Wadden Sea, 6-7 °C in Wales, Ireland and France and 14 °C in Portugal (Hughes 1972, Bachelet 1980, Desprez *et al.* 1991). Despite this large variation, there is no evidence, however, of a latitudinal variation in change in body weights during winter (Figs. 13-16).

The annual variations in the weights of the soft parts of the bivalves depend on the energy budget, and thus on the balance of total energy intake and energy demands. The intake rate depends on the food consumption and thus the available food supply, while the energy demands depend primarily on ambient temperature. The decrease in body weight of *Macoma* in mid summer can be explained by the decline in food supply at a time when energy demands reach a peak because of the high temperatures (Beukema *et al.* 1985, Hummel 1985c). The weight reduction in July may be as great as 20% in years when the sea water temperature is between 18 and 20 °C, but with July temperatures of 15 or 16 °C, *Macoma* are able to maintain their body weight (Beukema *et al.* 1985). Laboratory experiments (Hummel 1985b) confirm that a change in body weight depends on a combination of temperature and food supply. The apparent absence of a latitudinal variation in winter weight (Figs. 13 to 16) would suggest that the higher costs of living in the more southern areas are offset by a higher food intake (and food supply) during winter.

Implications for birds

Winter is a difficult period for waders. Firstly, the fraction of prey which is accessible to them is (much) lower than in the summer (Zwarts & Wanink 1989). The fraction of large *Scrobicularia* accessible for Oystercatcher *Haematopus ostralegus* is 40% in summer but nearly 0% in winter (Zwarts & Wanink 1989 and 1991). Secondly, they have to eat more prey to compensate for the poor condition of the prey. The data summarized in this paper show that waders have to find 1.5 to 2 times more prey in winter than in summer to maintain the same level of daily food consumption. For *Scrobicularia*, it has been shown that the seasonal variation in the weights of the prey actually accessible to Oystercatchers is even larger, because prey within reach of the bill has less-than-average body weight (Zwarts & Wanink 1991). Thirdly, the energy demands of waders increase when wind forces increase and temperatures decrease: the daily food consumption of an Oystercatcher increases by 40-50%, from 30-35 to 45-50 g AFDW, as the ambient temperature drops from 10 to 0 °C (Kersten & Piersma 1987). The effect of severe winter conditions on the energy demands of the birds themselves is thus not fully compensated by the better body condition of the prey that results from low temperatures (Fig. 10).

Chapter 2

HOW THE FOOD SUPPLY HARVESTABLE BY WADERS IN DE WADDEN SEA DEPENDS ON THE VARIATION IN ENERGY DENSITY, BODY WEIGHT, BIOMASS, BURYING DEPTH AND BEHAVIOUR OF TIDAL-FLAT INVERTEBRATES

Leo Zwarts & Jan H. Wanink

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HOW THE FOOD SUPPLY HARVESTABLE BY WADERS IN DE WADDEN SEA DEPENDS ON THE VARIATION IN ENERGY DENSITY, BODY WEIGHT, BIOMASS, BURYING DEPTH AND BEHAVIOUR OF TIDAL-FLAT INVERTEBRATES

For several reasons, waders in the Wadden Sea face a large seasonal and annual variation in their food supply. Observations on a tidal flat in the Dutch Wadden Sea have shown that:

- (1) The average energy density of ten invertebrate prey species varies between 21 and 23 kJ g^{-1} AFDW. In *Scrobicularia plana* and *Mya arenaria*, but not *Macoma balthica*, the energy density is 10% lower in winter than in summer.

- (2) Depending on the species, the body weights of prey of similar size are 30 to 60% lower in winter than in summer.

- (3) The year-to-year fluctuation in standing crop biomass is larger in some species than in others, the difference depending mainly on the frequency of successful recruitment. The overall biomass of the macrobenthos in winter is half of that in summer, but the timing of the peak biomass differs per species.

- (4) The burying depth varies per species: *Cerastoderma edule* live just beneath the surface, while *Macoma*, *Scrobicularia*, *Mya*, *Arenicola marina* and *Nereis diversicolor* bury more deeply and the majority of these prey live out of reach of the bird's bill. In all six species, burying depth increases with size. There is no seasonal variation in depth of *Cerastoderma* and *Mya*, but the four other species live at most shallow depth in early summer and most deeply in mid winter. Burying depths in winter vary from year to year, but are unrelated to temperature. Neither has temperature any effect on depth within months. For Knot *Calidris canutus* feeding on *Macoma*, the fluctuation in the accessible fraction was the main source of variation in the biomass of prey that is actually harvestable, i.e. the biomass of prey of suitable size that is accessible.

Accordingly, the paper reviews the available data on the temporal variations in accessibility, detectability, ingestibility, digestibility and profitability of prey for waders. Only a small part of the prey is harvestable since many accessible prey are ignored because of their low profitability, while many profitable prey are inaccessible. The profitability of prey depends on their size and weight but also on their depth in the mud, since handling time increases with burying depth. A simple biomechanical rule explains why the handling time of small prey increases with bill length and why large, long-billed waders ignore a disproportionately larger part of the small prey. The fraction detectable for visually feeding waders is usually very low, especially when the temperature of the substrate is below 3 to 6 °C. Waders vary their prey choice over the year in response to the changes in the availability and profitability of their different prey species. The food supply harvestable by waders is much lower in winter than in summer. For waders wintering in the Wadden Sea, the food supply may be characterized as unpredictable and usually meagre. Waders wintering in NW. Europe are concentrated in coastal sites where the average surface temperature is above 3 °C. This probably cannot be explained by a greater burying depth, and only partly by a lower body condition, of prey in colder areas. Yet the harvestable fraction is lower in colder sites, especially for sight-feeding waders, as invertebrates are less active at low temperatures. However, the lower energetic cost of living and reduced chances of the prey being covered by ice may also contribute to the waders' preference for warmer sites.

Introduction

This paper describes the seasonal and annual variation in the food supply of birds foraging on the intertidal flats in the Wadden Sea. A quantitative analysis of actual food supplies demands not only a description of the fluctuations in energy density, body condition and total biomass of the several potential prey species present, but also an investigation of the variations in the fraction of the prey that is available as well as profitable to the birds. Large prey are usually profitable (i.e. energetically worth consuming) but not available (i.e. detectable, accessible and ingestible). On the other hand, small prey are often readily available but are rejected because of their low profitability. Prey that are harvestable, defined as profitable as well as available, often comprise only a small fraction of the total biomass of prey present. In Knot *Calidris canutus*, a wading bird specializing on eating hard-shelled prey, 89% of the prey biomass consisted of animals that were too large or too small or lived too deeply to be taken (Zwarts & Blomert 1992, Zwarts *et al.* 1992).

Fluctuations in the harvestable food supply have to be measured precisely before answers can be given to questions such as: why do diet and intake rate in waders vary seasonally? why do waders leave the Wadden Sea to winter further south? Indeed, this kind of information is essential for any study of the relationship between predators and their food supply. It may also help us to explain how predators coexist, since it clarifies the degree to which there is overlap in the harvestable food supply exploited by different species (Zwarts & Wanink 1984).

Several aspects of the seasonal and annual variation in the food supply of shorebirds have already been described. Unique series of measurements are available on the year-to-year variation in the biomass of benthic prey in the Wadden Sea (Beukema *et al.* 1993). There is little seasonal variation in the energy density per g AFDW of tidal invertebrates (Beukema & de Bruin 1977, Chambers & Milne 1979). Beukema (1974) showed that in winter the biomass of all macrobenthic animals combined is about half of that in summer. This difference is mainly due to a decrease in the flesh content of individual prey (Hancock & Franklin 1972, Beukema & de Bruin 1977, Chambers & Milne 1979, Zwarts 1991). Seasonal variation in the burying depth of benthic animals has been studied by Reading & McGrorty (1978), Zwarts & Wanink (1989) and Zwarts & Esselink (1989).

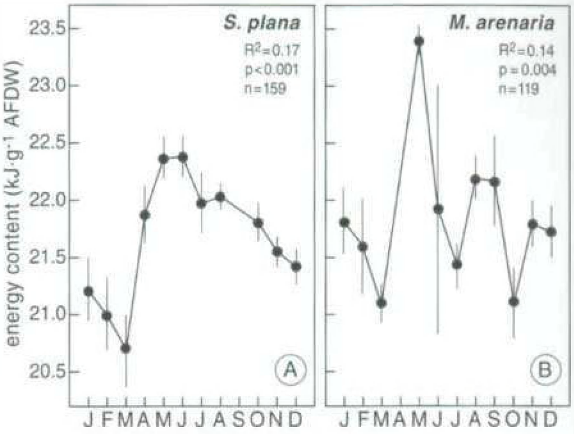


Fig. 1. Seasonal variation in the energy density (kJ g⁻¹ AFDW ± SE) of *Scrobicularia plana* and *Mya arenaria*. Results of one-way analyses of variance are given.

This paper presents additional data from the Wadden Sea on seasonal and annual variations in (1) the energy density, (2) flesh weight of prey of constant size, (3) total biomass, and (4) burying depth of shore bird prey. Taken together, these components comprise the main sources of variation in the harvestable food supply of the birds. We conclude that (1) the variation in the accessible fraction may be larger than the fluctuation in the total biomass of the prey actually present, (2) the extent of the seasonal variation in the flesh weight and in the accessible fraction differs greatly between prey species, (3) the food supply harvestable by waders is much lower in winter than in summer, and, therefore the most-studied shorebird, Oystercatcher *Haematopus ostralegus*, achieves a higher intake rate in summer than in winter, (4) low mud temperature in winter reduces the detectable prey fraction, but probably has no effect on the burying depth and body condition of the prey, and (5) large waders ignore a disproportionately large portion of the smaller, unprofitable prey.

Methods

The study sites were situated on a tidal flat in the eastern part of the Dutch Wadden Sea, along the mainland coast of the province Friesland (53°25'N, 6°04'E), and have been described before by Zwarts (1991) and Zwarts *et al.* (1992). The sites were situated just below mean sea level. Macrozoobenthos was sampled monthly in site N, while depth measurements were usually made in the nearby site D (Fig. 1 of Zwarts *et al.* 1992). The substrate in both sites was soft, averaging 5 to 6% clay (fraction < 2 µm).

Seventy-three or 292 sediment cores (15 cm Ø, 40 cm deep) were taken in site N almost every month from 1980 to 1986, and more infrequently between 1977 and 1979. The cores were sieved through a 1-mm mesh screen. The animals were taken to the laboratory to measure their length, dry weight and ash-free dry weight (AFDW) according to methods given by Zwarts (1991). The length of Ragworms, *Nereis diversicolor*, was defined as the maximum length of a worm creeping along a ruler in sea water (Esselink & Zwarts 1989). The length of broken worms was estimated from the relation between width of the tenth segment and the length of intact worms (Esselink & Zwarts 1989). The length of Lugworms *Arenicola marina* referred only to the body without tail, measured as the worm suspended for some seconds by the head in a pair of forceps.

The depth measurements were collected at low tide, once or twice a month over the seven-year period 1980 to 1986. We used a corer (Ø 15 cm) that was pushed 40 cm into the mud. The extracted core was laid down on a table and broken open. The burying depth of the bivalves was defined as the distance between the mud surface and the upper edge of the shell. The burrow depth of *Nereis* and *Arenicola* equalled the distance between the surface and the deepest point of their U- or J-shaped burrow. The methods are described more fully elsewhere (Zwarts 1986, Esselink & Zwarts 1989, Zwarts & Wanink 1989). The collected animals were taken to the laboratory to determine length and AFDW of each individual.

The energy density of the well-dried flesh was measured with a Parr-1665 adiabatic calorimeter. All determinations were done in duplicate or triplicate for each sample. The energy density is given per g AFDW; ash content was determined by furnace ashing at 550 °C. A correction was made for the endothermic reaction during the combustion of the Shore Crab *Carcinus maenas* (Paine 1966), since half of its dry weight consisted of $CaCO_3$.

Sea water temperature was measured daily by Rijkswaterstaat at 8 a.m. at the nearby station of Holwerd. SPSS (Norušis 1988) was used for all statistical analyses.

Results

Seasonal variation in energy density

Zoobenthos biomass is usually measured in terms of ash-free dry weight (AFDW). Predator consumption is often expressed the same way, the implicit assumption being that prey weight reflects food value and that the energy density does not differ between prey species or seasons. Enough data were available in three species to check for any seasonal variation in the energy density of flesh. No significant difference was found in the tellinid bivalve *Macoma balthica* according to a one-way analysis of variance ($R^2 = 0.04$, $p = 0.79$, $n = 60$). Energy density, however, varied seasonally in another tellinid bivalve, *Scrobicularia plana*, and in the Soft-shell Clam, or Gaper, *Mya arenaria* (Fig. 1). Both species reached lowest values in March and highest in May or June. This trend was evident within each year of sampling, even though the energy density of *Scrobicularia* also varied between the years (Zwarts & Wanink 1991). These seasonal differences were significant (see Fig. 1), but they amounted to not more than 2 kJ, or 10%.

Although previous studies had found no seasonal variation in the energy density of all three species (*Macoma*: Gilbert 1973, Beukema & de Bruin 1977, Chambers & Milne 1979; *Scrobicularia*: Hughes 1970b and *Mya*: Edwards & Huebner 1977, Winther & Gray 1985), a seasonal variation in energy density might be expected. Starvation in winter and spawning in summer lead to changes in the biochemical composition of the body (e.g. Ansell & Trevallion 1967, Beukema & de Bruin 1977, Pieters *et al.* 1980, Pekkarinen 1983, Dare & Edwards 1975, de Vooys 1975, Mayes & Howie 1985). Gametes alone may add

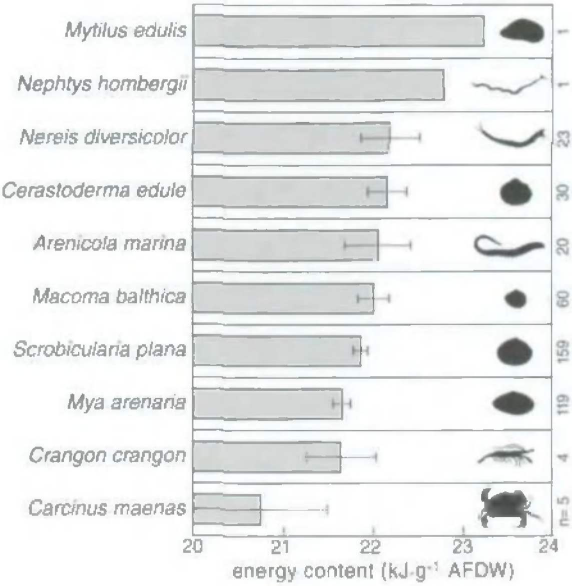


Fig. 2. Average energy density (kJ g^{-1} AFDW ± SE) of ten invertebrates; number of measurements are indicated. According to a one-way analysis of variance, the species differ significantly: $R^2 = 0.05$, $p = 0.027$, $n = 423$).

at least 20% to the body weight (e.g. de Wilde & Berghuis 1978, Zwarts 1991), so a difference between the energy value of gametes and other flesh would affect the energy density of the entire animal. However, de Wilde & Berghuis (1978) found that gamete production in *Macoma* would raise the energy density of females and lower it for males, since the energy density of eggs was 24.7 kJ g^{-1} and of sperm 18.9 kJ g^{-1}, 3 kJ above and below the average energy value of *Macoma* flesh, respectively. At the population level, it is thus unlikely that gametogenesis would cause the energy value of an average *Macoma* to vary 50 : 50. On the other hand, the study of de Wilde & Berghuis (1978) shows how food value may vary between individual prey and that predators may be able to increase their rate of energy intake by selecting female prey (see e.g. Szaniawska 1984 for Common Shrimp *Crangon crangon*; Zwarts & Blomert 1990 for Fiddler Crab *Uca tangeri*).

There were also significant differences in the energy densities of ten tidal invertebrates considered (Fig. 2). Although the worm species had, on average, a higher energy density than the bivalves, the highest energy density was found in the Common Mussel *Mytilus edulis*. Chambers & Milne (1979) found that, in the Ythan estuary, E. Scotland, the average energy density differed between *Mytilus* (22.2 kJ g^{-1} AFDW), *Nereis* (21.8 kJ g^{-1}), the Edible Cockle *Cerastoderma edule* (20.6 kJ g^{-1}) and *Macoma* (20.0 kJ g^{-1}). The species ranked in exactly the same order as in Fig. 2, but the values were in all cases below those found in our study area.

In most other studies, estimates of energy density are similar to those we found. Using conversion factors for fat, glycogen and protein, Dare & Edwards (1975) arrived at an average energy density for *Mytilus* of 23.3 kJ g^{-1}, very close to the value given in Fig. 2. The energy density measured by Bayne & Worrall (1980) was slightly higher (24 kJ g^{-1}, assuming that ash-content was 10%), but Heppleston (1971) found a slightly lower value: 22.6 kJ g^{-1}. The average value we found for *Macoma* is halfway between those given by Chambers & Milne (1979) (20.0 kJ g^{-1}) and Beukema & de Bruin (1977) (22.9 kJ g^{-1}). The published values for other bivalves are also similar to ours. Thus, Swennen (1976) found 21.7 kJ g^{-1} for *Cerastoderma*, Hughes (1970b) 21.4 kJ g^{-1} for *Scrobicularia*, and Edwards & Huebner (1977) and Winther & Gray (1985) found 20.8 and 21.7 kJ g^{-1}, respectively, for *Mya*.

Although a correction of 0.3 kJ g^{-1} was made for the endothermic reaction of $CaCO_3$ (see Methods), the energy density of *Carcinus* was low. This might be due to the low energy density of the organic component of the skeleton (Zwarts & Blomert 1990). This explanation is strengthened by Klein Breteler (1975) who found an energy density of 23 kJ g^{-1} in moulting *Carcinus* with little skeletal material. The presence of the skeleton probably also depresses the energy density of the amphipod *Corophium volutator* where, according to Chambers & Milne (1979) and Boates & Smith (1979), respectively, the energy density is only 19.9 or 20.2 kJ g^{-1}.

As fat has a higher energy density than proteins and carbohydrates, species differences in biochemical composition, as well as the amount of skeleton present, would be expected to cause species differences in energy density. The energy density of *Corophium* is less than that of bivalves, partly because its fat content is only 1.7% (Napolitano & Ackman 1989) compared with around 10% in bivalves *Tellina tenuis* (Ansell & Trevallion 1967), *Mytilus* (Dare & Edwards 1975) and *Macoma* (Beukema & de Bruin 1977). Fat content also varies regionally within a species; for example, the fat content of *Macoma* in the Baltic Sea is twice as high as in the Wadden Sea (Pekkarinen 1983). Such a regional variation in fat content may explain why the energy density of marine invertebrates from the northern region is, on average, higher than those from more southern shores. Thus Wacasey & Atkinson (1987) found a grand mean of 22.7 kJ g^{-1} for many invertebrate species from the Canadian Arctic. Brey *et al.* (1988) arrived at a mean of 23 kJ g^{-1} for invertebrates from the Baltic Sea. In contrast, this study found a mean of 21.8 kJ g^{-1} for the Wadden Sea, while Dauvin & Joncourt (1989) found a value of only 20.5 kJ g^{-1} in the English Channel.

In conclusion, the seasonal, regional and species variation in the energy density of estuarine invertebrates is not very large but, at 10%, might be enough to explain a diet shift of predators which might otherwise be difficult to understand if the simplification is accepted that prey weight is assumed to be equivalent to food value. But as will be shown in the next section, the variation in flesh weight of prey of constant size is much larger and thus likely to be ecologically more important.

Seasonal variation in body weight at the same length

The seasonal and annual variations in the condition of the four most important bivalve species in our study area have already been described (Zwarts 1991): *Macoma, Scrobicularia, Mya* and *Cerastoderma* of similar size contained, in May and June, 1.7 to 2.1 times as much flesh as in February and March. This section therefore deals only with the seasonal variation in the flesh weight of other benthic species. All available weight measurements were combined and the average weight per cm (in worms) and mm (in bivalves) size class calculated. The common regression between weight and body length was calculated for these average weights (Table 1). The slope of the weight-size regression differed seasonally in *Mytilus* as also found by Bayne & Worrall (1980), Craeymeersch *et al.* (1986) and Cayford & Goss-Custard (1990). The regression equation for *Carcinus* closely resembled that already published by Klein Breteler (1975). The equation for *Corophium* was similar to that given by Birklund (1977), but the predicted weights were somewhat below those given by Boates & Smith (1979) and Möller & Rosenberg (1982) and somewhat above those of Goss-Custard (1977a) and Hawkins (1985). A comparison was not possible in the worm species in view of the lack of standardisation in the measurement of body size. Weight measurements were expressed as deviations from the mean for each size class predicted by the regressions in Table 1.

The average monthly deviations from the long-term mean, set to 100, are shown in Fig. 3. The seasonal variations in *Mytilus* were very large compared with those recorded in the four bivalve species mentioned above. The change in condition is given separately for two size classes, since larger Mussels reach their peak

Table 1. Exponential relationship between body weight (AFDW of the flesh) and body size (shell length or worm length, but carapace width in *Carcinus maenas*). a and b are the intercept and slope, respectively, of the regression: ln(mg AFDW) against ln(mm, but cm in the worm species). The regressions were calculated for the mean weights of k size class, weighted for sample size (n). The data are from 10-12 years and all seasons, but *Corophium volutator* were only collected in summer.

species	*a*	*b*	*r*	*n*	*k*	*range*
Mytilus edulis	-4.596	2.840	0.995	10756	67	2-75 mm
Nephtys hombergii	-0.183	2.017	0.962	263	14	2-12 cm
Nereis diversicolor	0.898	2.208	0.996	3586	22	1-13 cm
Arenicola marina	+1.198	2.334	0.992	1831	13	1-13 cm
Carcinus maenas	-2.925	2.871	0.998	772	49	2-60 mm
Corophium volutator	-5.244	2.800	0.994	526	9	2-10 mm

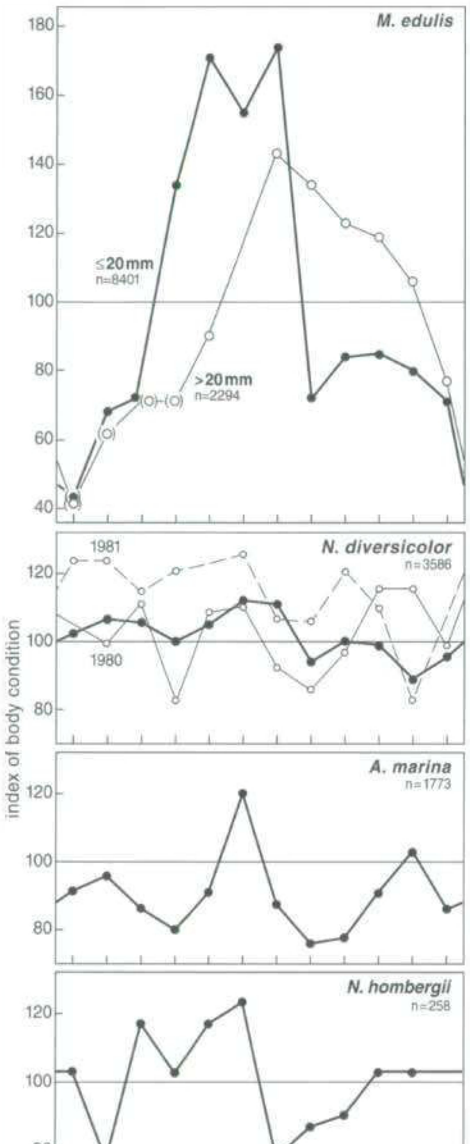


Fig. 3. Average seasonal variation in the body condition of *Mytilus edulis*, given separately for small and larger Mussels, and three worm species; small samples (< 10 animals) in parentheses. The average AFDW per size class, predicted by the regressions given in Table 1, were set to 100 and all weight measurements were expressed as percentage deviation and averaged per month; n is total number of individuals weighed. The trends also are shown for two separate years in *Nereis diversicolor* to show the year-to-year variation in body condition.

condition later in the year (Fig. 3; Dare 1975, Dare & Edwards 1975). A decrease in the body weight of Mussels in the Wadden Sea after late summer has already been observed by Everards (1973) and Pieters *et al.* (1979). In contrast, Craeymeersch *et al.* (1986) found the lowest body condition in June and the highest in winter in Mussels from the Eastern Scheldt (SW. Netherlands). A great weight loss in May or June due to spawning, and a weight recovery after that, was also noted for Mussels on the British Isles (Baird 1966, Dare 1975, Dare & Edwards 1975, Bayne & Worrall 1980, Cayford & Goss-Custard 1990). The geographical variation in winter condition will be discussed later.

At first sight, there seemed to be little seasonal variation in the body condition of *Nereis* (Fig. 3). However, when the data for different years were considered separately, (shown for two years in Fig. 3), large fluctuations emerged. Moreover, the seasonal timing of the peak and base weights varied between years by one or two months: the body condition was usually low in March or April, high in June or July and again low in July to November. Mettam (1979) found low body weights in winter, and to a lesser extent also in May. As spawning occurs when the temperature in spring rises above 6 °C (Bartels-Hartege & Zeeck 1990), the annual variations in the timing of the decrease in body condition in spring may reflect annual variations in the timing of gamete release associated with temperature. This may also explain the geographical variation in timing in the loss of condition which in southern England seems to be in March and April (Dales 1951, Olive & Garwood 1981), compared with April and May in the Wadden Sea (Essink *et al.* 1985) and May in southern Sweden (Möller 1985).

In accordance with de Wilde & Berghuis (1979b), *Arenicola* reached a low condition in late winter and again in late summer, following a peak in condition in June (Fig. 3). Beukema & de Vlas (1979) showed that large worms (common in sand but rare in muddy areas as our study area) reached their peak weight later in the season. Gamete release occurs in August to November (Farke & Berghuis 1979, de Wilde & Berghuis 1979b), which probably explains the low body weight in autumn.

As in *Nereis* and *Arenicola*, the seasonal variation in condition was relatively small in *Nephtys hombergii*

(Fig. 3). Peak condition was reached in June, while the poorest condition occurred in late winter and again in July, possibly due to emission of oocytes. The timing of spawning differs geographically (Smidt 1951, Kirkegaard 1978, Oyenekan 1986, Mathivat-Lallier & Cazaux 1991). Olive *et al.* (1985) also found that the pattern of seasonal change in body condition varied annually. When spawning occurred, the body weight was high in April and very low in June, due to the discharge of gametes. In contrast, in a year with spawning failure, the body weight in spring remained low.

No seasonal variation was found in the weight of *Carcinus*. Possible seasonal changes in the condition of *Corophium* could not be explored since this species was only collected in summer. However, Boates & Smith (1979) reported a decrease in body condition of *Corophium* after spring.

To conclude, the seasonal changes in body condition are caused by weight changes in reproductive and in other body tissues. In *Macoma*, *Mya* and *Cerastoderma*, the highest body condition is attained in early summer at a time of maximum growth. As a consequence, the weight loss due to spawning, which coincides with maximum growth, is masked by the rapid increase in body mass (Zwarts 1991 and sources cited in that paper). In contrast, spawning of *Scrobicularia, Mytilus* and several worm species takes place either before or after the period of maximum growth, with the result that the change in body condition during the year is more bimodal than unimodal.

Year-to-year variation in total biomass per species

The biomass of the prey in the substrate depends on densities of different size classes as well as on their condition. The previous section dealt with the variation in body weight in prey of similar size so, in order to understand the seasonal and annual variation in the total biomass present, it would also be necessary to show the mortality and growth in various cohorts. As this information will be published separately, we only show here the annual variation in biomass, accompanied by a brief description of the occurrence of the successive cohorts responsible for the year-to-year variation.

The biomass of *Macoma* (shell length 1 to 25 mm) varied between 7 and 66 g m^{-2} (Fig. 4A). This species occurred at a density of 200-300 m^{-2} in 1977 to 1979, but density increased to nearly 2000 m^{-2} at the time of the successful spatfall in 1979. Because of the small size of spat, however, the biomass at that time was only 7 g m^{-2}, the lowest level ever observed in the study area. But subsequently, as the animals grew, biomass increased and the year class 1979 dominated total *Macoma* biomass for several years, because the meagre spatfalls in 1981, 1983, 1984 amounted to less than 100 m^{-2}. The 1985 spatfall (500 spat m^{-2}) was the first large one in six years.

The biomass of *Scrobicularia* (shell length 4 to 50 mm) was high (40 to 70 g m^{-2}) in 1979 to 1982 (Fig. 4B) with all individuals belonging to the year class of 1976. Hardly any recruitment occurred during the ten years of sampling. The population born in 1976 died out in 1983 and the variation in biomass shown refers only to this one year class.

The year-to-year change in biomass of *Mya* (shell length 1 to 103 mm) (Fig. 4C) was dominated by two year classes: 1976 (from which 250 animals m^{-2} were still present in autumn 1977) and 1979 (800 spat m^{-2} in August). There were only 30 spat m^{-2} in August 1983, and even less in other years, so the year class 1979 largely determined the variation in biomass over the following 7 years. The peak biomass occurred when this cohort was 5 to 6 years old.

The biomass of *Cerastoderma* (shell length 1 to 41 mm) varied between 0 and 73 g m^{-2} (Fig. 4D), while its numerical density varied between 0 and 1550 n m^{-2}. Spatfall occurred in 1976, 1979 and in five successive years: 1982 to 1986. However, spat density in August was only about 100 m^{-2} in three of these years (1979, 1985 and 1986) and about 500 m^{-2} in 1982 and 1983. We found 1400 spat m^{-2} in August 1984, and the spatfall in 1976 must have been in the same order of magnitude, since the following year the density of 1+ Cockles was still 600 m^{-2}. *Cerastoderma* is a winter-sensitive species (Beukema 1989) so, as elsewhere in the Wadden Sea, hardly any survived the severe winters of 1978/79 and 1985/86 (Beukema *et al.* 1993). Although the winter of 1984/85 was as severe as the other two, the biomass was only reduced by a quarter, in contrast to other sampling sites in the Wadden Sea (Beukema *et al.* 1993). Sixty percent of the Cockles died, but this had only a small effect on the

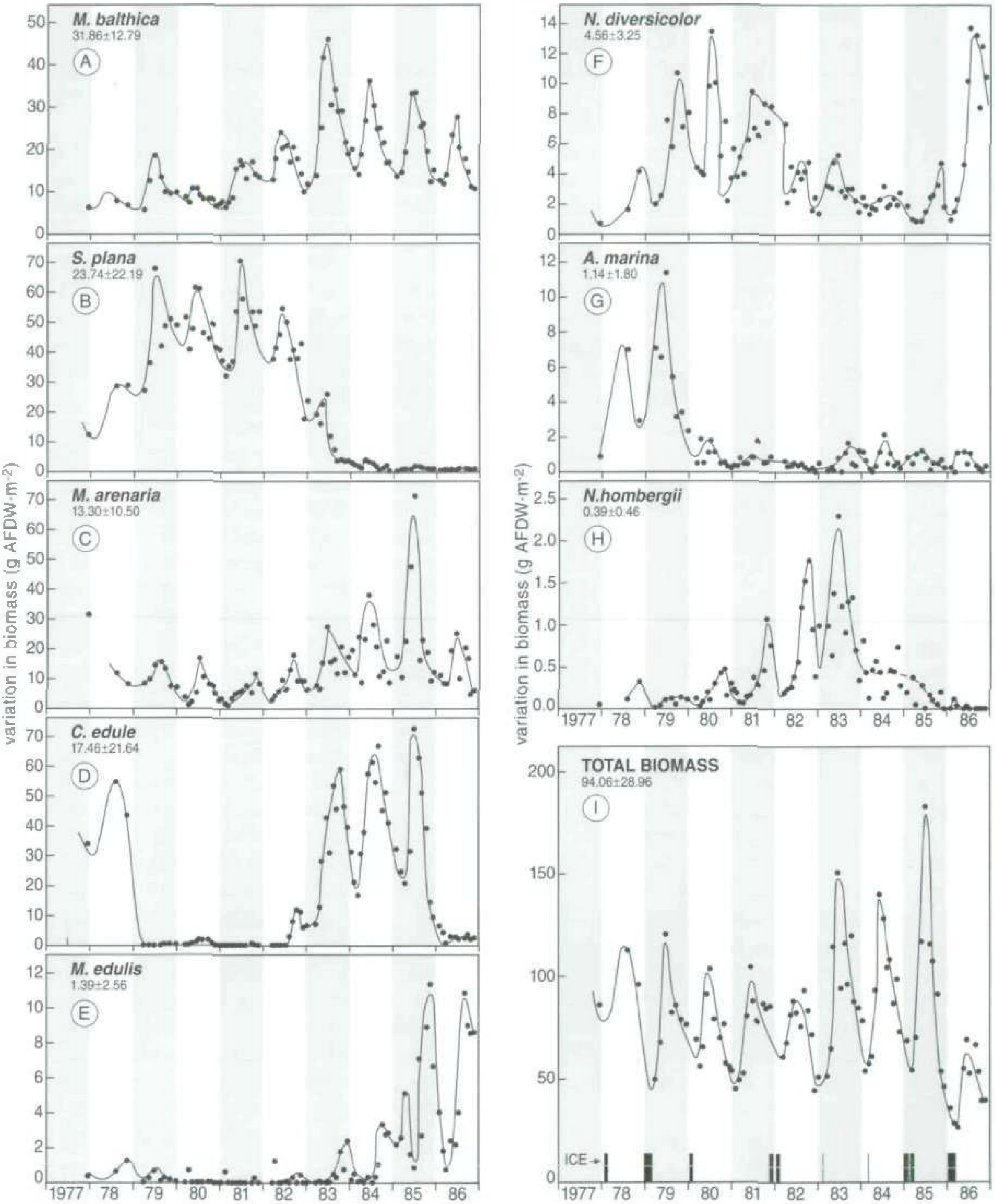


Fig. 4. Variation in the biomass (g AFDW m^{-2}) of five bivalve and three worm species, and in the total biomass of all species during nine years; mean ± SD, calculated over 84 sampling periods, is given; ice periods are indicated in the panel I.

total biomass since most of those that died belonged to the 0+ cohort, while most of the older age classes survived the winter, as has been reported elsewhere (Hancock & Urquhart 1964).

Mytilus (shell length 1 to 54 mm) was rarely found before 1983. Subsequently, there were three spatfalls with 45, 400 and 2000 spat m^{-2} in August 1983, 1984 and 1985, respectively. Most did not survive the autumn and only a few percent of the 1983 and 1984 cohort was still alive the following year; so the biomass curve (Fig. 4E) refers only to two year classes.

The biomass of *Nereis* (1 to 22 cm) varied between 1 and 14 g m^{-2} (Fig. 4F). The biomass was high in the autumn following a successful settlement of juveniles, as occurred in the summers of 1979, 1980, 1981 and 1986 when still 300 to 350 worms m^{-2} were found to be present in August.

There was recruitment of *Arenicola* only in 1978 when 30 juveniles m^{-2} were found. The biomass curve (Fig. 4G) refers to members of this cohort being 2 to 7 cm long in 1978 and 5 to 10 cm in 1979. The species was found only incidentally in later years.

Nephtys (1 to 12 cm) occurred at densities of 0 to 40 worms m^{-2}, equivalent to 0 to 2 g m^{-2} in biomass terms (Fig. 4H). The biomass reached, as in *Nereis*, a high value some months after a considerable settlement had occurred in the summers of 1982 and 1983. As in other Wadden Sea areas (Beukema *et al.* 1993), the species was absent or very rare after severe winters.

Four bivalve species, *Macoma, Scrobicularia, Mya* and *Cerastoderma*, contributed the lion's share to the total biomass of the macrozoobenthos (Fig. 4I). The highest biomass was about 70 g AFDW m^{-2} for each of these species, which is several times as much as the average biomass per species calculated over all sampling dates. *Cerastoderma* and *Scrobicularia* were absent in several years, and *Mya* also occurred at only very low densities in some years. The variability in biomass of *Macoma* was less extreme, as was also the case for *Nereis*.

The values given for the total biomass included not only the eight species shown, but also the contribution from four other species. *Nereis virens* (0.11 g m^{-2}, averaged over all sampling dates) was rare, except in 1980 when its biomass was over 1 g m^{-2}. *Carcinus* (0.12 g m^{-2}) occurred in late summer at a density of 5 to 15 specimens m^{-2}. *Corophium* was only found in 1977, with 270 individuals m^{-2} and a biomass of 0.2 g m^{-2}. *Lanice conchilega* was very rare and only observed before the severe winter of 1978/79.

Two worm species, *Heteromastus filiformis* and *Scoloplos armiger*, were not sampled and the Mud Snail *Hydrobia ulvae* was sampled only from 1981 onwards. During those 5 years, *Hydrobia* occurred at high densities of 10 to 20 thousand snails m^{-2}. But as most of the snails were juveniles, the total biomass was not high, varying between 2 and 5 g m^{-2}. Together with *Heteromastus* and *Scoloplos* the values for *Hydrobia* have not been included in Fig. 4I. On average, the resulting underestimation must have been about 5 to 10 g m^{-2}.

It should be noted that all biomass values were obtained with a 1-mm mesh screen. Hence bivalves ≤1 mm long were rarely found, and many somewhat larger specimens must also frequently have been missed. As a consequence, spatfall was never noticed before August. A 0.5 mm sieve, mounted below a 1 mm sieve, showed that the proportion of *Nereis* passing through the 1 mm sieve, but retained below on the finer sieve, increased from 22% for worms of 5 cm to 84% for worms of 1 cm (Zwarts & Esselink 1989). The error was even more serious for *Corophium* in which only the rare size classes > 5 mm were completely sampled; 90, 66, 51 and 28% of the size classes 2, 3, 4 and 5 mm, respectively, passed through the 1-mm sieve and were retained on the 0.5 mm sieve. However, we suspect that *Corophium* was the only species for which a 0.5 mm sieve, instead of a 1 mm sieve, would have resulted in much higher biomass estimates.

The total biomass in the study site (Fig. 4I) was about four times higher than the average biomass of the macrobenthos on the tidal flats of the Dutch Wadden Sea (Beukema 1976). The species composition in the samples was also different. *Scrobicularia* is rare in the Dutch Wadden Sea, but common along the Frisian mainland coast, while the reverse is the case in *Arenicola*. The intertidal substrate along the Frisian coast consists of mud and muddy sand, whereas 85% of tidal flats of the Wadden Sea are sandy with a clay content of < 3% (de Glopper 1967, Zwarts 1988b). The different species composition in our study area, compared with the Wadden Sea as a whole, can be understood as the distribution of macrobenthic species present is related to substrate composition and tidal height (Beukema 1976, Dankers & Beukema 1984, Zwarts 1988b). Nevertheless, it is remarkable that *Corophium*, a species that usually reaches high densities in soft substrates on the higher part of the shore (Beukema 1976), was not common in our study site. It has been shown that the presence of *Cerastoderma* and *Arenicola* prevented settlement of *Corophium* (Jensen 1985, Flach 1992), and probably the high densities of *Cerastoderma* and *Scrobicularia* in our study site has had the same negative effect.

The year-to-year variability in the biomass was large in several species, e.g. *Cerastoderma*, but rather small in *Macoma* (Fig. 4). The trends shown in Fig. 4, though referring to a relatively short period, fit the general pattern described for three sites in the Wadden Sea sampled for up to 25 years (Beukema *et al.* 1993). Following recruitment, the change in biomass is the result of the interaction between growth and mortality rates in one or more year classes. Thus, *Cerastoderma* and *Mytilus* grew fast and their mortality was high (Beukema 1982a), so that the maximum biomass of a cohort was reached only 1 or 2 years after settlement. In contrast, *Mya is* a long-lived species and it took 5-6 years before the total biomass of a cohort began to decrease (Fig. 4C; Beukema 1982b). *Macoma* is also a long-lived species (Fig. 4A; Beukema 1980), but in contrast to other bivalves in the tidal zone, recruitment failure occurred less often, so that several cohorts could be found simultaneously. Thus, regular recruitment contributed to the rather stable biomass of *Macoma*. The occurrence of severe and mild winters also had a strong impact on the year-to-year variation in biomass. In the severe winters of 1978/79, 1984/85 and 1985/86, there were mass mortalities in the cold-sensitive species *Cerastoderma*, *Nephtys* and *Lanice*, as already described by Beukema (1979, 1985). This was usually followed in the next summer by a very successful recruitment in both bivalves and worms (Beukema 1982b).

Seasonal variation in total biomass per species

Figure 5 shows seasonal variation in biomass over the last 8 years, during which the biomass was usually sampled each month. Sampling was not always possible, for instance when ice covered the mudflats. Data for missing months were therefore interpolated

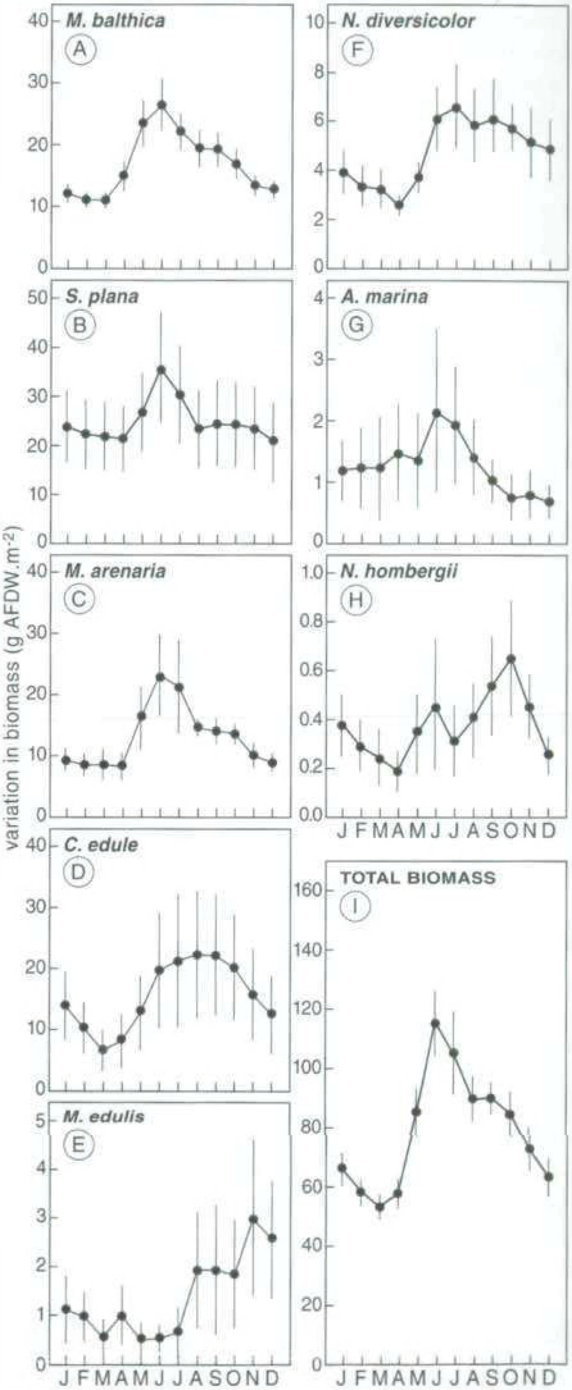


Fig. 5. Seasonal variation in the biomass (g AFDW m^{-2} ± SE) of five bivalve and three worm species, and in the total biomass of all species, calculated for eight years, 1979 to 1986.

on the basis of the preceding and the following month. *Macoma* (Fig. 5A) reached their maximum biomass in May and June, *Scrobicularia*, *Mya* and *Arenicola* (Fig. 5B, C & H) in June, *Cerastoderma* and *Nereis* (Fig. 5D & F) in June to October, and *Mytilus* and *Nephtys* (Fig. 5E & G) even later. The biomass remained at about the same level during the winter half of the year in *Macoma* and *Scrobicularia*, while it decreased during these months in *Cerastoderma*, *Nereis* and *Nephtys*. Taking all species together, the peak biomass occurred in June and the lowest value in March. The seasonal trend shown for the total biomass (Fig. 5I) closely resembled the graph given for the Balgzand area, 90 km to the west (Beukema 1974).

There was a considerable increase in biomass during the 3 to 4 months between late winter and mid summer. The ratio of the highest to the lowest biomass value was rather low in *Scrobicularia* and *Macoma* (1.6 and 1.8, respectively), but considerably higher in *Nereis* (2.6), *Mya* (2.9) and *Cerastoderma* (3.3). To establish the degree to which this difference was due to a change in the body weight of animals of similar size, we calculated the ratio between highest and lowest body weight as given in Fig. 3 and in Fig. 8 of Zwarts (1991). In all species, about 60% of the seasonal variation in biomass was due to a change in body condition. Thus, only 40% of the difference can be attributed to growth and change in numbers. In *Scrobicularia* and *Macoma*, however, the ratio highest/lowest biomass was about as large as the ratio highest/lowest condition, implying that, in these species, the increases in biomass due to growth were counterbalanced by decreases in biomass due to mortality.

The seasonal change in body condition explains nearly all the variation in biomass over the year in *Macoma*, *Scrobicularia* and *Mya* (Figs. 4, 5; Fig. 8 in Zwarts 1991). However, *Cerastoderma* reached the highest biomass in July to September, at a time when the average body condition had already decreased by 30%. This is also true for *Mytilus* which attained the highest biomass in autumn, despite the body condition peaking in June. The explanation for these exceptions is that the seasonal trajectories of somatic growth and shell growth were not identical. The shell continued to grow at a higher rate than the flesh, apparently causing flesh weights at a given length to stop increasing or

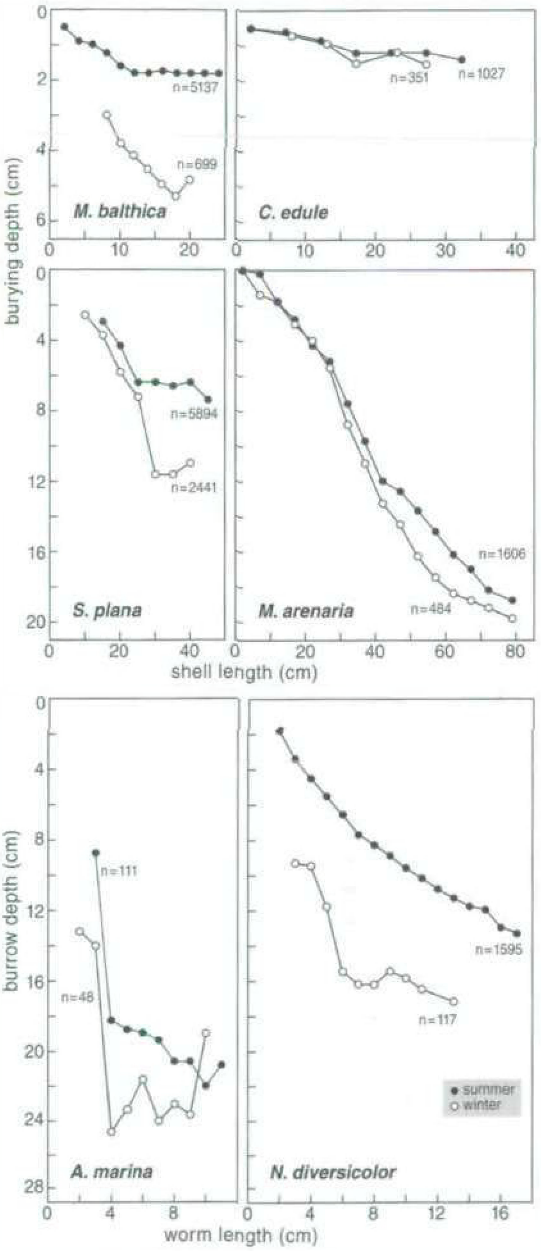


Fig. 6. Burying depth as a function of body size in summer and winter in six benthic species. Winter refers to the period December to February in *Macoma balthica*, December to April in *Arenicola marina*, and December to March in the four other species. Summer refers to the months June to August, except in *Macoma* (May to July) and *Arenicola* (May to August). Number of cases is given. Data from Zwarts & Wanink (1989) for the bivalves and Esselink & Zwarts (1989) for *Nereis diversicolor*.

even to start decreasing. Shell growth continued for longer periods in summer and autumn *Mytilus* and *Cerastoderma* than in any of the other bivalve species. Moreover, in these two species, the period of shell growth was shorter in the older than in young animals (Wanink & Zwarts in prep.). Since the contributions of the young 0+ and 1+ year classes to total biomass were higher in *Mytilus* and *Cerastoderma* than in *Macoma* and *Mya*, the biomass peak of the former two species fell even later than in the other bivalve species.

Seasonal variation in depth

Birds collect buried prey by probing their bill into the substrate. Since they do not dig for prey, bill length sets a limit to the fraction of the macrobenthos that is actually accessible to these birds. This section describes the seasonal variation in the burying depth of *Macoma, Scrobicularia, Cerastoderma* and *Mya*, and the burrow depth of *Nereis* and *Arenicola*. As the bivalve species remain immobile when attacked by surface predators or sampled by us, their accessibility to waders may be determined exactly by measuring the depth at which they live. Fortunately, the burrows of *Nereis* and *Arenicola* are sufficiently conspicuous to be traced in cores of muddy sediments to determine the maximum depth to which a worm may retreat when attacked.

Burying depth in bivalves and burrow depth in worms were a function of size (Fig. 6). In order to investigate the seasonal variation in depth, a selection was made of the length classes with the largest number of measurements, being 10 to 20 mm for *Macoma*, 30 to 40 mm for *Scrobicularia*, 30 to 50 mm for *Mya*, 10 to 35 mm for *Cerastoderma*, 7 to 14 cm in *Nereis* and 4 to 11 cm in *Arenicola*. Since depth increased within these size ranges (Fig. 6), all depth measurements were corrected to the mid-point length of the selected size classes. The burrow depth of *Arenicola* refers to worms living in mud and not in their usual habitat of (muddy) sand. It remains to be shown that the burrows made by *Arenicola* in sand are as deep as in mud.

There was little or no seasonal variation in the burying depths of *Mya* and of *Cerastoderma*, respectively. The other species lived close to the surface in June and burrowed deeply in winter (Fig. 7). Reading & McGrorty (1978) found a seasonal variation in the burying depth of *Macoma* in the Wash, eastern England, that was similar to the trend shown in Fig. 7 and suggest that depth is governed by day length and not by temperature. We also found that depth increased after June, when the sea water temperature continued to increase for two months, and decreased again after December, when the temperature continued to decrease for two months. The seasonal variation of the burying depth of *Macoma* (Fig. 7A) was thus synchronised with day length (Fig. 7C), resulting in a very high correlation of monthly averages of depth with day length (r = -0.98), and a lower one with sea water temperature (r = -0.79). As in *Macoma, Scrobicularia* burrowed more deeply from July onwards, but in contrast to *Macoma*, they remained at their winter depth until April. Hence, the average depth of *Scrobicularia* was better correlated with temperature (r = -0.93) than with day length (r = -0.85). This is also true for *Arenicola*: r = -0.81 for depth against day length, while r = -0.53 for depth against temperature. The two correlations were equal in the case of *Nereis* (depth-day length: r = -0.84; depth-temperature: r = -0.87).

To investigate the effect of temperature, independent of day length, we further analysed the depth measurements of *Macoma, Scrobicularia* and *Nereis* within separate months. The 126 sampling dates were divided per month into 7 classes of sea water temperature (Fig. 8). Two-way analyses of variance revealed that the differences in depth between the months were highly significant (R^2 was 0.569, 0.674 and 0.578 for *Macoma, Scrobicularia* and *Nereis*, respectively) while temperature did not add significantly to the explained variance in any of the three species. As Fig. 8 shows, depth was independent of sea water temperature in March and April, so temperature was obviously not a trigger for *Macoma, Scrobicularia* and *Nereis* to move up from their winter depth refuge (Fig. 8). Neither was there a relation between depth and temperature in the summer months, although it was noticeable that *Nereis* lived closer to the surface at lower temperatures in late summer.

The expectation that low temperatures in winter would prompt worms and bivalves to live at greater depths in order to reduce the risk of being frozen was based on the finding that the mortality among several species of macrobenthos is high during frost periods (Beukema 1989). Depth increases were not found.

However, for obvious reasons, we made no depth measurements when mudflats were actually frozen. The data for the December to February period revealed no relation between sea water temperature in the range from -1 to 6 °C and the burying depth of *Macoma*, *Scrobicularia* and *Nereis*. In contrast, Esselink & Zwarts (1989) concluded that in winter *Nereis* lived in deeper burrows at lower temperatures. However, their winter period referred to the longer period of 15 November to 30 March, during which there was a simultaneous decrease of temperature and burrow depth from November until February and an increase for both in March (Fig. 7): hence, seasonal and temperature effects were confounded. Nonetheless, it remains likely that *Nereis* do deepen their burrows as the winter temperature drops. First, the digging of deeper burrows by worms after a sudden fall in temperature was observed by Esselink & Zwarts (1989). Second, *Nereis* were found in remarkably deep burrows shortly after a cold spell by Linke (1939) and Beukema (1979). Although not confirmed in this study, a direct response in burrow depth by *Nereis* remains a distinct possibility.

There were large differences in the burying depths between the eight winter and seven summer periods studied (Fig. 9). *Macoma* lived at depths of only 3 to 4 cm in the winters of 1982/83 and 1984/85, but at depths of 6 to 7 cm in the winters of 1979/80, 1980/81 and 1986/87. The summer depth of *Macoma* also varied between years by between 1 and 2 cm. *Scrobicularia* reached a winter depth of 12 to 14 cm in the first three winters when the strong year class of 1976 was still abundant, but not subsequently as the population collapsed. Again, *Nereis* lived at greater depths in the first three winters than in the last five. Figure 9 confirms that these variations in depth were not associated with sea water temperature. For example, the two severe winters of 1984/85 and 1985/86 did not bring about an increase in burying depth of any of the three species.

We conclude that the seasonal variation in burying depth of *Macoma* and *Scrobicularia* was not regulated by changes in temperature. This was also true for *Nereis*, although this species is thought to burrow deeper when temperature decreases sharply. In separate papers, we will show that the seasonal variation in depth of *Macoma* and *Scrobicularia* can be at-

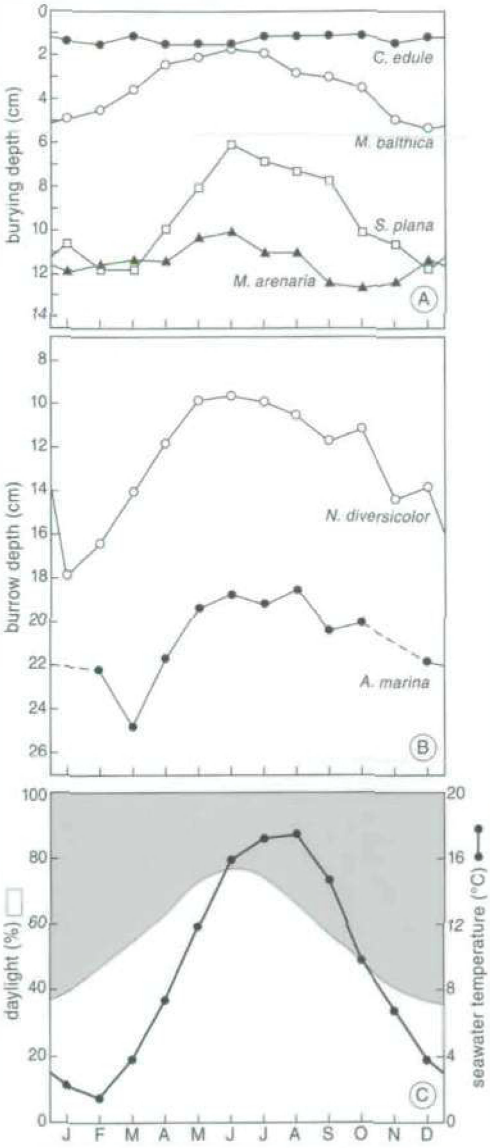


Fig. 7. Seasonal variation in **A.** burying depth of *Cerastoderma edule* (10-35 mm; n = 1802), *Macoma balthica* (10-20 mm; n = 12124), *Scrobicularia plana* (30-50 mm; n = 14305) and *Mya arenaria* (30-50 mm; n = 1396), **B.** burrow depth of *Nereis diversicolor* (7-14 cm; n = 1946) and *Arenicola marina* (4-11 cm; n = 161) and **C.** sea water temperatures and daylight period between civil twilights. The depth measurements were corrected for the increase of depth with size (Fig. 6) to a *Cerastoderma* of 20 mm, *Macoma* of 15 mm, *Scrobicularia* of 35 mm, *Mya* of 40 mm, *Nereis* of 10 cm and *Arenicola* of 8 cm. The depth measurements are averaged for seven years (1980 to 1986) and sea water temperature for 15 years (1972 to 1986).

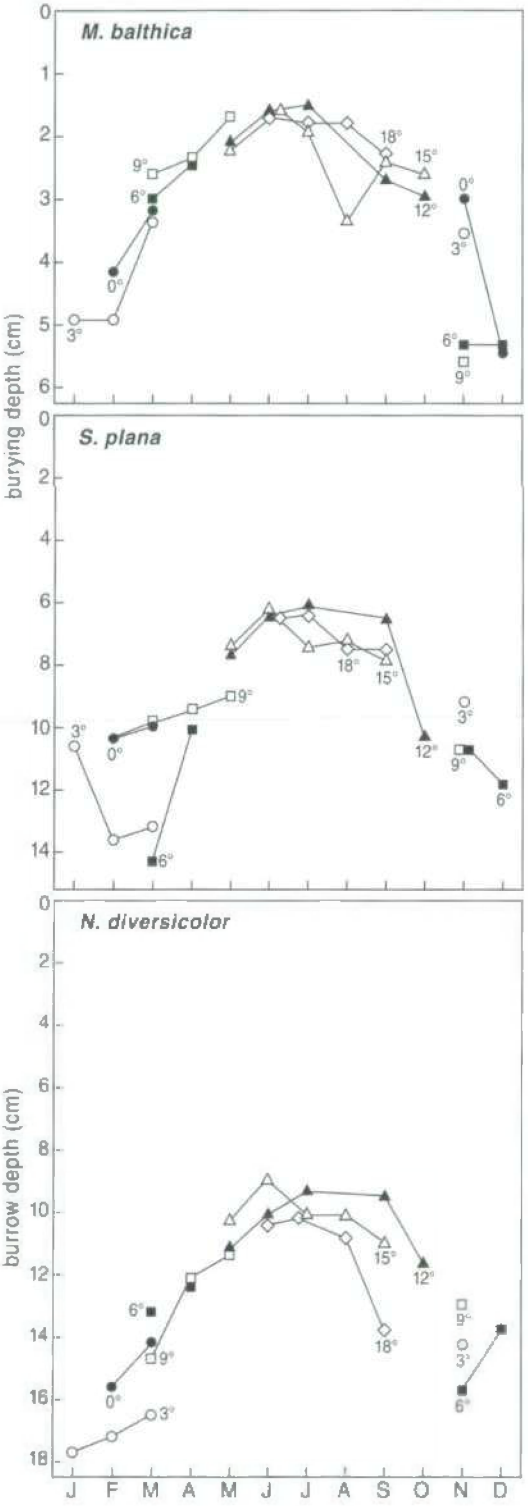


Fig. 8. Burying depth of *Macoma balthica* (15 mm) and *Scrobicularia plana* (35 mm) and burrow depth of *Nereis diversicolor* (10 cm) during the course of the year, split up for seven categories of sea water temperature. The graphs are based on the same data as in Fig. 7.

tributed partly to variation in siphon weight and also that the difference in depth between winters depends on the size of the siphon.

Seasonal variation in the accessible fraction of Macoma and Scrobicularia

Figures 7 to 9 show the average seasonal variation in the burying depth of *Macoma, Scrobicularia* and *Nereis*. In order to establish how many prey were really accessible to birds, it is necessary to measure the proportions that were out of reach of their bills. This is shown in Fig. 10 (the upper 2, 4, 6 cm, and below 6 cm, for *Macoma*) and in Fig. 11 (the upper 4, 6, 8 cm, and below 8 cm for *Scrobicularia*).

The data for *Scrobicularia* are only given for the first four years of sampling, since the species was too rare during the last 3 years to provide a reliable depth distribution. Data similar to those shown in Figs. 10 and 11, have already been given for *Nereis* by Esselink & Zwarts (1989). As the results show, the seasonal variation in the accessible fraction varied considerably between years. The response of the waders will be considered in several sections of Discussion.

Discussion

Response of waders to fluctuations in their food supply

The variation in biomass modifies the feeding conditions for waders in several ways. The greater part of the seasonal variation in biomass (Fig. 5) may be attributed to the variation in weight of individual prey of similar size (Fig. 3; Fig. 8 in Zwarts 1991), to growth in length and to changes in the prey density (Beukema 1976, Goss-Custard *et al.* 1977a). A decrease in the prey condition could directly affect the daily consumption rate, unless the birds are able to compensate by either an extension of the feeding period and/or an increase of their rate of attacking prey. A decrease in the prey density causes an increase of the search time per prey and may therefore reduce the intake rate (Goss-Custard 1970a, 1977c, Hulscher 1976, Goss-Custard *et al.* 1977c, Sutherland 1982b, Wanink & Zwarts 1985, Zwarts *et al.* 1992).

The year-to-year variation in the biomass of the individual species is so large (Fig. 4; Beukema *et al.* 1993), that the birds cannot restrict their diet only to one or two prey species. They have to learn how to search and handle different prey species, or move on to other areas. Depending on the pattern of occurrence of different prey, waders have to adjust their diet and, as a consequence, often have to switch between alternative feeding areas. For example, *Cerastoderma* was the major prey for Oystercatchers in our study area. However, this species was absent during four successive years (Fig. 4), so many birds left the area and spread out over surrounding mussel banks. The few birds remaining in the study area took *Macoma*, *Scrobicularia*, *Mya* and *Nereis*, whose biomass remained high (Fig. 4).

This raises the question as to whether birds that switch from one prey to another are able to achieve a similar intake rate, or whether they are forced simply to make the best of a bad job. The Oystercatcher is the only wader species for which enough data are available to indicate how the intake rate depends on the prey species and the size classes taken. The intake rate of Oystercatchers has been measured in 253 studies, compiled by Zwarts *et al.* (1996b). Intake rates vary between 1 and 3 mg s^{-1}, but, surprisingly, do not differ between prey species. Within a species, the greater part of the variance can be explained by prey size: the larger the prey, the higher the intake rate. In addition, the intake rate in the winter half of the year is significantly lower than in the summer half of the year (Table 2). When the data summarised in Table 2 are split up per month, the intake rate of Oystercatchers appears to peak in mid summer, than to decrease until mid winter and to increase from March onwards.

It was to be expected that intake rate should vary seasonally, since the condition of the prey is 30 to 60% lower in winter than in summer (Fig. 3; Zwarts 1991). Moreover, prey densities may decrease during winter, while at the same time the accessible fractions of *Macoma* and *Scrobicularia* decline (Figs. 10, 11). Zwarts & Wanink (1991) show that the seasonal

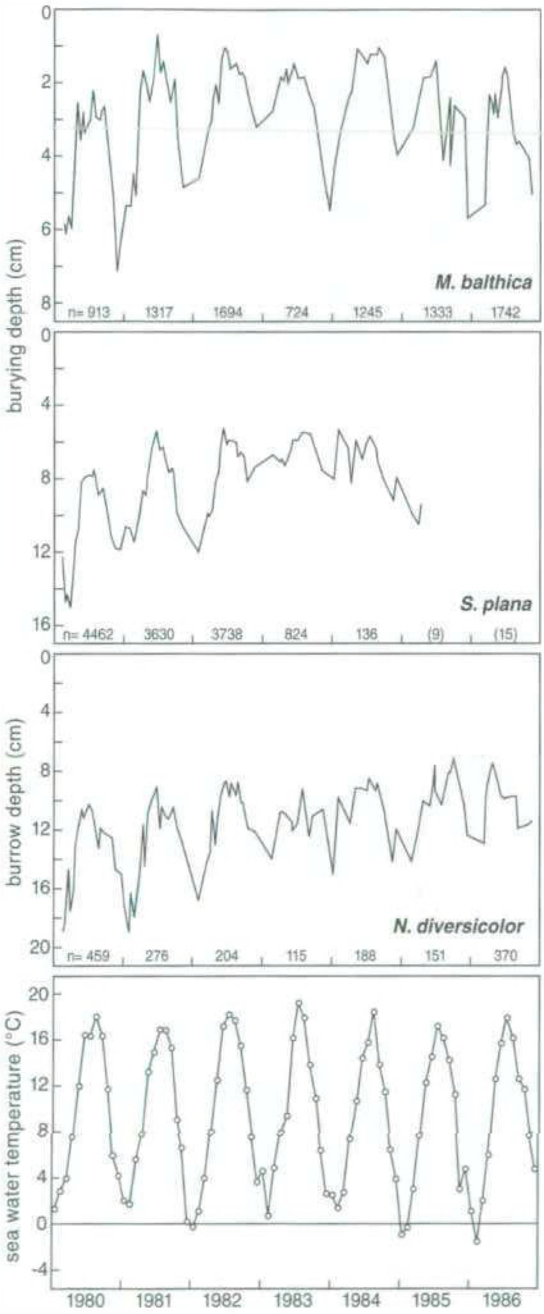


Fig. 9. Burying depth of *Macoma balthica* (15 mm) and *Scrobicularia plana* (35 mm) and burrow depth of *Nereis diversicolor* (10 cm) at each sampling date during the course of seven years; sample size in each year is indicated. The lower panel shows the average sea water temperature per month.

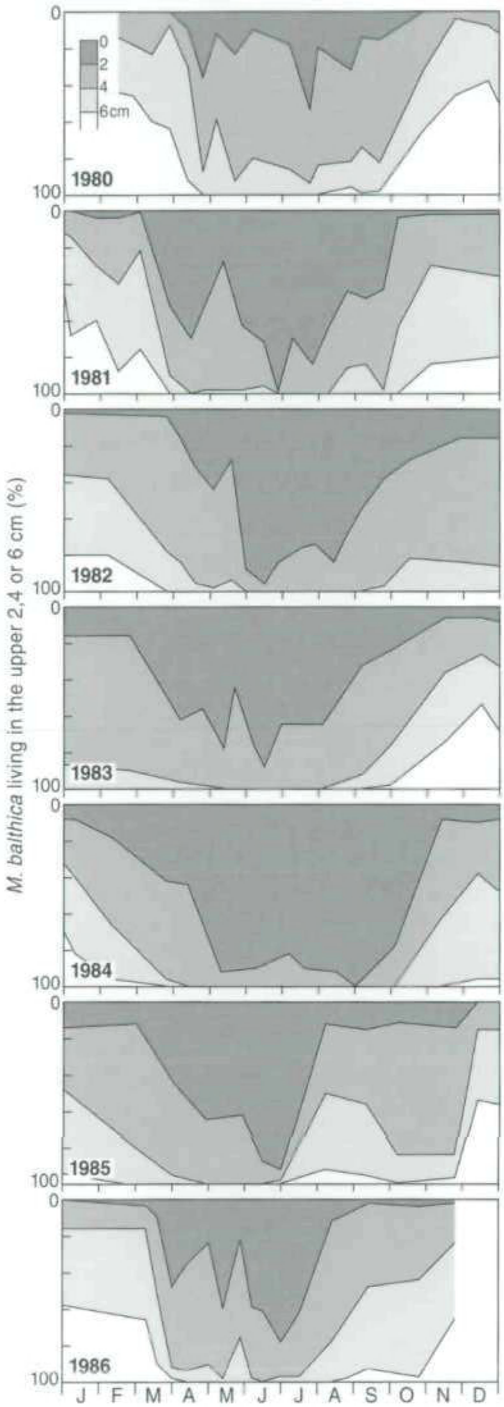


Fig. 10. Seasonal variation in the accessibility of *Macoma balthica* (15 mm) over 7 years. The proportion of the population living in the upper 2, 4 and 6 cm is shown.

variation in condition of the prey actually taken by birds may be even larger than indicated by the mean condition for the population as a whole. The condition of *Scrobicularia* varies with burying depth: the condition of shallow bivalves is about half of those that live more deeply and the same has been found in other bivalves and in *Nereis*. The consequence is that only lean prey are accessible in winter and that Oystercatchers feeding on *Scrobicularia*, for instance, face a seasonal variation in the flesh weight of the prey they actually take, which is 1.3 times greater than the variation in the entire population (Zwarts & Wanink 1991). Since most studies summarised in Table 2 have not taken this into account, the feeding conditions in winter are even worse than indicated.

It should be noted that Table 2 expresses the intake rate in terms of dry flesh, because energy density was rarely measured. Since our study showed that the energy density of *Scrobicularia* and *Mya*, is 10% lower in winter than in summer (Fig. 1), the seasonal difference in intake rate is even larger in these two species when expressed in terms of energy, the critical quantity.

Feeding waders must make many decisions: where to feed, for which prey species to search and which size class to select. These decisions can only be understood if the prey that are actually available are known and their profitability measured. In view of this, the next three sections attempt to define several aspects of prey availability in waders. After dealing with prey profitability, the results from all four sections are considered to describe the fraction of the prey that is harvestable. Finally, all this information is used to analyse prey switching in waders and to discuss to what degree the distribution of waders over the wintering areas is related to a deterioration of their harvestable food supply between late summer and winter in the tidal flats in NW. Europe.

The accessible prey fraction

Benthic prey are accessible to waders only if they live within reach of the bill. The accessibility of immobile prey (benthic bivalves) will be discussed first, followed by an analysis of the more complex situation of mobile prey (e.g. worms). Although bivalves are capable of changing their position in the substrate, the attachment of very thin nylon threads to *Macoma*,

Table 2. The intake rate of Oystercatchers feeding on eight prey species during the winter half of the year (October-March) and summer (April-September). The average intake rates (mg AFDW s^{-1}) ± SD refer to different studies (sample size indicated) summarized by Zwarts *et al.* (in press). A two-way analysis of variance shows that there was a significant difference between intake rate in winter and summer ($R^2 = 0.145$; $p < 0.001$), but that the intake rate did not differ between the prey species ($R^2 = 0.04$; $p = 0.58$).

	winter			*summer*		
	X	*SD*	*N*	*X*	*SD*	*N*
Macoma balthica			0	2.42	.66	9
Scrobicularia plana	1.72	0.61	8	2.20		1
Cerastoderma edule	2.19	0.98	12	2.58	.76	6
Mya arenaria	2.65		1	2.91		1
Mytilus edulis	1.87	0.61	27	2.90	1.23	12
Nereis diversicolor	1.74	.44	3	2.36	0.91	8
Arenicola marina			0	3.10		1
Littorina littorea	1.40		1			0
all species	1.92	0.71	52	2.61	0.92	38

Scrobicularia and *Mya*, that allowed their depth to be monitored continuously, revealed that they scarcely changed their position. Even more importantly, when attacked, they did not move their position but withdrew their foot and siphon(s) within the shell and closed the valves firmly (unpubl. data). Burying depth of the four bivalve species studied is thus a good measure of their accessibility to waders.

Clearly, an Oystercatcher with a bill length of 7 cm, cannot take *Scrobicularia* living at 8 cm or more, but where exactly is the limit between prey that have reached the depth refuge and those that are still in danger? There are two uncertainties in answering this question. First, the burying depth of bivalves has been defined as the distance between the surface of the substrate and the upper edge of the shell, but the birds must probe more deeply, either to grasp the prey before being able to lift it to the surface or to eat the flesh in situ. Second, the probing depth of birds may vary. The probing depth exceeds the bill length when birds probe up to their eyes in mud, although usually the probing depth is less than the bill length. For instance, Oystercatchers feeding on *Macoma* or *Scrobicularia* probe their 7.5 cm long bill on average 3 to 4 cm into the substrate (Hulscher 1982, Wanink & Zwarts 1985), and the 2.7 cm long bill of Sanderling *Calidris alba* is pushed only 2 cm into the substrate on average (Gerritsen & Meiboom 1986).

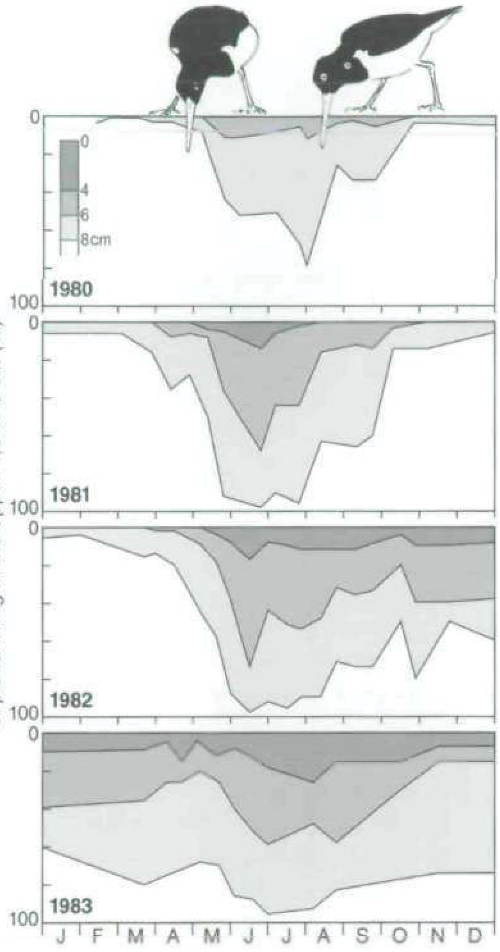


Fig. 11. Seasonal variation in the accessibility of *Scrobicularia plana* (35 mm) over 4 years. The proportion of the population living in the upper 4, 6 and 8 cm is shown.

Three studies have exactly determined the depth at which prey are taken: Sanderlings preying on three crustacean species, Curlews *Numenius arquata* feeding on *Mya* and Oystercatchers on *Scrobicularia*. Captive Sanderlings were offered frozen isopods or sand crabs buried at different depths (Myers *et al.* 1980). The feeding attempts varied between shallow surface pecks and deep probes that reached the base of the bill (2.7 cm). Sixty percent of the prey was taken from the upper 1 cm and none from below the maximum probing depth of 2.7 cm. Curlews probe their bill deeply into the substrate when searching for *Mya*. When a prey is found, they pull up the siphon and eat in situ the remaining flesh from the gaping shell. Zwarts & Wanink (1984) located *Mya* eaten by Curlews of known bill length and measured the burying depths. All the prey taken were at depths within the bird's bill length, but predation risk was much higher for those living less deeply (Zwarts & Wanink 1984, 1989). The same was found in an experiment with a captive Oystercatcher feeding on *Scrobicularia* living at various depths (Wanink & Zwarts 1985).

In conclusion, the risk of a bivalve being taken by a bird is zero when its burying depth exceeds the bill length, but increases closer to the surface. The data on depth distribution in bivalves (Figs. 6 to 11) may be used to identify for each wader species which prey are within reach of the bill. Irrespective of whether all prey from the upper 4 or 6 cm are assumed to be selected by Oystercatchers, all are accessible to these birds from April up to and including September (Fig. 10). The accessible fraction in mid winter varies from year to year. Hardly any *Macoma* were living in the upper 4 cm in the winters of 1979/80, 1980/81 and 1986/87, whereas in the winter 1982/83, all occurred within the upper 4 cm. Due to the large year-to-year variation in the accessible fraction (Fig. 11), *Scrobicularia* is clearly an unpredictable food source for Oystercatchers, at least in winter.

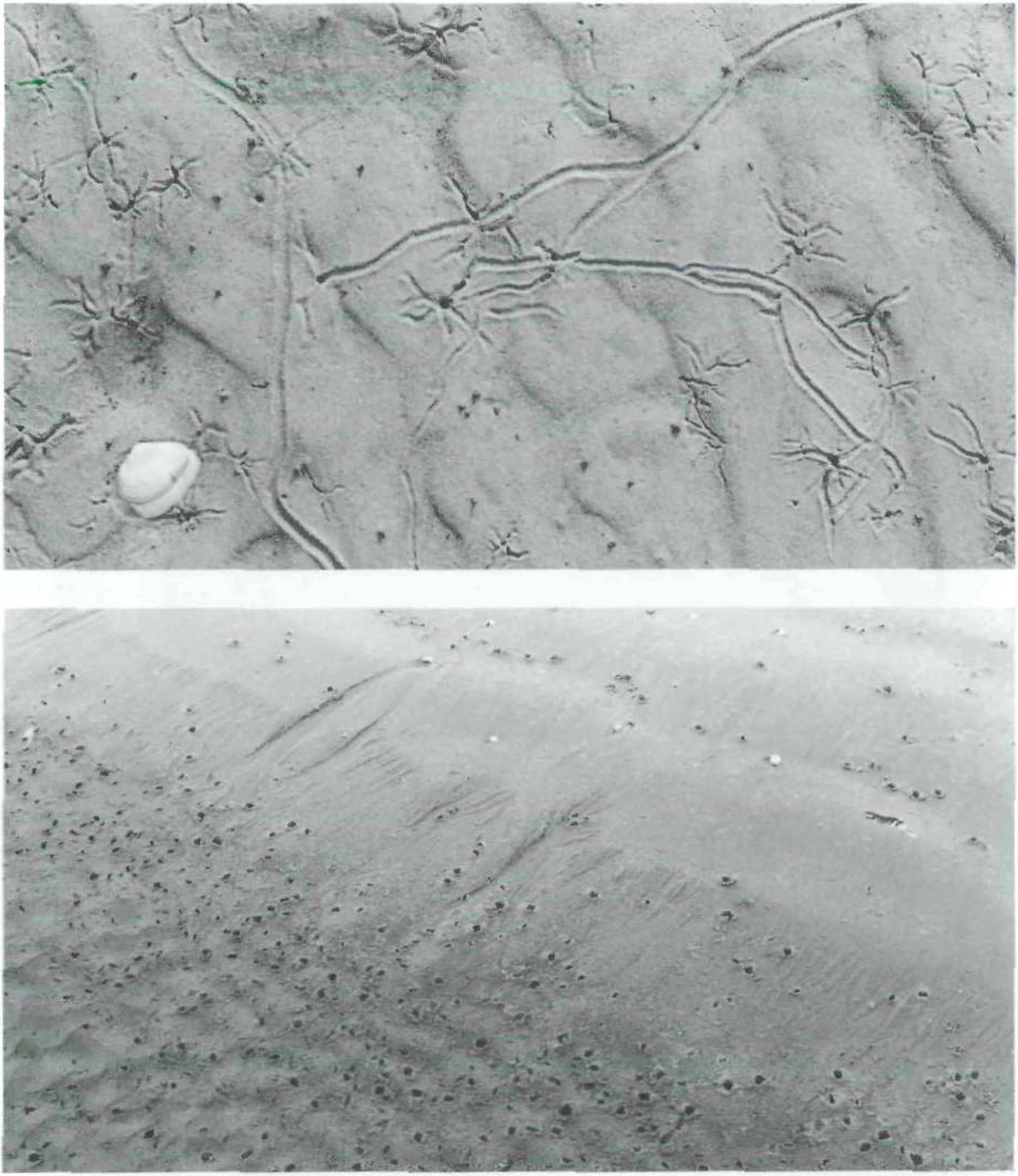
The bill length of Knot varies between 3 and 3.6 cm. Since it has been shown that the closely-related Sanderling took all prey from the upper 2 cm of the sediment, equivalent to 3/4 of its bill length (Myers *et al.* 1980), we assume that Knot can take the majority of *Macoma* from the upper 2 to 3 cm of the substrate. The seasonal variation in the accessible fraction of *Macoma* is very large for Knot, much greater than for Oystercatchers (Fig. 10; Reading & McGrorty 1978). The accessibility of *Macoma* to Knot also varies enormously between years. To migrant Knot passing through the Wadden Sea in August and in May, the accessible fraction may even vary between 0 and 100% (Fig. 10; Zwarts *et al.* 1992, Piersma *et al.* 1993b).

In contrast to bivalves, worms and *Corophium* move in their burrows and/or appear at the surface, and when in danger retreat to the bottom. Thus burrow depth is only a good measure of the fraction accessible to waders if prey are taken from the bottom. However, when waders exclusively select prey feeding at the surface, other definitions of accessibility are needed, as the following examples illustrate.

Arenicola live in burrows 20 to 25 cm deep (Figs. 6, 7), far beyond the reach of waders. Even the wader with the largest bill, the Curlew (bill length up to 16 cm), waits until a Lugworm appears at the surface which occurs when it defecates (Roukema & Zwarts unpubl.). As *Arenicola* defecate about once per hour and cast production takes some seconds, worms expose themselves to predation for about 1‰ of the low water period. Curlews run to catch a defecating worm at distances up to 2 m; chasing a defecating worm at about 3 m distance means that the bird will arrive too late or will only be able to grasp the tail. The accessible prey in this case can be defined as the number of defecating worms within about 2 m of a bird.

Many other benthic animals live in burrows and feed on the surface around the burrow, but retreat to the bottom to avoid predation. Foraging waders may thus reduce the fraction of prey at the surface. When fiddler crabs *Uca tangeri* feeding around their burrows are approached by a Whimbrel *Numenius phaeopus*, they disappear quickly into their deep burrows (Zwarts 1990). Whimbrels use two methods to counter this anti-predator response. Most crabs are taken by birds dashing at them before they can reach their burrow. The accessible fraction has been determined by measuring the distance from the burrows that crabs feed, the distance at which the crabs detect the approaching Whimbrel and the speed of both. The accessibility of *Uca* is easier to measure when Whimbrels wait motionless above a burrow for the emergence of a crab. In this case it is sufficient only to determine the waiting time.

Like *Uca*, *Corophium* retreat down their burrows when a wader walks over the mud (Goss-Custard 1970b). *Corophium* occur in densities of many thousands per m^{2}. Even if 99.9% of them retreat into their burrows, enough remain accessible to allow a



Only subtile traces reveal the presence of bivalves and worms that live hidden in the surface (upper photo). Although Oystercatchers concentrate their feeding effort on places where food is abundant, they have to probe at random to locate these hidden prey. The lower photo shows the imprints left behind by probing Oystercatchers.

slowly-walking bird to feed on them without the need to make dashes or to wait for emerging prey. However, since *Corophium* only return to the surface 5 to 10 minutes after a disturbance, birds feeding at high densities may severely depress the accessible fraction of the prey (Goss-Custard 1970b, 1976).

When disturbed, *Nereis* also retreat down their burrows, where they are safe from waders with short bills. Curlews use two methods for preying on *Nereis*. Since their bill is long enough for them to extract worms from their burrows in summer, Curlews may then search for burrows and probe deeply. However, when many worms feed at the surface, the Curlews concentrate their feeding effort entirely on these easy prey (Zwarts & Esselink 1989). The versatility in feeding techniques of both the worms and predator puts precise measurement of the accessible fraction of the prey beyond present capabilities. This is also true for plovers which peck at either an outflow of water from the hole when the worm is near the surface, or wait until it emerges from its burrow (Pienkowski 1983a, b, Metcalfe 1985).

The feeding activity of the benthos, and therefore the proportion that is accessible on the surface, can change considerably within a very short time, even within minutes. Filter-feeding bivalves, whose valves are firmly closed at low tide, start feeding as soon as incoming water covers the surface (Vader 1964). This may allow Oystercatchers to stab the bill between the gaping valves of *Mytilus* and *Cerastoderma* and so take them in a fast rate (Zwarts & Drent 1981, Swennen *et al.* 1983). *Corophium* are very accessible to waders when they leave their burrows for a short period on the receding tide (Linke 1939, Vader 1964, Hicklin & Smith 1984, Boates & Smith 1989): this may explain the tendency for waders feeding on *Corophium* to follow the tide edge. In contrast, waders feeding on surface-feeding *Nereis* have no reason to follow the tide line. This worm remains in its burrow as long as food can be filtered from the overlying water but, at low tide, they emerge from their burrows to feed on the surface (Esselink & Zwarts 1989). This may explain why Oystercatchers that feed on *Nereis* at low tide take alternative prey as the tide ebbs (de Vlas *et al.* 1996) and Curlews vary their feeding method over the low water period (Zwarts & Esselink 1989). It may also explain why plovers are able to remain on the high-level shores throughout the low water period, rather than move to lower levels with the receding tide edge.

The main conclusion of this section is that the accessible fraction varies enormously, often by more than the variation in the total biomass. It is also clear that the variation in accessibility differs between prey species, being relatively low in the more or less sessile bivalves (*Cerastoderma*, *Mya* and *Mytilus*), larger in bivalves with a seasonal variation in burying depth (*Macoma* and *Scrobicularia*), and very large in invertebrates that emerge from their burrows to defecate (*Arenicola*) or to feed (*Nereis*, *Corophium*).

The detectable prey fraction

Waders may probe at random to locate buried prey which live within reach of the bill, as Oystercatchers are known to do for *Cerastoderma* (Hulscher 1976) and *Macoma* (Hulscher 1982). In randomly probing waders we can calculate the exact encounter rate with benthic prey, provided the surface areas of the shells and bill tip are known, along with the probing depth of the birds and the depths at which the bivalves live (Hulscher 1976, 1982, Wanink & Zwarts 1985, Mouritsen & Jensen 1992, Zwarts & Blomert 1992). Dunlin *Calidris alpina* and Sanderling can detect buried prey by taste (van Heezik *et al.* 1983), thus enlarging the detection area of each probe. In contrast, Oystercatchers probably do not use taste perception since their encounter rate with experimental prey could be predicted precisely by touch alone (Hulscher 1982, Wanink & Zwarts 1985).

Waders may also search for tracks that betray the presence of prey beneath the surface and concentrate their probing in such places. Thus an Oystercatcher took more time to locate *Macoma* when all the surface clues on the mud surface had been erased experimentally (Hulscher 1982). The burrow entrance of *Nereis* is clearly visible on the mud surface when they filter water through their burrow or after they have fed on the substrate and so left starlike feeding tracks around their burrow. Curlews searching for *Nereis* do not probe at random, but look systematically for these small tracks. Siphon holes of *Mya* can be very conspicuous, especially in muddy substrate (Linke 1939: photo 50 to 52). Curlews probably know the size of *Mya* before they probe, since there is good correlation between siphon diameter and shell size

(Zwarts & Wanink 1989). In quiet weather, Curlews walk from one siphon hole to the next but when waves have eroded the upper layer of the substrate, no siphon holes are visible and Curlews feed by touch by continuously making swift pecks at the surface.

The detectability of prey affects the availability of prey to a bird in other ways. Prey must be detected within the visual range. *Arenicola* defecating within 2 m of a Curlew are accessible, but not detectable if the cast is produced behind the bird. Metcalfe (1985) found that *Corophium* was taken at a smaller distance by Lapwing *Vanellus vanellus* than *Nereis* and concluded that large prey may be detected at a greater distance than small and more cryptic prey. Though likely, there are two alternative explanations. First, *Corophium* may have been less accessible than *Nereis*, because it retreated more quickly into their burrows than *Nereis*. Second, the *Corophium* were smaller and less profitable than *Nereis* and so perhaps less worthwhile walking any distance to attack.

Waders may be able to increase their intake rate by increasing their rate of walking and thus, of encountering the prey. But, in doing so, more prey may be overlooked, and an optimal search rate would be a compromise depending on the crypticity of the prey (Gendron 1986). If so, waders would be expected to walk faster when they feed on easily detectable prey than when they search for cryptic prey or prey whose presence is only revealed by surface tracks. Redshank *Tringa totanus* do walk relatively fast when they feed on prey, such as *Corophium*, which appear to be easily detectable at the surface and search more slowly for the less visible surface tracks of *Nereis* (Goss-Custard 1977a, 1977b). Search rate may also vary within one type of a prey, depending on its detectability as four studies have shown. First, Semipalmated Sandpipers *Calidris pusilla* walk faster when they feed on *Corophium* crawling on the substrate on the ebbing tide than later at low water when most prey are found inside their burrows (Boates & Smith 1989). Second, Curlews feeding on *Mya* walk twice as fast when they walk from one siphon hole to the next as when they search for the same prey by continuous probing (unpubl. observations). Third, Oystercatchers that stab into *Mytilus* walk more slowly than those that hammer a hole in the shell, perhaps because the cues used by stabbers (i.e. slightly gaping bivalves) are particularly difficult to spot (Cayford & Goss-Custard 1990). Fourth, Curlews selecting *Nereis* adjust their search rate according to the number of conspicuous worms they take from the surface and cryptic ones they lift from the burrow (Zwarts & Esselink 1989). Although direct measurements of the conspicuousness and crypticity of these prey are needed to avoid circular argument, these results do seem to be consistent with the prediction that predators move faster when relatively more prey are conspicuous (Gendron 1986). Nonetheless, the main conclusion of this section must be that the detectability of prey remains extremely difficult to measure, especially in waders hunting by sight. For such waders, the rate of encounter with prey needs to be measured as a function of prey size and the width of the search path needs to be determined as has recently been described for sparrows (Getty & Pulliam 1993).

The ingestible and digestible prey fraction

Curlews eating large *Mya* take some minutes to pull up the siphon and consume the flesh piecemeal from the shell (Zwarts & Wanink 1984). Curlews also dismember large *Carcinus* and eat the pincers and legs separately from the carapace. In this way, some waders overcome the limit set by the width of their gape to the size of a food item that can be ingested. However, many prey cannot be broken into pieces, or it takes too long to do so, and must be swallowed whole. Thus, Knot eating whole bivalves and snails cannot swallow prey with a circumference exceeding 3 cm. This limit can be exactly quantified from the relationship between shell circumference and length (Zwarts & Blomert 1992). The round shape of *Cerastoderma* means that Knot cannot eat shells greater than 12 mm long, but they can eat longer bivalves that are more slender. That is why Knot are able to ingest *Macoma* up to 16 mm long, *Scrobicularia* up to 17 mm long, *Mya* up to 19 mm long and *Mytilus* up to 21 mm long. Hence, because of this size limit set by the gape, a large part of the bivalve biomass present is not ingestible by Knot.

Other factors may limit prey size. Thus Purple Sandpipers *Calidris maritima* take hard-shelled prey but, as suggested by Summers *et al.* (1990), they may reject some large prey that are probably small enough to be swallowed, but too strong to be crushed in the gizzard. The average weight, and so strength, of the stomach of different wader species may thus limit prey size. Three wader species that eat bivalves whole (Knot, Great Knot *Calidris tenuirostris* and Purple Sandpiper) have relatively heavier stomachs than species that eat soft prey (Piersma *et al.* 1993a). Moreover, Piersma *et al.* (1993a) also found indications that, within a species, individuals with a heavy stomach had taken more hard-shelled prey.

To conclude, bivalves contribute most to the total biomass of the intertidal invertebrates (Figs. 4, 5; Beukema 1976), but nonetheless, only a few wader species are specialized to exploit them because of their protective shells. Most waders cannot digest these prey because they are either too large to be ingested or too strong to be cracked in the stomach.

The profitable prey fraction

Waders ignore small prey. These prey are unprofitable, or uneconomical, because they give too low a return in terms of energy to be worth spending the time needed to handle them. Small prey are usually less profitable than large ones, because prey weight, and thus energy, increases exponentially with size while the increase in handling time is much less. In other words, small prey must be handled extremely fast to make them as profitable as large prey. Optimal foraging theory (e.g. Krebs & Kacelnik 1991) shows that, for a given prey size class to be taken, its profitability (i.e. intake rate during handling prey) must always exceed the intake rate during feeding (searching + handling). This rule has been used to explain the value of the size acceptance threshold for small prey observed in Oystercatchers feeding on four prey species: *Mytilus* (Zwarts & Drent 1981, Ens 1982, Sutherland & Ens 1982, Meire & Ervynck 1986, Cayford & Goss-Custard 1990), *Macoma* (Hulscher 1982), *Cerastoderma* (Sutherland 1982c) and *Mya* (Zwarts & Wanink 1984), in Redshank preying on *Nereis* (Goss-Custard 1977b), in Curlews feeding on *Mya* (Zwarts & Wanink 1984), *Nereis* (Zwarts & Esselink 1989) and *Uca* (Zwarts 1985), in Whimbrels feeding on *Uca* (Zwarts 1985) and in Knot feeding on *Macoma* (Zwarts & Blomert 1992). These studies showed that birds were more selective than predicted by theory, because barely profitable prey were usually taken much less frequently than expected.

It is not easy to identify the fraction of the macrobenthos that is profitable for waders, the main problem being that the profitability of a given prey varies between wader species. Large birds are usually able to handle prey of a given size much faster than a small bird. For instance, the average time needed to handle a Fiddler Crab 20 mm wide decreased from 90 to 4 s in four bird species that varied in weight between 100 and 1500 g (Zwarts 1985). This makes prey of a given size much more profitable for larger waders. On the other hand, large waders also need more food, so their lower prey size acceptance threshold will be elevated due to the need to maintain a higher intake rate.

It is possible to determine for each wader species the minimum weight of prey that are sufficiently profitable to eat, if we know the average intake rate and the handling time of small prey. The average intake rate of each wader species can be estimated because their total daily consumption is a function of metabolic requirements, and thus dependent on body weight. Zwarts *et al.* (1990b) estimated average daily consumption to vary with body weight of the wader (W, in gram) according to the equation:

$$\text{daily consumption (g dry flesh)} = 0.322W^{0.723} \quad (1)$$

Waders in tidal habitats forage for 6 to 13 hours in each 24 hour period, with the time spent feeding being lower for the larger wader species (Goss-Custard *et al.* 1977a, Pienkowski 1977, Engelmoer *et al.* 1984, Zwarts *et al.* 1990b). The average intake rate required to meet the energy demands equals the daily consumption divided by the feeding time. According to Zwarts *et al.* (1990b) this calculation gives the relationship between intake rate and body weight (W, in g) as:

$$\text{intake rate (mg dry flesh s}^{-1}\text{)} = 0.004W^{0.95} \quad (2)$$

Although this is a crude approach, the formula predicted quite well the intake rate in four species (Zwarts *et al.* 1990b). Equation (2) can be used to derive a generalised lower prey size acceptance threshold. Accepting that the profitability (mg s^{-1} handling) must at least be equal to the intake rate (mg s^{-1} feeding), the minimum prey weight can be defined as the product of intake rate and handling time. Thus, a general law relating handling time to prey size in birds of different weight needs to be formulated.

Waders can take up to 40 to 160 small prey per minute when feeding rapidly at one spot so that they hardly spend any time searching for prey. The minimum time to take then a prey varies between 0.4 and 1.5 s. Film and video analyses showed that the time taken to transport a small prey up the bill to the gape amounts to 0.4 s for Knot taking a small piece of flesh (Gerritsen 1988), 0.40 s for a Common Sandpiper *Actitis hypoleucos* taking a chironomid larva (Blomert & Zwarts unpubl.), 0.46 s for a Sanderling taking a small isopod (Myers *et al.* 1980), 0.70 s for a Black-tailed Godwit *Limosa limosa* taking a chironomid larva and 0.79 s for a Black-tailed Godwit taking a rice grain (Blomert & Zwarts unpubl.). In contrast to ducks (e.g. de Leeuw & van Eerden 1992), waders have to pick up and swallow each prey individually.

The total handling time must be longer than the time taken to mandibulate and swallow, because the prey must be (1) first recognized as edible, (2) grasped and, if necessary, lifted from the substrate, (3) shaken, or even washed, to clean it, (4) swallowed, (5) after which the bill can be lowered again to recommence searching for, or handling, the next prey. Myers *et al.* (1980) distinguished three components in the handling time of Sanderlings and measured their duration: the orientation time of 0.12 s preceded the swallowing time of 0.46 which was then followed by the time to return the bill to the surface, the down time of 0.12 s. The total handling time was 0.69 s, thus 1.5 times the swallowing time. Since Sanderlings took 0.86 s to consume each prey when the prey density was high, the average search and non-feeding time between successive prey was only 0.86 minus 0.69, or 0.17 s, per prey. A similar calculation can be made for Black-tailed Godwits feeding on chironomids or rice grains. On average, chironomid larvae were taken every 1.5 s (Blomert & Zwarts unpubl.), exactly as found by Dirksen *et al.* (1992) and Székely & Bamberger (1992). The handling time amounted to 1.0 s and was thus 0.5 s shorter than the time required to consume each prey. A quarter of this difference could be attributed to time lost in handling prey that were subsequently rejected. Thus, less than 0.4 s per prey was spent in non-handling time. The swallowing time of a rice grain was 0.79 s and the total handling time 0.97 s, or 1.13 s when the time wasted in rejected rice grains was included (Blomert & Zwarts unpubl.). A Black-tailed Godwit needed at least 1.71 s to find and eat a prey, so the minimum search time was 0.6 s. The three analyses show that the feeding rate actually achieved was 20 to 35% below the maximum feeding rate the birds would have attained if they only spent time in handling prey. Handling times of small prey were rarely measured, but feeding rates of waders taking small prey have been determined in several studies. Therefore we will compare handling times estimated as the inverse of the feeding rate and use the term 'composite handling time' to distinguish it from the 'true handling time'. 'Composite handling time' overestimates 'handling time', but it probably gives a more realistic description of the average minimum time needed to consume a prey since it includes the wasted handling times and the time needed to move the bill from one prey to the next.

At first sight, it would seem obvious that large waders handle prey of all size classes faster than small birds; for instance, their larger gape width would be expected to enable them to swallow prey much more easily. Surprisingly, the reverse trend has been found for small prey; it takes a large bird more time than a small one to eat tiny prey (Fig. 12A). The explanation may be found in Fig. 12B where long-billed birds are shown to take more time to handle a small prey than short-billed birds. Body weight and bill length are highly correlated in the sample of bird species used in Fig. 12 ($r = 0.88$). A multiple regression analysis (see Fig. 12B) revealed that the effect of body weight on composite handling time disappeared completely when bill length was taken into account while the influence of bill length on composite handling time became even more pronounced than in the simple regression.

As Fig. 12 includes the Black-headed Gull *Larus ridibundus* and Glossy Ibis *Plegadis falcinellus* and their composite handling times do not deviate from the trends found in the wader species, the relationships in Fig. 12 may apply to all birds taking one prey at a time. How to explain that the composite handling time depends on bill length? Waders transport a prey from the bill tip to the gape by a series of 'catch and throw movements' (Gerritsen 1988). Video analysis showed that the duration of the swallowing time, the major component of the handling time, depends on the number of catch and throw movements made. For instance, the time required by a Common Sandpiper to swallow a chironomid larva increased from 0.32 to 1.12 s if the number of such movements increased from 1 to 10. This species needed 0.43 s and 2.11 catch and throw movements, on average, to transport a chironomid from bill tip to gape. It took a Black-tailed Godwit

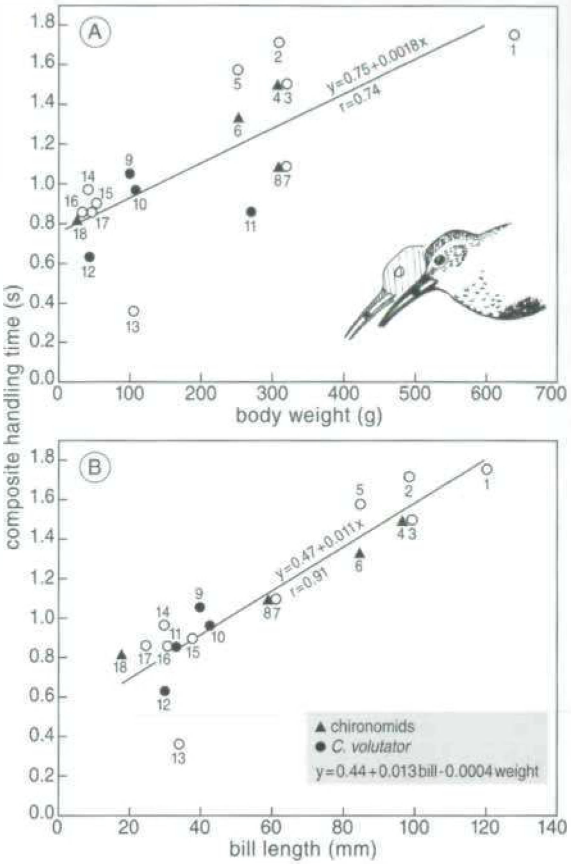


Fig. 12. The time needed to eat a small prey as a function of **A.** body weight and **B.** bill length of birds. As the times needed to eat small prey were calculated from the feeding rate (prey per unit time feeding) when small prey were taken in a high rate and the search time approaches zero, we use the term 'composite handling time' to distinguish it from directly measured 'handling times'. The composite handling time was determined in two ways. If frequency distributions of composite handling times were available, we used the average of the shortest 25% (study no. 1 to 9 and 11). In all other cases, we took the lowest average composite handling time per day, month, zone or experimental condition. All data were collected in the field, but study no. 5, 12, 13 and 17 were done in the laboratory. For adult Avocets an adjustment of bill length has been undertaken, since they touch *Nereis* at a point about 3/4 along the bill when they sweep the bill through the mud; no adjustment was necessary for juvenile Avocets as they pecked *Corophium* from the surface with the tips of their bill. The multiple regression equation is given in panel B. Further explanation in text.

no	*bird species*	*prey*	*source*
1	Glossy Ibis	*Corbicula fluminalis*	van der Kamp & Zwarts unpubl.
2	Black-tailed Godwit	rice grain	Zwarts unpubl.
3	Black-tailed Godwit	*Corbicula fluminalis*	van der Kamp & Zwarts unpubl.
4	Black-tailed Godwit	chironomid larvae	Dirksen *et al.* 1992
5	Bar-tailed Godwit	artificial pellets	Blomert & Zwarts unpubl.
6	Bar-tailed Godwit	chironomid larvae	Dirksen *et al.* 1992, Székely & Bamberger 1992
7	Avocet	*Nereis*	Blomert & Engelmoer unpubl.
8	Avocet	chironomid larvae	Dirksen *et al.* 1992
9	Young Avocet	*Corophium*	Engelmoer & Blomert 1985
10	Redshank	*Corophium*	Goss-Custard 1969
11	Black-headed Gull	*Corophium*	de Vries 1969
12	Dunlin	*Corophium*	van der Voet 1967
13	Knot	*Hydrobia*	Piersma *et al.* 1993
14	Dunlin	*Artemia salina*	Verkuil *et al.* 1993
15	Curlew Sandpiper	*Artemia salina*	Verkuil *et al.* 1993
16	Broad-billed Sandpiper	*Artemia salina*	Verkuil *et al.* 1993
17	Sanderling	isopods	Myers *et al.* 1980
18	Semipalmated Sandpiper	chironomid larvae	Ashkenazie & Safriel 1979

nearly twice as much time (0.79 s), and slightly more catch and throw movements (2.50), to swallow the same prey. The bill length of a Common Sandpiper is 2.5 cm and of a Black-tailed Godwit 9.8 cm, on average. Hence it is reasonable to assume that the increase of handling time with bill length is simply related to the distance along which the food item has to be transported.

It is also reasonable that prey taken from the surface, such as *Corbicula fluminalis*, *Corophium* and *Hydrobia*, may be handled faster than prey taken from the mud or out of the water (Fig. 12). This effect was indeed found when the residuals relative to the regression line in Fig. 12B were split up in these two categories. On average, non-surface prey were handled 13% faster than surface prey, but this difference was not significant ($p = 0.13$). Moreover, prey size explained a small part of the variation around the regression line of composite handling time against bill length: it took Black-tailed Godwits twice as much time to swallow a rice grain of 20 mg wet weight than a chironomid larvae of 10 mg (Blomert & Zwarts unpubl.). Also Bar-tailed Godwits *Limosa lapponica* spent 20% more time in handling an artificial pellet of twice the wet weight of a chironomid larva (Fig. 12B). However, prey size does not affect the close relationship between bill length and composite handling time, since the trends shown in Fig. 12 remain the same when a selection is made of prey about 1 mg AFDW (*Corophium* and chironomids).

Although it still has to be tested whether the relatively simple biomechanical rule that bill length negatively affects handling time, can fully explain the observed relationship between handling time and bill length, the function in Fig. 12B can be used to calculate for each wader species the lower prey size acceptance threshold for small prey. This was done by multiplying the predicted handling time (Fig. 12B) and the predicted average intake rate (equation 2). The smallest wader found along the East-Atlantic coast is the Little Stint *Calidris minutus* with a body weight of 22 g and a bill length of 18 mm. From Fig. 12B the predicted handling time of this species would be 0.8 s and thus a feeding rate of 1.25 s^{-1} is required. According to equation (2), the average intake rate would be 0.07 mg s^{-1}. Thus, the minimum weight of acceptable prey would be $0.07 / 1.25 = 0.05$ mg. Extrapolation of the regression function in Fig. 12B to the largest wader found along the East-Atlantic coast, female Curlew with a bill length of 16 cm, would give a composite handling time of 2.6 s $prey^{-1}$ or 23 prey min^{-1}. With a body weight of 900 g and an intake rate of 2.56 mg s^{-1}, the smallest acceptable prey for a Curlew should therefore be 6.7 mg.

These calculations were repeated for all the other wader species occurring in NW. Europe. When the calculated minimum prey weights needed to achieve the species characteristic intake rate according to equation (2), were plotted against body weight, the relationship between bird weight and the lower prey size acceptance threshold could be described as a function of body weight (W, in g) according to the equation:

$$\text{minimum prey weight (mg dry flesh)} = 0.0012\,W^{1.29} \qquad (3)$$

The exponent of equation (3) is much higher than the value of 0.75 associated with the dependence of metabolic requirements on body weight (equation 1). If the number of prey taken per unit time feeding were independent of body weight, average prey size would be a simple function of daily consumption (equation 1). If so, the average prey weight of a female Curlew would be 14.6 times as large as of a Little Stint. Taking into account the shorter feeding time for larger waders (equation 2) and their inability to handle small prey quickly (Fig. 12B), we arrive at an acceptance threshold for prey taken by female Curlews 120 times as high as for Little Stints. Thus this difference is some 8 times higher than the average prey weight predicted from the daily requirements under the assumption of size-independent feeding rate. This must mean that large birds are much more size-selective than small birds and so ignore a disproportionately large part of the small prey, which are unprofitable because of their low handling efficiency for small prey.

Large waders do indeed take relatively large prey compared to small waders (Zwarts *et al.* 1990a). The smallest prey ever recorded taken by Oystercatchers (body weight 550 g) was *Cerastoderma* 8 mm long and weighing 3.3 mg (Meire 1996b), but usually they feed on prey of 20 to 800 mg (Zwarts *et al.* 1996a, 1996b). The prey selected by Curlews weigh 100 to 300 mg (Ens *et al.* 1990) and are taken at an average rate of 1 prey min^{-1}. There are, however, two prey that weigh less. Both are taken at a high rate for Curlews: siphons of *Scrobicularia* (5 to 10 mg) up to 9 min^{-1} and juvenile *Carcinus* (40 mg) up to 7.4 prey min^{-1} (Zwarts unpubl.). However, Oystercatchers and Curlews feeding solely on such small prey achieve a relatively low intake rate, so these prey are usually ignored or taken while searching for larger prey.

The lower prey size acceptance rule may be tested by comparing its predictions with available measurements on both diet and size selection. By way of illustration, the following analysis considers waders feeding on one small prey species, *Corophium*. Fig. 13 shows the relation between size and weight in *Corophium* (from Table 1), and the predicted lower acceptance threshold for several wader species. The four lower panels give the observed size selection, expressed as 'index of selectivity' to correct for the varying frequency distribution of size classes on offer. As predicted, small waders, such as the Least Sandpiper *Calidris minutilla* (19 g; bill length 18.5 mm) and Semipalmated Sandpiper (21 g; bill length 19.4 mm) took small *Corophium* (Gratto *et al.* 1984); (*Corophium* > 4 mm are due to their size probably uningestible and/or unprofitable for these small waders). Redshank (110 g) was predicted to take prey larger than 5 mm, precisely as found by Goss-Custard (1969, 1977a: appendix b). Although *Corophium* is not a major prey of Bar-tailed Godwits (250 g), they do select the rare specimens larger than 7 mm (Zwarts unpubl.), which is also in line with expectation.

A further prediction is that waders which are heavier than Bar-tailed Godwit should ignore *Corophium* altogether. In line with this, it has never been found in the diet of any of the larger species. Black-headed Gulls are as heavy as Bar-tailed Godwits and eat *Corophium* (Curtis *et al.* 1985). They have a short bill in comparison to waders with a similar body weight and handle these prey quickly (Fig. 12); unfortunately no data are available on the size selection. *Corophium* is also one of the main prey of young Avocets *Recurvirostra avosetta*. However, when they pass a body weight of 100 g they switch to the more profitable *Nereis* (Engelmoer & Blomert 1985) as would also be predicted. Adult Avocets (320 g) do not take *Corophium* either (Engelmoer & Blomert 1985). Were Shelduck *Tadorna tadorna* (1100 g) only to pick up prey in the same way as waders, they would not be able to survive on a diet of such small prey as *Corophium* and *Hydrobia*. However, Shelduck are able to sieve mud through the bill lamellae and filter prey from the upper layer of the mud at the high rate of up to 3 prey s^{-1} (Buxton & Young 1981), much faster than waders.

Waders that take *Corophium* from the surface handle a prey in less than 1 s. But if waders have to take the same prey from beneath the mud surface, the handling time will be longer, due to the time needed to probe the bill into the mud and to extract the prey. Moreover, it is likely that mud would stick to such prey, requiring the waders to spend additional time in shaking or washing the prey before it is ingested. The profitability rule may therefore explain why waders only peck *Corophium* from the surface and do not probe for them, though they are accessible to most wader species in burrows 3 to 5 cm deep (Meadows 1964, Jensen & Kristensen 1990). If it is assumed that the handling time is twice as long for a Redshank probing for *Corophium* rather than pecking them from the surface, only prey > 6.5 mm would still be profitable, representing a considerable reduction in the accessible prey biomass. In this way, prey that are accessible may nonetheless be safe from predation if they make themselves unprofitable to their predator. This is also probably one of the reasons why *Hydrobia* bury themselves just below the surface when not actively grazing at the surface (Vader 1964, Little & Nix 1976, Dugan 1981, Barnes 1986, Mouritsen & Jensen 1992).

For the same reason Sanderlings, Curlews and Oystercatchers more often take shallow prey than just barely accessible prey. However, the risk of prey being taken is not solely a function of their depth, but also depends on their own density (Wanink & Zwarts 1985): an Oystercatcher offered a high density of *Scrobicularia*, became more selective and only consumed prey living in the upper 3 cm of the substrate. This is because the profitability of the prey decreased with depth due to the increase of the handling time with depth. The deep-living, less profitable prey were ignored at the higher prey density when the search time per prey decreased and the overall intake rate could be increased by concentrating on the shallow prey. This again shows that prey that under certain condition are known to be accessible can be ignored

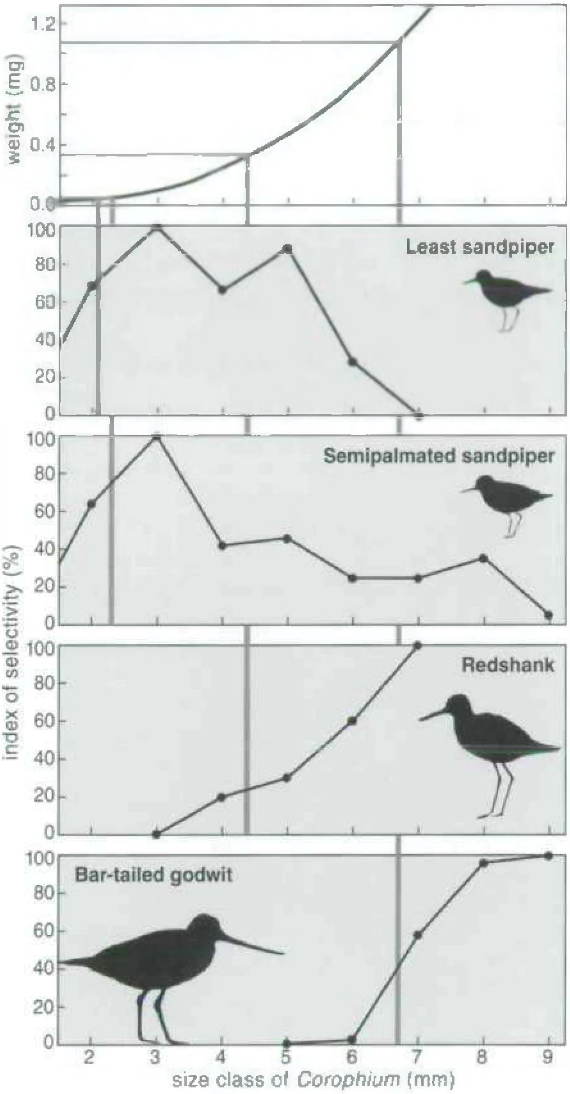


Fig. 13. The relation between weight and size in *Corophium volutator* (from Table 1) and the observed size selection by four wader species. The horizontal lines in the upper graph indicate the expected lower weight threshold according to equation (3) (see text) and the vertical lines show the corresponding expected lower size threshold. The lower panels give the measured size selection in Semipalmated and Least Sandpiper (Gratto *et al.* 1984), Redshank (Goss-Custard 1977a; averaged for two sites) and Bar-tailed Godwit (Zwarts unpubl.). The index of selectivity is obtained by dividing per size class the numbers of prey selected by the numbers on offer, set the maximum ratio to 100 and express all ratios relative to this maximum.

because their depth renders them unprofitable.

The variable depth selection of Oystercatchers also makes clear the point that the lower acceptance threshold must not be regarded as a fixed constant. By definition, the lower prey size acceptance threshold varies according to the intake rate during feeding. Birds add less profitable prey to the diet as their intake rate goes down. For example, as prey density declines, Oystercatchers accept all the *Cerastoderma* encountered and not only the open ones that can be handled quickly (Hulscher 1976). Redshank and Oystercatchers include the smaller size classes in their diet as prey density declines (Goss-Custard 1977b, 1977c, Zwarts & Drent 1981) and, as mentioned, Oystercatchers eat the less profitable *Scrobicularia* lying at a greater depth.

The profitability of prey may vary systematically between individual birds. Hulscher (1982) showed that Oystercatchers with blunt bills need more time to handle *Macoma* than birds with pointed bills. Similarly, Sutherland & Ens (1987) found that an Oystercatcher with a chisel-shaped bill was faster at stabbing *Mytilus* than a bird with a blunt bill, while it was other way around when the birds opened a Mussel by hammering. Again, Swennen *et al.* (1983) found individual differences in the time taken to handle *Cerastoderma* as did Wanink & Zwarts (1996) and Hulscher *et al.* (1996) for Oystercatchers eating *Scrobicularia*, *Mya* and *Macoma*, respectively. Individual differences in the handling efficiency would be expected to cause a variation in the lower acceptance level of size classes selected, but this possibility has still to be explored in the wild.

In conclusion, smaller prey are ignored by waders since they are unprofitable: large waders usually take prey of at least 10 to 20 mg, but usually larger, and waders weighing less than 100 g select prey of about 1 mg. Furthermore, prey that are not taken and so seem at first sight not to be available, may actually be detected but ignored because they are unprofitable.

The harvestable prey fraction

The information given in the former four sections, enables us to define the harvestable prey fraction. This will be illustrated in three examples. Fig. 14A shows the fraction of a benthic bivalve harvestable for Oystercatchers. Oystercatchers may locate their prey by randomly probing their bill into the mud, so prey detectability is determined by the surface 'touch area' of the shell (Hulscher 1976, 1982, Zwarts & Blomert 1992). Oystercatchers either open the prey in situ beneath the surface or lift them out of the substrate. The bivalves are opened by stabbing, or forcing, the bill between the valves, after which the flesh is eaten out of the shell (Hulscher 1982, Wanink & Zwarts 1985). Because no size limit is set by gape size and only the flesh is consumed, all prey are ingestible and digestible. Hence the harvestable fraction depends solely on the limits determined by the accessibility and profitability of the prey (Fig. 14A).

Oystercatchers lift deep-living prey more often than shallow ones (Wanink & Zwarts 1985). The lifting of prey prolongs the handling time and so makes them less profitable. As discussed above, deep-living, but accessible, prey may thus be ignored due to their low profitability (Wanink & Zwarts 1985). We therefore assume that the Oystercatchers (bill length 6.5 to 8.5 cm) take the majority of *Macoma* and *Scrobicularia* from the upper 4 cm of the substrate, and perhaps from the upper 6 cm when either the intake rate and/or the density of easily accessible prey is low.

Oystercatchers take large bivalves (e.g. Hughes 1970a, Goss-Custard *et al.* 1977a, Hulscher 1982, Bunskoeke *et al.* 1996, Zwarts *et al.* (1996a). *Macoma* smaller than 10 mm and *Scrobicularia* smaller than 13 mm are always ignored because they are unprofitable (Hulscher 1982, Zwarts *et al.* 1996a). Intake rate varies greatly and primarily depends on the presence of large bivalves. When, due to the high density of the large size classes, Oystercatchers achieve a high intake rate, they are more selective and ignore *Macoma* less than 15 mm long and *Scrobicularia* smaller than 25 mm long (Zwarts *et al.* 1996a). The harvestable fraction is thus highly variable for two reasons. First, the depth distribution and prey biomass fluctuates seasonally

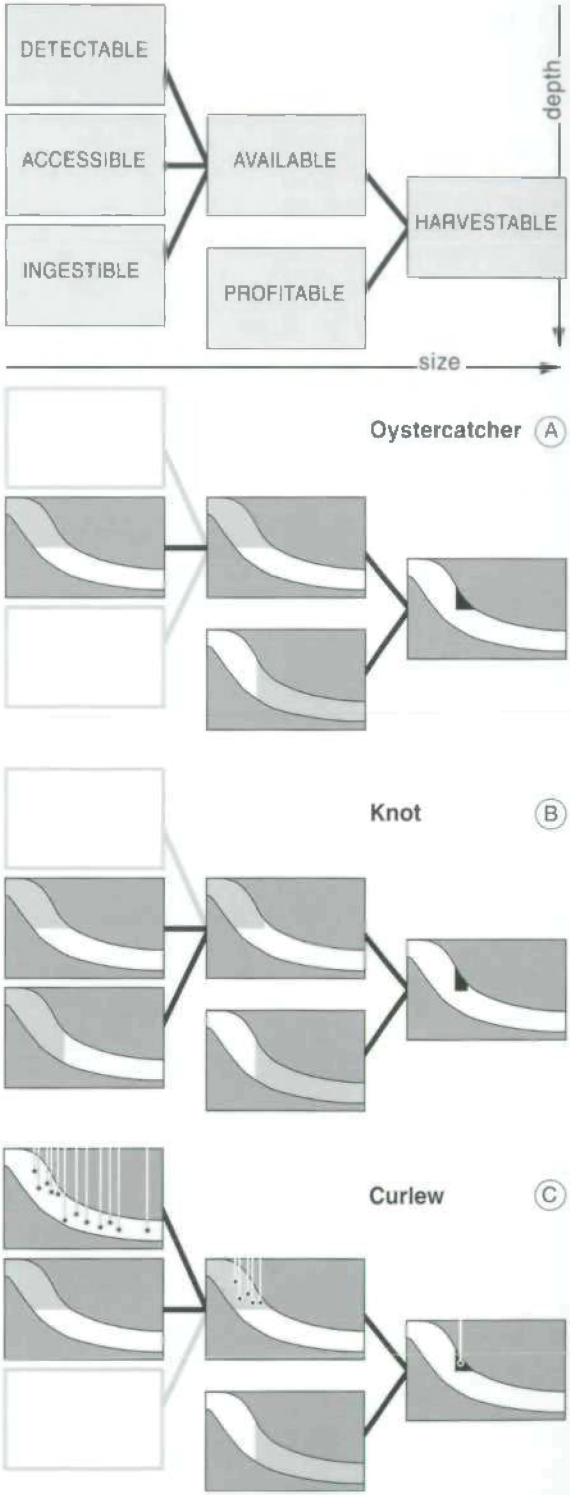


Fig. 14. The harvestable fraction of benthic prey depends on the fraction of prey being **A.** accessible and profitable in touch-feeding Oystercatcher; **B.** accessible, ingestible and profitable in touch-feeding Knot, and **C.** accessible, detectable and profitable in Curlew feeding by sight for siphon holes.

and annually. Second, the lower size acceptance threshold as well as the depth selection varies being a function of the intake rate.

Knot feed by touch when they search for benthic bivalves, but in contrast to Oystercatchers, they ingest their prey whole. This makes the harvestable fraction of prey for Knot much smaller than for Oystercatchers (Fig. 14B). *Macoma* is a preferred prey for Knot, but they ignore the size classes smaller than 10 mm long and reject *Macoma* larger than 16 mm long: the small prey are unprofitable, while the large ones are too wide to be swallowed (Zwarts & Blomert 1992).

Knot visited our study site only in August when the total biomass of *Macoma* over ten years varied between 6 and 35 g m^{-2}, with an average of 17.7 g m^{-2} (Fig. 15). On average, 44% of this biomass belonged to the suitable size classes, whereas only 31% was harvestable, i.e. both of suitable size and accessible (living in the upper 2 cm). The annual variation of 6 to 35 g m^{-2} in the total biomass of *Macoma* was small compared to those of other benthic species (Beukema *et al.* 1993), the standard deviation of 8.6 g m^{-2} being only 49% of the mean (17.7 g m^{-2}). The relative standard deviation (RSD) for suitable biomass (6 to 16 mm long) was 44%, and thus lower than that for the total biomass. The annual variation in the fraction of *Macoma* living within reach of the bill was much larger still: for instance, 98% of the prey was found in the upper 2 cm of the substrate in August 1984, against only 15% in August 1986 (Fig. 15). On average, 54% was accessible and the RSD was 60%. As a consequence of this large variation in prey accessibility, the RSD of the harvestable biomass increased still further to 77%. It was therefore the variation in depth distribution that was a major contribution to year-to-year fluctuations in the biomass of *Macoma* actually harvestable by Knot staging in our study area in August. Piersma *et al.* (1993b) arrive at the same conclusion in their study of Knot staging on Griend, western Dutch Wadden Sea. Knot did not stage in our study area when the biomass of the harvestable *Macoma* was low (Fig. 15).

The harvestable prey fraction in touch-feeding waders, such as the Knot, is less complex to measure than in most waders that feed by sight. Figure 14C illustrates the relatively simple situation of a Curlew searching for the siphon holes of *Mya*. This prey is harvestable if it lives within reach of the bill (13 to 16 cm), if it is profitable (size > 3 cm) and, at least for Curlews feeding by sight, if the siphon hole is visible at the surface (Zwarts & Wanink 1984). Only a small part of the profitable fraction is actually accessible. This is probably the main reason why short-billed male Curlews (bill length 10 to 13 cm) never feed on *Mya*, while it is the main prey for the females (bill length 13 to 16 cm) in areas where the prey species occurs (Zwarts & Wanink 1984). The detectable fraction also varies considerable. Siphon holes arise when *Mya* extend their siphon to the surface for suspension feeding. *Mya* cannot feed at low tide as no water lies on the surface, but the siphon holes may remain visible until they decay over the low water

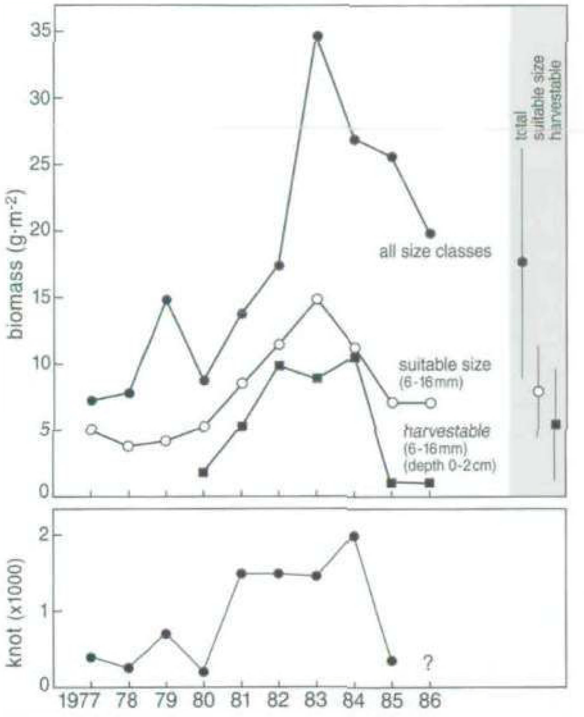


Fig. 15. The biomass of *Macoma balthica* in August 1977 to 1986, given for all size classes ('total'), for only the specimens in the range 6 to 16 mm ('suitable size') and for animals of 6 to 16 mm living in the upper 2 cm of the substrate ('harvestable'). The grey field gives the averages ± SD. The lower panel shows the response of the Knot (peak numbers in the study area). Data from Zwarts *et al.* (1992).

period. Our own unpublished work shows that Curlews systematically search for the detectable prey and usually avoid sites that they have already visited, suggesting that the detectable fraction is very small. Fortunately for the birds, new traces are formed at each ebbing tide. Hence waders that use tracks to locate prey are dealing with a renewable, but unpredictable, food resource since only an infinitely small fraction is removed each tidal cycle.

It is sometimes difficult or arbitrary to decide whether prey are not harvestable because they are unprofitable or because they are unavailable, as the analysis of depth selection illustrates. It seems obvious to define prey as inaccessible when the depth of prey exceeds the probing depth of the bird. However, probing depth may actually be less than the bill length would allow. Further, deep-living prey are least profitable and birds adjust their probing depth to maximize their intake rate (Wanink & Zwarts 1985). Thus, the actual depth selection is determined by the profitability rule and not simply by bill length. The same probably applies when waders feed on prey buried in substrates of varying degrees of hardness. Dunlin probe more deeply in soft substrate (Mouritsen & Jensen 1992), thus the depth at which prey are taken depends on the penetrability of the substrate. From this, it might be concluded that prey living deeply in sand are less accessible than prey found at the same depth in mud, because the bill is perhaps not rigid enough to probe deeply in sand. But an alternative possibility is that it takes too much time to search for and to take prey at greater depths in firm substrate thus reducing their profitability. Indeed, Myers *et al.* (1980) found that a Sanderling takes more time to probe to a certain depth as the substrate penetrability decreases, and Hulscher (unpubl.) showed that Oystercatchers spend more time lifting a bivalve from firm than from soft substrate.

A similar uncertainty regarding the distinction between unavailable and unprofitable prey is found in relatively large prey. The upper size limit for Knot feeding on *Macoma* has been attributed to the morphological constraint imposed by gape width. However, when the decreasing profitability of increasingly larger prey is taken into account (Zwarts & Blomert 1992), it might be found that the larger size classes are actually ingestible but that the increase in handling time makes them unprofitable. Oystercatchers hammering *Mytilus* provide another example. These birds may reject thick-shelled prey because they are too strong to allow Oystercatchers to hammer a hole in the shell. In this case, they may be said to be unavailable, but an alternative explanation is that the increase in handling time with thickness of the shell makes them also less profitable (Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Meire 1996a). As in Knot, this increase in handling time is due to an increasing proportion of prey being rejected, thus leading to a waste of time.

Finally, do birds take all harvestable prey species? This appears not to be so, at least when several prey species are available. We have calculated that 11% of the total biomass of all prey species was harvestable by Knot in our study area, but that they selected only from 3% of that, excluding all prey species except *Macoma*. Possibly Knot select prey to maximize the energy processing rate in the gut, since *Macoma* is thin-shelled while the other species all have thick shells (Zwarts & Blomert 1992).

The fact that individuals behave differently may also cause individual birds to be more selective than would be predicted solely on the basis of the fraction that is harvestable for a wader species. For example, the bill length of a Curlew determines the harvestable fraction of large *Nereis* and of medium-sized *Mya*. Yet Ens & Zwarts (1980a, unpubl.) found that, among Curlews feeding in the same area, individuals with a similar bill length took either *Nereis*, or *Mya*, or both over a period of several years. Probably these birds have learnt to search and handle efficiently some prey but not others. Oystercatchers are also food specialists (Goss-Custard & Durell 1983, Boates & Goss-Custard 1992), this partly being attributable to the overall morphology of the bill (Hulscher & Ens 1992, Durell *et al.* 1993). Moreover, individual waders may also differ in their ability to crack shelled prey depending on the structure of the gut (Piersma *et al.* 1993a). The harvestability of prey thus depends on the feeding decisions made by individual birds whose morphological and physiological constraints may differ. It will thus be more fruitful to study the relationship between predators and their harvestable prey at the level of the individual birds.

Prey switching

Waders feeding on tidal flats, face a huge variation in the relative occurrence of different prey species, this being particularly large when the fluctuations in the numbers of harvestable prey alone are considered. Waders would be expected continuously to adjust their diet as the food supply available varies. Goss-Custard (1969, 1970a, b) was the first to describe the reduction in the prey accessibility associated with short-term changes in an environmental factor and how the waders responded. He found that *Corophium* did not emerge from their burrows when the mud temperature was below 6 °C and that Redshank then switched to less preferred prey, *Nereis* and *Macoma*, these still being available. Similarly, Smith (1975) showed that when the temperature of the substrate dropped below 3 °C, *Arenicola* became inactive and Bar-tailed Godwits started to eat a smaller worm, *Scoloplos armiger*. Consequently, the intake rate decreased at low temperatures, and approached nil as the temperature came close to 0 °C. More recently, Pienkowski (1983a, b) found that, as mud temperature decreased, small worm species were less active at the substrate surface, (i.e. fewer outflows of water from the hole) and the intake rate of plover species decreased.

At a larger time scale, variation in diet also occurs as will be illustrated by six cases. (1) Blomert *et al.* (1983) studied the prey selection of individually marked Oystercatchers along the Frisian mainland coast in July to October. The birds took *Macoma* and *Scrobicularia* on a mudflat and *Mytilus* on a nearby mussel bed. The females with bill lengths of 7.5 to 8.5 cm, took twice as many *Scrobicularia* as *Macoma*. In contrast, *Scrobicularia* occurred in the diet of the males (bill length 6.5 to 7.5 cm) as much as *Macoma*. The long-billed birds thus seemed more specialized at taking deep-living prey than the short-billed ones. The expectation was that the birds would switch from *Scrobicularia* to *Macoma* in late summer, since the density of accessible prey would drop much more in *Scrobicularia* than in *Macoma* (Figs. 7, 10, 11). This was not the case, however. Instead, many males left the mudflats and started to feed on the nearby mussel bank. The result was that the total predation by Oystercatchers on *Scrobicularia* and *Macoma* was higher in late summer than in autumn. The intake rate of birds feeding on the mudflats decreased from July to October. In contrast, the intake rate of mussel-eating Oystercatchers was low in summer, but increased later on. The birds switched from mudflats to the mussel bank when *Mytilus* provided a higher intake than *Scrobicularia* and *Macoma*.

(2) The majority of *Scrobicularia* larger than 3 cm live out of reach of the Oystercatcher's bill (Fig. 11), but the smaller size classes burrowed less deeply, and were even accessible in winter (Fig. 6). Habekotté (1987), who studied Oystercatchers on the Frisian island Schiermonnikoog in winter, found that birds taking *Scrobicularia* about 20 mm long were able to achieve an intake rate sufficient for them to attain the required daily consumption. The feeding rate strongly depended on the density of *Scrobicularia*, increasing from 0.2 to 1 prey min^{-1} within the range of 100 to 600 m^{-2} at which *Scrobicularia* occurred. The majority of these prey lived at 4 to 7 cm below the surface. *Macoma* of suitable size occurred in the area at a density of 70 to 120 prey m^{-2}, but were hardly taken. They were accessible, but *Scrobicularia* were preferred above the smaller *Macoma* because of their greater profitability.

(3) *Macoma*, and to a lesser degree *Nereis*, were the major prey of Oystercatchers on the mudflats near Schiermonnikoog in spring and summer (Bunskoeke *et al.* 1996). *Nereis* were taken less during receding tide than during low tide, the reverse being the case for *Macoma* (de Vlas *et al.* 1996). This change in diet may be wholly attributed to a shift in the feeding behaviour of *Nereis* through the tidal cycle; they are filter feeders in the burrow during the receding tide, but feed on the surface around the burrow at low tide (Esselink & Zwarts 1989). The Oystercatchers switched from *Macoma* to *Nereis* during the summer (Bunskoeke *et al.* 1996). *Macoma* did not start to increase their burying depth before August (Fig. 7), hence this shift in diet could not be explained by a reduced accessibility of one of the prey. It is more likely that the decrease in the body condition of *Macoma* from June onwards (Beukema & de Bruin 1977, Zwarts 1991), made them less profitable. Indeed, the intake rate of Oystercatchers feeding on *Macoma* did decrease from May-June to August (Bunskoeke *et al.* 1996).

(4) Boates & Goss-Custard (1989) studied Oystercatchers wintering in the Exe estuary, SW. England. They observed a switch in October from *Nereis* to

Scrobicularia. There was hardly any change in the body condition of *Scrobicularia* during the winter, but a large decline in that of *Nereis* during autumn. As a consequence, there was a large decrease in the profitability of the worms which may explain the shift from worms to clams in autumn. Alternatively, the accessible fraction of worms and clams may have changed. For example, Oystercatchers took *Scrobicularia* c. 25 mm long in early winter but specimens of 30 to 35 mm long in early spring. This may indicate that *Scrobicularia*, as in the Wadden Sea, were buried more deeply in winter, so that only the smaller size classes remained accessible. Similar changes in the relative accessibility of clams and worms during autumn may explain the shift in diet observed at that time of the year. Unfortunately, the accessibility of the prey was not investigated, but it is likely that the switch in the diet was indeed a consequence of the relative change in the profitability of both prey, since the timing of the switch in diet occurred exactly when *Scrobicularia* became more profitable than *Nereis*.

(5) The diet of Dunlin was studied by Worrall (1984) who counted prey fragments found in droppings, pellets and gizzards. Although Dunlin took three prey species, the most important one was *Nereis*. The worms taken in winter were small (1 to 3 cm), but larger prey were selected in spring, probably because more became available due to their increased surface activity. The majority of the burrows of even the small *Nereis* were too deep for Dunlin (bill length 3 cm) (Fig. 6; Esselink & Zwarts 1989), which probably explains why they took such small prey in winter. *Hydrobia* were an important alternative prey in mid winter. *Macoma* were less important; the length classes 5 to 7.5 mm were most common in their diet and indeed still accessible in winter (Fig. 6; Reading & McGrorty 1978).

(6) Knot were only rarely present in our study area during winter, but had they overwintered, it would have been impossible in most winters for them to depend on *Macoma*, as they did in late summer, because the accessible fraction would have been too small (Fig. 10). Thus, Knot staging in the western part of the Wadden Sea in autumn (Dekinga & Piersma 1993, Piersma *et al*. 1993b) and in spring (Piersma *et al*. 1994) took only *Macoma* in August, but in September and October switched to two other prey that were still found at, or just beneath, the surface, *Hydrobia* and *Cerastoderma*, and returned to *Macoma* in March.

From these studies we conclude that the observed shifts in diet are a response to changes in the accessibility of different prey species. The studies on Oystercatcher also show that a seasonal change in condition of the prey, and thus in their profitability, can play an important role in switching from one prey to another. Two studies describe a switch from *Macoma* to *Nereis* in mid summer and from *Nereis* to *Scrobicularia* in autumn. In either of these cases this is due to a decrease in the prey condition and thus profitability in the prey eaten before the diet switch. *Macoma* are in good condition in early summer when they are a preferred prey for Oystercatchers, but these prey are ignored in winter, because they would yield too low an intake rate. As a consequence of this seasonal diet shift in the major predator of *Macoma*, its mortality is lower in winter than in summer (Beukema 1993a).

Do waders leave the Wadden Sea due to a deterioration in the harvestable food supply?

Some millions of waders spend the winter along the shores of NW. Europe. The winter density of waders is remarkably low on tidal flats in the Danish and German Wadden Sea, compared to tidal areas further to the south, in the temperate zone, as well as in the subtropics and tropics (Zwarts 1988a). Wader density decreases strongly with latitude within the continental wintering areas in NW. Europe, but weakly, although at a higher average level, in the British wintering areas (Fig. 16A). Great-Britain may harbour a higher winter density of waders because the surface temperatures do not fall below 4 °C, even in Scotland (Fig. 16B).

Why do wader densities decrease when the surface temperature is below 4 °C? One possibility is that in winter wader species feed at highest densities in estuaries where the biomass of their prey is largest (Goss-Custard *et al*. 1977c). However, it is unlikely that the relationships shown in Fig. 16, can be attributed to a high correlation between prey biomass and temperature or between prey biomass and latitude. If the winter densities were simply a response to prey biomass, we would likewise expect that but few waders would visit the northern tidal flats during autumn and spring, and the contrary seems to be the case. For example, the northeastern part of the Wadden Sea is visited by hundreds of thousands migrant waders in spring and Scotland, NW. England and the German and eastern part of the Dutch Wadden sea are relatively important staging areas for waders in late summer (Prater 1981, Smit 1984a, Prokosch 1988).

The average surface temperature in February is 1.5 °C in the northern and eastern part of the Wadden Sea and 7 to 8 °C along the English and French coasts (Fig. 16). The tidal flats in the Danish, German and eastern part of the Dutch Wadden Sea tidal flats are frozen and ice-covered for a period during more than half of winters, while this occurs only very rarely further south along the continental coast or in Great-Britain (Böhnecke & Dietrich 1951). Birds may thus avoid the northern continental tidal areas to reduce the mortality risk due to frost. In cold winters, many waders die of starvation or after they have left the area in a hard weather exodus (Hulscher 1990, Meininger *et al.* 1991).

Wintering in the north is energetically more expensive due to the lower prevailing temperatures and the associated higher costs of thermoregulation. A drop in temperature increases energy expenditure, especially in small birds (Kersten & Piersma 1987, Wiersma & Piersma 1994). This may explain why small waders are most common in the tropics while the majority of the waders wintering in the north are large (Smit 1984b, Zwarts *et al.* 1990a, Meininger *et al.* 1991, Piersma 1994). Thus, the two largest waders, Oystercatcher and Curlew, dominate in colder areas. However, this may also relate to their ability, as in Redshank (Goss-Custard 1969), to supplement their tidal flat feeding at low water with extra food from neighbouring grassland at high water (Heppleston 1971, Daan & Koene 1981, Townsend 1981). It is striking that during the winter these three species in the Dutch part of the Wadden Sea are most commonly on tidal flats lying adjacent to extensive inland grasslands and occur in only low numbers where such areas are not available (Zegers & Kwint 1992).

A third reason for not staying in northern intertidal areas might be that the day length is so short in winter that birds that cannot feed, or can only do so less successfully, at night face a considerable reduction in their feeding opportunities. However, variation in the

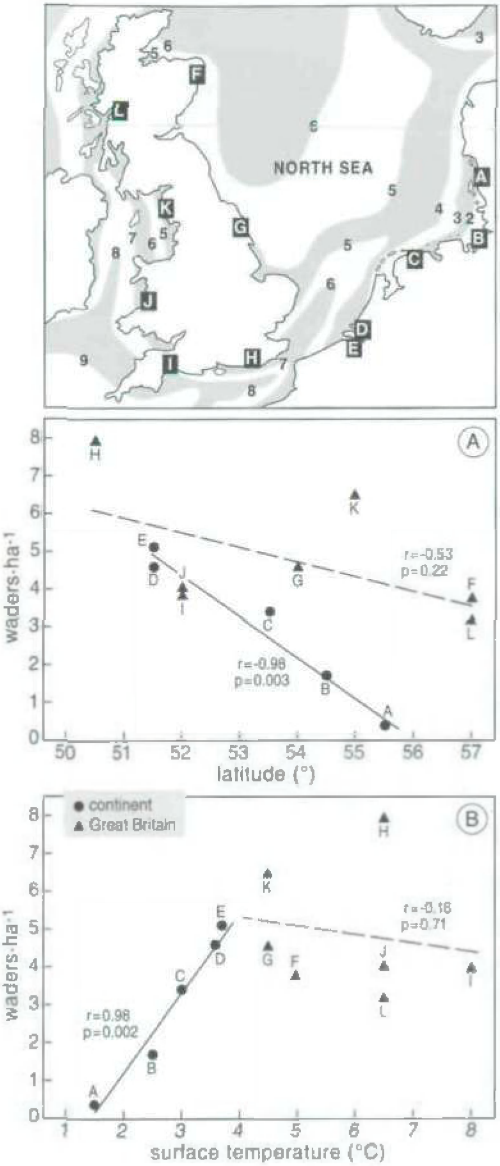


Fig. 16. Wader densities (birds ha^{-1} intertidal flat) in NW. Europe in winter as a function of **A.** latitude and **B.** surface temperatures; the map gives the average temperatures in February, based on Böhnecke & Dietrich (1951) and Anonymus (1962). The letters in the graphs correspond with the areas indicated on the map. The regression lines are given separately for five tidal areas along the continental coast (Danish, German and Dutch Wadden Sea, Grevelingen and Oosterschelde) and seven in Great-Britain (E. and W. Scotland, E., NW., S. and SW. England, and Wales). Wader densities are taken from Prater (1981), Smit (1982), Zwarts (1988a) and Wolff (1991).

duration of daylight with latitude is probably not responsible for the variation in densities shown in Fig. 16, as it differs in December by only 70 min, or 12%, between the latitudes of 50° and 58°.

The final possibility is that a decrease in the harvestable food supply in autumn forces waders to leave the area. For a variety of reasons, the feeding conditions for waders are worse in winter than in summer (Goss-Custard *et al.* 1977a). The question is whether the feeding conditions are even worse in areas with lower average surface temperatures. There are four arguments why this may be so.

(1) In summer, waders may choose between about 30 different prey species that occur in the intertidal zone, including various species of bivalves, worms, snails, shrimps, crabs and fish. However, the variety of prey species on offer in winter is restricted. Several epibenthic species, which are very common in summer, leave the tidal zone to winter in deep water, including the Common Shrimp *Crangon vulgaris* (Beukema 1992a), Shore Crab *Carcinus maenas* (Beukema 1991), Plaice *Pleuronectes platessa* (van der Veer *et al.* 1990), Flounder *Platichthys flesus* (van der Veer *et al.* 1991) and Common Goby *Pomatoschistus microps* (van Beek 1976, Jones & Clare 1977). Waders that feed on such epifauna, such as the Greenshank *Tringa nebularia* (Swennen 1971) and Spotted Redshank *Tringa erythropus* (Holthuijzen 1979), have no other choice than to continue their migration onwards in late summer and autumn. But as the entire epifauna vacate the tidal zone during the autumn everywhere in NW. Europe, this does not explain the differences in wader densities as shown in Fig. 16.

(2) As has been shown in this paper, some prey species live at a greater depth in winter than in summer. Hence they are either out of reach, or less profitable as prey because of the longer handling time. Furthermore, when only a small proportion of the prey is accessible, it is likely that the birds must eat marginal prey with poor body condition (Zwarts & Wanink 1991).

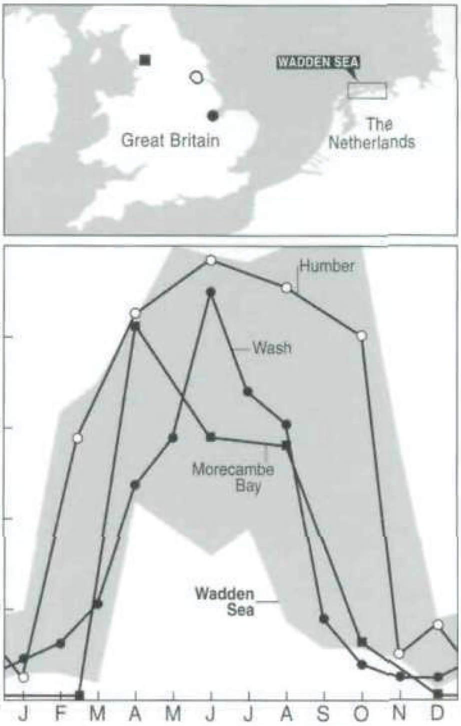


Fig. 17. Seasonal variation in the fraction of the biomass of *Macoma balthica* harvestable by Knot in the Wash (Reading & McGrorty 1978), Humber (Ratcliffe *et al.* 1981, Evans 1988), Morecambe Bay (Evans 1988) and along the Frisian coast (highest and lowest values found in seven years). Reading & McGrorty (1978), Evans (1988) and Ratcliffe *et al.* (1981) made slices in the sediment core and counted the number of *Macoma* per depth category. Accessible to Knot are *Macoma* found in the slices 0 to 3 cm. The slice technique gives in fact the distance between surface and a point halfway between the upper and lower edge of the shell, and not, as in the 'core sampling method' used by us, the distance between surface and the upper edge. To make our data comparable to the English measurements, we calculated the fraction of the biomass of prey found in the upper 2.5 cm.

It is unknown whether the depth distribution in winter differs geographically, but the burying depth of *Macoma* has been measured in six different places in NW. Europe. Unfortunately, the depth measurements in the Ythan estuary, Scotland (Chambers & Milne 1975a) and in the Danish Wadden Sea (Madsen & Jensen 1987) were presented with insufficient details to make the data comparable to the other studies (Fig. 17). Fig. 17 shows the variation in the fraction of biomass of *Macoma* (9 to 13 mm) living in the upper 2.5 cm. All studies found that 40 to 100% of these prey were accessible to Knot in summer, against less than 15% in winter. Many Knot leave the Wash in early autumn and spread out over other British estuaries where they switch to surface-living prey, *Mytilus* and *Hydrobia*, or continue to feed on *Macoma* (Evans 1979, 1988). Indeed, for Knot wintering in Morecambe Bay, *Macoma* remained the major prey item in at least two winters (Davidson 1971, Prater 1972). It is conceivable that Knot move from the Wash to the Morecambe Bay because the fraction of *Macoma* remaining accessible to Knot in the Morecambe Bay is higher than in the Wash. The scarce data available (Fig. 17) do not support this hypothesis. On the other hand, as shown in this paper, the year-to-year variation in the depth distribution is so large that it is hardly possible to compare sites if the sampling has not been continued for at least several years. This also implies that waders wintering in NW. Europe are not able to predict whether more prey are accessible when they move to other estuaries. We conclude from this that it is unlikely that systematic geographical variation in the accessible fraction of prey might explain why the cold coastal sites are avoided by waders.

(3) Many prey are less active at low temperature. Some no longer appear at the surface if the mud temperature is low, as shown for *Corophium* (Goss-Custard 1969, see also Meadows & Ruagh 1981), *Hydrobia* (Bryant & Leng 1975), *Arenicola* (Smith 1975, Cadée 1976) and *Scoloplos* (Pienkowski 1983a, b). Some bivalves feed less at low temperature (e.g. Hummel 1985a), so the valves will be closed more often, perhaps making the prey less profitable for Oystercatchers that use the stabbing technique to open these prey (Hulscher 1976, Wanink & Zwarts 1985). This may explain the marked decline in intake rate observed in stabbing Oystercatchers between August and February by Goss-Custard & Durell (1987). Assuming that the relation between mud temperature and either the defecation rate of invertebrates or the occurrence of surface feeding is not site dependent, the low prevailing temperatures in the north will tend to depress the accessibility and detectability of prey more often than in the south. Hence this factor could explain the lower winter densities of sight-feeding waders occurring in the cold coastal sites (Fig. 13 in Piersma 1996).

(4) The body condition of prey is 30 to 60% lower in winter than in summer. As a result more prey per unit time have to be eaten in winter to obtain a given intake rate, yet this option is not always available, as the lower intake rate of Oystercatchers in winter than in summer may illustrate (Table 2). At first sight, one might be tempted to assume that wintering waders in the north eat prey in a relatively poor condition because in the colder regions, macrobenthic animals feed less and thus lose more weight than their conspecifics in the warmer south. However, no geographical differences were detected in the body condition of *Macoma*, *Scrobicularia*, *Mya* and *Cerastoderma* during winter (Figs. 13 to 16 of Zwarts 1991). On the other hand, the year-to-year variation in the body weight of bivalves of similar length was shown to be so large that it would not be easy to show systematic differences. Series of measurements over at least three years are available for *Mytilus* (Dare 1975, Dare & Edwards 1975, this study: Fig. 3). Fig. 18 compares the seasonal variation in the average flesh weight of *Mytilus* 50 mm long for these three studies and also includes data from the Dutch Delta area and three estuaries in southern England, where the variation in the flesh content has been measured for one year. The differences between the seven sites are remarkably large. Oystercatchers wintering in the Lynher estuary would have to take three times as many Mussels as in the Exe to obtain a similar flesh consumption. These differences in condition may be due to the feeding conditions for *Mytilus* (e.g. emersion time). The eastern Dutch Wadden Sea is the only site where the body condition diminishes from mid summer to mid winter. In all other areas, the flesh content of Mussels of similar size increases from late summer to autumn and/or remain at the same level during autumn and early winter. We conclude from this that it is indeed worthwhile for Oystercatchers to leave the mussel beds in the Dutch Wadden Sea in autumn and move to the coast of the Irish Sea to winter there.

To test for latitudinal variations in the intake rate of Oystercatchers in winter, we re-analysed the data summarised in Table 2. We found, however, no significant differences between the intake rate of Oystercatchers in the winter half of the year in the Dutch Wadden Sea (2.02 mg s^{-1}; SD = 1.04, n = 13) and in the Dutch Delta area, England and France (1.91 mg s^{-1}; SD = 0.59, n = 40).

In conclusion, the more northerly tidal flats do seem to be less attractive as feeding areas for waders in winter than the more southern ones, because less prey are detectable and, in the case of *Mytilus*, the flesh

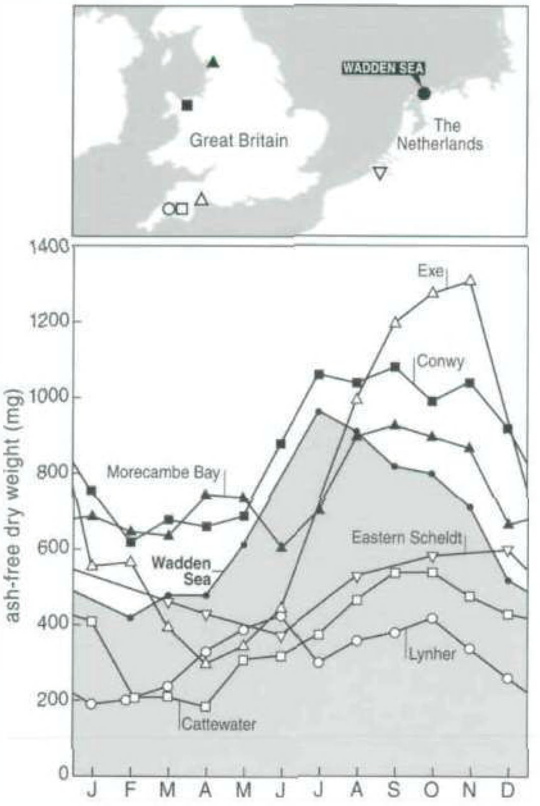


Fig. 18. Variation in body weight (AFDW, mg) of *Mytilus edulis* 50 mm long in seven areas. Sources: Exe (Cayford & Goss-Custard 1990), Conwy (Dare & Edwards 1975; averages for three years), Morecambe Bay (Dare 1975; averages for three years; correction has been made for weight loss due to formalin (12.8%); the paper gives DW; these were converted into AFDW, assuming that ash-content is 11%); Eastern Scheldt (Craeymeersch *et al.* 1986; corrected for weight loss due to formalin); Lynher & Cattewater (Bayne & Worrall 1980; weights are of Mussels 6 cm long; these were transformed to those of 5 cm using regressions given in their paper).

content per prey starts to decline earlier in the winter. It is not likely that the accessible fraction in winter differs much when areas at different latitudes or average sea water temperatures are compared.

However, it does not follow that, for all wader species, the feeding conditions are always worse when the ambient temperatures are low. First, the flesh content of prey may be better: *Macoma* and *Scrobicularia* lose more body weight in mild winters than in cold ones (Zwarts 1991, Beukema 1992b). Moreover, there are incidental occasions in winter, usually associated with a large drop in temperature, when the benthic food becomes highly available to birds. *Arenicola* and *Nereis* may leave their burrows to migrate to deeper water (Werner 1956, Verwey 1958, Dankers & Binsbergen 1984) and many worms become stranded and can be easily picked up from the mud surface (Zwarts unpubl.). Furthermore, during and after periods of frost, moribund *Cerastoderma* with gaping valves provide a rich food resource for gulls and waders that have remained (Zwarts unpubl.). Finally, during the winter half of the year, *Nereis* use a feeding method that makes them easy prey for birds. Whereas in summer they mostly remain in their burrows to filter food from the overlying water, in winter they feed more frequently on the substrate around their burrows, especially on sunny days in late winter and early spring (Esselink & Zwarts 1989). This is why Curlews feeding on *Nereis* achieve their highest intake rates in late winter, and not in summer or autumn (Zwarts & Esselink 1989). The surface feeding by *Nereis* also gives Redshank the opportunity to switch to *Nereis* at low mud temperatures when the surface activity of the preferred prey *Corophium* is already inhibited (Goss-Custard 1969).

Further research should focus on the profitability and availability of benthic prey for wintering waders along the East-Atlantic coast. This means that it is necessary to collect data on the body condition, burying depth, surface activity and defecation rates of the prey. It will not be easy to show latitudinal variation, however, since, as shown and discussed above, at any one place large annual differences may be expected in the profitability of the prey and in the fraction available to waders.

Chapter 3

BURYING DEPTH OF THE BENTHIC BIVALVE *SCROBICULARIA PLANA* (DA COSTA) IN RELATION TO SIPHON CROPPING

Leo Zwarts

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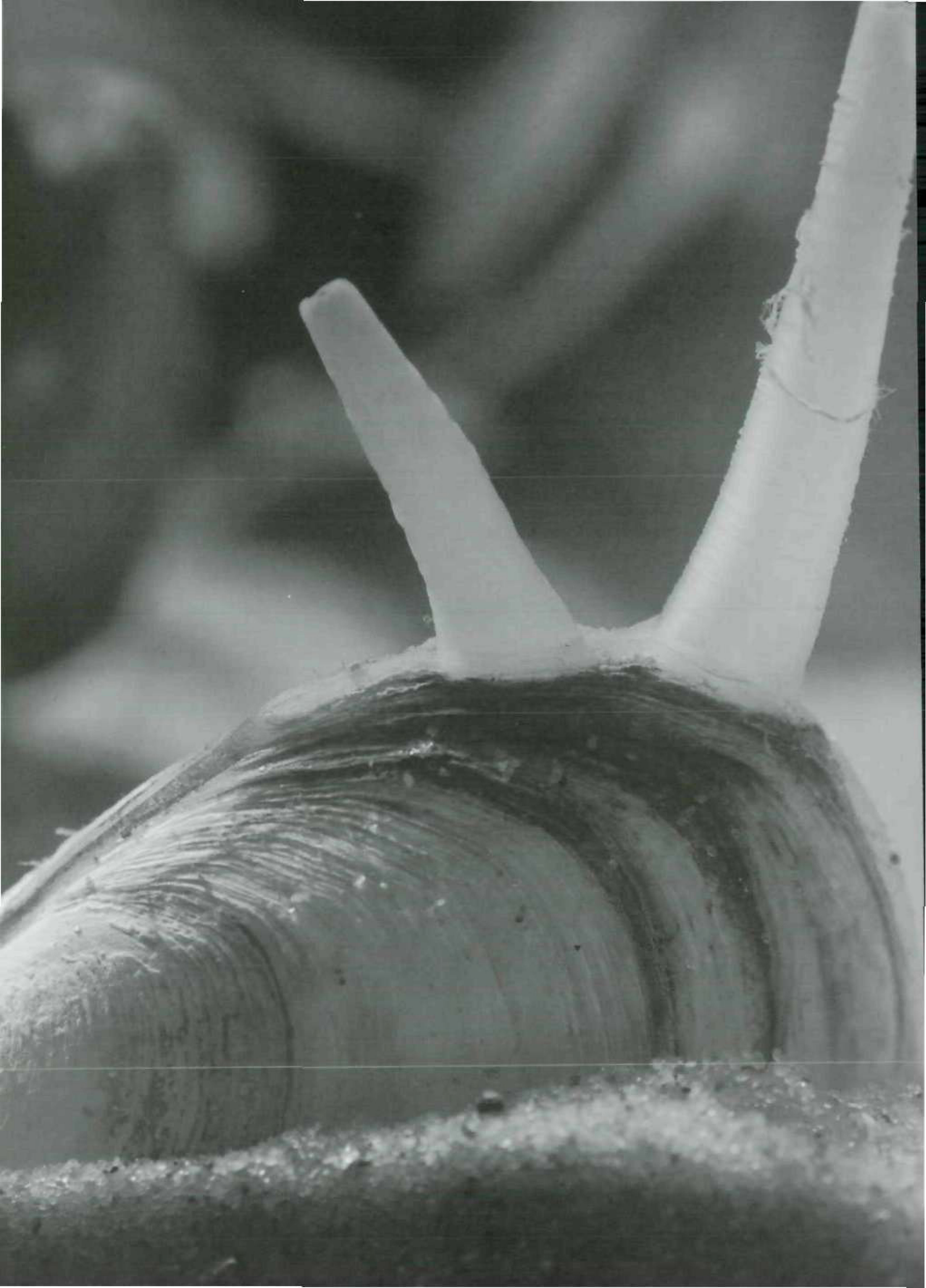


BURYING DEPTH OF THE BENTHIC BIVALVE *SCROBICULARIA PLANA* (DA COSTA) IN RELATION TO SIPHON CROPPING

A field experiment tested the hypothesis that siphon cropping influences the burying depth of the benthic tellinid *Scrobicularia plana* (da Costa). Cropping was simulated by removing part of the inhalant siphons and then burying the animals at the original depth. The depth was measured in situ each day afterwards with the aid of a nylon thread attached to the shell. The resulting increase of depth with siphon weight in the experimental animals resembles the relation between depth and siphon size in the natural population. Heavy cropping of the siphon reduced the body weight, whereas the loss of < 10 mg of the siphon had no discernible effect on the condition of the animals. When a *Scrobicularia* with a short siphon reduces its depth, it enlarges its feeding opportunity (radius around the burrows for deposit-feeding), but also increases the risk of being eaten by a predator. A short siphon alone does not force *Scrobicularia* to abandon the refuge provided by depth; only animals also in a poor body condition expose themselves to a larger predation risk. Siphon cropping reduces the burying depth and makes the bivalves more accessible for wading birds like Oystercatchers (*Haematopus ostralegus* L.). Burying depth is hence the outcome of conflicting demands; this implies that under each set of conditions an optimum can be defined.

Introduction

Benthic bivalves at first sight appear safe from predators, hidden as they are in the substratum. Many estuarine species, however, regularly suffer the loss of the siphon tips by 'cropping', 'nipping' or 'browsing' predators, mostly juvenile flatfish (Edwards & Steele 1968, Trevallion *et al.* 1970, Trevallion 1971, Kuipers 1977, de Vlas 1979a, 1985, Peterson & Quammen 1982).

Deposit-feeding bivalves are more vulnerable to these croppers than suspension feeders which can filter their food from the overlying water while the siphon is below the surface (Peterson & Quammen 1982). Even a typical deposit feeder, like the tellinid *Scrobicularia plana*, is, however, a suspension feeder at high water or limits its siphonal activities to the sides of mouth of the inhalant burrow, apparently to minimize the risk of losing a (big) part of the siphon to predatory fish (Hughes 1969). During deposit feeding at low water, *Scrobicularia* extend their siphon 5 to 8 cm out of the burrow, but they show an anti-predator reaction to feeding wading birds: there is a quick withdrawal of the inhalant siphon when there is any vibration through the mud (Linke 1939, Hughes 1969). Nevertheless, Curlews (*Numenius arquata*) manage to graze siphons of *Scrobicularia* at a rate of 1 to 10 per min (Ens & Zwarts 1980a, unpubl. data).

Bivalves are able to regenerate the siphon (Trevallion 1971, de Vlas 1979a, 1985, Hodgson 1982a), but siphon predation has several negative consequences for them. Regeneration of the siphon may take place at the expense of the development of the gonads (Trevallion *et al.* 1970, Trevallion 1971), the body condition (Trevallion *et al.* 1970, Trevallion 1971, Hodgson 1982a), or somatic growth (Peterson & Quammen 1982). The same sublethal effects have been shown for estuarine worms suffering tissue loss (de Vlas 1979b, Woodin 1984, Zajac 1985).

Zwarts & Wanink (1989) suggest another negative effect: regular amputation of the siphon would force the bivalves to live nearer to the surface and so expose themselves more to the risk of being eaten by birds. These authors show that *Scrobicularia* occur in a large vertical range within the substratum; animals of > 25 mm live in summer at a depth between 0 and 10 cm

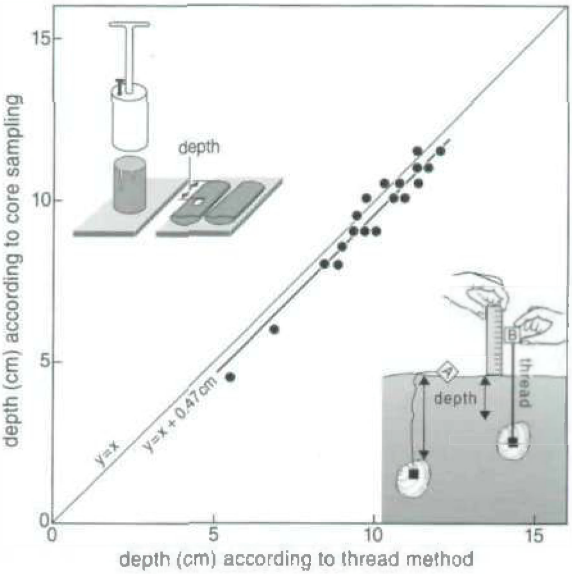


Fig. 1. The depth of 19 *Scrobicularia* measured with a thread, compared with the depth as measured afterwards with the aid of a core sampler: the mean discrepancy (0.47 cm) is shown.

and in winter between 4 and 21 cm. Zwarts & Wanink found that individual *Scrobicularia* having a low siphon weight live at a remarkably shallow depth compared with animals of the same size with a heavy siphon.

This paper describes a field experiment in which the cropping action is simulated by partly removing the inhalant siphon. It will be shown that burying depth of *Scrobicularia* not only depends on the siphon weight after cropping but also on the extent of siphon cropping itself and the body condition.

Materials and methods

Ninety one *Scrobicularia* of similar size (37.1 to 38.3 mm) were collected from a mudflat along the Frisian coast, Dutch Wadden Sea, in July 1982. Of these animals 25 were dissected immediately, separating the inhalant siphon from the body, to determine the ash-free dry weight of each. The other animals were placed in sea water until they exposed their inhalant siphons. Using forceps, portions of the extended inhalant siphons were removed and stored in a freezer to determine dry flesh weight. We tried to cut off small, moderate, and large amounts from an equal number of animals. As controls, some animals were handled, but the siphon was not cut.

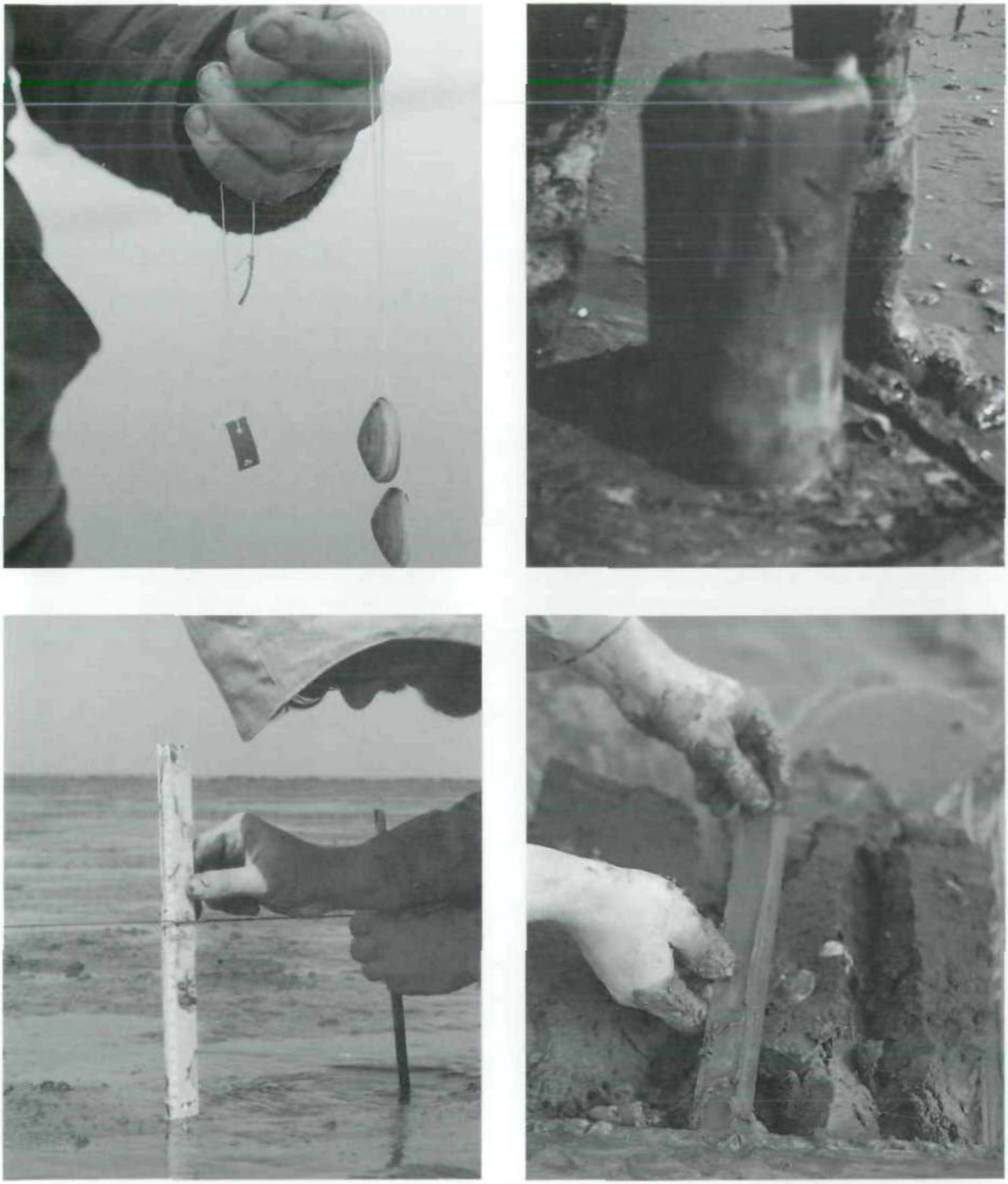
Using adhesive, a nylon thread with a numbered tag was attached to the shell. The animals were re-buried in the mud at the same spot from which they had been collected 8 h before. All were buried at roughly the same depth, i.e. between 4.5 to 6.5 cm (distance from substratum surface to top of shell; see Fig. 1). The depth to which the animal subsequently buried itself was determined every day afterwards for 5 days, by measuring the length of the thread remaining above the surface.

Zwarts & Wanink (1989) measured the depth of the local field population with the aid of a core sampler. This instrument was thrust into the mud, after which the core was extracted, placed horizontally and broken carefully. The core method underestimates the depth by 4 to 5 mm, when it is not taken into account there is a loss of the upper layer of the substratum during the handling of the core (see Fig. 1).

Each day a sample of c. 13 live animals was removed from the substratum. They were dissected, separating the body and the remaining length of the siphon, as described by Zwarts & Wanink (1989). The valves were opened by a short immersion in boil-

Table 1. The siphon weight after part had been removed as a function of the amount removed: mean ± SE and number of bivalves per category are indicated; also given is the total siphon weight, i.e. the sum of the amount remaining and the amount removed; in all cases the mean total amount would be 14 mg if there had been no regeneration; the observed values differ significantly (R^2 = 26.9%; p = 0.0002; n = 66).

	Siphon weight, mg		
n	*Removed*	*Remaining*	*Total*
11	0	14.0 ± 1.0	14.0
10	1 -3	11.5 ± 0.7	13.5
28	4 -6	10.3 ± 0.5	15.3
11	7 -9	8.2 ± 0.7	16.2
4	10-12	9.5 ± 0.7	20.5
2	13-15	7.0 ± 2.8	21.0



Burying depth of bivalves was measured either with thin nylon threads that were attached on the shell with super glue (left photos), or with a core sampler that was thrust into the mud, after which the core was extracted, placed horizontally and broken carefully (right photos)

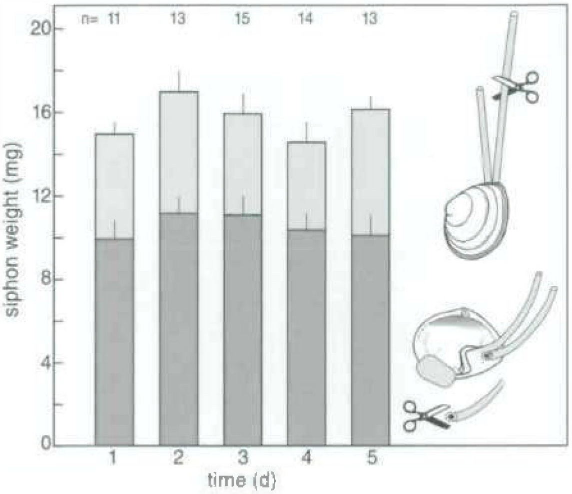


Fig. 2. The weight of the siphon (mean ± SE) of animals (37-38 mm) which were removed from the substratum 1 to 5 days after being buried; number of bivalves indicated; dark area, weight of the remaining siphon; grey area, weight of the removed siphon; time has no effect on the weight of the remaining siphon ($R^2 = 3.2\%$; $p = 0.73$; $n = 66$) nor on the weight of the total siphon (remaining + removed amount) ($R^2 = 8.7\%$; $p = 0.23$; $n = 66$); basic procedure elucidated in the accompanying sketches

ing water. The flesh was dried at 70 °C and burned at 550 °C.

SPSS (Nie *et al.* 1975) was used for all statistical analyses.

Results

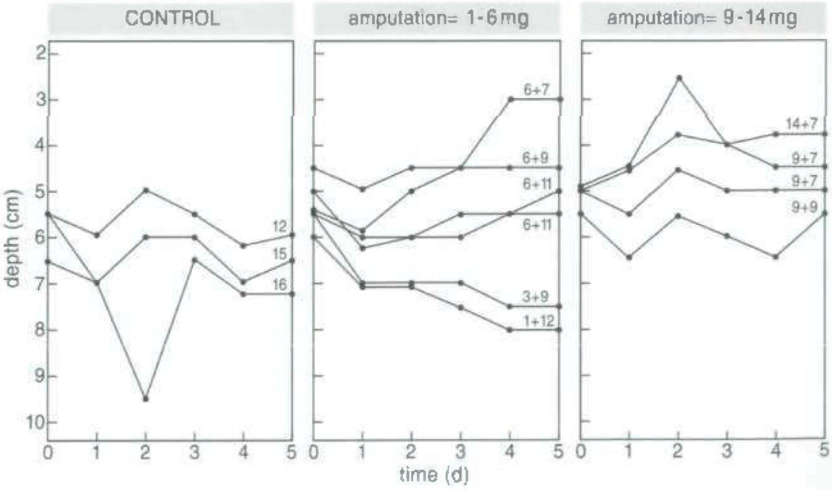
Amputation of the siphon

The siphon weight, as determined 1 to 5 days after the amputation, decreased more when a greater amount had been removed, but not as much as expected assuming an equal siphon weight for all categories before the amputation (Table 1). Two explanations are conceivable: there was regeneration of the siphon, or the initial siphon weights were in fact different.

Regeneration as rapid as this seems an unlikely explanation. Hodgson (1982a) found that *Scrobicularia* are able to regenerate their siphon at a rate of 3% per day and that regrowth starts after a lag of 24 h during which the wound heals. Assuming equal siphon weight before amputation, animals losing ≥ 10 mg would have regenerated c. 6 mg during a growing period of 4 days, i.e. a daily average of 21%. That would be extremely high compared with the rate of 3% measured in several bivalves (Trevallion 1971, Hodgson 1982a). In fact there was no increase in mean siphon weight during the experiment (Fig. 2).

It is much more likely that the experimental cropping was in fact not random. The siphon weight was

Fig. 3. The depth of 13 animals as measured with a thread in the course of 5 days after burial on Day 0; left panel shows the depth of three bivalves whose siphon was left intact; the siphon weight (in mg) on the last day is indicated; the two other panels show the depth of 6 animals from which 1 to 6 mg was removed and four animals which lost 9 to 14 mg; for each individual figures indicate amputated mg + remaining mg in that order.



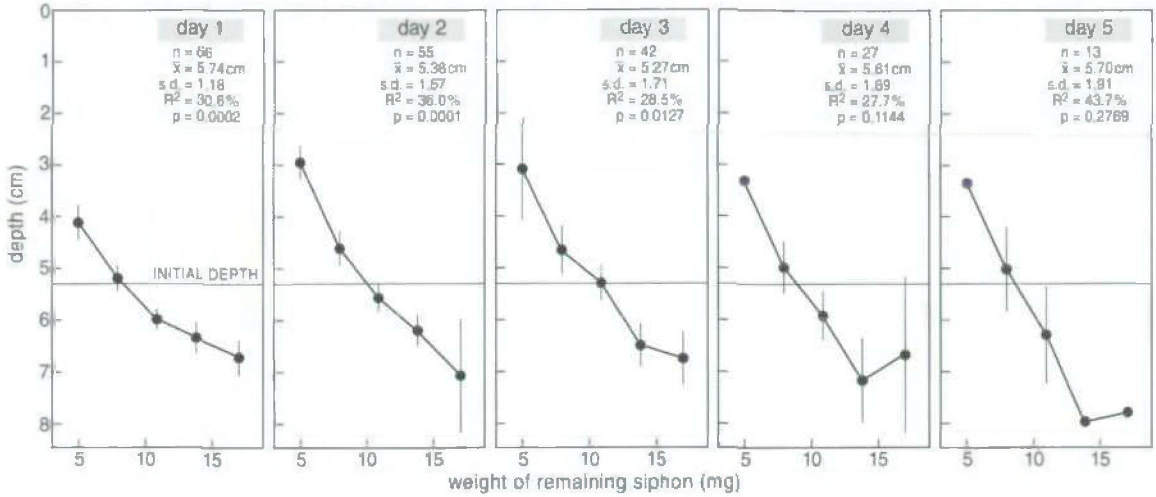


Fig. 4. The depth of animals (37 to 38 mm) with different siphon weights measured during the 5 days after they were buried (on Day 0) at an initial depth of 5.3 ± 0.4 cm (mean ± SD): the results of the five one-way analyses of variance are given.

very variable, ranging from 5 to 18 mg in the 25 animals dissected at the start of the experiment and from 7 to 17 mg in the 11 animals with intact siphons used as controls. It is clear that the animals losing 15 mg of their siphon must have had an initial siphon weight above the average weight.

To conclude, any regeneration during the experiment would have been negligibly small, so one can add the weight of the remaining siphon to the amount cut off to estimate the original total siphon weight.

Siphon weight and burying depth

The burying depth of the natural population of *Scrobicularia* during the experiment averaged 6 cm (n = 656 for the size class 35 to 39 mm). It was our intention to bury all experimental animals at exactly the same depth, but in practice a range of depth (± 1 cm) was achieved.

Figure 3 shows the daily measurements of the depth of a sample of animals during the course of the experiment. *Scrobicularia* were able to change their depth by 1 to 2 cm per day. Heavily cropped animals moved nearer to the surface than the animals losing little or no siphon. On the first day after the onset there was already a large contrast between the burying depths of animals with different siphon weights (Fig. 4). The divergence increased on the second day but re-

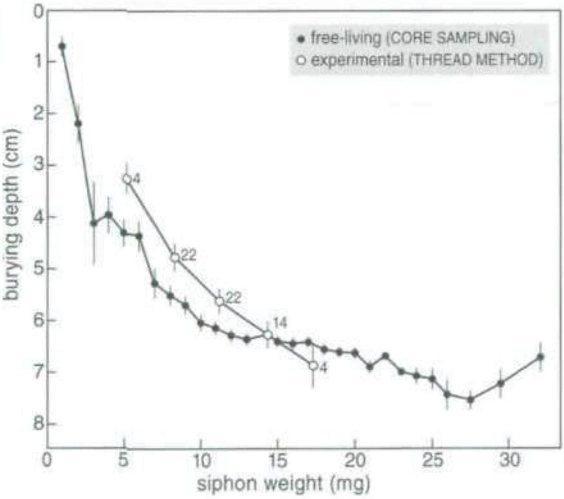


Fig. 5. The depth (mean ± SE) of animals (37 to 38 mm) with different siphon weight: number per category (4 to 6, 7 to 9 mg, and so on) is indicated; one-way analysis of variance: $R^2 = 35.4\%$; $p < 0.001$; also shown for comparison the relationship between depth and siphon weight as measured in free-living animals of the same size (35 to 39 mm) in the summer ($R^2 = 35.4\%$; $p < 0.001$; n = 3063; data from Zwarts & Wanink (1989)).

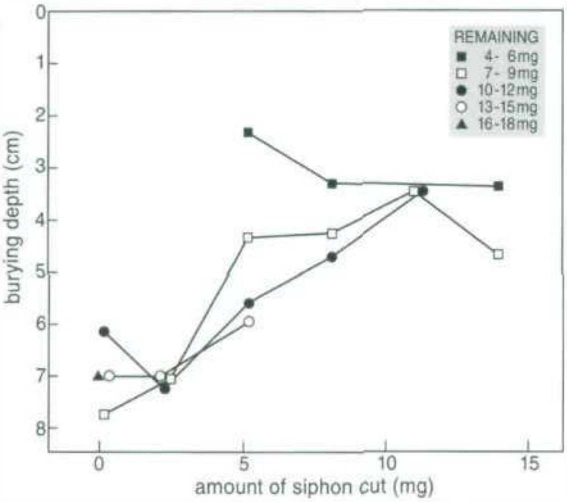


Fig. 6. The depth of animals (37 to 38 mm) as a function of the amount of siphon removed, given for five categories (see key) based on the weight of the remaining siphon; the results of an analysis of variance are given in Table 2.

Table 2. Three-way analysis of variance to test the effect of the amount of the siphon removed (0, 1-3, ... 13-15 mg), the weight of remaining siphon (4-6, ... 16-18 mg), and the time (day 1 ...5) on the depth of the animals (n = 66); see also Fig. 6; the table gives the explained variance (R^2) being unique for each variable; above that 'amount cut' and 'amount remaining' have 30.2% of the total variance in common, which is caused by the logical fact that the siphon from which much was removed, had a lower weight of the remaining siphon (see also Table 1).

	*R*², %	*p*
(a) Amount cut	26.3	0.001
(b) Amount remaining	8.2	0.010
(c) Time	4.6	0.081
(a) × (b)	5.3	0.256
(a) × (c)	7.9	0.159
(b) × (c)	3.0	0.843

mained the same for the next 3 days. The figure is based on all animals, controls inclusive, because, as will be shown lin Fig. 6, the burying depth of the controls did not differ from that of animals having an equal siphon weight after a small part was cut off.

Figure 5 shows the relationship between siphon weight and depth, as calculated for the entire experimental period. Because the siphon weight was determined on the day when the animal was taken from the substratum, the last depth measurement of each animal was used to construct Fig. 5 (and also Fig. 6). An animal having a siphon weight of 4 to 6 mg buried itself, on average, to a depth of 3 cm, whereas bivalves with a siphon of ≥ 13 mg buried themselves to a depth of 6 to 8 cm (Fig. 5). The relation between siphon weight and depth in the experimental animals did not differ from the natural population in the same area.

The extent of cropping, independent of the weight of the remaining siphon, also explains part of the depth distribution (Fig. 6; Table 2). *Scrobicularia* with a remaining siphon weight of 7 to 12 mg occurred at a depth of 4 cm when 7 to 15 mg was cut off, whilst the animals having the same weight of remaining siphon, but with a tissue loss of only 3 mg or less, settled at c. 7 cm.

Siphon weight and body condition

There was a good correlation between body weight and siphon weight in the control group and in the animals which had lost ≤ 9 mg of their siphon (Fig. 7;

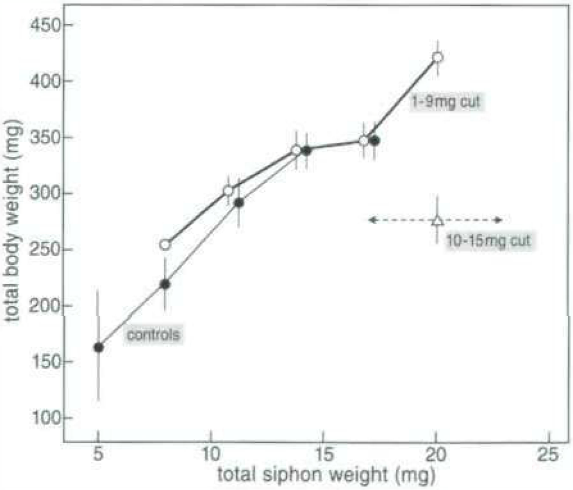


Fig. 7. The dry flesh weight of the body (mean ± SE) as function of the total siphon weight; in the cropping experiments the amount cut was added to the weight remaining; weights are given separately for the 36 controls (●), the 49 animals which lost 1-9 mg of the siphon (○) and the 6 animals from which 10-15 mg was taken, range indicated (Δ); the results of the analysis of variance are given in Table 3.

Table 3. Three-way analysis of variance to test the effect of the weight of the total siphon (4-6, ...22-24 mg), the experimental conditions (0, 1-9, 10-15 mg removed), and time (Day 0 ... 5) on the dry weight of the body (n = 91): see also Fig. 7.

	R^2, %	p
(a) Siphon weight	26.7	0.001
(b) Exp. condition	6.4	0.026
(c) Time	4.1	0.435
(a) × (b)	1.1	0.847
(a) × (c)	4.3	0.977
(b) × (c)	3.2	0.433

Table 3). The animals losing ≤ 9 mg were pooled because the regression of body weight on siphon weight was the same. The body weight was relatively low, however, in the bivalves from which ≥ 10 mg of the siphon was removed. All animals were alive when they were dug up 1 to 5 days after the siphon had been removed.

These results agree with the data collected by Hodgson (1982a) who showed that the energetic cost of regeneration was low when 15% of the siphon was removed but when 50% of more was cut off, regeneration took place at the expense of the body condition. *Some animals in his experiment died, but no information is given about survival and siphon loss.*

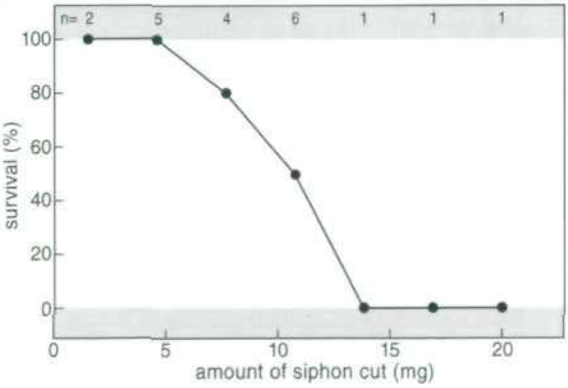


Fig. 8. Survival of *Scrobicularia* (37 mm) kept 2 weeks in an aquarium, in relation to the amount of the siphon removed (after Straat, Wanink & Zwarts unpubl. data).

Direct evidence on the effect of siphon amputation on subsequent survival is available from an experiment where *Scrobicularia* were held in a small aquarium filled with 20 cm mud and sea water for 14 days, without providing food. All animals from which 13 to 19 mg of the siphon weight has been removed were moribund or dead, whilst all animals remained in perfect condition when 0 to 6 mg was taken (Fig. 8).

Siphon weight, burying depth and feeding range

The relationship between depth and siphon weight (Fig. 9A, redrawn from Fig. 5), can be used to calculate the weight per cm of siphon from the upper edge of the shell to the surface, assuming that *Scrobicularia* have to reach the surface (Fig. 9B). It shows that free-living animals with a large siphon live at a depth that allows them 3 mg per cm. Of more interest is the minimum value: animals with a short siphon, although they minimize the distance to the surface, only have available about 1 mg per cm. Assuming that the maximum a feeding siphon can be stretched is 1 or 1.5 mg per cm, it is possible to estimate the potential reach of the inhalant siphon during surface feeding (Fig. 9C).

Linke (1939), Green (1967, 1968), and Hughes (1969) have given extensive descriptions of the feeding behaviour of *Scrobicularia*, but more detailed research is necessary to confirm that the range on the *surface over which the animals can reach really depends* on siphon weight and burying depth, as depicted in Fig. 9C. The model presented in Fig. 9 can, however, be used to derive some predictions.

One prediction is that about half the population will feed within a radius of 5 to 10 cm around the burrow. This can be measured directly, but can also be derived from the length of the starlike feeding tracks which a *Scrobicularia* makes during the sucking of the substratum. The predicted mean value of 5 to 10 cm agrees well with observations of a normal feeding range of 3 to 10 cm (Thamdrup 1935), 4 to 10 cm (Linke 1939) and 5 to 8 cm (Hughes 1969). The maximum feeding range of 20 cm *(Linke 1939) falls just within the predicted* range (Fig. 9C).

It is also to be expected that animals possessing a heavier siphon and thus a larger feeding space, are in a better condition than animals with a short siphon. This was indeed the case in the experimental animals (Fig. 7) as well as in nature; the body weight is 20 to 30%

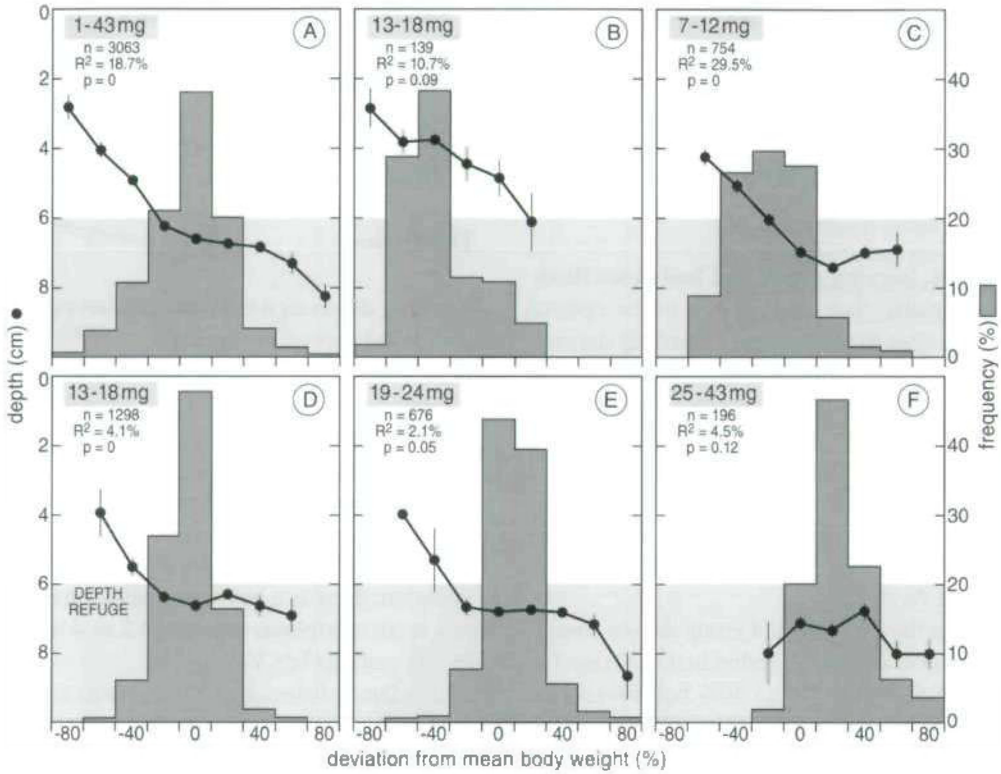


Fig. 11. The depth (mean ± SE) of free-living *Scrobicularia* (35-39 mm) in summer as a function of relative body weight expressed as per cent deviation from mean body weight: the histograms show the frequency distribution of relative body weight. Panel A concerns all animals; the other panels show the same data for different categories of siphon weight (see keys); results of the six one-way analyses of variance are given. Depth refuge (all animals beyond 6 cm) is defined by the bill length of the Oystercatcher, the chief predator.

out of reach of the bird's bill- are safe. Compared with animals living at a depth of 5 or 6 cm, the risk of being taken by an Oystercatcher is c. 6 higher for animals at 3 cm or less. So one would expect that *Scrobicularia* usually remain at a burying depth of at least 6 cm, and this was found to be the case. When the siphon is long enough, i.e. ≥ 10 mg, the average *Scrobicularia* live in summer below this danger line and there is scarcely any increase in burying depth when the siphon weight is three times as large (Fig. 5).

The natural variation in the siphon weight -between 1 and 43 mg for a *Scrobicularia* of 37 mm- is remarkable large, given the importance of a long siphon to attain a depth refuge of at least 6 cm. Figures 10 and 11 show that a short siphon alone does not force *Scrobicularia* to leave the depth refuge; only if animals are also in a poor body condition will they need to expose themselves to a larger risk of predation by approaching the surface.

Most *Scrobicularia* that have grown past the limit of 25 mm shell length live the greater part of the year at a depth of 6 cm of more, and are thus inaccessible to predators (Wanink & Zwarts 1985, Zwarts & Wanink 1989). Siphon cropping by juvenile flatfish in spring (Kuipers 1977, de Vlas 1979a) and by shrimps, Shore Crabs, and gobies in summer (de Vlas 1985) might be one of the reasons why c. 40% of the population in spring and summer lives above its depth refuge, i.e. at a depth of 6 cm or less, compared with nearly none during the rest of the year (Zwarts & Wanink 1989). Siphon cropping in summer might thus create a food supply within the reach of the birds' bills.

Chapter 4

SIPHON SIZE AND BURYING DEPTH IN DEPOSIT- AND SUSPENSION-FEEDING BENTHIC BIVALVES

Leo Zwarts & Jan Wanink

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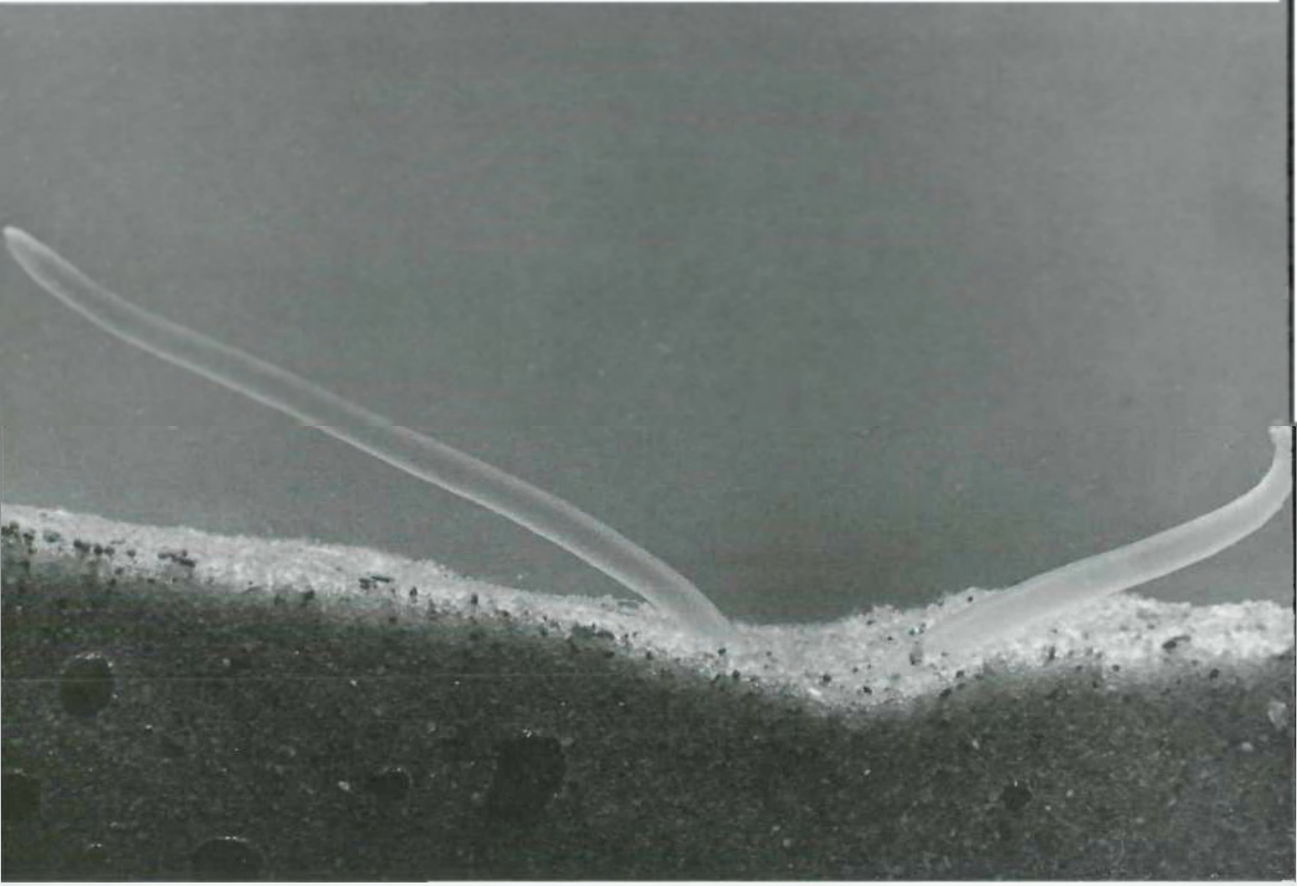

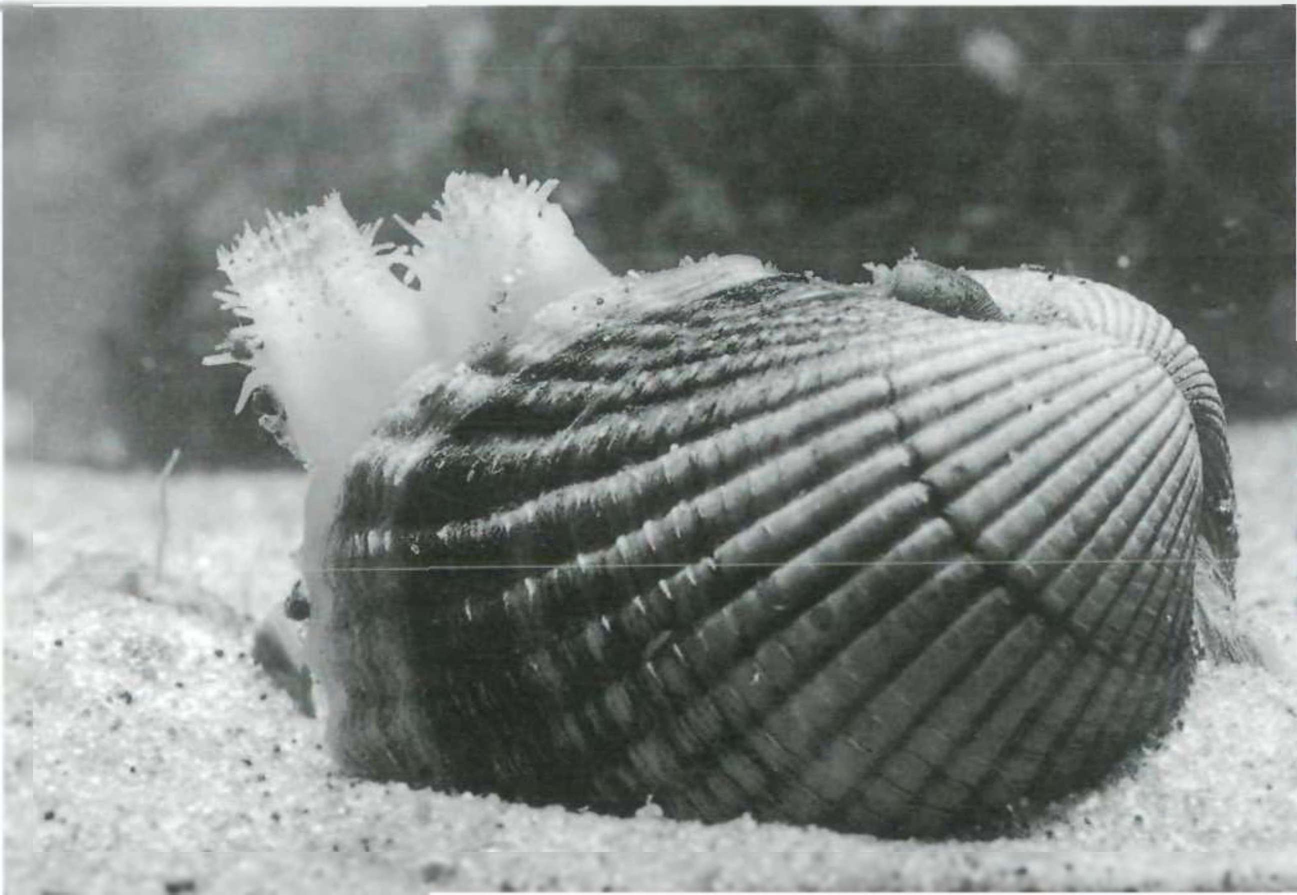

SIPHON SIZE AND BURYING DEPTH IN DEPOSIT- AND SUSPENSION-FEEDING BENTHIC BIVALVES

This paper analyses the significance of siphon investment in the life strategy of benthic bivalves. It describes the relationships between siphon weight, burying depth and shell size in *Mya arenaria*, *Cerastoderma edule*, *Scrobicularia plana* and *Macoma balthica*. All data were collected on an intertidal flat in the Dutch Wadden Sea during seven successive winter and summer periods. The four species have in common that (1) the increase of depth in relation to size can be described with an S-curve; (2) there is a linear relationship between log siphon weight and log shell size; (3) siphon investment is maximal for the size classes with the greatest increase in their depth; (4) siphon weight, in proportion to total body weight, decreases gradually for the larger size classes whose depth does not increase; (5) burying depth increases with siphon weight if individuals within a same size class are compared, but burying depth levels off above a certain siphon weight. *Macoma* and *Scrobicularia* live twice as deep in winter as in summer, although siphon weight for both seasons is about the same. In summer both species use a part of the siphon to graze the surface around the burrow, whereas deposit feeding does not occur in winter. This might explain the seasonal variation in burying depth. On the other hand *Cerastoderma* and *Mya*, which are both suspension feeders, show hardly any increase of depth in winter as compared to summer. For benthic bivalves the risk of being taken by a predator decreases with depth. The burying depth levels off where individuals reach the depth refuge (though in winter *Scrobicularia* live at greater depth). The conclusion is that siphon size is one of the main factors determining the burying depth of benthic bivalves and thus plays a critical role in their survival.

Introduction

It must be an essential part of the life-strategy of estuarine macrozoobenthos to select a burying depth which guarantees maximal survival and high offspring numbers. The deeper the burrow, the lower the risk of being washed out (Baggerman 1953, Kristensen 1957, Matthiesen 1960, Breum 1970, Hughes 1970a, Mosher 1972, Hulscher 1973, Ratcliffe *et al*. 1981, Sutherland 1982a), of being exposed to extreme temperatures (Thamdrup 1935, Brafield 1964, Johnson 1965, de Wilde 1975, de Wilde & Berghuis 1979a, Ratcliffe *et al*. 1981) or of being taken by a predator.

Predation risk is maximal for infauna living near the surface, because (with some exceptions e.g. some predatory worms) predators creep or walk on the surface or swim above it and do not usually dig for prey. Exclosure experiments show that the predation pressure on shallow-living species is much higher than on species, which bury deeper (Virnstein 1979, Holland *et al*. 1980, Reise (1985). Moreover, it has been shown that within species individuals living at greater depth in the substrate experience a decreased risk of being eaten by a predator (Table 1).

If a deep burrow offers a safe refuge, there must be

Table 1. Studies showing that predation risk of benthic animals decreases for individuals living at greater depth.

Predator	*References*
Starfish	Kim 1969, van Veldhuizen & Phillips 1978, Allen 1983
Crab	Reise 1979, Virnstein 1979, Blundon & Kennedy 1982b, Pearson *et al*. 1981, Haddon *et al*. 1987
Snail	Commito 1982
Fish	Kelso 1979
Shrimp	Reise 1978
Bird	Myers *et al*. 1980, Zwarts & Wanink 1984, Richardson 1985, Wanink & Zwarts 1985

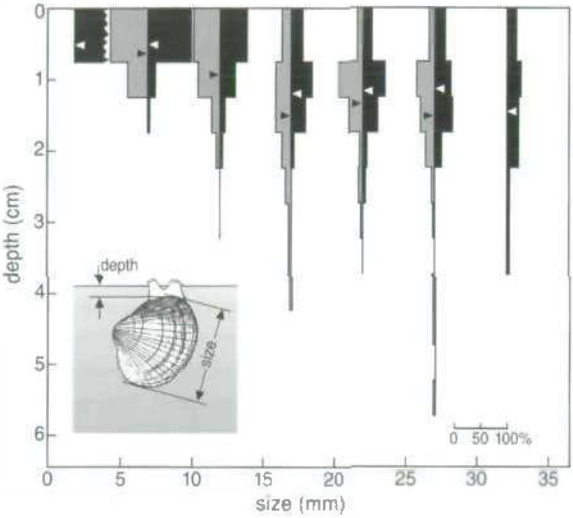

Fig. 3. *Cerastoderma edule*. Frequency distribution of depth per size class in winter (grey histograms; n = 453) and in summer (black histograms; n = 835). Mean depth indicated. Table 2 gives statistical analysis.

ber-March) and a summer period (July to September) during which, according to a preliminary analysis, the bivalves remained at a similar depth. SPSS (Nie *et al.* 1975) was used for all statistical analyses.

Results

Burying depth and shell size

The depth measurements of *Mya* are given in Fig. 2. The relation between burying depth and shell size can be described by an S-curve. *Mya* < 10 mm live in the upper 2 cm of the substrate. They increase their depth when they grow from 10 to 40 mm and remain at the same depth level when > 50 mm. In winter *Mya* live 10% deeper than in summer.

Cerastoderma remain near the surface, but there is an increase of depth with size and their burying depth in winter is larger than in summer (Fig. 3).

Large *Macoma* live deeper in the substrate than smaller ones, but the depth remains the same for all animals > 10 mm (Fig. 4). In summer *Macoma* > 10 mm live at a depth of 2 cm compared to an average of 5 cm in winter.

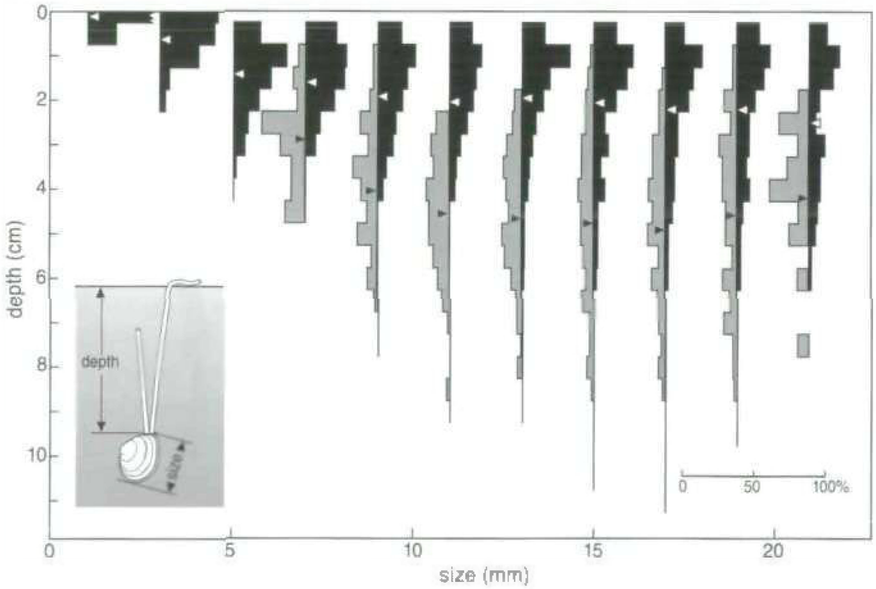

Fig. 4. *Macoma balthica*. Frequency distribution of depth per size class in winter (grey histograms; n = 1609) and in summer (black histograms; n = 6711). Mean depth indicated. Table 2 gives statistical analysis.

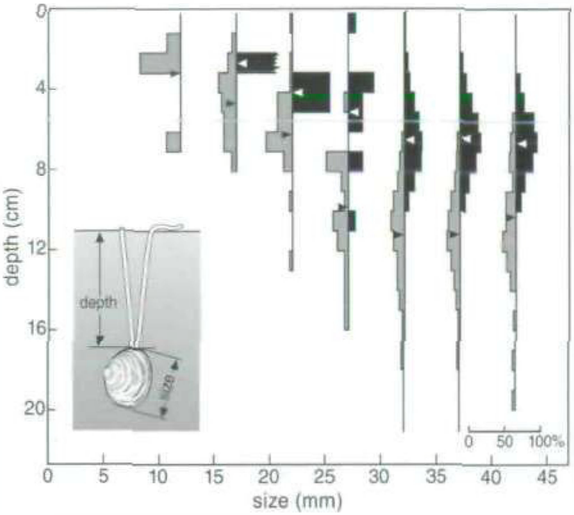

Fig. 5. *Scrobicularia plana.* Frequency distribution of depth per size class in winter (grey histograms; n = 3082) and in summer (black histograms; n = 5254). Mean depth indicated. Table 2 gives statistical analysis.

Scrobicularia which pass the limit of 30 mm remain at about the same depth, 6 cm in summer and 11 cm in winter (Fig. 5). Depth increases with size in the range of 10 to 30 mm length. Smaller individuals were not found because there was no new spatfall during the study period.

The depth/size relationship is significant in all four species (Table 2). There is a large difference between winter and summer depth in the deposit feeders, *Macoma* and *Scrobicularia*, but not in the suspension feeders, *Mya* and *Cerastoderma*. In all species there is remarkable variation in burying depth for a given size class, especially in the two deposit-feeding species.

Body weight, siphon weight and shell size

The increases of siphon weight and total body weight with size in the four species are shown in Fig. 6. There is a large variation in body and siphon weight on different sampling dates within the summer and winter periods, which explains why the exponential increase of body weight with size does not have as perfect a linear correspondence on a log-log scale as it does for each sampling date separately.

The increase of siphon weight with size is also exponential for all four species, though there is a levelling off in the siphon weight for the larger individuals (Fig. 6).

Burying depth and siphon weight

Siphon weight was measured instead of siphon length since length is very difficult to measure. Chapman & Newell (1956) showed that the siphon of *Scrobicularia* is elastic in nature: the siphon can be stretched more with a same amount of siphon mass by proportional thinning of the siphon wall (see also Hodgson & Trueman 1981). This elasticity of the siphon probably also occurs in *Macoma*. According to Zwarts *et al.* (1994) the siphon of this species can be stretched more if its weight is low. Average siphon weight and shell length appeared to be well correlated.

Vassallo (1971), Reading & McGrorty (1978) and Ratcliffe *et al.* (1981) suggested that the increase of depth with size in *Macoma* can be attributed to the increase of siphon length and thus siphon weight. The question, however, remains whether it is the increment of siphon weight that determines the observed relationship between burying depth and shell size. Indeed, burying depth as well as siphon weight increase with shell size (Figs. 2-5 and Fig. 6, respectively) but the in-

Table 2. Results of 4 two-way analyses of variance (ANOVA) to test effect of shell size and season on depth distribution (same data as in Figs. 2-5).

Species	*Size*		*Season*		*Size × Season*		*n*
	R^2, %	*p*	*R^2, %*	*p*	*R^2, %*	*p*	
Mya arenaria	76.4	0.001	0.6	0.001	0.7	0.001	2528
Cerastoderma edule	21.3	0.001	0.7	0.001	1.3	0.002	1288
Macoma balthica	1.8	0.001	33.3	0.001	0.4	0.001	8320
Scrobicularia plana	5.1	0.001	50.2	0.001	0.2	0.001	8336

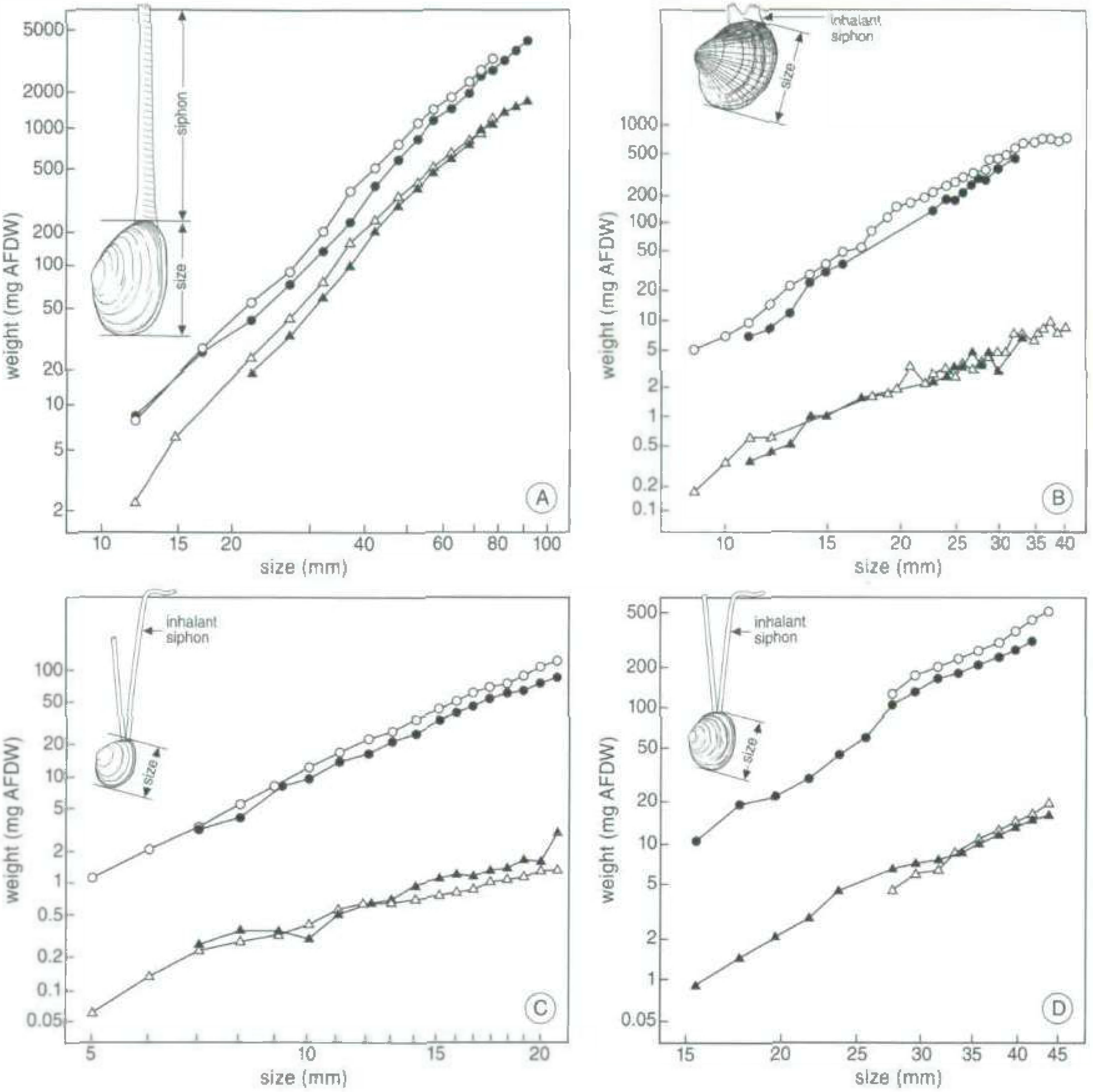

Fig. 6. Total body weight (mg AFDW) in winter (●) and in summer (○) and siphon weight (mg AFDW) in winter (▲) and in summer (△) as a function of shell size for **A.** *Mya arenaria* **B.** *Cerastoderma edule* **C.** *Macoma balthica* and **D.** *Scrobicularia plana*. Number of cases for body weight in winter and in summer, and siphon weight in winter and summer, respectively: **A.** 826, 1339, 173 and 1059; **B.** 461, 1218, 30 and 207; **C.** 880, 6593, 416 and 2284; **D.** 3082, 5254, 1989 and 4189.

crease of siphon weight might also be caused by its larger thickness, as will be shown below.

By comparing individuals of a same size class, one can rule out variations in siphon diameter leaving siphon weight as a better predictor for siphon length. *Cerastoderma* are not considered here because of the small variation in depth.

For *Scrobicularia* we selected the size class with the largest number of measurements (35 to 39 mm). An individual within this size class having less than 5

Table 3. Results of 2 two-way analyses of variance (ANOVA) to test effect of siphon weight on burying depth of individuals within a similar size class (same data as in Figs. 7-8).

Species	*Siphon*		*Season*		*Siphon* × *Season*		*n*
	R^2, %	*p*	R^2, %	*p*	R^2, %	*p*	
Macoma balthica	18.0	0.001	12.8	0.001	0.5	0.034	2077
Scrobicularia plana	5.9	0.001	55.1	0.001	0.5	0.001	4313

mg siphon mass increases its depth 1 cm for each extra mg in summer and 2 cm per extra mg in winter (Fig. 7, Table 3), so depth and siphon weight are proportional within that range. If the siphon weight, however, is more than 5 mg, a depth of 6 to 7 cm in summer and 10 to 12 cm in winter is maintained. There is scarcely any increase in burying depth if the siphon is 10 or 20 mg.

The relationship between burying depth and siphon weight in *Macoma* (Fig. 8) is the same as in *Scrobicularia* (Fig. 7), with one remarkable difference. All large *Scrobicularia* having no extremely low siphon weight, live at the same depth in summer as well as in winter (Figs. 5 and 7). This is also the case with large *Macoma* during the winter, but not in summer. Most large *Macoma* then live at 2 cm (Fig. 4), but individuals with a heavy siphon enlarge their depth to nearly 5 cm, which is their usual depth in winter (Fig. 8).

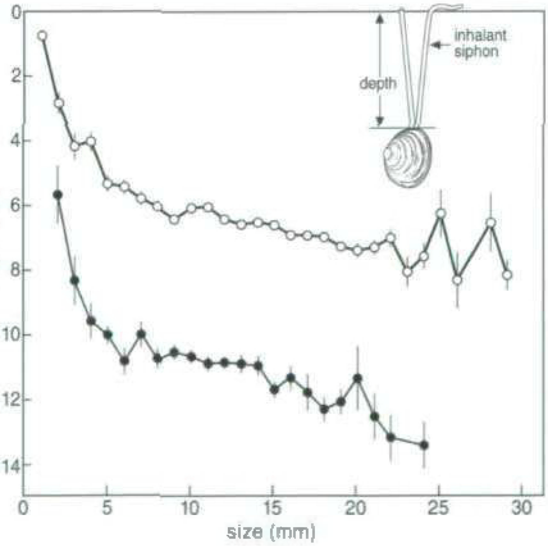

Fig. 7. *Scrobicularia plana* (35-39 mm). Burying depth (cm ± SE) in winter (●; n = 1253) and in summer (○; n = 3060) as a function of weight of inhalant siphon. Table 3 gives statistical analysis.

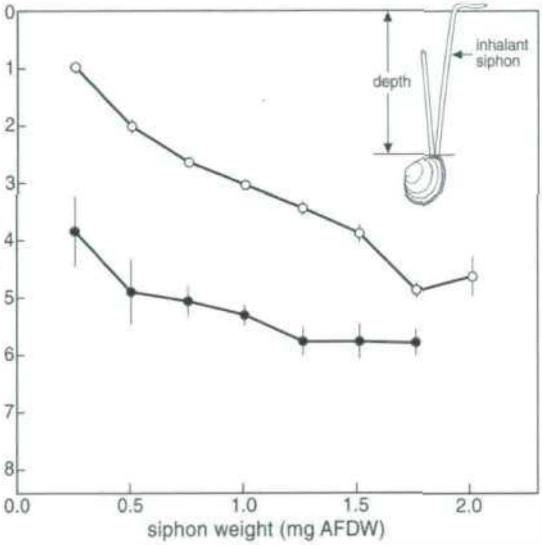

Fig. 8. *Macoma balthica* (10-22 mm). Burying depth (cm ± SE) in winter (●; n = 225) and in summer (○; n = 1852) as a function of weight of inhalant siphon. Siphon weights increase with size within the range selected. That is why all siphon weights are transformed into the siphon weight of a 15-mm individual. Table 3 gives statistical analysis.

It was possible to select three size classes with sufficient data to analyse the relation between siphon weight and depth in *Mya* (Fig. 9). Depth increases within each size class if the siphon is heavier, but size classes with a similar siphon weight are compared, it is found that smaller individuals bury deeper than larger ones. The explanation for this is indicated in Fig. 10: the siphon diameter of *Mya* increases with shell size;

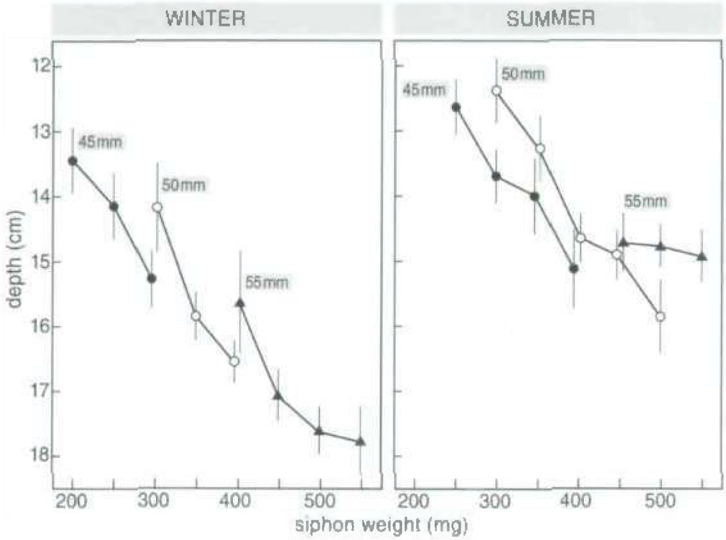

Fig. 9. *Mya arenaria*. Burying depth (cm ± SE) of three size classes as a function of siphon weight in winter (left panel; n = 246) and in summer (right panel; n = 321).

thus larger individuals use more siphon weight per unit length.

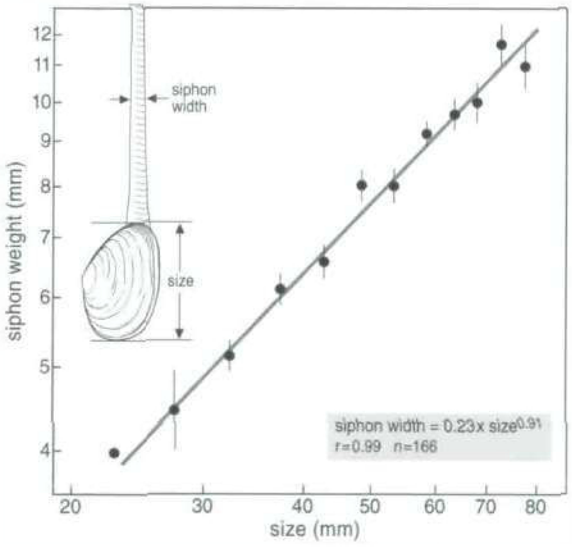

Fig. 10. *Mya arenaria*. Width of the siphon (mm ± SE) as a function of shell size.

Discussion

Burying depth and shell size

The depth/size relation of *Mya* (Fig. 2) corresponds with the qualitative descriptions given for the German and Danish Wadden Sea (Thamdrup 1935, Linke 1939, Kühl 1951, 1981) and with the data from California (Vassallo 1971) and the eastern coast of North America (Blundon & Kennedy 1982b).

Quantitative data of the burying depth of *Cerastoderma* were not found in the literature, but descriptions given by Thamdrup (1935), Linke (1939), Baggerman (1953), Kristensen (1957), Jackson & James (1979) correspond with Fig. 3.

Reading & McGrorty (1978) and Ratcliffe *et al.* (1981) measured the depth of *Macoma* on the English East Coast. They used the 'slice technique', but when a correction is made (see Materials and Methods), their depth/size relationship agrees with the depth measurements on Schiermonnikoog, the Dutch Wadden Sea (Hulscher 1973) and with our data: they found spat (< 4 mm) in the upper one cm during the whole year, whereas the large *Macoma* (8 to 15 mm) burrowed at 1 to 3 cm in summer and at c. 4 cm in winter. *Macoma* bury deeply along the North American coast, compared to their European conspecifics. The depth/size relationship, such as determined during the summer in San Francisco Bay (Vassallo 1971), looks like the winter curve in Fig. 4. Blundon & Kennedy (1982b) found individuals of 7 to 10 mm at no less than 5 to 10 cm in the Chesapeake Bay during the summer. *Macoma* which reach a size of 30 to 40 mm in the southern part of their American distribution area (Beukema & Meehan 1985) are also buried at very great depth: 10 to 35 cm (Vassallo 1971, Blundon & Kennedy 1982b).

Hughes (1970a) who measured the winter depth of *Scrobicularia* on a mudflat in Wales, found spat of 3 to 4 mm at a depth of 1 to 3 cm. His other measurements -individuals of 16 mm at 4 to 6 cm and the size class > 25 mm at 6 to 18 cm- correspond with our findings (Fig. 5).

Body weight, siphon weight and shell size

The body weight/size relationship in Fig. 6 corresponds with the already published data on *Mya* (Munch-Peterson 1973, Warwick & Price 1975, Möller & Rosenberg 1983), *Cerastoderma* (Hibbert 1976, Hancock & Franklin 1972, Chambers & Milne 1979, Newell & Bayne 1980, Sutherland 1982a, Möller & Rosenberg 1983), *Macoma* (Chambers & Milne 1975a, Beukema & de Bruin 1977, Bachelet 1980, Cain & Luoma 1986) and *Scrobicularia* (Hughes 1970b).

Hodgson (1982a) found the same siphon weights for *Scrobicularia* as shown in Fig. 6D. The relationship between siphon weight and shell size in *Macoma* (Fig. 6C) agrees closely with Pekkarinen (1984), but the siphon weights given by Reading & McGrorty (1978) are much larger than the 1-2 mg found by Pekkarinen (184), de Vlas (1985) and this study.

Mya invest 40 to 50% of their body weight in siphon mass (Fig. 12). That is extreme compared to the other three species, even if it is taken into account that the inhalant and exhalant siphon of *Mya* are fused, whereas they are separate in the other three species (Fig. 1). The weight of the exhalant siphon of *Scrobicularia* is 70% relative to its inhalant siphon (Zwarts unpubl.), which means that the weight of the inhalant and exhalant siphon equals 8 to 9% of the total body weight. The siphon weight of *Mya* is thus 4 to 5 larger than for *Scrobicularia*.

In the most shallow-living species, *Cerastoderma*, the relative weight of the inhalant siphon is minimal, viz. 1 to 2%. *Macoma* invest 1 to 4% of their body weight and *Scrobicularia* c. 5%. Comparing the four species, one sees a clear correlation between deeper burying depth and the increase of siphon weight in proportion to total body weight.

Burying depth and siphon weight

It is clear that burying depth depends to a large degree on siphon weight, as was already shown by Zwarts (1986) who manipulated the burying depth of *Scrobicularia* by reduction of the siphon weight. Burying depth is, however, not proportional to siphon weight (Figs. 7-9), a fact for which three explanations can be given. First, depth is not proportional to siphon weight because the relation between length and weight is also not proportional: the siphon is stretched more if its mass is less (Zwarts *et al.* 1994). Second, there is still some variation in siphon diameter when animals of a similar size class are compared (Fig. 10) so that, on the average, a heavy siphon might be thicker. Third, it is likely that deposit feeders with a relatively heavy siphon extend a greater part of their siphon out of their burrow to graze the surrounding surface (Zwarts 1986).

Suspension feeders like *Mya* and *Cerastoderma* do not extend their siphon far above the surface, which means that burying depth depends mainly on siphon length. The decision to select an optimal depth is more complex for deposit feeders like *Macoma* and *Scrobicularia*, since a part of their siphon is extended to graze the surrounding surface. The radius for deposit feeding in fact equals total siphon length minus burying depth, and hence a reduction of burying depth enlarges the surface for deposit feeding. For deposit feeders burying depth is a compromise between feeding and avoidance of predation. This trade-off is influenced by body condition in *Scrobicularia* (Zwarts, 1986): animals with a small siphon remain at larger depth if they are heavy, possibly because they are able to survive a period during which the feeding radius is limited. Individuals in poor condition have no choice and reduce their depth to increase their feeding opportunity, thus accepting an enlarged predation risk (Fig. 11B).

Macoma and *Scrobicularia* do not rely on deposit feeding only, for they are able to filter food from the

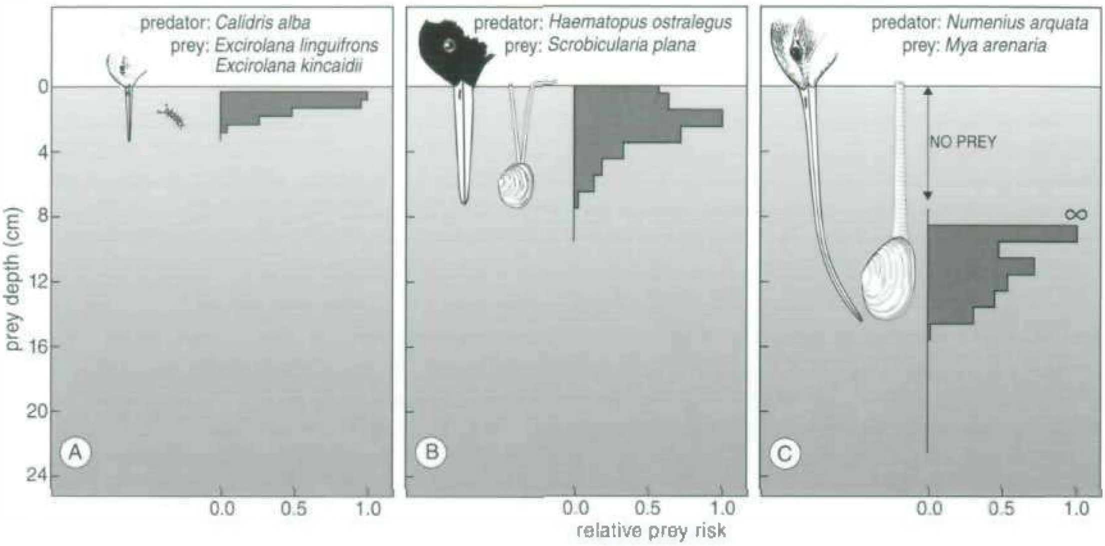

Fig. 11. Predation risk as a function of burying depth in three different studies: **A.** Sanderling *Calidris alba* preying on beach crustaceans (Myers *et al.* 1980). **B.** Oystercatcher *Haematopus ostralegus* feeding on a benthic bivalve (Wanink & Zwarts 1985) and **C.** Curlew *Numenius arquata* feeding on benthic bivalve (Zwarts & Wanink 1984). Prey risk is expressed in relation to the maximal predation risk of a single size class (set to 1); ∞ indicates a shallow prey taken by a Curlew, but not occurring in the sampling programme, resulting in an infinitely large prey risk.

overlying water while the siphon is just at the surface (Brafield & Newell 1961, Hughes 1969, de Wilde 1975, Earll 1975, Hummel 1985a). *Macoma* take deposit at a maximum of 4 to 6 cm from their burrow (Brafield & Newell 1961, Gilbert 1977) and *Scrobicularia* up to 10 cm (Thamdrup 1935, Hughes 1969) or even 20 cm (Linke 1939). Both species might be able to double their burying depth by shifting from deposit feeding to filter feeding. Since filter feeding is limited to the immersion period and deposit feeding can occur during immersion as well as during emersion, a vertical movement within a tidal cycle might be expected, as suggested by Yonge (1953). No evidence, however, was found for this in our laboratory (unpublished data) when we measured continuously the burying depth of individual *Macoma* with the aid of thin nylon threads, which connected the shells with a registration apparatus.

It is likely that the remarkable difference between the summer and winter burying depths of *Macoma* and *Scrobicularia* (Figs. 4 and 5) can be explained by the absence of deposit feeding in winter (Linke 1939, Hughes 1969, Hummel 1985a). Individuals with a similar siphon weight live 2-3 times as deep in winter as in summer (Figs. 7 and 8). The siphon weights in *Scrobicularia* are about the same in both seasons (Fig. 6D), whereas for *Macoma* the siphon is 35% heavier during winter than in summer (Fig. 6C), so that most individuals of both species are able to live at greater depths in the non-feeding season (Figs. 4 and 5). The relatively low siphon weight of *Macoma* during the summer can be attributed to heavy siphon cropping by fishes, crabs and shrimps (de Vlas 1985). It would be of interest to know to what degree the occurrence of suspension feeding during the summer in *Macoma* (Hummel 1985a) is caused by the reduction of siphon size.

The suspension feeders *Mya* and *Cerastoderma* remain at nearly the same depth during the whole year: *Cerastoderma* burrow to a 20% greater depth in winter than in summer (Fig. 3) and in *Mya* the difference is only 10 to 15% (Figs. 2 and 9).

Burying depth as a protection against predation

The relationship between burying depth and size can be described with an S-curve (Figs. 2-5). Burying

Tabel 4. Overview of existing knowledge about observed depth and size selection by different bird species on European tidal flats. Actual measurements on depth selection are rare. Figures given are derived from bill lengths, which seem to be a good predictor for exploited depth layer, although prey just within reach are rarely taken (Fig. 11).

Prey species taken by bird species	*Depth, cm*	*Size, mm*	*Sources*
Scrobicularia plana			
Haematopus ostralegus	7	?-max.	Hughes 1970a, Wanink & Zwarts 1985
Mya arenaria			
Haematopus ostralegus	7	> 17	Zwarts & Wanink 1984
Numenius arquata	14	> 30	Zwarts & Wanink 1984
Cerastoderma edule			
Calidris canutus	3	< 10	Goss-Custard *et al.* 1977b
Tringa totanus	4	< 7	Burton 1974
Somateria mollissima		< 30	Swennen 1976
Haematopus ostralegus	7	> 20	Hulscher 1976, Goss-Custard *et al.* 1977b, Sutherland 1982c
Macoma balthica			
Calidris alpina	3	3- 7	Worrall 1984
Tringa totanus	4	8-12	Goss-Custard 1969, Goss-Custard *et al.* 1977, Blomert & Zwarts unpubl. data
Calidris canutus	3	8-15	Prater (1972), Goss-Custard *et al.* 1977b, Zwarts & Blomert (1992)
Limosa lapponica	7-10	8-18	Goss-Custard *et al.* 1977b
Haematopus ostralegus	7	> 10	Goss-Custard *et al.* 1977b, Hulscher 1982

depth levels off for all four species when they reach a size which equals about 50% of their maximum size. The burying depth levels off at 1 to 2 cm in *Cerastoderma* and at 16 to 18 cm in *Mya*. It is different for summer and winter in the two deposit feeders: *Macoma* (2 and 5 cm, respectively) and *Scrobicularia* (7 and 11 to 12 cm, respectively).

As shown in Fig. 11, a deep burrow guarantees maximal survival and below a certain level predation risk is nil. We will analyse in this section whether the observed depth curves level off below which there is no predation ('depth refuge'). Since the depth refuges are determined by the predators which can probe at maximal depths, we will focus our attention on long-billed bird species (Table 4).

Invertebrate predators play no part in the predation on bivalves just beyond their depth refuges. Shrimp *Crangon crangon*, Shore Crab *Carcinus maenas*, Plaice *Pleuronectus platessa* and Flounder *Platichthys flesus* select the smaller bivalves present in the upper layer of the substrate. Their size selection is well documented for *Mya* (de Vlas 1979a, Pihl 1982, Jensen & Jensen 1985) and for *Cerastoderma* (Hancock & Urquhart 1965, de Vlas 1979, Pihl 1982, Möller & Rosenberg 1983, Pihl & Rosenberg 1984, Sanchez-Salazar *et al.* 1987a). The depth of the feeding holes made by Flounders is less than 2 to 3 cm (Summers 1980). Larger fish, such as the Cownose Ray *Rhinoptera bonasus*, are able to plough deeper while digging for large *Mya* (Orth 1975), but such large fish are not found in the tidal zone along the NW. European coast. Shore Crabs are also able to dig for prey. They make pits with a diameter of maximal 15 cm and sometimes also 15 cm deep (Smith & Chin 1953, Ropes 1968, Lindsay & Savage 1978). These observations from the American East Coast have not been duplicated for European tidal flats and it has also never been observed in our study area.

The Oystercatcher *Haematopus ostralegus* is the chief predator of large *Scrobicularia* (Hughes 1970a, Zwarts & Wanink 1996). It does not take individuals below a depth of 7 cm (Wanink & Zwarts 1985). The prey risk for an animal at a depth of 4 to 6 cm, though within the reach of the bird's bill, is much less than for an individual living near the surface (Fig. 11B). Optimal foraging theory (Krebs *et al.* 1983) offers the explanation: deep-living prey are ignored because handling time increases with depth, which makes them less profitable (Wanink & Zwarts 1985). *Scrobicularia* > 30 mm live the greater part of the year below a danger line of 4 to 6 cm (Fig. 5) and in fact individuals must have a poor condition as well as a low siphon weight before they expose themselves to a higher predation risk (Zwarts 1986). The conclusion is that in summer the 'average' *Scrobicularia* remain just below the danger line, but that from a point of view of minimization of predation risk there is no need to nearly double the burying depth in winter. This suggests that other factors may be involved in determining burying depth.

The Oystercatcher is also an important predator for large *Mya*, but it is the Curlew *Numenius arquata* which causes a high mortality among individuals living in the upper 14 to 15 cm (Fig. 11C). Oystercatchers select *Mya* > c. 17 mm from the upper 5 to 6 cm, while Curlews take *Mya* > 30 mm present in the upper 14-15 cm (Zwarts & Wanink, 1984). There is thus a small overlap in size and depth classes preyed upon by both bird species. When the part of *Mya* which is vulnerable to predation by Oystercatchers or Curlews is compared to the depth distribution (Fig. 2), it is clear that risk to be taken by an Oystercatcher or a Curlew is maximal for *Mya* of c. 25 mm and 35 to 45 mm, respectively, which closely resembles the observed size selection (Zwarts & Wanink 1984). It could also be shown that Oystercatchers and Curlews exert a heavy predation pressure on *Mya* > 2 cm, which makes it reasonable to assume that the depth/size curve is determined partly by Oystercatchers and Curlews creaming off the individuals living in the upper 6 and 14 cm respectively. Most animals > 50 mm live out of reach of all predators present on the intertidal flats.

Cerastoderma, unlike *Scrobicularia* and *Mya*, remain within reach of most of their predators during their life-time, but by growing, they get rid of many of them. Knot *Calidris canutus* prey upon *Cerastoderma* < 10 mm (Goss-Custard *et al.* 1977b, Ens unpubl. data), because the profitability of the prey increases with size (Sutherland 1982c).

Macoma have, like *Cerastoderma* and *Mya*, many different enemies during the first stage of their life. Five wader species, which are abundant on the intertidal flats from late summer till spring, are the chief predators for *Macoma* which have survived their first summer (Table 4). In winter most *Macoma* > 10 mm live out of reach of Dunlin *Calidris alpina*, Redshank *Tringa totanus* and Knot (Reading & McGrorty 1978), but a small number of the larger animals remain present in the upper 3 cm (Fig. 4) and hence available for these short-billed waders. They are, however, ignored even by the Bar-tailed Godwit *Limosa lapponica* with its longer bill. It is very likely that gape width determines the upper limit of acceptable prey size.

Contrary to the other waders, which swallow *Macoma* whole, the Oystercatcher takes the flesh out of the shell after hammering the shell or prising the bill between the valves (Hulscher 1982). This species selects *Macoma* > 10 mm (Goss-Custard *et al.* 1977b, Hulscher 1982). Large *Macoma* have thus to reckon with Oystercatcher and Bar-tailed Godwit as the only predators. It is still unknown from which depth layer the prey are actually taken by these waders, but if the profitability of the prey decreases with depth as shown for Oystercatcher feeding on *Scrobicularia* (Wanink & Zwarts 1985), it is also likely that with large *Macoma* the predation risk is maximal for those animals living in the upper 3 to 5 cm.

In winter, the depth of *Macoma* levels off at 4 to 5 cm (Fig. 4) and animals with a heavy siphon enlarge their depth till they reach a depth of c. 4.5 cm (Fig. 8). This suggests that also in summer the depth refuge is 4-5 cm, but that the reduced siphon size and the need to feed force most *Macoma* to move nearer to the surface.

The general conclusion is that benthic bivalves which attain a safe depth refuge do not increase their burying depth anymore. The great winter depth of *Scrobicularia* deserves another explanation. On European flats, large *Mya* have to deal with Curlews as their only predator and large *Macoma* with Oystercatchers and Bar-tailed Godwits only. That is why the upper limit of the depth refuge is set for both species at c. 14 and c. 4 cm, respectively. The Blue Crab *Callinectes sapidus* is an important predator for both species in Chesapeake Bay (e.g. Virnstein 1977, Blundon & Kennedy 1982b). Large Blue Crabs are able to crack

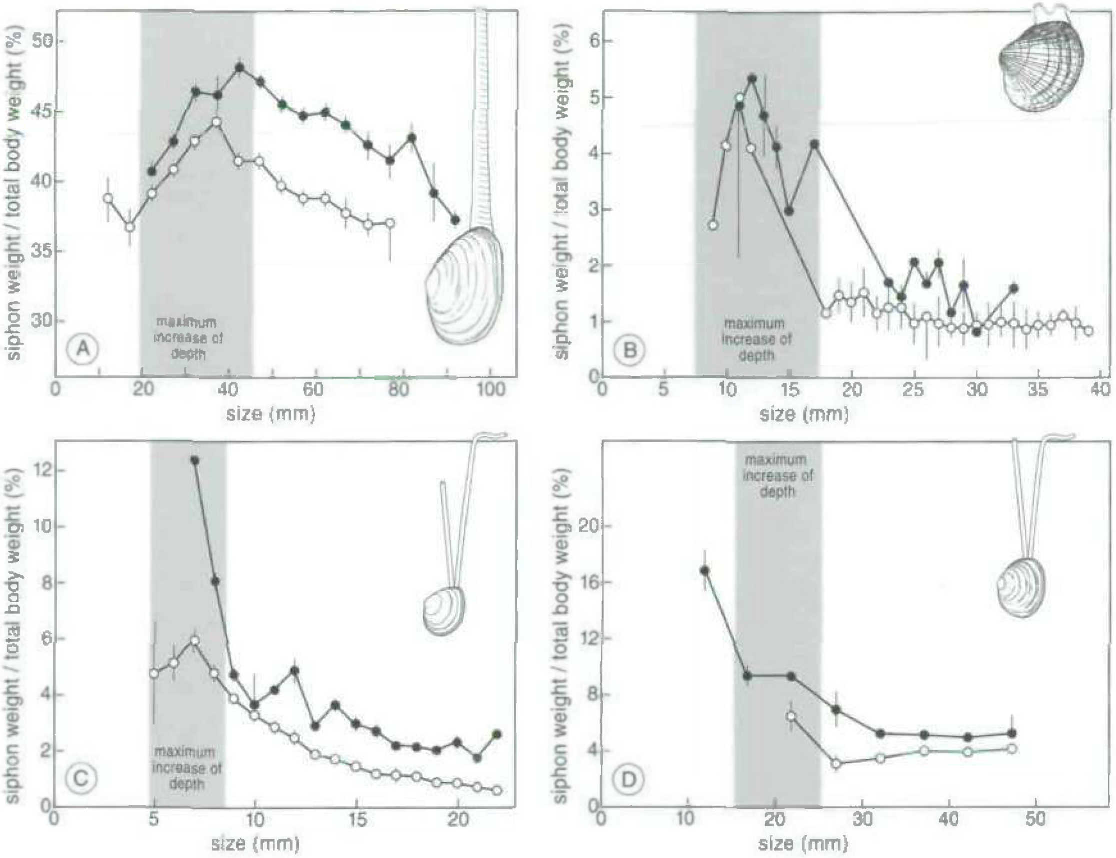

Fig. 12. Siphon weight (% ± SE) relative to total body weight in winter (●) and in summer (○) as a function of shell size of **A.** *Mya arenaria* **B.** *Cerastoderma edule* **C.** *Macoma balthica* **D.** *Scrobicularia plana*. Table 5 gives statistical analysis and number of cases.

Table 5. Results of 4 two-way analyses of variance (ANOVA) to test effect of shell size on relative siphon weight in winter and summer (same data as in Fig. 12).

Species	*Size*		*Season*		*Size × Season*		*n*
	R^2, %	*p*	*R^2, %*	*p*	*R^2, %*	*p*	
Mya arenaria	8.1	0.001	9.4	0.001	1.9	0.001	1816
Cerastoderma edule	55.8	0.001	3.5	0.001	1.3	0.233	237
Macoma balthica	50.6	0.001	4.1	0.001	0.8	0.001	2700
Scrobicularia plana	13.8	0.001	11.1	0.001	0.7	0.001	6178

Table 6. Size at which there is a maximal investment in siphon tissue (Fig. 12) and size at which egg production starts. The latter according to Brousseau (1978), Commito (1982) for *Mya arenaria*; Kristensen (1957), Seed & Brown (1977) for *Cerastoderma edule*; Caddy (1967), Commito (1982) for *Macoma balthica*; Hughes (1972) for *Scrobicularia plana*.

Species	*Maximal investment in siphon tissue*	*Start of egg production*
Mya arenaria	20-45 mm	> 20-45 mm
Cerastoderma edule	7-17	> 18
Macoma balthica	5-8	> 8-10
Scrobicularia plana	< 15-25	> 20

even the largest *Mya* and *Macoma* (Blundon & Kennedy 1982a). They dig up bivalves to a depth of c. 10 cm (Blundon & Kennedy 1982b), which is thus less than the probing depth of Curlews feeding on *Mya*, but more than the depth from which Oystercatchers take *Macoma*. This may explain why in Chesapeake Bay the latter species live at greater depths than their European conspecifics. It is worthwhile to do more comparative research to understand the importance of burying depth as a defensive adaptation.

Siphon investment and predation risk

The increase of burying depth with size (Figs. 2-5) corresponds with a larger investment in siphon mass (Fig. 6). The depth/size relationship in *Cerastoderma*, *Mya*, *Scrobicularia* and *Macoma* can be described with an S-curve (Figs. 2-5), so it is reasonable to suppose that siphon weight, known from Fig. 6, but recalculated here as a proportion of total body weight, is relatively low for juveniles, maximal for the size classes which burrow deeper, and gradually decreasing when burying depths level off. This is indeed the case (Fig. 12, see also Pekkarinen (1984) for a similar graph for *Macoma* in the Baltic Sea).

There is a very high mortality among juvenile benthic bivalves. A significant percentage of this mortality is caused by predation of flatfishes, shrimps and crabs (Hancock & Urquhart 1965, Reise 1977, de Vlas 1979a, Pihl 1982, Pihl & Rosenberg 1984, Jensen & Jensen 1985, Le Mao 1986, Sanchez-Salazar *et al.* 1987b). It is not yet clear to what degree size and depth offer protection against these shallow-feeding predators. In any case, quick growth is apparently a first priority, to be followed by increase in siphon mass to make possible a greater burying depth.

It has been suggested that reproduction in these benthic bivalves is delayed in order to divert its resources into rapid early growth (Lammers 1967 for *Macoma*; Seed & Brown 1978 for *Cerastoderma*, Brousseau 1979, Commito 1982 for *Mya*). Table 6 shows that maximal siphon growth also takes place before sexual maturity is reached. The three priorities during the course of the life of a benthic bivalve therefore seem to be: (1) to grow fast; (2) to increase burying depth; and (3) to produce offspring.

Chapter 5

FEEDING RADIUS, BURYING DEPTH AND SIPHON SIZE OF *MACOMA BALTHICA* AND *SCROBICULARIA PLANA*

Leo Zwarts, Anne-Marie Blomert, Piet Spaak & Bauke de Vries

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FEEDING RADIUS, BURYING DEPTH AND SIPHON SIZE OF *MACOMA BALTHICA* AND *SCROBICULARIA PLANA*

This paper investigates whether siphon weight limits the elongation of the siphon of deposit-feeding benthic bivalves under natural conditions. Were this to be so, it would imply that foraging and predator avoidance place conflicting demands on these animals, since an increase in the feeding radius on the surface would be associated with a decrease in the burying depth, and vice versa. The paper presents methods with which to measure siphon length and equations to transform siphon weight to siphon length in two benthic bivalves, *Scrobicularia plana* and *Macoma balthica*. Relatively heavy siphons are longer, but also thicker, than lightweight ones. We conclude that most individual bivalves stretch their siphons fully while feeding. However, bivalves with heavy siphons keep part of the siphon in reserve within the shell. Siphon cropping therefore results in an immediate reduction in siphon length, unless the siphon is heavy and a reserve is available. The feeding radius of *Macoma* and *Scrobicularia* is a linear function of shell size. *Scrobicularia* use half of their siphon length to feed on the surface and the other half to bury themselves, but if the siphon weight is below average, the proportion extended over the surface decreases with siphon size. However, among the animals with a short siphon, those with a good body condition take no risks and live as deeply as possible. A comparison between species reveals that the weight of the extended inhalant siphon per cm amounts, on average, to 0.6% of the total body weight.

Introduction

Bivalves that live buried in the substrate are usually surrounded by a hostile environment, without oxygen and food. Suspension-feeding benthic bivalves reach the surface for respiration and for filtering food from the water by pushing their inhalant siphon through the overlying mud. Deposit-feeding benthic bivalves have to protrude their inhalant siphon even further when they feed on the surface of the surrounding substrate.

It is of crucial importance to benthic bivalves to elongate their inhalant siphon as much as possible, since a long siphon enables them to live at a safe depth beyond the reach of surface predators (Zwarts & Wanink 1989). On the other hand, it is reasonable to suppose that deposit-feeding bivalves may increase their rate of food intake, and thus rate of somatic growth, by living near the surface so that they can extend the siphon on the surface over as large a feeding space as possible. Unless, and improbably, the siphon is so elastic that bivalves can simply extend it even more whenever they have to collect distant food and/or increase their burying depth to avoid surface predators, the minimization of prey risk (by burying deeply) and the maximization of feeding opportunity (by extending the siphon more) place conflicting demands on these animals.

Scrobicularia plana can achieve a remarkably long extension of the siphon (Chapman & Newell 1956, Green 1967, Hodgson & Trueman 1981). However, this does not necessarily mean that the extent to which an individual usually protrudes its siphon is highly variable. The burying depth of *Scrobicularia*, and also of *Macoma* balthica and *Mya arenaria*, increases with siphon weight when individuals of the same size are compared (Zwarts & Wanink 1989). Moreover, *Scrobicularia* reduce their burying depth when part of their inhalant siphon has been removed experimentally (Zwarts 1986). Furthermore, the degree to which these cropped *Scrobicularia* approach the surface also appears to depend on their body condition, defined as the individual's body weight relative to the average of its size class. Only animals with an underweight siphon that are also in poor condition move closer to the surface and so expose themselves to a greater predation risk.

These observations led Zwarts (1986) to hypothesise that the burying depth of deposit-feeding bivalves represents a compromise between foraging demands and predator avoidance. The hypothesis could not be tested because the feeding radius had not been simultaneously measured with burying depth and siphon weight. The aim of this paper is to present some measurements on the elongation of the siphon that are essential to answer the question about the trade-off between food and predation. We show that feeding radius, burying depth, and thus also siphon length, increase with shell size. We relate individual differences in feeding radius and burying depth in *Scrobicularia* and *Macoma* of different size classes to variations in siphon weight. We cut off siphons to determine the effect of siphon cropping on feeding radius and burying depth. The paper also describes techniques to measure the length of the inhalant siphon and gives equations to predict siphon length from siphon weight. These data will be used to estimate the feeding radius of a large sample of *Scrobicularia* in which burying depth and siphon weight has been measured.

Materials and methods

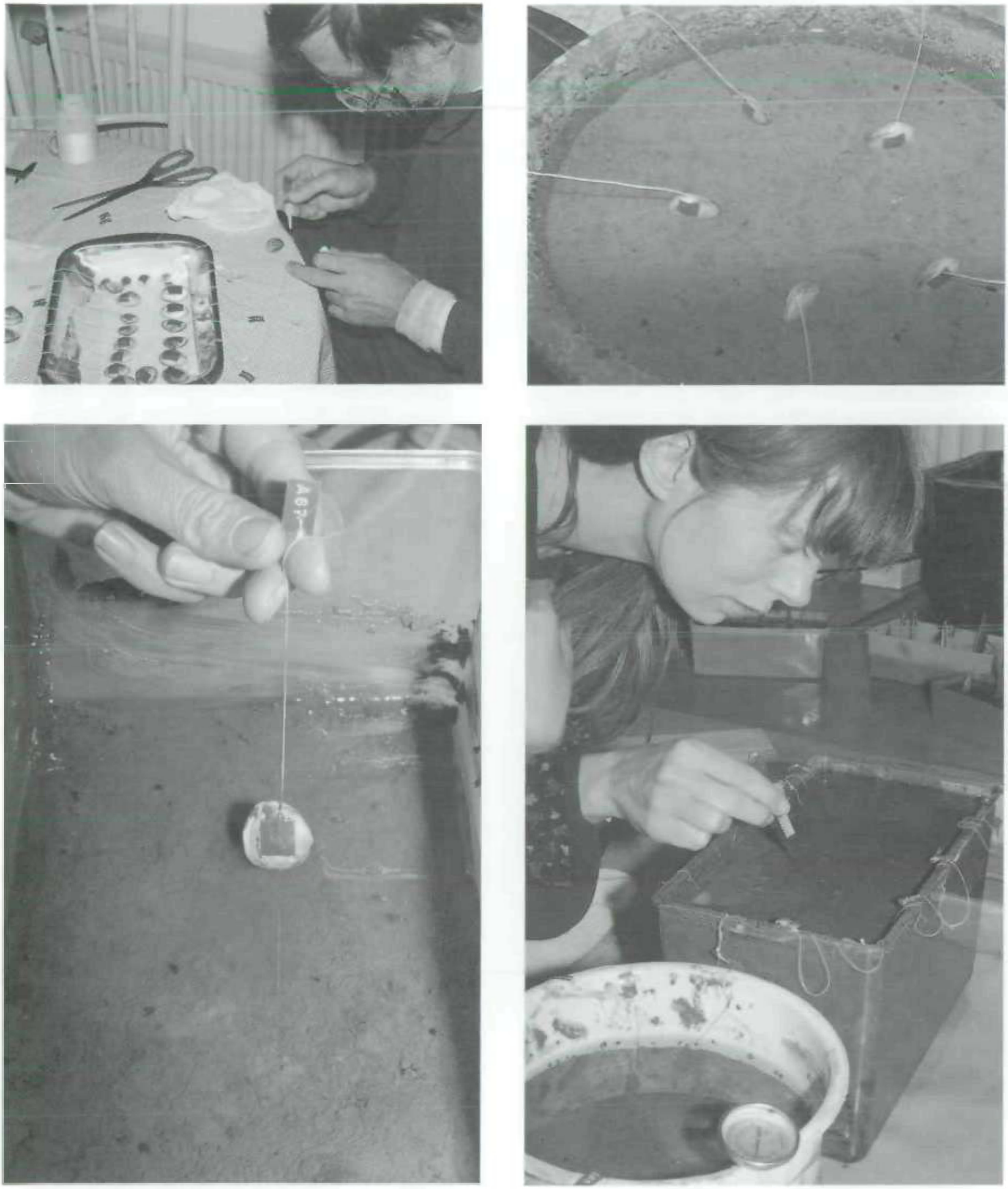
Burying depth, feeding radius and siphon weight: field data

The field data were collected on a tidal mudflat in the eastern part of the Dutch Wadden Sea along the mainland coast of the province Friesland (53° 25′ N, 6° 04′ E). We determined the maximal feeding radius of 75 *Scrobicularia* in June 1992 using two methods. First, we observed for 20 min the siphon activity of an individual bivalve, noted its maximum extension over the mud, using surface cues such as shell fragments as markers, and later measured the distance to the siphon hole. The second method was simply to measure the distance between the siphon hole and the maximum extent of the traces in the mud: like other deposit-feeding bivalves, *Scrobicularia* leave starlike tracks on the surface around the burrow caused by the siphonal activity (Hughes 1969, Hulscher 1973, Wikander 1980, Levinton 1971, 1991). Since both methods gave identical results, we subsequently only used the second method, selecting stars that were so clear-cut that the maximal feeding radius could be measured precisely. After that, the burying depth of the selected bivalve was determined using a circular corer pushed into the mud. After retraction, the core was laid horizontally and the burying depth of the focal bivalve measured to the nearest 0.5 cm. Burying depth is defined as the distance between surface of the mud and the upper edge of the shell; for a detailed description of the methods, see Zwarts (1986) and Zwarts & Wanink (1989). The animals were stored in sea water and taken to the laboratory where shell length was measured and the inhalant siphon separated from the body, as described elsewhere (de Vlas 1985, Zwarts & Wanink 1989). The siphons were dried for 3 days at 70 °C and burned at 550 °C for 2 h to determine the ash-free dry weight (AFDW).

To study the relation between burying depth and siphon weight after cropping, we collected 60 *Macoma* 16 to 17 mm long in May 1986. The animals were placed in dishes with shallow water, after which the extended part of the siphon was cut off in 44 individuals. Using adhesive, a thin nylon thread of known length was attached to the shell and the animals were reburied at a depth of 3 cm in the same mudflat from which they had been collected 8 hours before. The depth to which the animals subsequently buried themselves was determined each low water period over five days, by subtraction, from the length of the thread remaining above the surface. After that the animals were collected to determine the ash-free dry weight of the body weight and the remaining siphon, as well as of the weight of the part of the siphon that had been removed.

Experiments in the laboratory

Further experiments were conducted on the relationship between siphon weight, feeding radius and burying depth in the laboratory. Twenty-six *Scrobicularia*, 13 to 37 mm long, and 77 *Macoma*, 11 to 20 mm long, were collected in October 1992 and taken to the laboratory, where shell length was measured and thin nylon threads of known length were attached to the shell with super glue. The bivalves were then allowed to bury themselves in 20 cm of mud taken from the area where the bivalves had been collected. The mud temperature was kept constant at 15 °C. The water table above the



We took bivalves home to measure the siphon length of bivalves. Nylon threads were used to determine the depth of bivalves. We could determine the extension of the siphon by measuring the burying depth (using the threads) and the feeding radius on the mud surface.

surface in the containers was varied between 0 and 2 cm, but we took care to ensure that the mud was always moist. For practical reasons, the observations were restricted to the simulated low water situation. We first recorded the maximal feeding radius of individual animals that were actively engaged in deposit feeding during observation periods of 20 min. After that, we measured the length of the thread remaining above the substrate to determine, by subtraction, the burying depth (Zwarts 1986). Feeding radius and burying depth were determined 418 times in *Macoma* and 195 times in *Scrobicularia*. The bivalves remained in perfect condition during the ten days of experiment.

If bivalves make a trade-off between the distance over which they extend their siphon and burying depth, we would expect them to extend their siphon more, and to move nearer the surface, as the food supply declined. We expected a decline in the food supply to occur over the course of the experiment because of depletion around the siphon hole (Brey 1989, 1991). However, the bivalves stopped deposit feeding altogether after about one day. Therefore we had to turn over the upper layer of the mud regularly or add new substrate. This immediately stimulated deposit feeding, without exception.

The sum of the maximum feeding radius and of the burying depth for a single individual estimated its siphon length. Once a consistent estimate had been obtained, we tried to remove a part of the surface-feeding siphon with a sharp-pointed pair of tweezers to simulate the effect of siphon-cropping flatfish (de Vlas 1979a). We were able to measure the feeding radius and burying depth of 11 *Macoma* and 10 *Scrobicularia* after such cropping action.

Four alternative ways were used to measure siphon length as a function of siphon weight. These data were collected in May-June 1986 and October 1992 for *Macoma* and in June 1992 and October 1992 for *Scrobicularia*. First, we cut the inhalant siphon from the soft body of 2789 *Macoma* (4 to 21 mm long) and of 101 *Scrobicularia* (6 to 35 mm long) that were killed by a short emersion in boiling water, and measured the length of the unstretched siphon immediately afterwards. Second, we separated inhalant siphon and body in 35 *Scrobicularia* (18 to 45 mm long) which had been stored in a freezer, and measured in the unstretched siphon length, the width at the top, at the base and halfway along the siphon. Third, 26 *Macoma* 16 mm long were put in vertically-held test tubes filled with sea water. The length of the extended siphon was measured by reference to a scale at regular intervals, after which *Macoma* were sacrificed to separate inhalant siphon and body. Four, 81 *Macoma* 15 to 20 mm long were placed in a dish with 0.5 cm of sea water. When the siphon was extended, its length was measured and then it was cut off at the shell edge. Siphon weight was determined separately for the extended part and for the part remaining in the shell.

Analysis

The feeding radius, burying depth and siphon length are given as a function of shell size. In order to analyse the data with the effect of size ruled out, all weight and length measurements were transformed to a standard size class (*Scrobicularia* 35 mm and *Macoma* 15 mm long), using regression equations given in the paper. SPSS was used for all statistical analyses (Norušis 1988).

Results

Shell size, feeding radius and burying depth

Feeding radius and burying depth of individual *Scrobicularia* simultaneously were measured in the field (Fig. 1A) and in the laboratory (Fig. 1B). Burying depth increased with size, as was also found by Hughes (1970a) and Zwarts & Wanink (1989, 1993). In the field, *Scrobicularia* were buried more deeply in June 1992 compared with earlier measurements made in the same area over seven summers (Zwarts & Wanink 1989, 1993). The bivalves in the laboratory in October were buried at typical winter depths (Zwarts & Wanink 1989, 1993). The feeding radius in the field and in the laboratory varied between 0.5 and 7 cm, similar to the range mentioned by Thamdrup (1935), Linke (1939) and Hughes (1969). As expected, feeding radius increased with shell size, but, although significant, the effect was rather weak. The siphon length (i.e. sum of burying depth and feeding radius) of large *Scrobicularia* did not differ between field and laboratory. However, the smaller specimens extended the siphon more in the laboratory than in the field, due to their relatively large burying depth. The widening gap

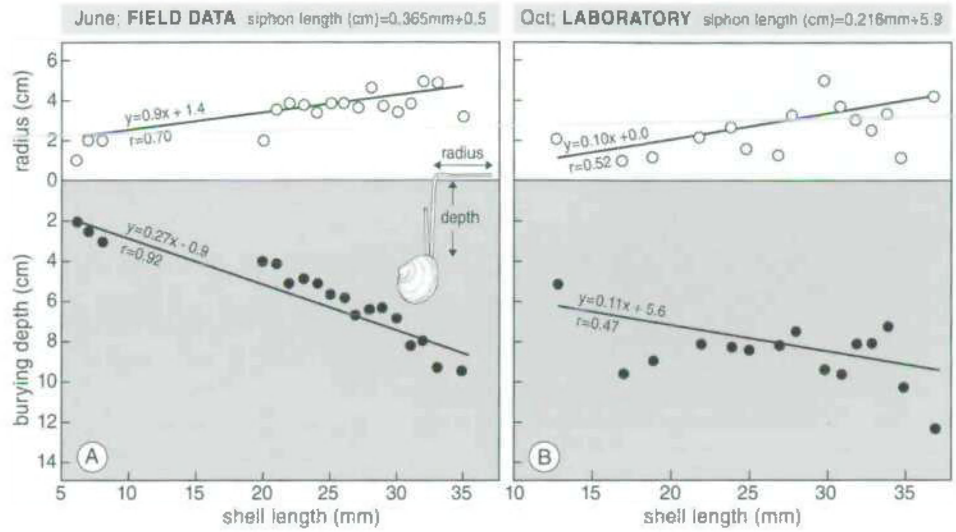


Fig. 1. Burying depth (cm) and feeding radius (cm) in *Scrobicularia*, as a function of shell length, measured **A.** in the field (n = 75) and **B.** in the laboratory (n = 26); data were pooled per mm shell length. All regressions shown are highly significant. The regression equations for siphon length are based on the sum of feeding radius and burying depth.

between burying depth and feeding radius in Fig. 1 shows that siphon length increased with shell size. The longest siphon measured 17 cm in a *Scrobicularia* 37 mm long. Green (1967) recorded a siphon length of 28 cm in an individual of 40 mm.

The feeding radius of individual *Macoma* varied between 0.2 and 4 cm and was related to shell size (Fig. 2). In contrast, no, or hardly any, increase of feeding radius with shell size was found in *Abra nitida* and *A. longicallus* (Wikander 1980) and *Macoma secta* (Levinton 1991). Brafield & Newell (1961), Gilbert (1977) and Kamermans & Huitema (1994) recorded for *Macoma* a maximal feeding radius of 4, 6 and 5 cm, respectively, close to present values. Lin & Hines (1994) mentioned a maximal radius of 10 cm, but their data referred to the larger American *Macoma* up to 39 mm long. Reid & Reid (1969) reported for seven species of *Macoma* a feeding radius of 1.5 to 3 cm. The variation in burying depth of *Macoma* (0 to 6 cm) was similar to values found in the field (Reading & McGrorty 1978, Zwarts & Wanink 1989). Contrary to the normal situation in the field, where depth was independent of size in *Macoma* larger than 10 mm (Zwarts & Wanink 1989, 1993), small animals buried more deeply than large ones. There was a weak, non-significant increase in siphon length (i.e. the sum of feeding radius and burying depth) with shell size for *Macoma* greater than 10 mm (Fig. 2). The longest

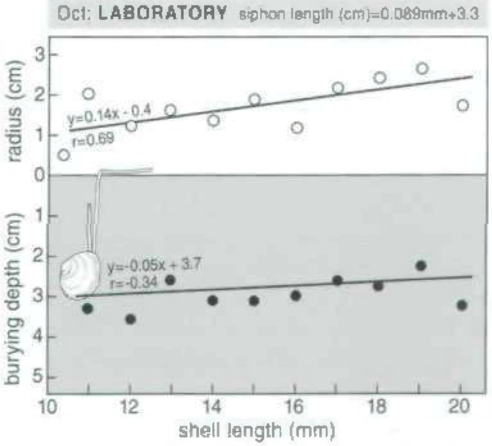


Fig. 2. Burying depth (cm) and feeding radius (cm) in *Macoma*, as a function of shell length measured in the laboratory (n = 77); data were pooled per mm shell length. All regressions shown are highly significant. The regression equation for siphon length is based on the sum of feeding radius and burying depth.

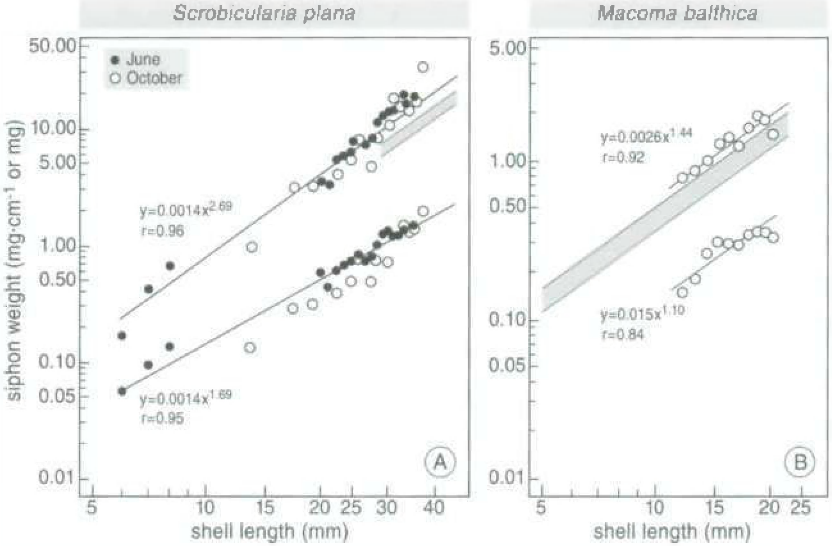


Fig. 3. Siphon weight (mg AFDW) of **A.** *Scrobicularia* (n = 112) and **B.** *Macoma* (n = 74) in June (○) and October 1992 (●). The upper line and symbols refer to the total weight. The grey fields indicate the range of siphon weights measured in the study area over several years (from Zwarts & Wanink 1989). The lower line and symbols give the total siphon weight divided by siphon length, calculated from data given in Figs. 1 and 2.

siphon measured 8.5 cm, below the maximum of 11 cm and 11.5 cm found by Kamermans & Huitema (1994) and Pekkarinen (1984), respectively for *Macoma* of similar size.

The siphons of *Scrobicularia* and *Macoma* were relatively heavy in June and October 1992, compared to the long-term average for the same months (Fig. 3), but the trends are similar: in both species, siphon weight is an allometric function of shell size, although the slope in *Macoma* is much lower than in *Scrobicularia*.

Siphon cropping, feeding radius and burying depth

There was little variation over time in the burying depth of the individual bivalves held in containers, but their feeding radius did vary. As an example, Fig. 4 shows the depth and radius measurements for two *Scrobicularia* and two *Macoma*. Simulated siphon cropping reduced the feeding radius, but did not cause a change in burying depth. Deposit feeding continued after the siphon top was lost, as was also observed by Hodgson (1982b) and de Vlas (1985); the wounded siphon heals very quickly (Hodgson 1981). An average of 10% of the siphon weight of *Scrobicularia* was removed and accounted completely for the smaller feeding radius. On average, *Macoma* (11 animals) lost 18% of the siphon weight, and the average siphon was shortened by 12% or 6 mm. The radius decreased by an even greater amount (38% or 10 mm) because, contrary to expectation, siphon cropping resulted in *Macoma* burying themselves more deeply (4 mm or 21%).

The contrary result was found in the field experiment. All *Macoma* had been buried by us at the same depth of 3 cm. The 44 individuals from which 20 to 70% of the siphon had been removed were found the next day at a depth of 1.4 cm and so had reduced their depth by 1.6 cm (SE = 0.1 cm). The 17 controls from which no siphon tissue had been removed had also moved closer to the surface, but only by 0.7 cm (SE = 0.2 cm). As the burying depth of both groups did not change over the following days, we calculated the average burying depth over this period for each individual and related this average to the weight of the remaining siphon and to the cut part of the siphon. Heavily cropped animals moved nearer to the surface

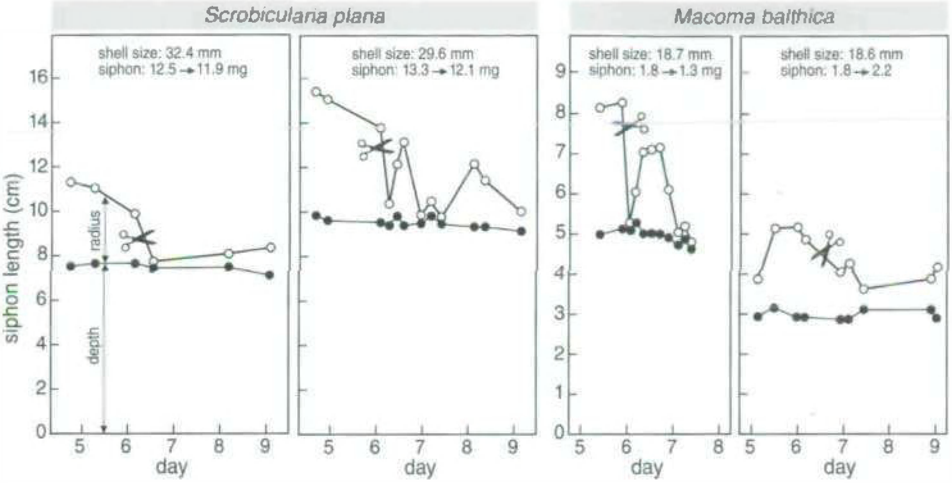


Fig. 4. Siphon length (cm) of 2 *Scrobicularia* and 2 *Macoma* measured from 5 days to 9 days after burial. Shell size, siphon weight (AFDW) before and after cropping and time of cropping (✂) are indicated.

than animals that had lost little or no siphon, just as found in similar experiments with *Scrobicularia* (Zwarts 1986). The burying depth increased with the weight of the remaining siphon and, as Fig. 5 shows, the relationship between siphon weight and depth was similar for the cropped animals and the controls. Statistical analyses confirmed that burying depths were highly correlated to the weight of the remaining siphon and that the weight of the amount that had been cut off did not add significantly to the explained variance.

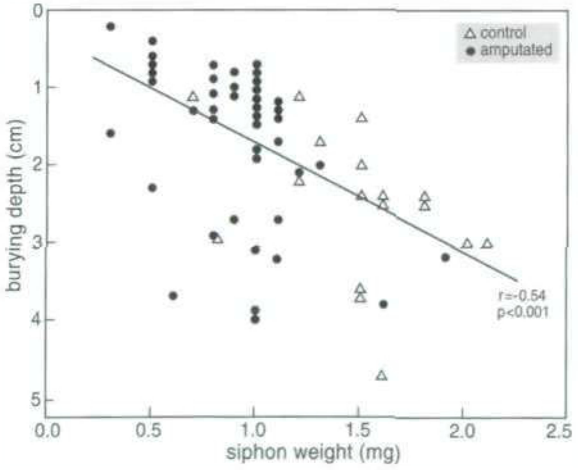


Fig. 5. Burying depth (cm) as a function of siphon weight of *Macoma* (16-17 mm) on a mudflat in May 1986 (n = 61). Except 17 controls, between 20 and 70% of the siphon weight has been removed shortly before the depth measurements were done.

Siphon length and siphon weight

Siphon length was 0.2-0.5 cm in *Macoma* and 0.5-2.0 cm in *Scrobicularia* after the siphons had been cut off in the animals killed in boiling water. These ranges correspond well with the measurements of Hodgson & Trueman (1981) and Pekkarinen (1984). In both species, the length of the dissected siphons, as well as the weight per cm of siphon, was highly correlated with shell length (Table 1). Also, the relationship between the dissected length and the maximum length of the extended siphon, measured in the same (still living) *Scrobicularia*, was highly significant ($r = 0.64$, $p < 0.0001$). The extended siphons were ten times as long as the dissected siphons, as also found by Hodgson & Trueman (1981). To investigate the relationship between siphon weight and siphon length independently of shell size, dissected siphon lengths and siphon weights were expressed as deviation from the average values of the corresponding size classes, using regression equations given in Table 1. The relation between siphon weight and dissected siphon length was not linear but curvilinear (Fig. 6).

Table 1. *Macoma* and *Scrobicularia*. Siphon length (cm) and siphon weight (mg AFDW per mm) as a function of shell length (cm). The length of the siphon was unstretched and measured directly after dissection. *Macoma* (n = 2789, range: 4 to 21 mm) were collected in April and May 1986 and *Scrobicularia* (n = 73, range: 6 to 35 mm) in June 1992. The regressions, which are both highly significant, were calculated over the means per mm class, weighed for the number of cases.

Siphon length (Y: cm) as a function of shell length (X: mm)		
Macoma balthica	$Y = 1.37 X + 0.24$	$r = 0.90$
Scrobicularia plana	$Y = 6.21 X - 4.22$	$r = 0.92$
Siphon weight (Y: mg cm^{-1}) as a function of shell length (X: mm)		
Macoma balthica	$Y = 0.145 X - 0.009$	$r = 0.95$
Scrobicularia plana	$Y = 0.386 X - 0.217$	$r = 0.97$

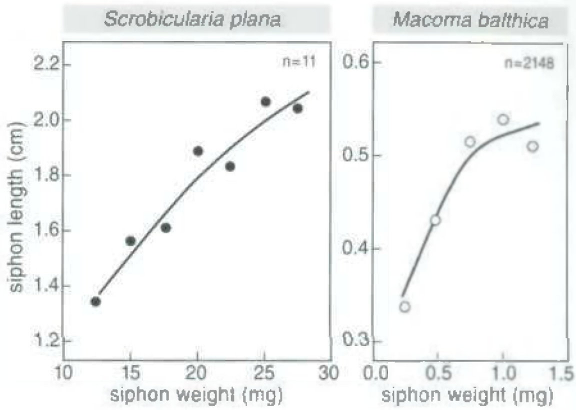


Fig. 6. Length (cm) of the inhalant siphon of *Scrobicularia* (35 mm) and *Macoma* (15 mm) after dissection as a function of the siphon weight: from data given in Table 1; data pooled per siphon weight category. Lines drawn by eye.

With *Scrobicularia* stored in the freezer, the unstretched siphon length was 2 to 10 cm, about five times longer than in boiled siphons. Siphon weight was again highly correlated with siphon length ($r = +0.58$) in these 34 *Scrobicularia*. The correlation was also significant when siphon weight was plotted against siphon width, measured at the top ($r = +0.44$), halfway along the siphon ($r = +0.50$) and at the base ($r = +0.34$). When siphon weight was plotted against the product of siphon length and the square of siphon width, the correlation was even higher, $r = +0.70$. Siphon weight is thus clearly a function of the combined effect of siphon length and siphon width. No relationship was found between siphon weight and shell size ($r = +0.10$), nor between siphon length and shell size ($r = -0.08$). The correlation between shell size and siphon width was non-significant with the width at the top ($r = +0.15$) or halfway up the siphon ($r = +0.14$), but highly significant with the width measured at the base ($r = +0.56$).

Macoma (15 mm long) that were held in vertical test tubes with sea water extended their siphons by 1 to 8 cm. We found for these 26 animals no significant relationship between the total siphon weight, which varied between 0.5 and 2.1 mg, and the maximal length of the extended siphon. The siphons weighed 1.4 mg, on average. The maximal extension of the siphon was, also on average, 4.5 cm, so 1 cm siphon length corresponded with about 0.31 mg siphon tissue.

In another experiment, *Macoma* (16 mm long) in some mm of sea water extended their siphons horizontally. There was again no relationship between the length of the extended siphon and its total weight. On average, the extension was 3.0 cm (SD = 1.1 cm) and the total weight 1.28 mg; this gives for an extension of 1 cm a siphon weight of 0.43 mg, or 0.39 mg cm^{-1} for a standard *Macoma* of 15 mm. However, the expected relationship between siphon length and siphon weight was found in this sample of horizontally stretched siphons when length was plotted against the weight of only the extended portion of the siphon (Fig. 7A). As part of the scatter in the data could be attributed to the total siphon weight, the relationship is given separately for total siphon weights of 1, 1.5 and 2 mg. If the siphon were elastic, the weight per cm extension would decrease the more the siphon was stretched. This is clearly not the case, since the weight per unit length of external siphon was 0.15 mg cm^{-1} for a total siphon weighing 1 mg and did not increase when the siphon was stretched by 2 or 7 cm (Fig. 7B). The same panel shows that with a total siphon weight twice as great, the weight per cm levelled off at the higher value of 0.3 mg cm^{-1}, also twice as high as in the relatively lightweight siphons. Since siphon extension is only

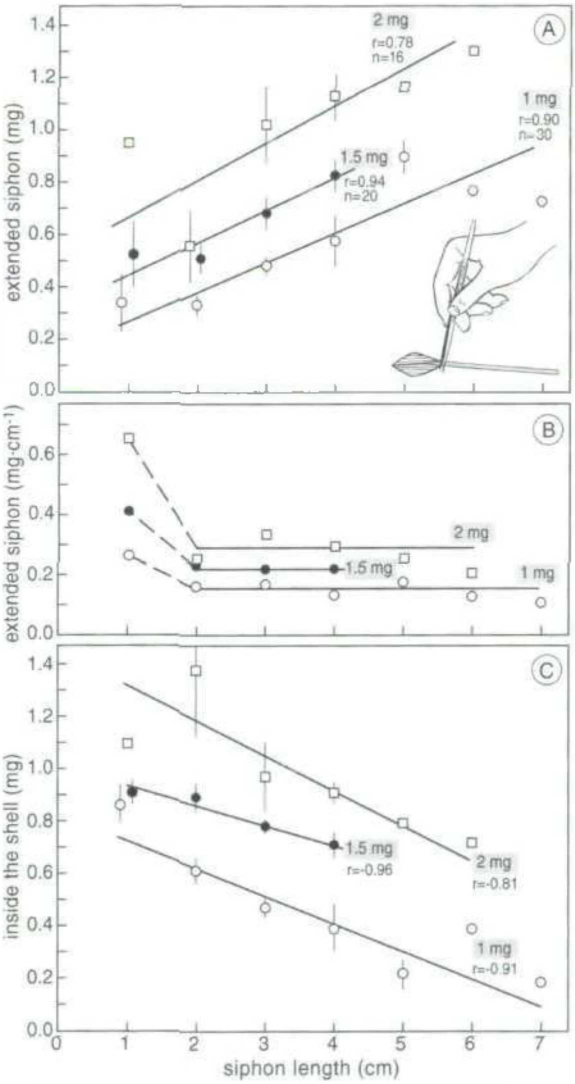


Fig. 7. **A.** Weight (mg AFDW) of the extended siphon, **B.** weight of the extended siphon (mg cm^{-1}) and **C.** weight of the internal siphon (mg AFDW) in *Macoma* 15 mm long as a function of the length of the extended siphon. The three regression lines in each panel refer to siphons with different total weights; number of cases given in the upper panel. The weight of the extended siphon depends on siphon length (R^2 = 0.281) and on total siphon weight (R^2 = 0.295); the interaction term was not significant.

possible if more siphon tissue is protruded, the weight of the siphon remaining within the shell must be less when the siphon is stretched more, and this is exactly what was found (Fig. 7C). When extending their siphon, *Macoma* kept part of it (20 to 70%) within the shell. The size of this 'internal' part of the siphon decreased if the siphon was extended further and was small in *Macoma* of a low siphon weight.

Discussion

Relation between feeding radius and shell size

As would be expected, there is a linear, rather than exponential, increase in average feeding radius with shell size (Figs. 1 and 2). If food is limiting and assuming that the proportion of the requirements taken from the surface, and the efficiency with which they are collected, is the same for the different size classes, the individual feeding area should be equivalent to the total food demands of a deposit-feeding bivalve. This means that the feeding radius should be a function of food intake$^{0.5}$. Other things being equal, energy requirements are a function of body weight$^{0.75}$, found both in comparisons between species and within individual *Scrobicularia* of different flesh weights (Hughes 1970b). The ash-free dry weight of the flesh in *Scrobicularia* and *Macoma* is an allometric function of shell length, with the exponent of 2.9 (Zwarts 1991). The prediction therefore would be that feeding radius would be function of shell length with an exponent of 0.5×0.75×2.9, or 1.09, and so close to observed linearity.

Other studies found no, or hardly any, relationship between feeding radius and shell size (Wikander 1980, Levinton 1991). This may indicate that larger individuals take relatively more food from the overlying water, and/or are able to graze the surface more efficiently. On the other hand, the individual variation in feeding radius of animals of the same size is very large and this is associated with the huge variation in siphon weight (see below: Figs. 8B and 9C). Hence the relationship between average feeding radius and shell size can easily be overlooked if the sample size is small.

Relation between siphon size and shell length

The exponent of the allometric relationship between siphon would not have to reach the surface but only the oxidation layer, which, in our study area, is only some mm below the mud surface in summer (Zwarts unpubl.). Thus, any overestimation of the length of the lightweight siphons is likely to have been small.

The data from Fig. 7 were recalculated to plot for *Macoma* the weight per cm of the extended siphon length against the weight of the total siphon (Fig. 9A). The regression in Fig. 9A was used to estimate siphon length from siphon weight (Fig. 9B), assuming that 0.1 to 0.4 mg of the inhalant siphon remains within the shell. The measurements of siphon length and siphon weight were also plotted in Fig. 9B, after a correction had been made for the weak increase of siphon length with shell size (Fig. 2) and of siphon weight with shell size (Fig. 3B). There was a reasonable fit between observed and predicted siphon length, but the observed average extension of the siphon was slightly less than predicted for the heavy siphons. As shown in Fig. 7C, the weight of the 'internal' siphon in a fully stretched siphon depended on the total siphon weight. The siphon weight of the *Macoma* collected in our study area varied between 0.1 and 2.7 mg, with the majority lying between 0.3 and 1.6 mg (Fig. 9C). This means that the expected 'internal' siphon mass for an extended siphon will be close to 0.2 mg in animals of average siphon weight, varying between 0.1 and 0.3 mg in animals with light and heavy siphons, respectively.

In conclusion, there is in both species a curvilinear relationship between siphon length and siphon weight, in both dissected (Fig. 6) and living (Figs. 8 and 9) animals. This curve may be partly explained by the variation in siphon thickness, as shown in Fig. 7B. However, even when a correction is made for this (Fig. 9A), the siphons appeared not to be fully stretched in *Macoma* when the siphon weight was above the average value of 1 mg (Fig. 9B). This may be attributed to the fact that a larger part of the siphon remains inside the shell when the siphon is heavy (Fig. 7C).

Effect of siphon cropping on siphon length

If the conclusion from the previous section is true, siphon cropping will result in a shorter siphon, unless the siphon is relatively heavy and a greater part of it can remain in reserve inside the shell. Clipping experiments in the laboratory were made on individuals with above-average siphon weights and thus siphon in reserve (Figs. 7-9). Hence, although our cropping them resulted in a loss of 10 and 18% of the siphon weight of *Scrobicularia* and *Macoma* respectively, no effect on siphon length was to be expected. There was indeed no adjustment in depth, but the feeding radius was reduced by 60% in *Scrobicularia* and 38% in *Macoma*. As a result, and in contrast to expectation, the lengths of the extended siphons were thus shorter.

Although siphon clipping was done to obtain additional data on the relationship between siphon weight and siphon length, we in fact unintentionally measured the behavioural response of bivalves to siphon cropping. In a clipping experiment with *Macoma* similar to the one described in this paper, Kamermans & Huitema (1994) also found a reduction in feeding radius: animals with siphons weighing 2 to 3 mg fed up to 3-5 cm from their burrow before cropping, but when siphon weights were reduced to 0.5 to 2 mg, the radius was also reduced to 1-4 cm. As in our experiment, Kamermans & Huitema (1994) worked with animals whose original siphons were relatively very heavy. Again as in our experiment, they found no decrease in burying depth after part of the siphon was removed.

Both experiments showed that siphon cropping affected siphon extension more than would be expected on the basis of the removal of a given fraction of the siphon weight. Siphon cropping did not stop deposit feeding but the surface feeding radius was reduced disproportionately, presumably to minimise the risk of losing yet more of the siphon. This might be expected because Kamermans & Huitema (1994) had shown that the presence of siphon-cropping shrimps inhibits deposit feeding in *Macoma*.

Contrary to the laboratory results, *Scrobicularia* and *Macoma* decreased their burying depth in a field experiment when bivalves were taken from the mud and reburied after part of the siphon had been removed (Zwarts 1986; Fig. 5). In both species, the weight of the remaining siphons was so low that a reduction in siphon length was to be expected.

The conclusion of this section is that siphon cropping results in an immediate reduction in feeding radius, usually followed by a decrease in the burying depth of bivalves whose initial siphon weights were low so that the animals had no siphon in reserve with which they could maintain their previous depth.

Burying depth as a compromise between feeding and predation avoidance

Siphon length in *Scrobicularia* and *Macoma* increases with shell size (Figs. 1 and 2). *Scrobicularia* use their longer siphon to increase both their burying depth and feeding radius (Fig. 1). Feeding radius also increases with shell size in *Macoma*, but larger animals reduce their burying depth (Fig. 2), which means that larger *Macoma* use an increasing proportion of the siphon length for deposit feeding. A decrease of burying depth with size had already been found in the first study on burying depth of *Macoma* (Hulscher 1973). However, burying depth is independent of size in *Macoma* larger than 10 mm when all field data, collected during seven summer periods, are taken together (Zwarts & Wanink 1989). When the data are analysed according to sampling date, the relation is usually positive and sometimes, especially in spring and summer, negative (Zwarts unpubl.).

The calculated relationships between siphon length and siphon weight may be used to estimate the feeding radius of individual *Scrobicularia* and *Macoma* of

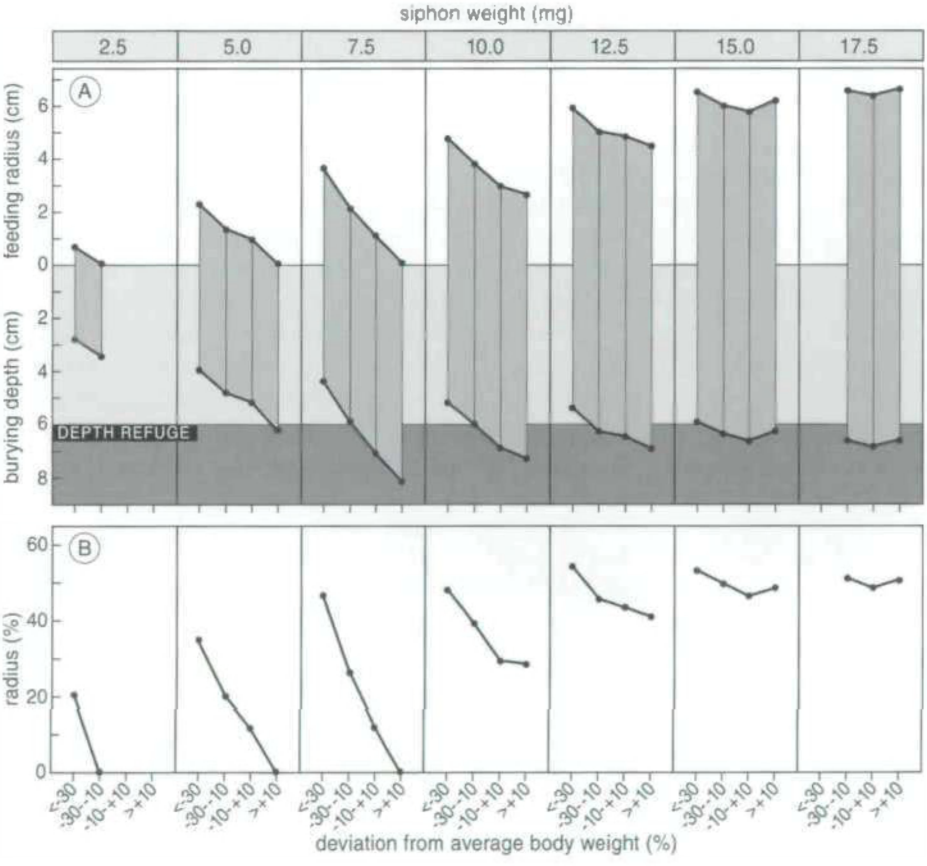


Fig. 10. **A.** Burying depth (cm) and estimated feeding radius (cm) in *Scrobicularia* (35-39 mm) as a function of body condition in animals with different siphon weights. Body condition is expressed as per cent deviation from average body weight. Feeding radius equals siphon length (using the equation in Fig. 9 to convert siphon weight to siphon length) minus burying depth (from Fig. 10 in Zwarts 1986). The graph is based on 3062 individuals collected in summer; for more details see Zwarts (1986). Animals living below the danger line of 6 cm are out of reach of the main predator, the Oystercatcher. **B.** Feeding radius as per cent of the siphon length as a function of body condition, using the data from the upper panel.

known siphon weight and burying depth. Zwarts (1986) showed that the burying depth of *Scrobicularia* was not only a function of siphon weight, but also of body condition. Using the equations from Fig. 8, the average feeding radius may be estimated for individuals living at different depths (Fig. 10). All animals having a body weight > 10% above the average, are able to take no risks and live in a depth refuge beneath the upper 6 cm of the substrate exploited by the main predator, the Oystercatcher *Haematopus ostralegus* (Wanink & Zwarts 1985). This means that in animals with a short siphon but reasonable body condition, the entire siphon length is used for living as deeply as possible so that there is no extra opportunity for deposit feeding on the surface. However, animals with a relatively low body weight have fewer reserves, making it more important for them to avoid further starvation, and so they accept a larger predation risk by living nearer to the surface. These animals extend about 40% of the siphon length over the surface to feed, even when the siphons are quite short. However, as Fig. 10 shows, if the siphon is very short, the bivalves put more emphasis on predator protection than on food input, presumably to avoid the extremely high predation risk associated with living at a very shallow depth (Wanink & Zwarts 1985). This supports the suggestion of Zwarts (1986) that the choice of the burying depth in deposit-feeding bivalves is the result of a trade-off between predator avoidance and feeding. The observation that the feeding radius becomes smaller and burying depth greater in *Macoma* whose feeding circumstances improve (Lin & Hines 1994), indicates that burying depth is the outcome of conflicting demands and that, under each set of conditions, an optimum can be defined.

An interspecific comparison between siphon length and siphon weight

The average siphon weight of *Scrobicularia* (35 mm) amounts to 10 mg, corresponding to an average siphon length of 10 to 11 cm (Fig. 8A). *Scrobicularia* live in winter at an average burying depth of 10 cm (Fig. 5 in Zwarts & Wanink 1989, 1993), so that they should just be able to reach the surface. On average, *Macoma* (15 mm) extend their siphon 5 cm (Fig. 9B), and they live at an average depth of 5 cm in winter (Fig. 4 in Zwarts & Wanink 1989). As in *Scrobicularia*, the estimated average siphon length agrees closely with the measured average burying depth in winter. This means that both bivalve species increase their depth in winter just to the point at which, on average, they are able to reach the surface to acquire oxygen from above the black mud where they live. This implies that they do not feed on the surface. Both species live at shallower depths in summer (Zwarts & Wanink 1989, 1993). At this time of the year, the predicted feeding radius is on average 4 cm in *Scrobicularia* (the gap between the two lines in Fig. 8) and 2 to 3 cm in *Macoma*, which is similar to the observed range in both species. These agreements between predicted and observed burying depths in winter and surface radius in summer suggest that the predictions of siphon length on the basis of siphon weight work out well.

Scrobicularia live in winter at twice the depth of *Macoma* and also invest, relative to total body weight, twice as much material in their inhalant siphon (Figs. 8 and 9). Siphon weight is 5% of the total body weight in *Scrobicularia* (35 mm), but this is only 2 to 3% in *Macoma* (15 mm) (Fig. 12 in Zwarts & Wanink 1989). The weight per cm of extended siphon (1.0 mg cm^{-1} in *Scrobicularia* and 0.2 mg cm^{-1} in *Macoma*, on average) is in both species equivalent to 0.5 to 0.6% of the total body weight (224 mg in *Scrobicularia* and 33.8 mg in *Macoma*, on average; Fig. 8 in Zwarts 1991). The closely-related *Tellina tenuis* is even smaller than *Macoma* (flesh content 15 to 25 mg), yet lives as deeply as *Scrobicularia* (10 cm) (Trevellion 1971). Its siphon weight of 1 to 2 mg (Trevellion 1971) is relatively high, representing 7.5% of the total body weight. However, the weight per cm extended siphon is similar to *Scrobicularia* and *Macoma* if we assume that the siphon is protruded 1 to 3 cm above the surface. Body and siphon weight and burying depth have also been determined of a filter-feeding bivalve, *Cerastoderma edule* (Zwarts & Wanink 1989). This species lives 1.5 cm below the surface and the weight of the inhalant siphon is 1% of total body weight. Since the siphon is extended only a short distance above the surface, the investment per cm siphon length is slightly below 0.7% of the total body weight. Comparable data for more bivalves are needed to know whether the apparent tendency for siphon investment to equal about 0.6% per cm extension, independent of size, is a general phenomenon in bivalves.

Chapter 6

THE MACROBENTHOS FRACTION ACCESSIBLE TO WADERS MAY REPRESENT MARGINAL PREY

Leo Zwarts & Jan H. Wanink

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THE MACROBENTHOS FRACTION ACCESSIBLE TO WADERS MAY REPRESENT MARGINAL PREY

The relationship between relative body condition (deviation from expected mean body weight) and burying depth was investigated in five macro-zoobenthic species living in a marine intertidal habitat. Body weight increased with depth when animals of the same size were compared. The increase amounted to 50% in the clam *Scrobicularia plana*, c. 40% in the worm *Nereis diversicolor*, 25% in the clam *Macoma balthica* and 20% in the Cockle *Cerastoderma edule* and the clam *Mya arenaria*. Only a part of the prey was within reach of some feeding wader species. Therefore prey value may be overestimated if one does not take into account the fact that shallow and accessible prey often have a relatively poor body condition.

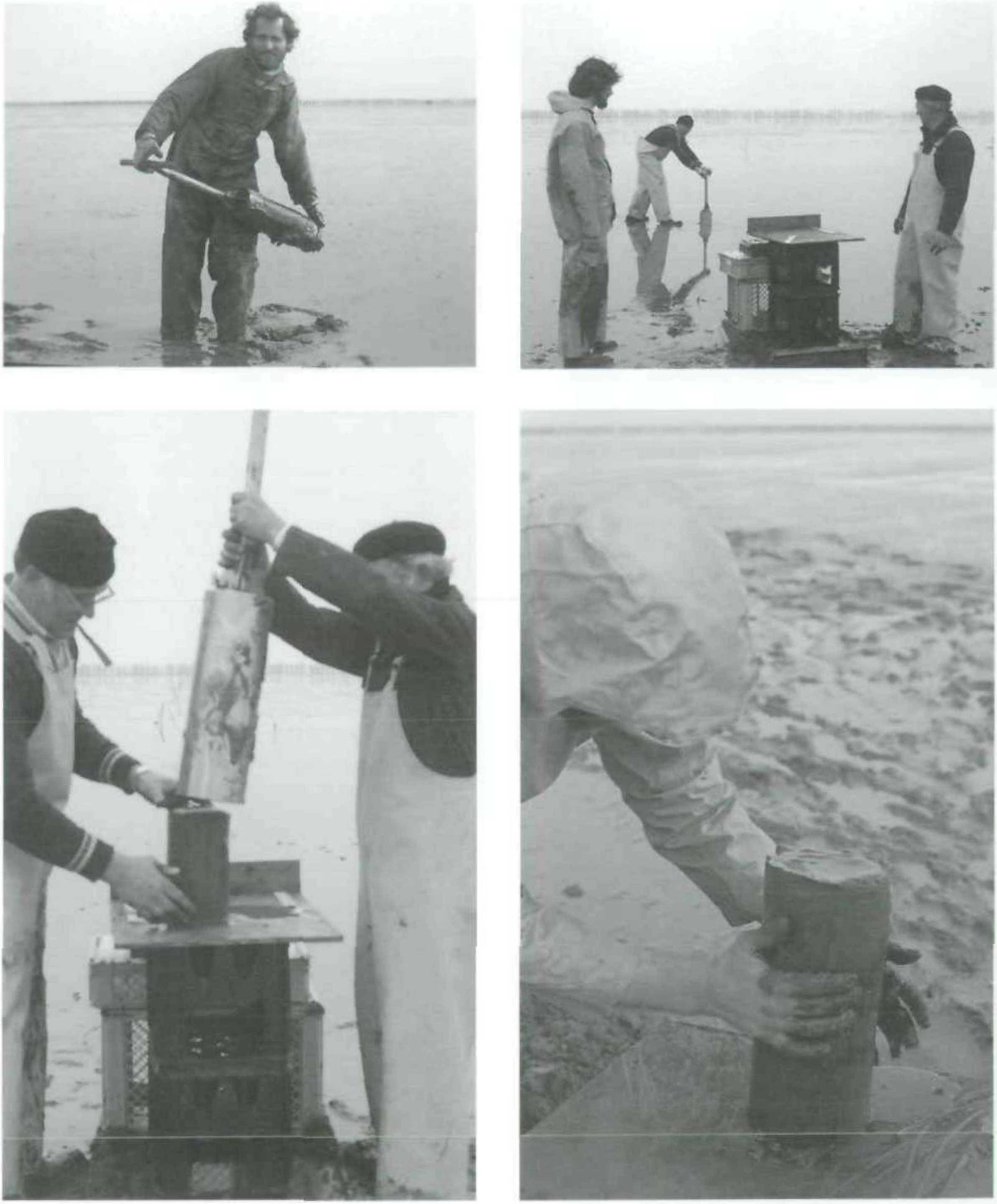
Introduction

In most studies it is impossible to determine exactly the biomass of the prey that are actually eaten by a predator. Rather an estimate of the mean weight of the average prey in the population is commonly used. However, the assumption that the biomass of a prey of a given size class selected by a predator is the same as that sampled by the investigator may be wrong. Investigators sample the prey population at random, while predators exploit that part of the prey population that is available, i.e. both detectable and accessible. The body condition of prey that are available may be lower than that of the whole prey population since prey which expose themselves to predation might be hungry (Dill & Fraser 1984, Lima 1988) and/or be diseased, injured or weakened (Curio 1976, FitzGibbon & Fanshawe 1989).

This paper examines whether prey caught by predators have a relatively poor body condition. The risk of fish and benthic animals being taken by predators on, or above, the surface depends on their own depth beneath the surface (e.g. Kramer et al. 1983, Zwarts & Wanink 1989). Hence the average weight of prey actually taken by these predators can be estimated provided that the body condition of prey at different depths is known (Wanink 1992). This possibility can be studied easily in some wader species feeding on estuarine macro-zoobenthos. Waders do not normally dig for prey so bill length limits the fraction that is accessible which, though variable, may be very small (Hulscher 1973, Reading & McGrorty 1978, Zwarts & Wanink 1984, Zwarts & Wanink 1989). In this paper, the food value of animals vulnerable to predation is compared to the average of the prey population as a whole.

Methods

All field data were collected on an intertidal flat along the mainland coast of the province of Friesland, Dutch Wadden Sea, (53°25′ N, 6°04′ E) over seven years, 1980-1986. The depth of the benthic animals was measured at low water with the aid of a circular corer as described elsewhere (Zwarts 1986, Esselink & Zwarts 1989, Zwarts & Wanink 1989). The depth of the Cockle *Cerastoderma edule* and of the clams *Mya arenaria*, *Macoma balthica* and *Scrobicularia plana* was defined as the distance between the surface of the mud and the upper edge of the shell. The burrow depth of the Ragworm *Nereis diversicolor* was measured as the distance between the surface and the deepest part of the burrow. The actual depth of *Nereis* was not measured because the worm moved in its burrow during sampling (e.g. Vader 1964, Goerke 1971, Esselink & Zwarts 1990). Instead, the greatest depth of the burrow was used as a measure of the depth to which it might retreat when attacked by a predator. Assuming worms can detect a predator, there is an inverse relation be-



It was always heavy work to measure the burying depth of bivalves in soft mud.

tween burrow depth and predation risk (Esselink & Zwarts 1989, Zwarts & Esselink 1989).

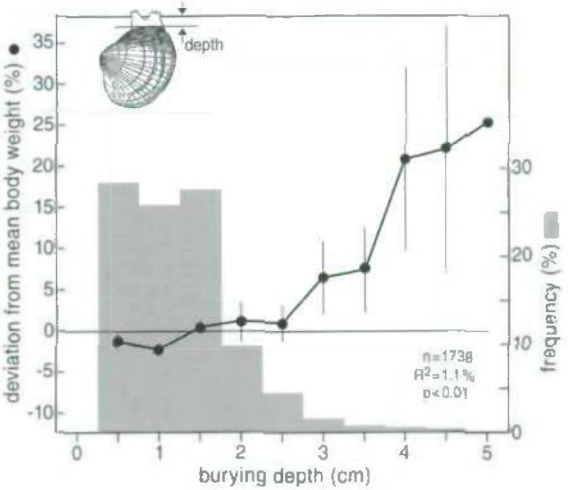


Fig. 1. *Cerastoderma edule* 20 mm long. Relative body condition (●, mean ± SE) as a function of burying depth. The histogram shows the depth distribution. Data are pooled for all seasons. The results of a one-way analysis of variance are given: burying depth explains a significant part of the variation in body condition.

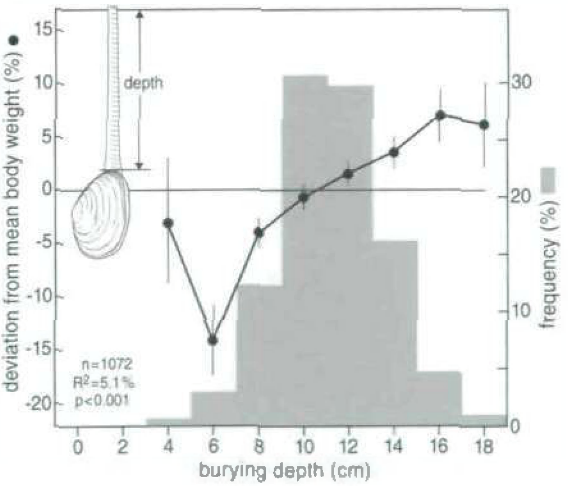


Fig. 2. *Mya arenaria* 40 mm long. Relative body condition (●, mean ± SE) as a function of burying depth. The histogram shows the depth distribution. Data are pooled for all seasons. The results of a one-way analysis of variance are given: burying depth explains a highly significant part of the variation in body condition.

The animals collected in the field were stored for up to 24 h in fresh sea water of 4 °C. The length of the bivalves was measured to the nearest mm along the anterio-posterior axis. The valves were opened by short immersion in boiling water and the flesh removed. We noted the infestation of *Macoma* by the parasitic trematode *Parvatrema affinis* (Swennen & Ching 1974). Since the length of a Ragworm is variable, we measured the maximum length of a worm moving in sea water (Esselink & Zwarts 1989). The flesh was dried at 70 °C for 2 to 3 days and burned at 550 °C for 2 h to determine ash-free dry weight (AFDW). All animals were weighed separately. Cracked bivalves and broken worms were not used. Energy values of prey were determined by bomb calorimetric analysis of dried flesh which had been deep-frozen for a maximum of 12 months.

Monthly mean body weights were calculated per cm size class for Ragworms and per mm size class for bivalves. The body weight of each individual animal was expressed as a percentage deviation from the monthly mean AFDW for the corresponding size class. This deviation from the average is called the relative body condition of the individual. The relation between relative body condition and depth was analysed only for a limited range of size classes: 10 to 30 mm in *Cerastoderma*, 30 to 50 mm in *Mya*, 10 to 20 mm in *Macoma*, 30 to 40 mm in *Scrobicularia* and 7 to 14 cm in *Nereis*. Nonetheless there was an increase in depth with body size even within these restricted size classes. Therefore all depths were adjusted relative to the average depth of an animal of a size halfway between the ranges of the size class (see Esselink & Zwarts 1989, Zwarts & Wanink 1989). After this transformation, both burying depth and relative body condition were independent of size, suggesting that the conversions had been made correctly. The data were analysed by using SPSS (Nie *et al.* 1975). Two-way analyses of variance revealed that the relationships between relative body condition and depth were different between seasons in *Macoma*, *Scrobicularia* and *Nereis*, but not in *Mya* and *Cerastoderma*. Accordingly the data for all seasons were pooled in the case of the latter two species, but treated separately for each season in the other three.

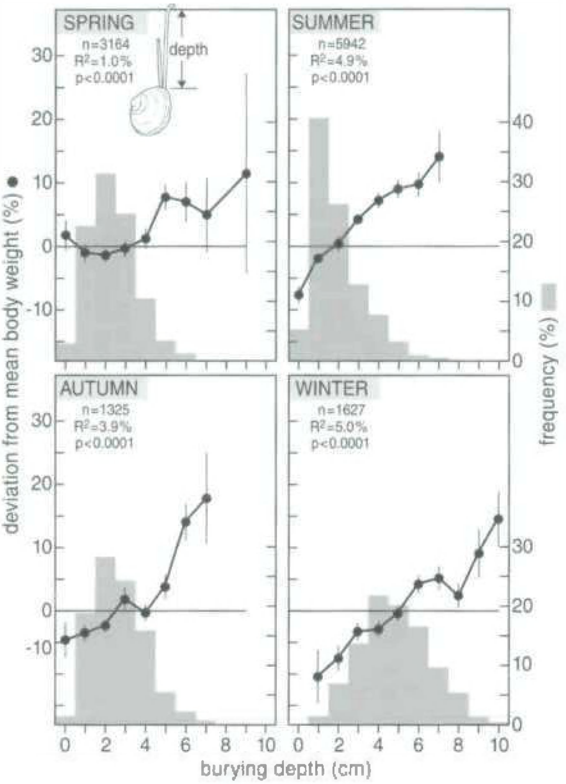


Fig. 3. *Macoma balthica* 15 mm long. Relative body condition (●, mean ± SE) as a function of burying depth during the four seasons. The histograms show the depth distributions. The one-way analyses of variance, given separately for each season, show that burying depth explains a highly significant part of the variation in body condition.

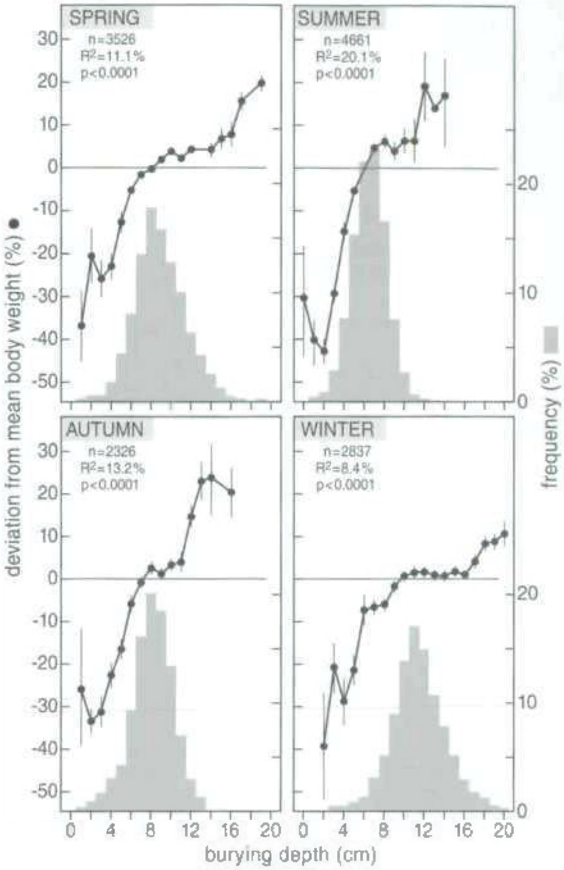


Fig. 4. *Scrobicularia plana* 35 mm long. Relative body condition (●, mean ± SE) as a function of burying depth during the four seasons. The histograms show the depth distributions. The one-way analyses of variance, given separately for each season, show that burying depth explains a highly significant part of the variation in body condition.

Results

Relative body condition per depth class

Most 20 mm *Cerastoderma* lived in the upper 1.5 cm of the substrate but the few animals burying to greater depths had a body weight which was 10-20% above the average (Fig. 1). *Mya* 40 mm long reached a burying depth of 10 to 12 cm. Shallow-living animals weighed c. 15% less than more deeply buried individuals of similar length (Fig. 2). The modal *Macoma* of 15 mm length had a burying depth of 1 cm in summer and 4 cm in winter, and a depth of 2 cm in spring and autumn. In all seasons, animals living at less than the average depth had a poor condition whereas animals at relatively great depths were in good condition (Fig. 3). The burying depth of *Scrobicularia* 35 mm long varied during the course of the year. It was greatest in winter (11 cm) and least in summer (6-7 cm). Individuals at a shallow depth had a relatively low body weight while those at relatively greater burying depths were heavy (Fig. 4). The burrow depth of a modal *Nereis* 10 cm long was 12 cm for most of the year, but it decreased to 10 cm in summer. Although fewer measurements were available, the same relationship between burying depth

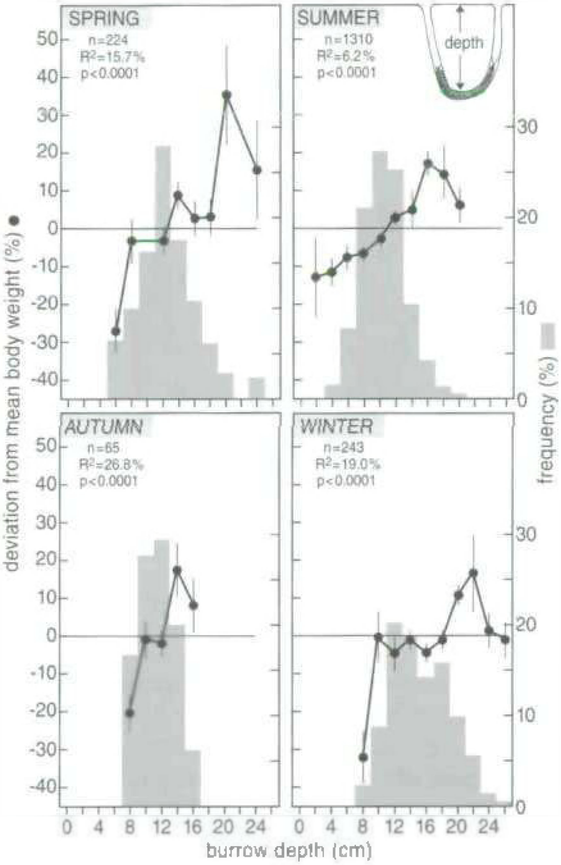


Fig. 5. *Nereis diversicolor* 10 cm long. Relative body condition (●, mean ± SE) as a function of burrow depth during the four seasons. The histograms show the depth distributions. The one-way analyses of variance, given separately for each season, show that burrow depth explains a highly significant part of the variation in body condition.

and relative body condition as was found in bivalves, was also found in this worm (Fig. 5).

The difference between the prey values of deep- and shallow-living animals would be even greater if deeper-burying animals of a given length also had a greater energy content per unit of mass, i.e. a greater 'energy density'. This would be expected if the lean, shallow-living individuals contained relatively less fat than the heavy, deep-living ones. No relationship was found, however, between energy density and burying depth in *Scrobicularia*, either in winter or in summer

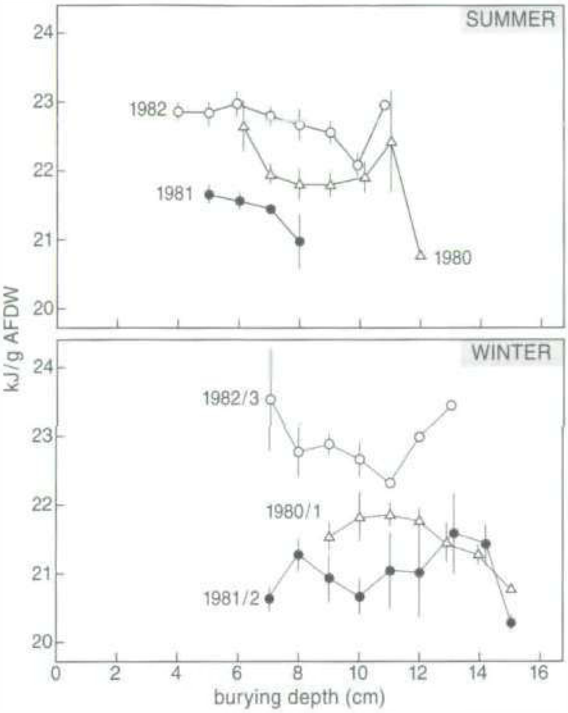


Fig. 6. *Scrobicularia plana* 35 mm long. Energy content (kJ ± SE) as a function of burying depth during three summers (12 sampling dates; upper panel) and three winters (14 sampling dates; lower panel). There are no significant relationships between depth and energy content; n = 146.

(Fig. 6). So in terms of energy, relative body mass condition remains a good predictor of prey value.

Relative body condition and depth for infested and uninfested animals

The Oystercatcher *Haematopus ostralegus*, the main predator of large *Macoma*, is able to distinguish prey infested with the parasitic trematode *Parvatrema affinis* (Hulscher 1982). Therefore the relationship between relative body condition and burying depth was also examined solely for non-parasitized individuals. For half a year, each *Macoma* was checked for infestation. With infested animals excluded, relative body condition was even less in the shallow-living animals (Fig. 7A). The reason is that infested individuals weighed on average 11% more, probably due to additional weight of the parasites, and a larger proportion they may take prey of relatively low value because they select *open* Cockles. First, Cockles in poor condition might be least able to shut their valves firmly when attacked. Second, Oystercatchers feed at low water when only a minority of Cockles do not close their valves (Twisk 1986). It is to be expected that it is predominantly those Cockles with low energy reserves that feed during the risky low water period.

The significance of our findings is that attempts to measure the daily intake rate of predators in the field may overestimate the energy consumed if the predators select relatively lean prey. Both Wanink (1992) and this paper demonstrate that the resulting overestimation of the food intake can be prevented by analysing the predator's selection criteria and determining the weight of prey likely to be taken. In some cases any selection for lean prey can also be tested directly by the analysis of prey remnants (e.g. FitzGibbon & Fanshawe 1989). Eutermoser (1961) found that man-trained falcons took twice as many diseased or injured crows as were shot by man, namely 40% against 21%. Healthy crows weighed 580 g compared with 490 g for the debilitated ones. Kenward (1978), also using the falconry technique, showed that the real weight of captured prey was 15% below the weight of the average pigeon in the population. An even larger discrepancy was found by Bijlsma (1990) who studied large falcon species preying upon Dunlin *Calidris alpina*. The average weight of birds in the population was 38 g, but the falcons caught juveniles which were extremely lean, some 26% below the population mean weight.

Predation risk and body condition

The depth to which a deposit-feeding bivalve *Scrobicularia* buries itself is a compromise between starvation and predation, and the compromise is different for each individual (Zwarts 1986). It is risky to be near the surface but by being there the animal enlarges the feeding range of its siphon on the surface. Siphon weight has a clear effect on burying depth, but if animals with the same siphon weight are compared, only *Scrobicularia* with a small siphon and in poor body condition should risk leaving the depth refuge to improve their feeding circumstances. Apparently animals with large energy reserves are able to survive a period of starvation and at the same time the siphon can grow.

Recently many papers have documented trade-offs that animals make between the risks of starvation and predation. There are a number of behavioural changes that reduce the risk of predation: an increase in scanning at the expense of feeding (Lendrem 1984, Glück 1987); a restriction of the total feeding time (Brown *et al.* 1988, Lima 1988); a change in habitat use (Stein 1977, Grubb & Greenwald 1982, Sih 1982, Cerri & Fraser 1983, Kramer *et al.* 1983, Werner *et al.* 1983, Holbrook & Schmitt 1988, Pitcher *et al.* 1988, Schlosser 1988) or a change in the diet (Dill & Fraser 1984, Lima & Valone 1986, Brown *et al.* 1988). Some papers have either argued theoretically or showed empirically that animals devote more time to predator avoidance when they are satiated (McCleerly 1978, Heller & Milinski 1979, Krebs 1980, Lima & Valone 1986, McNamara & Houston 1986, Weissburg 1986). Thus hungry fish flee less quickly from a predator than satiated ones (Dill & Fraser 1984, Morgan 1988); the vigilance of birds may decrease when they are hungry (Krebs 1980, Whitfield *et al.* 1988); birds with low energy reserves are more likely to feed during risky periods (Lima 1988); and birds may take more risks when their energy demands increase, e.g. due to premigration fattening up (Metcalfe & Furness 1984).

If starving animals do take more risks, predators would be expected to take prey with low energy reserves. Along with the results presented in this paper, there are two other reasons to think that such prey are more vulnerable to predators. First, starving animals are easy to catch because of their reduced speed (e.g. Yin & Blaxter 1987, Bijlsma 1990). Second, lean and subordinate individuals (Murton *et al.* 1971) feed more often in risky areas or during risky periods compared with dominant conspecifics (Fretwell 1972, Barnard 1980, Schneider 1984, Hegner 1985, de Laet 1985). Therefore we conclude that the selection of relatively lean prey by predators is a widespread phenomenon, which certainly deserves more attention in studies attempting to quantify the intake rate of predators in the field.

Chapter 7

DOES AN OPTIMALLY FORAGING OYSTERCATCHER OBEY THE FUNCTIONAL RESPONSE?

Jan Wanink & Leo Zwarts

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DOES AN OPTIMALLY FORAGING OYSTERCATCHER OBEY THE FUNCTIONAL RESPONSE?

We describe an experimental test of the optimal diet model. An Oystercatcher was offered bivalves *Scrobicularia plana* which were buried in the substrate at different depths. All prey were of equal length and thus of equal energy content. Since handling time increased with depth, deep-lying prey were less profitable. From the known increase of handling and search time with depth we were able to predict for each prey density which depth classes should be ignored by the bird so as to maximize its intake rate. The observed depth selection and intake rate were as predicted for the lower prey densities. At high prey densities the observed number of prey taken rose above the predicted intake rate. We suggest that the bird started to ignore closed bivalves with long handling times. The observed relationship between prey density and intake rate could not be described by Holling's type-2 functional response, because the handling time and the rate of discovery were density-related. A multi-species functional response is necessary to describe the intake rate of an optimally feeding predator.

Introduction

The functional response, the predation rate of an individual predator related to differences in prey density, has been much studied during the last decades. In the simple one-prey situation, the intake rate of the predator often rises decelerating to a plateau (type-2 functional response; Holling 1959). The curve has been described by the disc equation:

$$\frac{N}{T} = \frac{aD}{1 + aDh} \quad \text{(Holling 1959)} \qquad (1)$$

where N = number of prey taken, T = time predator and prey are exposed to one another, a = instantaneous rate of discovery, D = prey density and h = handling time.

Equation (1) can be simplified to:

$$\frac{N}{T} = \frac{\lambda}{1 + \lambda h} \qquad (2)$$

where λ = encounter rate: the inverse of searching time per prey item ($\lambda = aD$).

This one-prey model is based on the assumption that a predator takes every prey it encounters. However, predators are usually faced with a number of prey types from which they select their diet. When there are i prey types, Eq (2) can be rewritten as:

$$\frac{E}{T} = \frac{\Sigma \lambda_i E_i P_i}{1 + \Sigma \lambda_i h_i P_i} \quad \text{(Charnov 1976)} \qquad (3)$$

where E = energy intake, E_i = energy from one item of prey type i, P_i = probability the predator takes a prey item of type i after it is encountered, λ_i = encounter rate with prey type i and h_i = handling time of prey type i. It can be shown that to maximize the energy intake rate, $P_i = 1$ if $E/T < E/h_i$ and $P_i = 0$ if $E/T > E/h_i$ (Charnov 1976). So a predator should ignore a certain prey type when its profitability is below E/T and should take it if E_i/h_i is above that level. This prediction of the optimal diet model has now been confirmed in a lot of studies (see review by Krebs *et al.* 1983).

If the intake rate increases (because of rising prey density for instance), the model predicts exactly when a prey type should be dropped from the optimal set of prey types. This has been found in some studies (e.g. Davidson 1978, Pulliam 1980, Zwarts & Drent 1981). However, the functional response cannot yet be predicted quantitatively from the optimal set of prey types, since the encounter rate with the different prey types must also be known before Eq (3) can be solved.

This paper describes an experiment in which E, h and λ for the different prey types were quantified. This allowed us to compare the observed behaviour of a predator to the decisions it has to make to maximize its intake rate at different prey densities, and to describe the functional response of a predator feeding on several prey types.

We selected the Oystercatcher *Haematopus ostralegus* L. as the predator and the bivalve *Scrobicularia plana* (da Costa) as the prey. Oystercatchers locate buried bivalves like *Macoma balthica* L. and *Scrobicularia* entirely by touch. The number of prey encountered can be estimated by a simple random search model (Hulscher 1976, 1982). The prey types were bivalves of the same size and thus of the same energy content, but they were buried in the substrate at different depths. Handling time increases when the prey are buried at greater depth (Hulscher unpubl.) so varying prey depth also varies prey profitability. We selected a bird that showed the greatest increase in handling time for the less accessible prey so prey profitability could be manipulated most readily.

This paper attempts to answer the question whether the Oystercatcher obeys the functional response as predicted by Eq (3) and thus ignores less profitable prey as predicted by the optimal diet model. However, before the model can be tested, we have to show that the bird really searched at random for all prey densities.

Methods

The predator

We worked with an adult male Oystercatcher (bill length 70 mm; weight 460 g) caught near the Dutch Wadden Sea in April 1981. Before we conducted our experiments which took during 30 July-18 August 1981, the Oystercatcher had been foraging on *Scrobicularia* and *Mya arenaria* L. in pilot studies conducted by Hulscher in the same experimental set-up as we used.

The prey

Scrobicularia 35-36 mm long were dug out from the intertidal mudflats nearby. Their caloric value was 6.1 kJ (274 mg ash free dry weight; 22.2 J mg^{-1}). The prey were stored in fresh sea water at 4 °C for a period of up to 5 days, during which time they remained in perfect condition.

The experimental set-up

We used two cages connected by a small passage that we could open or close from our hide. A hide was placed next to the cage in which we had constructed an artificial mud-flat. The Oystercatcher was allowed to enter this cage only during the experiments.

The mudflat consisted of three plastic boxes in a row, filled up with mud taken from the intertidal flats and sieved to remove potential prey. The surface area was 0.663 m^2. The depth of the boxes was 12 cm, but by distributing at random 72 wooden blocks with a thickness of 1, 2, ..., 9 cm over the bottom, we made the depth of the mud-layer in the boxes irregular. The bivalves were placed on the bottom of the substrate in a vertical position. Prey depth was distance between the mud surface and the upper tip of the shell; since *Scrobicularia* of length 35-36 mm have a height of 3 cm, when placed vertical, we created 10 classes of prey depth (0, 1, ..., 9 cm). A grid system numbered in relation to the side and backside of the plastic containers allowed us to retrieve every buried prey afterwards.

The prey were buried in the substrate just before each experiment. All traces were erased from the surface to prevent the bird from using visual clues to locate the prey. The buried *Scrobicularia* quickly started feeding in their normal way by scraping their syphon over the mud surface. We never noticed the Oystercatcher responding to the moving syphons, thus reinforcing our opinion that the bird searched solely by touch. If necessary we added a little sea water to the mud surface so the bird could wash the flesh before eating as do Oystercatchers in the field.

We offered ten different prey densities. At the start of the experiment the Oystercatcher fed on an intermediate density (88 m^{-2}), after which we successively lowered the density to a level where the bird refused to search (Fig. 1). After that we increased the density progressively to the maximal value at the end of the experiment. This and not a random order was chosen to minimize the time the bird had to spend in adjusting its feeding behaviour to the changed prey densities.

The bird was not able to learn the location of the profitable prey because we changed the depth distribu-

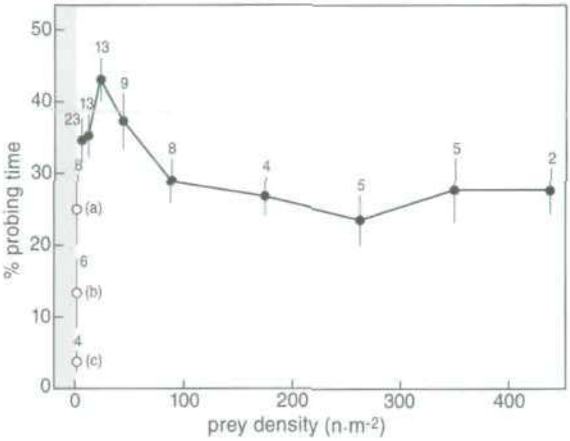


Fig. 1. Relationship between the time spent probing by the Oystercatcher (as a percentage of available foraging time minus total handling time) and the density (D) of *Scrobicularia plana*. Means ± SE (sample sizes indicated) are shown for all offered densities (●). During three successive sessions at $D = 2$ m^{-2} the bird found no prey at all and the amount of probing strongly decreased. Mean percentage probing time ± SE (○) per 5 min observation time is given for (a) first session (40 min); (b) second session after 40 min (30 min); (c) third session after 19 h (20 min).

tion completely before any session, and in most sessions the bird was only allowed to take a few prey.

We controlled hunger level by allowing the bird the same amount of food each day; viz. 35 g (AFDW): this is the mean food requirement of an Oystercatcher in captivity with a body weight of 460 g (Hulscher 1974). The extra food needed to make up this amount was given to the bird at the end of the daily experimental sessions in the form of opened Mussels *Mytilus edulis* L. and *Scrobicularia* in the non-experimental cage. Any remaining food was taken away every evening at 23.30 h. The experiments started each morning at 09.00 h, so the bird was deprived of food for 9.5 h. This is about 3 h longer than usually occurs in the field, so our captive bird was always motivated to feed.

The experimental sessions

The following were measured during a session:

(1) Available foraging time (duration of a session). The Oystercatcher always entered the experimental cage immediately after the passage was opened. After it had eaten the allowed number of prey, the passage was opened again and the bird driven out.

(2) Searching time. Since we assumed searching was by touch, only the period in which the bill was beneath the mud surface and no handling could be observed was scored as searching time. This 'probing time' amounted to 30-40% of the total time minus handling time (Fig. 1), but was lower at the lowest prey density offered (2 prey per m^2). In this case the bird did not find a prey after probing for 15 min, so this density was not used in the analysis.

(3) Depth of located prey. We noted the coordinates of prey that were found so that after the experiment we could determine its depth.

(4) Handling time. As with Oystercatchers feeding on *Macoma balthica* (Hulscher 1982) our bird handled prey in two ways: (a) opening the shell in situ, or (b) lifting the shell from the mud before opening. We always noted which method was used and measured total handling time by stopwatch. We also measured the lifting time (time needed to pull the shell to the surface and to put it down); cutting time (time needed to remove the flesh from the shell), and eating time (time needed to wash and swallow the flesh).

(5) Number of prey taken. The number of prey the bird was allowed to take in one session depended on prey density: one prey at $D = 2$ or 6 m^{-2}; two prey at $D = 12$ or 24 m^{-2}; three prey at $D = 44$ m^{-2}; five prey at $D = 88$ m^{-2} and ten prey (3-7%) from density 144 m^{-2} onwards. Because of the very low prey depletion, there was no need to correct for decreasing prey density during the course of a session (Rogers 1972). However, the fact that the number of prey the bird was allowed to take, increased with prey density, might have affected the decision making process of the Oystercatcher. As shown by Lucas (1983) the bird might lower its selection criterion when the remaining time available for feeding decreases. Since not time itself was limited, but the number of prey allowed, time constraints are unlikely to have affected the optimal diet choice in these experiments.

The analysis would have been complicated if the bird had increased its handling of searching time during long sessions because of decreasing motivation (Holling 1966). However, this appeared not to happen: in 21 of the 24 sessions in which the bird took 5 or more prey, there were no significant trends in the han-

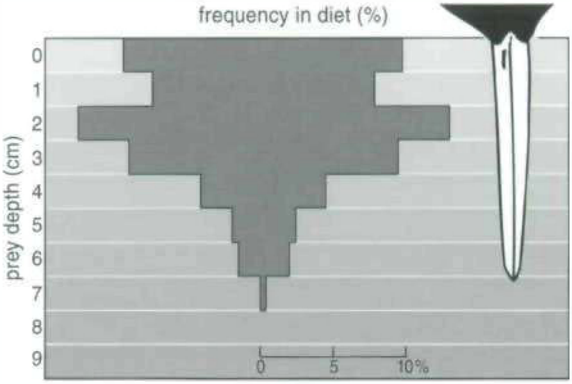


Fig. 2. Frequency distribution (%) of the selected depth classes in the Oystercatcher's diet. Prey on offer were distributed equally over 10 depth classes. Combined data of all experiments were used (n = 305).

dling time (Spearman rank correlation; $p > 0.05$). A significant increase ($p < 0.05$) occurred twice and a significant decrease ($p < 0.05$) once. In the 12 sessions where the bird took 10 prey and searching time per prey item was measured, there were no significant trends in searching time ($p > 0.05$) during the session.

After each session we checked the opened bivalves for remaining flesh, but fortunately our bird never performed partial predation.

Determining the effective touch area

In order to calculate the probability that a buried prey would be located by a randomly searching Oystercatcher, we needed to know the cross-sectional area (touch area) of the bivalve and of the bill tip. We measured the touch area of 47 specimens (range 33-46 mm) by pressing the bivalve vertically into modelling clay and measuring the impress of the largest cross section which, for our prey size (35-36 mm), was 1 cm below the top of the bivalve. The touch area was 0.22 ± 0.01 (mean ± SE) × shell length squared. We used Hulscher's (1982) value of bill tip touch area. The effective touch area was calculated as described by Hulscher (1982). The mean value for our prey size was 6.15 cm^2.

The film sessions

For a quantification of the duration and the depth of the probes, we filmed the bird in five 3 min sessions with intervals of 5 min between. A 16-mm camera was used, with a speed of 16 frames per s.

Analysis

SPSS (Nie *et al.* 1975) was used for all statistical analyses.

Results

Depth selection

Prey out of the reach of the bird's bill (7 cm) were never taken (Fig. 2). So prey density was defined as the prey number present in the depth classes 0-7 cm. Though prey were distributed equally over the depth classes, the deeper prey were taken less than the shallow prey (Fig. 2).

Handling time

Handling time increased with prey depth (Fig. 3), so prey profitability decreased with depth.

The analysis of the different components of han-

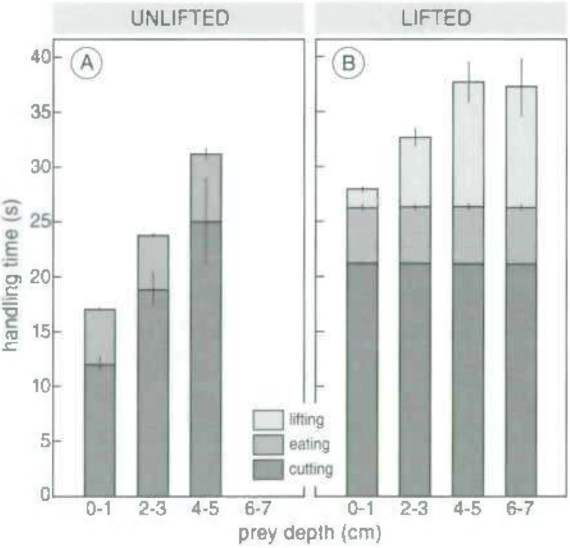


Fig. 3. Duration of handling components (mean cutting, eating and lifting time ± SE) as a function of prey depth, for **A.** Unlifted, and **B.** Lifted bivalves. The distinguished components are: cutting (dark), eating (grey) and lifting (light). See Table 1 for statistical analysis.

Table 1. Results of five one-way analyses of variance to test the effect of depth on several components of the handling time, for unlifted prey (n = 113; see Fig. 3A) and lifted prey (n = 186; see Fig. 3B).

	Unlifted prey		*Lifted prey*	
	R^2, %	p	R^2, %	p
Lifting time	-	-	11.2	0.026
Cutting time	12.0	0.001	1.0	0.838
Eating time	7.3	0.001	6.5	0.061

dling time, makes clear why the handling time is dependent on prey depth. For prey opened in situ, the Oystercatcher spent 25 s cutting out the flesh and 6 s eating a prey at 4-5 cm, but only 12 and 5 s respectively for a prey taken from the upper 0-1 cm (Fig. 3A). If the prey was lifted to the surface, cutting and eating time were independent of the depth, but the lifting time increased with depth (Fig. 3B; Table 1).

It would be expected that all prey from the upper 5 cm would be handled in situ if the Oystercatcher tried to minimize the total handling time. All prey should be lifted at depth 6-7 cm, because the increase of handling time with depth is greater for unlifted than for lifted prey (Fig. 3), by which the extrapolated handling time for unlifted prey at 6-7 cm would surpass the observed handling time for the lifted prey at that depth. The bird behaved as expected for prey at depth 0 and 1 cm (in situ) and 6-7 cm (lifted), but for the intermediate depth classes an increasing proportion of the prey were lifted (Fig. 4).

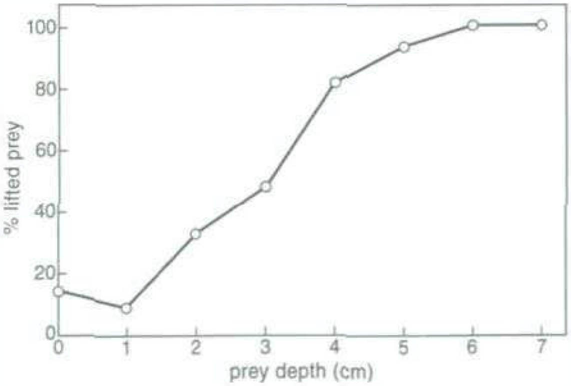


Fig. 4. Proportion of the prey being lifted (%), as function of prey depth.

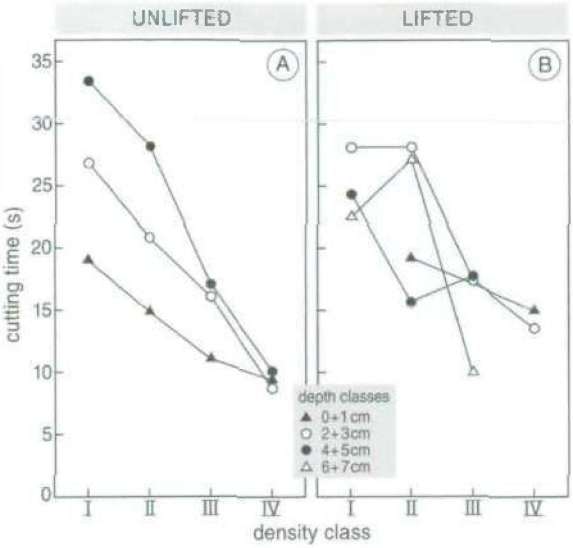


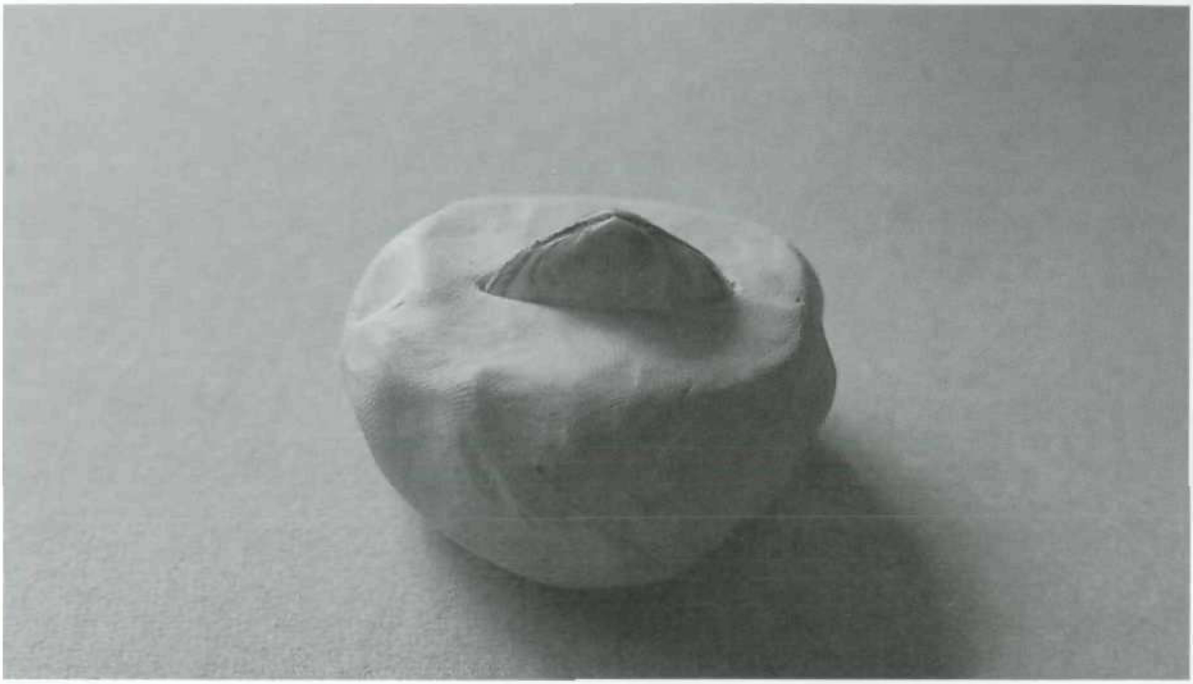
Fig. 5. Relationship between cutting time per depth class and prey density, for **A.** Unlifted prey, and **B.** Lifted prey. Four depth classes were distinguished: 0 + 1 cm, 2 + 3 cm, 4 + 5 cm and 6 + 7 cm; and also four density classes: 6 + 12 + 24 m^{-2} (I), 44 + 88 m^{-2} (II), 175 + 262 m^{-2} (III) and 350 + 437 m^{-2} (IV). See Table 2 for statistical analysis.

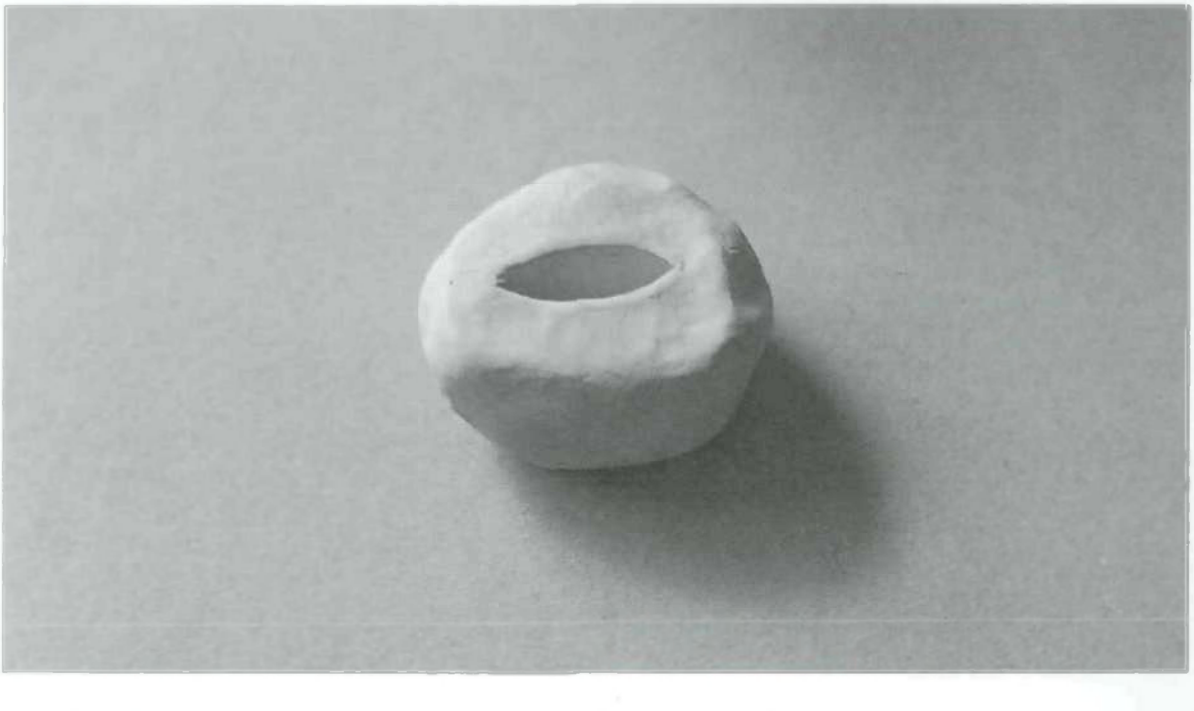
Cutting time at each depth class decreased as prey density went up (Fig. 5; Table 2), perhaps because the Oystercatcher rejected bivalves which were difficult to open when the prey density was high. It is possible that the bird was able to decide in a fraction of a second whether an encountered bivalve was gaping enough to stab into the shell immediately.

Lifting and eating time increased for deep-lying prey and were nearly independent of prey density (Fig. 6; Table 2). This was the other way around for cutting time. From this we can conclude that the profitability of the prey was related to the depth as well as to whether or not the valves were gaping. The depth was known, but the gaping of the bivalves could not be determined. Hence, the predictions of intake rates could be based on the depth-related profitability only.

Predicted encounter rate

Hulscher (1976, 1982) successfully tested his hypoth-





We used modeling clay to determine the surface area of bivalves measured in a horizontal plane in order to estimate the 'touch area' of a shell for a bird probing its bill vertically downward into the sustrate.

Table 2. Results of eight two-way analyses of variance to test the effect of depth and density on several components of handling time, for unlifted prey (Fig. 5A), lifted prey (Fig 5B.) and for all prey (Fig. 6). A hierarchical approach was chosen in which the higher priority was assigned to depth.

	Depth		*Density*		*Depth × density*	
	R^2, %	*p*	R^2, %	*p*	R^2, %	*p*
Unlifted prey						
cutting time	12.0	0.001	15.4	0.001	2.0	0.550
eating time	7.3	0.001	0.4	0.858	1.1	0.911
Lifted prey						
cutting time	1.0	0.813	14.7	0.006	4.9	0.484
eating time	6.5	0.054	6.1	0.067	4.9	0.437
All prey						
lifting time	31.6	0.001	2.1	0.039	4.2	0.035
cutting time	12.2	0.001	13.9	0.001	1.9	0.549
eating time	6.4	0.001	1.7	0.145	3.0	0.289
handling time	22.0	0.001	12.7	0.001	3.0	0.102

esis that Oystercatchers, feeding on *Cerastoderma edule* of *Macoma*, probe the substrate at random, when they locate their prey by touch. He calculated the probability (*P-loc*) that a bird would hit a prey at one probe from the formula:

$$P\text{-}loc = Ds/10^4 \tag{4}$$

where D = prey density (n m^{-2}) and s = mean effective touch area (cm^2).

To predict the encounter rate (λ) of the Oystercatcher with prey from a certain depth class, we must divide *P-loc* by the time it takes the bird to insert its bill to that depth into the substrate:

$$\lambda_i = P\text{-}loc_i / t_i \tag{5}$$

where λ_i = encounter rate with prey of depth class i (prey min^{-1}) and t_i = duration of a probe to a depth needed to locate a prey of depth class i (min). Since *P-loc* is based on the cross section 1 cm below the top of

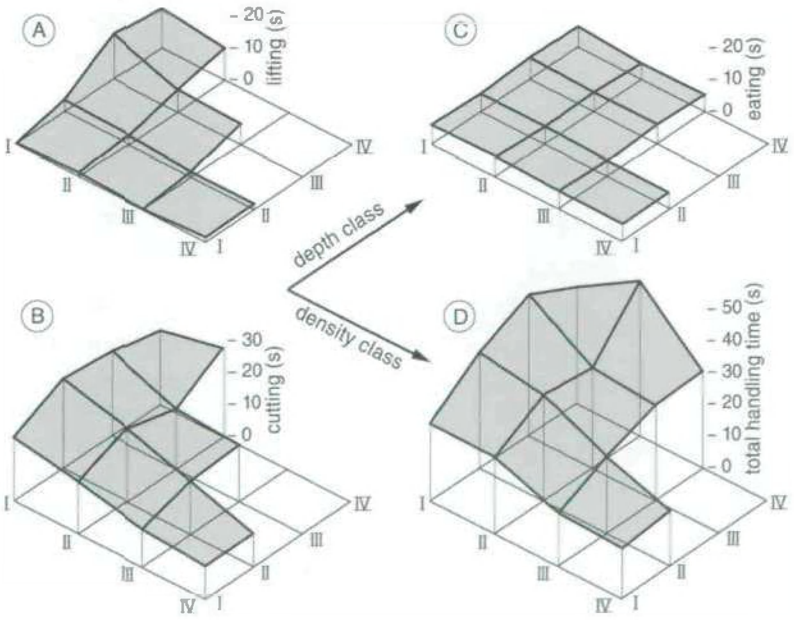


Fig. 6. A-D. The components of handling time related to prey density and burying depth. Where handling time is not shown we have no observations. Four density classes were distinguished: 6 + 12 + 24 m^{-2} (I); 44 + 88 m^{-2} (II); 175 + 262 m^{-2} (III) and 350 + 437 m^{-2} (IV); and also four depth classes: 0 + 1 cm (I); 2 + 3 cm (II); 4 + 5 cm (III); 6 + 7 cm (IV). See Table 2 for statistical analysis.

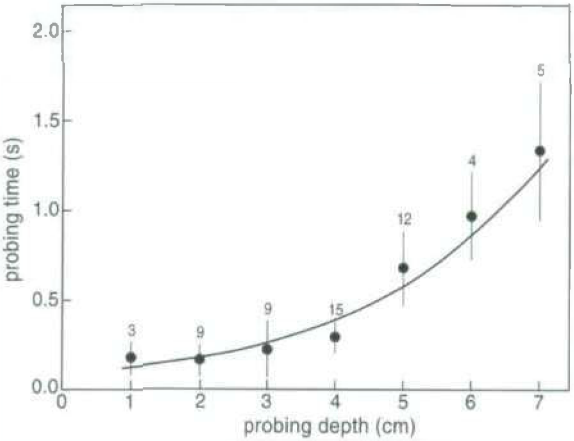


Fig. 7. Relationship between probing time and the depth of a probe. The values shown (means ± 95% C.L.; sample sizes indicated) are based on film analysis (resolution 1/16s) of searching behaviour at a prey density of 0 m^{-2}; ln(probing time) = 0.39 (probing depth) - 2.49 ($n = 7$, $r = 0.97$, $p < 0.005$).

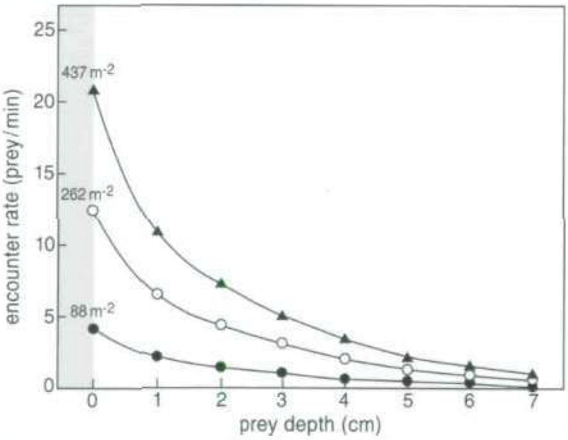


Fig. 8. Predicted encounter rate (λ) per depth class, for three different prey densities (prey m^{-2}).

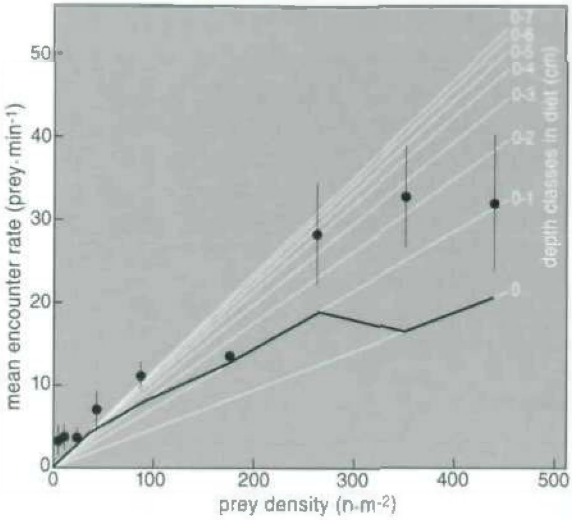


Fig. 9. Observed mean encounter rate (●) ± 95% C.L. The white lines represent values of λ ranging from no depth selection (upper line) to selection of depth class 0 cm only (lower line). The solid line gives the predicted λ for the bird selecting the optimal depth classes as calculated in Fig. 11.

the selected size class, we assume that the bird has to probe i+1 cm to locate a prey in depth class i. $P\text{-}loc_i$ depends on D_i only, because s is constant for all depth classes. D_i is known, so Eq (5) can be solved, for t_i has been measured using a film analyser (Fig. 7). The logarithmic increase of probing time with probing depth determines the way the predicted encounter rate decreased for prey which were buried at greater depth (Fig. 8).

Observed encounter rate

We never saw the Oystercatcher reject a prey it had discovered ('negative handling time'). That is why we used the observed searching time per prey taken to calculate the mean encounter rate. However, analysis of a high speed film showed that a prey can be located and refused too quickly to be noticed by an observer. We do not know how often we missed this kind of quick encounter, but it is certain that the observed encounter rate is an underestimation of the actual rate. Comparison of the predicted encounter rate for a random searching predator and the observed rate (Fig. 9) reveals that at low prey densities the Oystercatcher took all prey it found, whereas at high densities less prey than expected were taken, perhaps because the observer did not see encounters where prey were rejected.

Another explanation for the lower-than-expected rate at high prey densities was suggested by the film

The relationship between handling time and burying depth of bivalves, and between probing time and probing depth, was measured in a captive Oystercatcher that foraged on artificial mudflats, where we easily could manipulate density and burying depth of the prey.

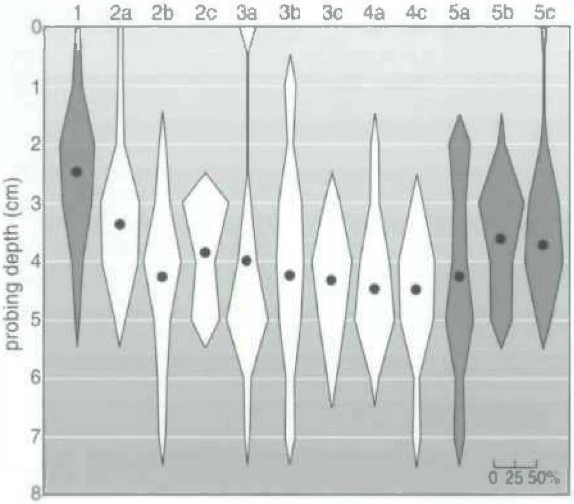


Fig. 10. Adaptation of the Oystercatcher's probing depth to prey density. Mean probing depth (●) and frequency distribution (%) are shown for five successive film sessions (3 min each; 5 min between the sessions) just after finishing the experiments at $D = 437\ m^{-2}$. Density during the film sessions 1 and 5 was $437\ m^{-2}$ and at sessions 2, 3, 4 it was $0\ m^{-2}$. Samples of 20 probes were taken from the start *a*, the middle *b* and the end *c* of each film. For film 1 the values of *a*, *b* and *c* were combined and at session 4b the bird made no probings at all.

analysis. The bird reduced its encounter rate with deep-lying prey by probing less deeply at high prey densities (Fig. 10). When the bird was allowed to feed for 15 min on a very high prey density, its mean probing depth at the end of this session was 2.5 cm only, against 4.5 cm at the end of the next three sessions (3 min each) when prey density was zero. Probing depth decreased gradually during the three minutes after the bird was given the same high prey density as in the initial session.

We conclude that the Oystercatcher took all prey it encountered at low prey densities, but when the prey density was high the bird became selective (1) by decreasing its probing depth and thus ignoring the deep-lying prey and (2) probably also by refusing a part of the prey that was encountered within the exploited layer of the substrate.

Predicted depth selection and intake rate

To solve Eq (3) we have to know λ_i, h_i and E_i. E_i has been set to 1, for all prey have the same energy value. The value of λ_i can only be estimated if it is known that the Oystercatcher took all prey encountered. This was definitely the case for the lowest prey densities (Fig. 9). That is why we selected the observations on handling time for the three lowest densities to measure the effect of depth on handling time:

$$h_i\,(s) = 3.7\,(\text{depth, cm}) + 24.9$$
$$(n = 72,\ r = 0.37,\ p < 0.005).$$

We are now able to predict the hypothetical intake rate, assuming an optimal selection of the depth classes by the Oystercatcher. The predicted intake rate for every possible selection level is presented in Fig. 11. The margin of the grey field in this figure connects the predicted maximal intake rates, and thus predicted depth selection for the different prey densities. According to these predictions the Oystercatcher should take all attainable prey for densities $6\ m^{-2}$ to $24\ m^{-2}$ but it should successively drop the deep-lying prey from its diet at higher prey densities. Only depth class 0 cm should be taken from density $350\ cm^{-2}$ onwards.

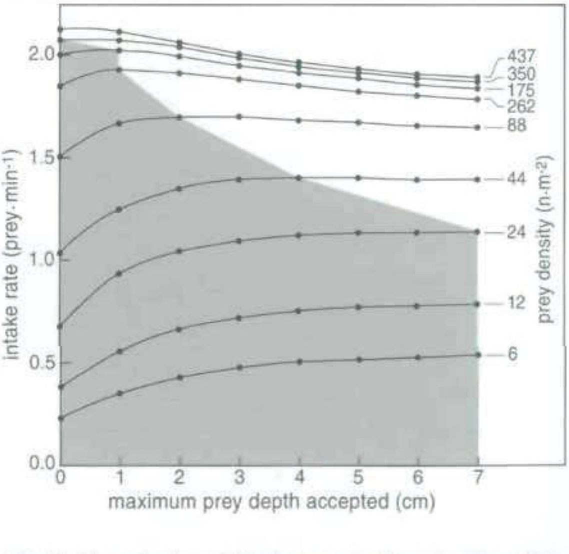


Fig. 11. The optimal set of depth classes predicted for all prey densities offered. The dots are solutions of Eq (3). The margin of the grey field connects values of maximal intake rate for the different prey densities. So, to maximize its intake rate, the Oystercatcher should take all the depth classes within the grey field and reject deeper lying prey.

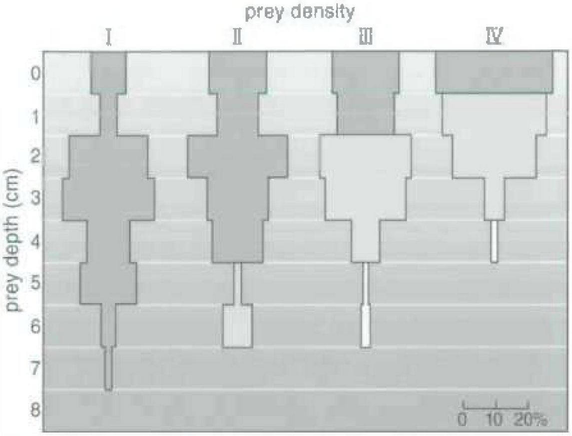


Fig. 12. Frequency distribution (%) of depth classes in the Oystercatcher's diet at four density classes: 6 + 12 + 24 cm^{-2} (I); 44 + 88 m^{-2} (II); 175 + 262 m^{-2} (III) and 350 + 437 m^{-2} (IV). From Fig. 11 we have calculated which depth classes the bird should take to obtain the maximal intake rate (dark grey) and which classes it might add to the diet (grey) before reducing its intake rate by more than 5% (white).

Observed depth selection and intake rate

Figure 12 shows the observed depth selection for four prey density classes. As predicted, the bird took all depth classes at the low prey densities and ignored the deep-lying prey when the density was high. The bird did not show exactly the predicted change in rejection threshold. However, the deviation is small and, as shown in Fig. 11A, deviation of 2-3 cm from the predicted depth selection limit hardly reduces the intake rate. The bird added in fact only those depth classes to the optimal set by which the intake rate was reduced not more than 5%.

The predicted intake rate for the bird selecting exactly the optimal set of depth classes fits quite well with the observed values for the five lower prey densities (Fig. 13). However, from density 175 m^{-2} onwards, the number of prey taken by the Oystercatcher rises above the predicted intake rate.

The predicted intake rate was based on the assumption that all prey must be taken from the optimal set of depth classes. However, by using as second selection criterion -ignore prey which are closed or not gaping enough, and so shorten the cutting time- the Oystercatcher was able to reduce the handling time and so increase its intake rate at higher prey densities by as much as 50% of the expected value. A density-related selection of shells which could not be stabbed immediately has already been suggested by Hulscher (1976) for an Oystercatcher feeding on Cockles all buried at the same depth.

We suggest that at prey densities below 175 m^{-2} optimal depth selection is the only decision rule, but above that density selection on depth as well as on 'easy' bivalves is optimized.

Discussion

Rate of discovery *a*

The disc equation of Holling (1959) is attractive because of its simplicity. The intake rate depends on two factors only, which should both be constant for all prey densities: the handling time and the rate of discovery *a*. Since *a* equals λD^{-1} (cf. Eq 2), *a* will be density-independent only if the search time increases n^{-1} times when prey density increases *n* times. This was the case in the 'touch experiment' of Holling (1959) but in the 'sound experiment' described in the same paper, *a* decreased when density went up. Holling solved this problem by dividing the search time into two compo-

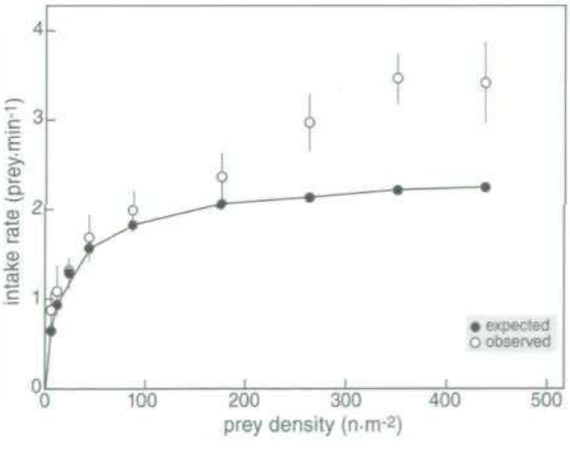


Fig. 13. Relationship between intake rate and prey density. Predicted values (●) are compared to the mean values observed ± 95% C.L. (○).

nents, real search time and an identification time. Assuming that the rate of discovery based on real search time was constant, Holling could estimate the identification time, which was then added to the handling time.

The reasoning of Visser & Reinders (1981) is also based on the idea that a part of the search time in reality belongs to the handling time. They assume there is a waiting time after a prey is swallowed (an internal handling time) during which the predator is unable to eat a new prey.

In the case of our Oystercatcher, it is unlikely that a recognition time or a waiting time after handling a prey, could explain the density-dependence of a. The recognition time must have been very short; prey which were located but refused were missed by us and could only be detected by film analysis. Also the waiting time cannot have been important. The bird was able to swallow prey after prey with very short intervals in between when we offered it opened bivalves, and we also saw no digestive pauses when the bird was eating prey containing much more flesh that the prey used in the experiments.

A decrease of a at higher prey densities could also be due to the predator spending less time in actively searching. For this reason, van Lenteren & Bakker (1976) stressed the importance of behavioural observations in the analysis of functional responses. Hassell *et al.* (1977) showed indeed the positive effect of the search effort on a.

We tried to minimize the effect of prey density on searching intensity by defining search time only as the time the bird is actively probing the substrate. In fact, percentage probing time if fairly constant over a large range of densities (Fig. 1), but we cannot rule out the possibility that the probing rate -and thus the relation between probe duration and probing depth (Fig. 7)- is related to prey density.

There are two other problems in estimating a: how to measure effective prey density and how to estimate the encounter rate. Measured prey density will be too high when part of the prey is unavailable to the predator (Murton 1971, Erichsen *et al.* 1980, Myers *et al.* 1980, Zwarts & Wanink 1984, this study: Fig. 2). This will not affect the calculation of a if the available fraction is the same for all densities, but when the selection criterion is related to prey density (Figs. 9 and 12) the effective prey density has to be estimated separately for each prey density.

Furthermore, some of the available prey may be ignored, thus making it still more difficult to determine encounter rate. In this experiment, as in most other studies, the encounter rate is derived from the number of prey attacked, but if some were ignored, encounter rate would be underestimated. This error becomes systematic and more serious if more prey are rejected at particular prey densities, as described by Hassell *et al.* (1976).

Optimal foraging theory predicts that the predator becomes more selective as prey density rises (MacArthur & Pianka 1966). Using the optimal foraging model of Charnov (1976) it is possible to predict for all prey densities the number of prey which should be ignored (Krebs *et al.* 1983, this study: Fig. 11).

Handling time *h*

The disc equation can only be solved if the handling time is independent of prey density (Holling 1959). Several studies have shown, however, that h decreased with increasing prey density (see review of Hassell *et al.* 1976). A common explanation of this might be a change in the feeding strategy of the predator. In cases where the predator eats the prey in several bites, it has been found that h decreases with higher prey density, because the prey is consumed completely at a low density whereas at high densities only the first, most profitable bites are taken (Haynes & Sisojevic 1966, Cook & Cockrell 1978, Giller 1980). Handling time also decreased in a predator which could act as a parasite too (Collins *et al.* 1981). Since an oviposition attack took less time than the consumption of a prey, and the proportion of oviposition attacks went up with prey density, the mean handling time decreased.

Hulscher (1976) showed a decreasing handling time at high prey densities in an experiment where an Oystercatcher fed on Cockles of the same size and with a same availability (just below the surface) (Fig. 14F). Hulscher suggests that eating time was constant but that cutting time decreased with prey density. At a high density the Oystercatcher started to select the Cockles 'where the right information concerning the orientation of the Cockle was known', this information is important for the feeding bird because the cutting time 'depends upon the extent to which the posterior

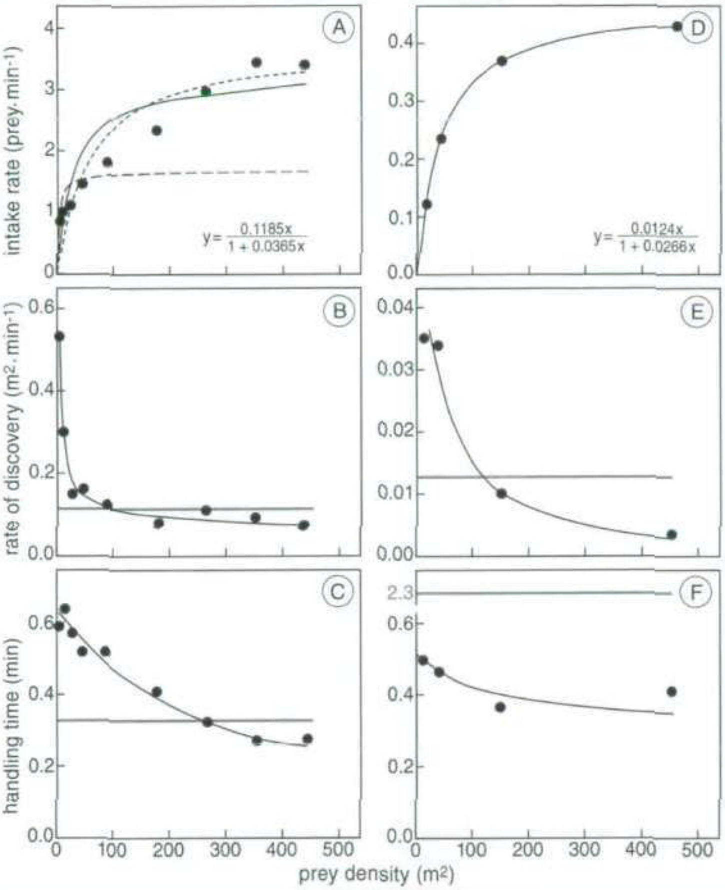


Fig. 14. Functional response and its components (solid lines) for this study (**A.**, **B.**, **C.**) and for Hulscher (1976) (**D.**, **E.**, **F.**). The grey horizontal lines in B, C, E and F show the values as predicted from the disc equations. For A we have constructed two curves, using the measured values of *a* and *h* for the lowest and the highest prey density (broken lines).

adductor muscle was severed at the first jab' (Hulscher 1976, p. 307).

The Oystercatcher in our experiment also became *more selective when prey density went up.* The bird reduced its handling time by ignoring deep-lying prey (shorter or no lifting time) and probably also by selecting prey it could stab into immediately (less cutting time).

Prey selection and functional response

A type-2 functional response is determined by the two constants *a* and *h* (Holling 1959), but as shown before (Fig. 14) a type-2 curve can occur where *a* and *h* are density-related. With the exceptions of Holling (1959) and Hulscher (1976), we could find no other papers where *a* and *h* were measured at all prey densities. We have found, however, several studies where the observed mean handling time could be compared to *h* as derived from the observed plateau-value of the functional response (Table 3). In most cases the measured *h* *was too small to explain the asymptotic value of the* feeding rate. The difference between predicted an observed handling times appeared to be greater in field studies than in the relatively simple experimental situations.

Krebs *et al.* (1983) suggested a model based on optimal diet theory to explain the limitation of feeding rate at the asymptote of the functional response. They constructed a family of functional responses for the different size classes of prey. If the predator takes only the largest (most profitable) prey, the curve will have a low asymptote since the handling time of large prey is high. Adding smaller prey to the diet will increase the asymptotic value. Optimal foraging theory predicts an

Table 3. Handling times (s) predicted from functional responses, and values observed. References: (1) and (2) Elliot 1983, (3) Green 1978, (4) Collins *et al.* 1981, (5) Feare *et al.* 1974, M.R. Berger & R. Veldhuis unpublished, (6) Hulscher 1976, (7) Sutherland 1982, (8) this study, (9) and (10) Holling 1959, (11) Davies 1977, (12) Tinbergen 1981, (13) Goss-Custard 1977a, (14) Goss-Custard 1977b.

Ref.	*Predator/Parasite**	*Prey/Host**	h_{pred}	h_{obs}	*Method*
(1)	*Agriotypus armatus**	*Silo pallipes**	1547	1032 - 1368	Expt.
(2)	*Agriotypus armatus**	*Silo pallipes**	979	1032 - 1368	Field
(3)	*Alauda arvensis*	weed seeds	11.3	1 - 2	Field
(4)	*Aphelinus basizonus**	*Drepanosiphum platanoidis**	829	456 - 1296	Expt.
(5)	*Corvus frugilegus*	grain	9.0	0.5-0.9	Field
(6)	*Haematopus ostralegus*	*Cerastoderma edule*	139.5	21 - 29	Both
(7)	*Haematopus ostralegus*	*Cerastoderma edule*	75.0	19 - 29	Field
(8)	*Haematopus ostralegus*	*Scrobicularia plana*	19.6	16 - 38	Expt.
(9)	*Homo sapiens*	sandpaper discs	2.8	2.4-2.6	Expt.
(10)	*Homo sapiens*	sandpaper discs	5.1	2.9-3.1	Expt.
(11)	*Motacilla alba/flava*	Scatophagidae	1.7	<1 - 10	Field
(12)	*Sturnus vulgaris*	*Tipula paludosa*	26.9	1.4-3.8	Field
(13)	*Tringa totanus*	*Nereis diversicolor*	12.0	0.4-6.0	Field
(14)	*Tringa totanus*	*Corophium volutator*	2.2	0.2-0.6	Field

increase in selectivity when prey density rises, so the predator is expected to jump successively to lower feeding rate curves.

In our experiment the most profitable prey took the shortest time to handle, since the energy contents of all the prey were equal. We therefore expected the bird to jump to higher plateau-values when prey density increased. This was found indeed, but, as can be seen from Fig. 13, the Oystercatcher managed to increase its intake rate at the higher prey densities even above the prediction based only on optimal depth selection. By selecting gaping shells the bird reduced the handling time and thus the asymptote of the intake rate curve went up even more.

Since we measured a and h for all offered prey densities, we could construct a family of functional responses based on real values for a and h. Figure 14A shows the curves, extrapolated from the lowest and the highest density. In this way we get a better fit with the observed intake data than when the disc equation was used to predict the functional response.

Chapter 8

PREY SIZE SELECTION AND INTAKE RATE

Leo Zwarts, John T. Cayford, Jan B. Hulscher, Marcel Kersten, Patrick M. Meire & Patrick Triplet

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PREY SIZE SELECTION AND INTAKE RATE

Oystercatchers ignore small bivalves. These prey have a lower probability of being encountered, but this alone is not sufficient to explain why they are not taken. Small bivalves are not profitable given the time needed to open and eat them, and consequently they allow only low rates of return of energy. The size rejection threshold is not fixed, but varies according to the average intake rate during feeding. Oystercatchers increase their intake rate in two ways: they reject unprofitable prey and they adjust their searching behaviour in order to increase the encounter rate with the more profitable prey. The intake rate depends predominantly on the prey size taken. When large prey are present, the intake rate is high (3 to 4 mg dry flesh s^{-1}) and small and medium-sized bivalves are rejected, due to their lower profitability. When only small prey are available, the intake rate decreases to 1 mg s^{-1}. The daily consumption varies between 36 and 50 g dry flesh. This means that even when the birds feed at the average year-round rate of 2 mg s^{-1}, 5 h feeding a day is sufficient to meet their normal maximum daily energy expenditure. Ninety-two percent of the intake rates observed in the field exceeded the rate at which the gut of Oystercatchers is able to process food (0.66 mg s^{-1}). Since processing rate forces the bird to stop feeding when their oesophagus is full (12 g), Oystercatchers must stop feeding for digestive pauses when their intake rate is high. Due to this digestive bottleneck, they have to feed 10 hours a day if there is one feeding period, or 8 hours a day if there are two feeding periods, digestive pauses included, to reach the minimum daily consumption of 36 g, required at thermoneutrality.

Introduction

Do predators take all the individual prey belonging to one species that they encounter, and if not, to what degree are some prey under-represented in the diet and why? These questions are important in every study of the interaction between predators and their food supply. This chapter first analyses the degree to which the selection of prey sizes within one prey species by Oystercatchers can be understood as a passive process in which a randomly searching bird takes all the prey it encounters; this will be referred to as 'passive size selection'. As we shall see, however, Oystercatchers reject certain size classes of prey which they actually encounter, and hence there is also 'an active size selection'. The rules that Oystercatchers obey when selecting size classes actively, and whether these can be derived from optimal foraging models, are then discussed. Finally, the chapter discusses how Oystercatchers maximize their intake rate and how the rate at which food can be processed sets a limit to the food intake.

The analyses are restricted to five bivalve species: the Edible Mussel *Mytilus edulis* and the Edible Cockle *Cerastoderma edule* and the three clams: *Macoma balthica*, *Scrobicularia plana* and *Mya arenaria*. There are three main methods for obtaining data on size selection by Oystercatchers eating these prey species: recovering opened and emptied shells, direct visual observations and size-specific depletion. Shell recovery is particularly convenient and is possible because, having eaten the flesh, the birds leave the opened shell behind. These are recognizable as prey by the damage done to the shell and/or by its position in the substrate. Recently emptied bivalves also contain some flesh, sometimes along the mantle edge and always where the adductors are attached on the valves. The collection of these shells is therefore an easy, reliable method of obtaining a frequency distribution of all the size classes taken by Oystercatchers in a certain area, although there may be a sampling bias in the case of Mussels (Ens 1982, Cayford 1988). It is thus no coincidence that there are more papers on prey size selection in Oystercatchers than there are in all the other wader species put together.

Predicted 'passive size selection'

If Oystercatchers locate prey beneath the surface of the substrate by randomly probing, the probability of a prey being encountered can be calculated from prey density provided that two other factors are also taken into account. Firstly, a proportion of the prey may live out of reach of the bill. Secondly, the probability that a prey is actually hit by the bill tip is a function of its size, or more precisely, the surface area the prey presents from above; this is referred to here as the 'touch area'. The observed size selection may only be compared with the predictions of passive size selection when the calculated encounter rate with prey of different size classes takes both these considerations into account (Hulscher 1982).

The proportion of prey that lie buried beyond the reach of the bill depends on bill length and on the depth to which Oystercatchers insert it. Bill length in Oystercatchers varies between 6.5 and 9 cm. When Oystercatchers extract bivalves from the substrate, they can probe so deeply that the base of the bill is pushed 0.5 cm below the surface. Even then, large *Mya* live out of reach (Zwarts & Wanink 1984, 1989) and the majority of large *Scrobicularia* are also inaccessible, at least during the winter (Zwarts & Wanink 1989). But, in fact, Oystercatchers do not usually probe to the maximum depth. The precise probing depth differs between prey species, but is, on average, always less than the bill length. Oystercatchers probe to a mean depth of 4 cm when searching for deep-living *Scrobicularia* (Wanink & Zwarts 1985), 3 to 4 cm when feeding on the more shallow-living *Macoma* (Hulscher 1982), and only 0 to 3 cm when taking Cockles which are found very near to the surface (Hulscher 1976). The fractions of each size class of each clam species living in the upper 4, 6 and 8 cm of the substrate are shown for the winter and summer period in Fig. 1. The data show, for example, that whereas most *Macoma* are accessible to Oystercatchers in summer, less than half are in winter. As Cockles live in the upper 4 cm of the substrate, with the majority being in the upper 1 or 2 cm, they are within reach of the Oystercatcher's bill throughout the year.

For Oystercatchers probing vertically downwards, the 'touch area' of a bivalve is equivalent to its surface area, measured in the horizontal plane (Hulscher 1982). This surface area has been determined by photographing from above the bivalve in its natural position with the substrate removed (Hulscher 1982) or by pressing the bivalve vertically into modelling clay (Wanink & Zwarts 1985, Zwarts & Blomert 1992). The 'touch area' of all bivalve species is elliptical, with the Cockle being the most circular and *Scrobicularia* the most slender, with *Macoma* and *Mya* lying between. The first estimates of the 'touch area' in Cockles (Hulscher 1976) and *Scrobicularia* (Wanink & Zwarts 1985) were given as a function of the squared length but, when calculated over a larger range of size classes, a better fit was obtained with exponents slightly larger than 2, since small shells are particularly slender (Zwarts & Blomert 1992). The details of this exponential increase of 'touch area' with shell size are given in Table 1.

The real, or 'effective', touch area for a probing

Table 1. The 'touch area' of the shell (mm^2) as a function of its length (mm). The 'touch area' is defined as the surface of a bivalve in its natural position, measured in a horizontal plane; from Zwarts & Blomert (1992). The corresponding surface area of the 'effective touch area' is equivalent to the surface area (set to a circle: πr^2) enlarged with the surface area of the bill tip itself (11 mm × 1.4 mm = 15.4 mm^2; Hulscher 1982) and the combined effect of the surface areas of bill tip and bivalve ($11 \times 2\pi + 1.4 \times 2\pi = 24.8\pi$ mm^2); from Habekotté (1987) and Zwarts & Blomert (1992). As an example, the surface areas of the 'touch area' and 'effective touch area' (mm^2) of two size classes (10 and 25 mm long) are given.

Species	*Equation*	*Touch area*		*Effective touch area*	
		10 mm	*25 mm*	*10 mm*	*25 mm*
Macoma balthica	$0.151\ mm^{2.16}$	22	87	158	334
Scrobicularia plana	$0.154\ mm^{2.09}$	19	129	80	287
Mya arenaria	$0.125\ mm^{2.04}$	14	89	66	221
Cerastoderma edule	$0.340\ mm^{2.07}$	40	266	128	494

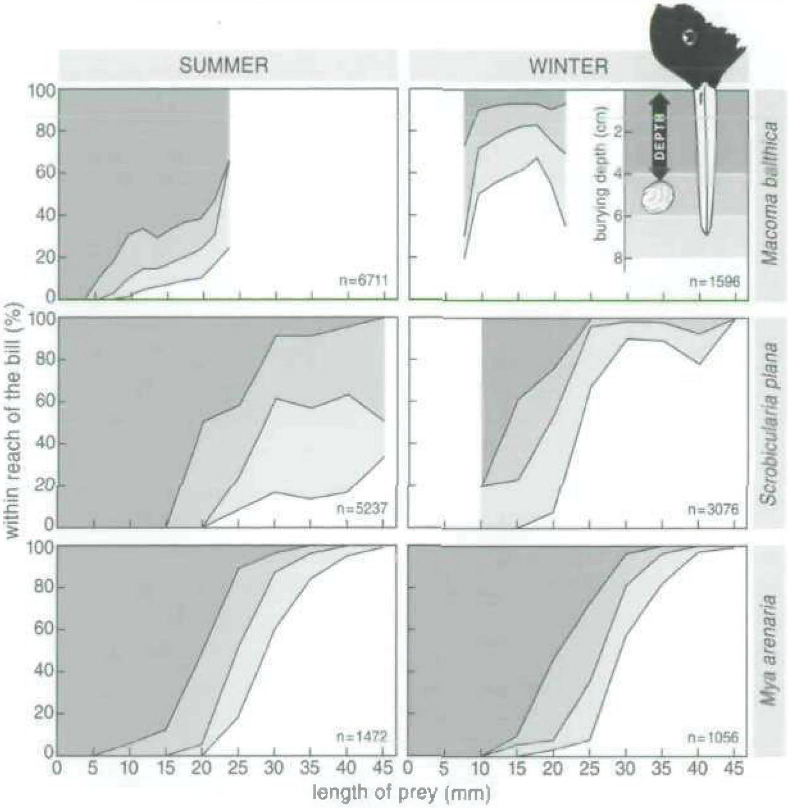
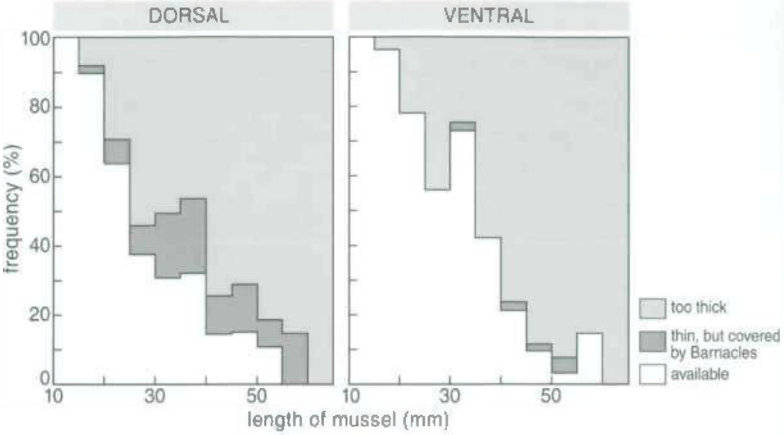


Fig. 1. Proportion of clams of three species living in the upper 4, 6 & 8 cm of the substrate as a function of shell size. The results are given separately for the summer months, July to September (left), and the winter period, November to March (right). The numbers of clams in the samples are shown (n) (Zwarts & Wanink 1989).

Oystercatcher is actually larger than the 'touch area' defined by the equations in Table 1, because the surface area of the bill tip needs also to be taken into account (Hulscher 1982). Probing Oystercatchers leave behind imprints in the mud (see photo in Davidson 1967), enabling the bill-tip surface area to be measured. With the small space between the slightly opened upper and lower mandibles included, the probing surface equals a rectangle measuring 11 × 1.4 mm (Hulscher 1982). As the touch area depends on the surface area of the shell and not on its shape, for simplicity it is treated as a circle. The 'effective touch area' is then equivalent to the 'touch area' (πr^2) enlarged by the surface area of the bill tip. Table 1 shows how to calculate 'effective touch area' from 'touch area' and gives, as an example, the surface areas for two size classes.

Mussel-eating Oystercatchers occasionally probe by touch, but usually appear to feed by sight (Hulscher 1996). This makes it impossible to use the method discussed above to measure the probability that prey will be detected at random. Ens (1982) argues that prey encounter rate in visually hunting Oystercatchers may also be a function of the surface detection area of the prey, and thus about equivalent to the squared length of the shell. Other papers on size selection of mussel-eating Oystercatchers have followed the same assumption (Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford & Goss-Custard 1990) and it will also be used here. Studies on mussel size selection have tended to focus on hammering Oystercatchers because it is possible to calculate the available fraction, i.e. those shells that are not covered with barnacles and which are thin

Fig. 2. Larger Mussels are less available than small ones to Oystercatchers hammering on the dorsal or ventral side of the shell, either because the shell is covered by barnacles or too thick to break Cayford & Goss-Custard (1990).



enough to break (Fig. 2). Since Mussels often grow on top each other, an unknown proportion of the Mussels are not actually visible to sight-hunting Oystercatchers (Goss-Custard *et al.* 1993, Meire 1996b, 1996c). This may affect the observed size selection, since large Mussels tend to cover small Mussels (Hulscher 1964, Norton-Griffiths 1967, Goss-Custard *et al.* 1993).

Observed size selection

Macoma balthica

Oystercatchers feeding on *Macoma* detect them by touch. Size selection in birds feeding on this clam has been studied on many occasions. To construct Fig. 3, the frequency distributions of the mm classes taken and of those on offer in the substrate were combined from all the studies because the size class distributions taken and on offer were similar, apart from the very large variation in the density of prey smaller than 10 mm long. However, these small *Macoma* were never selected, regardless of their contribution to the total prey population. On average, 81% of the prey taken were 15 to 20 mm long, compared with only 33% on offer at all depths in the substrate (Fig. 3A). In fact, Oystercatchers take *Macoma* only from the upper 4 cm

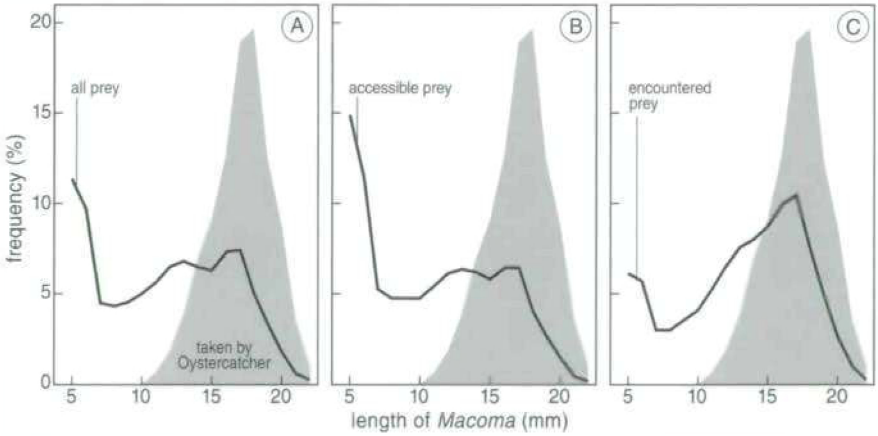


Fig. 3. Size classes of *Macoma balthica* selected by Oystercatcher (shaded) compared with the distribution of size classes in the prey population (solid line): **A.** Total prey population; **B.** Prey population in the upper 4 cm (see Fig. 1); **C.** Prey population in the upper 4 cm, corrected for 'effective touch area' (see Table 1) and so actually encountered. The graphs give the averages of 26 studies in which prey on offer and those taken were compared: Blomert *et al.* (1983), Goss-Custard *et al.* (1977b), Habekotté (1987), Hulscher (1982 and unpubl.), Triplet (1989a).

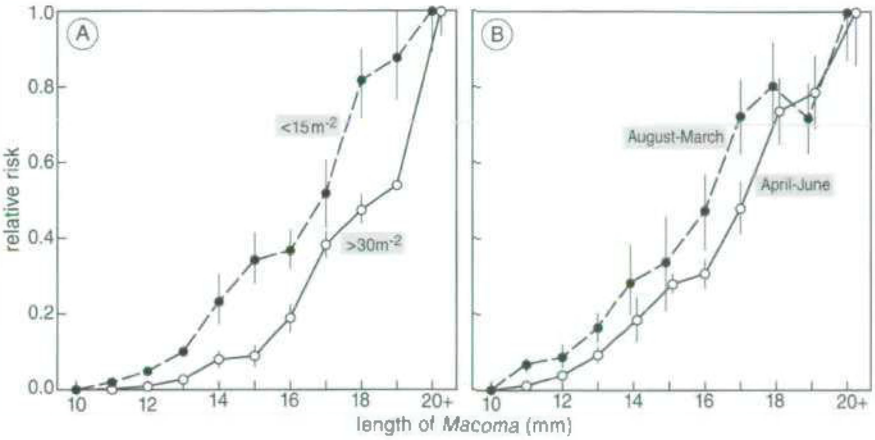


Fig. 4. *Macoma balthica*. The relative risk of bivalves of different lengths being taken by Oystercatchers, calculated as the ratio per size class of relative number of prey taken to the relative number in the prey population; data from Fig. 3. **A.** Relative risk (± SE) when the density of large *Macoma* (18 to 22 mm long) was lower than 15 m^{-2} (n = 10) or higher than 30 m^{-2} (n = 4); **B.** Relative risk (± SE) in April to June (n = 10) and in August to March (n = 6). To rule out the confounding effect of prey density shown in A., a selection is made for studies where the density of *Marcoma* 18 to 22 mm long is less than 30 m^{-2}.

of the substrate (Hulscher 1982). When the frequency distribution of the size classes actually within reach of the bill is calculated (Fig. 3B), the selection for larger size classes is even more pronounced because all small prey, but only a small proportion of the large prey, are accessible. But when the increase in effective touch area with size (Table 1) is also taken into account, the probability that small prey will be encountered dropped to a third of the previous value. Even so, there still remains a remarkable deviation between the observed size selection and that expected of a randomly probing Oystercatcher (Fig. 3C).

In all cases studied, Oystercatchers rejected *Macoma* less than 11 mm long, while the size classes 11 to 15 mm were taken much less frequently than would be expected on the basis of random searching. The relative risk of the medium-sized *Macoma* being taken appeared to depend on the density of the larger ones, 18 to 22 mm long (Fig. 4A), but not on their own density. There was also a difference in size selection between summer and the rest of the year (Fig. 4B); any confounding influence of the variable density of large *Macoma* was removed by restricting the analysis to studies where the density of large *Macoma* was less than 30 specimens m^{-2}. In conclusion, Oystercatchers concentrate their feeding on the largest *Macoma*, but when these are less common, they take relatively more of the medium-sized ones, especially in autumn and winter. Small prey are always rejected, however.

Scrobicularia plana

In contrast to *Macoma*, where different year classes regularly occur together, the frequency distribution of *Scrobicularia* size classes varies a lot depending on how many years have passed since the last recruitment took place. Three studies have been made of size selection in Oystercatchers taking *Scrobicularia* by touch. Blomert *et al.* (1983) studied Oystercatchers feeding on *Scrobicularia* between 24 and 48 mm long. The birds hardly took any prey larger than 37 mm because they were inaccessible (see Fig. 1). Prey smaller than 28 mm long were taken less than expected, whether or not a correction was made for the effective touch area and the fraction that was accessible. Hughes (1970a) found that Oystercatchers rejected prey smaller than 20 mm long when prey 25 to 40 mm long were available. Habekotté (1987) showed that small *Scrobicularia* were taken when there were few large specimens. In his study the birds rejected prey smaller than about 13 mm long and selected the largest size

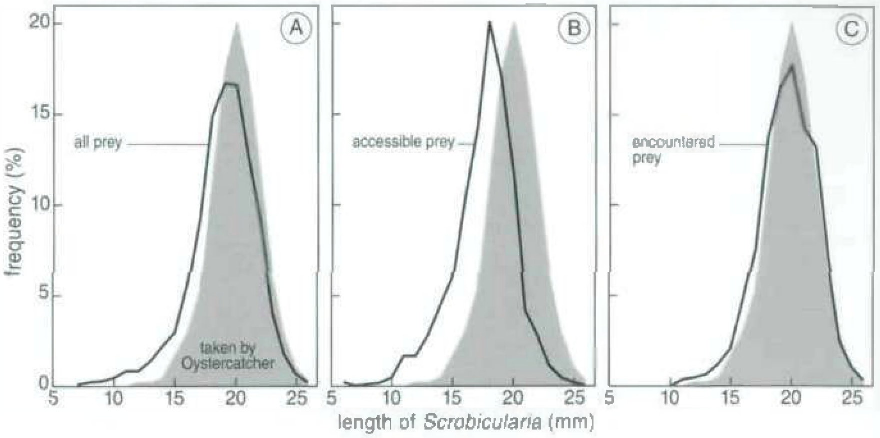


Fig. 5. *Scrobicularia plana*. Size classes selected by Oystercatchers (shaded) compared to the size classes in the prey population (solid line): **A.** Total prey population; **B.** Prey population in upper 6 cm (Fig. 1); **C.** Prey population in upper 6 cm corrected for 'effective touch area' and so actually encountered (Table 1) (Habekotté 1987).

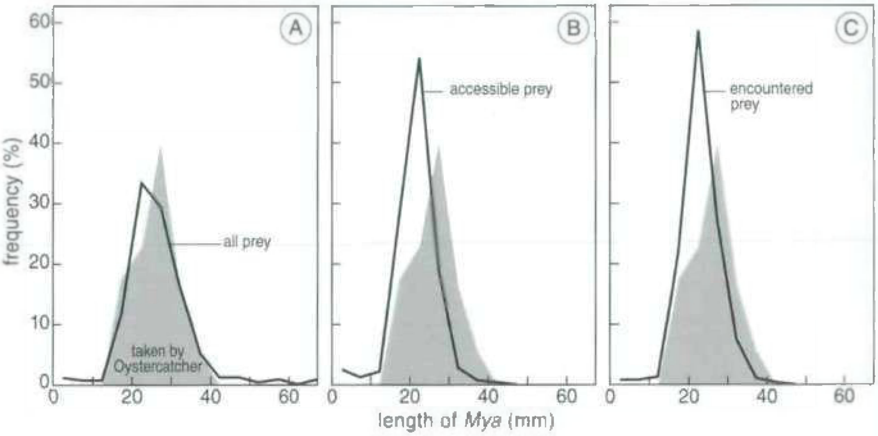


Fig. 6. *Mya arenaria*. Size classes selected by Oystercatchers (shaded) compared to the size classes in the prey population (solid line): **A.** Total prey population; **B.** Prey population in upper 6 cm (Fig. 1); **C.** prey population in upper 6 cm corrected for 'effective touch area' (Table 1) and so actually encountered (Zwarts & Wanink 1984 and Wanink & Zwarts 1996).

classes available more often than expected (Fig. 5). In conclusion, there is, as in Oystercatchers eating *Macoma*, a rejection minimum size threshold which cannot be explained by the random touch model. However, in contrast to *Macoma* (Fig. 4), the lower size threshold for *Scrobicularia* appears to vary greatly between 13 mm (Fig. 5) and 28 mm (Blomert *et al.* 1983), depending on the density of the large *Scrobicularia*.

Mya arenaria

Touch-feeding Oystercatchers select *Mya* of 15 to 40 mm long (Fig. 6). They reject the size classes smaller than 15 mm, although all are accessible (Fig. 1). In contrast, all clams larger than 40 mm live out of reach of the bill (Fig. 1). Taking depth distribution and effective touch area of the different size classes into account, Oystercatchers actively select *Mya* 20 to 30 mm long (Fig. 6C).

Mya may also be located by sight since, when feeding, they extend their siphon up to the surface. The siphon holes are sometimes visible during calm weather and the first hours of the receding tide. For visually hunting birds, large *Mya* are easier to find than small ones, since the surface area of the siphon hole is approximately proportional to its length squared (Zwarts & Wanink 1989). As Hulscher (unpubl.) showed, Oystercatchers hunting visually for *Mya* directed their pecks at siphon holes on the mud surface. The birds took *Mya* 20 to 75 mm long, even though some of them lived out of reach of the bill. Such prey were pulled from the mud by grasping the big siphon. Prey 75 to 105 mm long also occurred in the study area, but apparently lived too deep to be lifted since

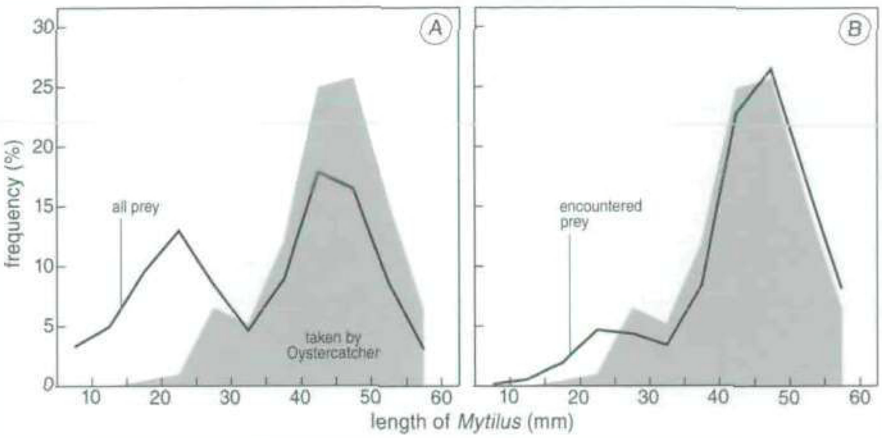


Fig. 7. *Mytilus edulis*. Size classes selected by Oystercatchers (shaded) compared to the size classes in the prey population (solid line): **A.** total prey population; **B.** prey population corrected for 'effective touch area' (i.e. squared length) and so actually encountered. The data are from 9 studies where Oystercatchers used the stabbing technique to open Mussels: Blomert *et al.* (1983), Hulscher (unpubl.), Koene (1978), Ens & Alting (1996b), Zwarts & Drent (1981), Zwarts (unpubl.).

captive Oystercatchers were able to eat these size classes when the prey were buried just beneath the surface (Zwarts & Wanink 1984).

Cerastoderma edule

Oystercatchers feeding on Cockles either make distinct pecks or move the bill through the substrate (Hulscher 1996). Pecking Oystercatchers taking Cockles use visual cues and do not peck at random (Hulscher 1976). This limits the validity of the random touch model even though the effective touch area (Table 1) correctly measures the expected encounter rate. When the bill makes straight furrows through the mud, another random touch model is more appropriate (Hulscher 1976).

Oystercatchers do not take first year Cockles less than 10 mm long, when older Cockles, 20 to 40 mm long, are available (Drinnan 1957, Brown and O'Connor 1974, Goss-Custard *et al.* 1977a, Sutherland 1982c, Triplet 1989b, Hulscher unpubl.). When only first-year Cockles are present, Oystercatchers may feed on them (Meire 1996b, Zwarts *et al.* 1996h, Piersma unpubl.), but this rarely occurs. When only second year, and older, Cockles are available, there is a reasonable coincidence between the observed size selection and the selection predicted on the basis of random searching (Hulscher 1976, Leopold *et al.* 1989).

Mytilus edulis

Oystercatchers use three techniques to open Mussels (Hulscher 1996). Briefly, ventral hammerers tear the Mussel from the bed, turn it over and hammer a hole on the weak ventral side (Norton-Griffiths 1967). Dorsal hammerers attack the Mussel in situ on its dorsal side (Ens 1982), while stabbers stab, or force, the bill between the valves. Each technique requires different measurements to define the fraction of prey actually available to Oystercatchers.

Stabbing Oystercatchers reject Mussels smaller than 20 to 25 mm long but take all larger size classes (Fig. 7A). Mussels larger than the apparent lower threshold of 20 to 25 mm are taken in proportions that conform to the assumption that the likelihood of a Mussel being attacked is proportional to its surface area, i.e. length squared (Fig. 7B). However, the rejection threshold differs between studies. When Mussels about 50 mm long are numerous, stabbing Oystercatchers may even reject Mussels as long as 40 mm (Zwarts & Drent 1981).

Hammering Oystercatchers reject thick-shelled Mussels covered by barnacles (Durell & Goss-Custard 1984, Meire & Ervynck 1986, Cayford & Goss-Custard 1990). This affects the frequency distribution of the size classes actually available to hammerers, since the larger Mussels are often encrusted by barnacles and many are too thick-shelled to be opened (Fig. 2). Like stabbing Oystercatchers, hammering birds reject Mussels below 20 to 25 mm long, but, in contrast to stabbers, Mussels larger than 60 mm are taken only infrequently. When a correction is made for the prey fraction that is unavailable due to shell thickness and barnacle cover (Fig. 2), the proportion of each large prey class taken roughly coincides with their available density (Meire & Ervynck 1986), or explains at least a part of the deviation between observed size selection and frequency distribution of size classes on offer (Cayford & Goss-Custard 1990).

Size selection and optimal foraging

Predicted 'active size selection'

The random touch model tests the assumption that birds take prey at random. In fact, as the results in the previous section show, the observed prey selection often deviates from the predictions of the model. Oystercatchers apparently prefer some size class to others. Why? Prey size selection in Oystercatcher is analysed here within the framework of optimal foraging theory (Emlen 1966, MacArthur & Pianka 1966, Krebs & Kacelnik 1991). The basic assumption is that predators are able to rank prey according to their profitability, defined as the intake rate while prey are being handled. They are predicted to reject prey for which the profitability is below the current average intake rate over both handling and searching combined. The decision rule governing the rejection threshold is therefore based on the relative profitability of handling compared with continuing to search, i.e. whether the bird can achieve a higher net intake rate by continuing to search for more profitable prey than it could achieve by handling a less profitable, although more frequently encountered, prey. This leads to the prediction that, when the profitability of the prey remains the same, the rejection threshold should increase as the intake rate increases. The rejection threshold should also increase when the intake rate remains the same but the profitability of all prey types decreases; for instance, because the prey are lean. The rejection threshold should therefore be flexible within clearly defined limits, as illustrated in Fig. 8.

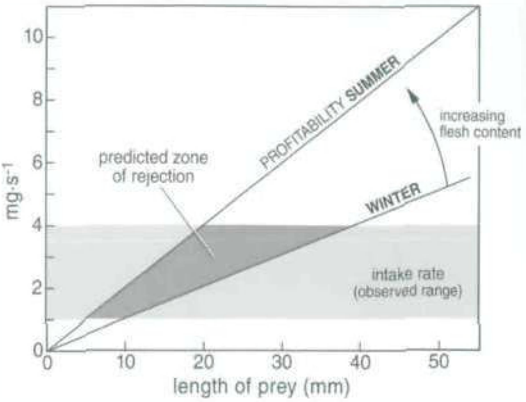


Fig. 8. The optimal prey size selection model. The two slopes delimit the seasonal variation in profitability (mg s^{-1} handling) as a function of prey size. Prey for which the profitability is below the intake rate (mg s^{-1} feeding, i.e. during both searching and handling) should be rejected. Which prey should be rejected thus depends on the level of the intake rate as well as on the length profitability slope. The dark shaded field shows the expected range within which the lower acceptance threshold should be found when the intake rate varies between 1 and 4 mg s^{-1} feeding.

Small prey are less profitable

Even after a correction has been made for the small 'effective touch area' of small prey, Oystercatchers appear to take fewer of them than would be expected on the basis of the frequency with which they are encountered (Figs. 2 to 7). The birds always completely reject prey less than about 10 mm long in *Macoma* and *Cerastoderma* and about 15 to 20 mm long in *Scrobicularia*, *Mya* and *Mytilus*. There might be a very simple explanation for this. Oystercatchers are specialized to open hard-shelled prey before they eat the flesh, in contrast to Knot *Calidris canutus* or Bar-tailed Godwits *Limosa lapponica* which swallow the prey whole and crush them in the stomach. There must be a size below which Oystercatchers are hardly able to separate the flesh from the shell. Whether or not this is close to the observed rejection threshold has still to be tested.

On the other hand, several papers have used the optimality approach to explain the size rejection threshold of Oystercatchers. The prediction is that, below a certain size threshold, prey are simply not worth taking since their energy value is too low given the time required to handle them; i.e. to open them and eat the flesh (Zwarts and Drent 1981, Ens 1982, Hulscher 1982, Sutherland 1982c, Zwarts and Wanink 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford & Goss-Custard 1990). Handling times have therefore been measured in both captivity and in the field. When determining the relationship between handling time and prey size in the field, prey sizes have to be estimated by eye against something of known length, normally bill length or the size of a colour ring. Fortunately, observers are quite consistent in their estimates and simple corrections are sufficient to give an accurate estimate of the size taken (Ens 1982, Blomert *et al.* 1983, Goss-Custard *et al.* 1987, Boates and Goss-Custard 1989).

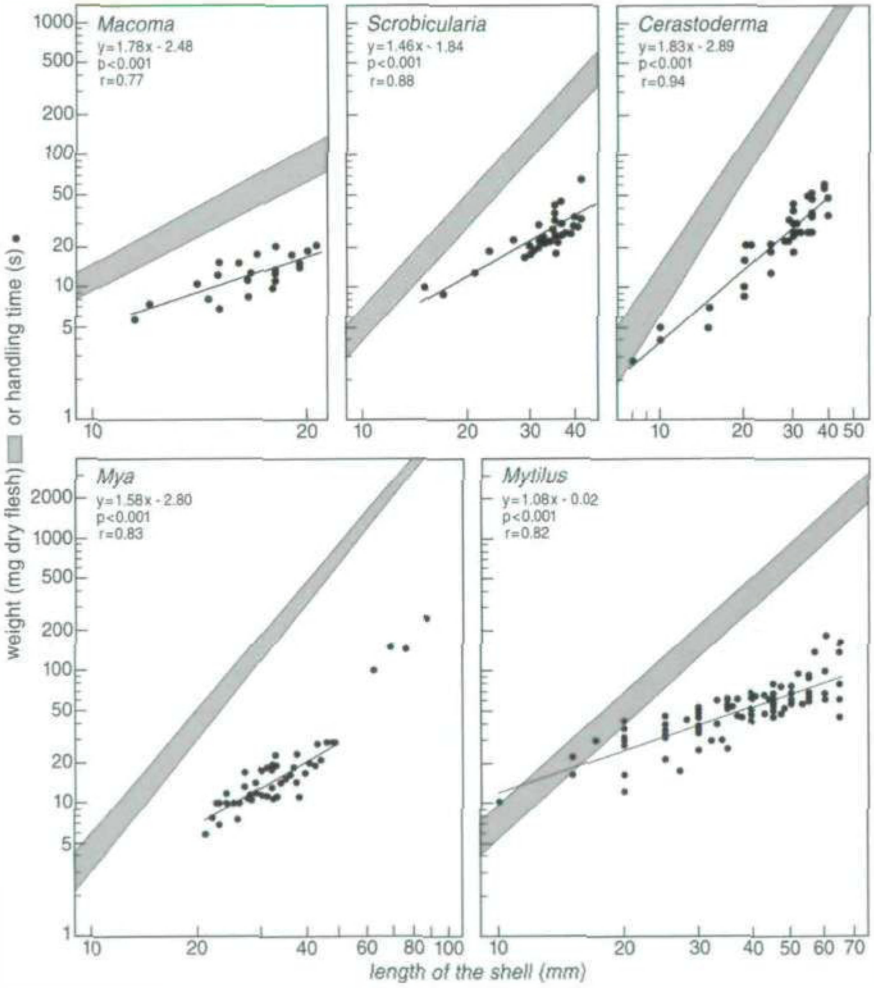


Fig. 9. Dry flesh weight (mg ash-free dry weight; shaded) and handling time (s; symbols) as a function of shell length (mm) in different studies. The seasonal variation in prey weights are from Cayford & Goss-Custard (1990) and Zwarts (1991). Data are from the following sources: *Macoma*: Blomert *et al.* (1983) and Hulscher (1982 and unpubl.). *Scrobicularia*: Blomert *et al.* (1983), Boates & Goss-Custard (1989), Habekotté (1987), Wanink & Zwarts (1985, 1996). *Cerastoderma*: Ens *et al.* (1996b & c), Hulscher (1982 and unpubl.), Meire (1996b), Sutherland (1982c), Swennen *et al.* 1989), Triplet (1990). *Mya*: Wanink & Zwarts (1996), Zwarts & Wanink (1984), *Mytilus* (stabbers): Blomert *et al.* (1983), Cayford & Goss-Custard (1990), Ens *et al.* (1996c), Hulscher (unpubl.), Koene (1978), Linders (1985), Speakman (1984a), Sutherland & Ens (1987). The allometric relations are given: y = ln(handling time, s), x = ln(shell length, mm).

The measurements of handling time in the five prey species are summarized in Fig. 9. Only times when prey were successfully taken are shown. Handling times for Mussels are for stabbing Oystercatchers. Depending on the prey size, it takes an Oystercatcher 3 to 300 s to open and eat the flesh in a bivalve. The flesh weight increases from 5 mg to over 1000 mg over the range of size classes studied. In all prey species, flesh weight increases exponentially with size, with an exponent of about 3. Handling time is also an exponential function of prey size, but the exponent is much lower (Fig. 9).

Dividing prey weight by handling time gives the profitability, i.e. the intake rate in mg dry flesh s^{-1} while handling the prey (Fig. 10). When all data are lumped, profitability is more variable than handling time. This is due to the considerable variation in the flesh content of the prey; for instance, in *Scrobicularia* and *Cerastoderma*, winter weight is almost half that in early summer (Zwarts 1991). But, despite this, there is

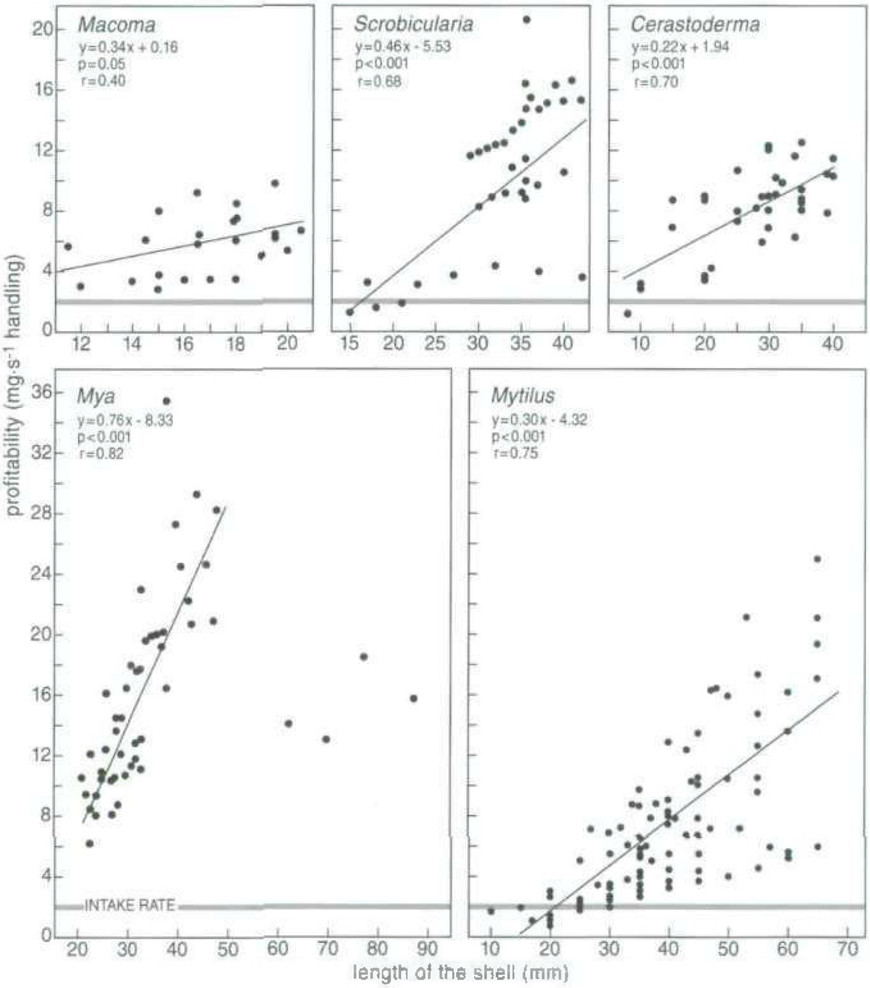


Fig. 10. Profitability (mg dry flesh s^{-1} handling) as a function of shell length; same data as in Fig. 9. The intake rate during feeding, averaged for all studies, is indicated by the horizontal line. The functions are given: y = profitability, mg s^{-1}, x = shell length, mm. The function for *Mya* refers to shells less than 50 mm long.

a highly significant relationship between prey profitability and size in all five bivalve species. This means that profitability can be ranked simply according to prey size.

Large prey are difficult and sometimes even dangerous to handle

Not all prey that are attacked are actually taken, so time is spent in failed attacks. When calculating the profitability of a particular size class, this wasted handling time has to be taken into account when calculating the average time needed to eat them. The difference this can make to the calculation of profitability can be illustrated by hammering birds. Oystercatchers successfully hammering into Mussels spend more time in breaking into a large one than into a small one, but this is worthwhile as the flesh content is disproportionately greater. But if the wasted handling times are included in the calculation, the profitability of hammered Mussels actually decreases in Mussels larger than 50 mm long (Fig. 11).

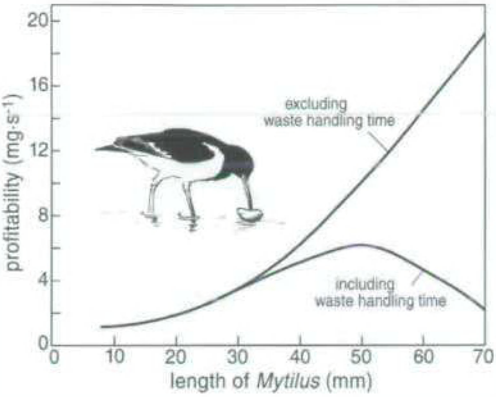


Fig. 11. Profitability (mg ash-free dry flesh s^{-1} handling) as a function of length for Mussels which are hammered on the ventral side. Upper line refers to Mussels that were actually eaten so the time cost was just the handling time for those Mussels. The lower line also includes all the time wasted on other Mussels of the same size class which were unsuccessfully hammered (Meire & Ervynck 1986).

Another factor which falls outside the scope of the simple optimality model being discussed here is the potential risk to the bill of attacking large prey. Both Sutherland (1982c) and Triplet (1989a) found that larger Cockles are refused more often than small ones. As the time lost is insignificant, the birds may be reducing the risk that the bill tip will be damaged. After being stabbed, Mussels may also close their valves firmly on the bill, so that an Oystercatcher may eventually die due to starvation (Hulscher 1988). But the risk appears to be small and, with exception of Mussels being hammered, the amount of time spent in wasted handling time is not large. The general conclusion from the previous section that the prey size predicts profitability is largely unaffected.

Oystercatcher can vary encounter rate

Another important consideration in calculating whether a particular size class of prey should be taken is the rate at which prey are encountered. Oystercatchers can control encounter rates with prey through changes in their search behaviour. For example, when Oystercatchers switch from touch to visual hunting (Hulscher 1976, 1982), they change from randomly probing into the mud to searching on the surface for signs of the prey beneath (Hulscher 1996). This means that the encounter rate with potential prey has to be defined according to the feeding technique used. Again, Oystercatchers visually hunting for tracks or inspecting bivalves on the surface may vary the encounter rate with different prey types by varying search speed (Cayford & Goss-Custard 1990). The speed at which a foraging animal searches has been described as an adaptation to the crypticity of the prey (Goss-Custard 1977a, Gendron 1986, Zwarts & Esselink 1989) and observations on the walking speed of Oystercatchers feeding on different prey types is consistent with this idea (Ens *et al.* 1996a).

Although randomly probing Oystercatchers provide a good opportunity to measure encounter rates, it would be wrong to assume that they are fixed for a given prey density and depth distribution. This is because Oystercatchers can modify probing depth. As already described, for example, Oystercatchers probe twice as deeply when searching for the deep-living *Scrobicularia* than when they feed on a shallow-living prey, such as the Cockle. Oystercatchers must therefore also make the decision on 'how deep to probe' and this too must be taken into consideration when the eco-

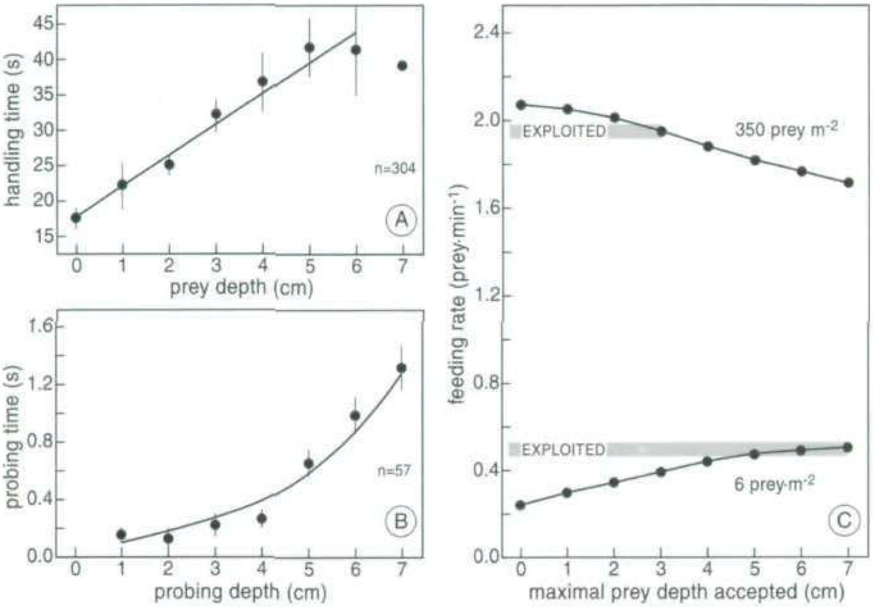


Fig. 12. Experiment to show why an Oystercatcher ignored deep, less profitable prey when the intake rate increased due to a high prey density. **A.** Time needed to handle *Scrobicularia* 37-38 mm long which were taken from different depths (s ± SE). **B.** Time needed to probe to different depths (s ± SE). **C.** Predicted feeding rate (*Scrobicularia* min^{-1}) at two prey densities when an Oystercatcher took prey from the upper 1, 2, ... 7 cm of the substrate. Actual observed depth selection is indicated with horizontal bars. As predicted, the bird took prey from all depths when the prey density was low and only shallow prey when the prey density was high. However, the bird did this at a much higher rate than predicted (explanation given in text). Data of Wanink & Zwarts (1985).

nomics of foraging are being calculated.

It has been shown experimentally that a captive Oystercatcher decreased its probing depth from 7 to 3 cm when the density of the prey on offer, *Scrobicularia* 36-37 mm long, increased from 24 to 350 prey m^{-2} (Wanink & Zwarts 1985). It took more time to handle deep-living prey (Fig. 12A), hence prey profitability decreased with depth. Moreover, it also took more time in the first place to locate a prey at greater depths (Fig. 12B). The encounter rate, defined in optimal foraging models as the inverse of the searching time, for prey at different depths could be calculated from the effective touch area and the probing time at each probing depth. Since the encounter rate and the handling time were both known for each depth class, the optimal set of depth classes, which should be included in the diet to maximize the intake rate, could be predicted exactly with a multi-species functional response equation (Charnov 1976) (Fig. 12C). The depth selection made by the bird was very close to that which was predicted. The Oystercatcher took prey from all depths when the density was low but rejected the deep, less profitable prey when prey density was high; by doing so, it increased its intake rate at high prey density by eating only the most profitable, shallow prey. It may be thought from Fig. 12C that the bird could have done slightly better by selecting prey only from the upper 1 cm, and not from the upper 3 cm, as it actually did. But, in fact, the Oystercatcher did even better than predicted by using a second selection criterion, as will be explained in the next section. The conclusion from this experiment is that Oystercatchers are indeed able to vary the rate at which they encounter different prey types and, in doing so, increase their intake rate.

Rejection of prey to increase intake rate

The previous section showed that Oystercatchers are able to adjust their searching behaviour in order to increase their encounter rate with more profitable prey. The next decision Oystercatchers have to make is which of the encountered prey they should take and which they should ignore. As noted above, the captive Oystercatcher studied by Wanink & Zwarts (1985) was able to attain an intake rate 50% above the predicted rate when prey density was high (Fig. 12C). Their explanation for this was that, at the high prey density, the bird only took prey from the upper 3 cm that were gaping and so could be stabbed immediately. As a result, the prey were opened and the flesh swallowed in less than 15 s, nearly twice as quickly as when a typical prey from the upper 3 cm was taken (Fig. 12A). The hypothesis that Oystercatchers may ignore closed, and thus less profitable, bivalves had already been proposed by Hulscher (1976) who observed that Oystercatchers spent less time handling *Cerastoderma* when prey density increased. By rejecting closed bivalves when prey are abundant, Oystercatchers are able to increase their intake rate substantially.

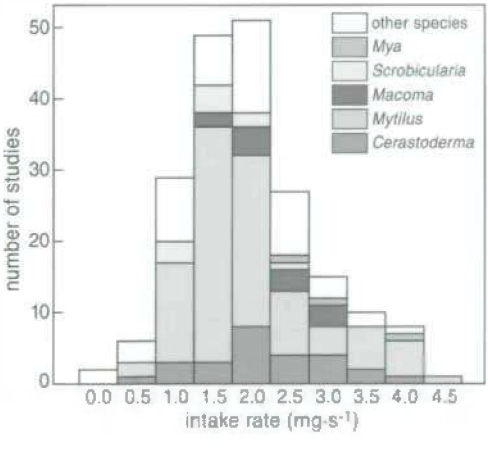


Fig. 13. Frequency distribution of intake rates (mg ash free dry flesh s^{-1} feeding) measured in 197 studies, given separately for five bivalve species; data for seven other prey species are lumped. The sources for the five bivalve species are given in the legend to Fig. 14. Other sources: Ragworm *Nereis diversicolor*: Boates & Goss-Custard (1989), Bunskoeke *et al.* (1996), Durell *et al.* (1996 & unpubl.), Triplet (1989b); Lugworm *Arenicola marina*: Bunskoeke (1988); earthworms: Heppleston (1971), Hosper (1978); Leatherjacket *Tipula paludosa*: Hosper (1978), Zwarts & Blomert (1996); Winkle *Littorina littorea*: Boates & Goss-Custard (1992); Giant Bloody Cockle *Anadara senilis*: Swennen (1990); Fiddler Crab *Uca tangeri*: Ens *et al.* (1993).

There seem to be large differences generally in the profitability of prey of similar size due to the large variation in handling time. In the same way that it takes less time to eat shallow-living and/or gaping bivalves (Hulscher 1976, Wanink & Zwarts 1985), there are also large variations in the profitability of hammered prey (Durell & Goss-Custard 1984). Despite the variation in profitability within a size class, size and prey profitability remain highly correlated (Fig. 10). This allows us now to focus on the question of why the small, less profitable prey are usually refused, but sometimes taken.

The optimal diet model predicts that birds should refuse prey for which the profitability is lower than the average current intake rate. Taking all studies together (Fig. 13), the average intake rate during feeding was 1.97 mg dry flesh s^{-1} ($SD = 0.84$, $n = 197$). The average intake rate differed significantly between the twelve prey species ($p = 0.006$, $R^2 = 0.137$), but there were also seasonal differences. The mean intake rate in 'summer' (April to October; 2.15 mg s^{-1}; $SD = 0.87$, $n = 126$) differed significantly from that in the 'winter' (November to March; 1.64 mg s^{-1}, $SD = 0.67$, $n = 71$, $p < 0.001$, $R^2 = 0.086$). Twenty-eight of the 31 studies recording an intake rate above 3 mg s^{-1} were made in summer, compared with 19 of the 37 studies with an intake rate below 1.5 mg s^{-1}. This difference was due to the seasonal variation in flesh content of prey (e.g. Zwarts 1991, Zwarts & Wanink 1993), which was higher in summer, making the prey more profitable than in winter. But taking 2 mg s^{-1} as an overall average for intake rate, the predicted average lower size threshold for prey may be read from the profitability curves given in Fig. 10. The average rejection threshold should be about 10 mm for *Macoma* and *Cerastoderma*, 15 mm for *Scrobicularia* and *Mya* and 20 mm for *Mytilus*. When these figures are compared with the actual selection of prey, there is a reasonable fit for *Macoma* (Fig. 3), *Cerastoderma* (see text on observed size selection), *Mya* (Fig. 6) and *Mytilus* (Fig. 7). On average, the optimal foraging model predicts the observed lower prey size thresholds quite well, although the size classes just above the predicted lower size threshold are under-represented in the diet.

Particular studies, however, have found some departures from prediction. Since the flesh content of bivalves may vary by a factor of two during the course of the year (Cayford & Goss-Custard 1990, Zwarts 1991, Zwarts & Wanink 1993), there is an opportunity to test whether seasonal changes in the profitability curves accurately predict a shift in size selection. Cayford & Goss-Custard (1990), for example, analysed the seasonal variation in the size selection for Mussels on the Exe estuary, SW. England. The birds actively selected those size classes predicted to maximize intake rate for most months of the year. However, in spring, the birds fed on smaller Mussels than were predicted from their profitability and availability. Cayford & Goss-Custard (1990) suggested that size selection may be influenced at certain times of the year by still unmeasured differences between size classes in prey quality and energy content.

However, other apparently contradictory results can be reconciled more easily with the optimal foraging model. Handling time does not increase as the flesh content of a bivalve increases because the time taken actually to eat the flesh is only a small fraction of the total (Wanink & Zwarts 1985). Most of the handling time is spent in lifting the bivalve to the surface, stabbing or forcing the bill between the valves, or hammering a hole in the shell. Hence the profitability of a given prey size may be as much as twice as high in early summer as in winter. The rejection threshold, therefore, should be lower in summer than during the rest of the year (Fig. 8). In fact, in *Macoma*, the reverse was found (Fig. 4B), as Oystercatchers were more selective in summer than at other times of the year. However, all data on size selection in early summer refer to breeding Oystercatchers which have the rather high intake rate of 3 mg s^{-1} (Ens *et al.* 1992, Bunskoeke *et al.* 1996). Such a high rate should have the effect of raising the rejection threshold for *Macoma*, thus countering the opposite effect on the rejection threshold of an increased prey condition (Fig. 8). Thus, in this case, two tendencies may be working in opposite directions.

The intake rates of Oystercatchers, measured over periods of several hours usually vary between 1 and 3 mg dry flesh s^{-1} (Fig. 13). When they feed at a rate of 1 mg s^{-1}, they would be predicted to accept all *Scrobicularia* or *Mytilus* larger than 15 mm long, whereas when the intake rate is three times higher, the rejection threshold should be raised to 20 and 25 mm, respectively (Fig. 10). The simple way to test these predictions would be to compare observed rejection thresholds with the lower thresholds predicted from the intake rate. There is, however, a methodological problem. In the field studies summarized in Fig. 13, intake rate is closely correlated with the size of the prey taken (see below); the expected dependence of the lower size threshold on intake rate may thus be attributed simply to size selection itself.

The intake rate is determined by a combination of three variables: the searching time, the handling time and the dry flesh weight of the prey taken. The search time primarily depends on prey density (Hulscher 1976, 1982, Sutherland 1982b, Wanink & Zwarts 1985). Both handling time and prey weight increase with prey size (Fig. 9), whereas there is a seasonal variation in the flesh content of individual prey. The major factor determining intake rate in the reviewed studies was the size of the prey (Fig. 14); for instance, 59% of the variance in intake rate on *Scrobicularia* could be explained by prey size. A covariance analysis performed on the 197 studies which measured intake rate (Zwarts *et al.* 1996b) revealed that prey weight explained 16% of the variance and that both the prey species and season had significant effects ($R^2 = 0.24$ and 0.19, respectively). When prey of different species, but of similar size, were compared, *Cerastoderma* and *Macoma* were shown to yield a higher intake rate than the other bivalves. The reason is that, for a given size class, *Cerastoderma* and *Macoma* are more profitable. This is due to their more globular shape (Zwarts & Blomert 1992), so that they contain more flesh than corresponding size classes in the other three bivalves (Fig. 10).

The increase in intake rate with prey size (Fig. 14) is thus due to the high profitability of the larger size classes (Fig. 10). The yield of the smallest prey taken (Fig. 10) is below the average intake rate of 2 mg s^{-1}. So even if the birds could eat these small prey continuously, without spending any time in searching for them, the average intake rate would fall to the low level of 1 or 2 mg s^{-1}. In contrast, the larger size classes can be handled at a rate of about 10 mg s^{-1} (Fig. 10), enabling the birds to attain an intake rate of 2 mg s^{-1}, even though as much as 80% of the feeding time is spent in searching. In fact, the searching time must have been less than this, as Oystercatchers taking large bivalves have an intake rate of 3 or 4 mg s^{-1} (Fig. 14).

The finding that the intake rate predominantly depends on size selection makes it difficult to interpret the field data on size selection. The prediction of the optimal foraging model is that the threshold size of acceptable prey should depend on the intake rate. However, the threshold level itself affects the intake rate. One way to break this circle is to examine studies where the density of the most profitable prey, and so the intake rate, varied considerably. When this was done, the lower size threshold changed in the direction predicted by the model; for example, Oystercatchers were more selective when the density of large *Macoma* was high (Fig. 4A). Similarly, Sutherland (1982c) found that Oystercatchers took fewer small Cockles as the abundance of the large ones increased. Such findings allow the direction of causality to be established. On the assumption that these findings can be applied across all studies, we conclude that, as predicted by the

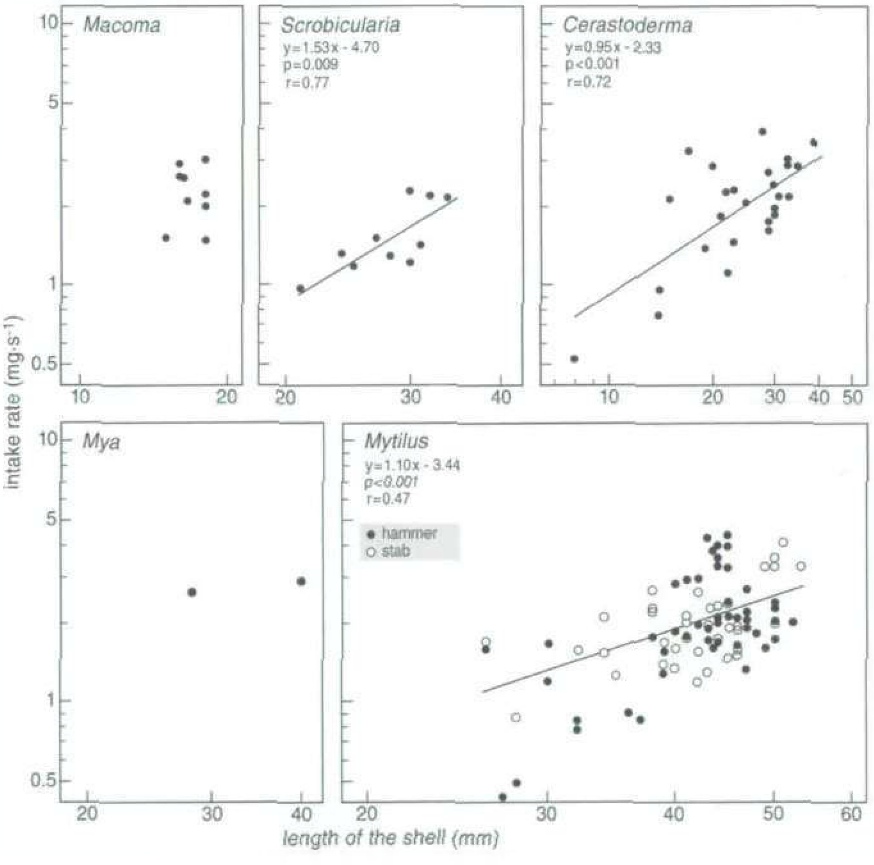


Fig. 14. Intake rate (mg ash-free dry flesh s^{-1} feeding) as a function of average length of bivalves taken. Data are from the following sources: *Macoma*: Blomert *et al.* (1983), Bunskoeke *et al.* (1996), Hulscher (1982 and unpubl.), Hulscher *et al.* (1996); *Scrobicularia*: Blomert *et al.* (1983), Boates & Goss-Custard (1989), Habekotté (1987), Hulscher (unpubl.), Wanink & Zwarts (1996); *Cerastoderma*: Brown & O'Connor (1974), Davidson (1967), Drinnan (1957), Ens *et al.* (1996b & 1996c), Goss-Custard (1977c), Hulscher (1976 & unpubl.), Leopold *et al.* (1989), Meire (1996b), Sutherland (1982b & c); *Mya*: Bunskoeke (1988), Hulscher (unpubl.), Wanink & Zwarts (1996), Zwarts & Wanink (1984), *Mytilus* (indicated separately for stabbers and hammerers): Blomert *et al.* (1983), Boates & Goss-Custard (1992), Cayford & Goss-Custard (1990), Drinnan (1958), Ens & Goss-Custard (1984), Ens *et al.* (1996c), Goss-Custard (unpubl.), Heppleston (1971), Hulscher (unpubl.), Koene (1978), Maagaard & Jensen (1994), Meire (1996b), Meire & Ervynck (1986), Speakman (1984a), Sutherland & Ens (1987), Zwarts & Drent (1981). The allometric relations are given: y = ln(handling time, s), x = ln(shell length, mm).

optimal foraging model, the minimum size rejection threshold is determined by the intake rate which itself depends predominantly on the abundance of the larger and most profitable size classes.

Intake rate, processing rate, feeding time and daily consumption

The central tenet of the classical optimal diet model is that predators attempt to maximize their intake rate. Given a fixed food requirement, intake rate determines the time required for feeding. Maximizing intake rate therefore implies minimizing the time spent feeding, assuming that birds are working towards a predetermined amount of food. Under thermo-neutral conditions, an Oystercatcher is able to maintain its body weight when its daily consumption is about 35 g of dry food pellets or dry flesh (Hulscher 1974, Kersten & Piersma 1987, Swennen *et al.* 1989, Goede 1993). Since the energetic values of food pellets and dry bivalve flesh are both 22 kJ g^{-1} ash-free dry weight, and does not vary much (e.g. Brey *et al.* 1988, Zwarts & Wanink 1993), this is equivalent to 770 kJ. About 15% of the ingested energy is not digested (Kersten & Visser 1996a), so the daily metabolized energy of an Oystercatcher is 650 kJ, or about 2.6 times the basal metabolic rate (BMR) of 250 kJ (Kersten & Piersma 1987). However, when the air temperature drops below 10 °C, the daily food requirements increase from 35 g per day to 50 g at an air temperature of 0 °C (Kersten & Piersma 1987, Goede 1993). The same high level may be reached when Oystercatchers increase their body weight before migration. These data refer to Oystercatchers held in outdoor cages. The requirements in wild birds are somewhat higher. First, free-living birds fly for 10 to 30 minutes per day. Assuming that flying costs are 12 times BMR (Masman & Klaassen 1987), this represents an expenditure of 20 to 40 kJ equivalent to 3 to 9% of daily energy expenditure. Second, the lean body weight in captive birds was in most studies below the normal range observed in free-living birds. Since the energy requirements vary with the lean body weight, the average cost of living in the field must be some percent above the estimated daily energy requirements in captive birds (Zwarts *et al.* 1996c). The daily food requirements of free-living Oystercatchers has therefore been estimated at 36 g.

Since tidal feeding areas are covered half of the time over high water, the daily feeding period is 12 hours if the birds feed at night. Given a daily consumption of at least 36 g dry flesh, Oystercatchers in the wild must consume 0.85 mg dry flesh s^{-1}, assuming they feed continuously over low water and at the same rate by day and by night (Hulscher 1996). An intake rate of about 0.85 mg dry flesh s-1 is thus the absolute minimum required to sustain energy balance, unless Oystercatchers can extend the foraging period over high water in day-time by feeding in fields. Feeding at high tide rarely occurs in summer, but is more common in the energetically more expensive winter, especially when, due to gales and floods, the tidal feeding areas are only exposed for a short time (Heppleston 1971, Daan & Koene 1981, Goss-Custard & Durell 1984).

The observed range of intake rates (Fig. 13) exceeds the minimum rate of 0.85 mg s^{-1} in 93.4% of the studies. One of the exceptions was a rate of 0.5 mg s^{-1} recorded in the Eastern Scheldt, SW. Netherlands (Meire 1996b). On this occasion, the tidal food resources were so poor that Oystercatchers had to rely on cockle spat 8 mm long, which in all other studies were rejected because of their low profitability.

When Oystercatchers feed at the highest observed rate of 4 mg s^{-1}, it will only take them 2.5 hours each day to obtain the minimum daily consumption of 36 g. In contrast, when the intake rate is at the low level of 1 mg s^{-1} and the daily energy requirements are at their highest level of 50 g, the birds will need to feed for 14 h. Thus, although the average feeding time would be expected to be only 5 h a day (intake rate 2 mg s^{-1} and daily consumption of 36 g), the large variation in both intake rates and daily energy requirements mean that the actual feeding time may vary between 2.5 and 14 h a day.

In some circumstances, then, Oystercatchers would be expected to collect food as fast as possible, notably when the tidal exposure period is reduced and feeding at high tide is not possible (Goss-Custard *et al.* 1996a). However, Oystercatchers cannot exceed the limit set by their digestive system. Kersten & Visser (1996a) studied the rate at which Oystercatchers process the flesh of bivalves. They found that the food processing rate could be described by three parameters: (1) a full

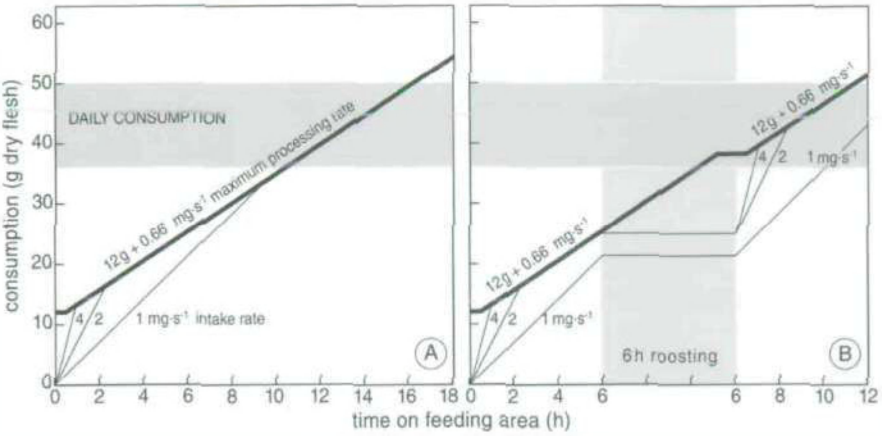


Fig. 15. Daily consumption as function of the time spent on the feeding area, when there is **A.** One feeding period per day or **B.** Two feeding periods with a roosting period of 6 hours in between. The intake rate determines how long it takes before the bird is forced to pause or reduce its intake rate due to the digestive bottleneck, this being set by the three parameters: (1) the oesophagus may contain 12 g ash-free dry flesh; (2) defecation starts 0.5 h after the beginning of the feeding period, and (3) the processing rate is 0.66 mg s^{-1} (after Kersten & Visser 1996a).

oesophagus contains 80 g wet (or 12 g dry) flesh; (2) the birds start to defecate 0.5 h after the beginning of the feeding period; and (3) the processing rate is 4.4 mg wet (or 0.66 mg dry) flesh s^{-1}. The processing rate is thus much slower than the range of intake rates observed in the field (1 to 4 mg s^{-1}). Indeed, Oystercatchers in captivity can achieve even higher intake rates. The highest rate of 16 mg s^{-1} was observed by Hulscher (unpubl.) in captive birds eating mussel flesh. At that rate, a digestive pause would be necessary after only 13 minutes of feeding, which was indeed the actual length of the feeding period in Hulscher's birds.

The finding that the processing rate is usually much lower than the intake rate during feeding has several implications. At least in the long run, birds must interrupt their feeding when their intake rate exceeds their processing rate (Zwarts & Dirksen 1990). The overriding effect of this digestive bottleneck on the daily consumption of the Oystercatcher is shown in Fig. 15. The maximum intake during a feeding period is set by the three parameters given by Kersten & Visser (1996a). At the very low average intake rate of 1 mg s^{-1}, the gut fills and forces the bird to reduce its intake rate to a level equal to, or below, the processing rate after 530 min of continuously feeding. But with intake rates of 2, 3 or 4 mg s^{-1}, the alimentary tract is full after only 135, 77 or 54 min, respectively.

The length of time an Oystercatcher has to spend on the feeding area, including digestive pauses, to achieve a given food consumption, is also shown by Fig. 15. The only assumption here is that the bird starts to feed with an empty stomach and leaves the feeding area with a full oesophagus. With one feeding period a day, the bird would have to feed for 10 hours to achieve the minimum daily energy requirements of 36 g (Fig. 15A). Remarkably, the average intake rate while feeding does not matter, as long as it exceeds 1 mg s^{-1}. Furthermore, if Oystercatchers leave the feeding area with a full gut, it takes just over 5 hours to process all the food, or nearly as long as the usual high water roosting period. Consequently, the total consumption is hardly affected when both the feeding and roosting periods are six hours long (Fig. 15B). The figure points to three important conclusions: (1) as long as the intake rate during feeding exceeds 1.16 mg s^{-1}, the gut processing rate determines the overall consumption during a low water period; (2) Oystercatchers cannot eat more than 25.1 g dry flesh during a low water period of 6 hours; so that (3) one low water feeding period of 6 hours is not long enough to obtain their food requirements.

What do birds do on the feeding grounds when their gut is full? Do they reduce their intake rate to the level of the processing rate of 0.66 mg s^{-1} or do they stop feeding and start again when the alimentary tract is partly or completely empty? Apparently Oystercatchers do not lower their intake rate when the alimentary tract is full, since intake rates as low as 0.66 mg s^{-1} are rarely recorded. Instead, Oystercatchers rest for a considerable part of the low water feeding period, just like Whimbrels *Numenius phaeopus* eating Fiddler Crabs *Uca tangeri* (Zwarts & Dirksen 1990). Active foraging is often restricted to the first and last hours of the low water feeding period (Brown & O'Connor 1974, Swennen *et al.* 1989). The higher intake rate on the incoming tide recorded in captive birds by Swennen *et al.* (1989) and in the field by Zwarts & Drent (1981) and Goss-Custard *et al.* (1984) probably guarantees that birds arrive at the high water roost with a full gut.

We have shown that Oystercatchers continuously make feeding decisions that enhance their intake rate. At the start of the chapter, we assumed they do this in order to minimize feeding time and thus maximize the time they can spend on other activities such as preening and aggressive behaviour. However, when the processing rate is usually so much lower than the intake rate, the birds can preen or be aggressive during their inevitable digestive pauses. This implies that feeding and, for example, preening are not necessarily competing activities. The question, already raised by Kersten & Visser (1996a) is this: why should we continue to expect Oystercatchers to always try to maximize their intake rate and thus minimize the time spent feeding? Maximizing intake rate would only seem to be relevant when the birds have difficulties in achieving an intake rate of about 1 mg s^{-1}; only in these circumstances is the total consumption determined by the intake rate itself (Fig. 15). It seems unlikely to be important for Oystercatchers to attempt to increase their intake rate and when it has already reached levels of 3 or 4 mg s^{-1} and when the only apparent consequence of doing so is that they must pause earlier to allow for digestion.

While these arguments seem to apply to many situations in winter, they do not do so in the breeding season. The amount of food brought to the young often limits reproductive success (Ens *et al.* 1992). Breeding birds have to feed in a hurry to return to their nest and/or defend their territory or young, and the rate of provisioning is not limited by the capacity of their own gut to process food. Indeed, breeding birds feed at higher average rates than non breeding Oystercatchers, which are not time-stressed (Zwarts & Drent 1981, Hulscher 1982, Ens *et al.* 1996c). Moreover, Oystercatchers were able to handle prey faster and to increase their intake rates when they were experimentally forced to collect their food over short feeding periods (Swennen *et al.* 1989). It seems that Oystercatchers do not normally feed at the highest possible rate they can attain, even though they usually seem to make the most profitable choices in the sizes of prey they select. The task now is to investigate the trade-offs that the birds presumably make under various conditions. One such trade-off might be to balance a higher intake rate against the need to minimize the risk of damage to the bill when breaking into their large and well-defended prey (Hulscher 1996). This would mean that the long-term advantage of an undamaged bill would be set against the short-term goal of a higher food intake rate and reduced feeding time. Another trade-off might be between a lower intake rate but a reduced chance of being infected by parasites (Goss-Custard *et al.* 1996a). What is clear, however, is that a model in which maximizing the intake rate is the only consideration is not adequate. More sophisticated models, which include trade-offs between a variety of changing influences, including the state of the bird's body reserves (Stephens & Krebs 1986), are now required.

Chapter 9

CAUSES OF VARIATION IN PREY PROFITABILITY AND ITS CONSEQUENCES FOR THE INTAKE RATE OF THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS*

Leo Zwarts, Bruno J. Ens, John D. Goss-Custard, Jan B. Hulscher & Sarah E.A. le V. dit Durell

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CAUSES OF VARIATION IN PREY PROFITABILITY AND ITS CONSEQUENCES FOR THE INTAKE RATE OF THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS*

Prey species have different morphological and behavioural adaptations to escape their predators. In this paper we review how these prey defenses affect prey profitability and intake rate for one predator, the Oystercatcher. Four rules govern profitability. First, within each species large prey are more profitable than small prey, because flesh content increases more steeply with prey size than handling time. Second, soft-bodied prey, such as worms and Leatherjackets, which can be swallowed whole, are much more profitable than armoured prey, such as bivalves, which Oystercatchers have to open before the flesh can be extracted from the shell. Third, heavily armoured surface-dwelling prey, like Mussels and Cockles, are the least profitable prey of all, even if the armour is bypassed through stabbing the bill between the valves. Fourth, within the burying prey species, the profitability of prey decreases with depth. Hence burying bivalve species that bury in winter at larger depth than in summer, are in winter, if not out of reach of the bill, anyway less profitable.

Despite the large differences between the profitabilities of the various prey species, the intake rates do not differ much when the prey species are compared, presumably because prey with a low profitability are only exploited if the search time is relatively short, i.e. if the density of harvestable prey is high. On the other hand, within each species, the intake rate goes up if larger, more profitable prey are taken. Thus, if the birds have to feed on smaller prey specimens, they fail to fully compensate for the low profitability by an increase in the rate at which these prey are found. Although the profitability of prey differs seasonally due to the variation in the prey condition, only a small seasonal variation in the intake rate was found. Because burying bivalves and soft-bodied worms bury deeper and are less active in winter, Oystercatchers necessarily rely on bivalves living at, or just beneath, the surface at that time of year.

Introduction

Oystercatchers *Haematopus ostralegus* feed on at least 15 different prey species along the NW. European coast (Cramp & Simmons 1983, Hulscher 1996). On intertidal sand and mudflats, their food consists of Cockles *Cerastoderma edule* and Mussels *Mytilus edulis*, and to a lesser degree also of other bivalves, such as *Macoma balthica*, *Scrobicularia plana* and *Mya arenaria*, worm species, such as *Arenicola marina* and *Nereis diversicolor*, and the Shore Crab *Carcinus maenas*. On rocky shores, Oystercatchers take Limpets *Patella aspara* and *P. vulgata*, Periwinkles *Littorina littorea* and Dogwelks *Nucella lapillus*, whereas in grassland they select mainly different earthworm species (Lumbricidae) and Leatherjackets (larvae of the crane fly *Tipula paludosa*).

Except for the worms and Leatherjackets, all species selected by Oystercatchers are armoured with a calcified exoskeleton. Nonetheless, Oystercatchers never swallow the hard skeletal parts. Instead, they eat the flesh from bivalves, snails or crabs after prizing, or stabbing, the bill between the valves or hammering a hole in the shell or carapace. Oystercatchers may easily find prey lying at the surface but they have to spend time breaking in and extracting the flesh. It takes more time for an Oystercatcher to locate benthic bivalves living hidden in the substrate, since these prey are usually found by randomly probing the bill into the mud (Hulscher 1976, 1982, Wanink & Zwarts 1985). Moreover, since these buried prey are also armoured against predation, Oystercatchers must, as with surface prey, spend time in opening them. In contrast, soft-bodied prey are ready to eat. They are also buried and must be searched for, but they are an easy prey for Oystercatchers when they come to the surface to feed themselves (Ragworms *Nereis*) or to defecate (Lugworms *Arenicola*).

The extent to which various prey species provide a staple food for the Oystercatcher varies dramatically with season. Inland fields are heavily exploited by breeding birds in spring and summer, but only used as a supplemental food resource by most Oystercatchers in winter (Heppleston 1971, Daan & Koene 1981, Goss-Custard & Durell 1984). On the tidal flats, *Macoma* is taken in early spring, whereas *Nereis* predominates in late spring (Bunskoeke *et al.* 1996). Both prey are only locally important. In contrast, as the papers reviewed below show, Mussels and Cockles are universally important winter foods. The fact that Shore Crabs are only taken in summer is easily explained by their migration to deeper water in autumn (e.g. Beukema 1991). However, the other prey occur year-round in the same habitat, with many individuals growing for several years. We take as a working hypothesis that the seasonal changes in the utilization of these prey by the Oystercatcher population are primarily due to seasonal changes in harvestability of the prey, i.e. the prey fraction that is both accessible and profitable (Zwarts & Blomert 1991, Zwarts & Wanink 1993). By definition, harvestability is negatively related to the effectiveness of the morphological and behavioural anti-predator defenses of the prey. Since each prey species has different adaptations to reduce predation risk, we may also expect differences between prey species in the time of year when the defenses are most effective.

The intake rate is defined as mg s^{-1} feeding, thus the quotient of weight of the prey and feeding time. Feeding time consists of two components: searching and prey handling. Hence the intake rate is the product of two ratios:

prey weight/handling time ×
handling time/(search + handling time).

The first ratio, the intake rate during prey handling, is called the profitability. The second ratio is the relative handling time, the proportion of the feeding time during which the bird handles the prey.

It is obvious that the intake rate will increase when the prey are large, are handled in a short time, and/or when the search time between prey is limited. Several studies (Hulscher 1976, 1982, Wanink & Zwarts 1985, Habekotté 1987, Goss-Custard *et al.* 1996b) show that search time of Oystercatchers decreases as prey density increases. Several others support the corollary that the rate at which prey are taken increases with prey density (Goss-Custard 1977, Sutherland 1982b, Triplet 1990, Ens *et al.* 1996c). Most of these positive results were obtained on Oystercatchers feeding on Cockles which, due to their shallow depth, are always within reach and detectable by touch. In contrast, the depth distribution of burying bivalves differs seasonally and locally (Zwarts & Wanink 1993) and this, as will be discussed, affects the profitability and the intake rate. Due to variation in the thickness of the shell, the degree in which barnacles cover Mussels, and several other variables (Goss-Custard *et al.* 1996b), the fraction of harvestable Mussels is even more variable and very hard to assess.

To understand the variation in intake rate it is not sufficient to measure the relationship between intake rate and prey density. This paper focus on the dependence of intake rate on prey profitability. One of the main conclusions of this paper is that, within each prey species, the weight of the prey greatly affects the profitability and thereby the intake rate. To investigate to what degree prey profitability and intake rate differ between surface and buried prey, and between hard-shelled and soft-bodied prey, we review all available Oystercatcher studies on prey profitability and intake rate. First, we explore whether, within a species, the handling time depends not only on prey size, but also on prey condition, i.e. the relative deviation from the average weight per size. The next step is to relate handling time and prey profitability to prey weight and to examine whether prey species differ in the time Oystercatchers need to eat a given amount of flesh. The paper analyses the feeding time per prey (i.e. searching + handling time) as a function of prey weight separately for the species and for all species taken together. Since the prey condition varies seasonally, we also test whether this affects intake rate. The companion paper (Zwarts *et al.* 1996h) will investigate whether the described relationships of prey profitability and intake rate as a function of prey size and prey weight can be used to predict in detail the decision of Oystercatchers to take only certain prey from a mixture of different size classes and prey species.

Methods

Studies

The data presented in this paper have been taken from 57 articles, 6 student reports, 4 unpublished theses, but also from unpublished data files of Anne-Marie Blomert, Klaus-Michael Exo, Kees Hulsman, Cor Smit and the five authors; all sources are listed in the appendix. The studies were performed in 20 areas (Fig. 1), of which ten are situated in Great Britain and Northern Ireland, six in the Netherlands and one in Denmark, France, Morocco and Mauritania. All studies were done in the field on free-living Oystercatchers, except those indicated as C in column 'Cap' of the appendix which refer to caged birds. Captive birds were either taken to the mudflats where they were allowed to feed in temporary cages (Hulscher 1976, 1982, unpubl.) or they were offered food on artificial mudflats (e.g. Swennen *et al.* 1989). Captive birds thus fed in an almost natural situation, but occasionally the food supply was manipulated either by erasing surface tracks that might reveal the presence of the prey (Hulscher 1982), or by implanting prey at different depths (Wanink & Zwarts 1985, 1996).

Prey size

Size classes taken were known because prey remnants could be collected, and/or the prey size was estimated when the birds held the prey in the bill. In the latter case, bill length or the size of the colour ring could be used as a ruler of known size. Calibration experiments showed that observers could estimate prey size this way rather consistently (Ens 1982, Goss-Custard *et al.* 1987, Boates & Goss-Custard 1989, Ens *et al.* 1996b). Such estimates were usually accurate. In others, errors could be corrected. For instance, comparison of the size frequency distribution of remnants of fiddler crabs *Uca tangeri* taken by Oystercatchers (Ens unpubl.) and

Fig. 1. Map of the study areas in NW. Europe indicated by three letter codes. Two study areas were situated in Africa: the Bay of Dakhla, Morocco (formerly Western Sahara) and the Banc d'Arguin, Mauritania.

size of estimates of *Uca* obtained visually, as they were being taken (Ens *et al.* 1993), showed that the visual estimates were systematically 5 mm too low.

Since Oystercatchers only ingest soft flesh, faecal analysis did not reveal information on prey size selection. However, if Oystercatchers swallowed the prey whole, hard prey fragments found in the excreta could be used to predict the prey size taken, as shown by Durell *et al.* (1996), who measured the jaws of Ragworms, and Zwarts & Blomert (1996) who did the same for jaws and head capsules of Leatherjackets.

Prey weight

Although the best measure of prey value would be assimilated energy, we have to rely on gross intake of biomass for two reasons. First, except for a few studies (Speakman 1984a, Kersten & Visser 1996a and Zwarts & Blomert 1996), the digestibility of the natural food of Oystercatchers has not yet been measured. However, since the biochemical composition of the flesh of marine bivalves does not vary much (e.g. Beukema & de Bruin 1979, Dare & Edwards 1975), we assume also that the digestibility of this type of food for Oystercatchers does not vary much either and will remain close to 85%, such as found by Speakman (1984) and Kersten & Visser (1996a) for mussel flesh. Second, too few studies have measured the caloric content of the food taken by Oystercatchers. However, the available studies (e.g. Brey *et al.* 1988, Dauvin & Joncourt 1989, Zwarts & Wanink 1993) suggest that the variation is not large, usually between 22 and 23 kJ g^{-1} ash-free dry weight (AFDW). Hence we take the rate of AFDW consumption as a general measure of prey profitability and intake rate.

Dare (1975) found a weight loss of 12.8% if Mussels were stored in formalin. Corrections for weight loss due to formalin have been made in the studies of Meire & Ervynck (1986), Meire (1996b) and Exo *et al.* (unpubl.); these studies are indicated with F in column 'Lab' of the appendix. The first quantitative studies in the fifties and sixties expressed food consumption not in terms of AFDW, but as volume, wet weight or dry weight. Column 'Lab' in the appendix indicates which studies give intake rate as volume (V), wet weight (W) or dry weight (D). Volume (ml) of flesh, determined by emersion in water, is equivalent to 90-93% of its wet weight (mg) (Drinnan 1958b, Hulscher 1982). The dry weight of bivalve flesh is 15% to 20% of the wet, or fresh, weight (Hulscher 1974, 1982, Kersten & Visser 1996a). The variation in this ratio depends on the laboratory procedures used. The water content varies between 79 and 82% if the flesh is briefly patted dry, but is some percentage points lower if it remains longer on a filter paper and higher if water on the surface of the flesh is not removed (Zwarts unpubl.).

Dry weight includes inorganic material. The ash-free dry weight (AFDW) of the flesh of marine invertebrates varies between 75 and 90% of the dry weight. A part of this variation may be attributed to the season (Zwarts 1991), but the main source of variation is again the laboratory procedure. The ash content of the flesh drops to 10-15% if the animals have been stored in clean sea water, but if their alimentary tract is still full of sediment, the ash percentage can be as high as 25 or even 30%. For estuarine prey species, we take a common conversion factor of 0.16 to estimate AFDW if only wet weight is known and 0.17 if only volume has been determined. If the AFDW of prey has not been measured but derived from the volume or wet weight by using these conversion factors, the error of the estimate may be as much as 25% due to variation in the water content of the prey and, especially, the variable amount of ash. The error is still larger in earthworms in which the ash content varies between 25 and 55%.

The relationship between size and weight of the prey has been determined in all studies. If a paper did not give the average prey weight, we calculated it from the frequency distribution of the size classes taken and the size-weight relationship. In a few studies, the frequency distribution was not given. In those cases the weight of the average length class was taken as the average weight. This underestimates, inevitably, the average prey weight, especially if the range of size classes taken was large due to the exponential increase of weight with size.

Some prey were incompletely consumed and additional data have to be collected to know how much flesh remained in the shell (Zwarts & Wanink 1984, Swennen 1990). For instance, Oystercatchers feeding on fiddler crabs (Ens *et al.* 1993), opened the carapace and took the flesh piecemeal but refused the pincers and legs, hence ignoring half of the biomass of the large specimens (Zwarts & Dirksen 1990). A more difficult error of estimate arose if prey were stolen as they were being eaten, or when Oystercatchers leave behind considerable amounts of flesh in the prey, which were subsequently consumed by other waders. This makes it hard to estimate the fraction of the prey biomass that was actually taken, a problem faced by Swennen (1990) in quantifying the intake rate of birds feeding on Giant Bloody Cockles *Anadara senilis*.

These problems did not arise when the weight of the flesh taken was not derived indirectly from the prey size but instead from direct estimates of the amount of flesh swallowed. The size of pieces of flesh extracted from the prey was estimated and converted to prey weight using calibration experiments with model Oystercatchers in which observers estimated the size of morsels of flesh held near the bill (Blomert *et al.* 1983, Goss-Custard *et al.* 1987, Kersten & Brenninkmeijer 1995, Ens & Alting 1996b). This alternative way of estimating prey weight is the only one that can be used if the size of the individual prey was unknown as, for instance, when the flesh was extracted from prey opened beneath the surface.

Profitability

Profitability is defined as mg AFDW per second prey handling. Unless stated to the contrary, this only refers to prey which are actually consumed. Profitability can also be calculated taking into account the time lost on prey that were handled but not taken. The time spent in handling prey taken, and not taken, is known as the 'positive' and 'negative' handling times, respectively. To include negative handling times in the calculation of the profitability, it is necessary to known how often prey of a given size class are not taken and how much time is lost each time. Usually, the inclusion of lost handling times does not matter much, since either the negative handling times are very short, and/or very few prey are rejected, as shown for Ragworms and *Macoma* by Ens *et al.* (1996a). Important exceptions are Mussels being hammered on the dorsal, and especially on the ventral side (Meire & Ervynck 1986, Cayford & Goss-Custard 1990). The feeding method used when eating Mussels is indicated in column 'Mus' of the appendix.

Intake rate

Intake rate is defined as mg AFDW consumed per second of feeding. Feeding time excludes preening and resting pauses, but includes short bouts of aggressive behaviour. Most data are based on observation periods of 5, 10 or 15 minutes. In some cases, however, individual birds were watched continuously for the entire low water period (Blomert *et al.* 1983, Ens & Goss-Custard 1984), or both methods were used (Ens *et al.* 1996b).

Some studies concerned Oystercatchers taking a mixture of prey species. In these cases, observation periods were selected during which at least 80% (and occasionally 100%) of the ingested biomass belonged to one species. This may cause errors of estimation. If an Oystercatcher generally feeds only on a small prey and only incidentally takes a large one, 5 min. periods during which only the large species are taken tend to give untypically high intake rates which birds may seldom attain were they to feed solely on these prey. This was presumably the case in Oystercatchers taking large *Mya* or *Arenicola* while their main prey, *Macoma* and *Nereis*, were smaller (Bunskoeke 1988). According to the same reasoning, estimates of intake rate of small prey taken from feeding bouts with large prey may be spuriously low.

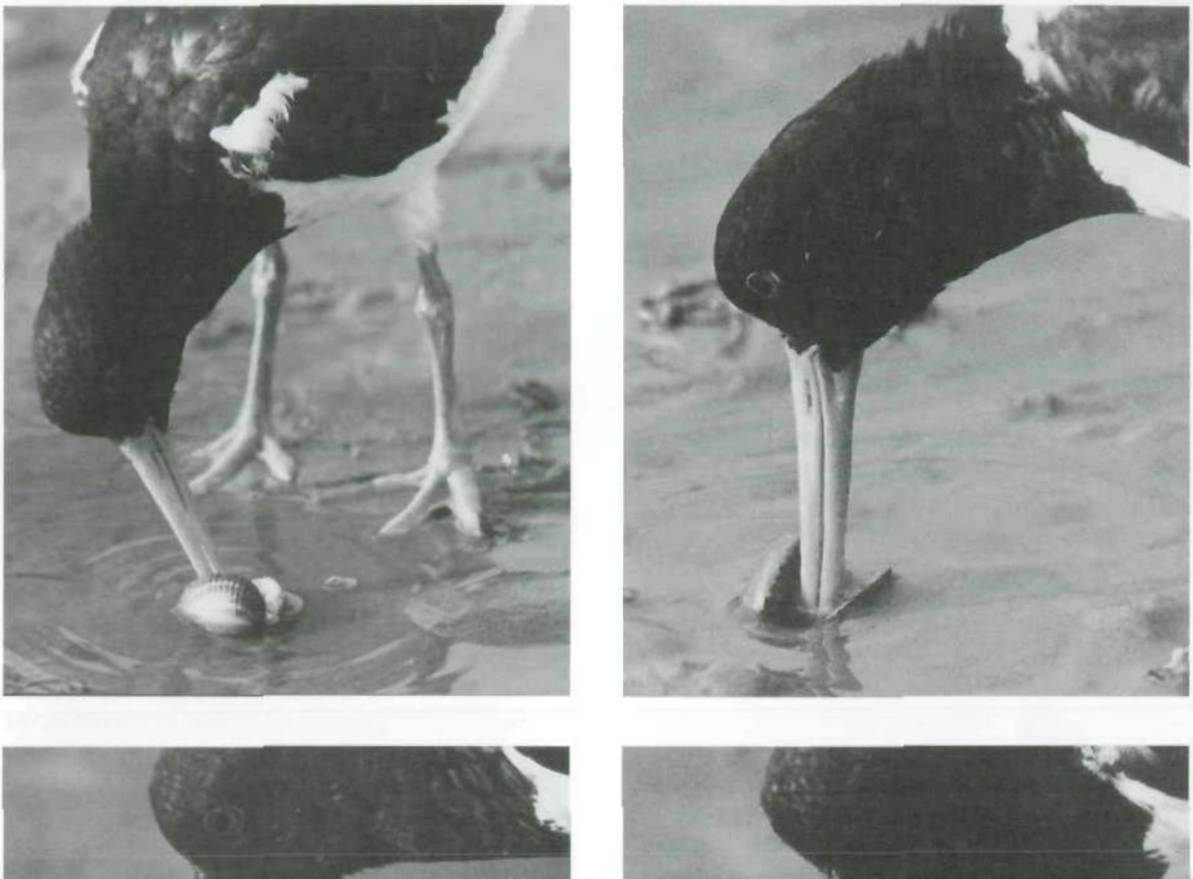
We will investigate the relationship between intake rate and the prey density for Oystercatchers feeding on *Cerastoderma*, but not in the other prey species; see Goss-Custard *et al.* (1996b) for mussel-eating Oystercatchers. Column 'n m^{-2}' in the appendix gives the cockle densities.

Available feeding period

The maximal duration of the feeding period in tidal areas is determined by the exposure time of the feeding area which is usually situated at, and below, mean sea level. The main feeding areas of Oystercatchers, cockle and mussel beds, are available for 5-6 h over an average low water period. The exposure time would overestimate the duration of the feeding time for breeding birds, since they visit the low water feeding areas only in short bouts (e.g. Ens *et al.* 1996b). These measurements are marked with a B in the column 'Br'. The available, sometimes extremely short, feeding periods in captive birds were varied experimentally. Column 'Time' in the appendix gives the duration of the feeding period.

Feeding activity

The feeding activity was determined in two ways.



After an Oystercatcher has opened a Cockle, it only takes some seconds to separate the soft body from the shell and swallow the flesh.

Counts of feeding and non-feeding birds were conducted at regular intervals over the entire low water period. The alternative was to measure continuously the non-feeding time in individual birds of which the feeding behaviour was registered over long periods. Column 'Feed' in the appendix gives the percentage of the time actually spent feeding.

Consumption

The product of intake rate, duration of the feeding period and the percentage of time spent feeding estimates the total consumption during the feeding period, given in column 'Cons' of the appendix. The feeding period refers to the total daylight period in non-tidal habitats and to the low water period by day in tidal habitats. The appendix gives in column 'Cons' the available estimates of consumption.

Analysis

We assembled two data files from the literature and our own unpublished data. One contained measurements of the handling time by prey species and by prey size and/or prey weight. The other contained the intake rates of Oystercatchers feeding on a single prey species. If studies spanned several months or years, the data were subdivided by month if intake rates were available for each month and based on sufficient measurements and prey weight and intake rate differed between the months. The same criteria were used to decide whether data would be given separately or lumped for different study plots within the study area or for different individual birds being studied. The intake rates were lumped in the few cases that the intake rates were known per Oystercatcher age class. Since the paper investigates the effect of prey density on intake rate in *Cerastoderma*, the intake rates from four studies have been split up for different subareas where prey size, prey density and intake rate were measured. SPSS (Norušis 1990) was used for all statistical analyses.

Results

Handling time of armoured prey in relation to prey size, opening technique and burying depth

The smallest armoured prey opened by Oystercatchers were spat Cockles 8 mm long with an AFDW of 3.3 mg (Meire 1996b). The largest prey taken were Giant Bloody Cockles *Anadara* which is the food supply of Oystercatchers wintering on the Banc d'Arguin, Mauritania (Swennen 1990). These birds ate prey that were, on average, 78 mm long containing 3300 mg AFDW. Even larger prey were taken by Oystercatchers in captivity, as well as in the field, when offered large *Mya* 88 mm long with a flesh content of 4200 mg AFDW. However, since these prey usually lie out of reach of the bill (Zwarts & Wanink 1984), they cannot be considered as normal prey for Oystercatchers. Cockle spat could be handled in some seconds, but it took an Oystercatcher 212 s and 265 s, on average, to consume the flesh from the large *Anadara* and *Mya*. Thus, the handling time increases with flesh weight, as is further analysed in this section.

Although prey size explained a substantial part of the variation in handling time, there remained a large residual variation within each size class. In Mussels, a large part of this variation could be attributed to the technique used to open the Mussel (Fig. 2). Oystercatchers using the stabbing technique took less time than those which hammered Mussels on the dorsal side of the shell. The handling times were especially long when Mussels were torn off the bed, turned upside down and hammered on the ventral side (Cayford & Goss-Custard 1990, Fig. 2). Cockles were usually opened by stabbing, or forcing, the bill between the valves, but sometimes by hammering the shell. Ens *et al.* (1996b) found that it took Oystercatchers more time to open Cockles by hammering than by stabbing, just as in Mussels (Fig. 3).

The handling time also increased with shell length and flesh weight in *Scrobicularia* but it also depended on the depth at which the prey lived beneath the surface (Fig. 4). Wanink & Zwarts (1985) found that the time needed to handle *Scrobicularia* 37 mm long increased from 18 to 42 s as the burying depth increased from 0 and 5 cm (Fig. 4). Wanink & Zwarts (1996) offered Oystercatchers prey of different size but buried at a depth of 2 cm beneath the mud surface. All size classes were handled rapidly. The handling time of *Scrobicularia* of different size has also been measured in the field, but no attempts have been made to estimate the depth from which the prey are extracted. It is obvious, however, that most prey in winter were taken after the bill had been inserted fully into the substrate,

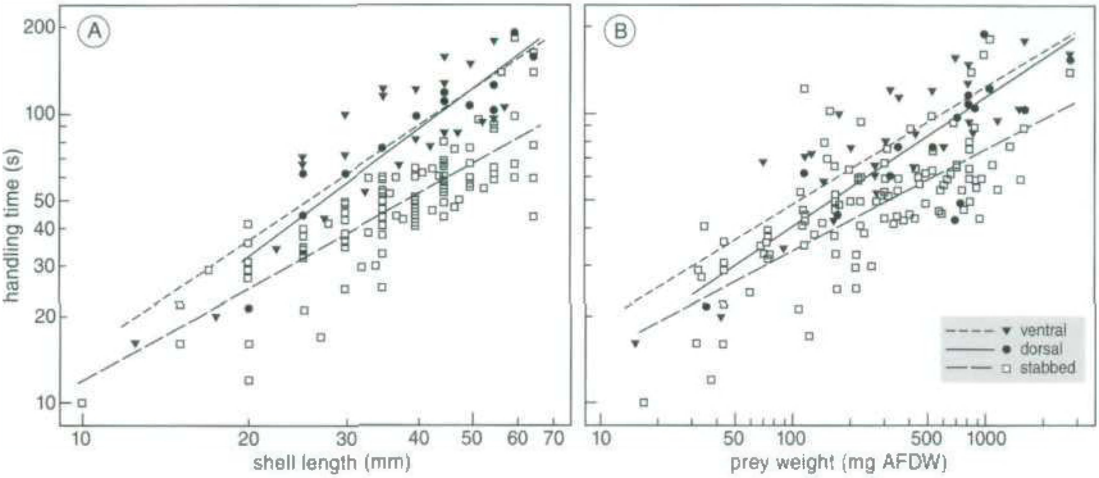


Fig. 2. Handling time as a function of **A.** prey length or **B.** prey weight in *Mytilus* opened by Oystercatchers stabbing the bill between the valves, or hammering the shell on the dorsal or ventral side. Sources: Blomert *et al.* (1983), Cayford & Goss-Custard (1990), Ens (1982), Ens *et al.* (1996b), Hulscher (unpubl.), Koene (1978), Linders (1985), Meire & Ervynck (1986), Speakman (1984), Sutherland & Ens (1987), Zwarts & Drent (1981). The three regression lines (see also Table 1) differ significantly ($p < 0.001$) from each other according to covariance analyses: $R^2 = 0.593$ for prey length and $R^2 = 0.168$ for the three techniques (left); $R^2 = 0.620$ for prey weight and $R^2 = 0.100$ for the three techniques (right).

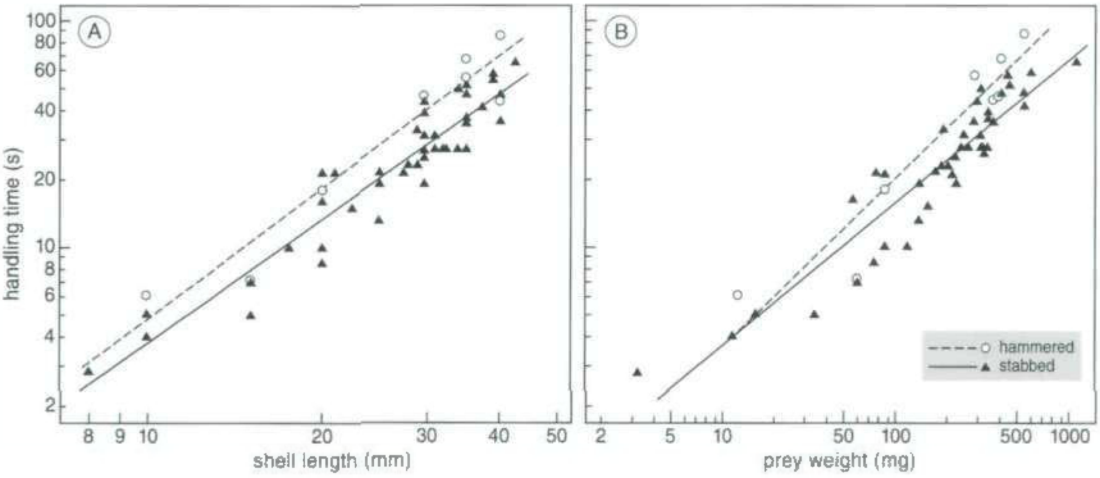


Fig. 3. Handling time as a function of **A.** prey length or **B.** prey weight in *Cerastoderma*, given separately for Oystercatchers opening Cockles by stabbing the bill between the valves or hammering the shell. Sources: Hulscher (1976 & unpubl.), Ens *et al.* (1996b & 1996c), Sutherland (1982c), Swennen *et al.* (1989), Triplet (1994). The two regression lines (see also Table 1) differ significantly ($p = 0.002$) from each other according to covariance analyses: **A.** $R^2 = 0.875$ for prey length and $R^2 = 0.024$ for both techniques; **B.** $R^2 = 0.868$ for prey weight and $R^2 = 0.016$ for both techniques.

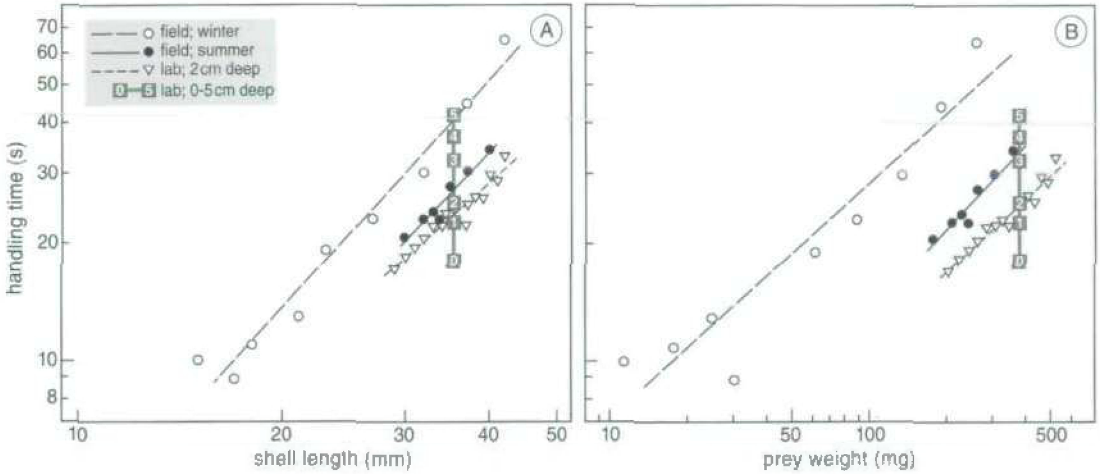


Fig. 4. Handling time as a function of **A.** prey length or **B.** prey weight in *Scrobicularia*, given separately for field data collected in winter (Boates & Goss-Custard 1989, Habekotté 1987) or in summer (Blomert *et al.* 1983) and for captive birds offered prey of similar size at different depths (Wanink & Zwarts 1985) or for different size classes buried to the same depth of 2 cm (Wanink & Zwarts 1996). The three regression lines (see also Table 1) differ significantly ($p < 0.001$) from each other, according to covariance analyses: **A.** $R^2 = 0.848$ for prey length and $R^2 = 0.089$ for the three groups; **B.** $R^2 = 0.674$ for prey weight and $R^2 = 0.219$ for the three groups.

whereas in summer the majority were taken from nearer the surface. Such a difference was to be expected, since most *Scrobicularia* in winter live out of reach of the Oystercatcher's bill (Zwarts & Wanink 1991, 1993); probably, all prey taken are only just accessible at a depth of 6 cm or 7 cm beneath the surface. In contrast, *Scrobicularia* live at shallower depths in summer, and some prey may be found at a burying depth of just a few cms only. In winter it took 1.4 times more time as in summer to handle *Scrobicularia* of similar size (Fig. 4). We conclude that the longer handling times in winter were entirely due to the greater burying depth of the prey.

The handling times of *Macoma* also increased with size (Fig. 5). It also seems likely that, just as in *Scrobicularia*, handling time increased with prey depth. *Macoma* live in the upper three cm of the substrate from April through July, increase their depth from Au-

Table 1. Handling time as an exponential function of length (L, mm) or weight (W, mg) of the prey. The last column gives the number of the figure where the regression lines are depicted.

Species	*Category*	*Regression*	*R*	*n*	*Fig.*
Mytilus	ventral	$0.712L^{1.313}$	0.86	26	2A
Mytilus	dorsal	$0.443L^{1.432}$	0.93	14	2A
Mytilus	stabbed	$0.975L^{1.081}$	0.82	99	2A
Cerastoderma	hammered	$0.054L^{1.945}$	0.96	8	3A
Cerastoderma	stabbed	$0.053L^{1.840}$	0.95	42	3A
Scrobicularia	field; winter	$0.046L^{1.905}$	0.98	9	4A
Scrobicularia	field; summer	$0.041L^{1.823}$	0.96	7	4A
Scrobicularia	lab; 2cm deep	$0.093L^{1.549}$	0.98	14	4A
Macoma	Aug; lifted	$0.262L^{1.466}$	0.83	7	5A
Macoma	Apr-Jun; lifted	$0.076L^{1.778}$	0.87	16	5A
Macoma	Apr-Jun: in situ	$0.408L^{1.055}$	0.67	5	5A
Mya	lab; 2 cm deep	$0.070L^{1.546}$	0.80	44	6A
Mytilus	ventral	$7.258W^{0.411}$	0.84	26	2B
Mytilus	dorsal	$5.114W^{0.451}$	0.92	14	2B
Mytilus	stabbed	$6.549W^{0.355}$	0.78	99	2B
Cerastoderma	hammered	$0.625W^{0.750}$	0.95	8	3B
Cerastoderma	stabbed	$0.817W^{0.637}$	0.93	42	3B
Scrobicularia	field; winter	$1.821W^{0.508}$	0.95	9	4B
Scrobicularia	field; summer	$0.541W^{0.701}$	0.96	7	4B
Scrobicularia	lab; 2cm deep	$0.675W^{0.610}$	0.98	14	4B
Macoma	Aug; lifted	$2.212W^{0.487}$	0.83	7	5B
Macoma	Apr-Jun; lifted	$0.694W^{0.655}$	0.87	16	5B
Macoma	Apr-Jun; in situ	$0.508W^{0.642}$	0.83	10	5B
Mya	combined	$0.661W^{0.586}$	0.91	54	6B
Nereis		$0.378W^{0.481}$	0.96	35	7
Arenicola		$0.387W^{0.530}$	0.98	7	7
Earthworms		$1.489W^{0.216}$	0.52	10	7

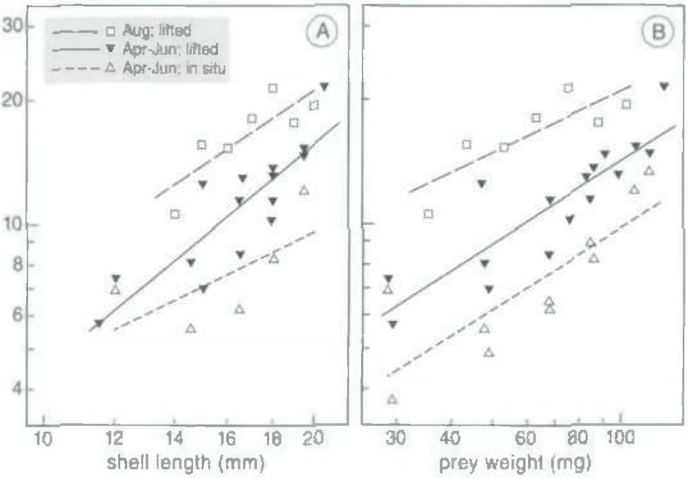


Fig. 5. Handling time as a function of **A.** prey length or **B.** prey weight in *Macoma*, given separately for prey eaten in situ or lifted to the surface and eaten there; the latter is divided into two periods (April-June, August). Sources: Hulscher (1982 & unpubl.), Hulscher *et al.* (1996), Blomert *et al.* (1983), Ens *et al.* (1996a). The three regression lines (see also Table 1) differ significantly ($p < 0.001$) from each other, according to covariance analyses: **A.** $R^2 = 0.490$ for prey length and $R^2 = 0.326$ for the three groups; **B.** $R^2 = 0.402$ for prey weight and $R^2 = 0.445$ for the three groups.

gust onwards and live about twice as deep in winter as in summer (Reading & McGrorty 1978, Zwarts & Wanink 1993). No studies were available for Oystercatchers feeding on *Macoma* in autumn and winter, probably because they are not taken then. However, within the summer half of the year, handling time varied seasonally, being in August 1.5 times as long as in spring and early summer (Fig. 5A); this is presumably due to the greater depth from which the prey were obtained in August. This comparison refers to field studies in which prey were lifted to the surface. However, *Macoma* are also eaten in situ, and in this case handling times are much shorter (Fig. 5A & B). Captive Oystercatchers lifted deep-living prey more often than shallow prey (Wanink & Zwarts 1985, Hulscher *et al.* 1996), so we assume that prey were eaten more often in situ during summer, whereas in early spring and late summer when they live at greater depth they were more lifted. Bunskoeke *et al.* (1996) provided some tentative support for this idea from free-living birds. As a consequence, the combined handling time of *Macoma* being lifted and eaten in situ will be short when the prey live close to the surface from April to July, the difference between late summer and early spring being perhaps twofold.

There is no variation in the burying depth of *Mya* during the year, so we expected no seasonal, prey depth-related variation in the handling time, as found in *Scrobicularia* and in *Macoma*. All the handling times in Fig. 6A were obtained in the laboratory, except for those obtained in one field study. Figure 6A shows the handling time of clams up to 90 mm long. Free-living Oystercatchers never find *Mya* larger than 40 mm long, since these large clams live out of reach of the bill (Zwarts & Wanink 1984, 1989, 1993). All clams in the laboratory experiments were buried, however, at a depth of about 2 cm and so at an extremely shallow depth compared to the natural situation, at least for the larger size classes. This means that, as in *Scrobicularia*, the handling times of the larger size classes would be about twice as long if the prey were taken from a depth of 5 or 6 cm, as would be usual in the field. The single field study found that, in contrast to the expectation, Oystercatchers handled the prey in less time than in the laboratory (Fig. 6A). However, while the Oystercatchers in the laboratory ingested all the flesh from the shell, the birds in the field often only took the siphon and left behind the remaining part of the body (Zwarts & Wanink 1984). Another field study (Bunskoeke *et al.* 1996, pers. comm.) estimated the

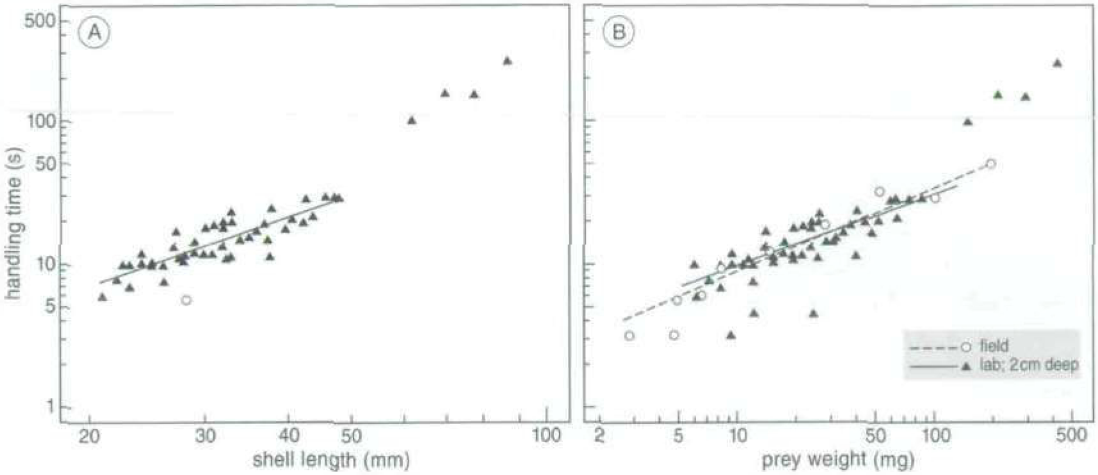


Fig. 6. Handling time as a function of **A.** prey length or **B.** prey weight in *Mya* in captive Oystercatchers feeding on prey lying at a depth of 2 cm (Wanink & Zwarts 1996) or wild birds feeding on clams from which the flesh is eaten in situ (Zwarts & Wanink 1984, Bunskoeke *et al.* 1996 & unpubl.). The regressions are calculated without the four largest clams since their handling times were untypically long. The handling times as a function of prey weight are not significantly different ($p = 0.33$ in panel B). Results of covariance analyses: **A.** $R^2 = 0.853$ for prey length; **B.** $R^2 = 0.869$ for prey weight and $R^2 = 0.002$ for the two groups; Table 1 gives more details.

weight of the flesh extracted from *Mya* of unknown size, so more field data were available when handling time was plotted against the prey weight (Fig. 6B). As Fig. 6B shows, the relationship between handling time and prey weight was the same as in the laboratory, where all the flesh from shallow prey was eaten, and field studies, where a variable amount of flesh was extracted from deep-living prey.

In conclusion, the handling time of all armoured prey species increases with prey size. An additional, and substantial, part of the variation in handling time may be explained by four other variables: (1) depth from which prey are taken; (2) whether prey are hammered or stabbed; (3) whether prey are opened in situ or opened after being pulled up from or off the sediment; and (4) portion of the prey eaten.

Handling time of bivalves in relation to prey condition

Figures 2-6 show the handling times as a function of prey length and of prey weight. If most of the handling time is spent in eating the flesh, we expect that the handling time would depend on the amount of flesh ingested and that the close relationship between handling time and prey size is due only to the high correlation between prey size and flesh weight. On the other hand, if handling time consists mainly of time spent in breaking the shell, handling time would be primarily determined by size-related strength of the shell and not by the amount of flesh ingested. Prey weight and prey size are so highly correlated, that it is hardly surprising that it is not possible to tell from Figs. 2-6 whether handling time depends on prey weight, and thus indirectly on size, or on prey size, and thus indirectly on the amount of flesh to be ingested.

Although flesh weight and prey size were highly correlated when both were plotted on a log-log scale, the weight variation within each size class was large enough to investigate whether the amount of flesh, independent of prey size, affected the handling time. Most of the species preyed upon by Oystercatchers contained in late winter 40% less flesh than specimens of similar size in early summer (Chambers & Milne 1979, Zwarts 1991, Zwarts & Wanink 1993, Ens *et al.* 1996b). Prey condition had been defined as percent deviation of the average prey weight, such as obtained by regressing log(weight) against log(size), using all data given in Figs. 2-6. Multiple regression analyses showed that handling time increased with prey length and that it also took, as expected, more time to handle Cockles and Mussels containing more flesh. These increases were not significant, however (Table 2). The relationships were even significantly negative in *Scrobicularia* and *Macoma*. The explanation is that in the latter two species prey condition and burying depth varied concurrently: they were meagre and buried deep in winter and had a good condition and were close to the surface in summer. As shown in the previous section, handling time increased with burying depth, so the negative correlation between handling time and prey condition was most likely due to the positive correlation between prey condition and burying depth (e.g. Zwarts 1991, Zwarts & Wanink 1993).

In conclusion, the increase of handling time with flesh content, such as shown by Ens *et al.* (1996b) for his data, is not found by us when data from different mussel and cockle studies were pooled. *Scrobicularia* and *Macoma* are even handled significantly more rapidly if they contain more flesh, but this is because body condition varies seasonally in accordance with burying depth.

Handling time of soft-bodied prey in relation to prey weight and burying depth

Figure 7 shows the relationship between handling time and prey weight in four soft-bodied prey: Ragworms, Lugworms, earthworms and Leatherjackets. Handling time quadruples as prey weight increases thirtyfold. The handling times are short in these species for several reasons. First, no time was spent in opening, or preparing, the prey, since they were eaten whole. Moreover, soft-bodied prey were usually swallowed in one piece and not piecemeal. Further, most of these prey were picked up from, or taken from just beneath, the surface. Handling times were longer when the prey were extracted from the substrate. It took Oystercatchers, on average, 4 s to remove Leatherjackets from their burrows, 2-4 cm deep, and only 1.3 s to mandibulate them (Blomert & Zwarts unpubl.). Hence, depending on the position of the Leatherjacket in its burrow, the handling time varied between 2 and 6 s. We might expect an even larger difference in earthworms. When prey are found at, or just beneath, the surface, they can be grasped easily and transported up the bill in only one catch-and-throw movement (see Gerritsen 1988). But when prey are extracted from the turf, they often break and must therefore be eaten piecemeal. Whether the prey are at or beneath the surface presumably also explains the average differences in handling time between species. Lugworms, and the majority of the Ragworms, were grasped while they were close to the surface and at depth in their burrows. In contrast, the Leatherjackets and earthworms were, at least partly, extracted from the turf.

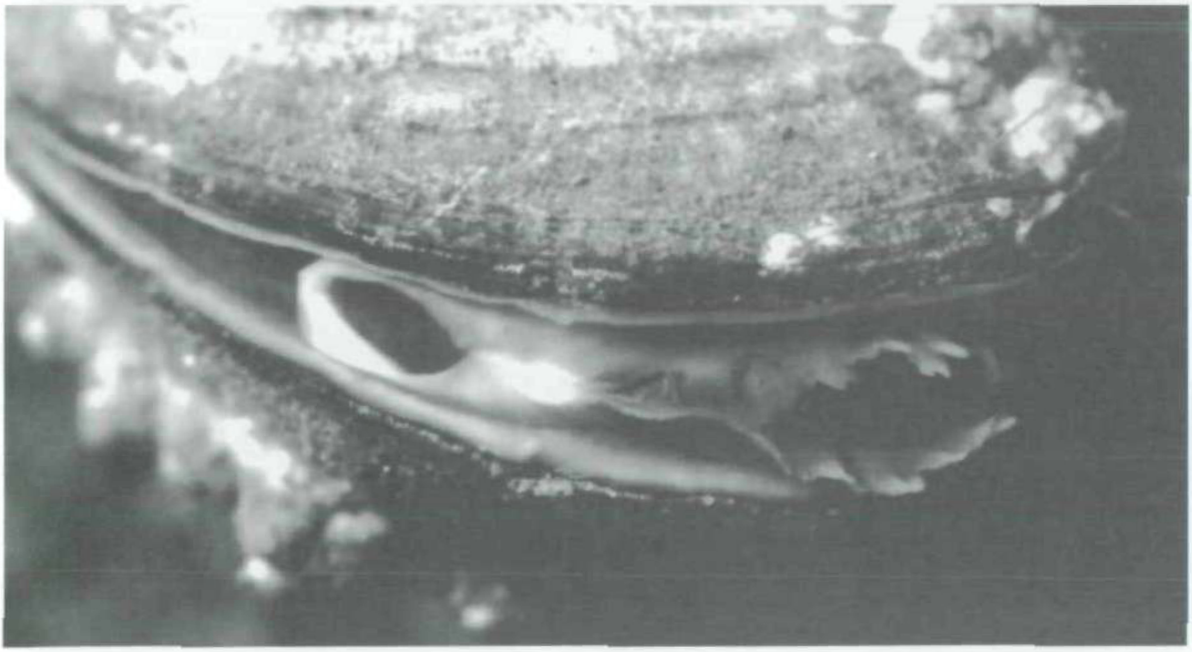
Table 2. Handling time as a function of prey size and prey condition according to multiple regression analyses: a is the intercept, $b_1 \pm SE$ is the prey size (ln(mm)) and $b_2 \pm SE$ is the prey condition (ln(percent deviation from average weight for each mm class)). The average weights are obtained by plotting for each species all weights against all sizes in Figs. 2-6. The analysis in *Mytilus* and *Cerastoderma* is limited to prey opened by stabbing. The prey condition has a non-significant, positive effect on the handling time in *Mytilus* and *Cerastoderma* and a significant, negative effect on the handling time of *Scrobicularia* and *Macoma*.

Species	*a*	b_1	*SE*	b_2	*SE*	*R*	*n*
Mytilus	-0.029	+1.081	.075	+0.041	.074	.681	99
Cerastoderma	-2.950	+1.851	.112	+0.273	.200	.945	36
Scrobicularia	-1.255	+1.254	.157	-0.572	.155	.582	61
Macoma	-2.452	+1.746	.328	-1.093	.511	.754	28

We conclude that soft-bodied prey are handled rapidly, unless they are extracted from the substrate. We assume that because Oystercatchers usually feed on estuarine worm species that appear at the surface, they are handled in less time than the grassland species which are more often extracted from the turf.

Profitability of armoured and soft-bodied prey

Figures 2-7 show the relation between handling time and prey weight in five armoured and four soft-bodied prey species. The profitability, the amount of flesh consumed per unit time handling, was calculated for these species, and also for *Anadara* and *Uca*, and plotted against their prey weight (Fig. 8). Worms and Leatherjackets were, on average, 4.43 times more profitable than armoured prey of similar size. Although there was a large scatter in the profitability of the armoured prey, it is clear that the profitability of soft-bodied, as well as armoured prey, increases with prey weight.



Fiddler crabs (upper photo) are the least profitable prey, because it takes an Oystercatcher a lot of time to open the carapace and eat the flesh; by not eating the pincers and the jaws, they ignore 50% of the flesh. Also Mussels are no profitable prey, even if the birds encounter Mussels which are open and the bill can be stabbed immediately between the valves (lower photo).

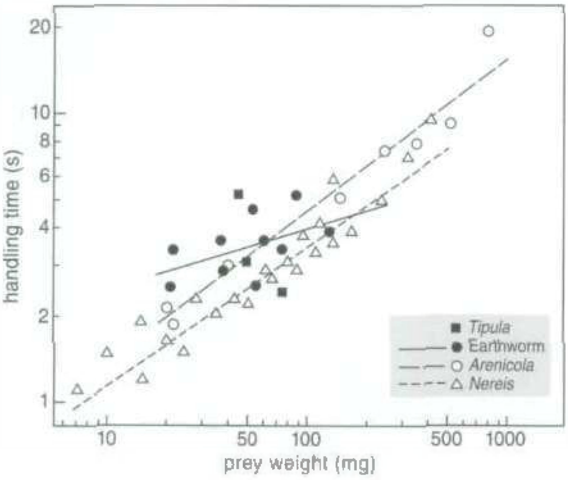


Fig. 7. Handling time as a function of prey weight (mg AFDW) in earthworms (Ens unpubl.). *Nereis* (Boates & Goss-Custard 1989, Ens *et al.* 1996a, Hulscher unpubl.), *Tipula* (Blomert & Zwarts unpubl., Ens unpubl.) and *Arenicola* (Bunskoeke 1988 & unpubl.). The handling times of the four species differ significantly according to a covariance analysis ($R^2 = 0.918$ for prey weight and $R^2 = 0.025$ for the species).

The large scatter in the profitability of armoured prey could largely be explained by the species concerned and the technique used to open them. An analysis of covariance revealed that the 11 prey species alone explained 39.1 % of the variance, prey weight 15.1%, whereas 24.0% could be attributed to both. To visualize the differences in profitability between species, independently of prey weight, we regressed profitability against prey weight for the armoured and soft-bodied prey, without distinguishing among the species, and calculated for each species the average deviation from the regression line. Fig. 9 is based upon these calculations and shows the average profitability per species, standardized to a prey weight of 200 mg. Four types of prey can be distinguished. First, soft-bodied prey taken from the surface had a profitability of 30-35 mg s^{-1}. Second, if soft-bodied prey were extracted from the substrate, their profitability was reduced to about half, as indicated for Leatherjackets, but not shown as a separate category in Fig. 9. Third, the average profitability of bivalves living buried in the substrate was 10-15 mg s^{-1}, but was about half this value when prey had to be taken from a great depth. Fourth, hard-shelled prey found just beneath, or from the surface, were the least profitable prey (4-8 mg s^{-1}).

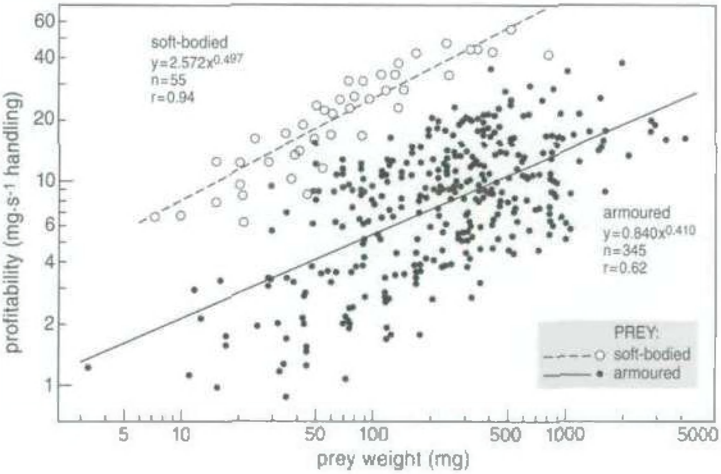


Fig. 8. Profitability (mg s^{-1} handling) as a function of prey weight (mg AFDW), given separately for soft-bodied prey (same data as Fig. 7) and armoured prey (in addition to the data given in Figs. 2-7, also *Anadara* (Swennen 1990), *Littorina* (Boates & Goss-Custard 1992), *Patella* (Safriel 1967) and *Uca* (Ens *et al.* 1993 & unpubl.). The regression lines are shown separately for soft-bodied and armoured prey. A multiple regression analysis revealed that non-parallel regression lines did not explain more variance than parallel ones ($R^2 = 0.515$ and 0.514, respectively). Hence a common exponent (0.421) may be used with different intercepts: 0.788 for armoured prey and 3.490 for soft-bodied prey.

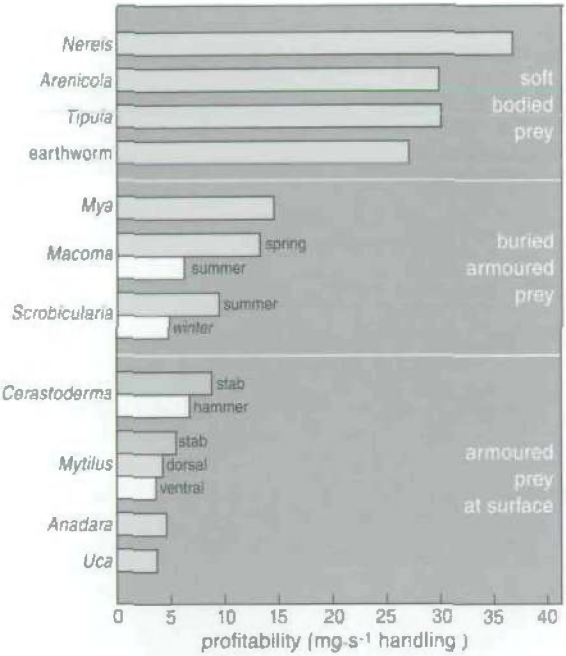


Fig. 9. Comparative profitabilities of different prey species, calculated as a relative deviation from the relationship between profitability and prey weight (Fig. 8, using a common slope but different intercepts for armoured and soft-bodied prey) and then standardized for a prey of 200 mg. According to a one-way analysis of variance, the standardized profitabilities differ significantly between the species and categories concerned ($R^2 = 0.87$, $p < 0.001$, $n = 400$). The values are extrapolations for some small prey always weighing less than 200 mg.

Of these prey, hammered bivalves were less profitable (4-6 mg s^{-1}) than those which were stabbed (6-8 mg s^{-1}). Taking the ratio shell weight to flesh weight as a measure of the amount of armour, profitability was directly related to prey armour (Fig. 10); clearly, it was least for the most heavily armoured prey.

Figures 2-10 show the time actually taken to handle prey and so ignores the waste handling time spent on rejected prey. If waste handling times due to prey being rejected or stolen prey were included, the graph for the soft-bodied prey in Figs. 8 and 9 would not change much because few prey were refused and waste handling time was very short (Ens *et al.* 1996a). In contrast, waste handling times had a significant effect on prey profitability in armoured prey, such as Mussels hammered on the dorsal or ventral side (Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996a, Meire 1996c). As a consequence, the difference in profitability between soft-bodied and armoured prey at the surface is even larger than shown.

In conclusion, prey weight varies by a factor of 1000 whereas, over this range, handling time increases only about 100 times. The relationship between handling time and prey weight is different for the various prey species. It takes 4.4 times more time to prepare and consume the flesh of armoured prey compared with a soft-bodied prey of a similar energy value. Among the armoured prey, surface prey take more time to handle than burying species. The handling time of burying prey increases, however, if they are taken from deep beneath the surface.

Intake rate and prey weight

If the time taken to search for prey is negligible, the intake rate during feeding is equal to the prey profitability, the intake rate as the prey is being handled. The profitability of the prey thus sets the upper limit to in-

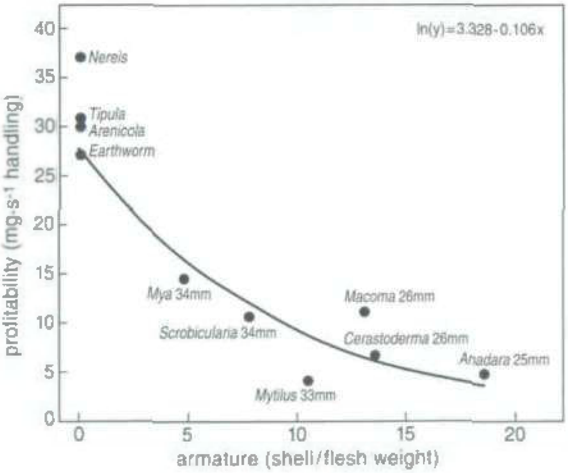
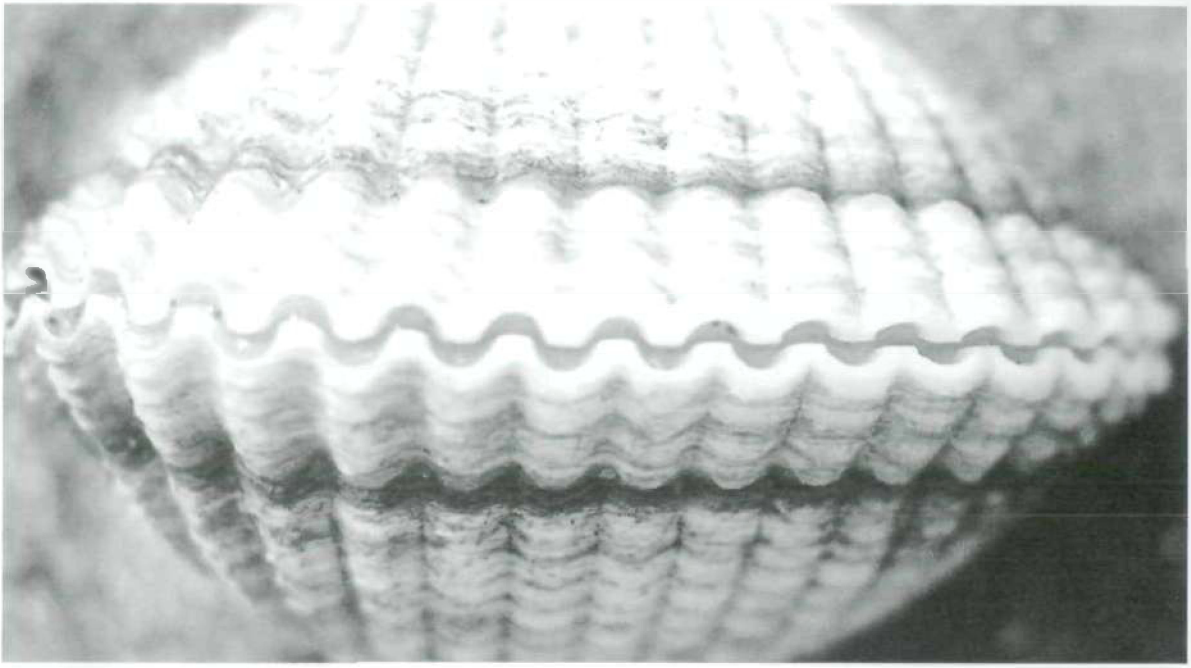
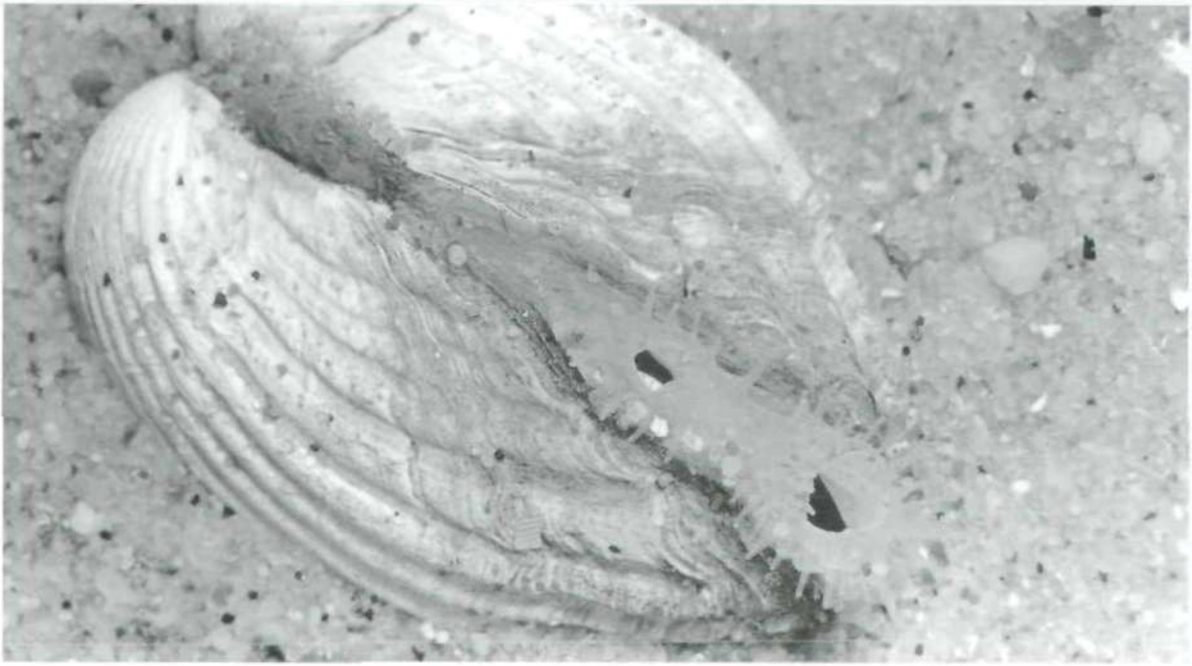


Fig. 10. Profitability as a function of the armour index in prey containing 200 mg flesh. The corresponding shell length of the bivalves is indicated. The fitted curve is highly significant ($r = -0.91$, $p = 0.0003$). Profitability of the different prey species was standardized for a prey of 200 mg (see Fig. 9). Armature index is defined as the ratio shell to flesh weight for the size classes concerned. Shell weights from Wolff *et al.* (1987), Zwarts & Blomert (1992); flesh weights from Zwarts (1991) and Zwarts & Wanink (1993).





Oystercatchers are able to eat Cockles by hammering a hole in the shell, but the handling times are much shorter when the birds can surpass the armature of the shell by prising the bill directly between the opened valves. This situation occurs when Cockles protrude their siphons to filter food particles from the overlying water.

take rate. We might therefore expect that the maximum recorded intake rate, and possibly also the average, to increase when Oystercatchers feed on the more profitable prey. As large prey are more profitable than small ones, we would expect an increase of intake rate with the average weight of the prey taken. There was indeed an effect of prey weight on intake rate, but intake rates were always relatively high when the birds foraged less than 1 h after a long resting period. We focus here on intake as a function of prey weight and exclude the 11 studies in which feeding time was less than 1 h. We analyse elsewhere the relation between intake rate, feeding activity and duration of the feeding time (Zwarts *et al.* 1996b).

Most of the prey taken by Oystercatchers weighed between 30 and 1000 mg. Within this range, the aver-

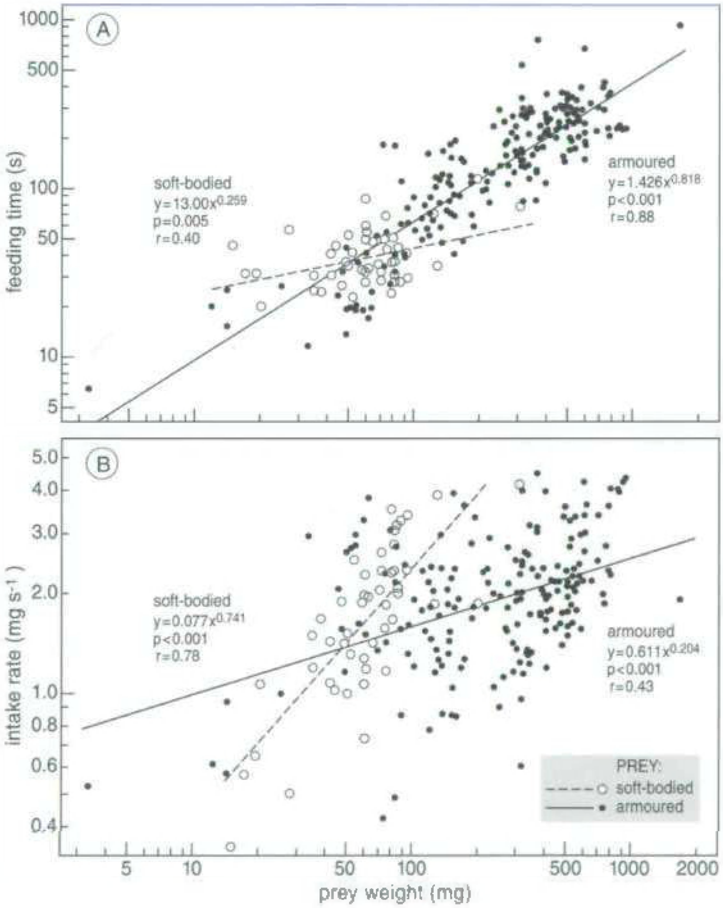


Fig. 11. **A.** Feeding time per prey (s) and **B.** intake rate (mg s^{-1} feeding) as a function of average prey weight, given separately for soft-bodied and armoured prey species. Sources: *Anadara* (Swennen 1990), *Arenicola* (Bunskoeke 1988), earthworms (Heppleston 1971, Hosper 1978, Ens unpubl.), *Littorina* (Boates & Goss-Custard 1992), *Macoma* (Bunskoeke *et al.* 1996, Hulscher 1982 & unpubl., Hulscher *et al.* 1996), *Mya* (Bunskoeke 1988, Hulscher unpubl., Zwarts & Wanink 1984), *Patella* (Safriel 1976), *Tipula* (Hosper 1978, Safriel 1976, Zwarts & Blomert 1996, Ens unpubl.), *Uca* (Ens *et al.* 1993); for other species see the legends of Figs. 12-15, or the appendix for a complete list. Feeding time is not given in the appendix, but can be calculated by dividing prey weight by intake rate. Eleven studies for which the feeding time was less than 1 h are not included. The two lines in panel A differ significantly from each other according to an analyse of variance: $R^2 = 0.814$ for prey weight and $R^2 = 0.011$ for the two groups; the regression lines in panel B explain each less variance, but differ more from each other: $R^2 = 0.214$ for prey weight and $R^2 = 0.020$ for the two groups ($n = 240$).

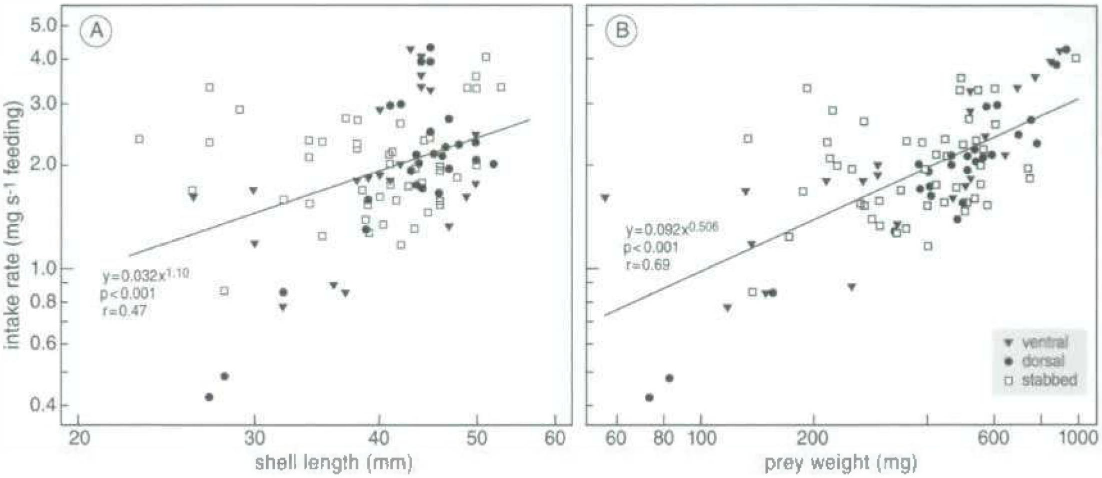


Fig. 12. The intake rate as a function of **A.** shell length and **B.** average weight of *Mytilus* taken. Sources: Boates (1988), Boates & Goss-Custard (1992), Cayford & Goss-Custard (1990), Drinnan (1958a), Ens & Goss-Custard (1984), Ens & Alting (1996b), Ens *et al.* (1996b), Goss-Custard (unpubl.), Heppleston (1971), Hulscher (unpubl.), Koene (1978), Maagaard & Jensen (1994), Meire (1996b), Meire & Ervynck (1986), Speakman (1984), Sutherland & Ens (1987), Zwarts (unpubl.), Zwarts & Drent (1981).

age feeding time per prey, the time to find and consume one prey, increased with prey weight, but the rate of increase seemed to differ between soft-bodied and hard-shelled prey (Fig. 11A). The exponent was 0.82 in hard-shelled prey, so clearly sub-proportional, and was only 0.26 in soft-bodied prey. Since the increase in average feeding time with prey weight was less than proportional, the intake rate, being the ratio of prey weight and feeding time per prey, increased with prey weight (Fig. 11B). The increase was more pronounced in soft-bodied prey than in hard-shelled prey for which the variation was very large over the range of 1 to 3 mg s^{-1} within which the majority of the intake rates occurred.

Figures 12 to 15 relate intake rate to the weight and length of the prey, separately for each species. Intake rate increased with prey length in Mussels (Fig. 12A), although the relationship was more pronounced when intake rate was plotted against prey weight (Fig. 12B). Feeding method did not explain a significant part of the variation (prey size: $r = 0.001$, $p = 0.96$, $n = 95$; prey weight: $r = 0.013$, $p = 0.35$, $n = 97$). Prey weight was also a better predictor of intake rate (Fig. 13B) than prey size in cockle-eating Oystercatchers (Fig. 13A). Similarly intake rate increased with length and weight in *Scrobicularia* (Fig. 14). However, there was no relationship in *Macoma*, probably because the variation in the range of size and weight classes taken was too limited.There were insufficient data for *Mya* (see appendix). In contrast, the increase of intake rate with prey weight was very steep in Ragworms (Fig. 15). Indeed, the increase was proportional, implying that the feeding rate (number of worms taken per unit time feeding) was independent of the average weight of the prey taken. Apparently, Oystercatchers that fed on small Ragworms were not able to compensate for the low prey weight by a higher rate of feeding.

We used multiple regression analysis, with the species as dummy variables, to explore the degree to which the variation around the regression lines in Fig. 11 could be attributed to differences between prey species. In soft-bodied prey, the variance explained increased from 60% to 69% if we assumed a similar slope for the each species (exponent = 0.656) but different intercepts. By using four parallel slopes, the regression lines became less steep than the one used for all four species species combined (exponent = 0.741). However, using different slopes for the different soft-bodied prey increased the explained variance by less than 1% and has thus not much sense. In the armoured prey species, using parallel slopes for all species (exponent = 0.375) added 31% to the 18% of the explained variance that could be attributed to prey weight using the single regression line (exponent = 0.204) in Fig. 11B. On the assumption that all the regression lines for the armoured prey species were not parallel, the explained variance increased again, but from only 49% to 56%. We therefore conclude that (1) in each species, the intake rate increases with prey weight, (2) the rate of increase differed between soft-bodied and armoured prey species, (3) the rate of increase did not differ much among the four soft-bodied and among the

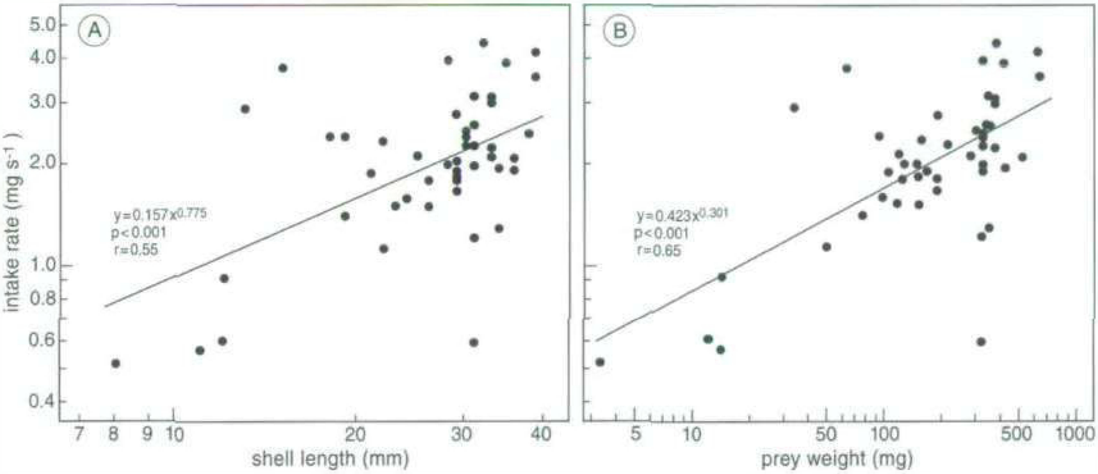


Fig. 13. The intake rate as a function of **A.** shell length and **B.** average weight of *Cerastoderma* taken. Sources: Brown & O'Connor (1974), Davidson (1967), Drinnan (1957), Ens *et al.* (1996b & 1996c), Exo, Smit & Zwarts (unpubl.), Goss-Custard (1977), Hulscher (1976 & unpubl.), Leopold *et al.* (1989), Meire (1996b), Sutherland (1982b & 1982c).

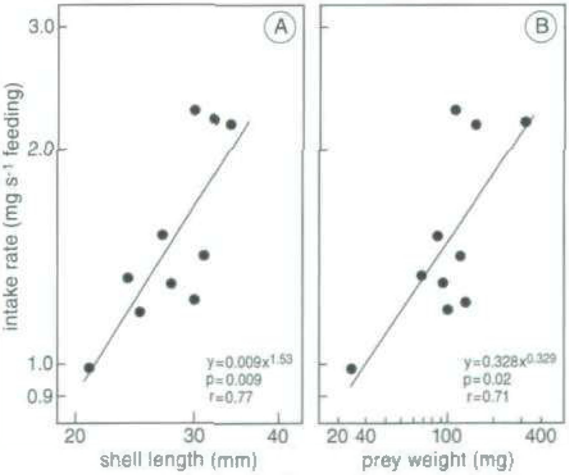


Fig. 14. The intake rate as a function of **A.** shell length and **B.** average weight of *Scrobicularia* taken. Sources: Blomert *et al.* (1983), Boates & Goss-Custard (1989), Habekotté (1987), Hulscher *et al.* (unpubl.), Wanink & Zwarts (1985 & 1996), Zwarts (unpubl.).

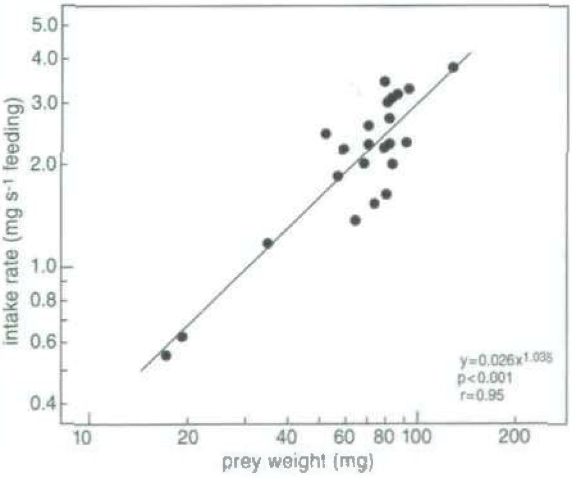


Fig. 15. The intake rate as a function of the average weight of *Nereis* taken. Sources: Boates & Goss-Custard (1989), Bunskoeke *et al.* (1996), Durell *et al.* (1996 & unpubl.), Hulscher (unpubl.), Triplet (1989).

Table 3. Average intake rate (mg s^{-1} ± SD) and prey weight per prey species; n is the number of studies (given in appendix). Eleven studies with a feeding period < 1 h and two studies with extremely low intake rates (nrs. 196 & 197 in appendix) have been excluded.

Species	*mg s^{-1}*	*SD*	*mg*	*n*
Anadara	1.85		1637	1
Arenicola	2.96	1.64	216	2
Cerastoderma	2.17	0.93	230	48
Earthworms	1.18	0.53	71	5
Littorina	1.24	0.27	138	8
Macoma	2.34	0.59	67	12
Mya	3.14	0.64	172	3
Mytilus ventral	2.04	0.92	418	26
Mytilus dorsal	2.10	0.93	513	27
Mytilus stab	2.05	0.69	409	48
Nereis	2.00	0.95	67	23
Patella	2.35		120	1
Scrobicularia	1.74	0.75	178	11
Tipula	1.34	0.48	53	18
Uca	1.78		78	61
all species	2.00	0.85		240

12 armoured prey species, and (4) intake rate differed between the species when prey of similar weight were taken.

Table 3 gives the average intake rate per prey species. According to a one-way analysis of variance, the differences were significant ($R^2 = 0.185$, $p < 0.001$, $n = 240$). The highest intake rate was found in birds feeding on *Mya* or *Arenicola* and the lowest in birds eating earthworms, *Tipula* or *Littorina*. Since intake rate increased with prey weight in each prey species, a similar relationship might be expected between average intake rate and average weight across prey species. There was, however, no such relationship ($r = 0.00$). But in order to rule out any possible effect of prey size on intake rate, the intake rate was standardized to a prey weight of 200 mg, using the predicted values from the multiple regressions with a common slope but different intercepts for the different soft-bodied and armoured prey species. Intake rate averaged for each species now differed more from each other. In conclusion, prey weight determines to a large degree the intake rate, but differences between the prey species are even larger.

Intake rate and prey density

A review of the effect of prey density on intake rate was only attempted for Oystercatchers feeding Cockles. We selected ten cockle studies, from the 12 available. As discussed by Zwarts *et al.* (1996b) intake rate was presumably overestimated by Goss-Custard (1977), while Triplet (1994a) does not present sufficient details to be included in the analysis.

If birds do not vary their search rate and prey selection with prey density, a type 2 functional response would be expected (Holling 1959). Although the levelling off in the intake rate at high prey density in the experiments of Hulscher (1976) resembled this type of response (redrawn in Fig. 16), the assumptions underlying the model were not met (Wanink & Zwarts 1985). As had already been suggested by Hulscher (1976), the birds increasingly specialized on easy prey with short handling times when prey density increased. Thus, even in a controlled experiment, Holling's functional response equation was too simple to describe the feeding behaviour of Oystercatchers.

The situation in the wild is still more complicated, because changes in prey density are usually accompanied by variation in prey condition and prey size (e.g. Goss-Custard 1977, Sutherland 1982a). Sutherland (1982a, b) compared the feeding behaviour of Oystercatchers visiting 12 plots where the cockle density varied between 10 and 600 prey m^{-2}. He found a levelling off in the feeding rate at about 9 Cockles min^{-1}. However, the highest intake rate was achieved at low prey densities because prey were large where their density was low: $r = -0.90$ for ln(density) against prey weight. A multiple regression analysis revealed that the intake rate was highly dependent on prey weight ($R^2 = 0.417$, $p = 0.0002$) as well as on prey density ($R^2 = 0.407$, $p = 0.001$). With the exception of the plot with the lowest prey density of 10 Cockles m^{-2}, all these values of intake rate fitted rather well with the general relationship between intake rate and prey weight (Fig. 13).

Intake rate as a function of prey weight and density has also been calculated in a multiple regression of the combined data set for the 38 measurements taken from the ten studies on cockle-feeding birds depicted in Fig. 16. Again, the effect of prey weight was highly significant ($R^2 = 0.577$, $p < 0.001$) as well as prey density ($R^2 = 0.093$, $p = 0.004$), with a highly negative correlation between ln(density) and ln(prey weight) (r =

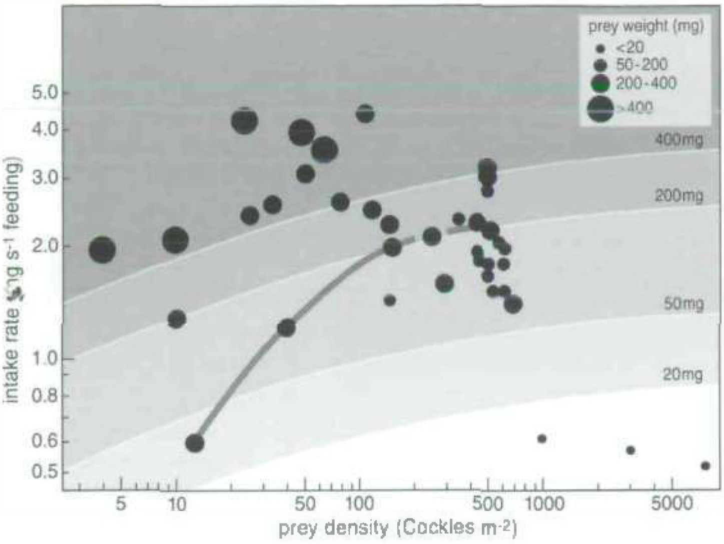


Fig. 16. Intake rate of cockle-feeding Oystercatchers as a function of prey density (n m^{-2}) assembled from ten studies. Hulscher (1976) and Leopold *et al.* (1989) offered caged birds different prey densities. Drinnan (1957), Sutherland (1982a, b, c), Ens *et al.* (1996b & 1996c), Meire (1996b), Exo *et al.* (unpubl.), Hulscher (unpubl.) and Hulsman (unpubl.) observed birds in the wild. All details are given in the appendix. The four curves are based upon the multiple regression equation: $Y = 0.238X_1 - 0.012X^2_1 + 0.476X_2 - 2.727$ ($R^2 = 0.670$, $n = 38$, $p < 0.001$), with Y = ln(intake rate), X_1 = ln(prey density) and X_2 = ln(prey weight). The grey line connects the measured intake rate of a captive Oystercatcher offered Cockles of 313 mg in different densities (Hulscher 1976).

-0.72). Figure 16 shows the intake rates predicted by the multiple regression analysis as a function of prey density for Cockles weighing 20, 50, 200 and 400 mg. These curves can be compared directly with the 38 measurements, since the prey weight has been indicated by four different symbols. It is obvious that intake rates are well predicted at high prey density but not at low. This may be due to the inevitably larger sampling error when prey density is low. Moreover, there are no studies of birds feeding on small Cockles occurring in low densities. Hence the curves for small Cockles at low prey densities must be considered as extrapolations. The regression analysis may systematically overestimate the intake rate at low prey densities because the samples refer to average density within a plot, whereas the birds would presumably select the richer patches within a plot. This typical problem for field studies was absent in Hulscher's (1976) experimental study in which Oystercatchers fed in a small plot with homogeneous prey density. As would be predicted, the intake rate at low prey densities in that study is indeed below the prediction of the regression model based on all the studies (Fig. 16).

More detailed data are needed to determine intake rate of Oystercatchers on extremely low densities of Cockles. The general conclusion remains, however, that most of the variation in intake rate depends on the profitability of the average prey taken. The effect of prey density may only become apparent at very low densities.

Seasonal variation in intake rate and consumption at low water

Are Oystercatchers able to attain the same intake rate in winter as in summer, given that the food value of the prey in winter may be reduced as much as 40% below those in summer, whereas the harvestable fraction may be considerably reduced in winter due to the greater burying depth and the reduced surface activity of worms (Zwarts & Wanink 1993)? Although a lower intake rate is to be expected. Oystercatchers have to raise their daily consumption to cover the increased thermoregulation costs when winter temperatures drop below the critical level of 10 °C. Hence, to keep their body weight constant, they must raise their intake rate and/or extend their feeding period. Since intake rate is highly correlated with the time spent on the feeding area (Zwarts *et al.* 1996b), we exclude in this analysis the intake rates of breeding birds visiting the feeding areas only during short intervals (< 1 h).

Figure 17 plots the average intake rate, measured in the field, against the season. The data are shown separately for Mussels and all other estuarine prey combined because Mussels have a very poor condition in May (Dare 1975, Dare & Edwards 1975, Cayford & Goss-Custard 1990, Zwarts & Wanink 1993), whereas all other prey species reach their maximum condition in early summer (Chambers & Milne 1979, Zwarts 1991, Zwarts & Wanink 1993, Ens *et al.* 1996b). For birds feeding on Mussels, intake rate reaches its highest level in late summer. For those taking other prey, the highest rate is in early summer. Hence, the seasonal trends in intake rate follow the seasonal variation in the prey condition.

This raises the question as to whether there was also a seasonal variation in the total consumption over the low water period in daylight. To remove the effect of variation in exposure time and low water consumption, only those studies in which the available feeding period was 4-6 h were used. With this rather typical exposure time, Oystercatchers consume 24.2 g AFDW (SD = 5.2 g). No significant differences were found, however, in the low water consumption between seasons ($R^2 = 0.20$, $p = 0.06$, $n = 51$; 13 studies that overestimated the consumption (Zwarts *et al.* 1996b) have been excluded). Despite the higher energy demands, consumption during daytime low water periods did not increase in winter. On the other hand, the poorer prey condition had no apparent effect on average low water consumption. This implies that feeding activity must be high in winter, as was shown indeed by Goss-Custard *et al.* (1977) and the studies reviewed here: the average feeding activity is in winter 80-90% compared with 70-80% in summer, although the difference is only weakly significant ($R^2 = 0.22$, $p = 0.04$, $n = 51$).

In conclusion, the higher intake rate in summer may be attributed to the variation in prey condition, the shallower depth of burying bivalves and the greater activity of the worms. The birds apparently compensate for lower intake rates in winter by feeding for more

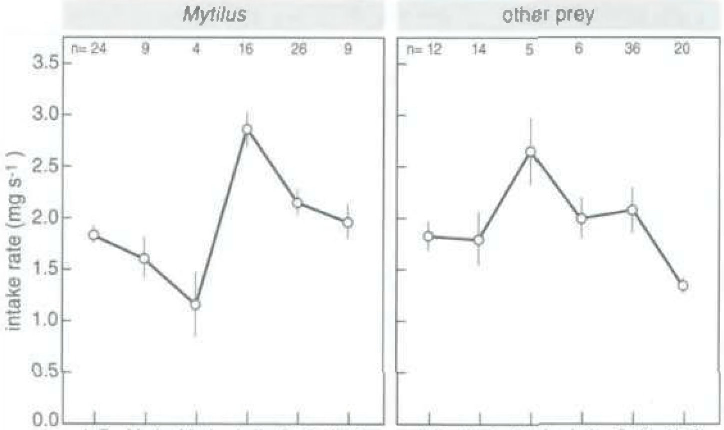


Fig. 17. Seasonal variation in the intake rate (± SE) of birds feeding on *Mytilus* (left) or other estuarine prey (right). Excluded are breeding birds, birds feeding for less than 1 h, birds feeding in grassland and in Africa, and 13 studies that apparently overestimated intake rate (see Zwarts *et al.* 1996b). The number of studies are shown along the X-axis. All sources are given in the appendix. A 2-way analysis of variance showed that the intake rate differed significantly between birds feeding on Mussels and the other estuarine prey species, and between the six bimonthly periods ($R^2 = 0.149$, $p = 0.013$, $n = 181$).

time during the feeding period. As a consequence, there is no seasonal variation in the amount of food consumed during an average low water period in daylight.

Discussion

Does profitability matter?

Predators cannot choose prey that are not available. For instance, bivalve prey are in any case not available to Oystercatchers if they live out of reach of the bill. Depending on whether bivalves are opened by stabbing or hammering, prey may be defined as available if the bill can be stabbed between the valves, or if the shell is not too strong to hammer a hole in it. Yet, Oystercatchers do not simply take all prey from the available stock. As has been well documented, Oystercatchers refuse small prey due to their low profitability (reviewed by Zwarts *et al.* 1996a). For the same reason, the birds may also select from the available prey only the most profitable prey that are living at a shallow depth (Wanink & Zwarts 1985), that have slightly opened valves (Hulscher 1976, Wanink & Zwarts 1985) and/or that have thin shells (Durell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Ens & Alting 1996a & 1996b, Meire 1996a & 1996c). Finally, as predicted by the optimal prey choice model (e.g. Krebs & Kacelnik 1991), Oystercatchers are more selective when their intake rate is high (review Zwarts *et al.* 1996a): as intake rate rises, Oystercatchers successively drop the least profitable prey from their diet. For instance, Oystercatchers take prey from the upper 7 cm of the substrate when their intake rate is low but only from the upper 3 cm when the intake rate is high (Wanink & Zwarts 1985).

What determines prey profitability?

Having firmly established the importance of profitability as a criterion for prey selection in the Oystercatcher, we must enquire in more detail into the factors that determine profitability. The data summarized in Fig. 8 show that the profitability of prey taken by Oystercatchers varies between 1 and 100 mg s^{-1}, i.e. two orders of magnitude! A large part of this variation may be attributed to the way in which prey, through their defenses, are able to prolong the time the predator needs to attack and eat them. For hard-shelled prey, we may hypothesize that the decrease in profitability with the degree of armouring, depicted in Fig. 10, can be explained by the extra time needed to prepare and open the prey. To explore this hypothesis, we must break down the handling time into its consecutive components. First, Oystercatchers must recognize prey as edible. However, it is likely that the time-cost of recognition is so small that it can be safely ignored. For instance, Wanink & Zwarts (1985) found that detection and rejection of prey happened so quickly in Oystercatchers feeding on buried prey that it could not be measured, not even with the aid of a high speed camera. Thus, handling time may be subdivided into three significant components: (1) lifting and preparing time; (2) opening and cutting time and (3) eating time (Speakman 1984a, Wanink & Zwarts 1985, 1996). What is known about the relative duration of these components?

(1) Lifting and preparing time. When prey located in the substrate are lifted to the surface to be opened, lifting itself takes, on average, a quarter of the total handling time (Wanink & Zwarts 1985, 1996). The handling time is 1.25-1.50 times longer when burrowing prey, such as *Macoma*, *Mya* and *Scrobicularia*, are extracted from the substrate rather than being eaten in situ (Wanink & Zwarts 1985, 1996, Hulscher *et al.* 1996; see also Fig. 5). A soft-bodied prey taken from the surface, such as the Leatherjacket, is handled at least twice as fast than those which have to be extracted from the substrate. Grasping or lifting time is also zero in Oystercatchers that stab the bill directly between the valves of Mussels and Cockles, or hammer Mussels in situ on the dorsal side of the shell. In contrast, the handling times of Mussels hammered on the ventral side are relatively long because the Mussels have to be torn off the bed and turned upside down (Cayford & Goss-Custard 1990; see also Figs. 2 & 3).

(2) Opening and cutting time. Armoured prey must be opened by hammering or stabbing, after which the flesh can be separated from the shell. Opening and cutting are absent in prey eaten whole, but it takes about 2/3 of the handling time of bivalves, and even more when prey are hammered. Before lifted bivalves are opened, they are sometimes transported. Oystercatchers may walk for several seconds with their prey to a site with a substrate firm enough to exert the force to break into the shell. This occurs more often when the substrate is soft and Oystercatchers have to walk to a nearby creek, or to a site where the shells of bivalves that have been opened earlier serve as an anvil. Although untested, the part of the handling time involved in transporting the prey must increase if bivalves are taken from soft substrates.

(3) Eating time. Finally, the flesh must be mandibulated and swallowed, sometimes after being washed to get rid of the mud clinging to the flesh. Most prey taken by Oystercatchers are swallowed as one large bit of flesh, after which one or two remaining small morsels are taken from the shell. If bivalves contain more than about 1 g AFDW (*Anadara*, large *Mya*), the flesh is taken in more than one large piece, but such large prey are rarely taken. Eating time is 20 to 30% of the total handling time in Oystercatcher eating bivalves. Since 100% of the handling time of soft-bodied prey is spent in eating the prey, one might expect that the average profitability of soft-bodied prey is about four times as large as those of hard-shelled prey, which is indeed close to what has been found (Fig. 9).

Apart from supporting the contention that prey armouring affects prey profitability through its effect on opening time, the review indicates that we may be able to predict the profitability of novel prey from measurements on the prey only, i.e. without observing its consumption by Oystercatchers first. But before we can do this, it is necessary to make a more detailed assessment of the effect of prey size and prey depth on profitability.

Profitability and prey size

Handling time increases with prey size (Figs. 2-7), but the increase in flesh weight is larger, so that large prey are always more profitable (Fig. 8). Why does it take more time to handle large prey? In *Scrobicularia* and *Mya*, it takes more time to lift a larger prey to the surface, to open the shell and to remove the flesh from the shell and to eat it (Wanink & Zwarts 1996). The relative contributions of these three components of handling time are, however, similar for small and large clams. The same was found by Speakman (1984a) who studied the handling of Mussels opened by stabbing Oystercatchers. Independently of mussel size, 65% of the handling time is spent in cutting (called 'manipulation time' by Speakman) and 29% in eating the flesh. An increase with prey size in time spent in prey transport was found in stabbing Oystercatchers feeding on Cockles (Exo, Smit & Zwarts unpubl.). Prey of 20-35 mm were eaten in situ, but prey 30-40 mm long were taken to a nearby creek, extending the handling time in the latter case by an extra 31 s, on average.

The greater profitability of the larger size classes is reduced if the greater risk of larger prey being stolen and the greater waste handling time are taken into account. First, Cockles are more often refused after they have been stabbed when they are large (Sutherland 1982c, Triplet 1990). Second, Mussels being hammered are often given up and waste handling time increases steeply with size (Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996a, Meire 1996c) Third, Oystercatchers lose prey to dominant conspecifics and to crows and gulls (Zwarts & Drent 1981, Goss-Custard *et al.* 1982, Ens & Goss-Custard 1984, Swennen 1990). We might expect kleptoparasitism to be more common in large prey as the longer handling time gives the parasite more time to attack, while the higher biomass gives a greater benefit (e.g. Ens *et al.* 1990). However, reviewing the literature on Oystercatchers, Ens & Cayford (1996) found evidence for this relationship across prey species, but not within a prey species. Recently, Triplet (1994b) found that large Cockles were stolen more often by gulls than small ones.

Profitability and prey depth

Experiments with Oystercatchers in cages have shown that the handling time of benthic prey increases with burying depth for three reasons (Wanink & Zwarts 1985, Hulscher *et al.* 1996). First, when prey are eaten in situ, the eating time is longer when prey live at greater depths. Second, if prey are lifted, the lifting time increases with depth. Third, it always takes more handling time to lift prey to the surface than to eat them in situ and deep-living prey are lifted more often than shallow ones. Two lines of evidence suggest that similar relationships hold in the field. First, *Scrobicularia* are handled about twice as fast in summer, when they live at shallow depth, as prey of similar size in winter (Fig. 4A). As prey in summer contain about 1.5 times as much flesh as they do in winter, the profitability of *Scrobicularia* is three times greater in summer than in winter. Similarly, handling time in *Macoma* in August is 1.5 longer than in spring (Fig. 5A), presumably because the prey have to be pulled from greater depths: *Macoma* live closest to the surface in June and July (2 cm) and burrow more deeply from July onwards to reach the greatest depth in December-January (5 cm) (Zwarts & Wanink 1993). Although *Macoma* do remain the entire year within reach of the Oystercatcher's bill, the birds do not feed on them between September and March. If the 50% increase of handling time in August is indeed due to the increased depth of *Macoma*, their greater depth in mid-winter would make *Macoma* a highly unprofitable prey. The profitability of *Macoma* 18 mm long would decrease from 10 mg s^{-1} in mid-summer to 3-4 mg s^{-1} in August and possibly less than 1 mg s^{-1} in mid-winter. Since profitability also decreases due the decline in body condition (Zwarts 1991), an increasing proportion of the medium-sized *Macoma* would be dropped from the diet from June onwards. Hence, only the largest prey are still sufficiently profitable to be taken in August (Bunskoeke *et al.* 1996) and *Macoma* finally disappears from the diet altogether in September (Blomert *et al.* 1983).

Predicting the profitability of new prey

Exotic species are often introduced into ecosystems, either by accident, or on purpose. The effects of such introductions are hard to predict. It would therefore be of great practical value if we could predict the profitability of a prey to a predator before the predator ever ate one. It would also be a good test whether we fully understand the determinants of profitability. In our case, the American razor clam *Ensis directus* is an obvious candidate for prediction. This bivalve did not occur in the Wadden Sea until 1979. It has spread rapidly and now occurs in many places (Swennen *et al.* 1985, Beukema & Dekker 1995). In contrast to related endemic razor clam species, which only live subtidally, it occurs on intertidal mudflats and therefore constitutes a potential prey to which the Oystercatcher cannot have evolved any special adaptations, yet Oystercatchers have been seen taking *Ensis* by Swennen *et al.* (1985). The birds took *Ensis* 83 mm long, on average, containing 331 mg dry flesh. Since the weight of the shell was 1640 mg, the shell/flesh ratio was 4.95. This is a rather low value for the armouring index, but comparable to *Mya* (Fig. 10). Given the value of this index, we would predict from Fig. 10 that *Ensis* 83 mm long would have a profitability of 15 mg s^{-1} and thus be handled in 22 s. Although Swennen *et al.* (1985) did not measured handling times, they noted that the prey were handled in less time than Cockles of 280 mg occurring in the same area. The handling time of such a Cockle is about 30 s (Fig. 3, Table 1) and thus indeed longer than the predicted 22 s. *Ensis* is a difficult prey to attack since it is highly mobile and dig very rapidly into the substrate when attacked (Schneider 1982, Henderson & Richardson 1994), but if the prey can be pulled out the sand, it is easy to open as the valves gape.

Some dozens of Oystercatchers were recently observed feeding on another razor clam, *Solen marginatus*, in Dakhla Bay and Khniffiss lagoon, S. Morocco (Exo, Smit & Zwarts unpubl.). These birds took prey 4 to 9 cm long that were present just beneath the surface. The clams were handled in 10-20 s. This implies that, as expected, their profitability resembles those of *Mya* and *Ensis*.

Consequences of variation in profitability for intake rate

The intake rate of Oystercatchers usually varies between 1 and 3 mg s^{-1} (Zwarts *et al.* 1996a, 1996b, this paper) and is the mathematical product of three variables: the searching time, the handling time and the prey weight. Since profitability is simply the ratio of prey weight to handling time, intake rate will necessarily increase with profitability if searching time remains constant and with decreasing searching time if profitability remains constant. However, this is difficult to test as our review does not deal with controlled experiments, but with field data gathered in many different localities under many different circumstances. We might from these field data equally suggest that intake rates are more or less constant and vary independently of prey profitability, because the birds will choose not to feed in poor areas with small prey at low densities and interference will depress intake rate in the best feeding areas with high densities (e.g. Zwarts & Drent 1981).

Within a prey species, profitability (Figs. 2-7, Table 1) as well as intake rate (Figs. 11-15), increase with prey size. Hence, intake rate increases with profitabil-

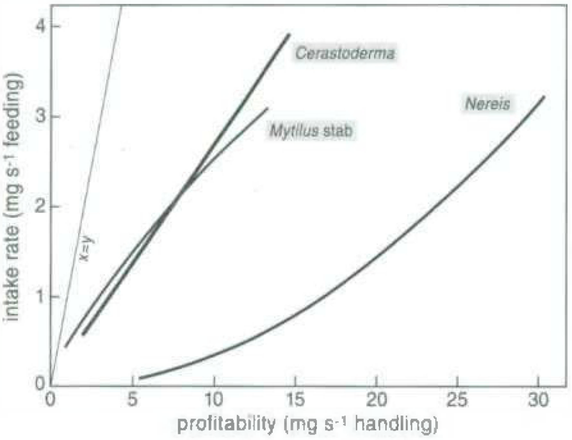


Fig. 18. The intake rate (mg s^{-1} feeding) as a function of profitability (mg s^{-1} handling) were Oystercatchers to feed on *Mytilus*, *Cerastoderma* and *Nereis* of different weights. The graphs are based upon the relationships between profitability and prey weight (Table 1) and between intake rate and prey weight (Figs. 12, 13 & 15). For *Mytilus* a selection is made of birds using the stabbing technique.

ity (Fig. 18). All else being equal, a doubling of profitability will have little impact on the intake rate when the birds spend most of their time searching, but will nearly double intake rate when the birds spend most of their time handling. It is therefore not surprising that in Fig. 18 profitability differences strongly affect intake rate in Cockles and Mussels, in which handling time is very long, but have much less effect when the birds search for *Nereis*, in which most time is spent in searching.

To investigate the relationship between profitability and intake rate between prey species, we plotted the average intake rate per species (Table 3) against the average profitability (Fig. 19A). This comparison shows that, even when profitability increases sixfold, the intake rate remains the same. This implies that when the prey species are compared, the average time spent handling as proportion of total feeding time, i.e. handling and search time combined, decreases with profitability (Fig. 19B). Soft-bodied prey are so profitable that, even when 95% of the feeding time is spent in searching, the intake rate remains at 2 mg s^{-1}. If Oystercatchers were also to search for 95% of the feeding time when they take Mussels, their intake rate would reach the extremely low level of 0.1 mg s^{-1}, and they would starve as shown in the next section.

Since average prey weight differed so much between species, we standardized the profitability and intake rate to prey of similar weight choosing 200 mg (Fig. 9). We calculated the intake rate for each species with the same weight, using the multiple regression equations for soft-bodied and armoured prey with different intercepts but parallel slopes. When prey species with similar body weight are compared, the intake rate doubles within the range of profitabilities observed (Fig. 19C) and the handling time as proportion of the total feeding time halves (Fig. 19D). Thus, when prey species of similar weight are compared, intake rate strongly depends on the profitability, such as was also found within the species.

Profitability and minimal intake rate

What is the minimal intake rate of food on which Oystercatchers can sustain themselves? Oystercatchers in the wild need at thermoneutrality 36 g a day to keep their body weight constant (Zwarts *et al.* 1996b). If they feed for all the five to six hours per low water period during which the feeding areas are usually exposed, the intake rate must be at least about 1 mg s^{-1}. If it is less than this, they have to collect extra food either on the upper shore during the incoming and receding tides and/or on inland grasslands at high tide. The intake rate on the high shore is low, however (Sutherland 1982, Ens *et al.* 1996c, Meire 1996b), because the large prey taken by Oystercatchers do not occur there or only at very low densities (e.g. Zwarts *et al.* 1996c) and their condition is often poor (Goss-Custard 1977, Sutherland 1982a). Inland grasslands may provide some compensation, but these opportunities are only available locally. Thus, an intake rate of 1 mg s^{-1} may be considered as a limit below which food consumption will in the long term usually be too low.

If the average weight and handling time of the prey taken are known, it is possible to calculate the length of the searching time at which the intake rate reaches the lower acceptance level of 1 mg s^{-1}. Since the relationships between prey weight and handling time are known (Figs. 2-6, Table 1), we can easily calculate the search time per prey needed to achieve an intake rate of 1 mg s^{-1}. The resulting Fig. 20 shows that if Oystercatchers feed on prey containing more flesh, they may

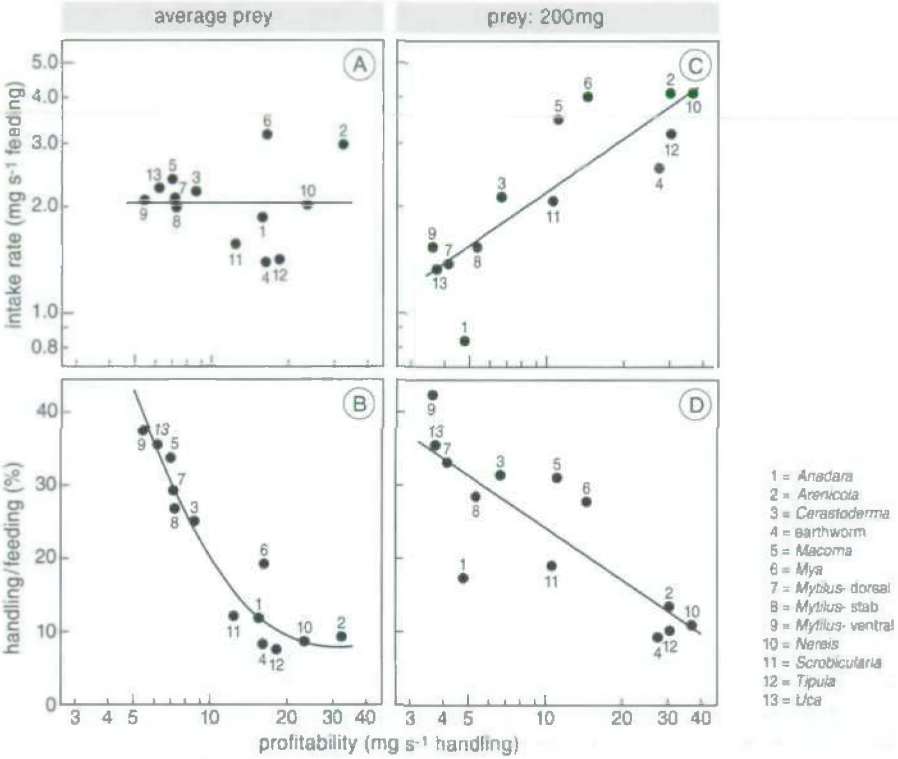


Fig. 19. **A.** Intake rate and **B.** handling time relative to total feeding time, both averaged per prey species, as a function of the average prey profitability. Per cent handling time, shown in panel B, was calculated from the averages shown in panel A. Similar relationships are shown in **C.** and **D.**, with the profitability and intake rate standardized to prey of 200 mg. The standardized profitability of the different prey species was taken from Fig. 8. The intake rate was calculated for prey weighing 200 mg, such as predicted by two multiple regression analyses on the effect of prey weight on the intake rate with soft-bodied or armoured prey species as dummy variables (see text). The values are extrapolations for some small prey always weighing less than 200 mg.

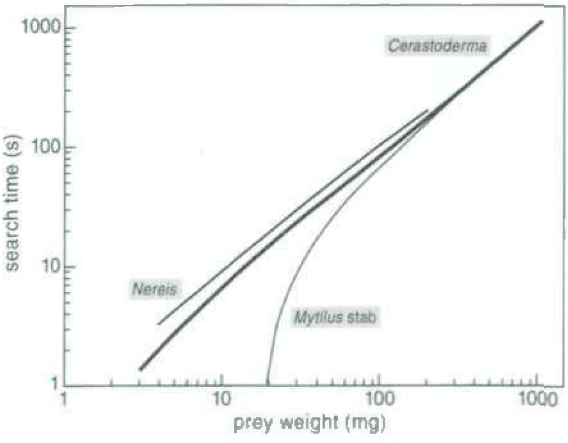


Fig. 20. The time Oystercatchers are allowed to search for prey of a certain weight to achieve an intake rate of 1 mg s^{-1} when they feed on *Mytilus*, *Cerastoderma* and *Nereis*. The searching time is derived from the functions describing the relationship between handling time and prey weight (Table 1). For *Mytilus* a selection is made of birds using the stabbing technique.

spend much more time in searching to attain a sustainable intake rate. For instance, Cockles > 30 mm long in good condition may contain as much as 1000 mg flesh and are handled in 70 s. Even if the birds have to search for 930 s for each prey, their intake rate is still 1 mg s^{-1}. However, if they feed on cockle spat 8 mm long containing 3 mg flesh, they have to take one prey each 3 s; with a handling time of 1.7 s, the birds cannot search for longer than 1.3 s which requires the spat to be very dense. Cockle spat are indeed found in high densities of many thousands m^{-2} in their first summer. However, although the density of Cockles is usually reduced to about 100 and 10 Cockles per m^2 after one or two winters respectively (Beukema 1982a, Zwarts *et al.* 1996h), Oystercatchers nonetheless achieve a higher intake rate at a low density of these old Cockles than on the high density of spat.

Are there alternative prey for Cockles and Mussels in winter?

Cockles and Mussels are reported as the main prey of the Oystercatchers wintering in NW. Europe (Hulscher 1996). Since Oystercatcher and man compete for the same food resource (e.g. Goss-Custard *et al.* 1996a), it is highly relevant to know to what degree Oystercatchers may switch to other food resources if, for instance due to intensive fishing, few Cockles or Mussels are left. The data summarized in this paper show that, especially in winter, these are only limited possibilities of taking alternative prey.

Burying bivalve species are, on average, more profitable than bivalves living at, or just beneath, the surface (Fig. 9). However, burying bivalve species, such as *Scrobicularia* and *Macoma*, live in winter at twice the depth they do in summer. The increase of handling time with depth makes them, therefore, in winter much less profitable than in summer, by which they become even less profitable than surface-living prey (Fig. 9). Moreover, the search time increases with burying depth (Wanink & Zwarts 1985). Hence, the intake rates would be usually very low were Oystercatchers to feed on *Scrobicularia* an *Macoma* in winter (Zwarts *et al.* 1996h).

In some years, *Mya* is an alternative winter prey, as it does not increase its burying depth during the winter and so many remain accessible all winter. Moreover, this prey is highly profitable, even if taken from deep beneath the surface (Fig. 6). However, only prey of about 20-30 mm are harvestable by Oystercatchers since smaller prey are unprofitable and an increasing proportion of the larger clams burrows out of reach of the Oystercatcher's bill (Zwarts & Wanink 1984). Consequently, Oystercatchers can only feed on *Mya* when they are about 1.5 years old, and since there is no spatfall in most of the years (Beukema 1982b, Beukema *et al.* 1993), Oystercatchers can harvest this food supply in only in a minority of the winters (Zwarts *et al.* 1996h).

Two large worm species, *Arenicola* and *Nereis* might provide other alternative source of prey. However, since both species live at depth, especially in winter (Zwarts & Wanink 1993), Oystercatchers can only feed on them when they come to the surface. Oystercatchers have to wait till Lugworms emerge at the surface to defecate, which means that even actively feeding worms are inaccessible for 99.9% of the time. As Lugworms reduce their feeding activity at lower mud temperatures (Smith 1975, Cadée 1976), they are inaccessible for 100% of the time on many winter days. This is also true for Ragworms which leave their deep burrows to graze at the surface or filter food in the mouth of the burrow. They feed actively on the surface on sunny days in late winter and early spring, but are also inactive on many cold winter days (Esselink & Zwarts 1989, Zwarts & Esselink 1989, Vedel *et al.* 1994).

Another option is to switch to inland grassland areas, where Oystercatchers can feed on earthworms and Leatherjackets. The latter prey is still extremely small in winter, and possibly only large enough to feed upon from April to August (Laughin 1967, Blomert & Zwarts unpubl.). Earthworms may be an important prey in winter as long as the fields are not frozen. The 22 studies on the intake rate of Oystercatchers feeding on earthworms and Leatherjackets (Heppleston 1971, Hosper 1978, Ens unpubl., Zwarts & Blomert 1996) all arrive at a rather low intake rate (see appendix). This may explain why grassland is only used as supplemental food resource at high water in winter (Goss-Custard *et al.* 1984), especially after the proceeding low water feeding period was short (Daan & Koene 1981).

What can Oystercatchers do in winter if there are no large Mussels and Cockles? Beukema (1993a) describes the exceptional winter of 1990/91 when this situation arrived in the western part of the Dutch Wadden Sea. The Oystercatchers did not leave the area. The disappearance rate of the alternative prey (small Cockles, *Macoma*, *Mya* and *Arenicola*) was exceptionally high (Beukema 1993a), suggesting that the birds started to take prey that they usually ignored and continued to do so, even when the prey density became very low. The intake rate of the Oystercatchers was not measured, but must have been extremely low. Indeed, it may even have been lower than the 0.5 mg s^{-1} observed in the Eastern Scheldt during the autumn of 1986 (Meire 1996b) when the only food source available for Oystercatchers was 0-year Cockles of 8 mm long. Although the winter 1990/1991 was mild, the mortality of Oystercatchers in the Wadden Sea was relatively high (Camphuysen *et al.* 1996). Apparently, the consumption rate in the western Wadden Sea was too low to meet their energy requirements, so that part of the birds starved to death.

Appendix

Overview of all studies that measured size and weight of prey taken by Oystercatchers, as well as their intake rate and total consumption in different areas (indicated in last column with a three letter code, but see Fig. 1 for full names and their geographical position in NW. Europe; dak = Baie of Dakhla, S. Morocco and arg = Banc d' Arguin, Mauritania). Size is expressed as prey length (mm), weight as mg AFDW and intake rate as mg AFDW s^{-1} feeding. Column 'Time' gives the time spent on the feeding area (h), 'Feed' the proportion of the time spent feeding while present on the feeding area, 'Cons' the total consumption (g AFDW) during the time spent feeding; 'B' in column 'Br' indicates whether the data concern breeding birds; nm^{-2} gives the prey density (only for Cockles); 'Mus' shows whether Mussels were opened by stabbing (S), ventral hammering (V) or dorsal hammering (D). Column 'Cap' shows whether birds were held in captivity (C); all other studies were done on free-living birds. Column 'Lab' shows whether it was necessary to estimate AFDW from prey volume (V), wet weight (W) or dry weight (D); all other studies measured AFDW; 'F' refers to studies using formaline to store the prey, making a weight correction necessary. For further general explanation see methods, but for details the notes in this appendix. The number of the notes corresponds with the digit in first column.

No	*Species*	*mm*	*mg*	*mgs^{-1}*	*Month*	*Year*	*Time*	*Feed*	*Cons*	*Br*	*nm^{-2}*	*Mus*	*Cap*	*Lab*	*Sources*	*Area*
1	*Anadara*	73	1637	1.85	2	86	7.30	39.4	19.16						Swennen *et al.* 1990	arg
2	*Arenicola*		309	4.12	5/7	86/7				B					Bunskoeke 1988	sch
3	*Arenicola*		124	1.80	8	86									Bunskoeke 1988	sch
4	*Cerastoderma*	22	49	1.13	2	73	8.50	58.8	20.33					D	Brown & O'Connor 1974	str
5	*Cerastoderma*	21	102	1.86	11/3	61/5	8.50	55.0	31.30					W	Davidson 1967	bur
6	*Cerastoderma*	22	154	2.31	1	54	7.50	42.0	26.20		349			V	Drinnan 1957	mor
7	*Cerastoderma*	30	291	2.45	10	54	7.50	50.0	33.08		115			V	Drinnan 1957	mor
8	*Cerastoderma*	12	12	0.61	2	84					1000				Ens *et al.* 1996c	tex
9	*Cerastoderma*	38	316	2.42	2	84									Ens *et al.* 1995c	tex
10	*Cerastoderma*	36	313	1.88	2	84									Ens *et al.* 1996c	tex
11	*Cerastoderma*	12	14	0.93	3	84									Ens *et al.* 1996c	tex
12	*Cerastoderma*	13	33	2.87	4	84									Ens *et al.* 1996c	tex
13	*Cerastoderma*	15	62	3.75	5	84				B					Ens *et al.* 1996c	tex
14	*Cerastoderma*	18	92	2.38	6	84				B					Ens *et al.* 1995c	tex
15	*Cerastoderma*	19	92	2.38	7	84									Ens *et al.* 1996c	tex
16	*Cerastoderma*	34	411	1.91	9	83					4				Ens *et al.* 1995d	tex
17	*Cerastoderma*	36	504	2.05	9	83					10				Ens *et al.* 1995d	tex
18	*Cerastoderma*	39	606	4.19	9	83					23				Ens *et al.* 1995d	tex
19	*Cerastoderma*	31	338	3.09	9	83					49				Ens *et al.* 1995d	tex
20	*Cerastoderma*	39	616	3.54	9	83					64				Ens *et al.* 1995d	tex
21	*Cerastoderma*	31	328	2.57	9	83					79				Ens *et al.* 1995d	tex

No	*Species*	*mm*	*mg*	*mgs*$^{-1}$	*Month*	*Year*	*Time*	*Feed*	*Cons*	*Br*	*nm*$^{-2}$	*Mus*	*Cap*	*Lab*	*Sources*	*Area*
22	*Cerastoderma*	32	366	4.45	9	83					107				Ens *et al.* 1995d	tex
23	*Cerastoderma*	11	14	0.57	9	83					3000				Ens *et al.* 1995d	tex
24	*Cerastoderma*	33	274	2.08	1	95	5.00	41.4	15.50		250			F	Exo, Smit, Zwarts unpubl.	dak
25	*Cerastoderma*	28	317	3.94	1	74	5.00	80.3	56.95						Goss-Custard 1977	was
26	*Cerastoderma*	31	313	0.60	7	66					13		C	D	Hulscher 1976	sch
27	*Cerastoderma*	31	313	1.21	7	66					40		C	D	Hulscher 1976	sch
28	*Cerastoderma*	31	313	1.95	7	66					150		C	D	Hulscher 1976	sch
29	*Cerastoderma*	31	313	2.23	7	66	4.00	54.4	17.47		450		C	D	Hulscher 1976	sch
30	*Cerastoderma*	19	76	1.40	8	61	4.76	66.0	15.83		680			V	Hulscher unpubl.	vli
31	*Cerastoderma*	25	117	2.10	10	80	4.50	67.0	22.79		600				Hulscher unpubl.	pac
32	*Cerastoderma*	23	148	1.49	8	78	5.10	63.2	17.29		147				Hulsman unpubl.	pac
33	*Cerastoderma*	33	365	3.05	10	84	2.00				500		C		Leopold *et al.* 1989	tex
34	*Cerastoderma*	33	365	2.97	10	84	3.00				500		C		Leopold *et al.* 1989	tex
35	*Cerastoderma*	33	365	2.19	10	84	5.00				500		C		Leopold *et al.* 1989	tex
36	*Cerastoderma*	29	185	2.74	10	84	2.00				500		C		Leopold *et al.* 1989	tex
37	*Cerastoderma*	29	185	1.64	10	84	3.00				500			C	Leopold *et al.* 1989	tex
38	*Cerastoderma*	29	185	1.77	10	84	5.00				500			C	Leopold *et al.* 1989	tex
39	*Cerastoderma*	8	3.3	0.52	10	87					7600			F	Meire 1996b	oos
40	*Cerastoderma*	34	337	1.28	2	79					10				Sutherland 1982a, b	tra
41	*Cerastoderma*	30	314	2.37	2	79					25				Sutherland 1982a, b	tra
42	*Cerastoderma*	31	336	2.55	2	79					33				Sutherland 1982a, b	tra
43	*Cerastoderma*	35	403	3.88	2	79					49				Sutherland 1982a, b	tra
44	*Cerastoderma*	30	209	2.25	2	79					145				Sutherland 1982a, b	tra
45	*Cerastoderma*	24	95	1.57	2	79					287				Sutherland 1982a, b	tra
46	*Cerastoderma*	29	162	1.87	2	79					442				Sutherland 1982a, b	tra
47	*Cerastoderma*	29	146	1.80	2	79					450				Sutherland 1982a, b	tra
48	*Cerastoderma*	26	114	1.50	2	79					542				Sutherland 1982a, b	tra
49	*Cerastoderma*	29	143	2.00	2	79					582				Sutherland 1982a, b	tra
50	*Cerastoderma*	28	124	1.97	2	79					598				Sutherland 1982a, b	tra
51	*Cerastoderma*	26	120	1.77	2	79					609				Sutherland 1982a, b	tra
52	Earthworms		38	1.62	5	84				B					Ens unpubl.	tex
53	Earthworms		27	0.49	6	83				B					Ens unpubl.	tex
54	Earthworms		44	1.00	6	84				B					Ens unpubl.	tex
55	Earthworms		50	0.98	12	66									Heppleston 1971	yth
56	Earthworms		197	1.80	4	77	15.00	33.1	32.17					D	Hosper 1978	fri
57	*Littorina*	18	147	1.29	9/3	81/2	6.00	91.8	25.58					D	Boates & Goss-Custard 1992	exe
58	*Littorina*	18	128	1.31	1	81								D	Boates & Goss-Custard 1992	exe
59	*Littorina*	18	127	1.13	2	81								D	Boates & Goss-Custard 1992	exe
60	*Littorina*	18	89	0.85	3	81								D	Boates & Goss-Custard 1992	exe
61	*Littorina*	18	166	1.16	9	81								D	Boates & Goss-Custard 1992	exe
62	*Littorina*	18	150	1.03	10	81								D	Boates & Goss-Custard 1992	exe
63	*Littorina*	18	145	1.40	11	81								D	Boates & Goss-Custard 1992	exe
64	*Littorina*	18	154	1.76	12	81								D	Boates & Goss-Custard 1992	exe
65	*Macoma*		54	2.70	4	86									Bunskoeke *et al* 1996	sch
66	*Macoma*		59	3.20	5	86				B					Bunskoeke *et al* 1996	sch
67	*Macoma*	16	54	2.90	6	86				B					Bunskoeke *et al* 1996	sch
68	*Macoma*	18	79	3.00	7	86									Bunskoeke *et al* 1996	sch
69	*Macoma*	18	45	2.00	8	86									Bunskoeke *et al* 1996	sch

No	*Species*	*mm*	*mg*	*mgs^{-1}*	*Month*	*Year*	*Time*	*Feed*	*Cons*	*Br*	*nm^{-2}*	*Mus*	*Cap*	*Lab*	*Sources*	*Area*
70	*Macoma*		110	1.73	5	84				B					Ens *et al.* 1996d	tex
71	*Macoma*	17	83.1	2.09	5	79	6.07	90.9							Hulscher 1982	pae
72	*Macoma*	17	83.1	2.67	5	79				B					Hulscher 1982	pae
73	*Macoma*	18	74	2.21	6	66	5.50	85.0	37.19	B				D	Hulscher 1982	sch
74	*Macoma*	20	92	2.32	6	66	0.17	100.0	1.42				C	D	Hulscher 1982	sch
75	*Macoma*	18	60	1.47	8	63	4.58	76.5	18.54					V	Hulscher 1982	vli
76	*Macoma*	16	49	2.58	5	81	1.02	76.0	7.20						Hulscher 1982, unpubl.	pae
77	*Macoma*	16	49	3.68	5	81	0.30	75.0	2.98	B					Hulscher 1982, unpubl.	pae
78	*Macoma*	16	64	2.67	6	86	0.50	100.0	4.81					C	*Hulscher et al.* 1996, *unpubl.*	sch
79	*Macoma*	16	64	3.31	6	86	0.50	100.0	5.96					C	Hulscher *et al.* 1996, unpubl.	sch
80	*Macoma*	15	47	1.51	5	85									Hulscher unpubl.	sch
81	*Mya*		154	3.87	4/8	86/8				B					Bunskoeke 1988	sch
82	*Mya*	40	135	2.91	5	85				B					Hulscher unpubl.	sch
83	*Mya*	36	350	3.00	7	81	0.40	100.0	4.32					C	Wanink & Zwarts 1995	pae
84	*Mya*	28	51	2.65	10	80	5.00	88.0	41.98						Zwarts & Wanink 1984	pae
85	*Mytilus*	39	332	1.27	9/2	81/2	5.25	93.6	22.47			S		D	Boates & Goss-Custard 1992	exe
86	*Mytilus*	39	328	1.27	9/2	81/2	5.25	91.3	21.91			D		D	Boates & Goss-Custard 1992	exe
87	*Mytilus*	36	249	0.89	9/2	81/2	5.25	93.0	15.64			V		D	Boates & Goss-Custard 1992	exe
88	*Mytilus*	40	320	1.12	1	82								D	Boates & Goss-Custard 1992	exe
89	*Mytilus*	39	288	1.13	2	82								D	Boates & Goss-Custard 1992	exe
90	*Mytilus*	35	342	1.20	9	81								D	Boates & Goss-Custard 1992	exe
91	*Mytilus*	34	261	1.09	10	81								D	Boates & Goss-Custard 1992	exe
92	*Mytilus*	39	315	0.95	11	81								D	Boates & Goss-Custard 1992	exe
93	*Mytilus*	38	234	1.03	12	81								D	Boates & Goss-Custard 1992	exe
94	*Mytilus*	43	400	1.89	1	84						D			Cayford & Goss-Custard 1990	exe
95	*Mytilus*	44	379	1.67	1	84						V			Cayford & Goss-Custard 1990	exe
96	*Mytilus*	50	540	2.03	2	84						D			Cayford & Goss-Custard 1990	exe
97	*Mytilus*	50	571	2.37	2	84						V			Cayford & Goss-Custard 1990	exe
98	*Mytilus*	52	461	1.98	3	84						D			Cayford & Goss-Custard 1990	exe
99	*Mytilus*	47	332	1.31	3	84						V			Cayford & Goss-Custard 1990	exe
100	*Mytilus*	37	149	0.85	4	84						V			Cayford & Goss-Custard 1990	exe
101	*Mytilus*	28	83	0.48	4	84						D			Cayford & Goss-Custard 1990	exe
102	*Mytilus*	27	73	0.42	5	84						D			Cayford & Goss-Custard 1990	exe
103	*Mytilus*	32	118	0.77	5	84						V			Cayford & Goss-Custard 1990	exe
104	*Mytilus*	32	156	0.84	6	84						D			Cayford & Goss-Custard 1990	exe
105	*Mytilus*	44	692	3.30	8	84						V			Cayford & Goss-Custard 1990	exe
106	*Mytilus*	42	610	2.94	8	84						D			Cayford & Goss-Custard 1990	exe
107	*Mytilus*	44	773	3.53	9	84						V			Cayford & Goss-Custard 1990	exe
108	*Mytilus*	45	873	3.90	9	84						D			Cayford & Goss-Custard 1990	exe
109	*Mytilus*	45	931	4.29	10	84						D			Cayford & Goss-Custard 1990	exe
110	*Mytilus*	43	903	4.20	10	84						V			Cayford & Goss-Custard 1990	exe
111	*Mytilus*	44	853	3.93	11	84						V			Cayford & Goss-Custard 1990	exe
112	*Mytilus*	44	872	3.90	11	84						D			Cayford & Goss-Custard 1990	exe
113	*Mytilus*	38	216	1.76	3	56	9.00	75.0	42.77			V		V	Drinnan 1958a	con
114	*Mytilus*	26	56	1.58	12	55	7.00	85.6	34.08			V		V	Drinnan 1958a	con
115	*Mytilus*	45	697	2.41	10	80	3.89	66.5	22.44			D			Ens & Goss-Custard 1984	exe
116	*Mytilus*	42	606	2.59	10	80	3.60	89.5	30.04			S			Ens & Goss-Custard 1984	exe
117	*Mytilus*	38	498	2.25	10	80	4.44	54.2	19.49			S			Ens & Goss-Custard 1984	exe

No	Species	mm	mg	mgs⁻¹	Month	Year	Time	Feed	Cons	Br	nm⁻²	Mus	Cap	Lab	Sources	Area
118	*Mytilus*	41	570	2.91	10	80	3.89	81.0	33.01			D			Ens & Goss-Custard 1984	exe
119	*Mytilus*	39	522	1.80	10	80	3.61	87.2	20.40			V			Ens & Goss-Custard 1984	exe
120	*Mytilus*	40	533	1.58	10	80	4.00	91.2	20.75			S			Ens & Goss-Custard 1984	exe
121	*Mytilus*	39	505	1.55	10	80	4.00	90.9	20.29			D			Ens & Goss-Custard 1984	exe
122	*Mytilus*	41	551	1.73	10	80	4.03	90.6	22.74			S			Ens & Goss-Custard 1984	exe
123	*Mytilus*	47	749	2.67	10	80	4.33	56.4	23.47			D			Ens & Goss-Custard 1984	exe
124	*Mytilus*	41	551	1.98	10	80	4.00	94.0	26.80			S			Ens & Goss-Custard 1984	exe
125	*Mytilus*	38	271	2.64	7	83						S			Ens *et al.* 1996a	sch
126	*Mytilus*	45	520	3.22	7	83						V			Ens *et al.* 1996a	sch
127	*Mytilus*	35	390	2.30	2	84						S			Ens *et al.* 1996c	tex
128	*Mytilus*	34	351	2.31	3	84						S			Ens *et al.* 1996c	tex
129	*Mytilus*	27	191	3.28	4	84						S			Ens *et al.* 1996c	tex
130	*Mytilus*	29	224	2.84	5	84				B		S			Ens *et al.* 1996c	tex
131	*Mytilus*	23	134	2.33	6	84				B		S			Ens *et al.* 1996c	tex
132	*Mytilus*	27	217	2.30	7	84						S			Ens *et al.* 1996c	tex
133	*Mytilus*	37	518	2.68	7	83						S			Ens *et al.* 1996d	tex
134	*Mytilus*	44	380	1.69	1	82						D			Goss-Custard unpubl.	exe
135	*Mytilus*	40	300	1.33	1	82						S			Goss-Custard unpubl.	exe
136	*Mytilus*	47	509	1.91	1	83	4.68	89.4	28.77			D			Goss-Custard unpubl.	exe
137	*Mytilus*	49	469	1.58	1	94						V			Goss-Custard unpubl.	exe
138	*Mytilus*	43	404	1.72	2	83	4.68	90.0	26.08			D			Goss-Custard unpubl.	exe
139	*Mytilus*	44	425	1.73	2	83	4.68	100.0	29.15			S			Goss-Custard unpubl.	exe
140	*Mytilus*	50	502	1.71	2	94						V			Goss-Custard unpubl.	exe
141	*Mytilus*	39	285	1.38	3	82						S			Goss-Custard unpubl.	exe
142	*Mytilus*	44	379	1.99	3	82						D			Goss-Custard unpubl.	exe
143	*Mytilus*	43	350	1.29	3	83						S			Goss-Custard unpubl.	exe
144	*Mytilus*	46	408	1.62	3	83						D			Goss-Custard unpubl.	exe
145	*Mytilus*	42	444	1.55	9	83	4.68	99.0	25.85			S			Goss-Custard unpubl.	exe
146	*Mytilus*	44	538	2.31	9	83	4.68	85.7	33.35			S			Goss-Custard unpubl.	exe
147	*Mytilus*	43	481	1.70	9	83	4.68	94.2	26.98			S			Goss-Custard unpubl.	exe
148	*Mytilus*		480	1.36	9/10	81						D			Goss-Custard unpubl.	exe
149	*Mytilus*		400	1.50	9/10	81						S			Goss-Custard unpubl.	exe
150	*Mytilus*	45	504	1.45	10	82	4.68	91.3	22.30			S			Goss-Custard unpubl.	exe
151	*Mytilus*	46	559	2.08	10	82	4.68	81.3	28.49			D			Goss-Custard unpubl.	exe
152	*Mytilus*	48	748	1.81	11	81	4.95	92.5	29.84			S			Goss-Custard unpubl.	exe
153	*Mytilus*	41	424	2.12	11	81						S			Goss-Custard unpubl.	exe
154	*Mytilus*	50	779	2.27	11	81	4.95	82.5	33.37			D			Goss-Custard unpubl.	exe
155	*Mytilus*	44	461	2.10	11	81						D			Goss-Custard unpubl.	exe
156	*Mytilus*	47	530	2.19	11	82	4.68	80.6	29.74			D			Goss-Custard unpubl.	exe
157	*Mytilus*	46	503	1.54	11	82	4.68	91.6	23.77			S			Goss-Custard unpubl.	exe
158	*Mytilus*	39	340	1.67	12	81						S			Goss-Custard unpubl.	exe
159	*Mytilus*	43	394	1.93	12	82	4.68	94.6	30.76			S			Goss-Custard unpubl.	exe
160	*Mytilus*	45	513	2.10	12	83	4.68	84.6	29.93			D			Goss-Custard unpubl.	exe
161	*Mytilus*	42	404	1.17	12	83	4.68	94.6	18.65			S			Goss-Custard unpubl.	exe
162	*Mytilus*	45	647	2.11	12	84	4.68	84.6	30.07			V			Goss-Custard unpubl.	exe
163	*Mytilus*	45	591	2.12	12	84	4.68	84.6	30.22			D			Goss-Custard unpubl.	exe
164	*Mytilus*	30	132	1.66	10	66	11.20	80.9	54.15			V		D	Heppleston 1971	yth
165	*Mytilus*	30	136	1.18	12	66	8.90	94.5	35.73			V		D	Heppleston 1971	yth

No	*Species*	*mm*	*mg*	*mgs⁻¹*	*Month*	*Year*	*Time*	*Feed*	*Cons*	*Br*	*nm⁻²*	*Mus*	*Cap*	*Lab*	*Sources*	*Area*
166	*Mytilus*	34	220	2.07	10	80	6.00	66.4	29.69			S			Hulscher unpubl.	pae
167	*Mytilus*			16.00			0.22	100.0	12.48				C		Hulscher unpubl.	sch
168	*Mytilus*	46	580	1.52	3	77	4.70	65.5	16.85			S			Koene 1978	tex
169	*Mytilus*	46	740	1.94	10	76	4.68	65.5	21.41			S			Koene 1978	tex
170	*Mytilus*	46	251	1.92	3	92	5.00	78.8	27.23			S			Maagaard & Jensen 1994	ska
171	*Mytilus*	45	448	2.35	9	92	4.00	83.6	28.29			S			Maagaard & Jensen 1994	ska
172	*Mytilus*			1.60	10	86	4.08	74.0	17.39			V		F	Meire 1996b	oos
173	*Mytilus*			1.67	10	86	4.12	92.0	22.79			V		F	Meire 1996b	oos
174	*Mytilus*	39	270	1.50	10	86						S		F	Meire 1996b	oos
175	*Mytilus*			1.94	10	86	4.57	52.0	16.60			V		F	Meire 1996b	oos
176	*Mytilus*	41	450	2.10	10	86						S		F	Meire 1996b	oos
177	*Mytilus*	35	172	1.24	10	86						S		F	Meire 1996b	oos
178	*Mytilus*	40	296	1.84	10	86						V		F	Meire 1996b	oos
179	*Mytilus*	41	270	1.77	10	86						V		F	Meire 1996b	oos
180	*Mytilus*	42	297	1.95	10	86						V		F	Meire 1996b	oos
181	*Mytilus*	40	524	2.82	9	82						V		F	Meire & Ervynck 1986	oos
182	*Mytilus*	50	230	1.95	9/4	81						S			Speakman 1984	for
183	*Mytilus*	51	785	4.02	9	73	5.90	76.3	65.15			S			Zwarts & Drent 1981	sch
184	*Mytilus*	53	604	3.30	5	74	1.38	88.0	14.43	B		S			Zwarts & Drent 1981	sch
185	*Mytilus*	50	545	3.27	5	75	1.38	90.2	14.65	B		S			Zwarts & Drent 1981	sch
186	*Mytilus*	50	492	3.53	5	76	1.38	87.4	15.33	B		S			Zwarts & Drent 1981	sch
187	*Mytilus*	49	487	3.27	5	77	1.38	85.3	13.86	B		S			Zwarts & Drent 1981	sch
188	*Mytilus*	26	186	1.65	5	78	1.38	88.9	7.29	B		S			Zwarts & Drent 1981	sch
189	*Mytilus*	38	614	2.19	5	78	5.00	76.4	30.12			S	C		Zwarts & Drent 1981	sch
190	*Mytilus*	32	299	1.56	5	78	5.00	76.4	21.45			S	C		Zwarts & Drent 1981	sch
191	*Mytilus*	34	264	1.52	9	78	6.00	79.0	25.94			S			Zwarts & Drent 1981	sch
192	*Mytilus*	28	137	0.86	3	79	6.00	84.1	15.62			S			Zwarts unpubl.	pae
193	*Nereis*		17	0.56	8/11	81	7.00	96.1	13.56						Boates & Goss-Custard 1989	exe
194	*Nereis*		35	1.17	8	81									Boates & Goss-Custard 1989	exe
195	*Nereis*		19	0.63	9	81									Boates & Goss-Custard 1989	exe
196	*Nereis*		9	(0.13)	10	81									Boates & Goss-Custard 1989	exe
197	*Nereis*		5	(0.19)	11	81									Boates & Goss-Custard 1989	exe
198	*Nereis*		93	2.30	4	86									Bunskoeke *et al* 1996	sch
199	*Nereis*		84	3.10	5	86				B					Bunskoeke *et al* 1996	sch
200	*Nereis*		94	3.30	6	86				B					Bunskoeke *et al* 1996	sch
201	*Nereis*		82	3.00	7	86									Bunskoeke *et al* 1996	sch
202	*Nereis*		69	2.00	8	86									Bunskoeke *et al* 1996	sch
203	*Nereis*		81	1.63	8	84	6.83	100.0	40.08						Durell *et al.* 1996, unpubl.	exe
204	*Nereis*		80	2.25	8	84	6.25	92.8	46.98						Durell *et al.* 1996, unpubl.	exe
205	*Nereis*		58	1.82	9	82									Durell *et al.* 1996, unpubl.	exe
206	*Nereis*		71	2.56	9	82									Durell *et al.* 1996, unpubl.	exe
207	*Nereis*		80	3.46	9	83	6.25	93.4	72.71						Durell *et al.* 1996, unpubl.	exe
208	*Nereis*		87	3.18	9	83	6.83	100.0	78.19						Durell *et al.* 1996, unpubl.	exe
209	*Nereis*		82	2.71	9	84	6.83	99.4	66.23						Durell *et al.* 1996, unpubl.	exe
210	*Nereis*		53	2.44	10	82									Durell *et al.* 1996, unpubl.	exe
211	*Nereis*		60	2.21	10	82									Durell *et al.* 1996, unpubl.	exe
212	*Nereis*		71	2.27	10	83	6.25	100.0	51.08						Durell *et al.* 1996, unpubl.	exe
213	*Nereis*		82	2.27	10	83	6.83	100.0	55.81						Durell *et al.* 1996, unpubl.	exe

No	*Species*	*mm*	*mg*	*mgs*$^{-1}$	*Month*	*Year*	*Time*	*Feed*	*Cons*	*Br*	*nm*$^{-2}$	*Mus*	*Cap*	*Lab*	*Sources*	*Area*
214	*Nereis*		85	2.00	10	84	6.25	96.3	43.34						Durell *et al.* 1996, unpubl.	exe
215	*Nereis*		129	3.82	7	83									Ens *et al.* 1996d	tex
216	*Nereis*		65	1.38	5	85				B					Hulscher unpubl.	sch
217	*Nereis*		74	1.53	12	84									Triplet 1989	som
218	*Patella*		96	2.35	5/7	65/6								D	Safriel 1976	sko
219	*Scrobicularia*	32	310	2.20	7	79	4.58	70.0	25.39						Blomert *et al* 1983	pae
220	*Scrobicularia*	30	132	1.22	10/3	81/2	7.00	98.4	30.25						Boates & Goss-Custard 1989	exe
221	*Scrobicularia*	31	121	1.42	1	82								D	Boates & Goss-Custard 1989	exe
222	*Scrobicularia*	34	149	2.17	2	82								D	Boates & Goss-Custard 1989	exe
223	*Scrobicularia*	30	110	2.27	3	82								D	Boates & Goss-Custard 1989	exe
224	*Scrobicularia*	25	101	1.18	10	81								D	Boates & Goss-Custard 1989	exe
225	*Scrobicularia*	27	89	1.51	11	81								D	Boates & Goss-Custard 1989	exe
226	*Scrobicularia*	24	68	1.32	12	81								D	Boates & Goss-Custard 1989	exe
227	*Scrobicularia*	21	25	0.98	3	84	7.00	80.0	19.76						Habekotte 1987	sch
228	*Scrobicularia*	39	303	4.43	10	81	0.46	100.0	7.34				C		Hulscher *et al.* unpubl.	pae
229	*Scrobicularia*	39	303	8.06	10	81	0.25	100.0	7.25				C		Hulscher *et al.* unpubl.	pae
230	*Scrobicularia*	39	303	9.99	10	81	0.20	100.0	7.19				C		Hulscher *et al.* unpubl.	pae
231	*Scrobicularia*	35	300	3.00	7	81	0.40	100.0	4.32				C		Wanink & Zwarts 1996	pae
232	*Scrobicularia*	36	274	3.40	8	81	0.40	100.0	4.90				C		Wanink & Zwarts 1985	pae
233	*Scrobicularia*	28	94	1.29	4	79	5.50	89.1	22.76						Zwarts unpubl.	pae
234	*Scrobicularia*	29	169	3.55	5	79									Zwarts unpubl.	pae
235	*Tipula*		50	1.47	7	91									Blomert & Zwarts unpubl.	fri
236	*Tipula*		49	1.37	8	93									Blomert & Zwarts unpubl.	fri
237	*Tipula*		60	1.24	4	84									Ens unpubl.	tex
238	*Tipula*		60	1.92	5	84				B					Ens unpubl.	tex
239	*Tipula*		75	1.14	6	83				B					Ens unpubl.	tex
240	*Tipula*		60	1.04	6	84				B					Ens unpubl.	tex
241	*Tipula*		60	0.72	7	84									Ens unpubl.	tex
242	*Tipula*		76	1.80	4	78	14.00	35.7	32.39					D	Hosper 1978	fri
243	*Tipula*		62	1.89	5	77				B				D	Hosper 1978	fri
244	*Tipula*		47	1.84	5	78	17.00	22.0	24.77	B				D	Hosper 1978	fri
245	*Tipula*		42	1.05	6	77				B				D	Hosper 1978	fri
246	*Tipula*		61	1.15	6	78				B				D	Hosper 1978	fri
247	*Tipula*		85	1.95	7	78								D	Hosper 1978	fri
248	*Tipula*		42	1.40	5/7	65/6								D	Safriel 1976	sko
249	*Tipula*		15	0.34	3	77	13.00	59.1	9.40						Veenstra 1978	fri
250	*Tipula*		20	1.04	4	95	14.70	57.3	31.54						Zwarts & Blomert 1996	fri
251	*Tipula*		35	1.45	5	91		39.9		B					Zwarts & Blomert 1996	fri
252	*Tipula*		52	1.28	5	91									Zwarts & Blomert 1996	tex
253	*Uca*		786	2.23	9	88									Ens *et al.* 1993	arg

Notes to appendix:

1: AFDW of *Anadara* taken was 3300 mg, but 56% of the prey could not be eaten completely, due to kleptoparasitism by other bird species. Since Swennen estimated that in these cases, on average, 10% of the flesh was eaten, the *weight of the average prey taken was estimated to be 1637* mg.

2-3: Since the birds also took *Macoma* and *Nereis*, a selection was made of 5 min periods during which *Arenicola* was the dominant prey.

4: Cockle height has been converted to length using Table 5 in Zwarts (1991); ash assumed to be 20% (being the average winter level; Zwarts 1991).

5: *The intake rate varied between 1.4 and 2.2. mg* s^{-1} *during* six different winter months. The data were pooled since the observation times were limited.

8-15: Since the birds also took *Mytilus*, a selection was made of 5 min periods with *Cerastoderma* as dominant prey.

25: Feeding area was exposed 5 h during daylight in January; this is equivalent to 6.5 h per low water period. Goss-Custard (1977) noted that the avarage prey weight was overestimated since small prey were probably missed and flesh also remained in the shell.

26-29: Ash assumed to be 13% in summer (being the average summer value; Zwarts 1991).

31: The flesh remaining in the shell has been measured (14.8% relative to total AFDW).

33-38: The same data are given separately for individuals by Swennen *et al.* (1989).

52-54: Since the birds also took *Tipula*, a selection was made of 5 min periods during which earthworms were the dominant prey.

55: It is assumed that the birds took the average prey present.

56: It is assumed that the ash content is 40% (data for the same area in later years; Blomert & Zwarts unpubl.).

57-64: Ash of *Littorina* in winter is assumed to be 10% (Chambers & Milne 1979).

65-69: Since the birds also took *Nereis*, a selection was made of 5 min periods during which *Macoma* was the dominant prey.

70: Since the birds also took *Cerastoderma*, a selection was made of 5 min periods during which *Macoma* was the dominant prey.

71-72: The estimation of the consumption per low water feeding period is based upon measurements of the feeding rate in colour-marked non-breeding birds (study 71) and breeding birds (study 72), but the feeding activity and mean prey weight were based on counts and prey collection, respectively, in which breeding and non-breeding birds could not be distinguished. That is why a calculation of the low tide consumption (41 g AFDW) would be too high for the non-breeding, even if they remained 6 h on the feeding area, since presumably their feeding activity would be lower than for the breeding birds.

74: Intake rate of captive birds averaged for two experimental conditions (erased and non-erased surface).

76-77: *A pair of individually marked Oystercatchers visited tidal* mudflats adjacent to their nest during short feeding bouts; Studies 76 and 77 give the averages for the week before and after eggs were laid, respectively; feeding rate already given by Hulscher (1982: Fig. 29).

81: Since the birds also took *Macoma*, a selection was made of 5 min periods during which *Nereis* was the dominant prey.

82: *The birds usually only took the siphon. This partial consumption* did not cause an overestimation of the consumption, since the flesh taken was estimated from the size of the pieces of flesh extracted from the shell.

83: The birds took small *Mya* in one jerk, taking the siphon but leaving a part of the body behind in the shell. When this was imitated in the laboratory 22% of the flesh remained behind. This was taken as a correction factor.

85-87: *Study 85 and 86 give same data as study 87-93 averaged* for all months and split up for stabbers, dorsal and ventral hammerers. Intake rates are given by Boates (1988). Exposure time according to Goss-Custard (unpubl.).

94-112: details in Cayford (1988)

117-126: Summary of the data are published by Ens (1982), Ens & Goss-Custard (1984), Sutherland & Ens (1987).

127-132: Since the birds also took *Cerastoderma*, a selection was made of 5 min periods with *Mytilus* as dominant prey.

134-163: The majority of the data are given in Goss-Custard *et al.* 1984, Goss-Custard & Durell 1987 & 1988. The intake rates were recalculated, however, from the actual AFDW/mussel length relationships measured on the mussel bed, month and year in question, whereas the original paper gave standardized intakes rates.

164-165: Ash assumed to be 20% in winter. Observations were restricted to 5 h around low water, and give according to Heppleston (1971) an overestimation when extrapolated to the extreme long exposure times in October (study 164), when the birds were less active at the end of the feeding period.

167: Hungry, captive Oystercatchers were offered shelled *Mytilus*.

182: The flesh remaining in the shell has been measured (7.6% relative to total AFDW).

184-191: The intake rates deviates from those orginally published (Zwarts & Drent 1981), due to recalculation. Exposure time of the musselbed in May was, as in the other months, 6-6.5 h, but the watched adults were breeding birds and visited the mussel bed during bouts of 83 min, on average, only.

193-197: AFDW is assumed to be 81% of DW (Zwarts unpubl.). Exposure time according to Goss-Custard (unpubl.).

198-202: Since the birds also took *Macoma*, a selection was made of 5 min periods during which *Nereis* was the dominant prey.

203-214: Intake rates of adult and juveniles are pooled.

217: Intake rates pooled over adults and immatures and over three winter periods.

218: AFDW assumed to be 80% of DW.

220-226: AFDW assumed to be 83% of DW (Zwarts 1991). Exposure time according to Goss-Custard (unpubl.).

228-230: Three birds were allowed to take 24 prey each in different sessions with a prey density > 200 prey m^{-2}.

231-232: Intake rate averaged for the experimental sessions with prey density ≥ 100 m^{-2}.

237-241: Since birds took also earthworms, a selection was made of 5 min intervals during which Leatherjackets were the dominant prey.

242-247: The diet consisted not solely of *Tipula*, since sometimes large earthworms were also taken, especially in April and July. The ash content of Leatherjackets and earthworms assumed to be 21% and 40%, respectively (data of the same area in later years; Blomert & Zwarts unpubl.). The feeding activity and consumption refer to the day-light period.

248: AFDW assumed to be 79% of DW (Blomert & Zwarts unpubl.).

249: Birds fed from sunrise to sunset. The feeding activity according to the activity counts was 59.1% (but the observed birds fed 83.5% of the time). Weight of the Leatherjackets taken was not measured, but assumed to be 15 mg AFDW, being the average weight of prey collected in the same area and the same month in later years (Blomert & Zwarts unpubl.).

253: Ens *et al.* (1993) give feeding rate and size selection. Collection of prey remnants showed, however, that prey size was underestimated (Ens unpubl.). Intake rate was calculated on the basis of corrected size selection. The birds opened the carapace to remove the flesh from it; by not eating the pincers and legs, they ignored 50% of the flesh (Zwarts & Blomert 1990, Zwarts & Dirksen 1990). Not all flesh was eaten from the carapace, since other wader species took flesh from it after Oystercatchers had finished. Whimbrels *Numenius phaeopus* opening *Uca* of similar size left behind 100 mg in the carapace (Zwarts & Dirksen 1990); it is assumed this was the same for Oystercatchers.

Chapter 10

WHY OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* CANNOT MEET THEIR DAILY ENERGY REQUIREMENTS IN A SINGLE LOW WATER PERIOD

Leo Zwarts, Bruno J. Ens, John D. Goss-Custard, Jan B. Hulscher & Marcel Kersten

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WHY OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* CANNOT MEET THEIR DAILY ENERGY REQUIREMENTS IN A SINGLE LOW WATER PERIOD

Captive Oystercatchers consume daily 25-40 g dry flesh or 550-850 kJ, of which they metabolize 450-700 kJ. Free-living Oystercatchers eat more than captive birds but, contrary to expectation, this is not due to greater activity costs but to a higher body weight. When body weights are equal, free-living and captive Oystercatchers consume the same amount of food. The intake rate of Oystercatchers generally varies between 1 and 3 mg dry flesh s^{-1} feeding, but if non-feeding times are included, the crude intake rate usually varies between 1 and 1.5 mg s^{-1}. Extremely high intake rates, above 4 mg s^{-1}, are only observed in birds feeding during a short bout after a long resting period. According to Kersten & Visser (1996a) such high intake rates cannot be sustained for long, because a maximum of 80 g wet flesh, equivalent to 12 g dry flesh, can be stored in the digestive tract and the processing rate does not exceed 4.4 mg wet flesh s^{-1} or 0.66 mg ash-free dry weight (AFDW) s^{-1}. Due to this digestive bottleneck, the birds are forced to spend much time on the feeding area each day. Since the exposure time of their intertidal feeding areas is usually 5-6 h, Oystercatchers cannot meet their daily energy requirements in a single low water period, which would often suffice if intake rate was the limiting factor. For a given length of the feeding period, the bottleneck model predicts the maximum crude intake intake, called CIR_{max}, that can be achieved, i.e. the highest intake rate including the non-feeding time. When the birds are able to feed for less than 3 h, the achieved crude intake rate usually remains far below this maximum, suggesting that the rate at which prey are found and eaten determines the intake rate. The consumption is also usually less than would be allowed by digestive constraint when the birds feed for 12 h or longer, because the birds at thermoneutral conditions do not need more than 36 g a day. When the birds spend 3 to 12 h on the *feeding area, the average consumption is usually close to, or below the predicted maximum. However,* in a few cases, the maximum was clearly exceeded. These studies do not invalidate the bottleneck model, because there is ample reason to believe that food consumption was overestimated. A detailed investigation of the many sources of error indicates that food consumption is more likely to be overestimated than underestimated in field studies.

Introduction

The present-day consensus is that birds may fail to collect a sufficient amount of food in the time available, if they fail to choose correctly the prey species to take or the place to feed. Recently, Kersten & Visser (1996a) challenged this view by suggesting that Oystercatchers cannot process the food sufficiently fast during the time available for digestion, so that the digestion rate is often a more important constraint on consumption than the rate at which food is ingested. At first sight, this is a remarkable view as the time available for digestion will always exceed the time available for feeding. Thus, internal processing of the food may commence immediately after the first prey item has been ingested and continue long after the incoming tide prevents feeding. According to Kersten & Visser (1996a), food is processed at a constant rate, so that intake rates can only exceed this processing rate during periods when the digestive tract has not yet been filled to capacity.

The digestive bottleneck hypothesis has important implications, quite apart from challenging the traditional emphasis placed on maximization of intake rate in optimality models. It throws, for example, a differ-

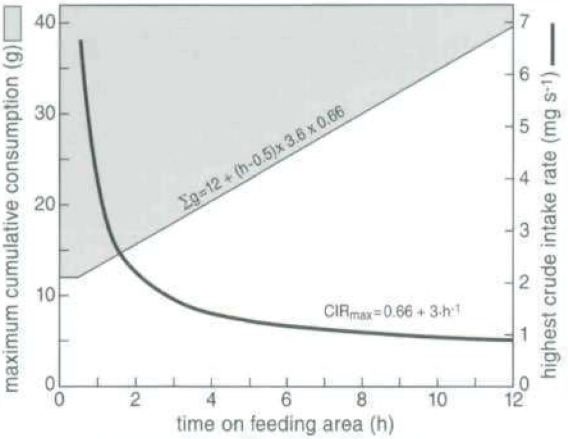


Fig. 1. Highest cumulative food consumption by Oystercatchers (g AFDW) as a function of the time spent on the feeding area (h), based upon the digestive constraint according to Kersten & Visser (1996a): (1) the storing capacity is 12 g AFDW, (2) defecation starts 0.5 h after the start of feeding, (3) the processing rate is 0.66 mg s^{-1}. Thus, in a normal low water period of 5 to 6 h, not more than 22.7 to 25.1 g can be consumed. From the predicted highest consumption, the highest crude intake rate (mg s^{-1} feeding, including non-feeding bouts: CIR_{max} (left axis)) can be calculated. In the first 0.5 h, CIR_{max} equals the storage capacity (12 g) divided by the time of spent feeding. Subsequently it decreases according to an inverse relationship that approaches the processing rate of 0.66 mg s^{-1} in the long term.

ent light on the occurrence of inactive birds during the time spent on the feeding area. These are not necessarily birds that are idling away their time, but could be birds whose digestive tract has been filled to capacity so that further feeding is impossible. Birds may not therefore always be able to fully exploit times of good feeding as, for example, when intake rate is high, and/or energy expenditure is low, and/or predation risk is low and/or risk of attracting parasites is low. If so, they may sometimes be forced to exploit less good feeding times as well. Evidently a bird that loses one hour of feeding time due to disturbance will suffer more if it has an empty gut than if its stomach is full because it loses irrecoverable processing time.

The bottleneck hypothesis dates back to Kenward & Sibly's (1977) work on Woodpigeons *Columba palumbus* eating vegetables and the work of Diamond *et al.* (1986) on hummingbirds feeding on nectar. The study of Zwarts & Dirksen (1990) on Whimbrel *Numenius phaeopus* eating crabs seems to be the only other case of this idea being applied to a carnivorous shorebird. As Kersten & Visser (1996a) derived their conclusions from only a limited number of experiments on captive Oystercatchers, before it is accepted as a fact in future Oystercatcher studies, it seems prudent to the hypothesis and assess the potential for variability in the parameters.

If there is a digestive constraint, it follows that for a given length of the feeding period the total food intake cannot exceed the sum of the storage capacity and the amount of food that can be processed during that period ('broken stick' in Fig. 1). A necessary corollary is that maximal crude intake rates, or the intake rates calculated over a period which includes the digestive pauses, will decrease with an increasing length of feeding period ('curved line' in Fig. 1). Since Oystercatchers start to defecate 30 min after the beginning of feeding (Kersten & Visser 1996a), the only limit to the intake rate during the first 30 min of feeding is the 80 g storage capacity for wet food, equivalent to 12 g dry flesh, i.e. ash-free dry weight (AFDW). Therefore, if Oystercatchers feed for 10 or 20 min, the highest possible intake rate will be 20 and 10 mg AFDW s^{-1}, respectively, and will decrease linearly to 6.67 mg s^{-1} if the birds feed for 30 min. If the feeding time is longer than 30 min, the intake rate further decreases with time but not any longer linearly because the birds start to defecate. There is thus an inverse relationship between the highest possible crude intake and the length of time spent on the feeding area (Fig. 1). When the birds feed for an infinitely long period, the crude intake rate cannot exceed the processing rate of 0.66 mg s^{-1}. However, when the feeding time is limited, the influence of the storage capacity increases as the feeding time shortens, because the highest crude intake rate (CIR_{max}) can exactly be described by the equation:

$$CIR_{max} = 0.66 + 3\ h^{-1}.$$

The digestive constraint has one important consequence for the birds. If the daily requirement for food exceeds the maximum consumption that is predicted from the bottleneck hypothesis for a low-tide period, the birds will need to feed during both low-tide periods, irrespective of the intake rate that can potentially be achieved. In this paper, we will address two questions: (1) Do the many studies on food intake of Oystercatchers conform to the predictions of the bottleneck hypothesis, i.e. do the crude intake rates not exceed the curved line in Fig. 1? (2) Do birds rest more, or do they reduce their intake rate, if their consumption is restricted by the digestive bottleneck, or do they both?

To test the prediction of the bottleneck hypothesis, we use the data set on food intakes of Oystercatchers assembled from published and unpublished sources, of which a large part is summarized in Zwarts *et al.* (1996a). None of these studies was undertaken as an explicit test of the bottleneck hypothesis, but properly combining reported data on intake rate, feeding activity and time spent on the feeding area should yield figures that can be used for this purpose. The review shows that, except for a few cases, the prediction is met. In these anomalous cases, the intake rate exceeds the predicted maximum. This caused us to explore possible sources of error in the estimation of total food intake and whether they are most likely to overestimate, rather than to underestimate, intake rate. Furthermore, to evaluate whether the digestive bottleneck prevents free-living Oystercatchers from fulfilling their daily energy needs during a single tide, we need to know how much food an Oystercatcher in the wild needs per day. Several papers measured precisely the daily food consumption in caged birds and we convert these data into an estimate of the requirements of free-living Oystercatchers.

Methods

Data

The data summarized in this paper have been taken from several sources, usually already published, but also unpublished theses, reports and data files. Zwarts *et al.* (1996a) give a full list of all sources. They also describe how these data were combined and how all measurements on prey size, prey weight, intake rate, time spent on the feeding time, and feeding activity were assembled into one data file, of which the essential measurements are given as an appendix; the intake rate were averaged per month of Oystercatchers feeding on a certain prey. In addition to these studies, their paper also includes long-term observations on individual birds studied in the Exe estuary (Ens & Goss-Custard 1984, Urfi *et al.* 1996), and the Dutch Wadden Sea (Blomert *et al.* 1983, Ens *et al.* 1996a, 1996b, Kersten 1996).

Nearly all field studies give food consumption of Oystercatchers as AFDW. Hence we also use this as the measure of food intake. Since, as discussed by Zwarts *et al.* (1996a), the energy content of marine invertebrates usually varies between 22 and 22.5 kJ g^{-1} and Oystercatchers digest 85% of the ingested energy, the factor 19 can be used as a common multiplier to convert gross intake (mg AFDW) into metabolized energy (kJ) if necessary.

Definitions

Food consumption is measured as dry flesh (AFDW), gross energy (kJ) or metabolized energy (kJ). Intake rate is defined as food consumption per unit time of feeding, excluding the time spent resting and preening over the period the bird is on the feeding area. The feeding period is defined as the time spent on the feeding area, including any time not spent feeding. Feeding activity is the percentage of the time actually spent in feeding over the whole duration of the feeding period. Crude intake rate is the rate of food consumption over the entire feeding period, including all the non-feeding intervals. Finally, the highest possible crude intake rate, derived from the digestive bottleneck model and indicated by the curved line in Fig. 1, is called maximal crude intake rate (CIR_{max}).

Results

Food consumption and feeding time

Figure 2A shows that the food consumption by captive birds lies, on average, just below the maximum predicted by the food processing model of Kersten & Visser (1996a). This is also true for field studies in which the consumption by individual, usually colour-banded, birds was measured over long periods (Fig. 2B). Most birds were observed over an entire low water period, but all observations longer than 8 h, and some of the shorter observation periods, refer to breeding birds or to non-breeding birds feeding in grasslands by day. Grassland-feeding birds foraged for less than half of the observation time, sometimes for even less than 20%, and therefore had very low crude intake

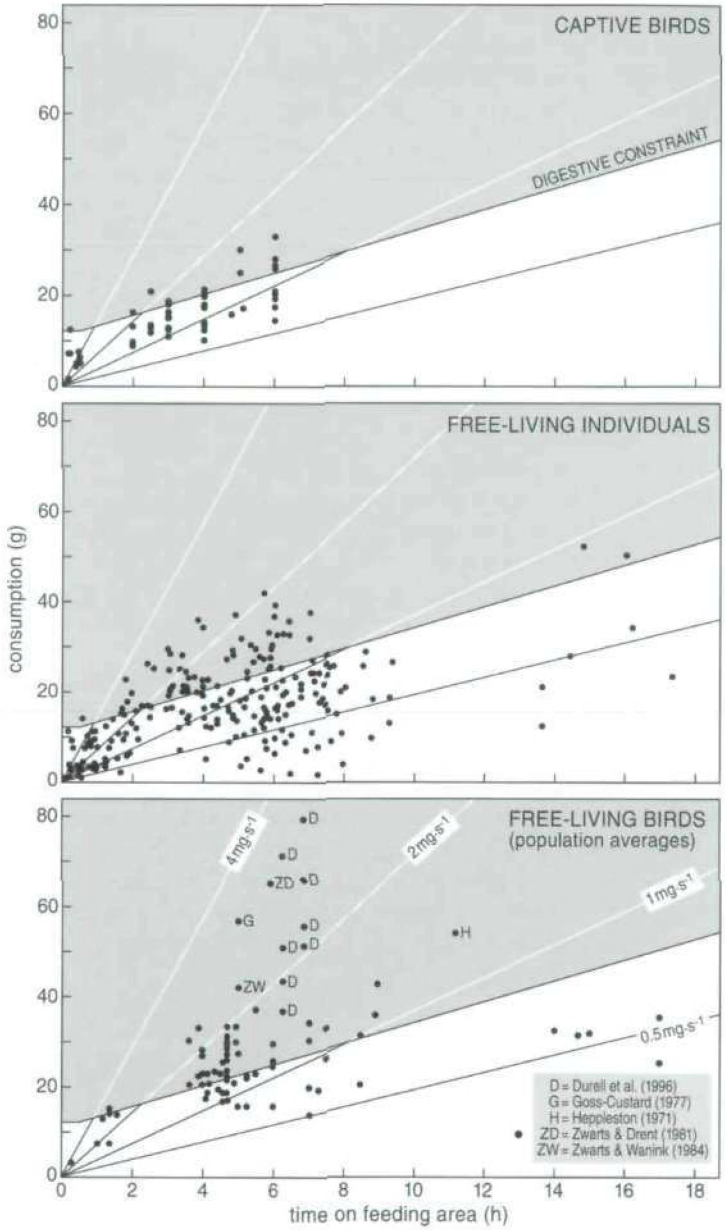


Fig. 2. Total food consumption (g AFDW) as a function of the time spent on the feeding area, given separately for **A.** captive birds (n = 53), **B.** free-living birds (long-term observations of individuals; n = 244) and **C.** free-living birds (population averages; n = 83). The grey field indicates the predicted maximal consumption determined by the digestive bottleneck (Kersten & Visser 1996a). The solid lines give the consumption with the crude intake rate (during feeding and non-feeding periods combined) set at 0.5, 1, 2 or 4 mg s^{-1}. The sources of the data shown in panels A and C are listed in the appendix of Zwarts *et al.* (1996a). In addition, panel A gives the 34 measurements of Swennen *et al.* (1989) on captive birds. The data in B refer to the consumption of individual birds over a certain time, usually an entire low water period; sources: Blomert *et al.* (1983), Ens & Goss-Custard (1984), Ens *et al.* (1996a, 1996b), Kersten (1996), Urfi *et al.* (1996) and Zwarts & Blomert (1996). Studies marked with a capital in panel C are discussed in the text.

rates. Across all data, most crude intake rates fall below the predicted maximum, but a few do exceed this level. In contrast, there are several outlying points for the population averages, i.e. calculated for free-living birds feeding on a certain prey species (Fig. 2C). Some of these estimates are even three times higher than the predicted maximum consumption.

There are three possible explanations when the food intake exceeds the predicted maximum: (1) the bottleneck hypothesis is false; (2) the hypothesis is true, but the actual level of the digestive constraint is not constant but varies between conditions and (3) the food consumption is estimated incorrectly. If (3) is true, we would expect the frequency of excessively high food intakes to increase with the potential for errors being made. Our next step is therefore to assess the possible sources of error in the estimation of food intake and the most likely direction of these errors.

Food consumption in the field is often overestimated

To estimate the total food consumption over a feeding period it was necessary in most studies to measure the length of prey taken, their weight, the feeding rate (the number of prey taken per unit time feeding), the feeding activity (percentage of time spent feeding) and the duration of the feeding period. Since the estimation errors are multiplicative, even a few small errors in the component estimates may easily lead to a large overall error in the estimated total consumption.

Estimating prey size When prey size is estimated from emptied prey found on the substrate surface, small prey may be overlooked more often than large ones. This error is possibly small when prey are collected on bare sand and mudflats, or from 'anvils', where each shell may be easily located. Small prey are possibly more easily being hammered under the surface, so one always needs to search with care. The error may be more serious on mussel beds (Ens 1982, Speakman 1984b, 1990, Cayford 1988). However, even if the sizes of prey found on the surface are representative of those eaten at the surface, the estimates may be biased if Oystercatchers eat certain size classes of burying bivalves in situ, and so beneath the surface. Although this possible error has not yet been investigated, we might expect them to be errors of overestimation for two reasons. First, prey in situ are eaten in less time than lifted prey (Wanink & Zwarts 1985, 1996, Hulscher *et al.* 1996), allowing small prey eaten in situ still to be profitable. Moreover, captive Oystercatchers lifted deep-living prey more often than they lifted shallow prey (Wanink & Zwarts 1985, Hulscher *et al.* 1996), which would generally be smaller than those at greater depths (Zwarts & Wanink 1993). Thus, collecting samples of emptied prey at the surface presumably causes large prey to be over-represented in the diet.

Converting prey size into prey weight Prey size is usually converted to prey weight from allometric relationships based on random samples of prey, thus estimating the average weight of each size class. Oystercatchers, however, do not take 'average' prey. They select thin-shelled Mussels *Mytilus edulis* when hammering; they search for bivalves that are slightly gaping when stabbing; and when they probe for buried prey, they take those living closest to the surface. Such accessible prey are often in a relatively poor condition (Esselink & Zwarts 1989, Zwarts & Wanink 1991, Goss-Custard *et al.* 1993). The greatest overestimates arising this way probably occur in Oystercatchers feeding in winter on *Scrobicularia plana*. The majority of these live out of reach of the bill and the few that are still accessible are in very poor body condition.

Prey not completely eaten It is usually assumed that Oystercatchers clean a bivalve completely, whereas some flesh often remains along the mantle edge and where the adductors are attached to the valves. When in the laboratory, the bivalves are briefly immersed in boiling water so that all flesh can be easily removed from the shell, the stub of the adductor muscle remains attached to the shell, just as when Oystercatchers clean a shell. However, it is not clear in how many studies the adductors are entirely cut free from the valves instead. Obviously, the amount of flesh extracted in the laboratory is never below, but always exceeds the amount eaten by Oystercatchers, although the differences may usually be small. Occasionally, however, the error may be large; for example, Oystercatchers left behind 11.7% of the AFDW of Cockles *Cerastoderma edule* (Hulscher unpubl.); 7.6% of Mussels (Speakman 1984a) and some 50% in Giant Bloody Cockles *Anadara senilis* (Swennen 1990). The error is also serious when Oystercatchers pull out the siphon of the Soft-bodied Clam *Mya arenaria* only and leave the rest of body behind; an estimated 22% of the prey flesh can be lost in this way (Zwarts & Wanink 1984).

It would be worthwhile in future studies to measure the amount of flesh remaining in the opened shell, but there are two problems. Prey opened by Oystercatchers may be systematically cleaned by Oystercatchers or other waders, such as Turnstones *Arenaria interpres* (Swennen 1990). Secondly, part of the prey may be stolen by gull and crow species (Zwarts & Drent 1981, Ens & Goss-Custard 1984, Swennen 1990). As such prey cannot be distinguished from prey eaten by Oystercatchers, they will cause an overestimation of the amount of flesh left behind if gulls and crows are less adept than Oystercatchers at removing the flesh from the valves.

Estimating time spent feeding The time spent feeding is estimated in two ways, but both tend to overestimate the percentage of time actually spent feeding. When birds are observed for fixed intervals of 5 or 10 minutes, birds should be chosen at random, but observers will be inclined to start with a feeding, and not a resting, bird. Inevitably this overestimates the feeding activity when such observations are used to estimate the time spent feeding. For instance, the feeding activity of Oystercatchers on Leatherjackets *Tipula paludosa* in a grassland from sunrise to sunset was estimated as 83.5% from birds observed for 15 min periods, but 59.1% from group scans made every 15 min (Veenstra 1977). Most studies overcome this difficulty by determining feeding activity from regular scans of feeding and non-feeding birds, but this method may also be biased because birds may leave the feeding area to rest (Brown & O'Connor 1974, Zwarts *et al.* 1990).

Estimating total time on the feeding area The estimate of the time spent on the feeding area by the average bird is too high when the feeding duration is based on the time birds are present on the feeding site, because individual birds may arrive later and/or leave earlier than the average (Ens & Goss-Custard 1984). The feeding time of individual birds was 1 h less than the 4 to 6 h estimated across all birds (Zwarts *et al.* 1996d). The difference is of course much larger during the breeding season when individual birds feed in bouts of only 1 h and spend, in total, only 10 to 30% of the available low water period actually on the feeding area (Ens *et al.* 1996a).

Can high food intakes be explained as estimation errors?

To what extent can the extremely high crude intake rates in some studies plotted in Fig. 2C be attributed to these five types of error? The studies which estimated an extremely high consumption will be discussed in turn.

(1) Heppleston (1971) made all his measurements between 2.5 h before and after dead low water. He warned that extrapolation to the entire exposure time would overestimate the total consumption, because the mussel bed was exposed for 11 h and the birds hardly fed over the last few hours. However, as this was not quantified, it could not be taken into account.

(2) Goss-Custard (1977) feared that his consumption estimate was too high because his shell-collections may have been biased towards large Cockles. Nor did he take into account that Oystercatchers did not eat all the flesh from the Cockles.

(3) Zwarts & Wanink (1984) studied Oystercatchers feeding on small *Mya* in autumn. The birds used a mixture of three techniques: the birds either only grasped the siphon, or they ate the whole prey in situ or they lifted the prey to the surface. Although we know now (Hulscher *et al.* 1996, Wanink & Zwarts 1996) that larger prey are lifted more often than small ones, that study implicitly assumed that *Mya* found on the surface were representative of all size classes taken, independent of the feeding technique used. Since the majority of prey were eaten in situ, the collection of prey lifted to the surface, probably caused the average size of *Mya* to be overestimated. Most clams in the mud were 16 to 30 mm long. The average length of the prey on offer was 22.8 mm, compared with 28.2 mm for the prey collected from the surface, a difference of 5.4 mm. Oystercatchers removed, in total, 80% of the prey over the months of observation. As *Mya* do not grow in autumn and winter, we would expect the size of the sampled prey to have gradually decreased over the season if Oystercatchers only took the larger prey. The extensive sampling programme showed, however, that the average size of the prey remained exactly the same, which implies that the frequency distribution of the prey taken did not differ from that on offer. Consequently, the prey weight was overestimated by 30%: the average prey taken was not 28.2 mm and 65.4 mg, but 22.8 mm and 50 mg. This error alone reduces the

consumption over the 5 h spent on the low water areas to 32 g. However, this is still 8 g above the maximum predicted by Kersten & Visser (1996a) suggesting a second estimation error was possibly made. The majority of *Mya* were eaten in situ. To estimate the amount of flesh remaining in the shell when the bird only took the siphon, the Oystercatchers were imitated by grasping the extended siphon with a pincer and pulling it from the shell. From this, it was estimated that 22% of the dry flesh remained behind. But perhaps Oystercatchers in the field left an even greater amount of flesh in the shell. If so, the estimated food consumption would no longer exceed the predicted maximum.

(4) Zwarts & Drent (1981) may have made three of the errors. First, they calculated from shell collections that Mussels of 50.5 mm long were taken. Although small prey were uncommon on their mussel bed, the average size of the prey taken would decrease by 5 mm if is assumed there was no size selection for prey size by Oystercatchers. If this is correct, the average AFDW of the prey taken would decrease from 981 to 687 mg, a reduction of 30%. Second, no correction was made for the flesh remaining in the shell, although it was clear that this was as much as 10-20%; juvenile Oystercatchers and several small wader species often took rather large bits of flesh left behind in the opened Mussels. Third, the activity counts were limited to the mussel bed itself, whereas birds sometimes roosted outside the counting site, causing the average feeding activity to be overestimated by some percent. There may have been a further error. Rather more measurements were made of the intake rate at the beginning and the end of the exposure time when the feeding rate was high. Correcting for this decreases the intake rate by a further 5%. Although each error in itself is not very large, in combination they result in a corrected estimate of the low water consumption being less than half of the original 61 g. However, this is still some g above the physiological constrained highest consumption, perhaps because the Oystercatchers took prey in a poor condition.

(5) All eight estimates of the consumption of Oystercatchers in the Exe estuary feeding on Ragworms *Nereis diversicolor* (Durell *et al.* 1996) are above the digestive ceiling level. These authors collected droppings and measured the jaws of the worms to calibrate their size estimates. Since the majority of the large *Nereis* selected by Oystercatchers live in deep burrows out of reach of the bill, the birds usually feed on the rare worms that make grazing excursions to the surface and do not retreat fast enough into their burrow at the approach of a bird (Esselink & Zwarts 1989). Thus, it is conceivable that Oystercatchers do not take 'average' prey, but marginal ones with a low body weight. This is true even if Oystercatchers probe for worms down in their burrow, because within each size class, the heavy worms live in deeper burrows, so that only the relatively lightweight worms can be reached by a probing bird (Esselink & Zwarts 1989).

The studies discussed above, marked with capitals in Fig. 2C, have been omitted from further analysis. It is nonetheless possible that the same errors may also have been made in field studies recording a much lower consumption. However, if the average consumption in the field, without these outliers, is compared with consumption in controlled, experimental conditions, where most of sampling errors discussed above cannot be made, it is clear that the difference is not large (Fig. 2). From this we conclude that consumption may easily be overestimated in the field, but that the degree to which this occurs varies and is probably small in the majority of the studies.

Daily consumption

To investigate whether a digestive bottleneck forces Oystercatchers to feed during both low-tide periods, we must know how much food the birds need each day. These data are hard to get for free-living birds due to the difficulties in accurately measuring intake rate at night. There are two ways around this problem. First, we can exploit situations where the birds only feed by day. For intertidally-feeding birds, this occurs in the summer when the short night falls over the high water period. Blomert *et al.* (1983) selected such a day to measure the total consumption of a marked individual over 24 h. Inland birds usually feed only during the daylight period and habitually roost communally at night, and a few studies have been made. Veenstra (1977) measured the feeding rate and feeding activity of inland Oystercatchers in March over the entire daylight feeding period, but since he did not measure prey weight, his data allow only a very crude estimate of the daily consumption to be made. Zwarts & Blomert

no	*prey*	*month*	*age*	*free*	*°C*	BW_c	*BW*	*g*	*xkJ*	*kJ*	*Q*	*kJQ*	kJQ_c	*source*
1	*Cer*	6		F		-2.25	518	33.8	20.7	700	0.85	595	640	Ens *et al.* unpubl.
2	*Cer*	6					461	36.2	22.0	796	0.85	677	677	Hulscher 1974
3	*Cer*	6					468	36.2	22.0	796	0.85	677	677	Hulscher 1974
4	*Cer*	7					474	39.8	22.0	876	0.85	744	744	Hulscher 1974
5	*Cer*	6					426	24.4	22.0	536	0.85	456	456	Swennen *et al.* 1989
6	*Cer*	12			6.3		444	29.6	22.0	652	0.85	554	442	Swennen *et al.* 1989
7	*Cer*	12			6.3		450	37.8	22.0	832	0.85	707	595	Swennen *et al.* 1989
8	*Cer*	10					467	35.6	22.0	782	0.85	665	665	Swennen *et al.* 1989
9	*Cer*	6					469	31.4	22.0	691	0.85	587	587	Swennen *et al.* 1989
10	*Cer*	10					490	37.7	22.0	829	0.85	705	705	Swennen *et al.* 1989
11	*Cer*	6					495	26.9	22.0	593	0.85	504	504	Swennen *et al.* 1989
12	*Myt*	12	1				420	26.2	22.6	591	0.85	502	502	Heppleston 1971
13	*Myt*	7					442	24.0	23.0	552	0.85	469	469	Hulscher 1974
14	*Myt*	7					453	25.8	23.0	593	0.85	504	504	Hulscher 1974
15	*Myt*	7					453	26.8	23.0	616	0.85	524	524	Hulscher 1974
16	*Myt*	7					456	31.8	23.0	731	0.85	622	622	Hulscher 1974
17	*Myt*	7					459	33.9	23.0	780	0.85	63	663	Hulscher 1974
18	*Myt*	7					461	26.9	23.0	619	0.85	526	526	Hulscher 1974
19	*Myt*	8					467	34.0	23.0	782	0.85	665	665	Hulscher 1974
20	*Myt*	7					469	26.1	23.0	600	0.85	510	510	Hulscher 1974
21	*Myt*	7					473	23.5	23.0	541	0.85	459	459	Hulscher 1974
22	*Myt*	7					522	35.1	23.0	807	0.85	686	686	Hulscher unpubl.
23	*Myt*	3			6.5	-1.92	466	29.6	23.0	681	0.85	578	511	Koene 1978
24	*Myt*	3			6.5		512	40.7	23.0	937	0.85	796	690	Koene 1978
25	*Myt*	3			6.5		519	38.7	23.0	891	0.85	757	652	Koene 1978
26	*Myt*	3			6.5	1.46	521	39.1	23.0	899	0.85	764	629	Koene 1978
27	pel	8	3			0.86	428	32.4	19.9	644	0.67	432	415	Exo & Freimüth unpubl.
28	pel	7	3			-0.60	428	38.0	19.9	757	0.67	507	519	Exo & Freimüth unpubl.
29	pel	7	3			0.40	444	41.8	19.9	833	0.67	558	550	Exo & Freimüth unpubl.
30	pel	8	3			1.21	460	39.1	19.9	778	0.67	521	497	Exo & Freimüth unpubl.
31	pel	7					510	32.9	22.8	750	0.85	638	638	Goede 1993
32	pel	6					465	28.5	25.8	734	0.85	624	624	Kersten & Piersma 1987
33	pel	7					480	29.4	25.8	759	0.85	645	645	Kersten & Piersma 1987
34	pel	5					495	30.1	25.8	775	0.85	659	659	Kersten & Piersma 1987
35	pel	1					515	27.5	25.8	711	0.85	604	604	Kersten & Piersma 1987
36	*Scr*	7	F				525	33.3	22.2	739	.85	628	628	Blomert *et al.* 1983
37	*Tip*	6	F				470	31.3	24.5	767	0.83	636	636	Ens *et al.* unpubl.
38	*Tip*	4	F				500	31.5	22.8	719	0.89	640	640	Zwarts & Blomert 1996

Table 1. Daily consumption (g AFDW) and body weight (g) of Oystercatchers feeding on Cockles (*Cer*), Mussels (*Myt*), commercial food pellets (pel), *Scrobicularia* (*Scr*) or larvae of *Tipula* (*Tip*). Source numbers (used in Fig. 3) and sources are given in the first and last column. All birds were adults except one 1-year and four 3-year old birds (see column 'age'). All birds were held in captivity, but studies marked with F in column 'free' were free-living birds. All data were collected in thermoneutral conditions, except four and two birds held at an average air temperature of 6.5 and 6.3 °C (see column '°C'). Body weight was constant in all studies over the periods concerned, but decreased in study 1 (18 g in 8 days), 23 (50 g in 26 days), 28 (19 g in 30 days), and increased in study 26 (38 g in 26 days), 27 (24 g in 28 days), 29 (13 g in 30 days) and 30 (34 g in 34 days); column 'BW_c' gives weight change (g day^{-1}). Change in body weight was unknown in field studies 36 and 38, but assumed to be constant. Average body weight (g, column 'BW') and month of observation are indicated. Body weight was not known for the days of observation in field study 36 and 38, but assumed to be equal to the average weight of the birds of the same sex, such as measured in other birds in the same time of the year and the same site. Columns 'g', 'kJ' and 'kJQ' give total daily consumption in terms of gross AFDW (g), gross energy (kJ) and metabolized energy (kJ), respectively. Kersten & Piersma (1987) found in pellets 22.8 kJ g^{-1} fresh weight being equivalent to 25.8 kJ g^{-1} AFDW, Goede (1993) 22.3-25.1 kJ g^{-1} AFDW for different kind of food pellets, Exo & Freimüth (unpubl.) 19.9 kJ in the pellets they used, Heppleston (1971) 22.56 kJ g^{-1} AFDW in Mussels, Merck (1983) 20.7 and 21.9 kJ g^{-1} AFDW in Cockles and Mussels, respectively, taken by the birds studied by Ens (unpubl.), Blomert & Zwarts (unpubl.) 24.5 kJ in Leatherjackets in the same area where Ens collected his data (same month but later years), Zwarts (unpubl.) 22.2 kJ for *Scrobicularia* taken by the bird studied by Blomert *et al.* (1983), and Zwarts & Blomert (1996) 22.9 kJ for Leatherjackets in April. It is assumed that in the remaining five studies the average energy content of Mussels was 23 kJ and of Cockles 22 kJ g^{-1} AFDW; column 'xkJ' gives the average energy content (kJ g^{-1} AFDW; printed in italics if estimated). Column 'Q' gives the digestibility and 'kJQ_c' the metabolized energy consumption (kJQ) corrected for weight change and thermoregulation costs (see text). Each measurement concerns an individual bird, except Kersten & Piersma (1987) and Goede (1993) whose measurements averaged 6 and 12 birds, respectively. Studies 32 to 34 concern the same six individuals being weighed each week. After a selection was made of weeks with a temperature > 10 °C and constant body weights, the average consumption was calculated separately for three categories of body weight.

(1996) observed some breeding pairs from sunrise until sunset in April, in the week before egg-laying, and measured prey fragments in the droppings to reconstruct prey weights. Second, it is possible to estimate nocturnal food consumption in nesting birds from weight changes recorded on an electronic balance placed under the nest (Kersten & Visser 1996b, Ens, Dirksen, Nieuwenhuis & Smit unpubl. and Exo & Scheiffarth unpubl.). The relation between weight change and consumption was calibrated by comparing weight changes to measured food consumption during the day.

Compared to these few field studies, many studies *have measured daily consumption in captive birds* (Table 1). With daily consumption expressed as AFDW, the variation is large. The average gross consumption is 32.3 g AFDW with a SD of 5.1 g, or 15.8% of the mean. This large variation is not due to daily variation in consumption, since the data in Table 1 for captive birds all refer to studies that averaged the consumption over longer periods, and in some cases over several individuals. We therefore first investigate to what extent this variation was due to differences in (1) energy content of the prey, (2) digestibility of the prey, (3) costs of thermoregulation, (4) weight changes, (5) body weight, (6) activity costs, (7) age and (8) season. This will then allow us to assess whether a difference in food consumption occurs between captive and free-living birds.

(1) Energy content of the prey The captive Oystercatchers were fed artificial food pellets, Cockles or Mussels. The four field studies refer to breeding birds feeding mainly on Cockles (Ens *et al.* unpubl.) and Leatherjackets (Zwarts & Blomert 1996, Ens *et al.* unpubl.) and to a non-breeding bird feeding on *Scrobicularia* (Blomert *et al.* 1983). As different prey types contain different amounts of energy, this diversity of food types makes it likely that the variation in daily consumption would be less if it was expressed as gross energy intake. Hulscher (1974) found that three Oystercatchers alternately offered Cockles and Mussels, consumed, on average, per day 37.4 g AFDW if Cockles were taken, but 33.2 g, or 11% less, if their food was Mussels. The energy content of both prey was not measured, but other studies have found that the energy content of Mussels is 5-10% higher than that of Cockles (Chambers & Milne 1979, Merck 1983, Zwarts &

Wanink 1993). The energy content of the food offered has been determined in 8 of the 13 studies and was estimated by us for the remaining ones (Table 1). The daily consumption of Oystercatchers averaged for all studies is 728 kJ (SD 103); SD as percentage of the mean is 14.1% and thus marginally smaller than the variation in the daily AFDW consumption.

(2) Digestibility of the prey A further reduction in the variation may occur were the digestibility of the food to be known so that the daily metabolizable energy could be calculated. Digestibility in Oystercatchers feeding on Mussels was 85% of the energy (Speakman 1987, Kersten & Visser 1996a), whereas it varies between 65% and 89% in various types of food pellet (Kersten & Piersma 1987, Exo & Freimüth unpubl.). Even though a low digestibility might be expected for Leatherjackets because this prey has a thick skin, 83 to 89% of the energy is actually metabolized (Zwarts & Blomert 1996). The metabolized energy consumption, averaged for all studies, amounts to 605 kJ per day on average (SD = 93; relative SD = 15.4%). Thus, in contrast to expectation, the variation in consumption did not decrease when expressed as net, rather than gross, energy.

(3) Thermoregulation The air temperature in most studies was above 10 °C, the critical temperature below which the costs of thermoregulation increase (Kersten & Piersma 1987). However, two studies held birds at average temperatures of about 6 °C. The extra amount of energy needed to meet these additional thermoregulation costs is estimated to be 30 kJ for each °C below 10 °C, using the regression equation and conversion factors given by Kersten & Piersma (1987). The thermoregulation costs of waders along the shore are more effected by wind force than by temperature alone (Wiersma & Piersma 1994). The captive birds lived in sheltered cages, however, whereas the data for free-living birds were collected at air temperatures of > 15 °C. Hence there is no need to estimate the extra costs due to wind flow.

(4) Gaining or losing body weight Another source of variation is whether birds were changing body weight. However, body weight remained constant in most of the experiments, the exceptions being indicated in Table 1. We assume that if Oystercatchers gain, or lose, 1 g fresh body weight per day, their net energy intake would be 20 kJ above, or below, the energy consumption required to keep their body weight constant. Oystercatchers are able to keep their body weight constant at a daily gross consumption of 36 g and a net consumption of 670 kJ (see below). They lose 30 g a day if they take no food at all (Kersten & Visser 1996b). Hence, daily food consumption (C, AFDW) is a function of the daily change in body weight (ΔW, g):

$$C = 36 - 1.2\,\Delta W.$$

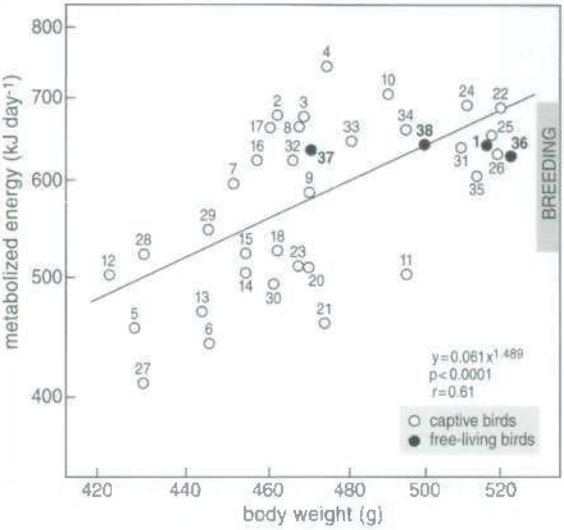


Fig. 3. The daily consumption (kJ metabolized energy) as a function of body weight in captive and free-living Oystercatchers according to several data sources given in Table 1. The digit codes in the figure correspond with the source numbers in Table 1. The grey field indicates the variation in daily energy expenditure of adult birds during the breeding season (Kersten 1996: Table 8). The daily consumption was measured at constant body weight and under thermoneutral conditions, and if this was not so, a correction was made (see text and Table 1).

A slope of 1.2 g AFDW was found indeed in captive Oystercatchers by Kersten & Piersma (1987).

After correction for weight changes (20 kJ for each gram change of body weight) and costs of thermoregulation (30 kJ for each degree below 10 °C), the maintenance metabolism in the birds amounts to, on average, 588 kJ day^{-1} (SD=85). The coefficient of variation is 14.5%, and thus still quite large.

(5) The effect of body weight Body weight explains a significant part of the variation in daily energy intake. The correlation of the linear regression is +0.59 and +0.61 on a log-log scale (Fig. 3) with an exponent of 1.49 (SE = 0.32). The SD of the residuals from the regression line shown in Fig. 3 is 69, or still 11.7% of the average consumption. The effect of the three remaining variables -activity costs, age and season- has been investigated after removing the effect of body weight by analysing the residuals.

(6) Activity costs The costs of feeding might vary between the studies, being higher for free-living birds (Blomert *et al.* 1983, Zwarts & Blomert 1996, Ens *et al.* unpubl.) than for captive birds. Within the captive birds, the feeding costs might differ too, being high if the birds had to feed on an artificial cockle bank (Swennen *et al.* 1989) or a mussel bank (Koene 1978), and low if the birds were offered opened bivalves (Heppleston 1971, Hulscher 1974 & unpubl.) or pellets (Kersten & Piersma 1987, Goede 1993, Exo & Freimüth unpubl.). Although the energy expenditure has not been measured, the possible costs of feeding might be derived from an increase in the metabolized energy consumption. However, the daily consumption did not differ among the four categories of studies distinguished ($p = 0.81$), nor when free-living and captive birds were compared ($p = 0.89$).

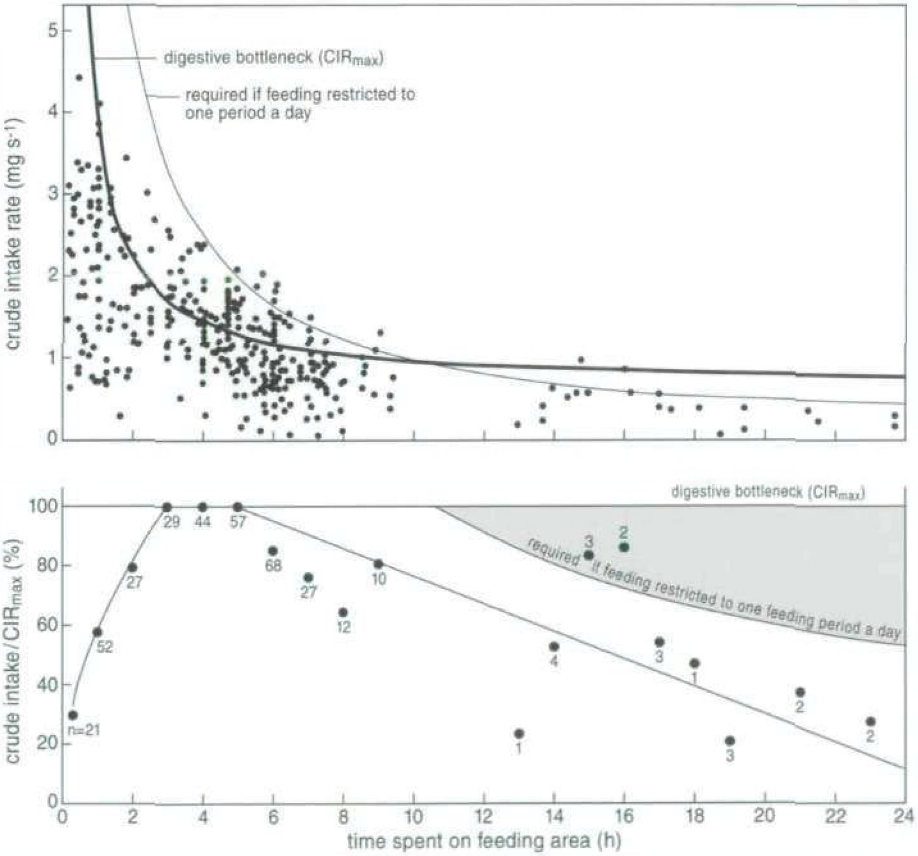


Fig. 4. A. Crude intake rate (mg AFDW s^{-1}) as a function of the time spent on the feeding area. A selection was made of the studies summarized in Fig. 2A, B and C: $\Sigma n = 370$ studies. One curved line shows the highest possible crude intake rate such as determined by the digestive system (CIR_{max}; Fig. 1). The other line shows the intake rate required to keep their body weight constant, assuming that feeding is restricted to one feeding period a day. **B.** Average deviation of the crude intake rate from CIR_{max} (set to 100%) or from the required crude intake rate at one daily feeding period (calculated from the data given in panel A); number of cases indicated.

(7) Age All studies dealt with adult birds, but Heppleston (1971) worked with a yearling and Exo & Freimüth (unpubl.) with two subadults three years old. The few data available suggest no reason to assume that the consumption is different for the age classes when birds of similar body weight were compared ($p = 0.87$).

(8) Season There is also no seasonal variation in the consumption at thermoneutrality ($p = 0.31$).

In conclusion, the daily consumption of Oystercatchers with constant body weight and living in thermoneutral conditions greatly depends on their body weight but not on whether they live in captivity or in the wild. Oystercatchers in the wild weigh 520 g during most months of the year. From Fig. 3, their daily net energy intake can be estimated at 672 kJ, which is equivalent to a gross consumption of 790 kJ or 36 g AFDW.

Crude intake rate and the digestive constraint

Although the amount of food consumed increases with the amount of time spent on the feeding area (Fig. 2), the rate at which food is taken nonetheless decreases. This is illustrated in Fig. 4A, where the crude intake rates are plotted against feeding time, using the data from Figs. 2A, B and C. The curved lines in Fig. 4A show CIR_{max} and the required crude intake rate, assuming that the birds need 36 g a day at thermoneutrality and take all this food during one feeding period a day. It is clear from Fig. 4 that, under these conditions, they cannot meet their daily energy requirements in less than 11 h.

The highest crude intake rate ever observed was 16 mg AFDW s^{-1} and was measured in a hungry Oystercatcher, offered opened Mussels, that fed for 13 min (Hulscher unpubl.). This bird must have filled up its digestive tract completely during this short feeding bout. The three other studies with crude intake rates exceeding 5 mg s^{-1} concerned birds foraging for less than 30 min. Even so, these extremely high intake rates still lie below CIR_{max}. But as Fig. 4A also shows, even though the observed crude intake rates decrease with the time spent on the feeding area, they do not all fall below CIR_{max}, perhaps because of errors of estimation. In fact, the observed crude intake rates follow, on average, the CIR_{max} curve over the feeding time range of 3 to 5 h. To show this, we turned all crude intake rates into deviations from predicted CIR_{max} and plotted the hourly average deviation from CIR_{max} against time (Fig. 4B).

Figure 4 shows that if the birds forage less than 3 h, the CIR_{max} is so high, that the achieved crude intake rate usually remains far below this maximum. In other words, the rate at which prey are found and eaten determines the intake rate. The consumption is also usually less than CIR_{max} when the birds are able to feed for longer than 11 h, because they have time enough to consume the 36 g they need. However, when low water feeding areas are exposed only for during 3-5 h, the average crude intake rate is equal to CIR_{max} (Fig. 4B). On these occasions, the birds consume, on average, as much food as the digestive system allows.

Feeding activity and the digestive constraint

What do wild Oystercatchers do if the digestive system sets a limit to their consumption? Do they feed at the low level of 0.66 mg s^{-1}, set by the processing rate, throughout the feeding period, or do they feed more quickly and stop feeding intermittently to resume feeding later on? The relationship between average intake rate and feeding activity over the entire feeding period in relation to the duration of the feeding period will be analysed in the next section, using the same data as shown in Fig. 4. However, to know what birds do as their digestive tract is filling, we need data on the change in intake rate and feeding activity within the feeding period. We therefore reanalysed the data of Zwarts & Drent (1981) who, over many days, counted the number of feeding and non-feeding Oystercatchers on a mussel bank each quarter of an hour. We restricted the analyses to counts made in late summer and autumn, since those from spring and early summer partly refer to breeding birds that visited the mussel banks during short bouts of only 1 h.

Figure 5 shows that the Oystercatchers arrived on the mussel bed between 3 and 2 h before low water and left between 2h 30' and 3 h after. The average Oystercatcher was present on the mussel bank between 2h 45' before low water until 2 h 52' after low water, making a total of 5h 37'. On the digestive bottleneck hypothesis, the highest possible consumption over this time span would be 24.16 g (Fig. 1) and so CIR_{max} would be 1.20 mg s^{-1}, on average. The average feeding activity was 81%. Hence, the average intake rate must

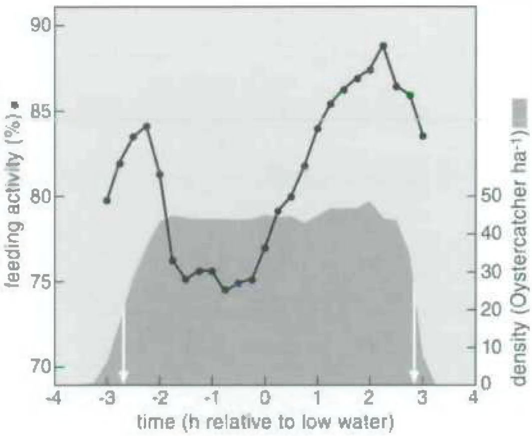


Fig. 5. Average feeding activity (% of Oystercatchers feeding) on a mussel bank over the low water period and the average total numbers (birds ha^{-1}) at which they occurred. Data of Zwarts & Drent (1981); a selection was made for the 220 low water periods that completely fell in daylight period between July and November.

have been 1.49 mg s^{-1} at the most. Can the dip in the feeding activity in the 1.5 h before low water be explained by a digestive bottleneck? Were the birds to feed from the beginning of the exposure period at a rate of 1.49 mg s^{-1}, the digestive tract would not be full even after several h of feeding. We know, however, that the feeding rate during the first 1.5 h of the exposure period was twice as high as during the hours around low water (Zwarts & Drent 1981). Hence the intake rate would be 2.6 mg s^{-1} during receding tide and 1.3 mg s^{-1} around the moment of low water. At such a rate of consumption, a digestive pause would be necessary 1.5 h after the start of feeding. From this we conclude that the low feeding activity in the 2 h before low water was indeed due to the digestion constraint and that the intake rate after low water must have been lower than 1.49 mg s^{-1}.

The Oystercatchers foraged, on average, 81% of the time they spent on the mussel bank, but the birds fed continuously when the feeding area was exposed for a short time and they were more often inactive when the exposure time was long. To what extent can this decrease in the feeding activity with the duration of the exposure time be explained by a digestive constraint? Figure 6 gives for four different intake rates the predicted relationships between feeding activity and exposure time. With an intake rate of 2 mg s^{-1}, a full digestive tract would force them to feed for not more than 77% of a 4 h exposure period and 59% of a 6.5 h period. The circles show how often different combinations of exposure time and feeding activity occurred. It is obvious that the intake rate must usually have been 1.5 to 2 mg s^{-1}, and thus in agreement with the estimate given above. The large scatter in the feeding activity may largely be explained by season. The birds fed more actively later in the season, apparently to compensate for the 30% decline in the condition of the Mussels, and thus for the probably lower intake rate.

Figures 5 and 6 show that the variation in the feeding activity during the course of the exposure period, as well as between different days, may also be explained by the digestive constraint. Both figures are based on population averages, but the intake rate, and possibly also the processing rate, may differ between individuals. It is thus of interest to analyse in more detail the consumption and time budget of individual

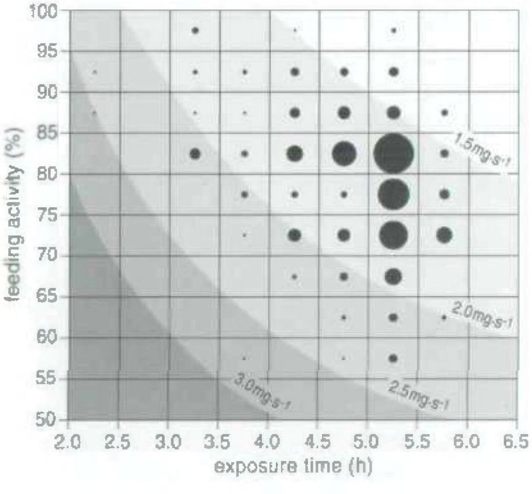


Fig. 6. Average feeding activity (%) during a low water period as a function of the duration of the exposure time of the mussel bank (i.e. water level below mean sea level). The surface of the circles indicates the number of low water periods, varying between 1 and 24 (Σn = 220). The curves show the expected relationship between feeding activity and exposure time, if the birds fed at a certain intake rate and the total consumption was as high as digestion allows. Data of Zwarts & Drent (1981).

birds over long periods. As an example, Fig. 7 shows the cumulative consumption in three individual birds observed over complete exposure water periods of 4-6 h duration. Hulscher (1976) allowed three captive birds to feed for exactly 4 h on a cockle bed at a density of 13 to 450 large Cockles m^{-2}, whereas Blomert *et al.* (1983) observed free-living, colour-banded birds from their arrival on the feeding area until their departure to the high water roost.

The birds studied by Hulscher (1976) only reached a crude intake rate equal to CIR_{max} at the highest prey density on offer (Fig. 7A). On one day, bird WR fed continuously for 3 h and consumed 17 g. Its digestive tract must have been filled completely, and indeed its consumption did slow down over the last h of feeding. A week earlier, the bird had consumed as much, but rested halfway during the feeding period when the digestive tract was not yet full (Fig. 7A). This suggests that the strategy of Oystercatchers is not to fill their digestive tract as fast as possible when they begin feeding at the start of the feeding period, but to store the maximal amount of food at the end of the feeding period. The data on free-living birds studied by Blomert *et al.* (1983) suggest the same. Bird WW2023 (Fig. 7B) rested several times for 20 to 30 min even though its storage capacity had not yet fully been used, but after spending 4 h on the feeding area, it foraged for relatively less time, apparently due to the digestive bottleneck. The same pattern was observed even more evidently in bird GW2126 (Fig. 7C), which during one day rested for 100 min after it had filled its digestive tract completely and resumed feeding during the last 40 min. However, on the other day the bird rested at the beginning of the low water period, but ultimately reached the same result: the highest possible consumption set by the digestive constraint (Fig. 7C).

Figure 7 shows a selection of 5 days in which the birds filled their digestive tract to the maximum possible. On not one day did any of the birds studied by Hulscher (1976) or Blomert *et al.* (1983) ever reach a consumption exceeding the digestive maximum. During the majority of the days, the consumption was 20 to 40% below this and, in some cases, it was even less. For instance, after GW2126 consumed 26.9 g (Fig. 7C) during an evening low water period it took during the next early morning low water period only 6.3 g, even though the duration of the exposure time would

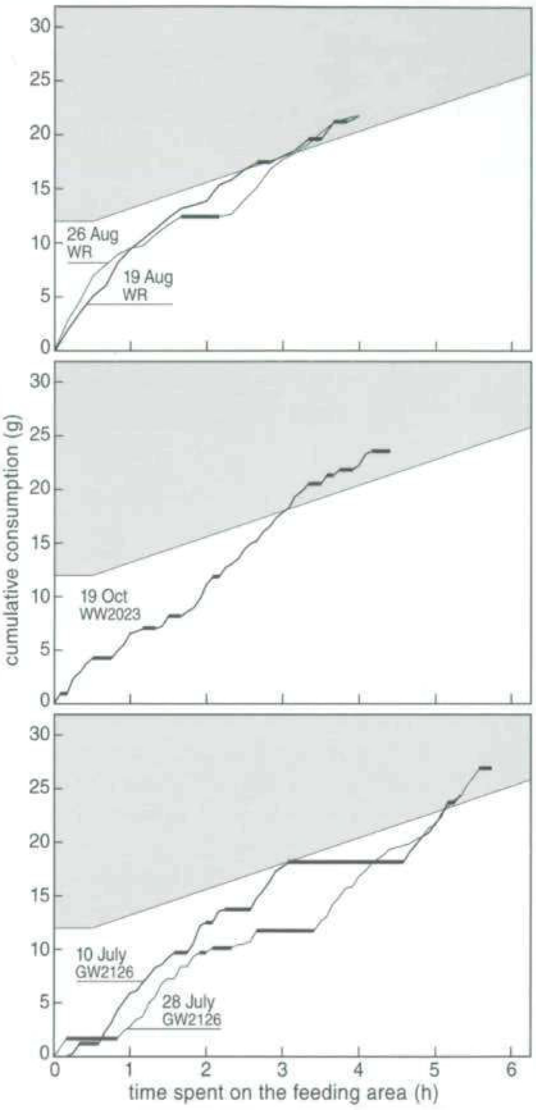


Fig. 7. Cumulative consumption (g) of three individual birds during the feeding period: **A.** captive bird allowed to feed on a cockle bed in a temporary cage (Hulscher 1976), **B.** and **C.** two free-living, colour-banded birds feeding on *Mytilus* and *Scrobicularia*, respectively (Blomert *et al.* 1983) compared to the predicted maximal consumption determined by the digestive bottleneck (Kersten & Visser 1996a). Thick, horizontal lines indicate the resting periods > 5 min.

have allowed the bird to take three times as much. There was no need for the bird to consume any more, because its intake over the 24 h was sufficient to maintain its body weight (Fig. 3).

Do birds feed at a lower rate over long feeding periods?

The processing capacity is not being fully used if the actual intake rate remains below CIR$_{max}$. How often does this occur? Figure 8A plots intake rate against the time spent on the feeding area, using again the data from Figs. 2A, B and C. The intake rate is usually 1 to 3 mg s^{-1}. However, if the birds feed for less than 2 h, the intake rate is more often 2 to 4 mg s^{-1}, whereas it is usually 1 to 2 mg s^{-1} if they remain for longer than 6 h. Although the intake rate decreases when the birds spend more time on the feeding area, CIR$_{max}$ decreases more. Hence the proportion of studies with an intake rate above CIR$_{max}$ increases with the duration of the feeding period. If the intake rate exceeds the CIR$_{max}$, the birds have to interrupt feeding for digestive pauses. That is why the feeding activity decreases with the time spent on the feeding area (Fig. 8B). In conclusion, Oystercatchers have more digestive pauses, and also feed at a lower intake rate, if they can spread out their food consumption over long periods.

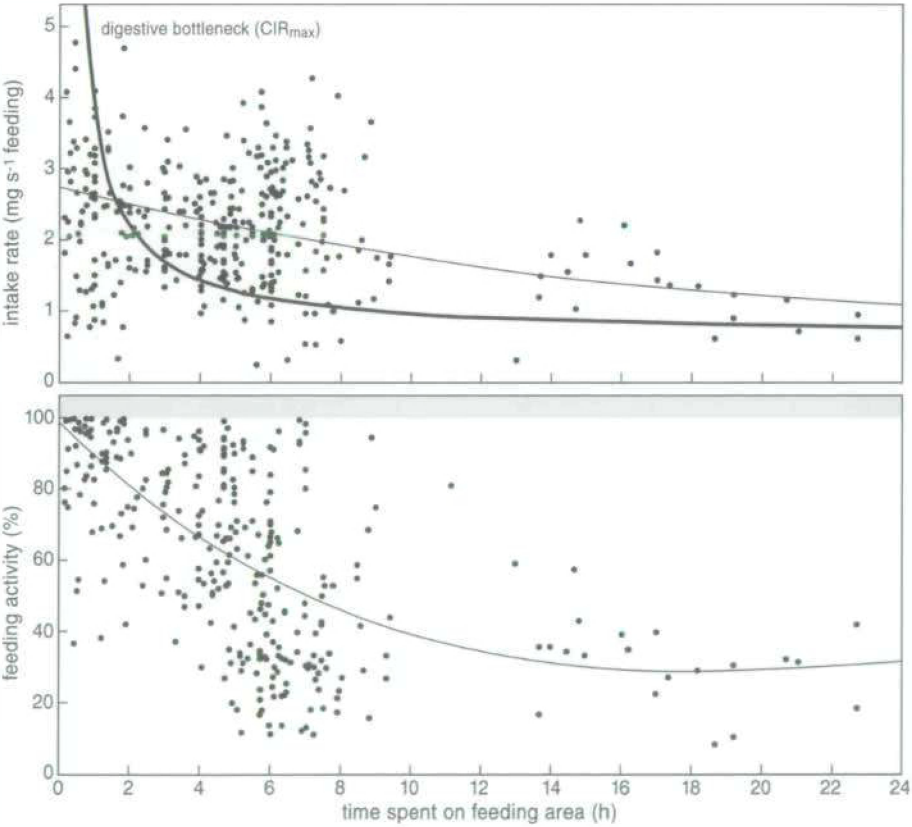


Fig. 8. A. Intake rate (mg s^{-1} feeding) and **B.** feeding activity (%) as a function of the time spent on the feeding area. A selection was made of the studies summarized in Fig. 2A, B and C; $\Sigma n = 370$. The heavy line in panel A shows the highest possible intake rate if the birds feed as fast as digestion allows (CIR$_{max}$; Fig. 1) and for 100% of the time. Thin lines (based on polynomial regressions) give the average decrease of intake rate and feeding activity with time.

Discussion

There is no difference in food consumption between wild and captive birds

We did not find a difference in food consumption between wild and captive birds. Since birds in the field fly, and possibly walk, more, than captive birds, some difference between cage and field metabolism had been expected, even for studies where the captive birds had to search and handle their own food. However, a theoretical calculation shows that the expected magnitude of this difference is actually quite small. Free-living Oystercatchers fly four times a day some 2 to 5 km between roost and feeding area and occasionally make short flights due to disturbance or interference. Assuming that (1) for an Oystercatcher weighing 520 g, the average energy expenditure is 7.8 W at thermoneutrality (Fig. 3; 672 kJ day^{-1} = 7.8 kJ s^{-1}), (2) captive birds never fly and free-living birds fly for 10-30 min a day (authors' unpubl. data), and (3) the flying costs are 36 W (Pennycuick 1989; given that the wingspan of an Oystercatcher is 83 cm (Welham 1994)), the energy budget of wild birds would only be about 3-8% above that measured in captive ones. As the three studies of free-living Oystercatchers refer to birds just before or during the breeding season that foraged close to their nest or on a tidal flat nearby, and flew even less than average (Zwarts & Blomert 1996, authors' unpubl. data), it is perhaps not surprising after all that their daily consumption did not differ from that of the captive birds. Also the estimates of the daily energy expenditure of adult breeding birds throughout the breeding season (Kersten 1996: Table 8) confirm that the life of breeding Oystercatchers is not expensive.

Food requirements and body weight

Daily consumption increases with body weight in Oystercatchers weighing between 420 and 520 g (Fig. 3). The body weight of wild Oystercatchers varies, however, over a higher range, between 500 in summer and 620 g in midwinter or just before migration (Dare 1977, Goss-Custard *et al.* 1982, Johnson 1985, Zwarts *et al.* 1996b). We therefore seek to identify the underlying cause of the relationship before deciding if we can safely extrapolate the regression line in Fig. 3 beyond the weight range of the captive birds to the generally higher weights of the free-living birds.

Oystercatchers with long wings (280 mm) weigh, on average, 12% more than birds with short wings (250 mm) (Zwarts *et al.* 1996c). Wing or bill lengths have not been measured in most studies summarized in Table 1 and Fig. 3. Therefore, it is not possible to standardize the body weights to birds of the same size. Were this correction possible, the scatter along the slope in Fig. 3 would possibly have been smaller and the slope less steep.

Variation in energy requirements due to intraspecific variation in body weight, were expected to scale with the exponent 0.73, the exponent that applies across species (Kersten & Piersma 1987). However, we found the much higher exponent of 1.49. The exponent is about 1.35 if basal metabolic rate (BMR) is plotted against body weight in an other wader, the Knot *Calidris canutus* (Piersma *et al.* 1995).

There are two explanations for this steep increase of metabolism with intraspecific variation in total body weight, as has also been found in other bird species (Bryant & Tatner 1991, Tinbergen & Dietz 1994 for parent birds provisioning their chicks). First, the much higher maintenance metabolism of heavy individuals must be due to a change in the metabolic machinery. Skin, feathers and the skeleton weigh the same for fat and lean birds of the same size, but since these parts of the body require less energy (Daan *et al.* 1990), the costs of living are relatively low in lean birds.

Second, if birds increase the weight of their body, they also increase the costs of living because walking and flying become much more expensive. Taylor *et al.* (1980) showed that the oxygen consumption increased in direct proportion to the added load. In other words, the exponent is 1 if log(energy expenditure) is plotted against log(body weight). The costs of flying increase much more with body weight: the exponent against body weight is 1.52 (Pennycuick 1989). Thus, the exponent of the allometric relationship between body weight and maintenance metabolism depends on the activities of the birds, i.e. how much they fly. Per 24 h, Oystercatchers rest during more than half of the time, they walk 30 to 40% and fly during 1 to 2%. Hence, the exponent of energy expenditure against body weight should be closer to 1 than to 1.52.

In conclusion, the steep increase of maintenance metabolism with body weight (exponent 1.49) may in a small part be attributed to the unmeasured variation

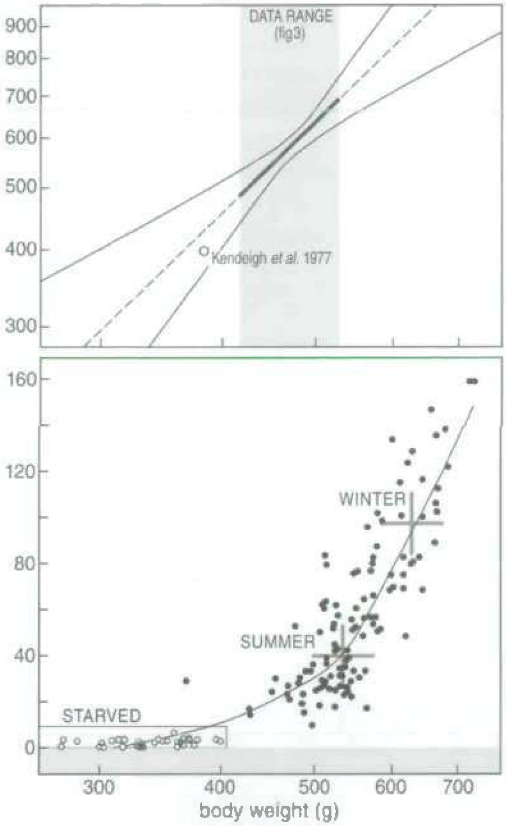


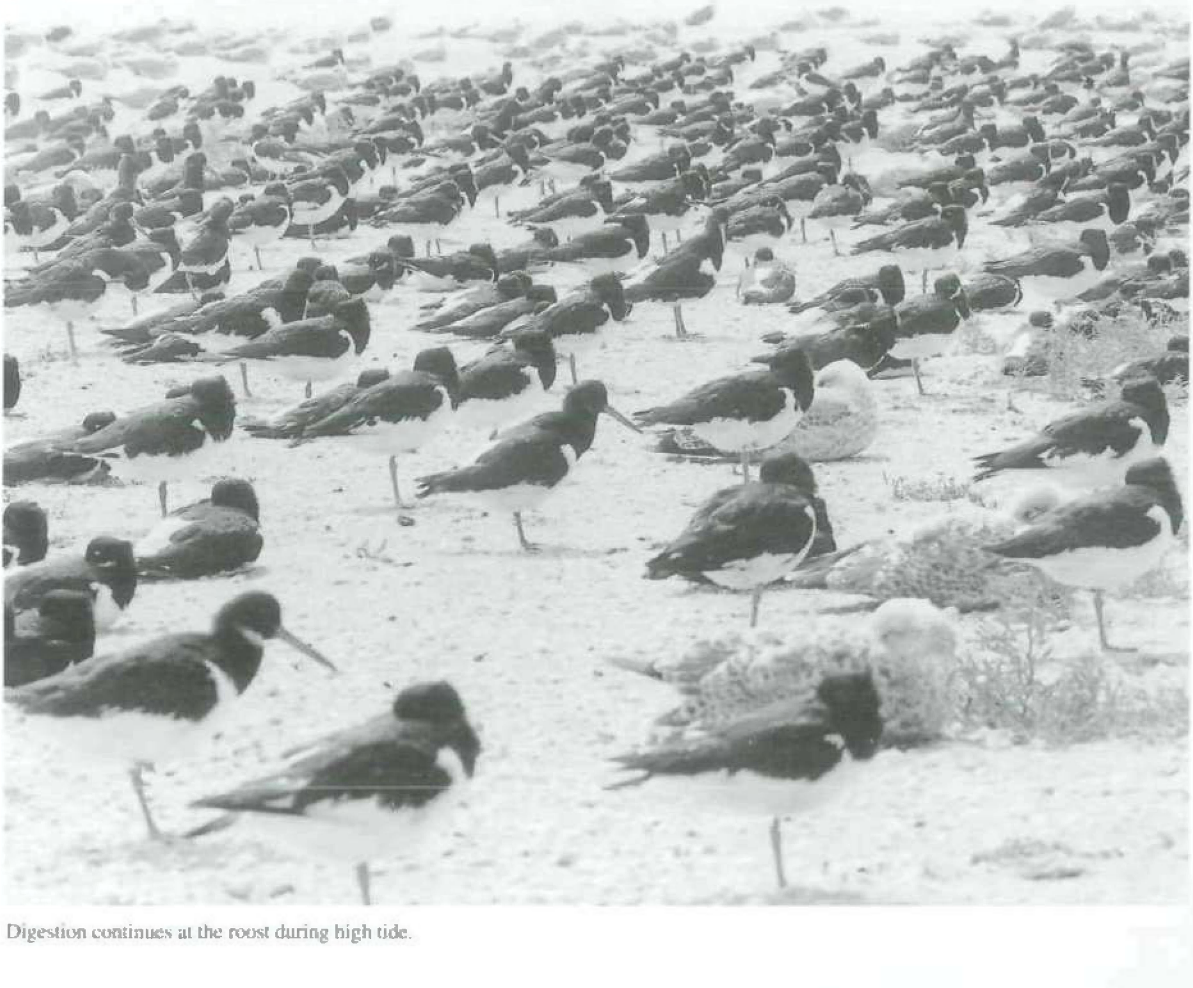
Fig. 9. A. Net energy consumption (kJ day^{-1}; with 95% confidence interval) as a function of body weight in Oystercatchers, based upon the data from Fig. 3 (range shown), compared to the maintenance metabolism of an extremely lean Oystercatcher studied by Kendeigh *et al.* (1977). **B.** Fat as a function of total body weight in birds starved in winter and living birds collected in all months of the year; crosses give the average fat and body weight in summer and winter birds; data from Zwarts *et al.* (1996b). The line was calculated with a running mean procedure ('lowess smoothing'; Norušis 1993).

in body size, but for the larger part to an increase of the costs of the basal metabolism and the costs of transport. Hence, although extrapolation of the regression line in Fig. 3 shows that a heavy Oystercatcher of 620 g would need 873 kJ per day, twice as much as an extremely lean bird of 394 g, this difference would be smaller if birds of similar body size could be compared. The only evidence that the regression line may be extrapolated downwards comes from the study of Kendeigh *et al.* (1977) who gave the maintenance metabolism of an extremely lean Oystercatcher of 385 g. Their measurement falls within the extrapolated confidence interval (Fig. 9A). We badly need data on the energy consumption of extremely heavy birds at thermoneutrality and constant body weight to know whether the regression line in Fig. 9A may also be extrapolated upwards. Possibly the increase of energy expenditure with body weight becomes less steep above a body weight of about 520 g because, from then on, an increase of the body weight is mainly due to fat deposition (Fig. 9B). However, even if fat deposition would not raise basal metabolic rate, the costs of transport will still continue to increase, thus a higher body weight must enhance the costs of living.

How (in)flexible is the digestive constraint?

In our test of the bottleneck hypothesis, we found several estimates of food intake that exceeded the maximum predicted by the hypothesis, although the most extreme values could be explained as the result of errors of estimation. It is well known, however, that gut morphology is flexible depending on the types of food taken, as reviewed by Piersma *et al.* (1993). Although Oystercatchers take different prey species, their food always consists of soft flesh only. Hence no variation in the gut morphology, and thereby rate of food processing, in relation to their diet is to be expected. However, an enhanced rate of food processing in winter might be expected because more food has then to be processed to deal with the prevailing low temperatures, strong winds and increased body weight.

The size of the digestive tract determines the amount of the food, i.e. the volume, that can be stored, whereas the rate at which food can be processed is presumably constrained by the rate at which energy can be metabolized. A seasonal variation in the rate of digestion may therefore only be expected if the size of the digestive system varies during the season. If this does happen, the processing rate may increase with body weight either because more food can be stored in the larger gut and/or because the energy can be processed at a faster rate due to an increase in the length of the digestive tract. However, when a bird increases its body weight, it acquires more muscles and fat, but does not increase its structural size. An intraspecific comparison between the weight of the gut and the total body of some wader species (Piersma *et al.* 1993) shows that the exponent of the slope is usually less than 1. Furthermore, the seasonal variation in body weight in Oystercatchers is not as large as in migratory birds, even though a winter weight of 600 g is 20% above the body weight of inland Oystercatchers during the summer. Since Kersten & Visser (1996a) did their experiments in summer and their birds had a low body weight, the consumption in winter might exceed the digestive constraint these authors defined. However, our analysis of the crude intake rates (Fig. 4) revealed no seasonal variation. Hence we take the model of Kersten & Visser (1996a) as a general description of the constraint in the rate at which also the food can be processed at a maximum.



Digestion continues at the roost during high tide.

Chapter 11

PREDICTING SEASONAL AND ANNUAL FLUCTUATIONS IN THE LOCAL EXPLOITATION OF DIFFERENT PREY BY OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS*: A TEN-YEAR STUDY IN THE WADDEN SEA

Leo Zwarts, Jan H. Wanink & Bruno J. Ens

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PREDICTING SEASONAL AND ANNUAL FLUCTUATIONS IN THE LOCAL EXPLOITATION OF DIFFERENT PREY BY OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS*: A TEN-YEAR STUDY IN THE WADDEN SEA

We predict the intake rate and prey choice of Oystercatchers feeding along the Frisian coast, Dutch Wadden Sea, combining the optimal prey choice model (Charnov 1976) with detailed measurements of the widely fluctuating food supply. Assuming that the birds maximize their intake rate, the birds should never eat Mussels *Mytilus edulis* during 10 years of observations, *Mya arenaria* during two short periods, *Macoma balthica* and *Scrobicularia plana* during most summers and Cockles *Cerastoderma edulis* in most winters. Observations on feeding Oystercatchers confirmed the predictions. Due to the seasonal variation in burying depth of *Scrobicularia* and *Macoma*, these prey were in winter, if not inaccessible, hardly worthwhile exploiting because of the increase of handling time and searching time with burying depth. Hence, the seasonal variation in intake rate was very large in these deep-living prey compared to surface prey, such as Cockles and Mussels. Consequently, Oystercatchers usually switch from surface to deep-living prey in spring and back to surface prey in autumn in order to maximize their intake rate. Oystercatchers will never achieve a high intake rate when they feed on small prey, even when these prey would occur in extremely high densities. The reason for this is that the yield of small prey during handling is even less than the intake rate during feeding of 1 mg ash-free dry weight (AFDW) s^{-1}, which Oystercatchers need to meet their energy demands during the limited feeding periods in the tidal habitat. Since Oystercatchers eat only large bivalves, they might be vulnerable because cohorts of prey may disappear completely before they can be harvested. Despite the very large annual variation in the biomass of the different prey species in the Wadden Sea, the total food supply harvestable by Oystercatchers is large enough for them to stay in the area, unless ice covers the tidal flats. However, Oystercatchers cannot survive in the Wadden Sea when their diet is restricted to one or two prey species. They need to switch between at least 3 or 4 prey species. For the same reason, the birds have to roam over feeding areas measuring at least some ten's km^2. The winter remains a difficult period, however. The mortality is higher in winter than in summer and increases with the severity of the winter. Besides, the winter mortality increases when the food consumption is reduced, due to either a low intake rate and/or a short feeding time. Therefore, the wintering numbers of Oystercatchers in the Wadden Sea are limited during circumstances which occur in only some of the winters, viz. when ice covers the feeding areas and the harvestable food supplies are low.

The total biomass of the five bivalve species in the study area amounted to 81 g ash-free dry flesh (AFDW) m^{-2}, on average. The annual production was 56 g m^{-2}, but only 32 g m^{-2} can be considered as exploitable by Oystercatchers. Oystercatchers did not harvest the 9 g m^{-2} $year^{-1}$ produced by large *Mya* living out of reach of the bill, nor the 5 g m^{-2} produced by bivalves too small to be eaten by Oystercatchers. Moreover 9 g m^{-2} disappeared during disasters (e.g. frost) and could not be eaten by birds. Oystercatchers consumed 12 g m^{-2} $year^{-1}$, on average, thus more than the 10 g m^{-2} taken by all other shorebird species together. Half of the prey biomass disappearing due to mortality between August and March could be attributed to Oystercatcher predation. The predation pressure by Oystercatchers was much lower in *Scrobicularia* and *Macoma*. In contrast, 80% of the second year *Mya* was eaten by Oystercatchers in some months. The numbers of Oystercatchers feeding in the study area were weakly related to the annual variations in the total food supply, but strongly related to those of the harvestable food supply. This high correlation must be due to two causal relationships: the bird density increases with the intake rate, and intake rate increases with the harvestable food supply.

Introduction

Many workers have attempted to answer the question whether the numbers of shorebirds feeding on the intertidal flats are limited by their food supply. It is commonly assumed that such a limitation can occur either through actual depletion of the food supply or interference, where high densities of feeding birds impair the ability of the individual to collect food (Goss-Custard 1980). There is abundant evidence that Oystercatchers interfere with each other at high feeding densities (Zwarts & Drent 1981, Ens & Goss-Custard 1984, Goss-Custard & Durell 1987, 1988) and this may explain why many birds are often found feeding in poor areas, instead of all concentrating in the best feeding areas (Goss-Custard *et al.* 1982, 1984).

In this paper we explore the hypothesis that low intake rates limited the number of birds that used our study area. We refine our measurements of what part of the food supply can be considered harvestable for the birds (sensu Zwarts & Wanink 1993) and the extent to which the harvestable fraction is actually harvested in any given year. To this end we apply the optimal prey choice model developed by Charnov (1976). It is necessary to consider several potential prey species, because the Oystercatchers have to take more prey species due to the wide year-to-year fluctuations in the prey densities (Beukema *et al.* 1993).

After parameterizing our application of the prey choice model, the paper will give a description of the seasonal and annual variation in the food supply of Oystercatchers. These data will then be used to make quantitative predictions on the intake rate. Assuming that the birds maximize their intake rate, the predicted diet can be ascertained. The next step is to compare the predicted intake rates and diet to the quantitative data on intake rate and diet. The data on predicted intake rate will then be combined with the bird count data to investigate whether the study area attracts more birds at high intake rates and/or a certain food supply. Finally, the calculated total predation pressure exerted by the Oystercatchers on the different prey species will be compared to the observed mortality of the different potential prey species. This will give a further check on the predicted diet. More important, it will allow us to determine the predation pressure of Oystercatchers on their tidal-flat invertebrates and the extent to which the harvestable prey are actually harvested. The data will be used to analyse whether the winter mortality in the oystercatcher population in our study area is related to the food supply and the intake rate.

Predicting prey choice, intake rate, biomass consumption and exploitable biomass

Our aim is to predict the optimal prey choice and the associated intake rate of the Oystercatchers, as well as the exploitable part of the biomass, for each sampling of the food supply in our study area. Optimal foraging theory (see e.g. Krebs & Kacelnik 1991) has proven a useful tool for achieving the first two goals and, as we will show, it can also help to achieve the third goal. There are three simplifications in our study. We ignore (1) spatial variation in prey density through averaging over larger areas, (2) feeding specializations among the birds, and (3) interference.

A common and convenient assumption of optimal foraging models is that animals attempt to maximize their intake rate of energy while feeding. A realistic model of intake rate should therefore take into account (1) the weight and associated energy gain E_i (J) from an item of prey type i, (2) the handling time h_i (s) of each prey of type i and (3) search times of different prey types, which can also be characterized by λ_i, the encounter rate (s^{-1}) with prey type i. The multi-species functional response equation, also known as the simple or 'classic' optimal prey choice model (Charnov 1976), is based upon these three variables. In the model, prey of different species and sizes are ranked by their profitability, i.e. the rate of energy gain during handling. The ranking may include prey characteristics like prey size, but also shell thickness and burying depth. From the rate at which prey of a given class are encountered during searching, which classes should or should not be taken to achieve the maximum rate of energy gain during feeding can then be calculated. For i prey types:

$$\frac{E}{T} = \frac{\Sigma \lambda_i E_i P_i}{1 + \Sigma \lambda_i h_i P_i}$$

where E is total energy intake (J) during observation time T (s) and P_i is the decision variable. P_i represents the probability that the predator takes a prey item of type i after it is encountered. When prey with a profitability below the critical threshold are encountered, it is more efficient to continue searching than to handle and eat those prey, i.e. $P_i = 1$ if $E/T < E_i/h_i$ and $P_i = 0$ if $E/T > E_i/h_i$ (Charnov 1976). The optimal P_i, i.e. the prey choice that maximizes intake rate of energy, can be found if the encounter rates λ_i are treated as fixed constants.

How then should we deal with spatial heterogeneity in the food supply and temporal variability in the searching behaviour of the bird? First, the prey species of the Oystercatcher usually occur in different patches within the tidal zone. For instance, the birds have to decide whether to go to a mussel bed to feed on Edible Mussels *Mytilus edulis* or to a mudflat to feed on the clam *Scrobicularia plana*. Second, even if Oystercatchers feed on a mudflat where two prey species, for instance Edible Cockles *Cerastoderma edule* and *Scrobicularia*, occur together, they may be forced to adapt their searching behaviour depending on which species they exploit. For instance, it is sufficient to bring the bill tip into contact with the mud surface to encounter *Cerastoderma* but the birds have to probe their full bill into the mud to find *Scrobicularia*, so searching for surface prey and deep-living prey is not easily compatible. For the same reason, Oystercatchers have to compromise if they search simultaneously for conspicuous and cryptic prey. They search slowly if they feed on prey hidden in the substrate, but speed up their walking rate if they feed on easy prey, such as Ragworms *Nereis diversicolor* that graze at the surface around their burrow (Ens *et al.* 1996a).

In the following we therefore assume as a first approximation that, with one exception, searching for prey species i implies a zero encounter rate with all other prey species. To find under these conditions the prey choice that maximizes intake rate, we first have to calculate the optimal prey selection within a prey species. This will yield a profitability threshold for each prey species and an associated intake rate. We then choose the highest one among these intake rates and identify this prey and the associated selection criteria as the optimal choice for that sampling date. As we will discuss when deriving parameter estimates, the one exception that we currently allow is where the bird can choose between *Scrobicularia* and the Baltic Tellin *Macoma balthica*, both of which live buried in the mud.

We find the harvestable biomass at any one time by extracting the biomass of all prey that cannot be harvested from the total biomass. First of all, prey are excluded that are unavailable, i.e. buried beyond reach of the Oystercatcher's bill. Second, for each prey species, we exclude all prey with a profitability below the minimal intake rate required for the birds to maintain energy balance.

The fraction of prey actually being exploited may be smaller than the harvestable fraction. Moribund Cockles found at the surface with gaping valves are highly profitable and extremely accessible and thus harvestable prey, but only a fraction of these prey can be consumed if they are all dying at the same moment. Moreover, for the sufficiently profitable prey, we can imagine that they are exploited until the density is so low that the minimal intake rate is reached. With a further decrease in density, the prey remain profitable and accessible, but the search time will become so long that the intake rate will drop below the acceptance level.

What should we take as the minimal intake rate for a given date? The available feeding time determines the minimum intake rate required for the birds to achieve the daily consumption. Oystercatchers need at thermoneutrality 36 g ash-free dry flesh weight (AFDW) per day (Zwarts *et al.* 1996c). If they could feed 24 h a day, their intake rate during feeding must be at least 0.42 mg s^{-1}. It must always be higher than this, because the birds need some time for other activities. Furthermore, their feeding areas in the tidal zone are exposed for only 4 to 6 h per low water period. This amounts to about 10 h a day, assuming that the birds also feed at night (Table 2.1 in Hulscher 1996). Therefore, an intake rate of at least 3.6 g AFDW h^{-1} or 1 mg AFDW s^{-1} is obligatory. The minimal intake rate may be a bit lower when the birds are able to extend the feeding period, or to catabolize their own energy stores. The latter gives only temporary relief, while extension of the feeding period is only locally possible, i.e. where birds can feed in grasslands at high tide. Futhermore, the energy requirements increase by 50% if the temperature drops from thermoneutrality (10 °C) to freezing point (Kersten & Piersma 1987). Therefore, the minimal intake rate will increase by 5% for every degree that the average daily temperature falls below the lower critical temperature of 10 °C.

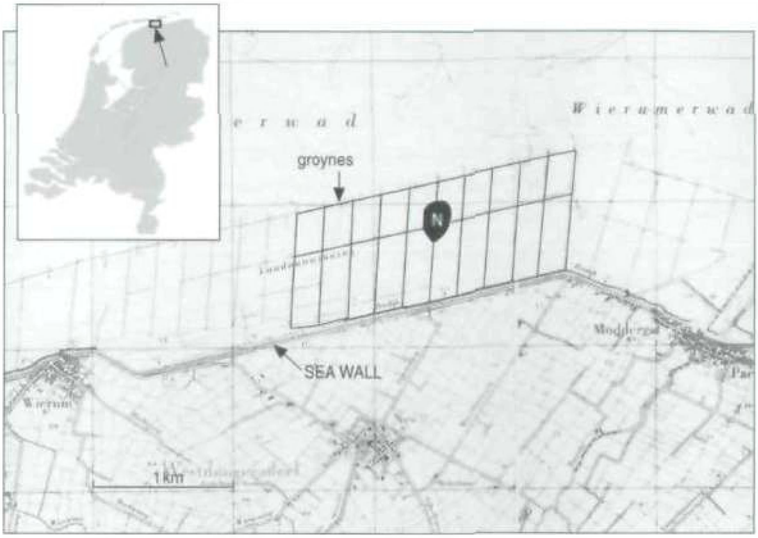


Fig. 1. Map of the study area along the Frisian coast. The food supply was measured in the Nes area (7.3 ha; site N). The birds were counted in the Nes area and in twenty counting areas around the Nes area, in total 100 ha of tidal flats. See also the map of Fig. 19.

Methods

Study area

The study was performed between 1977 and 1986 on intertidal flats along the Frisian coast in the Dutch Wadden Sea (Fig. 1). The study area was intersected by long rows of poles, these being the remnants of brushwood groynes made in the sixties to enhance sedimentation. The former groynes delimited the study area, in total 396 ha, and divided it into 53 subareas. The eastern subareas were situated around mean sea level and the clay fraction (< 2 µm) in the substrate was 2-5%. The more western subareas were at about 25 cm above mean sea level and the substrate was soft with a clay content of 10-20%. For a more extensive description of the study area, see Zwarts *et al.* (1992).

The Oystercatchers feeding in this area used several roosts in the immediate surroundings, but at high tide the majority were found in the Paesenserpolder or on the island Engelsmanplaat. In total, about 20 000 Oystercatchers foraged on the tidal flats between the Frisian coast and the island Engelsmanplaat. We individually marked more than 3000 birds with the aid of 3 colour rings per bird, of which one with bar-codes. Most were captured with mist and cannon nets on the tidal roost in the Paesenserpolder.

Measuring the food supply

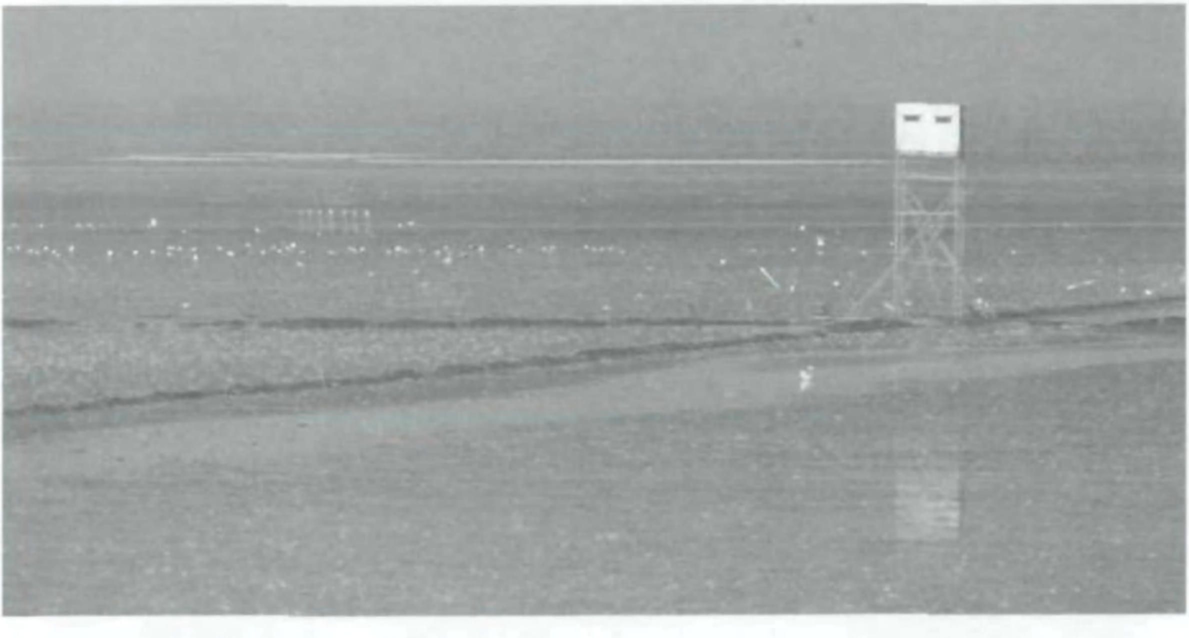
Sampling Samples of the macrozoobenthos inhabiting the mudflats were taken along 27 transects in August during four years (1977-1980). More detailed data were collected in the eastern part of the study area, where 146 plots of 0.1 ha were pegged out around two observation towers. One to four samples of the benthic fauna (179 cm^2) were taken nearly every month during seven years (1980-1986, and less frequently in 1978 and 1979) in the 73 sites around one of these towers, the Nes area, in earlier papers also indicated as site N. This series of measurements is used here. A comparison between the Nes data and the samples taken along the transects covering the entire area showed that the Nes samples were representative for the area as a whole, especially for the most eastern part of the area (Zwarts 1988). The measurements in the Nes area started in December 1977 but, to extend the series of measurements, we will use for August 1977 the samples of two of the 27 transects that crossed the Nes area.

Condition, growth and mortality The laboratory procedures used to determine the biomass of the benthic animals have been described in Zwarts (1991). The growth of the bivalves could sometimes be calculated directly from the length frequency distribution in the monthly samples, but this was usually impossible because two or even more year classes occurred together. The year classes were identified using the Bhattacharya method for separating cohorts (MPA module of the Compleat ELEFAN software package, version 1.0; Gayanilo *et al.* 1988). This technique made it possible to estimate the monthly mortality and growth in length for the separate cohorts.

Estimating prey production Using the relationships between size and flesh weight, determined for all sampling data, we also calculated for each cohort the fluctuation in the biomass of the average individual and for the cohort population as a whole. This allowed us to calculate the production per species, separately for the age classes. The production can be estimated by adding either the growth increments or the weight losses caused by size-dependent mortality (Crisp 1984). We estimated the production by calculation of the monthly weight loss since this made it possible to indicate to what degree the elimination of biomass due to prey mortality had been determined by the predation pressure of the Oystercatchers.

The elimination of the prey biomass is determined by the product of two terms: the mean weight of the prey averaged over two consecutive sampling dates and the decrease in the prey density between both sample dates. Both, prey weight and the numbers disappeared, were calculated separately per cohort and recalculated per month if the intervening period was longer than a month. The eliminated biomass per cohort was summed to arrive at the total monthly elimination of biomass per prey species. Since Oystercatchers do not take Cockles < 10 mm, *Macoma* < 11 mm and the Soft-shell Clam *Mya arenaria* < 17 mm (Zwarts *et al.* 1996a), the elimination of biomass belonging to the size classes ignored by Oystercatchers will be given separately, as well as for prey living out of reach of the bill, i.e. *Mya* living more than 6 cm below the surface (Zwarts & Wanink 1984).

Burying depth The burying depth of the bivalves was measured once or twice a month during seven years (1980-1986). The methods have been described by Zwarts & Wanink (1989). The combination of biomass samples and the depth measurements was used to describe the annual fluctuation in the biomass actually



View from the sea wall over the study area. The observation tower was built in the middle of the Nes area at the cross of two groynes.

accessible to Oystercatchers; see Zwarts & Wanink (1993) for a detailed description of the seasonal and annual variation in biomass and prey accessibility.

Human impact There was no human impact on the food supply in the study area. There was no dredging for Cockles within the study period and the few people digging for Lugworms *Arenicola marina* did not do so within the Nes area.

Counting and observing the birds

The Oystercatchers, and other bird species, were counted twice a month at low tide from the top of the sea wall which offered a splendid view over the whole area; in total 166 fortnightly counts were made between summer 1977 and autumn 1985. The birds were dispersed over the feeding area and were counted one by one. Counts of the birds feeding in the 73 0.1 ha plots in the Nes area were also often made from the observation tower, but since only a few of these counts were available for the winter months, the series of counts made from the sea wall will be used instead. For two reasons we took the bird counts from the eastern 100 ha (Fig. 1), and not from the entire area, as measure of the bird density. First, as already indicated, our measure of the food supply in the Nes area was more representative for the eastern part than for the entire area. Second, prey and size selection and intake rate were studied in Oystercatchers feeding around the towers in the eastern part of the study area. These data were collected during the first five years of observations (1977-1981) by Hulscher (1982 & unpubl.), Blomert *et al.* (1983), Hulsman (unpubl.), Zwarts (unpubl.) and Zwarts & Wanink (1984); see Zwarts *et al.* (1996b) for a summary. Only qualitative data on the prey selection are available during the latter five years (1982-1986).

Comparison of the low water counts in the 100 ha and the 7.3 ha around the Nes hide in the centre of this area showed that the Oystercatcher density in the Nes area as a whole was highly correlated ($r = 0.93$, $n = 35$) with the density measured on the same day in the 100 ha being, on average, 1.3 times higher. This difference was to be expected since the upper 1/4 of the 100 ha, situated along the dike, was hardly used when the tide was out. All bird numbers were therefore expressed as bird densities for the lower 3/4 of the study area, i.e. situated between 10 cm above and 20 cm below mean sea level. Despite the high correlation between bird densities on 100 and 7.3 ha, there was one period where the counts of 100 ha would highly overestimate the density on the 7.3 ha. In November 1979, most birds left the Nes area for some months but remained to feed on the lower shore within the 100 ha. Therefore, we used the bird densities measured in the Nes area for these months.

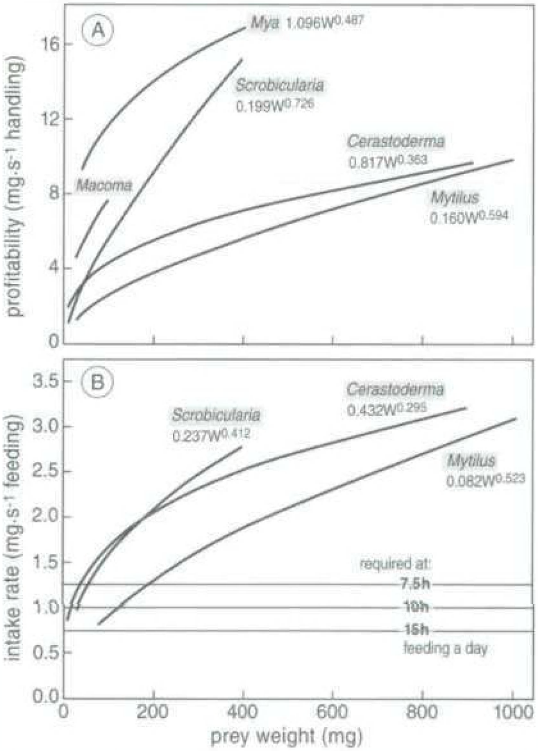


Fig. 2. **A.** Average profitability (mg s^{-1} handling) and **B.** average intake rate (mg s^{-1} feeding) as a function of average weight of the prey taken by Oystercatchers feeding on five different prey species. The profitabilities and intake rates are taken from Zwarts *et al.* (1996b). The minimal intake rate required to meet the energy requirements at thermoneutral conditions is indicated for the usual daily range in the available feeding time.

Estimating parameters of the prey choice model

For each prey species, we need to know the profitability of the various prey classes and their respective encounter rates. For profitability we can draw on a recent review (Zwarts *et al.* 1996b). The profitability is defined as mg ash-free dry weight (AFDW) s^{-1} handling and varies between 1 and 16 mg AFDW s^{-1} for the hard-shelled prey usually taken by Oystercatchers. In all prey species, the profitability increases with size (Fig. 2A, based on Table 2 in Zwarts *et al.* 1996b).

Oystercatchers feed only on middle-sized and large bivalves. Small size classes are ignored as being extremely unprofitable. The intake rate, defined as mg AFDW s^{-1} foraging varies between 0.5 and 3 mg AFDW s^{-1} and also increases with prey size (Fig. 2B, based on Figs. 12-14 in Zwarts *et al.* 1996b). This increase is a logical consequence of the positive relationship between profitability and prey weight (Zwarts *et al.* 1996b). Nonetheless, this cannot be the whole story, as the density of the prey also influences intake rate, through its effect on encounter rate. Thus, prey density must be included in the prediction of intake rate.

We describe below for each species, or combination of species, how we estimated encounter rates and intake rates, or, if we failed to estimate these, what alternative procedure we used to predict intake rate from prey characteristics.

Scrobicularia Assuming that Oystercatchers probe their bill at random in the mud when they search for buried bivalves, it is possible to predict the searching time from the prey density (Hulscher 1976, 1982). To make precise predictions on intake rate, it is necessary to divide the prey into different depth categories and to measure the effect of burying depth on handling as well as on searching time (Wanink & Zwarts 1985). One also needs to know the relationship between burying depth and prey weight since the accessible shallow-living bivalves may represent marginal prey compared to the prey of similar size living at larger depths (Zwarts & Wanink 1991). The encounter rate $\lambda = aD$, where a is the instantaneous rate of discovery ($m^2 s^{-1}$) and D ($n\ m^{-2}$) the density of the prey. The searching time is the inverse of the encounter rate , which is the product of three variables: (1) the time needed to thrust the bill a certain distance into the mud, (2) the number of probes that has to be made to encounter a prey and (3) the proportion of the searching time spent in probing. All three relationships were measured: (1) the relation between probing time (T, s) and probing depth (P, cm) was quantified using a high-speed film:

$T = \exp(0.39P - 2.49)$ (Wanink & Zwarts 1985);

(2) the encounter rate was derived from the prey density and the 'effective touch area', i.e. the surface area of the prey (S, cm^2) as a function of prey length (L, mm):

$S = 0.154\ L^{2.09}$ (Zwarts & Blomert 1992),

enlarged with the surface area of the bill tip (Hulscher 1982, Zwarts *et al.* 1996a: Table 2.1); (3) the probing time appeared to be a fixed proportion of the total searching time, 30% independent of the prey density of *Scrobicularia* (Wanink & Zwarts 1985).

Wanink & Zwarts (1985) offered a captive bird *Scrobicularia* 35-36 mm long, buried at different depths and predicted the intake rate, using the multispecies functional response equation (Charnov 1976). Extrapolation of this model to free-living birds was possible because the relationship between effective touch area and prey size has been quantified for different bivalve species (Zwarts & Blomert 1992), as well as the relationship between handling time and prey weight for the same prey species (Zwarts *et al.* 1996b). Based on this information, Wanink & Zwarts (1996b) have estimated the encounter rate of free-living Oystercatchers feeding on *Scrobicularia* using the six-year data base of the bimonthly depth measurements (Zwarts & Wanink 1989, 1993). The handling time (H, s) of *Scrobicularia* as a function of burying depth (B, cm) and prey length (L, mm) was based on the empirical relationship:

$H = (0.093\ L^{1.549} / 23.4) - (3.7B + 24.9)$

The flesh weight of all mm classes was known per cm depth class, so it was possible to calculate the intake rate under the assumption that Oystercatchers probe their bill at random into the mud. The calculation was repeated for birds probing 2, 3, ... 8 cm deep. If all prey were deeply buried, the birds would achieve the highest intake by probing as deeply as possible, but if many live close to the surface, the optimal depth selection could be attained by ignoring all deep-living *Scrobicularia*.

Macoma The intake rate of Oystercatchers feeding on

Macoma could be predicted in the same way as in *Scrobicularia*. However, whereas the relationships between handling time and burying depth and shell length were available for *Scrobicularia*, this must be estimated for *Macoma*. Our only clue was the relationship between handling time and prey weight for two periods where prey depth could be estimated, i.e. spring and late summer, when the animals lived 2 and 4 cm, on average, beneath the surface of the mud, respectively (Fig. 5 in Zwarts *et al.* 1996b). From that figure it could be concluded that prey weight correlated better with handling time than prey length, so that for practical reasons we used prey weight, instead of prey length to predict the handling time. To obtain the handling time of *Macoma* as function of prey weight (W, mg) for other burying depths, we performed linear interpolation, resulting in the following equation:

$$H = 0.231B \times 0.602W^{0.571} = 0.139B \times W^{0.571}$$

Since we know that Oystercatchers never take *Macoma* < 11 mm long (Hulscher 1982, Zwarts *et al.* 1996a), the calculations were based on the assumption that the birds took all *Macoma* ≥ 11 mm that they encountered.

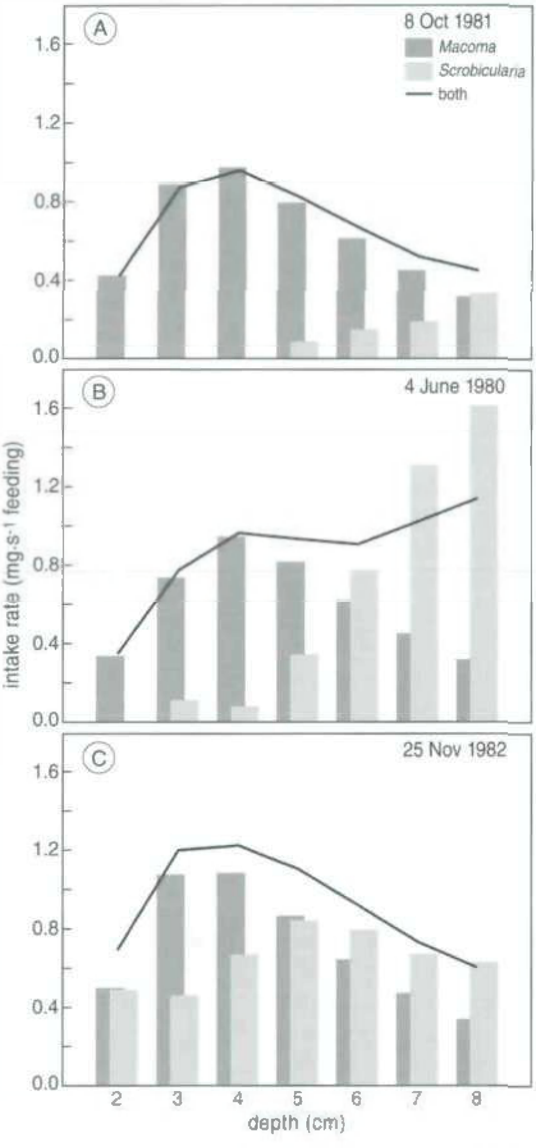


Fig. 3. Predicted intake rate (mg s^{-1} feeding) in free-living Oystercatchers on three different days when they had selected only *Scrobicularia* or *Macoma*, or taken both species, as a function of depth selection. The intake rate would have been maximized if the birds had selected only *Scrobicularia* on 4 June, only *Macoma* on 8 October and taken both species on 25 November. The optimal depth selection was also different.

Scrobicularia* + *Macoma *Scrobicularia* and *Macoma* occurred in the same habitat, reaching the highest density on the mid-shore and living buried in the substrate. Hence, Oystercatchers encountered both prey if they probed the mud with their bill. Assuming that Oystercatchers took all *Scrobicularia* and *Macoma* ≥ 11 mm, it was possible to calculate the intake rate for both species combined. As an example, Fig. 3 shows for three different days the predicted intake rate of Oystercatchers feeding either solely on *Scrobicularia* and *Macoma*, or on both species together.

On 8 October 1981, the birds should select *Macoma* from the upper 4 cm in order to maximize their intake rate (Fig. 3A). The birds would have to probe as deeply as possible were they to feed solely on *Scrobicularia*, but their intake rate would remain very low because only a small fraction of these prey would be accessible and none would be found in the upper 5 cm. If the birds were to feed on both species, they would be able to increase their intake rate if they probed deeply, but since a higher intake rate still could be reached by selecting only prey from the upper 4 cm, the prediction remained that only *Macoma* would be taken.

The second example shows that, on 4 June 1980,

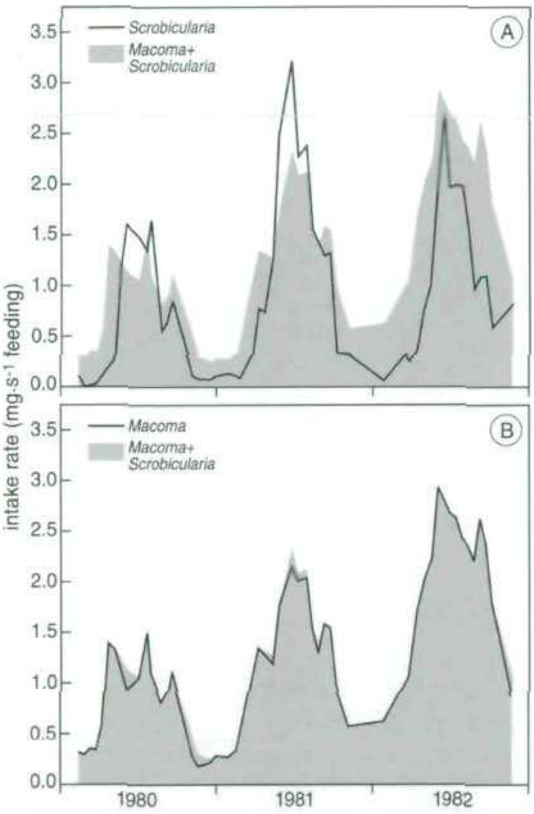


Fig. 4. Predicted intake rate in Oystercatchers feeding on **A.** *Scrobicularia*, **B.** *Macoma* compared to when an optimal mixture of both prey species is taken. The intake rates are calculated on the assumption that the birds performed optimal depth selections, as shown for three days in Fig. 3.

Oystercatchers feeding on *Macoma* would reach the highest intake rate if they took all prey from the upper 4 cm of the substrate and ignored all prey living more deeply (Fig. 3B). In contrast, if Oystercatchers restricted their diet to *Scrobicularia*, they would have to probe as deeply as possible and take all prey within reach of the bill. In the latter case, the intake rate would be higher than if only *Macoma* were taken. Hence, the prediction was that the birds would take *Scrobicularia*. The intake rate would decrease if the birds added *Macoma* to a diet of *Scrobicularia*, so for this day the prediction remained that only *Scrobicularia* would be selected.

On 25 November 1982, the highest intake rate could be achieved by selecting *Macoma* living in the upper 3 cm or *Scrobicularia* from the upper 5 cm (Fig. 3C). However, the birds would maximize their intake rate if they selected prey of both species from the upper 4 cm, in which case 85% of the biomass would consist of *Macoma*.

Calculations such as depicted for these three days (Fig. 3) were repeated for all 88 days of sampling. There were 53 sampling days out of a total of 88 during which both prey species were common. In this period, Oystercatchers rarely raised their intake rate by taking both species (Fig. 4). They even lowered their intake rate on seven days by adding *Macoma* to a diet of *Scrobicularia* (Fig. 4A); in contrast, it hardly affected their intake rate when added *Scrobicularia* to a diet of *Macoma* (Fig. 4B). Since the intake rates predicted for birds feeding on *Macoma* or on both species did not differ much, we decided to treat these two prey species as a single species for calculations on intake rate and prey choice.

Mya In principle, a similar depth-related model might be developed to predict the intake rate for Oystercatchers feeding on *Mya*. However, in this prey, the siphon holes are sometimes visible at the surface, by which they may be located by sight. This made a model based on randomly probing the mud less appropriate. *Mya* are only harvestable by Oystercatcher during a short period of their lives, being too small to be profitable before the second growing season and buried too deeply to be accessible after the third (Zwarts & Wanink 1984). Hence, the prey was harvestable by Oystercatchers during only 2 of the 10 years of observation. The intake rate was actually measured in one of these two winter half years.

The birds achieved an intake rate of 1.86 mg s^{-1} in October 1980 (correcting for the 30% overestimation of prey weight by Zwarts & Wanink 1984; see Zwarts *et al.* 1996c). We know that the birds continued to feed on *Mya* in the following months but did not measure the intake rate. The body condition of the prey decreased gradually by 20% from November to February, but the decline in intake rate would have been larger because the Oystercatchers depleted their food. The birds eliminated 80% of all the *Mya*, and 90% of the shallow, most profitable prey (Fig. 5). Consequently, the search time must have increased during

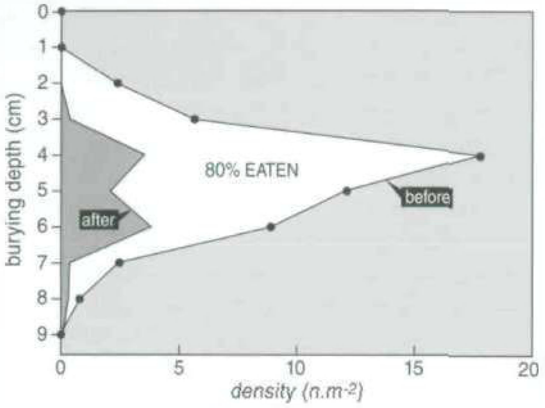


Fig. 5. Depth distribution of second year *Mya* in winter 1980/81, before and after Oystercatchers had removed 80% of the prey, between September (n = 82) and February (n = 40), to show that Oystercatchers took the most shallow prey.

these months of heavy exploitation. The decrease in intake rate could be estimated, because the *Mya*-eating Oystercatchers in autumn foraged in 73 plots where the prey density was known. The feeding rate was significantly correlated with prey density (r = 0.27, n = 80 observation periods of 10 min, p = 0.01) and decreased from 4 clams min^{-1} at 100-250 clams m^{-2} to 2.2 clams min^{-1} at 50 clams m^{-2}. When the linear regression was extrapolated downwards to below 50 clams m^{-2}, the feeding rates must be too high. Therefore, we used a third-degree polynomial to describe the sigmoidal function of feeding rate (F, *Mya* min^{-1}) against prey density (D, *Mya* m^{-2}):

$$F = -0.21 + 0.66D - 0.00033D^2 + 0.00000056D^3$$

The density of the harvestable clams was reduced to only 15 clams m^{-2} at the end of the winter. Hence, by extrapolation downwards the intake rate must have dropped from 1.86 mg s^{-1} in October to the extremely low level of about 0.30 mg s^{-1} some months later.

The intake rate was unknown for the *Mya*-eating Oystercatcher in winter 1977/78. Although the prey density was higher than in early autumn 1980, we estimated that the intake rate was 1.86 mg s^{-1} as in October 1980.

Cockle Cockles live close to the surface. Therefore it was sufficient to know the density and frequency distribution of the size classes to calculate the encounter rate with the prey, using the random touch model of Hulscher (1976). However, as Hulscher (1976) also showed, in daylight Oystercatchers hunt visually for Cockles. Moreover, he could show that the birds became more selective at high prey densities by ignoring the closed bivalves that could not be opened in a single stabbing movement. That is why random touch models could not be used to predict the intake rate of cockle-feeding Oystercatchers. Instead, the intake rate was predicted from the empirical relationship between intake rate (I, mg s^{-1}), prey density (D, n m^{-2}) and prey weight (W, mg AFDW). The function was based on a multiple regression as a function of both, performed on the 38 available studies (Fig. 16 in Zwarts *et al.* 1996b):

$$I = \exp(0.476W + 0.238D - 0.0124D^2 - 2.727)$$

Sometimes the Oystercatchers could feed on Cockles that had recently died, e.g. due to frost bite after a cold spell. In these circumstances the birds simply extracted the flesh from the gaping valves and achieved intake rates well exceeding 3 mg s^{-1} (Hulscher & Zwarts unpubl.). For sampling dates where this happened, we used 3 mg s^{-1} as an estimate for intake rate on adult Cockles, irrespective of density and size.

Mussel The Oystercatchers in our study area used the stabbing technique to open Mussels. The slightly open Mussels were located by eye as well as by touch. In both cases, we needed to know the fraction of open Mussels before the encounter rate with accessible prey could be estimated. These data were lacking, but we knew that the intake rate strongly depended on the weight of the Mussels taken (Fig. 2B). Hence, we used the curve from Fig. 2B to estimate the intake rate from the flesh weight of Mussels.

Ragworm, Lugworm and Shore Crab There were potentially three alternative non-bivalve prey species in the study area: the Ragworm, the Lugworm and the Shore Crab *Carcinus maenas*. Of these three species, only Ragworms were common in the study area, but rarely taken by Oystercatchers. Their biomass varied between 2 and 14 g m^{-2} (Zwarts & Wanink 1993: Fig. 4F). The worms were large, 10 cm and longer (Zwarts & Esselink 1989: Fig. 9), and thus large enough to be highly profitable (Zwarts *et al.* 1996b: Fig. 8). This was surely the case in spring and early summer when worms fed at the surface (Esselink & Zwarts 1989). Indeed, Bunskoeke *et al.* (1996) found that the majority of the Oystercatchers took Ragworms at this time of the year on the mudflats near Schiermonnikoog, only 10 km from the study area, and this was also the case on the mudflats 2 km eastern of the Nes area (Hulscher & Zwarts unpubl.). Because Ragworms were obviously a summer prey taken by a few specialists among the small number of Oystercatcher that were present, we excluded them from the analysis.

Lugworms were rare in our study area, because the substrate was too soft. Their contribution to the prey biomass was only 1 to 2 g m^{-2} in most years, although they occurred with 4 to 11 g m^{-2} in 1977-1979 (Zwarts & Wanink 1993: Fig. 4G). Since we never saw an Oystercatcher take this prey species in the study area, there is no reason to take it into account.

First year Shore Crabs were very common on the tidal flats, but Oystercatchers ignored them. Older crabs were rare in our study area. Since only a few specimens were observed to be taken in early summer, also this species could safely be ignored in the calculation of the total food supply.

Estimating biomass consumption

We assumed that the Oystercatchers counted during low tide in the study area obtained all their food there, i.e. they did not consume appreciable amounts of food elsewhere either earlier or later in the tidal cycle, and that if night feeding occurred, the distribution over the area did not differ from those by day. The daily consumption varies between 36 g in summer and 40-50 g in winter and amounts, on an annual basis, to 39.4 g. The predation pressure by the other shorebirds was estimated from the relationship between body weight and basal metabolic rate (BMR), according to Kersten & Piersma (1987), and further based on the general assumptions (e.g. Smit 1984b, Zwarts *et al.* 1990a & b) that the daily energy expenditure is equivalent to 2.2 x BMR, the energy content of flesh is 22 kJ g^{-1} and 85% of the ingested energy is digested.

To calculate for each period how much biomass of a particular prey was removed by the Oystercatchers, it

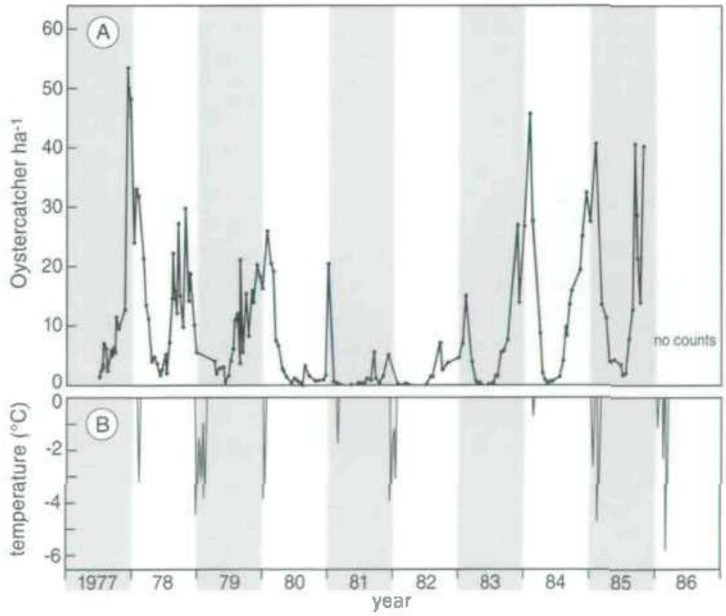


Fig. 6. A. Annual and seasonal variation in Oystercatcher density (birds ha^{-1} at low water); **B.** average air temperature per ten days, if below 0 °C.

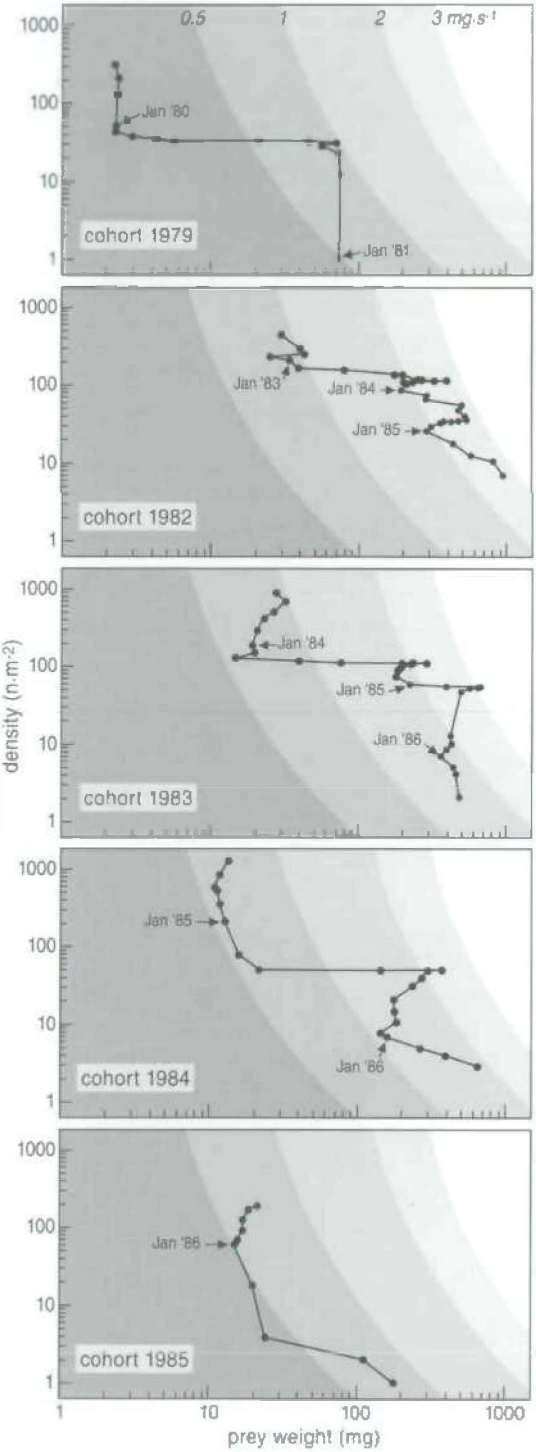


Fig. 7. *Cerastoderma.* Plot of density (n m^{-2}) against average flesh weight (mg AFDW) for five different cohorts during one to three years. The lines connect the course of the change in density and average prey weight for as long as the cohort existed; based on monthly samples in the Nes area, from August in the year of settlement onwards. In each winter there was a decrease of the prey weight. Grey fields indicate the predicted intake rate of Oystercatchers as the combined function of prey weight and prey density (based on Fig. 16 in Zwarts *et al.* 1996b).

was assumed that all Oystercatchers fed on the prey predicted to yield the highest intake rate. Except for *Macoma* and *Scrobicularia*, we assumed that the birds could prey on only one prey species at a time. As shown before, the actual choice between these two species did not matter much for the predicted intake rate, so that it was hard to reliably predict the optimal mix. Fortunately, *Scrobicularia* was absent during the last four years. For the first four years, it was assumed that both prey were taken in an equal amount of biomass.

Results

Bird density

The Oystercatcher was the most common shorebird in the study area with 8.4 birds ha^{-1}, averaged over the entire year, but there was a large variation in the density during $8^1/_2$ years of counting (Fig. 6A). Hardly any Oystercatcher fed in the area in 1981 and 1982. Nonetheless, the peak numbers were present each year in mid-winter and the lowest numbers occurred between mid-March and mid-August. No counts were made when ice covered the mudflats (Fig. 6B), but usually no Oystercatchers fed in the study area during such periods, since most birds left the area altogether and those remaining stayed on the roosts. If birds fed on the mudflats during frost periods, they did so outside the study area on the water's edge near the low water mark, the only place where the substrate was not frozen.

Oystercatchers and Cockles

The intake rate of Oystercatchers depended closely on the weight of the prey taken and, to a lesser degree, on the density in which these prey occurred. Figure 7 depicts how the intake rate was determined by both variables, according to the multiple regression equation given in 'Methods'. It also shows for five important cohorts the relationship between the increase of the flesh weight of the average Cockle and the concurrent decline in the density. After their settlement in summer, Cockles occurred at densities of many thousands per m^2. There was a high mortality among these spat during their first summer, as a result of which the density was usually reduced to some hundreds per m^2 by September.

The change in the density and the average body weight in the five cohorts was based on monthly samples, and shown from August in the first year onwards (Fig. 7). The decrease of weight in winter was caused by the declining body condition. Obviously first year Cockles could never provide Oystercatchers with an intake rate exceeding the acceptance level of 1 mg s^{-1}.

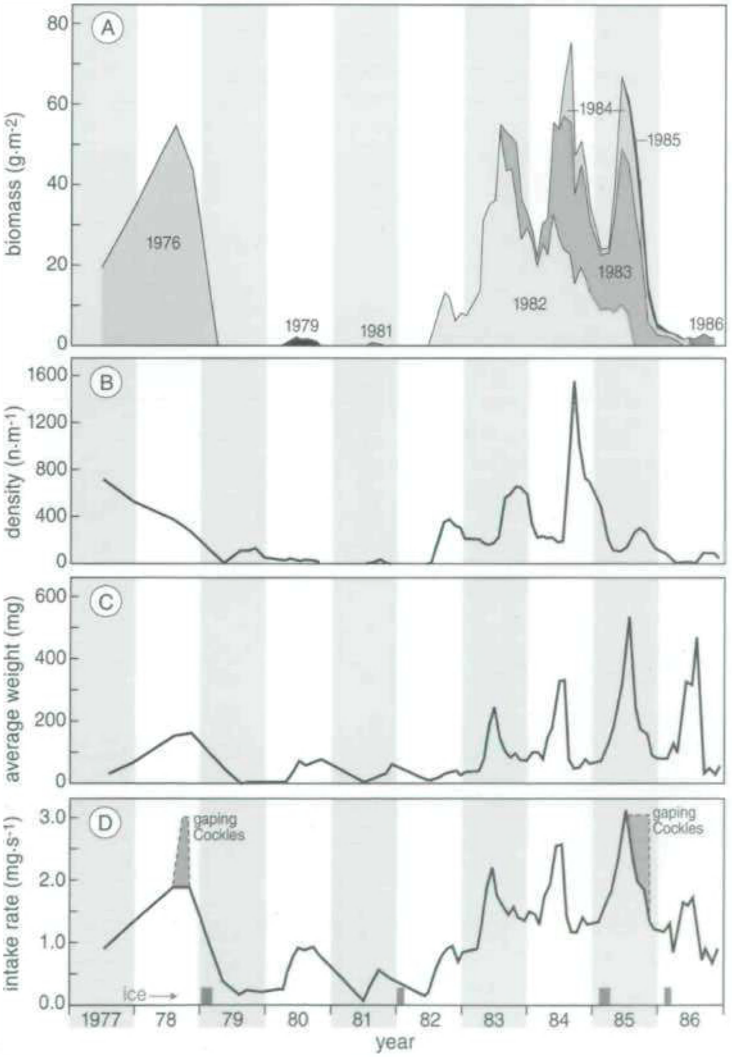


Fig. 8. *Cerastoderma.* **A.** Biomass (g m^{-2}), **B.** density (n m^{-2}), **C.** average weight (mg AFDW) and **D.** predicted highest intake rate (mg s^{-1} feeding) of Oystercatchers feeding on Cockles during 10 years. The intake rate increased to 3 mg s^{-1} when the birds could feed on dying Cockles with gaping valves.

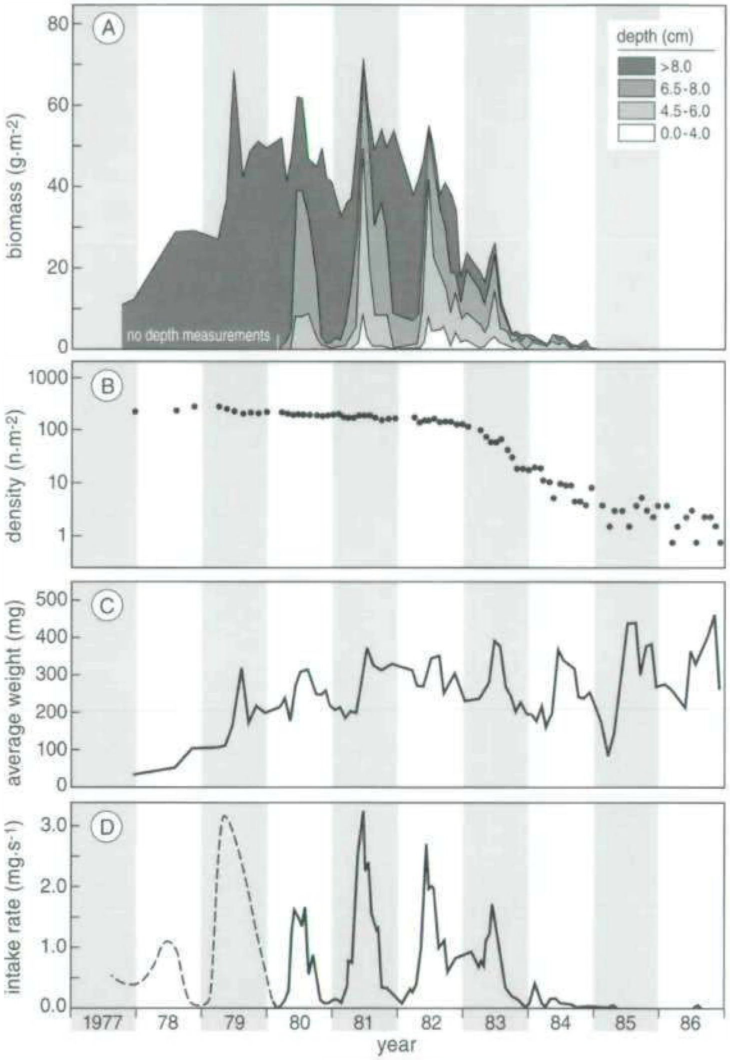


Fig. 9. *Scrobicularia*. **A.** Biomass (g m^{-2}), **B.** density (n m^{-2}), **C.** average weight (mg AFDW) and **D.** predicted highest intake rate (mg s^{-1} feeding) of Oystercatchers solely feeding on this prey during 10 years. The biomass from 1980 onwards is given separately per depth class. The predicted intake rate before 1980 is based on the assumption that the burying depth of the prey did not deviate from the average seasonal depth variation recorded in 1980-1982.

Although the prey numbers steadily decreased later, the intake rate usually increased to 2 mg s^{-1} in the second year and, if the cohort still existed, to about 3 mg s^{-1} in the third.

Spatfall of Cockles did not occur each year. In our study area, there was settlement of Cockles in seven of the eleven summers, of which only three were substantial. Figure 8A shows the course of the biomass, given separately per year class. Each cohort reached its maximal biomass in the second summer. This implied that the decrease in the population after that (Fig. 8B) was larger than the increase of the average body weight (Fig. 8C). The intake rate was the combined function of both variables and therefore could be predicted for the entire observation period (Fig. 8D). The Oystercatchers encountered many dying Cockles after frost periods in January-February 1979, 1985 and 1986, and there was also a mass mortality in October 1978 and October/November 1985. As explained in the methods, Oystercatchers achieved very high intake rates under these circumstances.

Oystercatchers and *Scrobicularia*

There was no spatfall of *Scrobicularia* during the years of observation, but the course of the year class born in 1976, the year before the observations started, could be followed completely (Fig. 9). The average prey size gradually increased from 22 mm after their second

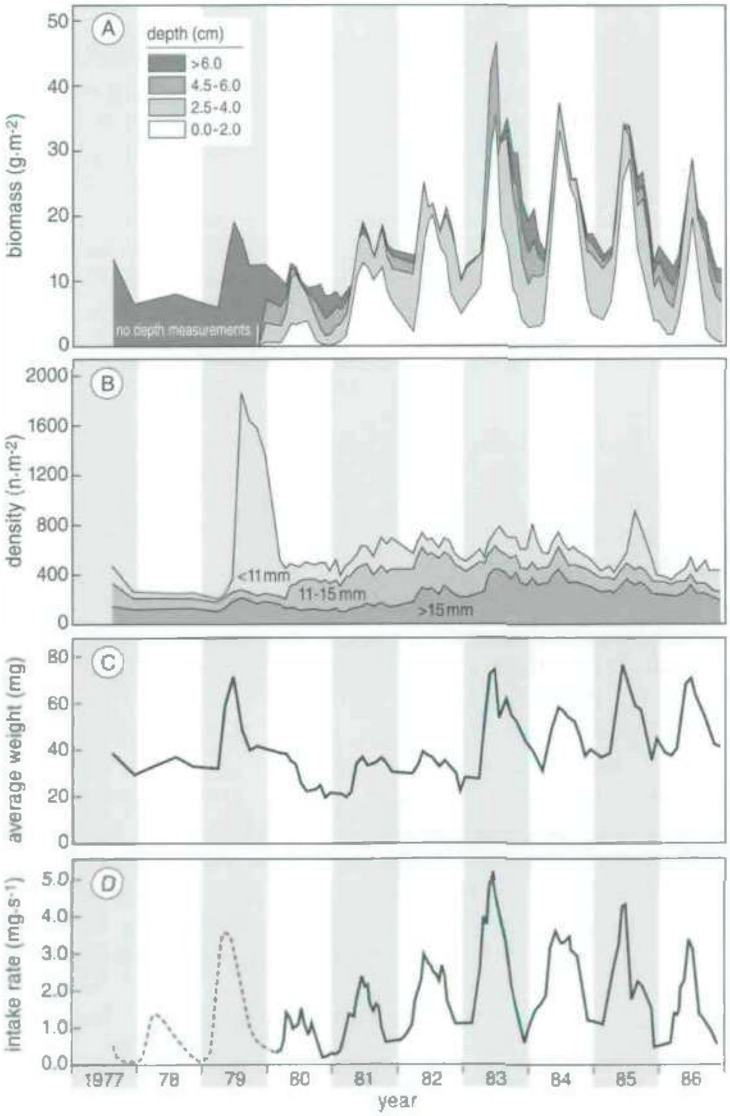


Fig. 10. *Macoma*. **A.** Biomass (g m^{-2}), **B.** density (n m^{-2}), **C.** average weight (mg AFDW of specimens > 15 mm) and **D.** predicted highest intake rate (mg s^{-1} feeding) of Oystercatchers solely feeding on this prey during 10 years. The biomass from 1980 onwards is given separately per depth class. The predicted intake rate before 1980 is based on the assumption that the burying depth of the prey did not deviate from the average seasonal depth variation recorded in 1980-1986.

growing season in 1977 to 35 mm in 1979. From then on the length increment was 1 mm per year. Over the same period, the body weight increased from 50 mg in 1977 to about 300 mg from 1981 onwards (Fig. 9C). The seasonal variation in the body weight was large, however, being in March 40% below the level reached nine months before in June (Fig. 9C; see also Fig. 8 in Zwarts 1991). There was a rather low mortality between 1977 and 1982, but the population collapsed in 1983 when the animals were seven years old (Fig. 9B). In the three years before, the biomass varied seasonally between 40 and 60 g m^{-2} (Fig. 9A). However, the seasonal variation in biomass accessible to Oystercatchers was much larger, between 0 and 60 g m^{-2}, because *Scrobicularia* lived in winter out of reach of the bill, except during the winter of 1982/1983 (Fig. 9A).

The predicted intake rate of Oystercatchers feeding on *Scrobicularia* depended mainly on the burying depth of their prey (Fig. 9D), being high in June when the burying depth was minimal and close to zero in winter when the majority of the prey lived out of reach of the bill. Again, the exception was the winter 1982/1983 when the intake rate was predicted to have been 0.8 mg s^{-1}. The intake rate before 1980 was estimated by assuming that the seasonal variation in burying depth did not deviate from the average depth in 1980-1982. The high intake rate in 1979 was due to the very good prey condition of the individual *Scrobicularia* (Fig. 9C). *Scrobicularia* were still small before the growing season of 1979 (Fig. 9C), which explains the low intake rate in 1978. Although they were still smaller, and thus less profitable, in 1977 and 1978, this was compensated by a higher fraction of the prey being accessible. Whereas *Scrobicularia* > 25 mm buried in winter out of reach of the Oystercatcher's bill, specimens < 25 mm remained accessible (Zwarts & Wanink 1989), and were indeed taken by Oystercatchers in winter (Habekotté 1987).

Oystercatchers and *Macoma*

There was spatfall of *Macoma* during six of the eleven years, but only the 1979 recruitment was extremely large (Fig. 10B). Oystercatchers always ignore *Macoma* < 11 mm (Hulscher 1982) and take above this lower size limit relatively much more of the largest size classes (Zwarts *et al.* 1996a). *Macoma* > 15 mm were rare between 1977 and 1982, but 2-3 times more common in 1983-1985 (Fig. 10B). *Macoma* grew slowly. The year class 1979 measured 6 mm after one growing season, reached the length of 12 mm in 1980, after which the growth in length was 1 mm per year (Zwarts *et al.* 1992). The first heavy spatfall after 1979 took place in 1985. In the years between, the population density remained remarkably stable, which would suggest there was no mortality. However, a closer look on Fig. 10B shows there was a seasonal variation in the numbers. The population increased each year in March-May and decreased over the rest of the year. The increase in the Nes area in early spring must have been due to a change in distribution pattern of *Macoma* by which animals living further upshore resettled in the Nes area, such as has been documented by Beukema (1993b) elsewhere in the Wadden Sea. Careful inspection of the monthly size-frequency distribution revealed that the immigrating animals were small compared to those from the Nes area. This difference was to be expected since growth is retarded on high-level mudflats (Wanink & Zwarts 1993). The immigrating specimens were each year larger than in the preceeding year, which suggests that the immigration was of clams of the strong year class 1979 and thus the migration from high to low flats continued over several years.

The biomass varied seasonally (Fig. 10A). This was mainly due to the variation in the average weight of the larger prey (Fig. 10C; see also Fig. 8 in Zwarts 1991). Clearly, the winter would be a very difficult period for Oystercatchers if they were to depend solely on *Macoma*. Not only was the body condition of the prey 40% below the summer level, but the prey also had to be located at a larger depth (Fig. 10A). Consequently, the predicted intake rate was much lower in winter than in summer (Fig. 10D). Since no depth measurements were made before 1980, the predicted intake rate could not be calculated, but on the assumption that the seasonal variation in burying depth did not deviate from average, the intake could be estimated. The intake rate was expected to have been low in the first years of observation due to the low density of large *Macoma* (Fig. 10B); the exception was in the summer of 1979 when the bivalves had an exceptionally good body condition (Fig. 10C; Zwarts 1991: Fig. 8).

Oystercatchers and *Mya*

There was recruitment of *Mya* in 1976 and in 1979 but not in the other nine years. The relationship between density and prey weight is shown for both cohorts in Fig. 11. Oystercatchers did not feed on *Mya* < 17 mm, and thus ignored prey containing less than 10-15 mg. Hence, the decline in the population during the first year of life was not due to Oystercatcher predation.

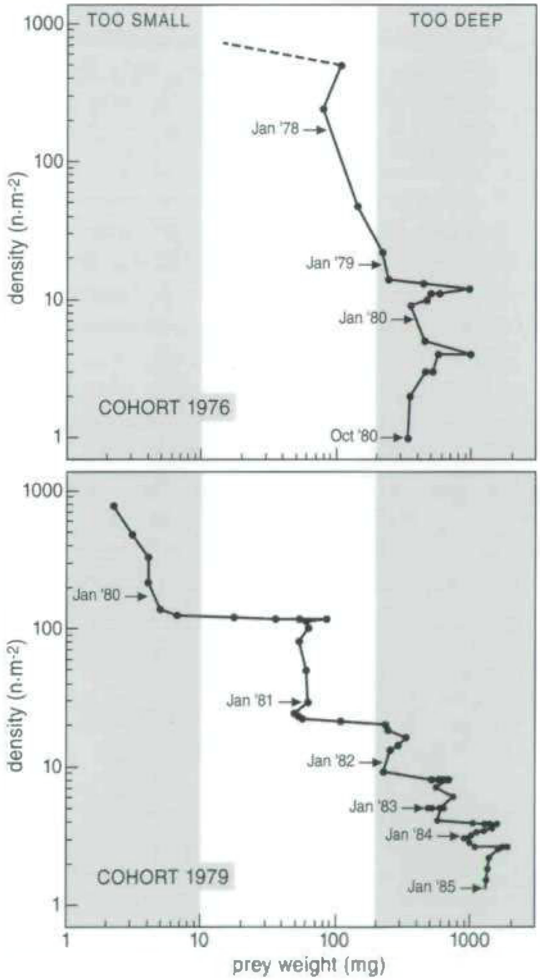


Fig. 11. Density of *Mya* belonging to two different cohorts as a function of flesh weight during four years. The lines connect the course of the change in the density and average prey weight as long as the cohort existed; based on monthly samples in the Nes area. In each winter there was a decrease of the prey weight due to a decline in the body condition. Prey < 10 mg are too small to be harvested by Oystercatchers, whereas prey > 200 mg live too deeply buried to be accessible.

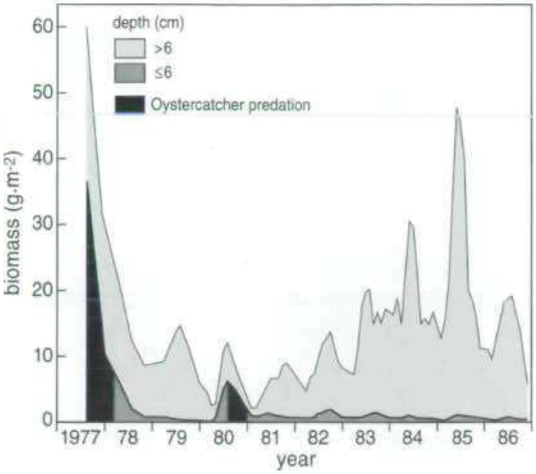


Fig. 12. *Mya*. Total biomass and biomass of the specimens living in the upper 6 cm of the substrate (g m^{-2}) during 10 years. Periods during which Oystercatchers heavily exploit this food resource are indicated.

During the second year, however, Oystercatchers exerted a heavy predation pressure on the remainder. After the next growing season, *Mya* measured 45 mm and weighed 700 to 1000 mg. At this size, they all lived out of reach of the Oystercatcher's bill (Zwarts & Wanink 1984, 1993).

There was a large annual and seasonal variation in the total biomass of *Mya* (Fig. 12). The year-to-year variation was still larger for the biomass accessible to Oystercatchers (Fig. 12). In fact, only in two years were Oystercatchers able to feed on this prey. From the observations in October 1980, we estimated the intake rate that the birds achieved (see 'Methods'). The Oystercatchers also foraged on *Mya* in the winter of 1977/78, when they took prey of about the same size as in autumn 1980 but the prey density was higher. Since the intake rate was not measured, we assumed that it did not differ from that three years later.

Oystercatchers and Mussels

Mussels might have been an alternative prey for Oystercatchers in 1985 and 1986, when the biomass of this prey reached a level of 10 g m^{-2} (Zwarts & Wanink 1993: Fig. 4E). In both years, the population consisted of spat. There was a huge mortality: 99% of the population disappeared in the first year of life (Fig. 13) by which time the survivors had attained 30 to 60 mg AFDW. It is unlikely that Oystercatchers will take first year Mussels. Even second year Mussels provide a rather low intake rate. Hence, in our study period, the Mussels did not reach a weight sufficient to make them a harvestable prey for Oystercatchers (Goss-Custard *et al*. 1996c).

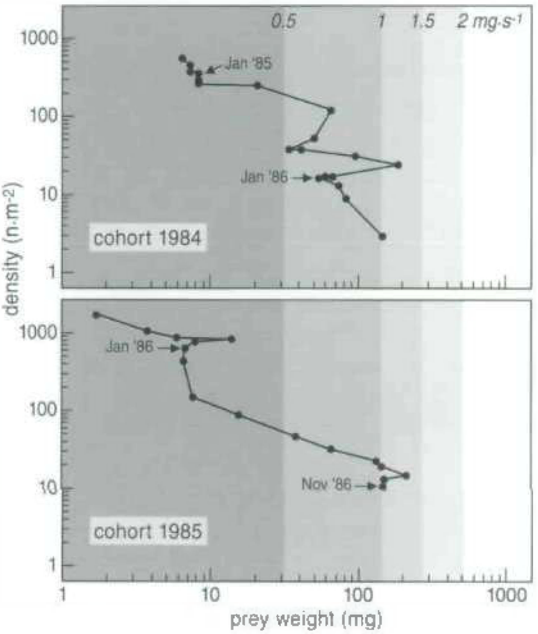


Fig. 13. *Mytilus*. Density of Mussels belonging to two different cohorts as a function of flesh weight during two years. The lines connect the course of the change in density and average prey weight as long as the cohort existed; based on monthly samples in the Nes area, from October or August in the year of settlement, 1984 and 1985 respectively, onwards. In each winter there was a decrease of the prey weight due to a decline in the body condition.

Did prey selection conform to prediction?

The previous sections predicted the highest possible intake for birds feeding on Cockles (Fig. 8D), *Scrobicularia* (Fig. 9D), *Macoma* (Fig. 10D), *Scrobicularia* + *Macoma* (Fig. 4), *Mya* (see text) and Mussels (Fig. 13). If birds maximized their intake rate, we would expect that they selected the prey species that delivered the highest intake rate. The predicted highest intake rate varied between 0.2 and 5 mg s^{-1} (Fig. 14). To achieve this intake rate, the birds had to change their prey choice as indicated in Fig. 14. Mussels should never be taken in the study area. *Scrobicularia* and *Macoma* were predicted to be the dominant food resources in summer, whereas Oystercatchers were expected to take *Mya* and Cockles predominantly in winter. Did the birds behave as predicted in Fig. 14? There were four periods for which this could be checked.

(1) It was predicted that the birds should take *Mya*

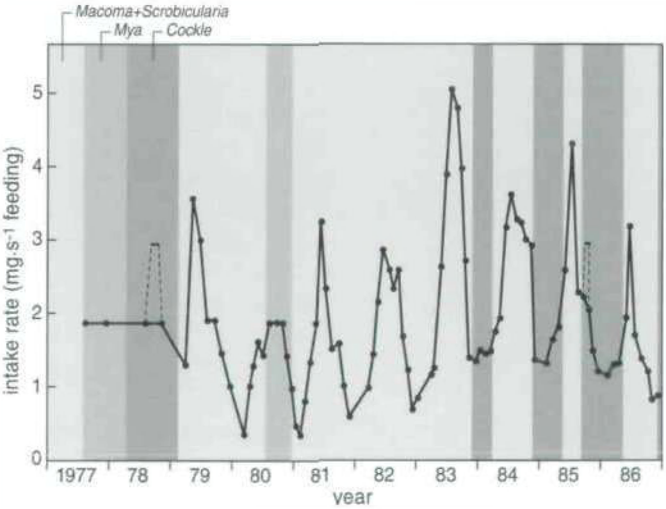


Fig. 14. Predicted intake rate when the food supply consists of Cockles, *Scrobicularia*, *Macoma*, *Mya* and Mussels, assuming that the birds take the prey providing the highest intake rate; based on Figs. 8D, 9D, 10D and 13; for *Mya* see text. The predicted prey selection is indicated. Mussels should never be selected.

in the winter of 1977/78, which the Oystercatchers were indeed observed to do (Zwarts & Wanink 1984). The low mortality rates of Cockles (Fig. 8B), *Scrobicularia* (Fig. 9B) and *Macoma* (Fig. 10B) also suggested that these alternative prey were either not, or hardly ever, taken.

(2) After the growing season of 1978, *Mya* lived beyond the reach of Oystercatchers and the birds were expected to feed on Cockles. Extensive observations of Hulsman (unpubl.) between March and November 1978 showed that the Oystercatchers did indeed take Cockles. The birds achieved an intake rate of 1.49 mg s^{-1} (Zwarts *et al.* 1996b), which was close to prediction.

(3) There was a mass mortality of the Cockles in late autumn 1978 and none was still alive after the severe winter of 1978/79. Therefore, only *Scrobicularia* and *Macoma* were left as prey. Since the depth distribution was not measured, the estimations of the predicted intake rate are rough. Oystercatchers observed in March 1979 fed on *Scrobicularia*, even though *Macoma* was calculated to yield a higher intake rate. They took small specimens (29 mm long weighing only 94 mg) which they took from great depths at a low intake rate of 1.29 mg s^{-1} (Zwarts *et al.* 1996b). The birds took in May mainly *Macoma*, achieving a rather high intake rate of 2.09 mg s^{-1} (Hulscher 1982; Zwarts *et al.* 1996b). The prey selection and intake rate was studied in detail between July and October 1979 by Blomert *et al.* (1983). In July, the birds took *Scrobicularia* and *Macoma*, but later in the season the proportion of *Scrobicularia* increased; again this was against prediction that they should have switched increasingly to *Macoma*. The intake rate of birds feeding on both prey combined, was 1.84 and 1.92 mg s^{-1} in July and August, respectively and decreased to 1.54 in September and 1.02 mg s^{-1} in October. The last data were collected on the few birds that remained to feed around the tower, since the majority of the birds moved 0.5 km to the NE, just outside the study area, where they started to feed on small Cockles some months old. There had also been some cockle spatfall in the Nes area (Fig. 8A), but the Cockles had grown larger at the lower-level and less muddy tidal flats which the birds started to exploit: the Cockles there were 10 mm, instead of 5 mm such as in the Nes area (Wanink & Zwarts 1993). However, even *Cerastoderma* of 10 mm delivered an extremely low intake rate (Fig. 7), so it is certain that 1979/1980 was a very meagre period for the Oystercatchers remaining in the study area. Summarizing, the 1979 measurements of the intake rate agreed with the predictions: the intake rate was low in late winter, high in summer and decreasing in autumn. In contrast, predicting whether the birds should select either *Macoma* or *Scrobicularia* proved impossible, providing further arguments in favour of lumping these two prey species.

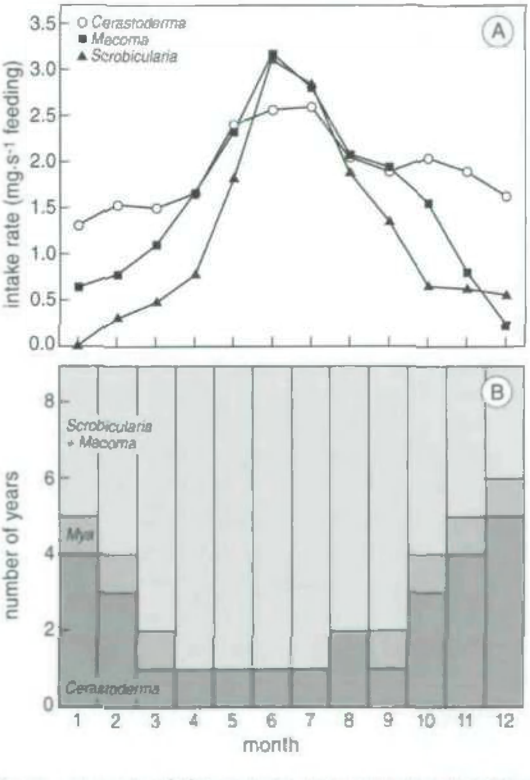


Fig. 15. Seasonal variation in **A.** the predicted intake rate of Oystercatchers feeding on Cockles, *Scrobicularia* or *Macoma* averaged over the years when the prey were present and **B.** the predicted diet during 9 years (from data shown in Fig. 14).

(4) A year later, in the autumn of 1980, the Oystercatchers preyed upon *Mya* (Zwarts & Wanink 1984) as predicted.

In conclusion, when we lump *Scrobicularia* and *Macoma*, all measurements on intake rate and prey selection were in agreement with the predictions (Fig. 14).

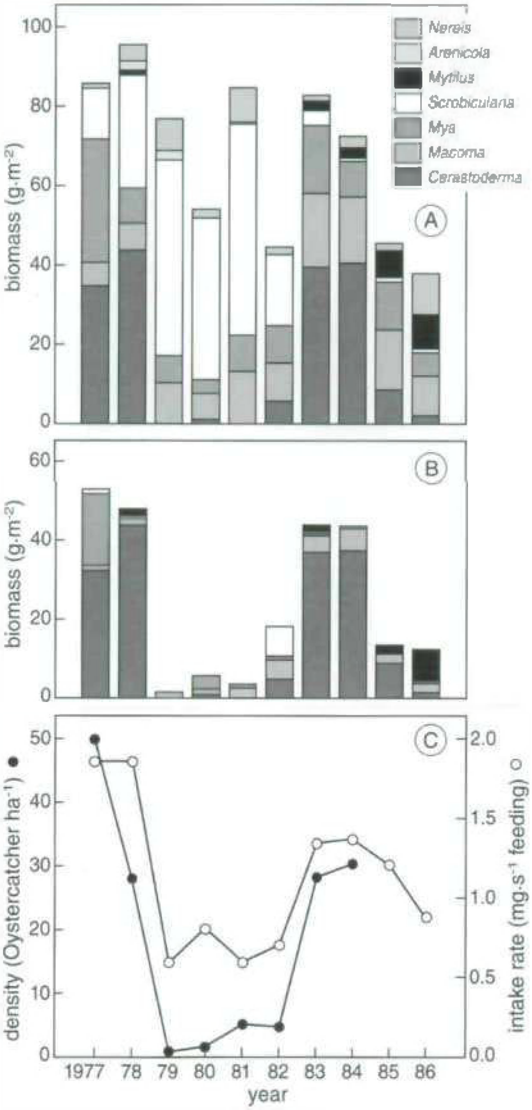


Fig. 16. Variation in **A.** total biomass, **B.** harvestable biomass, **C.** the average bird density and predicted intake rate in December. Harvestable biomass is defined as the summed biomass, excluding Cockles < 10 mm long, *Scrobicularia* < 13 mm long or living > 6 cm deep, *Macoma* < 11 mm long or living > 4 cm deep, *Mya* < 17 mm or living > 6 cm deep, and Mussels < 25 mm. Original data are given in Figs. 8A, 9A, 10A and 12 for biomass values, Fig. 14 for predicted intake rates and Fig. 6A for bird densities; no bird counts are available for December 1985 and 1986.

Seasonal variation in intake rate and prey selection

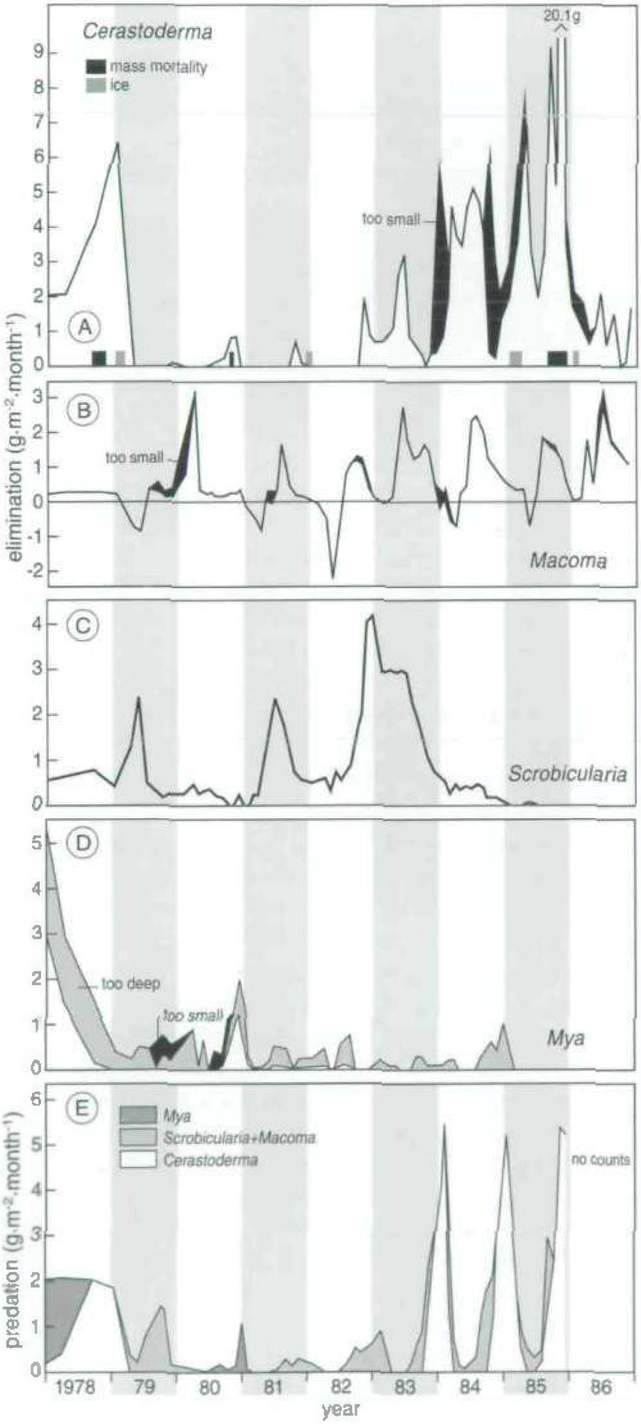
In all prey species there was a seasonal variation in the predicted intake rate, particularly in birds feeding on *Scrobicularia* (Fig. 9D) or *Macoma* (Fig. 10D). The intake rate of cockle-eating Oystercatchers was also predicted to be higher in summer than in winter (Fig. 8D), but the seasonal variation was not as large as in the two deep-living bivalve species (Fig. 15A). The explanation for this difference was that the seasonal variation in burying depth of the deep-living bivalves made them very unattractive to feed on in winter, because the majority of prey were inaccessible to the probing bird, and if the prey were accessible, they were hardly profitable (Zwarts *et al.* 1996b). In contrast, Cockles remained living at, or just beneath, the surface for the entire year, so that the accessible fraction did not vary seasonally.

Since the seasonal amplitude in intake rate differed so much between the prey species, Oystercatchers achieved the highest intake rate when they took the buried prey, *Scrobicularia* and *Macoma*, in summer and Cockles in winter (Fig. 15B). In this figure we lumped *Scrobicularia* and *Macoma* because, as explained before, we could not predict accurately enough which of the two species should be taken.

Annual variation in bird density, intake rate, prey selection and food supply

Although the number of Oystercatchers present in the study area varied seasonally, a close look at Fig. 6 reveals that, in some years, the monthly numbers were systematically lower than in other years. To analyse whether these year-to-year variations were due to variation in the food supply, we examined the data from December. There was a gradual decrease in the total winter biomass of the prey species combined over the years, but the annual fluctuations were large, varying between 40 and 100 g m^{-2} during ten years (Fig. 16A). After subtraction of the biomass of prey either too small or too deep to be taken, the biomass harvestable for Oystercatchers appeared to differ even more, being extremely low in 1979-1982 (Fig. 16B). In the first three of these years, *Scrobicularia* contributed about 3/4 to the total biomass, but this part of the food supply was largely not accessible to Oystercatchers. The variation in wader density was even larger, being less than

Fig. 17. Elimination of biomass for **A.-D.** four different bivalve species (g m^{-2} month) and **E.** calculated consumption (g m^{-2} $month^{-1}$) by Oystercatcher assuming that all birds foraged each month only on the prey species that delivered the highest intake rate (Fig. 14). The elimination, summed for *different cohorts, has been defined as the product of average* prey weight and the numbers that disappeared m^{-2} $month^{-1}$. The apparent negative elimination in *Macoma* is due to resettlement by which the density rose from March to May. The elimination of the small size classes, which would have been ignored by Oystercatchers, and the large *Mya*, that would have been out of reach of the Oystercatcher's bill, are marked separately. The total bird consumption is the product of Oystercatcher density (Fig. 6A) and consumption per bird (varying between 36 g day^{-1} in summer, and depending on ambient temperature, increasing to 50 g on cold winter days).



3 Oystercatchers ha^{-1} *in the three years when Scrobicularia* was the dominant food supply and more than 25 birds ha^{-1} in four years when the prey biomass of the Cockles reached high values. The predicted intake rate was clearly below the critical lower acceptance level of 1 mg s^{-1} in the four poor winters in succession, 1979-1982.

Comparing elimination of biomass and predation pressure

The average total predation pressure by Oystercatchers was estimated at 12 g m^{-2} $year^{-1}$, but due to the very large variation in density (Fig. 6A), the predation pressure varied considerably between and within years. Assuming that the birds only took the prey which would have given the highest intake rate (Fig. 14), the predation pressure on the different prey species could be compared to the total biomass that was actually eliminated (Fig. 17). Note that the production by *elimination of the small prey was usually very* low, except for first year Cockles in 1985 and 1986, and *Macoma* and *Mya* in the first year after the spatfall 1979.

Cockles The prediction was that Oystercatchers would have fed on Cockles in 1978 and in the winters of 1984, 1985 and 1986 (Fig. 17E). Indeed, these were periods of high losses of cockle biomass (Fig. 17A). Oystercatchers were not responsible for the sometimes considerable summer mortality. Taking all data together, Oystercatchers would have consumed 6.3 g Cockles m^{-2} year^{-1}, whereas the total annual elimination of cockle biomass was estimated at 27.1 g m^{-2}, of which 24.5 g m^{-2} was contributed by specimens ≥ 10 mm.

There are two main reasons why the mortality of Cockles was so erratic. First, many Cockles died in the frost periods of February 1979, 1985 and 1986: 26% of the average annual loss of biomass through mortality took place in these periods. Second, for unknown reasons, there was mass mortality in October 1978, 1980 and 1985, when there were so many dying and gaping Cockles on the surface that the mudflats, over many km^{2}· gave off a nasty smell of decay. In October 1978 and 1985 about 15 and 20 g m^{-2} respectively disappeared within a couple of weeks. Oystercatchers and other waders were observed to eat from the gaping Cockles, but the majority of the flesh disappeared without being eaten by birds.

Scrobicularia* and *Macoma A comparison between the elimination of biomass and predation pressure was more complicated in *Scrobicularia* and *Macoma* than in Cockles. First, the predictions for the intake rate of birds feeding on one of these prey species, or on both combined, usually did not differ much from each other (Fig. 4). Hence, it made little sense to distinguish when the birds should take one of both, or both, species. The second problem was that the elimination of *Macoma* was negative in March-May (Fig. 17B), which was due to the increase, instead of the decrease, of the densities of the cohorts in spring. Since we had no independent estimate of the immigrated biomass, we could give no estimate of the eliminated biomass for the period March-May. It is clear from Fig. 17B, however, that more biomass was eliminated in summer than in winter. Oystercatchers were predicted to take *Macoma* in summer (Fig. 17E), but the predation pressure was usually only a fraction of the total amount eliminated actually (Fig. 17B).

The elimination of biomass in *Scrobicularia* was also higher in summer than in winter, except for the winter of 1982/83 (Fig. 17C), when the population started to decline at a fast rate (Fig. 9B). Oystercatchers were predicted to take *Scrobicularia* in summer, and also in the winter of 1982/83, when *Scrobicularia* did not return to the safe, deep winter depth which makes them for Oystercatchers hardly worthwhile exploiting. The calculated predation pressure by Oystercatchers in this winter was, however, not high enough to explain the huge loss of biomass.

Mya The predation pressure of Oystercatchers on *Mya* was restricted to second year clams, because after the first growing season, the prey were still too small to be exploited, while after the third growing season, they were buried too deeply. Oystercatchers exerted a heavy predation pressure on *Mya* in the intervening period. The estimated predation was close to the total of eliminated biomass (Fig. 17D).

Species combined The Cockle was the major prey for the Oystercatchers in our area. More than half of their average annual consumption consisted of cockle flesh. Cockles also attributed about half of the total elimination summed over the five bivalve species (Table 1). Oystercatchers took 25% of the total elimination by Cockles and *Macoma*, 22% of *Mya*, 17% of *Scrobicu-*

Table 1. Average annual consumption by Oystercatcher in the Nes area (g m^{-2}), compared to the average annual production, due to the annual elimination of biomass (g m^{-2}) for all cohorts combined ('total'), for the size classes large enough to be profitable for Oystercatchers (exluding Cockles < 10 mm long, *Scrobicularia* < 13 mm long, *Macoma* < 11 mm long, *Mya* < 17 mm and Mussels < 25 mm), and for prey being exploitable i.e. beside profitable and accessible (*Mya* < 45 mm; *Scrobicularia* in winters when all specimens live > 6 cm deep), also not dying in mass starvation during extremely short periods, as occurred in Cockles. The calculations refer to the period August 1977 to December 1985.

		elimination		*consumption*
	total	*profitable*	*exploitable*	
Cerastoderma	25.3	23.1	16.6	6.3
Scrobicularia	8.8	8.8	8.2	1.9
Macoma	6.8	6.4	6.4	1.6
Mya	12.9	12.3	3.0	2.2
Mytilus	2.4	0.4	0.4	0.0
TOTAL	56.2	51.0	34.6	12.0

Table 2. As Table 1, but calculated for 15 August-15 March.

	elimination			*consumption*
	total	*profitable*	*exploitable*	
Cerastoderma	17.0	15.4	8.9	5.7
Scrobicularia	4.7	4.7	4.1	1.6
Macoma	5.1	3.4	3.4	1.2
Mya	9.3	9.0	2.8	2.0
Mytilus	1.2	0.3	0.3	0.0
TOTAL	36.6	33.6	20.3	10.5

laria and 0% in Mussels. These percentages refer to the entire year, but Oystercatchers were hardly present in summer. To investigate to what degree the elimination of winter biomass was due to oystercatcher predation, the data were divided into two periods: 15 August-15 March ('winter') and the remaining five months ('summer'). Oystercatchers took during the seven winter months seven times as much food as during the five summer months, respectively 1.5 and 10.5 g year^{-1}. The total elimination was in the winter twice as high as during the summer, 19 and 37.3 g year^{-1} respectively (Table 2). Hence, Oystercatchers took only 8% of the elimination in summer, against 28% of the winter elimination.

These calculations show that the predation pressure by Oystercatcher was not a very important cause of mortality for these bivalve prey, but the risk of a bivalve being taken by Oystercatchers varied enormously between different categories. First, Oystercatchers ignore the small, unprofitable prey. The elimination of these prey was relatively small, except in Mussels (Tables 1 & 2). It was more important to take into account the elimination by prey living out of reach of the bill. All *Mya* > 45 mm were inaccessible for Oystercatchers, as a result of which only 1/4 of the elimination of *Mya* could be harvested by Oystercatchers. All *Scrobicularia* were also out of reach of the bill during most of the winters. This reduced the annual harvestable elimination from 8.8 g to 8.2 g. Gaping Cockles during short periods of mass mortality are an example of a food resource that, although harvestable, could not be fully utilized. On an annual base, 4.7 and 4.6 g Cockle biomass disappeared during mass starvation in October and during ice periods in winter, respectively. Assuming that Oystercatchers took in these periods not more than what they needed to meet their daily energy demand, they consumed 1.3 and 1.5 g of these amounts, respectively. Hence, 3.4 g during the October starvation periods and 3.1 g during the cold spells were, for the Oystercatchers, wasted. This reduced the annual elimination of profitable Cockles from 23.1 to 16.6 g. The elimination of prey after the above-mentioned restrictions was called the elimination of prey *exploitable* by Oystercatchers. The percentage of the exploitable elimination actually taken by Oystercatchers varied between the prey species, being extremely high in *Mya* and Cockles and low in the other species (Table 1). In the winter period, 3/4 of the eliminated *Mya* biomass and 2/3 of the cockle biomass could be attributed to oystercatcher predation (Table 2).

Year-to-year variation The average winter predation by Oystercatchers amounted to 10.5 g m^{-2} (Table 2), but it was only 1.3 g m^{-2} in 1981/82 and 23.2 g in 1985/86, respectively 0.12 and 2.2 × the long-term average. The variation in the total elimination during the seven winter months was less extreme, being between 7.3 g m^{-2} in 1979/80 and 66.9 in 1985/86. The total loss of biomass from August to March was larger than the elimination, due to the loss of condition in the individual bivalves, which varied between 15.9 and 89.9 g m^{-2}. Figure 18 plots the total loss of biomass during the seven winter months in relation to the biomass on 15 August. Four types of biomass loss were distinguished. First, loss of body weight in the macrozoobenthos still alive on 15 March, and three types of elimination of biomass due to mortality: oystercatcher predation, mass starvation of Cockles not consumed by Oystercatchers, and other sources. The higher the biomass, the higher the loss (Fig. 18A). The macrozoobenthos lost about 20% of their body weight between 15 August and 15 March, and this fraction was independent of the initial density. In contrast, the total elimination was highly positively density dependent (Fig. 18B). This was completely due to the response of the Oystercatchers, because the elimination of prey which was not due to oystercatcher predation only weakly increased with density from 10 to 15%. In contrast, Oystercatchers consumed only some per cent

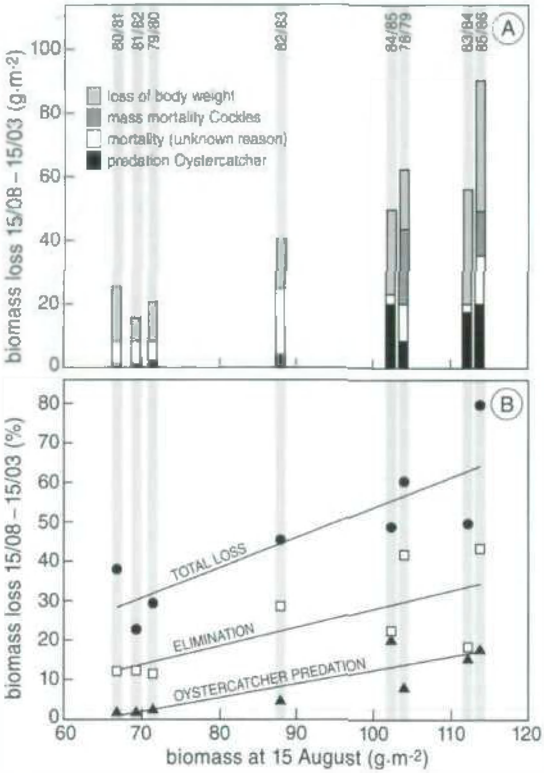


Fig. 18. Loss of biomass by Cockles, *Scrobicularia*, *Macoma*, *Mya* and Mussels between 15 August and 15 March of the next year in relation to the total biomass present at 15 August. The loss of biomass is due to a decrease in the body condition and to mortality, the latter given separately for Oystercatcher predation, mass mortality in Cockles (see text) and other causes. Panel **A.** gives the absolute loss of biomass (g m^{-2}), and **B.** the loss as percentage.

when the food supply was poor and this increased to 17% in winters with a rich food supply.

Discussion

Model assumptions

In this paper we predicted the feeding behaviour of the Oystercatcher on the basis of measurements on the prey. This required several simplifying assumptions. Before we discuss our results in some detail, it seems prudent to investigate some limitations in our approach.

Spatial variation In our model calculations we ignored the spatial variation in prey density. The samples of the macrozoobenthos in the Nes area were taken at 73 sites and we know from this that *Macoma* and *Scrobicularia* on the rich sites were twice as common as on the poor sites and that the ratio was even three in Cockles and *Mya* (Zwarts 1988b). In principle, it would have been possible to repeat all calculations done for the Nes area as a whole for the 73 sites individually. This would not have changed the average trends shown for prey choice and intake rate. However, whereas we predicted that all birds would everywhere have switched at the same moment from one prey to the other, the timing would have been different between sites, so that more gradual changes would be expected for the Nes area as a whole.

Feeding specializations First, we assumed that all birds selected one prey species, with the exception that they could take a mixture of *Scrobicularia* and *Macoma*. This was certainly not the only exception, because birds also took Cockles and *Macoma*. This was only observed, however, in summer when *Macoma* lived close to the surface at the same depth as Cockles (Hulscher 1976, Hulsman unpubl.). Consequently, we were probably wrong in predicting that birds would have taken only *Macoma* in summer 1984 and 1985 and ignored Cockles.

Another simplification was that all birds should perform the same prey selection, whereas direct observations also showed that this was not true. For instance, one female took only Ragworms among the 29 other colour-banded birds feeding in the Nes area on *Scrobicularia* and *Macoma* (Blomert *et al.* 1983). Bill length has a large effect on the prey selection. The last birds feeding on *Scrobicularia* in October 1979 and the first ones in early spring 1980 were all females with long bills, because the prey then lived out of reach of the shorter bill of the males. Also the depletion of the second year *Mya* in autumn 1980 was due to predation by females. The bill length of the birds feeding on *Mya* was, on average 1 cm longer than for the birds feeding at the same time on a cockle bed, just north of the study area. Hence, it is to be expected that the seasonal variation in intake rate and harvestable food supply, of which the averages has been given in this paper, were larger for males and smaller for females.

Interference Our predictions of the intake rate of the birds only depended on the characteristics of the food supply, and not on the feeding density of the birds. Thus, we ignored the possibility that high feeding densities may have depressed the intake rates of some or all of the birds. Yet, there is a considerable amount of field evidence for such interference in Oystercatchers (Koene 1978, Zwarts & Drent 1981, Ens & Goss-Custard 1984, Goss-Custard *et al.* 1984, Goss-Custard & Durell 1987, Boates 1988, Cayford 1988a). However, as the review by Ens & Cayford (1996) shows, strong evidence comes exclusively from Oystercatchers feeding on Mussels. Ens & Cayford (1996) also conclude that interference may ultimately be due to food stealing, which triggers adaptive responses in the individuals that are most susceptible to such kleptoparasitism, at the cost of a reduced capture rate. Food stealing occurs primarily for prey that are profitable to steal, i.e. prey that are large and require a long time to open. None of the prey in our study area reached the sizes nor needed the handling times that would bring them on a par with the Mussels that are so regularly kleptoparasitized. It follows that, in most years, interference may have been minimal and was therefore safely ignored.

Estimating parameters The estimates of the intake rate of birds feeding on *Scrobicularia* and *Macoma* were based on three variables: density, weight and burying depth of the prey. The estimates for birds eating Cockles were based on two variables, density and weight of the prey, whereas the predictions for birds consuming second year *Mya* were based on prey density and for Mussel-eaters on prey weight. The predictions for the five prey species were all based on prey variables, but there is one important difference. The predictions for birds eating *Scrobicularia* and *Macoma* were based on the principles of the random touch model and the optimal prey choice model, whereas the other three extrapolated intake rates from prey density and/or prey weight. Although refinements of the predictions are still desirable, the models do seem to give realistic estimates.

Other predators The Oystercatcher was by far the most important bird predator on the benthic food supply in our study area. The oystercatcher density was 8.4 birds ha^{-1}, averaged over the entire year. All other bird species together foraged at an average annual density of 9.3. birds ha^{-1}, of which only four species reached a density above 1 bird ha^{-1}: Curlew *Numenius arquata* 2.6, Redshank *Tringa totanus* 1.7, Black-headed Gull *Larus ridibundus* 1.3 and Dunlin *Calidris alpina* 1.1 birds ha^{-1} year^{-1}. Oystercatchers took 12 g m-2 year^{-1}, but all the other bird species together only 10.3 g m^{-2} year^{-1}, with three species taking more than 1 g m^{-2} year^{-1}: Curlew 4.8, Herring Gull *Larus argentatus* 1.4 and Black-headed Gull 1.1 g m^{-2} year^{-1}.

There was hardly any overlap in the choice of the prey species by Oystercatchers and the other species. In the few cases that the Oystercatcher and other bird species fed on the same prey species, different size

The bill length of individual Oystercatchers varies between 6 and 9 cm and was measured in all colour-banded birds. The majority of the Oystercatchers which were observed to feed on deep-living prey had long bills. In contrast, most birds feeding on surface prey, such as mussels and cockles, had short bills.

classes were selected: (1) Herring Gulls took Mussels in 1985 that were still too small to be taken by Oystercatchers (Zwarts unpubl.); (2) Knot *Calidris canutus* selected medium-sized *Macoma* hardly taken by Oystercatchers (Zwarts & Blomert 1992); (3) Oystercatchers took second year *Mya* still ignored by Curlews (Zwarts & Wanink 1984). Hence, although different bird predators successively contribute to the decline of the prey cohorts, there was no reason to take into account the predation pressure of the other bird species when we compared oystercatcher predation to the elimination of the prey biomass harvestable by Oystercatchers.

Seasonal variation in intake rate and prey selection

The intake rate of Oystercatchers varied seasonally, being high in summer and low in winter. This trend was more pronounced in the burying prey species, *Scrobicularia* and *Macoma*, than in the surface prey, the Cockle (Fig. 15A). The seasonal variation in intake rate was even smaller in Mussel-eating Oystercatchers (Goss-Custard & Durell 1987; Fig. 17 in Zwarts *et al.* 1996b). The explanation is that, due to the variation in burying depth, the encounter rate with burying prey was reduced in winter. There was no such a difference in surface prey, although birds stabbing the bill between the valves may more often encounter closed bivalves in winter than in the summer, when Cockles and Mussels feed more often themselves. This may explain why the seasonal variation in intake rate in Mussel-eating Oystercatchers was larger in stabbers than in hammerers (Goss-Custard & Durell 1987).

According to the predictions (Fig. 15B) and direct observations (see text), burying prey were selected in summer and only taken in winter when there were no surface prey. Several other studies provide similar evidence for such a seasonal shift in the diet of the Oystercatcher. Bunskoeke *et al.* (1996) and Hulscher *et al.* (1996) show that *Macoma* was the main prey on Schiermonnikoog in spring and completely disappeared from the Oystercatcher's diet in late summer. That *Macoma* is indeed a summer prey, hardly taken by Oystercatchers in winter, is also evident from the work of Beukema (1993a) on the Balgzand in the western part of the Wadden Sea. He found that the monthly mortality of *Macoma* between mid-March and mid-August (five months) was, on average, three times as large as in the remaining seven winter months (Beukema 1993a: Fig. 6). Bird counts indicated that the monthly predation pressure by Oystercatchers was only 1/4 the level in the five summer months compared to the seven winter months (Beukema 1993a: Fig. 4). Assuming that the mortality of adult *Macoma* was completely due to oystercatcher predation, it follows

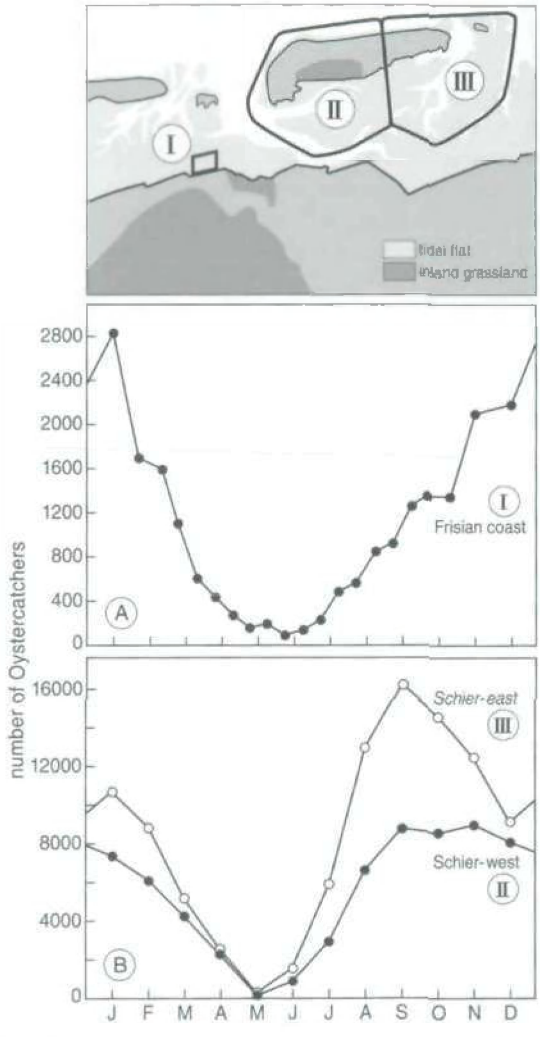


Fig. 19. Seasonal variation in the number of Oystercatcher feeding along **A.** the Frisian coast, **B.** the west and east side of Schiermonnikoog. The map indicates the three tidal feeding areas and adjacent grassland where the birds may feed at high tide. The birds on Schiermonnikoog were counted on roosts at high water, but the birds along the Frisian coast on 100 ha of tidal flats at low tide (see Fig. 1).

Thousands of Oystercatchers roost in the grassland polder on west Schiermonnikoog, but most continue to feed during the high water period, at least in autumn and winter, when the feeding time during the preceding low water period was short.

that an individual Oystercatcher took *Macoma* in spring and summer 12 times as often as in autumn and winter. The significance of *Macoma* as autumn + winter prey for Oystercatchers must be still lower, because large numbers of Knot winter on the Balgzand (Zegers & Kwint 1992), and this species must be responsible for a major part of the mortality in autumn and winter.

Another source of information on the seasonal variation in prey selection may be derived from the many field studies assembled from different areas in NW. Europe (Zwarts *et al.* 1996b, 1996c). Not one of the 276 studies from September to March refer to *Macoma*-eating Oysteratchers, but 77 of 311 studies during the four summer months. This suggests again that *Macoma* disappears from the diet in late summer.

Winter predation by Oystercatchers of *Scrobicularia* must be impossible during the majority of the winters because the prey live too deep. There are, however, two winter studies of Oystercatchers feeding on *Scrobicularia*. In one case, this concerned birds on Schiermonnikoog feeding on relatively small prey 20 mm long, of which the majority lived just within reach of the bill (Habekotté 1987). The other study was done by Boates & Goss-Custard (1989) in the Exe estuary. Although the majority of the birds in the Exe are found on the mussel beds, some birds feed each winter on *Scrobicularia*. Perhaps this prey on the Exe in winter do not live as deeply buried as in the Wadden Sea. If so, the seasonal variation in intake rate would not be expected to be as large as in the more northern tidal flats where the accessible fraction of *Scrobicularia* is much lower in winter than in summer (Zwarts & Wanink 1993).

Seasonal variation in bird density

Despite the large variation in the number of Oystercatchers feeding in the area from year to year, the trends were similar each year (Fig. 6A). The seasonal course of the change in numbers in the study area (Fig. 19A) deviated from those elsewhere in the eastern part

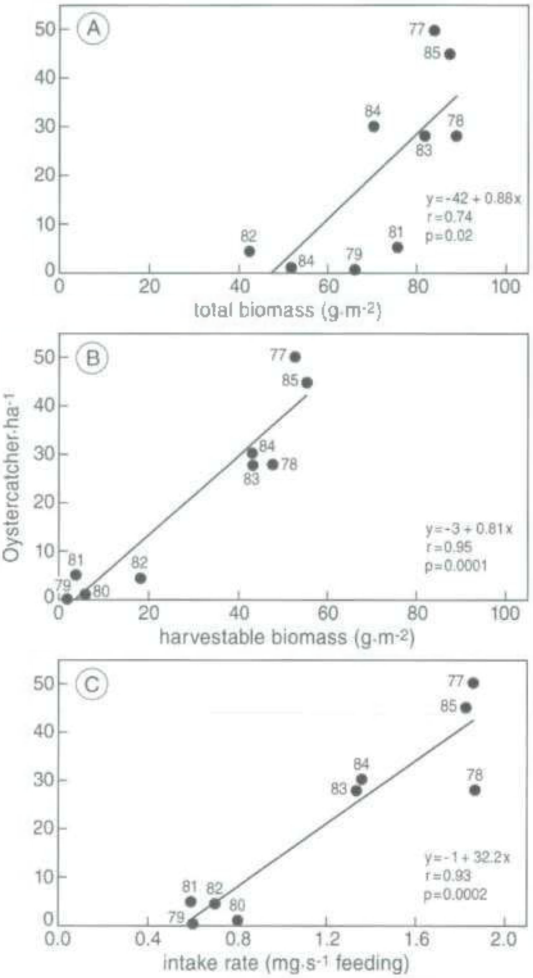


Fig. 20. Average feeding density in December (Oystercatcher ha^{-1}) as a function of **A.** total biomass, **B.** harvestable biomass and **C.** predicted intake rate (mg s^{-1} feeding); same data as Fig. 16. Since no bird counts were available for December 1985, we compared for that year food supply and bird density at the end of October. Bird density in December was, on average, 1.5 times as high as in October (Fig. 19); hence this multiplying factor was used to estimate the density in 1985.

of the Wadden Sea, where the Oystercatchers decreased from October onwards. As an example, Fig. 19B shows the monthly averages for nearby Schiermonnikoog, given separately for the eastern and western part of the island.

How can we explain why our study area attracted so many Oystercatchers in mid-winter? The simplest explanation is that birds leave a feeding site if they can achieve a higher intake rate elsewhere. If so, birds feeding in summer on mudflats with buried bivalves and Ragworms as the only prey would leave these areas in late summer to move to mussel and cockle beds (Fig. 15A). Since cockle and mussel beds are usually found on the lower part of the shore, and *Macoma* and Ragworms occur on mudflats often situated above mean sea level, the high shore is in summer a relatively more important feeding area than in winter. However, it is unlikely that this explains why our study area attracted so many Oystercatchers in winter. The tidal flats in our study area consisted of mud and the greater part were situated above mean sea level, so fewer birds would be expected to remain to feed in winter. In fact, the reverse was found (Fig. 19). Possibly, the tendency of Oystercatchers to concentrate from October onwards on tidal flats adjacent to inland feeding areas (Fig. 19) explains this unexpected finding. This would explain the relatively low numbers remaining to winter on the eastern part of Schiermonnikoog, where there is no grassland, and the relatively high numbers wintering along the Frisian coast and on western Schiermonnikoog where grassland is available. The bird census data of the Dutch Wadden Sea (Zegers & Kwint 1992) also revealed that the number of Oystercatchers on Vlieland, an island without inland feeding areas, is in winter 47% lower than in late summer, whereas the winter numbers along the mainland coast of the provinces Noord-Holland, Friesland and Groningen, with extensive grasslands next to the sea wall, are 28% higher, on average, than in late summer; this calculation is based upon a comparison between the January counts from the four mild winters 1981, 1983, 1989 and 1991, and preceding counts from August or September. As shown elsewhere (Zwarts *et al.* 1996d), the daily variation in exposure time of the low water feeding areas in the Wadden Sea is much larger in winter than in summer. Consequently, the ability to compensate at high tide for short feeding periods is more important in the winter half of the year than in the summer half. This opportunity is apparently important enough for Oystercatchers to move to parts of the Wadden Sea where compensatory feeding on grassland is available.

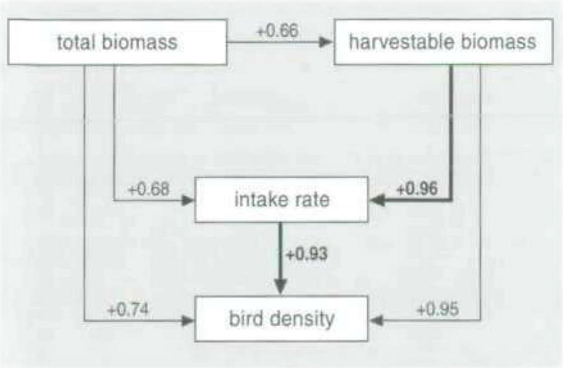


Fig. 21. Dependence of bird density on food supply and predicted intake rate. The correlations are shown along the arrows; same data as Fig. 20.

Response of Oystercatchers to variation in harvestable prey biomass

The Nes area was certainly not a marginal feeding area. The biomass of the food supply and the feeding density of Oystercatchers were, on average, respectively, 4 and 10 times as high as the average for the tidal flats of the Dutch Wadden Sea as a whole (Beukema 1976, Zwarts & Wanink 1993). The bird density fluctuated in accordance with the food supply, as shown in Fig. 20A, using the December data from Fig. 16.

There is a good correlation between bird density and 'total biomass', r = 0.74, which is actually surprising, because total biomass is an inaccurate measure of the food supply, due to the highly variable fraction that is unharvestable. Because of this, we expect a better correlation between bird density and the biomass of the prey that is both profitable as well as available, and this indeed appeared to be the case, r = 0.95 (Fig. 20B). Very likely, this response is caused by the birds acting on the intake rates that they achieve (Fig. 20C). Figure 21 summarizes the causal relationships, as we see them. Two relationships are essential: bird density depends on intake rate, which in turn rate depends on the harvestable biomass. The high correlation between intake rate and harvestable biomass is not surprising, because the intake rate has been predicted from the density, size and burying depth of the prey, three variables which all contribute to harvestable biomass. It is already obvious, however, that many wintering Oystercatchers only occur in the study area when older Cockles or second year *Mya* are abundant and the intake rate is > 1.2 mg s^{-1}. In contrast, when the wintering birds have to feed on *Scrobicularia* or *Macoma*, hardly any birds remain to feed in the area because of the extremely low intake rate.

The correlations shown alongside the arrows in Fig. 21, are based upon linear regressions. However, instead of a linear relationship between bird density and intake rate (Fig. 20C), we rather expect a J- or S-curve. No birds should ever feed in the area when the intake is < 1 mg s^{-1}, as we confirmed in this study (Fig. 20C). What will happen above this level will also depend on what the birds can obtain elsewhere. In other words, even at a rather high intake rate, few birds may be concentrated in the area if the situation elsewhere is even better. Once intake rates are so high that the area ranks among the best in the region, the bird density will increase until all 'available' birds have been attracted to the area, after which the density will level off at still higher intake rates because the supply of recruits dries up. How many birds are 'available' will depend on the total number of birds in the region and the size of the region, which will depend on the size of the home range of the birds. With extreme site fidelity, home ranges and therefore the region will be very small, so that the pool of 'available' birds is quickly depleted and very little relationship between bird density and food supply is to be expected when years are compared. If, on the other hand, home ranges are large and variation in food supply between years quite extreme, a high correlation between bird density and intake rate can occur, as was probably the case in our study. The sightings of the colour-banded birds certainly proved that movements of 1 to 3 km regularly occurred, although individuals could stay for months, and some even for years, on the same spot of less than 0.5 ha. The site fidelity of the Oystercatchers in our study area seems intermediate between that in the Exe estuary, where the mussel beds are extremely stable and home ranges often less than 1 ha (Goss-Custard *et al.* 1982), and the estuary of the Ribble, where an exceptionally large spatfall of Cockles caused a massive influx of Oystercatchers (Sutherland 1982d).

Oystercatcher in the waiting room?

When different bird species feed on the same prey, the larger ones usually take the larger size classes. Pehrsson (1976) observed this trend in seven duck species feeding on Mussels and the same was found in waders feeding on the Shore Crab (Zwarts 1981), the fiddler crab *Uca tangeri* (Zwarts 1985), or the amphipod *Corophium volutator* (Zwarts & Wanink 1993). However, when the size selection of the Oystercatcher is compared to those of other bird species, the species seems to be an exception to this general rule because it usually takes large bivalves that are even rejected by the Herring Gull (e.g. Harris 1965) and Eider *Somateria mollissima* (e.g. Nehls 1995), bird species that weigh 2 and 4 times as much, respectively, as the Oystercatcher.

The unique ability of Oystercatchers to open large hard-shelled prey facilitates exploitation of a rich food resource that cannot be harvested by bird species that eat bivalves and other armoured prey by swallowing them whole (Hulscher 1996). Bird species that swallow bivalves whole are limited by their gape width in the sizes they can take and are forced to maintain a large stomach to crush the shells. For instance, the stomach of an Oystercatcher is, relative to body weight, half as heavy as that of a Knot, a wader species that cracks small hard-shelled prey after swallowing them (Piersma *et al.* 1993). The quick reduction in stomach size of Knot during periods that they do not need it to crack shells (Piersma *et al.* 1993) suggests a high cost to maintaining it. Thus, Oystercatchers probably do not have the ability to crack shells in their stomach, because it did not pay to maintain a heavy stomach. Hence, Oystercatchers must also open small armoured prey which they could easily have ingested whole. It always takes them some seconds to handle even the smallest bivalve (Zwarts *et al.* 1996a, b), whereas the same prey might be handled in less than 1 s if ingested whole (Zwarts & Wanink 1993: Fig. 12). Since Oystercatchers never swallow hard-shelled prey entirely, we do not know for sure how much faster they would be able to handle these small prey. Curlews, which usually extract the flesh from the shell when they feed on *Mya*, sometimes take these prey including the shell. The extraction of flesh from a 25 mm *Mya* takes them twice as much time as clams of similar size swallowed whole. Consequently, prey swallowed whole are twice as profitable as prey from which the flesh is eaten (Zwarts & Wanink 1984).

Table 3. Variation in food supply in August and December in the Nes area between 1977 and 1986. The RSD, or relative standard deviation, is the SD as percentage of the mean. The total biomass is summed for five bivalves (g m^{-2}; the August data are shown per bivalve species in Zwarts *et al.* 1992; Fig. 16A gives the December values per year). The harvestable biomass is defined as the summed biomass, excluding Cockles < 10 mm long, *Scrobicularia* < 13 mm long or living > 6 cm deep, *Macoma* < 11 mm long or living > 4 cm deep, *Mya* < 17 mm or living in > 6 cm deep, and Mussel < 25 mm (Fig. 16B gives the December values per year).

biomass	*August*		*December*	
	mean (g m^{-2})	*RSD (%)*	*mean (g m^{-2})*	*RSD (%)*
total	73.3	26.6	63.6	30.7
harvestable	40.3	65.9	24.17	9.5

Since Oystercatchers depend on large prey, the predictability of their food supply might decrease due to the mortality of the prey before reaching the size taken by Oystercatchers. Oystercatchers would be able to overcome this possible problem by eating these small prey themselves, but when they do, they only lower their intake rate (Fig. 1B). To investigate whether the food supply harvestable by Oystercatchers is less predictable than the total biomass, we calculated for 2 months, August and December, the variation in the total and the harvestable biomass (Table 3). The total biomass varied between 53 and 111 g m^{-2} in August, with a standard deviation (SD) of 19.5. The annual variation in the harvestable food supply was much larger with a range from 10 to 83 g m^{-2} and a SD of 26.6. This result may be compared directly to similar data for the Knot (Zwarts *et al.* 1992: Table 1 & 2). The variation in the food supply harvestable by Knot in August was twice as large as the variation in the total biomass, but in Oystercatcher it was even 2.5 times as large. The biomass harvestable by Oystercatchers was even still less predictable in winter: it varied between 2 and 53 g m^{-2} in December.

It would be worthwhile to do the same calculations for the food supply of Oystercatchers elsewhere. It is striking, for instance, that the mussel beds in the Exe estuary (SW. England) provide Oystercatchers with a stable food supply (Goss-Custard *et al.* 1996b). In contrast to the Wadden Sea, mussel beds in the Exe do not disappear from gales and ice, such as occurs in the Wadden Sea (Dankers & Koelemaij 1989, Obert & Michaelis 1991). Moreover, since the annual recruitment of Mussels in the Exe is less erratic than in the Wadden Sea and the survival of spat strongly negatively density-dependent, the density of large Mussels does not vary much (McGrorty *et al.* 1990).

Were Oystercatchers dependent on one or two prey species in the Wadden Sea, they would not be able to survive a period longer than one to four years. The birds in our study area could only stay alive by switching regularly from one to another bivalve species and take, *in total, four bivalve species during the ten years* of observation (Fig. 14). Nevertheless, the intake rates would be insufficient during four years, and the birds had to move to alternative feeding areas. The high water counts showed that the total number of Oystercatchers did not decrease during these years along this part of the Frisian coast and the nearby island Engelsmanplaat (Zegers & Zwarts unpubl.). Therefore, the birds must have moved to feeding areas still within reach of the same high water roosts. Sightings of colour-banded birds showed that many of the Nes birds moved to mussel beds on the lower shore, at 1 to 4 km from the Nes area. In other words, the birds could not survive a ten year period if they restricted their feeding range to 1 km^2 of mudflats. However, by extending their individual feeding ranges to an area of 10-20 km^2, they could probably find enough food.

The large majority of Oystercatchers in the Wadden Sea depend in winter on Cockles and Mussels. The year-to-year variation in the occurrence of both prey is very large (Beukema *et al.* 1993). Unfortunately for their predators, recruitment and mortality of both species is related to the winter temperature, by which the fluctuations of the food stock of both species tend to be synchronized (Beukema *et al.* 1993). Hence, Oystercatchers wintering in the Wadden Sea must deal with a varying, and sometimes low, food supply.

Are Oystercatchers limited by their food supply?

Several prey species contribute to the benthic production, and since each bird species restricts its diet to a limited number of prey species and size classes, each bird species harvests only a part of the total production. Oystercatchers restrict their diet mainly to bivalves. They consumed in the Nes area yearly 12 g m^{-2}, on average, or 21% of the total yearly elimination of the five bivalve species combined (Table 1). The predation pressure by Oystercatchers on their prey has already often been measured, although usually not as fraction of the annual prey elimination, but as fraction of the total biomass being removed over the winter (see recent reviews by Meire 1993 and Goss-Custard *et al.* 1996b). Oystercatchers are able to remove between 10 and 80% of their prey in a winter, but in most studies it is 20 to 40%. Also this study reveals a large variation in the predation pressure between prey species (Tables 1 & 2), and between years (Fig. 18). In

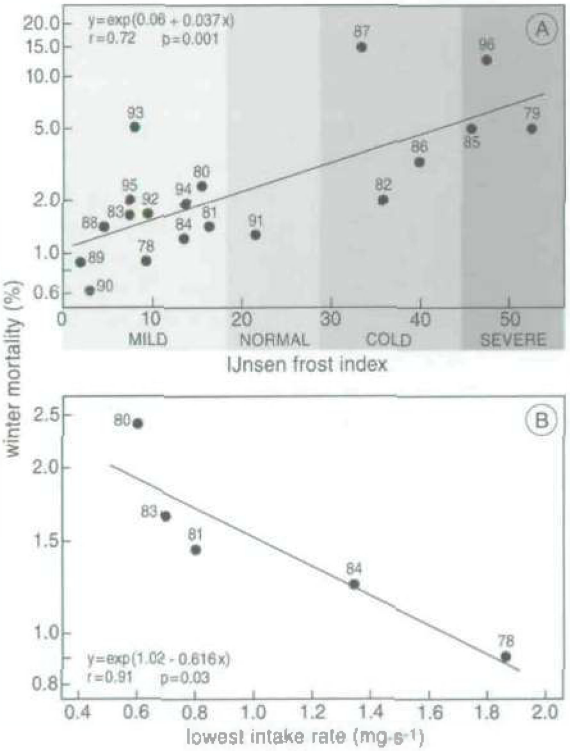


Fig. 22. Winter mortality of Oystercatchers captured along the Frisian coast as a function of **A.** the IJnsen frost index and **B.** the predicted lowest intake rate in winter in the Nes area; a selection is made for recoveries in January-April. The analysis is based on 3424 colour-banded Oystercatchers and excluded the yearlings; from Zwarts *et al.* (1996e). The frost index of IJnsen (1991) is defined as $0.000275v^2 + 0.667y + 1.111z$, where v is the number of days with a minimum temperature < 0 °C, and y and z the number of days with a maximum temperature < 0 °C and < -10 °C, respectively.

both cases, the variation in the predation pressure may be attributed to the intake rate. Oystercatchers exert a high predation pressure on prey such as Cockles and second year *Mya* which can be consumed with a high intake rate, whereas *Macoma* and *Scrobicularia* are hardly taken in winter due to their low intake rate. For the same reason, the predation pressure as fraction of the total biomass of the five prey species increases with the intake rate: r = +0.87 when the winter predation as per cent of the biomass (Fig. 18B) is plotted against intake rate in winter (Fig. 20C).

From the point of view of the predators, it is not in the first place the size of the harvestable food supply, or its production, that actually counts, but whether they can meet their daily energy requirements. Thus to answer the question: 'is there enough food for the predators, or could they have taken more?', it makes sense to reformulate this as: 'how often is the harvestable food supply too low to yield an intake rate sufficient to get the necessary amount of food within the restricted time the tidal feeding areas are exposed?'; see Goss-Custard *et al.* (1994, 1996d) for an extensive discussion why carrying capacity may be reached before the birds have depleted their food supply.

Oystercatchers deposit body reserves as an insurance against periods with too low a daily consumption. Their energy buffer is large enough to survive a starvation period of at least some days (Hulscher 1990, Zwarts *et al.* 1996e). Therefore, a possible short-term variation in the daily consumption due to adverse weather conditions does not affect the survival of Oystercatchers. However, if the daily consumption is systematically less than, for instance, half what the Oystercatchers need, they will die within two to three weeks. Hence, the birds will do all to attain the intake rate of at least 1 mg s^{-1} during feeding.

The optimal diet model assumes that, not only in critical, but in all, circumstances, the birds will attempt to maximize their intake rate and select the prey species, and the feeding area, that yield the highest intake rate. Hence, predators are creaming off the most profitable fraction of their food supply and, after depletion, switch to lower-ranking prey initially ignored. This may be prey that are less profitable since they are of smaller size (Meire *et al.* 1994, Zwarts *et al.* 1996b, and sources given there), but also specimens of similar size living more deeply buried below the mud surface (Fig. 5; Wanink & Zwarts 1985) or armoured prey with a thicker shell (Sutherland & Ens 1987, Meire 1996a, Ens & Alting 1996). Thus, Oystercatchers by creaming off the most profitable prey, exert a high predation pressure on only a fraction of the prey and ignore not only the unprofitable prey, but also the majority of prey which, by definition, still would be harvestable. Consequently, the predation pressure on the harvestable prey fraction as a whole is usually low.

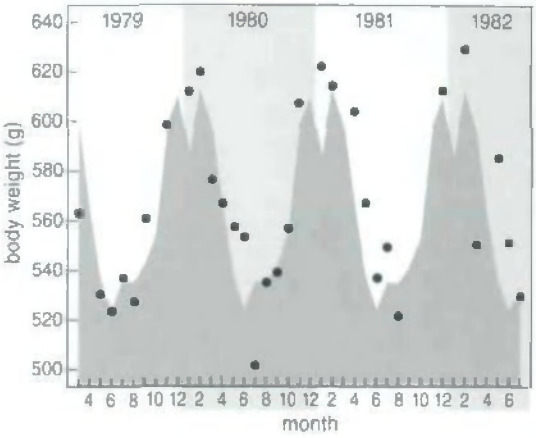
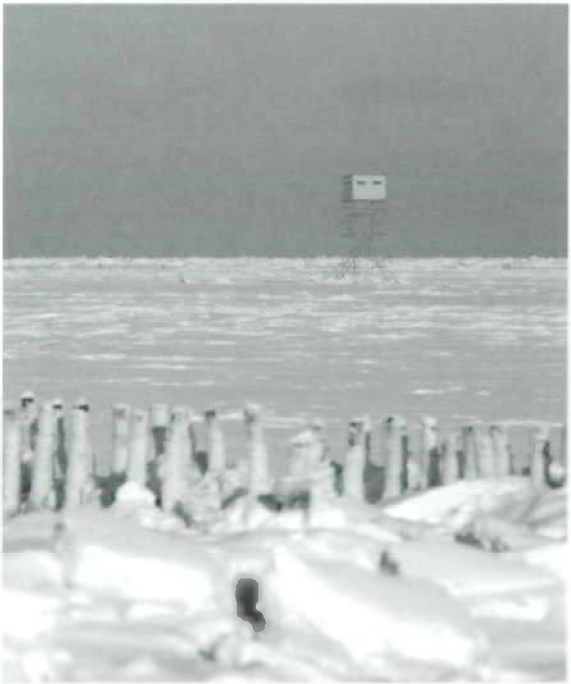


Fig. 23. The average body weight of Oystercatchers in 1979 (n = 627), 1980 (n = 534), 1981 (n = 627) and 1982 (n = 255) (●), compared to the average monthly mean in other years (n = 4434 for 1977, 1978 and 1983 to 1986; shaded field), to show that the poor food supply in the four intervening years did not negatively effect the average body condition of the Oystercatchers; from Zwarts *et al.* (1996e).

The question remains then why are there not more Oystercatchers than there are now. The Oystercatcher is a long-living species with a low yearly recruitment and thus cannot increase its numbers immediately in a year with a high food supply. This implies that the predation pressure by Oystercatchers in the Wadden Sea might increase were the yearly variation in their harvestable food supply to decrease. It is thus of importance to study feeding Oystercatchers in the worst feeding conditions.

How often do poor years occur and do Oystercatchers die from starvation in these years? Winter mortality primarily depends on winter temperature (Hulscher 1990, Camphuysen *et al.* 1996, Goss-Custard *et al.* 1996a), so this has to be taken into account studying the possible effect of food supply on winter mortality. IJnsen (1991) has classified the severity of the winters. During the study period there were no 'normal' winters, because five winters were mild, three cold and two severe (IJnsen 1991). To analyse the winter mortality, we took 3424 adult Oystercatchers which were colour-banded along the Frisian coast between 1977 and 1984 (Zwarts *et al.* 1996e). Assuming that the annual mortality of adult Oystercatchers in the long-term, including severe winters, was 6.1% (J.B. Hulscher pers. comm.; Goss-Custard *et al.* 1996e) 1206 of these birds would still be alive on 1 October 1996. Until this datum, 426 birds, or 12.4%, were recovered, which would imply that 19.2% of our colour-banded birds were recovered after death. Using this as a correction factor, the variation in the absolute mortality can now be calculated. The risk to die in January or February was nearly 4 times as large as during the rest of the year (Zwarts *et al.* 1996e). To compare the winter mortality, we will also include March and April, because winter victims are still found in these months. The mortality between May and December was 2.7%, on average, and independent of the frost index of the foregoing winter period.



Intertidal flats in the study area completely covered by ice.

In agreement with other studies, the winter mortality was much higher during severe winters (Fig. 22A), which is equally due to hunting in France and to starvation in birds staying behind after the inset of the frost (Zwarts *et al.* 1996e). To exclude the effect of severity of the winter, we took the five mild winters to plot winter mortality against the lowest intake rate in the winter concerned (Fig. 22B). In these five winters, no birds were shot and nearly all were found dead in the study area. However, the winter mortality in the three poor years appeared to be nearly twice as high as in the two years during which, due to the presence of large Cockles, the intake rate in winter could stay at a high level.

The biomass measurements in the Nes area ended in November 1986, some months too early, because the winter mortality of Oystercatchers was extremely high in winter 1987 when 17% of the population died, even though the winter was not extremely cold. The November samples showed that there were no *Scrobicularia* (Fig. 9) or second year *Mya* (Fig. 12) left and hardly any large Cockles (Fig. 8), whereas also large *Macoma* (Fig. 10) and second year Mussels (Fig. 13) had decreased. As a consequence, the intake rate was already extremely low in autumn 1986 (Fig. 14), and must have been so in the following months, and at least as low as in the poor winters 1980-1982. Hence, the remarkably high mortality in the winter of 1987 was probably due to the combination of a cold winter and a poor food supply. A remarkably high number of our birds were shot in France in 1987. This suggests that more Oystercatchers left the Frisian coast in a cold rush than usual in other cold winters. As Fig. 22A shows, there were three winters with an exceptional high mortality. The high mortality in 1987 was explained with a low food supply but, unfortunately, we do not know whether the food supply was also extremely low in the winters of 1993 and 1996.

When the Nes area could only offer a poor harvestable food supply, and consequently a low intake rate, most birds left to feed further downshore. Apparently, the intake rate in these alternative areas was not high enough to prevent a higher mortality. We only know that these alternative feeding areas were exposed a shorter time, so possibly the reduced feeding time increased the risk of starvation.

Mortality due to starvation implies an exhaustion of the nutrient reserves. The feeding circumstances in our study area were poor between autumn 1979 and spring 1982, compared to the time before and after. However, the body weight of the Oystercatchers in these four years appeared not to deviate from the long-term average monthly means (Fig. 23). Hence, the average Oystercatcher was, even in these winters, able to satisfy its energy requirements. This seems inconsistent with the higher mortality in the poor years (Fig. 22B). However, as shown elsewhere (Zwarts *et al.* 1996e), Oystercatchers attempt to increase their body weight as soon as their food supply is less predictable. Thus a higher body weight is to be expected if the average intake rate is low. On the other hand, some marginal birds will possibly not be able to attain the required higher consumption. If this is so, we would expect a larger variation in the body weights within the population in years with a poor food supply. The frequency distribution of the body weights in the three poor years, however, appeared not deviate from those of the other years. Possibly, the fraction of marginal birds which run a high risk of dying in periods of low temperatures and/or reduced daily consumption is too small to be detected in the bird catches we made.

Our general conclusion is that there are large local variations in the food supply harvestable to Oystercatcher, but that the Wadden Sea, unless the mudflats are covered by ice, offers enough food for the birds, provided that they either switch between prey species and/or between areas. This is probably generally true for waders in Wadden Sea, since Zwarts & Drent (1981) and Zwarts *et al.* (1992) arrive at the same conclusion in their work on Oystercatchers on Schiermonnikoog and Knot along the Frisian coast, respectively. Nonetheless, the increase of winter mortality at a lower food supply, suggests that the winter remains a difficult period for the Oystercatcher, as also found by Camphuysen *et al.* (1996) who could show that, over a long series of 27 years, more Oystercatchers beached when the food supply for Oystercatchers in the western part of the Wadden Sea reached low levels (Beukema 1993a).

Chapter 12

WHY KNOT *CALIDRIS CANUTUS* TAKE MEDIUM-SIZED *MACOMA BALTHICA* WHEN SIX PREY SPECIES ARE AVAILABLE

Leo Zwarts & Anne-Marie Blomert

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WHY KNOT *CALIDRIS CANUTUS* TAKE MEDIUM-SIZED *MACOMA BALTHICA* WHEN SIX PREY SPECIES ARE AVAILABLE

We quantified the prey selection and intake rate of a wading bird, Knot *Calidris canutus*, when six different, intertidal prey species, the Mud Snail *Peringia ulvae* and the bivalves *Macoma balthica*, *Cerastoderma edule*, *Mya arenaria*, *Scrobicularia plana* and *Mytilus edulis*, were abundant. Knot usually search for food by randomly probing into the mud. Prey selection may be described by five rules: (1) Prey are not ingestible by Knot if the circumference is more than 30 mm. (2) Prey are not accessible to Knot when they lie buried deeper than 2 to 3 cm. (3) The probability of a prey organism being detected depends on its surface area, measured in the horizontal plane. (4) Prey are ignored when they are unprofitable, i.e. when the rate of intake while handling the prey is below the current overall average intake rate during feeding. (5) Knot prefer thin-shelled to thick-shelled prey species, possibly because a high inorganic content has an inhibitory effect on the rate at which energy can be extracted from the food. The first rule of ingestion is set by the gape width, and is therefore invariable. The fraction of the prey which is accessible varies according to the probing depth of the bird. The lower size threshold of prey taken is determined by the profitability rule and so varies according to the current feeding rate of Knot. Unfortunately for Knot, the majority of the preferred thin-shelled prey live out of reach of the bill, whereas the thick-shelled species live at the surface. Medium-sized *Macoma* is the best compromise available in the six-species mix.

Introduction

Worms, crabs and shrimps are the most important prey for the majority of the fourteen wader species occurring on the intertidal areas in NW. Europe (Cramp & Simmons 1983). Although bivalves form the bulk of the biomass of the macrozoobenthos living in the intertidal zone (Beukema 1976), only two waders, Oystercatcher *Haematopus ostralegus* and Knot *Calidris canutus*, are specialized to such a degree that they depend on bivalves almost entirely. Oystercatchers take the larger bivalves, which they open by stabbing or forcing the bill between the valves, or by hammering a hole in the shell (Hulscher 1976, 1982, Goss-Custard & Durell 1988, Cayford & Goss-Custard 1990). In contrast, Knot swallow bivalves and snails whole (Ehlert 1964, Davidson 1971, Prater 1972, Goss-Custard *et al.* 1977b).

This paper considers why Knot were observed to select some prey and not others from six potential prey species. Two species occur on the surface of the substrate, the Mud Snail *Peringia ulvae* and the Mussel *Mytilus edulis*. Another, the Cockle *Cerastoderma edule*, is found just below the surface, and three species, the clams *Macoma balthica*, *Mya arenaria* and *Scrobicularia plana*, are buried several cm deep.

To understand prey selection by a predator, it is essential to know whether prey are detected but rejected or are simply inaccessible by virtue of their excessive depth below the surface. It is thus important to know which prey are actually available. Our first goal was therefore to test whether prey selection by Knot could be explained simply by their rate of encounter with different kinds of prey. To determine the fraction available, three factors need investigation:

(1) Which prey are *ingestible*. Since Knot eat prey whole, the width of their gape sets an upper limit to prey size. The prey species have different shapes, so the circumference of the shell, rather than its length, is likely to form a measure of the upper size threshold of prey that can be swallowed.

(2) Which prey are *accessible*. Since Knot probe

some three cm into the mud and the prey remain immobile when attacked, the proportion of prey living within reach of the bill can be determined exactly (Hulscher 1973, 1982, Goss-Custard *et al.* 1977a, Reading & McGrorty 1978, Zwarts & Wanink 1989).

(3) Which prey are *detectable*. Since Knot locate their benthic prey by probing (Gerritsen *et al.* 1983), the probability of finding prey of different sizes was measured using a modified version of the random touch model developed by Hulscher (1982) for touch-feeding Oystercatchers.

When the prey selected differs from what would be expected on the basis of the density of accessible and detectable prey that could be swallowed, Knot can be assumed to prefer some prey types to others. The possibility that such a selection could be predicted within the framework of an optimal foraging strategy was next investigated. This problem can conveniently be divided into two questions:

(4) Which prey are *profitable*. Since Knot take one bivalve at a time, the time needed for handling one prey item can be measured. Optimal foraging theory predicts that prey sizes for which the intake rate during actual handling is below the overall average intake rate during feeding as a whole (i.e. handling + searching measured over long intervals) have to be ignored in order to maximize intake rate (e.g. Hughes 1980).

When even prey which are both available and profitable are ignored, a short-term strategy of maximizing gross intake rate may fail to explain the observed selection. And, since food must also be processed, the final question becomes (Sibly 1981):

(5) Which prey give the *highest rate of energy yield*. Since Knot ingest the shell of the molluscs, inorganic content of the food is extremely high. If the rate at which food can be processed limits the intake rate, Knot may maximize their rate of energy gain by selecting prey with a lower inorganic content.

Methods

Knot

Data were collected on the Wierumer flats along the Frisian coast in the eastern part of the Dutch Wadden Sea (53°25′ N, 6°04′ E; see Zwarts *et al.* 1992). The majority of the Knot arrive at the end of July and leave the area by mid-August *en route* to their African wintering areas (Boere & Smit 1980, Zwarts *et al.* 1992). Observations were made on 4 August 1983, when a flock of 30 Knot fed within 20 to 30 m of the observation tower at site M (see Fig. 2 in Zwarts *et al.* 1992). The Knot fed on a plot that was situated 23 cm below mean sea level where the clay content (< 2 μm) in the upper 25 cm of the substrate was 4.8% (Zwarts 1988b). Individual Knot were watched without interruption from the tower (height 6 m) for three hours before the flood tide covered the area. The birds were observed with a mirror (40×) and a zoom (15-45×) telescope. Prey size was estimated in 1/4 cm categories with reference to the bill length (3.5 cm). The handling time of each prey lifted to the surface was measured by digital stopwatch. The time spent searching and preening was also noted. Faeces were collected from the area immediately after the observations had ended.

Prey taken by Knot

Actual prey size was reconstructed from fragments found in the faeces and in eighteen gizzards from Knot collected on the island of Vlieland (Dutch Wadden Sea) between 23 August and 24 October 1982. In bivalves, the relation between umbo width and shell length was used: as an example, *Macoma* is shown in Fig. 1. Body length of the Ragworm *Nereis diversicolor* was estimated from jaw length (calibration curve

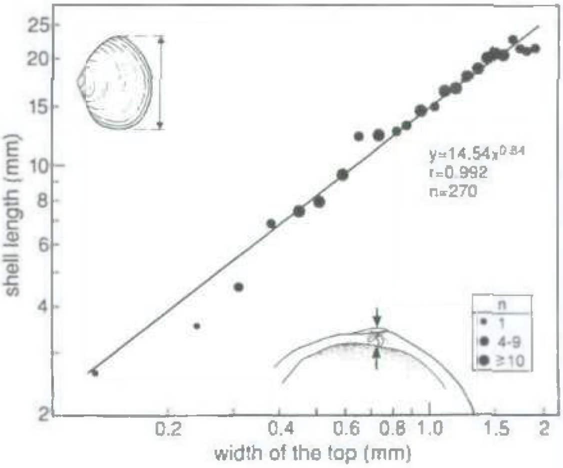


Fig. 1. *Macoma*. Length predicted from width of the umbo. The function is calculated for 24 means, weighted for sample size.

in Zwarts & Esselink 1989). The length of *Corophium volutator* was derived from the relationship between the length of the second antennae and body length. The size of Shore Crabs *Carcinus maenas* was estimated from the relationship between carapace width and the size of the propodus of the pincer. Intact *Peringia* were measured directly.

Prey available

Prey were divided into 1 mm size classes, and the density of each class was determined at the time the observations were made using a standard sampling programme, sixteen samples of 1/56 m^2 being taken (Zwarts 1988b). The burying depth of the bivalves was measured using methods described in Zwarts & Wanink (1989).

The laboratory procedures for measuring the flesh weight of each mm class (ash-free dry weight, AFDW) are given in Zwarts (1991). The allometric relationships between AFDW and shell length in the six potential prey species (Fig. 2) are based on data collected in the study area in August, at the time the observations were made. No data for *Peringia* are available, so published values are used (Chambers & Milne 1979, Dekker 1979). Since Knot swallow the shell, Fig. 2 also shows the relation between length and dry weight of the empty and cleaned shell. In order to be able also to measure food intake in terms of wet weight, samples of *Macoma*, *Cerastoderma* and *Mytilus* were weighed immediately after being collected, without any surface water being removed. Table 1 gives the allometric relationships for wet weights. The percentage of water hardly differed among the three bivalve species. Normally, the proportion of water in marine benthos is around 78% (own unpubl. data), but the three species in Table 1 had a much greater proportion: 91 to 93%, excluding the shell. The reason for this was that, when collected and so disturbed, bivalves shut their valves firmly and enclosed some seawater. *Cerastoderma* contained 1.5× as much water relative to the amount of flesh as did *Macoma* and *Mytilus*. The salinity of the water in the shells was 27.5‰ (n = 3, SD = 0.2), similar to that in the surrounding water.

Results

Gizzard analysis

Seven of the eighteen gizzards contained no prey fragments. One contained ten umbos of *Macoma*, with an estimated shell length of 15 to 16 mm. Shell fragments of *Cerastoderma* (but no umbos) and four pincers of *Carcinus* (estimated carapace width c. 8 mm) were found in another gizzard. The remaining nine gizzards held a total of 1022 *Peringia*. Though many were damaged, the shell length of 17% and shell width of 44% of the *Peringia* were determined (left inset in Fig. 3). Width was converted to shell length (right inset in Fig. 3). Larger snails were more often fragmented than small ones (Fig. 3), so it was difficult to quantify size selection. Prey length averaged 2.36 mm (SD = 0.60) in the subsample of specimens for which length could be measured directly. However, length was 2.86 mm (SD = 0.79) in the subsample for which only the width was intact. Most likely the average size for the entire sample was 3 mm or more, because the unmeasurable fraction were probably above average sizes. Though differences among shell lengths were small, the three

Table 1. Relations between total wet weight and length in three bivalve species, freshly taken from the substrate in September 1988. Since the relation between ln(weight) and ln(length) appeared to be concave in two of the three species, polynomial lines were fitted. The functions were calculated for the means per mm class, weighted for the number of observations; $y = \ln(mg)$ and $x = \ln(mm)$. Water content (± SE) and flesh content are given as a percentage of the total wet weight, including the shell. Dry flesh content was not measured in the sample itself, but estimated from weight-length equations calculated for samples taken from the same area in the same period.

Species	*n*	*r*	*Equation*	*Water, %*	*Flesh, %*
Macoma	298	0.998	$y = 2.559 + 0.803x^2 - 0.743x$	54.12 ± 0.24	5.5
Cerastoderma	320	0.999	$y = -1.226 + 3.0234x$	55.72 ± 0.22	3.8
Mytilus	173	0.998	$y = 4.083 + 0.526x^2 - 0.642x$	51.90 ± 0.21	5.0

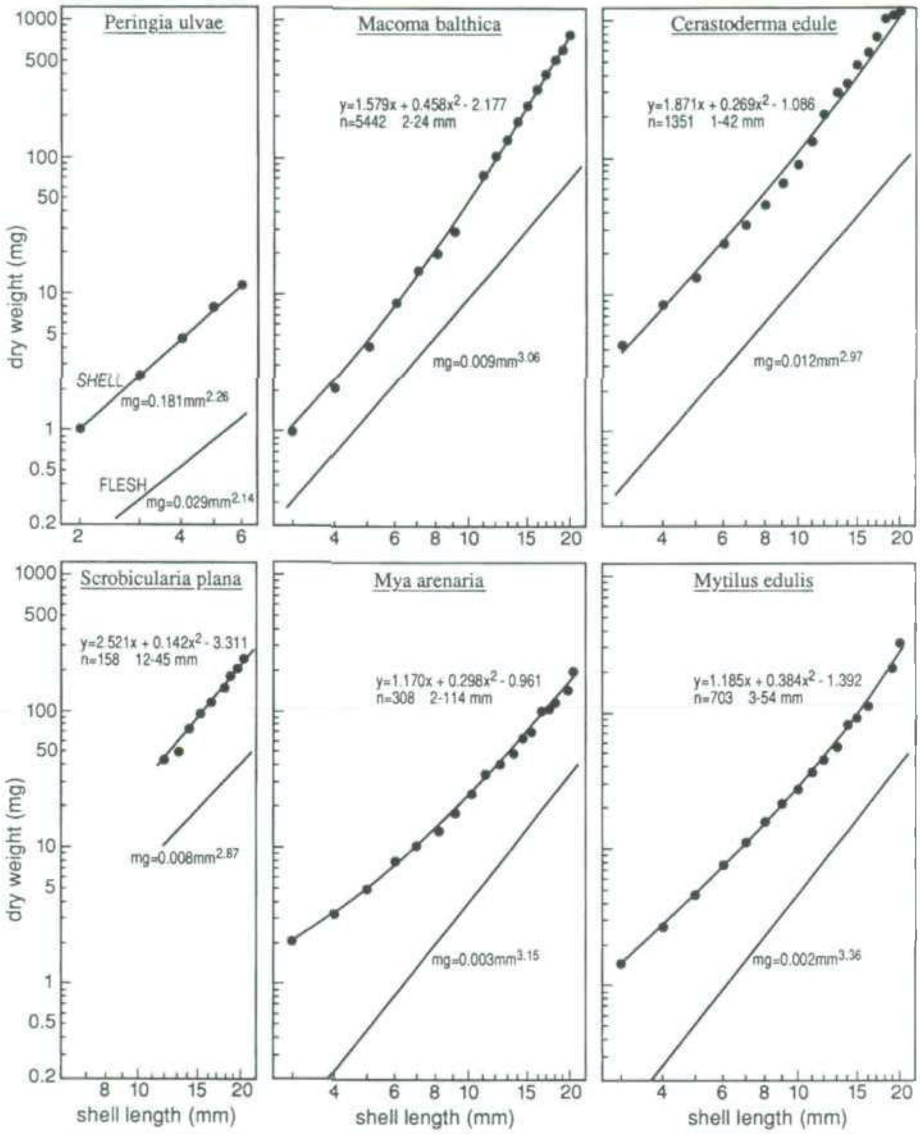


Fig. 2. Relations between dry weight of the cleaned shell (mg dry weight) and shell length (upper line), and between flesh weight (mg ash-free dry weight) and shell length (lower line) in six hard-shelled species. All data, except for *Peringia*, were collected in the study area in August; data were pooled for 11 years of sampling (from Zwarts 1991 and unpubl.). Data for *Peringia* were taken from Chambers & Milne (1979) and combined for May and November; a correction is made for the 3% organic matter found in the shell (Dekker 1969), representing 10 to 15% of the total organic mass. Since the relation between ln(shell weight) and ln(length) appeared to be concave in the bivalves, a polynomial line was fitted. The functions were calculated for the means per each mm size class, weighted for the number of observations. All correlations were larger than 0.995. The functions are indicated in the panels ($y = \ln(mg)$ and $x = \ln(mm)$), as well as the number of measurements and the range over which the regressions were calculated.

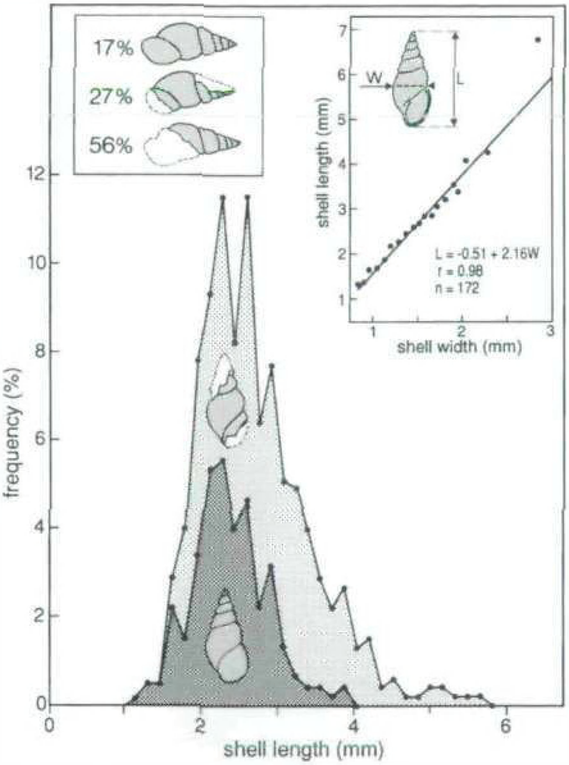


Fig. 3. *Peringia*. Size frequency distribution of 450 individuals found in nine gizzards of Knot collected on Vlieland, Dutch Wadden Sea, during the period 15 August to 24 October 1982. Dark shading: snails for which the length could be determined. Light shading: crushed snails for which width at the base, but not length, could be measured and for which length was derived from the relationship between width and length in undamaged snails (see right inset). Left inset shows that in more than half of the snails width nor length could be measured (100% = 1022).

estimates of shell length give values of average flesh weight of prey taken by Knot which differ by 50%, due to the fact that flesh weight allometrically relates to shell length with a power of 2.14 (Fig. 2).

Prey selection

According to our observations, not all prey taken from the mud were actually swallowed: 63 of the 84 *Macoma* brought to the surface, were ingested, and only one in four of the *Cerastoderma*. Two shrimps *Crangon crangon* 5 cm long were handled for several seconds but finally not eaten. Rejection of the latter two prey species was unexpected as *Cerastoderma* is a major prey elsewhere (Goss-Custard *et al.* 1977b, Boere & Smit 1980, Nehls 1992) and faecal analysis showed that Knot can feed on shrimps 43 to 63 mm long (own unpubl. data).

Both the field observations and faecal analysis indicate that *Macoma* was the main prey and that *Cerastoderma*, *Nereis* and *Corophium* were rarely taken (Table 2). Even though very few of the prey seen eaten were too small to identify, 360 Mud Snails *Peringia* (1 to 3 mm) and six very small bivalves (1 to 2 mm) were found in the faeces. However, all were intact and contained flesh, so they must have been accidentally scraped from the surface while the faeces were being collected.

One of the Knot observed produced 15 faeces during 21 min of continuous observation. All but one of the intervals between faeces depositions varied between 58 and 88 s. The exception was 174 s long, suggesting that we missed one faecal packet during one interval. If so, Knot produced one faecal packet per 80 s. Therefore the faeces that were collected reflected a period of 20 × 80 s, or 26 min, feeding. Since the total time spent watching the birds was 83 min, the number of prey seen taken should have been 83/26 or 3.2 times as large as the number found in the faeces, and

Table 2. Prey taken by Knot during 82 min (left column) and prey found in 20 faeces from the same individuals (right column), Wierumer flats, Dutch Wadden Sea, 4 August 1983. Among the prey taken, three were so small that the species could not be identified. The number of prey in the faeces was determined by counting unique fragments (jaws of the Ragworm *Nereis*, second antennae of *Corophium*, umbos of *Macoma* and *Cerastoderma*); since each animal has two such fragments, the numbers found were divided by two. Animals accidentally scraped from the surface are indicated in parentheses.

	No. prey observed	*No. prey in faeces*
Macoma > 9 mm	63	19
Cerastoderma 12 mm	1	0.5
Nereis	1	0.5
Corophium	3	0.5
Macoma spat	3	(2)
Cerastoderma spat		(4)
Peringia		(360)

this was indeed so (Table 2): in *Macoma* the ratio was 3.3. Thus, faecal analysis confirmed the visual observations of prey selection.

Size selection

Estimates of prey size made by eye in the field suggested Knot took *Macoma* between 3/4 and 2 cm long, but faecal analysis showed that the size range was narrower (0.9 to 1.6 cm; Fig. 4). It appears that the observers overestimated the sizes of the larger prey and underestimated those of the smaller ones. In order to correct the visual estimates, a cumulative frequency distribution was made of the size classes found in the faeces. This allowed the average size of the six categories used for estimating prey size visually in the field to be superimposed on the frequency distribution of the actual size classes taken (inset in Fig. 4). To increase the sample size for the smallest prey categories, the few prey classified in the field as 0.75, 1 or 1.25 cm long are combined for purposes of this study.

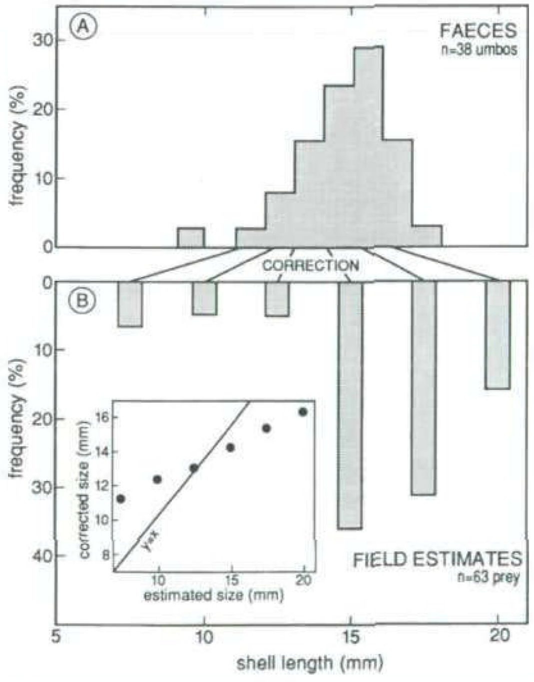


Fig. 4. *Macoma*. Size frequency distribution of prey taken by the same Knot according to **A.** faecal analysis and **B.** visual estimates in the field. Inset gives the function used to correct the visual estimates of prey size.

A quarter of all *Macoma* handled by Knot were not swallowed. Although occasionally small *Macoma* were lost during handling, most rejections concerned large prey, refused after a 5 to 6 s frantic handling effort. The larger the prey, the more were rejected (Fig. 5A). Since half of the *Macoma* 16 mm long were re-

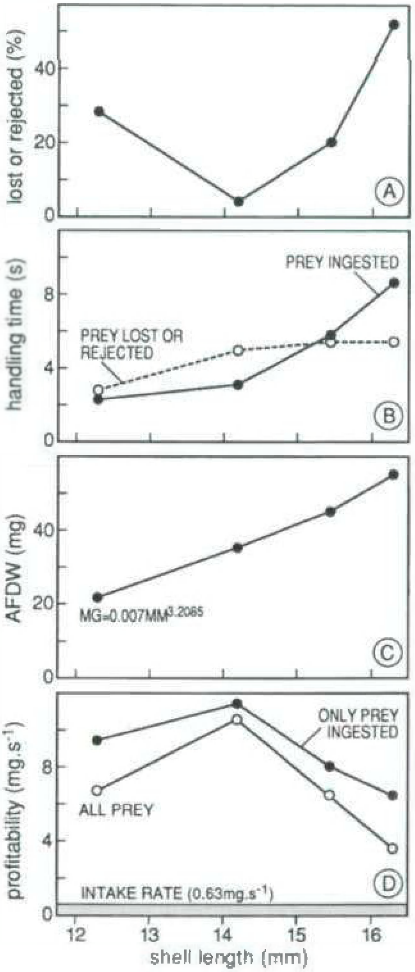


Fig. 5. *Macoma*. The handling of different sizes by Knot. **A.** Percent prey lost or rejected. **B.** Handling time of prey swallowed by Knot and lost or rejected. **C.** Ash-free dry weight (AFDW) as determined in 1062 specimens collected, r = 0.999. **D.** Profitability (mg AFDW s^{-1} handling) of prey swallowed. The upper line represents only the prey that were swallowed; the lower line reflects the profitability after taking into account the time lost during handling of rejected prey (see panel A); the intake rate (mg AFDW s^{-1}) during feeding is indicated by grey shading.

fused, specimens larger than this were clearly too large for Knot. Knot handle *Macoma* with a series of 'catch and throw movements' during which the food is transported up the bill (Gerritsen 1988). The larger the prey, the greater the number of catch and throw cycles required, and so handling time increased with prey size (Fig. 5B).

The profitability of each prey size, expressed as mg AFDW s^{-1} handling, was calculated from the relation between prey size and handling time (Fig. 5B) and between prey size and AFDW (Fig. 5C). As handling time increased disproportionably to the amount of flesh, the profitability decreased in the larger size classes (Fig. 5D). This decrease was even larger when the time lost in handling rejected prey finally was taken into account (Fig. 5D).

Intake rate

During 67 min of feeding, Knot took 63 *Macoma* whose average weight was 39.6 mg AFDW. The contribution of the three other prey species to the total food intake was only 1%. AFDW of the single 11 mm Cockle taken was 16.2 mg, of the three *Corophium* 3×0.4 mg, and of the single 4 cm Ragworm 7.6 mg. The total intake rate was 0.63 mg s^{-1}, excluding 18.8% of the observation time spent preening, usually in short bouts. With this non-feeding time included, the overall intake rate decreased to 0.51 mg s^{-1}.

Density of available prey

Though the Knot fed in a rich area (Fig. 6), not all prey may have been available. Below we attempt to quantify which prey were actually available to Knot.

Ingestible prey

Though *Macoma* between 3 and 21 mm were present (Fig. 6), no prey larger than 16 mm long were taken (Fig. 4). Since more than half of *Macoma* 16 mm long were rejected (Fig. 5A), this is presumably the largest prey that is normally ingested. The same upper size limit was also found by Prater (1972), Goss-Custard *et al.* (1977b), Nehls (1992) and Piersma *et al.* (1993b). This limit is probably not determined by length *per se*, but by the combined effect of shell width and height. The 'catch and throw movement' made by Knot handling a large shell (Gerritsen 1988) is intended to bring the prey with its longest axis parallel to the bill. Since the gape has to be stretched wide to allow a large, hard-shelled prey to be swallowed, the upper size limit is determined by the circumference of the shell in a plane perpendicular to the length axis.

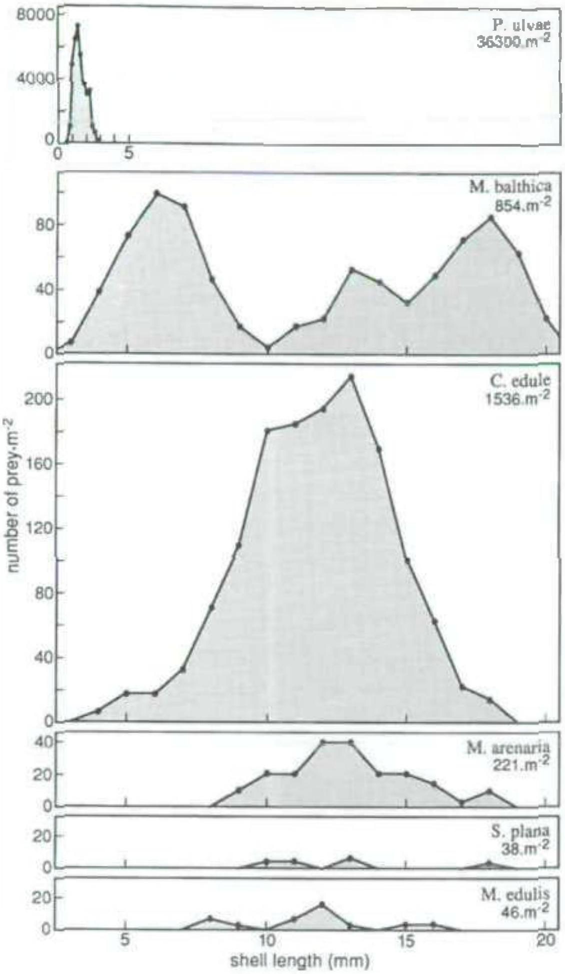


Fig. 6. Density of each size class of the Mud Snail *Peringia* and five bivalve species (*Macoma*, *Cerastoderma*, *Mya*, *Scrobicularia* and *Mytilus*) on the site where Knot fed. Note different vertical scales. Large *Cerastoderma* (23 to 33 mm; 150 specimens m^{-2}); *Mya* (23 - to 41 mm; 21 m^{-2}) and *Scrobicularia* (38 to 43 mm; 21 m^{-2}) are not shown. See table 3 for the total biomass m^{-2} for the six species.

These considerations of dimensions of course apply to all bivalves. In all species studied, a size-independent ratio was found, whereby the shell circumference of the prey was 1.5 to 1.6 times greater than the sum of its width and height. This shape index was lowest in *Mytilus* (1.51; SE = 0.007, n = 11) and highest in *Scrobicularia plana* (1.62; SE = 0.01, n = 10) (see Fig. 7C). There was a very close relationship between shell length and shell width (Fig. 7A) and between shell length and shell height (Fig. 7B), so the circumference could be predicted accurately for each length class (Fig. 7C).

The circumference of 16 mm long *Macoma* is 30.6 mm (Fig. 7C). As shown in Fig. 7C, all *Cerastoderma* longer than 12 mm could not be ingested, whereas the predicted upper limits for the more slender *Mya arenaria*, *Scrobicularia plana* and *Mytilus* would be 17, 19 and 21 mm, respectively. Data to test the predicted upper size limits are scarce, but agree with these values. Knot rarely took *Cerastoderma* longer than 10 mm (Goss-Custard *et al.* 1977b, Nehls 1992, Piersma *et al.* 1993b), but did swallow prey 18 to 19 mm long among the more oblong *Mytilus* (Prater 1972, Piersma pers. comm.). Though length itself also might set a limit to the size of prey Knot could swallow, there are no data available for this, so the circumference of 30.6 mm measured in *Macoma* is taken as the limit for all species. Even the largest *Peringia* length 6 mm, remained far below this limit.

Accessible prey

All *Peringia* and Mussels *Mytilus* were considered accessible, as they live at the surface. The other four bivalve species occurred at various depths beneath the surface. Based on work done in the same locality (Zwarts & Wanink 1989), the proportion of the prey living in the upper two or three cm of the substrate is shown in Fig. 8.

Which prey would be within reach of a bill 35 mm long? Assuming that a Knot needs c. 5 mm purchase on a shell of 10 mm or longer, the distance between the mud surface and the upper edge of the bivalve (burying depth) would have to be less than 30 mm for a Knot to take a prey. However, not all of this upper 30 mm would be fully exploited, as only some probes were made to the base of the bill. The upper 10 to 20 mm must have been searched more thoroughly than the deeper layer. Most probes of the closely related

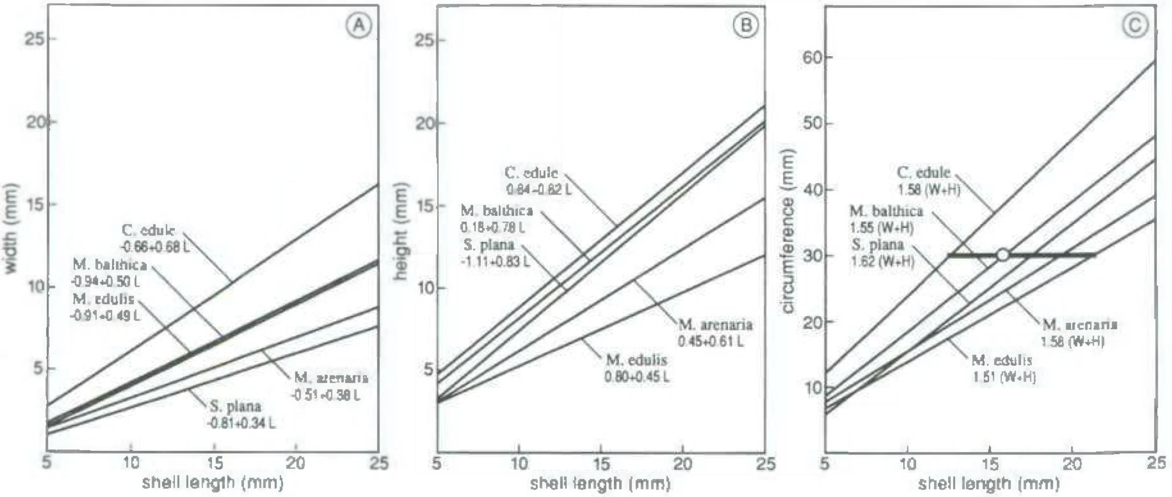


Fig. 7. A. Shell width, **B.** shell height and **C.** shell circumference as a function of shell length in five bivalve species. Length, height and width were measured in 608 *Macoma* (r = 0.984, r = 0. 993 for width versus length and height versus length, respectively), 400 *Cerastoderma* (r = 0.995 and 0.998), 292 *Mya* (r = 0.995 and 0.997), 347 *Scrobicularia* (r = 0.985 and 0.993) and 304 *Mytilus* (r = 0.995 and 0.996). The circumference (panel C) is derived from the 'shape index', the ratio between the measured circumference and the sum of width and height. The shape index differed significantly in the five species according to a one-way analysis of variance (n = 51, $R^2 = 0.60$, $p < 0.0001$); the standard errors for the five species were less than 1% of the average shape index. In C, the predicted critical upper size threshold for Knot, based on Knot eating *Macoma* (○), is indicated by a bar.

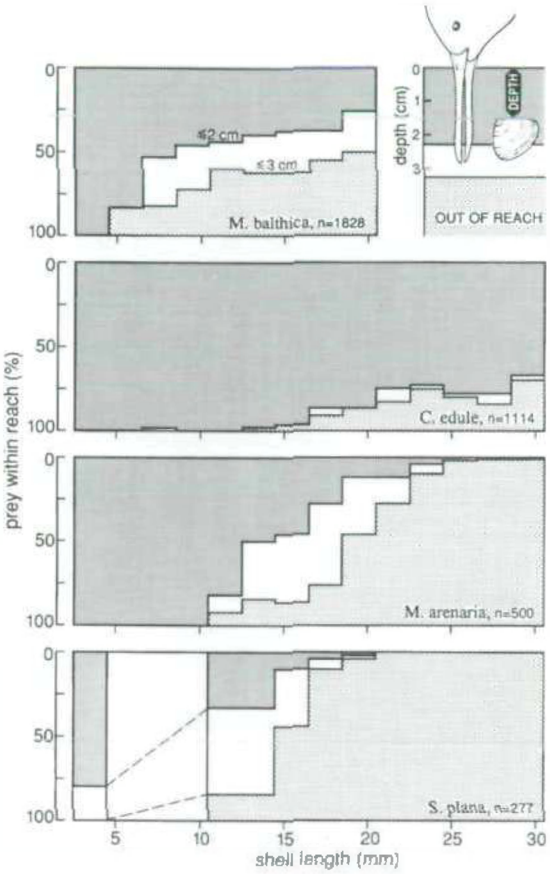


Fig. 8. Percentage per size class of four bivalve species living in the upper 2 cm or upper 3 cm of the substrate, as a measure of the fraction of prey accessible to Knot. The data, collected in the study area, are based on Zwarts & Wanink (1989) and are from August for *Macoma* and July to September for *Cerastoderma* and *Mya*. Since small *Scrobicularia* rarely occurred in the study area during the years of sampling, the data were lumped for the entire year and supplemented with depth measurements from Wales (Hughes 1970).

Sanderling *Calidris alba* (bill length 26 to 27 mm) were 20 mm deep (Gerritsen & Meiboom 1986) and the probing depths of an Oystercatcher (bill length 70 mm) averaged 40 mm (Wanink & Zwarts 1985). This suggests that prey living in the upper two cm (Fig. 8) likely would be accessible to Knot.

Detectable prey

Taking into account the fraction of prey that is too large to be eaten or are living too far down to be reached, the density of the available prey in the study site is reduced from 2705 to 1412 bivalves m^{-2}. But not all of these may be detectable, except perhaps *Mytilus*, which is visible on the surface. The other bivalves were found by probing vertically downward, in the same way Oystercatchers search for *Macoma* (Hulscher 1982). The probability of a prey being touched depends primarily on its surface area measured in the horizontal plane. Hulscher (1982) measured this 'touch area' by photographing bivalves in their natural position from above, the mud having been carefully removed beforehand. Wanink & Zwarts (1985) measured 'touch area' in *Scrobicularia plana*, by determining the surface area left by prey pressed into modelling clay. The latter technique was also used here. The natural position of the bivalves in the substrate is shown in Fig. 9. Touch area was closely re-

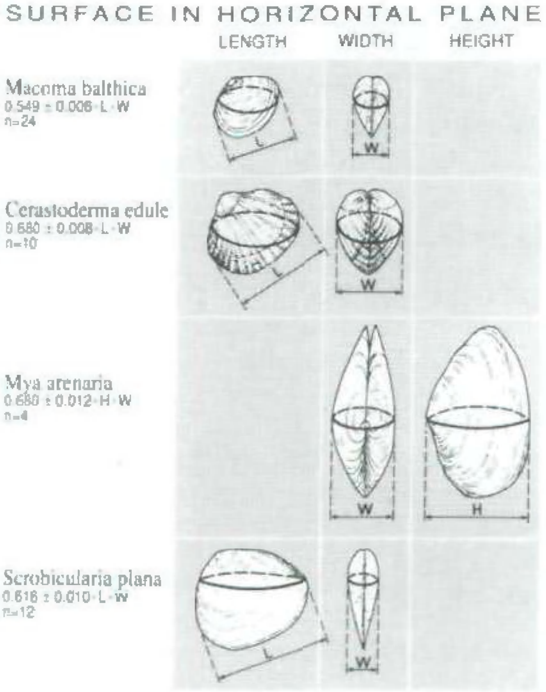


Fig. 9. Surface area ('touch area') of four bivalve species given as a function of the ratio of shell length and width, except in *Mya arenaria* for which shell height and width were used. Number of measurements and standard error of the ratios are given. 'Touch area' refers to the maximal surface area of bivalves buried in their natural position, measured in a horizontal plane.

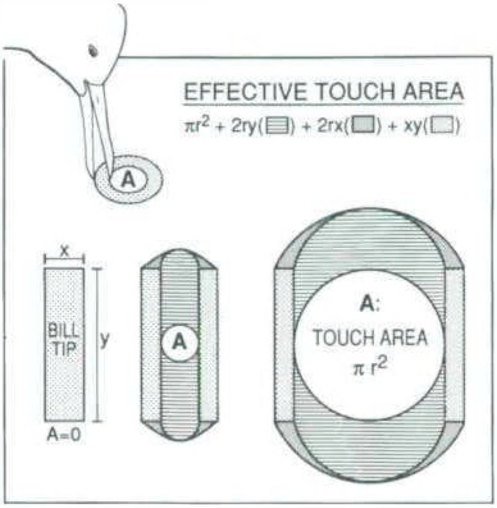


Fig. 10. 'Effective touch area' of a bivalve as a function of the 'touch area' of the shell, enlarged by the surface of the bill tip, shown for three situations: zero, small and large 'touch area'. For simplicity, 'touch area' is shown as a circle. The surface of the tip of the two (opened) mandibles is indicated with a rectangle; see text for further explanation.

lated to the product of shell width and shell length (Fig. 9); width and height were used in *Mya arenaria*, due to their different position in the mud. The index was similar for different size classes; the standard errors were very small (Fig. 9).

Like Oystercatchers (Hulscher 1982), sandpipers, such as Knot, probe with an open bill, apparently to increase the effective touch area (Gerritsen & Meiboom 1986, Gerritsen 1988). The touch surface of a slightly opened Knot bill is about 3×7 mm (Gerritsen 1988, own unpubl. data). For simplicity, the prey is considered a circle (with radius r) and the (opened) bill a rectangle (with x and y as sides). The 'effective touch area', which equals the touch area of the prey enlarged by the surface area of the bill tip, can then be expressed as a function of the three variables r, x and y (Habekotté 1987). Figure 10 shows that the surface of the bill adds an important increment to the touch area, especially for the smaller prey.

Since the touch area is a simple function of shell length and width or, in *Mya arenaria*, shell width and height (Fig. 9), the surface area can be calculated from the shell dimensions (Fig. 7A, B). The calculated surface is given in Fig. 11 as an allometric function of length. The expected exponent of this equation would be 2 if the shape of the shell was the same in all size classes. In fact, the exponent is larger than 2, and greatest in *Macoma*. The reason is that small bivalves are more slender than large ones, particularly in *Macoma*. The data in Fig. 11 for *Macoma* coincide well with those of Hulscher (1982), taking into account that his measurements are for more slender specimens (Hulscher pers. comm.), as were the data for *Cerastoderma* obtained by Hulscher (1976) and for *Scrobicularia plana* obtained by Wanink & Zwarts (1985).

To calculate the effective touch area, the touch area given in Fig. 11 was transformed to a circle to find the derived variable r. With r and bill dimensions x and y known, the touch area was converted into effective touch area. The calculated effective touch area is shown as a function of shell length for *Cerastoderma* in Fig. 11. The risk of prey being encountered by a probing Knot increased 25-fold for all species within the range of size classes shown. The effective touch

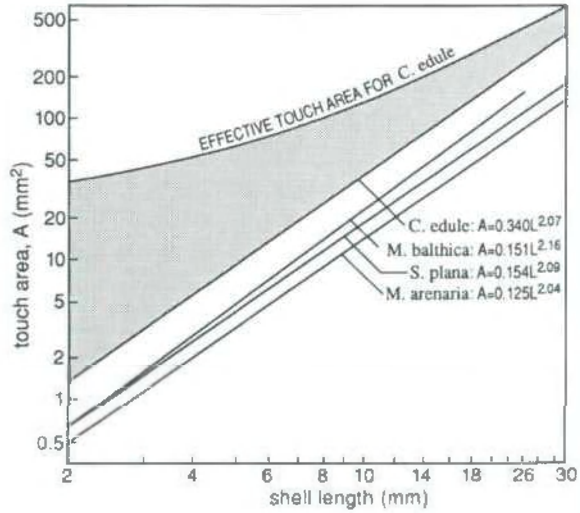


Fig. 11. 'Touch area' of four bivalve species (*Cerastoderma*, *Macoma*, *Scrobicularia* and *Mya*) as a function of shell length. The 'touch area' is calculated from the same data used in Fig. 7A & B. The relations between surface and dimensions of the shells (Fig. 9) were used to calculate the regressions shown. The grey field shows the enlargement of the 'touch area' for *Cerastoderma* when the surface of the bill is taken into account: this gives the 'effective touch area' (see Fig. 10 and text for further explanation).

area is twice as large as the touch area for bivalves > 10 mm, but more than 20 times as large for bivalves 2 mm long. This confirms the importance of the large touch area of the bill tip itself.

Selection of available prey

In this section we derive the relative risk of prey being taken by Knot, according to the random touch model, but without *Mytilus* and *Peringia*, which Knot could locate visually. The total effective touch area of all benthic prey together is the product of effective touch area per size class (Fig. 11) and density per size class (Fig. 6). Assuming that during a probe a prey is either hit or missed completely, and that two prey are never hit in one probe, the bill must encounter a prey 44% of the times the Knot is probing (no depth restriction). However, if it is assumed that the probing depth was only 2 cm (see Fig. 8), the percentage of hits decreases to 35%. If the prey that are too large to be ingested are also excluded, the percentage is reduced to 15%.

This 15% represents the effective touch areas of all available prey, i.e. the accessible fraction of the ingestible size classes of all species. Assuming that Knot took all ingestible prey which they encountered, they would take hardly any *Scrobicularia* (1%), only a few *Mya* (8%), and some *Macoma* (21%), but the majority would be *Cerastoderma* (70%). In fact, however, 98% of the 64 prey ingested were *Macoma* and only 2% were *Cerastoderma*. Clearly, Cockles were rejected. A similar comparison between the frequency of occurrence of the various *Macoma* size classes in the diet of Knot (Fig. 4A) and the predicted frequency distribution according to the random touch model (Fig. 12) shows that many small *Macoma* also must have been completely rejected.

The observed Knot walked slowly and probed continuously in the manner described earlier by Goss-Custard (1970b). The data suggest that a Knot had to probe, on average, 6.5 times to a depth of 2 cm before a prey was encountered. However, since the diet was restricted to *Macoma* 9 to 16 mm long, 91% of the prey encountered were ignored. A Knot thus had to probe 71 times before a prey of the preferred type was found. The average searching time per prey captured, whether ingested or not, was 43 s, which means that on average, 1.6 probes were made per second of searching.

Discussion

Small prey are unprofitable

Why did Knot ignore *Peringia*, which occurred at such a high density, while in other areas and at other times of the year this prey is the only food taken (Ehlert 1964, Lange 1968, Höfmann & Hoerschelmann 1969, Goss-Custard 1970b, Prater 1972, Piersma 1989, Nehls 1992, Piersma *et al.* 1993b, Fig. 3 in present study)? Why did Knot refuse small *Cerastoderma*, even though 70% of the ingestible benthic prey encountered were of this species (Fig. 12)? Why did Knot ignore the many small *Macoma* (Fig. 12), as was also found by Prater (1972) and Goss-Custard *et al.* (1977b)?

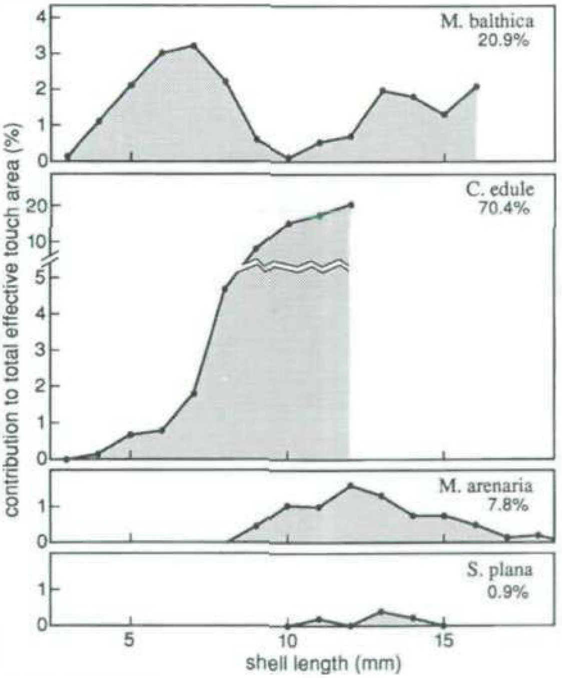


Fig. 12. Probability that Knot encounter prey of different species (*Macoma*, *Cerastoderma*, *Mya* and *Scrobicularia*) and size classes. Prey densities, given in Fig. 6, were adjusted by omitting size classes too large to be swallowed (Fig. 7C) and by determining the number of prey lying in the upper 2 cm (Fig. 8). The 'effective touch area' for the available prey was calculated with the functions given in Figs. 10 & 11. The panels give thus the relative contribution of each size class to the summed total 'effective touch area' of all bivalves available for Knot.

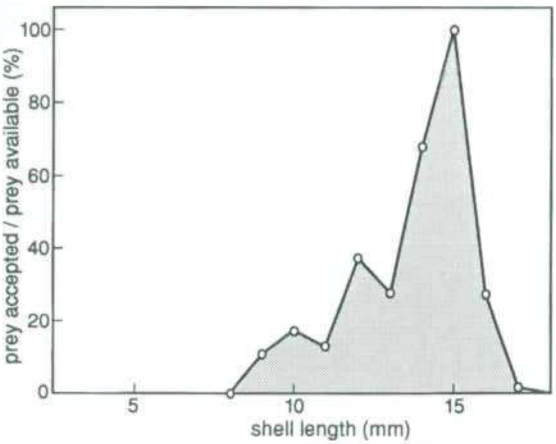


Fig. 13. Selectivity of Knot feeding on *Macoma* living in the upper two cm of the substrate. The frequency distribution of the size classes taken by Knot (Fig. 4A) was divided by the predicted frequency distribution on the basis of size and depth (Fig. 12, upper panel). The ratio was highest for prey of 15 mm; selection ratios for all other size classes are expressed relative to this maximum, set at 100%.

Predators maximizing their intake rate while feeding must ignore prey for which the intake rate during handling ('profitability') is lower than the average current overall intake rate, which includes the time spent both handling and searching for prey. The reason for this is that a predator taking such unprofitable prey would inevitably lower its overall intake rate (see reviews by Hughes 1980, Krebs & Kacelnik 1991). Figure 5D shows that the profitability (energy intake / handling time) of the size classes selected by Knot varied between 3 and 11 mg s^{-1}, thus being far above the current intake rate (0.63 mg s^{-1}). All the size classes taken were profitable. In the following section, we explore the implications of introducing a more stringent acceptance threshold.

According to our observations, the handling time of small *Macoma* levelled off at about 2 s. Taking these 2 s as the minimal handling time and using the allometric relation between AFDW and shell length (Fig. 5C), the profitability of *Macoma* 7, 6, 5 and 4 mm long decreased from 1.8 to 1.1, 0.6 and 0.3 mg s^{-1} respectively. With an overall intake rate of 0.63 mg s^{-1}, Knot should ignore any *Macoma* they encounter smaller than 6 mm long. The prediction is thus that all shells below 6 mm should be rejected and all larger ones accepted. However, as shown in Fig. 13, prey below 9 mm were refused. Moreover there was not a step-wise acceptance threshold level, as we predicted, because prey 9 to 11 mm long were taken much less frequently than expected. By ignoring such profitable prey, Knot would not maximize their intake rate. The effect on intake rate of ignoring profitable prey may be calculated, since encounter rate, λ_i, handling time, h_i, and flesh weight, E_i, are known for each size class i. The encounter rate, λ, is the inverse of the searching time. Assuming that a Knot made 1.6 probes s^{-1}, λ_i can be estimated from the random touch model (see Fig. 12). The two other variables were measured directly.

The overall intake rate, total energy E obtained in total time T, is calculated from a multi-species functional response equation (Charnov 1976):

$$\frac{E}{T} = \frac{\Sigma \lambda_i E_i}{1 + \Sigma \lambda_i h_i}$$

The intake rate was calculated assuming that (1) all *Macoma* (size 9 to 16 mm) encountered were pulled to the surface, and (2) the proportion of prey lost or rejected was as observed in the field (Fig. 5A, accepting the proportion of the 12 mm size class as applying to all smaller prey). The change in intake rate when the acceptance threshold for prey size was varied is shown in Fig. 14. Clearly, it did not matter whether Knot accepted all *Macoma* larger than 3 mm or larger than 11 to 12 mm. The reason for this is that the profitability of the size classes around 6 mm long was close to the current intake rate.

The profitability rule also can be used to calculate the lower size threshold for other prey species. The relation between shell size and dry flesh weight is taken from Fig. 2. These data represent average weights in August, calculated for a data set from 11 years (Zwarts 1991); note that the body condition of *Macoma* at site M during the year of observation was 18% above this average (see Figs. 2 & 5C). Assuming that only a single size class is available for a given period, the rate at which prey must be taken to achieve an intake rate of 0.63 mg s^{-1}, as found in this study, can be calculated (Fig. 15). To achieve this rate, from 22 to 341 prey 1

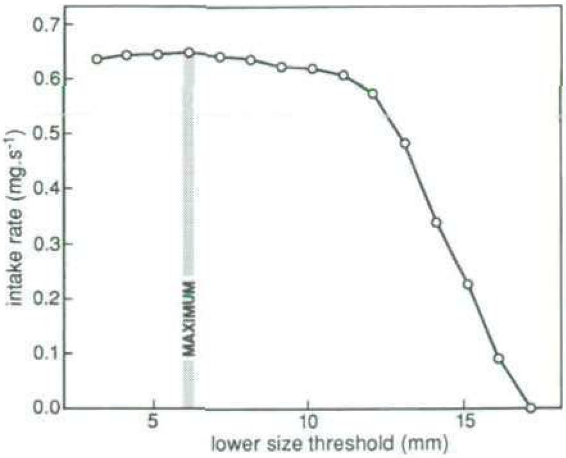


Fig. 14. Effect of a shift in the lower acceptance threshold on intake rate of Knot while feeding. The calculations are based upon three variables: encounter rate, handling time and weight of the prey of each size class; see text for further explanation. According to the prediction, prey smaller than 6 mm should be refused but, as shown, intake rate did not change much when the lower limit was several mm lower or higher than this.

mm long have to be taken per second, depending on the prey species selected. This is quite impossible, however. A Knot already requires 0.4 s to transport a small piece of flesh up the bill (Gerritsen 1988). Taking this as the absolute minimum, the lower limit of profitable prey is indicated in Fig. 15 (Threshold A). The resulting prediction is that all size classes below 3 or 4 mm would be ignored by Knot. There are three reasons why this lower size threshold may, in fact, be higher. Firstly, if prey have to be extracted from the mud, a more realistic estimate of the shortest handling time may be one prey item per 2 s. The lower acceptance threshold must therefore be higher for the buried bivalves (Threshold B in Fig. 15) than for prey found at the surface (Threshold A).

Secondly, the foregoing calculations assume that prey recognition is instantaneous once prey have been encountered, which only seems plausible if Knot rely solely on visual cues. Since Knot are touch-feeders (Gerritsen *et al.* 1983), they must take a certain amount of time to recognize prey types buried in the substrate, and this recognition time should be added to handling

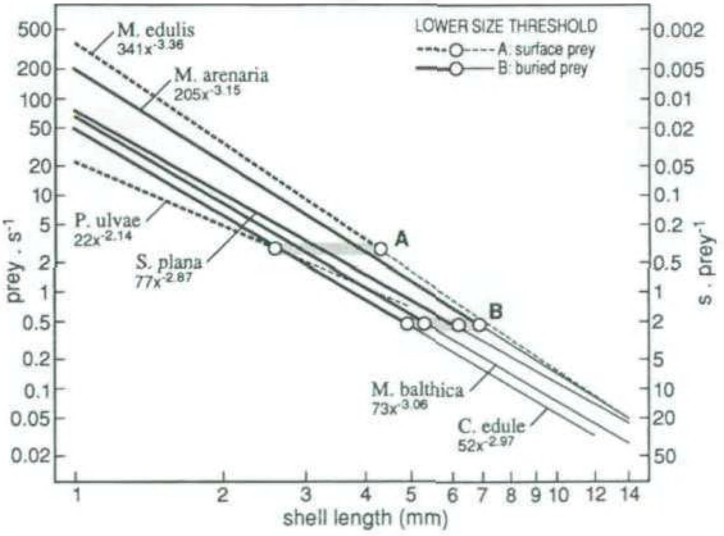
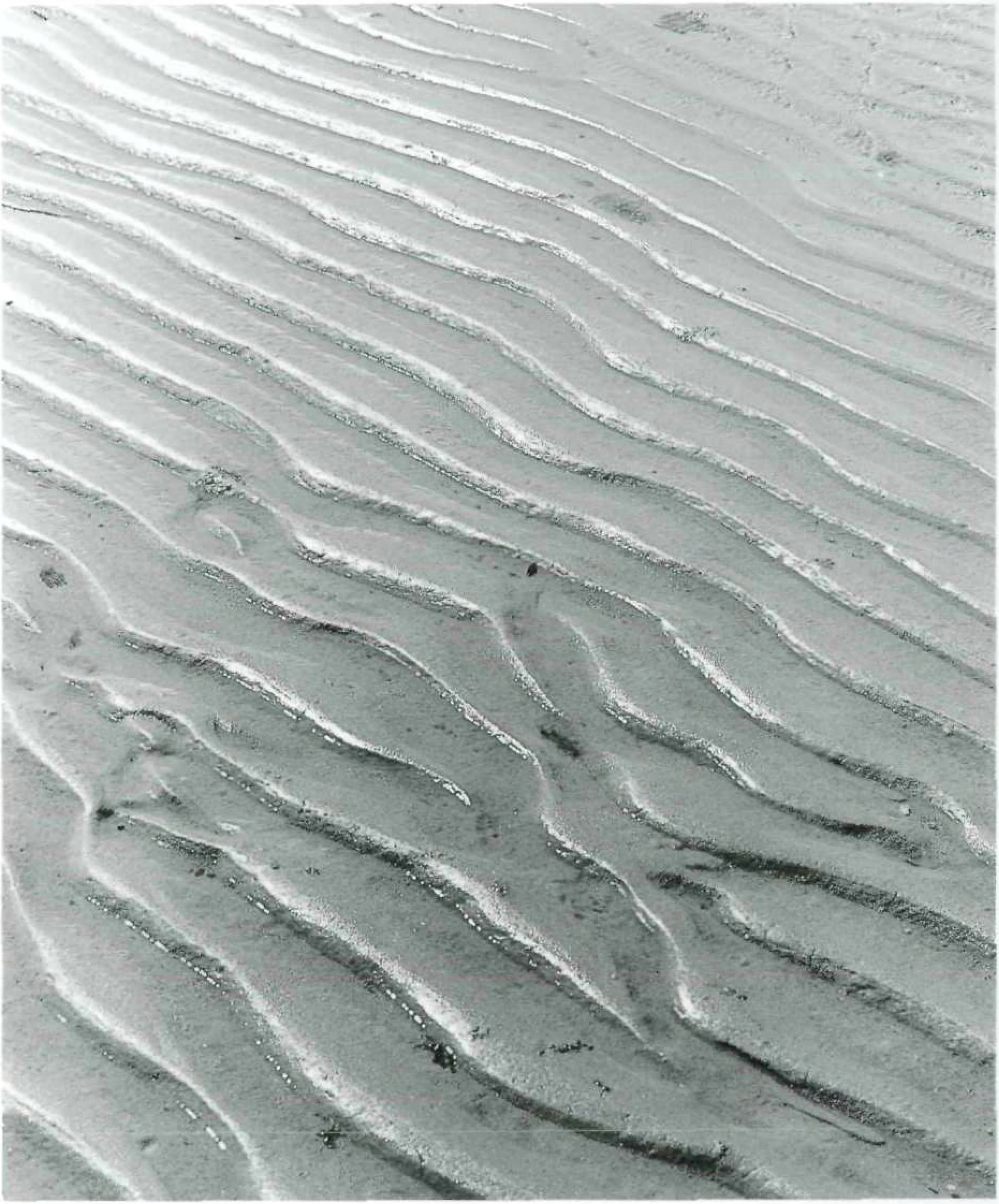


Fig. 15. Maximum feeding rate (prey in summer condition swallowed s^{-1}; see Fig. 2) for five bivalve species (*Mytilus, Mya, Scrobicularia, Macoma* and *Cerastoderma*) and *Peringia*, assuming that Knot eats prey of the same size class while its intake rate remains at a level of 0.63 mg s^{-1}. The graph shows that a Knot has to take small prey at an improbably high rate to achieve this intake rate. The size thresholds reflect situations when prey can be taken without spending time searching; the handling time is set at 0.4 s (Threshold A), thought to be the shortest handling time for prey taken from the surface, or 2 s (Threshold B), assumed to be the shortest time needed to extract and ingest prey from the mud (Threshold B).



Knot have to probe their bill into the substrate to locate their bivalve prey.

time (Hughes 1979). This would further reduce the profitability of all size classes, and would cause an upward shift in the lower acceptance threshold.

Thirdly, when only prey similar in size to the lower size thresholds are available, Knot cannot lose time searching for them; they must handle prey continuously. This situation is rarely found. However, *Peringia* occur at densities of several individuals cm^{-2}, one of the rare situations where it seems possible to feed on prey without spending time searching. The Knot on Vlieland took *Peringia* 2 to 4 mm long (Fig. 3), as was also the case in Wash Bay, England (Goss-Custard *et al.* 1977b). *Peringia* of 2, 3 and 4 mm contain 0.12, 0.30 and 0.55 mg dry flesh, respectively (Fig. 2). Assuming these snails are handled in 0.4 s, the highest possible intake rate would be 0.5, 0.8 or 1.4 mg s^{-1}, according to whether all the prey were 2, 3 or 4 mm long. In other words, Knot should be able to reach the observed 0.6 mg s^{-1} only if snails 3 mm and larger were taken. However, in the study area, most *Peringia* were less than 2 mm long (Fig. 6). This may explain why these extremely abundant and readily available prey were completely ignored. The Knot on Vlieland took *Peringia* c. 3 mm long, weighing 0.3 mg on average (Fig. 3). Two of these prey would have to be taken per second to achieve an intake rate similar to that of Knot eating *Macoma*. The rate at which Knot take *Peringia* has been measured previously: 980 snails were taken in a feeding period of 20 min (Swennen unpubl., cited in Glutz *et al.* 1975), or one prey per 1.2 s, meaning that an intake rate of 0.6 mg s^{-1} might have been achieved if the snails were 4 mm long.

Table 3. *Total biomass of six potential prey species for Knot* (g AFDW m^{-2}) in the study area (corresponding to data given in Fig. 6) and that of prey individuals too large, too deep or too small for Knot (see Fig. 16). The remaining biomass is harvestable for Knot.

species	*total biomass*	*too large*	*not too large, but too deep*	*too small for Knot*	*harvestable for Knot*
Peringia	3.7	0	0	3.2	0.5
Cerastoderma	87.1	77.0	0	0.1	10.0
Macoma	28.2	19.6	4.6	0.3	3.7
Scrobicularia	12.7	12.4	0.2	0	0.1
Mya	6.5	4.1	1.2	0	1.2
Mytilus	0.4	0	0	0	0.4
TOTAL	138.6	113.1	6.0	3.6	15.9

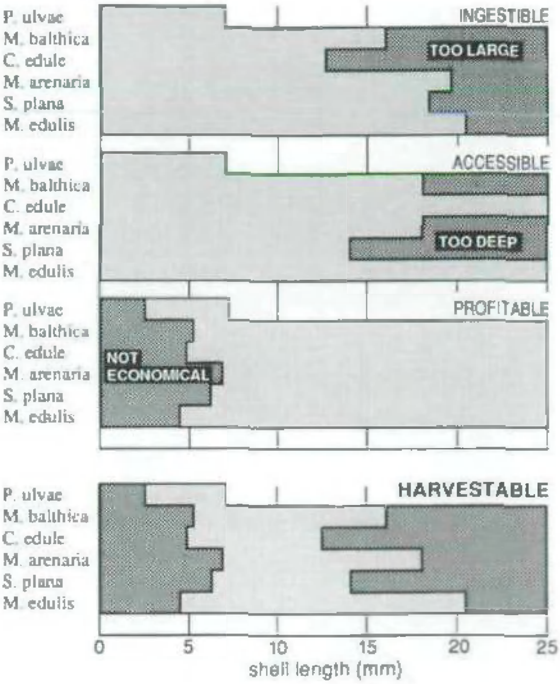


Fig. 16. Size classes of the six hard-shelled prey species (*Peringia*, *Macoma*, *Cerastoderma*, *Mya*, *Scrobicularia* and *Mytilus*) which are ingestible by, accessible and presumably profitable to Knot (light shaded areas). Prey sizes are defined as harvestable when (1) they can be swallowed, (2) they lay within reach of the bill, and (3) their handling efficiency is higher than the average feeding rate (mg s^{-1} handling > mg s^{-1} feeding). As explained in the text, the thresholds are not to be considered as fixed limits.

Size classes of prey which are harvestable by Knot

Figure 16 summarizes, for each of the six prey species, the size classes that are most likely to be taken. The biomass harvestable by Knot is only a fraction of the total biomass, because the majority of the flesh is found in prey too large to be swallowed (Table 3). The upper threshold is set by gape width (size threshold) and, to a lesser degree, by bill length (depth threshold), and the lower size threshold is set by the speed at which prey may be handled (profitability threshold).

The upper size threshold has been investigated in relation to gape width, but it is also conceivable that there is a size limit related to the ability to crush prey in the gizzard, as suggested for the Purple Sandpiper *Calidris maritima* (Summers *et al.* 1990). Work in progress (T. Piersma unpubl.) will show whether in Knot the digestibility of prey decreases with size.

The upper size threshold is probably fixed for the most part. It should be noted, however, that the relation between shell circumference and shell length (Fig. 7C) may vary locally and geographically. Variation in shape has been attributed to age and density in *Mytilus* (Seed 1968) and to growth rate and ambient salinity in *Cerastoderma* (Eisma 1963, Hancock 1967). *Macoma* in the southern part of their range are more slender than those in the north (Beukema & Meehan 1985). The effect of this is that the critical length for Knot varies by 2 to 3 mm.

Though Knot do not take bivalves that live too deep, they can vary the depth to which they probe. Oystercatchers probed more deeply when the density of prey within reach was low (Wanink & Zwarts 1985). The fraction of prey living in the upper two and three cm is given in Fig. 8 for our study site in late summer. *Macoma* and *Scrobicularia* live much deeper in winter than in summer, with the proportion accessible to Knot varying between 0 and 100% (Reading & McGrorty 1978, Zwarts & Wanink 1989, Zwarts *et al.* 1992). There is no seasonal variation in the burying depth of *Mya* and *Cerastoderma* (Zwarts & Wanink 1989).

In addition, according to the profitability rule, the lower size threshold should be variable, because it is closely linked to the current intake rate. When only the less profitable prey are available, the intake rate will inevitably decrease, so that the low-ranking prey then become profitable (e.g. Zwarts & Drent 1981). Profitability will also depend on the condition of the prey. Cayford & Goss-Custard (1990) have shown the implications of variations in the condition of *Mytilus* for size selection by Oystercatchers. Similar variations in AFDW occur in *Macoma*: individuals of similar size contain about 1.5 times as much flesh in May and June as in February and March. This seasonal variation is even larger in *Cerastoderma* (Zwarts 1991). Thus, the lower acceptance level should increase in winter as the condition of prey decreases. This is only true, however, if Knot are able to maintain their intake rate at a constant level. The lower size threshold would not change if the intake rate decreased at the same rate as did prey condition.

Whether Knot can survive on a lower intake rate depends on the available feeding time and on their energy requirements. The available feeding period does not vary much between intertidal areas used by Knot, but the energy requirements do differ: when wintering in Africa, for example, energy requirements may be half those in NW. Europe during a cold spell (Kersten & Piersma 1987, Piersma *et al.* 1991) or during the pre-migration period when Knot are fattening up (Klaassen *et al.* 1990). The Knot in the study area in late summer were on migration, so the high intake rate observed was probably required to enable them to accumulate body reserves. This would imply that the small prey ignored during this pre-migration period might be profitable under other circumstances, and so might be taken when Knot require a lower daily food consumption. The average intake rate of Knot wintering in Africa was estimated to be about 0.37 mg s^{-1} (Zwarts *et al.* 1990b), 40% below the 0.63 mg s^{-1} found in this study. This may be one of the reasons why Knot in Mauritania accept very small prey (Zwarts *et al.* 1990a).

Does a digestive bottleneck explain prey selection? The rate of food processing in Oystercatchers is constrained by the capacity of the gut to digest food, because, although they can ingest 100 mg wet weight s^{-1}, the gut processing rate is only 4.4 mg wet weight s^{-1} (Kersten & Visser 1996). Thus, when the ingestion rate over a long period exceeds 4.4 mg s^{-1} digestive pauses are necessary to empty the digestive tract. Are there any reasons to believe that the rate of food intake of Knot was also constrained by such a digestive bottleneck? When the preening periods are included as possible digestive pauses, the overall intake rate was one prey item per 82 s. Knot produced one faecal packet per 80 s and the faeces contained, on average, 0.98 prey, which means that the defecation rate was one prey item per 78 s. This suggests that the observed ingestion rate was equal to the processing rate, as derived from the defecation rate, and that higher intake rates while feeding would not be possible, unless the birds were to take more digestive pauses (or increase their

Table 4. Rate at which three waders process their food in terms of mg total wet weight s^{-1}, mg dry weight s^{-1} and mg dry flesh s^{-1}. The food composition is also given. 'Non-flesh' refers to inorganic dry matter (shell, sand, salt). Knot fed on *Macoma* including the shell (present paper). Whimbrel took crabs of the genus *Uca* (the maximal processing rate is taken from Zwarts & Dirksen (1990) and the food composition from Zwarts & Blomert (1990)); 30% of the organic matter, found in the skeleton of the crab, was indigestible and therefore added to the non-flesh component. Oystercatchers ate only the flesh of Mussels (Kersten & Visser 1996).

Species	*Body weight, g*	*Processing rate, mg s^{-1}* wet	dry	dry flesh	*Food composition, %* water	non-flesh	flesh
Knot	119	9.0	4.2	0.51	54	40	6
Whimbrel	413	11.1	2.8	1.0	75	16	9
Oystercatcher	525	4.4	0.9	0.7	80	4	16

processing rate and probably decrease the digestibility of the food).

Knot ingested the wet flesh and shells along with the water included in the shells. Knot eating *Macoma*, ingested 54% water, 6% dry flesh and 40% inorganic matter in the form of shell, salt and sand (Table 4). When the equation in Table 1 is used to convert the prey taken to total wet weight, Knot appeared to have ingested and processed 9 mg wet weight s^{-1} (Table 4). Kersten & Visser (1996) compared the weight of ingested food with the weight loss by defecation in Oystercatchers. Behavioural observations on Whimbrels *Numenius phaeopus* showed that the intake rate, with digestive pauses included, levelled off above a certain value (Zwarts & Dirksen 1990). The data for these three wader species are not easy to compare, as the body weights vary between the species and their diet is completely different. Oystercatchers removed flesh from the shell, so the food consisted mainly of water and the non-food ballast was low. Whimbrels eating whole fiddler crabs *Uca tangeri* ingested a much higher proportion of non-food matter, although it was not as high as for Knot eating *Macoma* (Table 4). Since a constant proportion of the body in birds is allocated to the digestive tract, it would be expected that meal size is proportional to body weight (Calder 1974). However, the rate of food processing must be proportional to the birds' requirement, i.e. (body weight)$^{3/4}$ (Zwarts *et al.* 1990b). On this basis, the expected processing rate of Knot would be 0.4 times that of Oystercatcher and Whimbrel. Whether the processing rate is expressed in terms of wet weight, total dry weight or dry flesh weight, Knot digest their food at a rate much faster than 0.4 times the rate observed in the other two species (Table 4). The defecation rate observed in Knot (one per 80 s) was indeed much faster than in Oystercatchers which produced one dropping per 10 min (Kersten & Visser 1996).

This comparison with the two other waders might suggest that Knot are adapted to processing food having a low flesh content. However, when the processing rate is 9 mg wet weight s^{-1} at maximum, a switch from *Macoma* to *Cerastoderma* would lead to a great reduction in the yield, measured in terms of energy. Indeed, the ratio of shell weight to flesh in *Cerastoderma* is nearly twice that in *Macoma* (Fig. 17), and when calculated for wet weight the ratio is even more un-

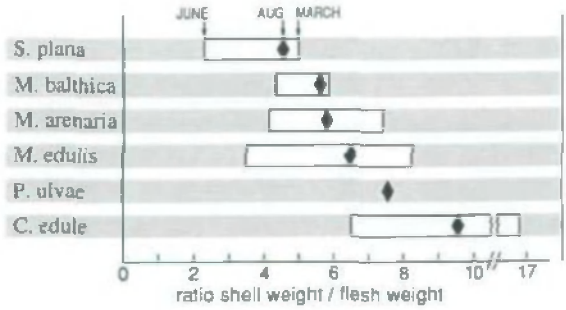


Fig. 17. Ratio of shell weight (DW) and flesh weight (AFDW) for five bivalves (*Scrobicularia*, *Macoma*, *Mya*, *Mytilus* and *Cerastoderma*) 12 mm long and for *Peringia* 6 mm long. The August data are taken from Fig. 2. Also shown is the average ratio in June, when body condition peaks, and in March, when body weights are at the lowest level (from Zwarts 1991 and unpubl.).

favourable (Table 1). *Cerastoderma* is extremely unfavourable food in winter when the flesh content, relative to the total dry weight, is reduced to about 5%, one third that in *Macoma* during winter (Fig. 17).

Thin-shelled prey may therefore be preferred to thick-shelled species, because of the more favourable rate at which their energy can be processed. Thus, deeply buried bivalves should be preferred to *Cerastoderma* and *Peringia*, which live at or just below the surface. Indeed, just this was observed. *Macoma* was preferred to *Cerastoderma* (this study) and to *Peringia* (Prater 1972, Piersma 1989). Contrary to expectation, the shell weight of *Mytilus*, which also lives on the surface, was actually lower than in these latter two species. Figure 17 shows that the shell/flesh ratio of *Mytilus* is just above those of the benthic species and two thirds that of the average value for *Cerastoderma*, but in many areas, the flesh/weight ratio of *Mytilus* would resemble that of *Cerastoderma* (Seed 1979, Fisher 1983, Bustnes & Erikstad 1990).

There is also variation in the shell weights of benthic species. The shell weights of *Cerastoderma* from brackish waters are only half of those of the same species in the Wadden Sea (Kristensen 1957, Eisma 1963, present study). The shells of *Macoma* were thinnest in the sheltered areas near the shore, with the individuals further offshore being 1.5 times heavier (Kristensen 1957, Beukema 1980). Bonsdorff & Wenne (1989) found that the shells of individuals living in sand were 17% heavier than those living in mud. Assuming that Knot prefer thin-shelled bivalves, also within prey species, such variations in shell thickness may well influence the distribution of Knot over the feeding areas. It is to be expected that Knot feeding on *Macoma* prefer sheltered, muddy areas along the shore, where the shells are thin. In fact, it was found that these areas were ignored (Zwarts *et al.* 1992), so other factors must also be involved.

A relatively thick shell is an obvious impediment to predators attempting to break it with their bill (Cayford & Goss-Custard 1990) or pincers (Boulding 1984), increasing the handling time and decreasing the value of the prey. Furthermore, a thick shell also makes prey less attractive to Knot, and perhaps other predators which swallow prey whole, because it leads to a digestive bottleneck and so results in a reduction of processing rate.

Chapter 13

ANNUAL AND SEASONAL VARIATION IN THE FOOD SUPPLY HARVESTABLE BY KNOT *CALIDRIS CANUTUS* STAGING IN THE WADDEN SEA IN LATE SUMMER

Leo Zwarts, Anne-Marie Blomert, Jan H. Wanink

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ANNUAL AND SEASONAL VARIATION IN THE FOOD SUPPLY HARVESTABLE BY KNOT *CALIDRIS CANUTUS* STAGING IN THE WADDEN SEA IN LATE SUMMER

The biomass of the macrobenthic animals living in intertidal flats of the Wadden Sea varies annually and seasonally. However, the variation in prey biomass harvestable by wading birds such as Knot *Calidris canutus*, which feed mainly on the middle range of their prey size classes, is even larger. The majority of first-year *Cerastoderma edule*, *Mya arenaria* or *Mytilus edulis* are too small to be profitable as prey for Knot. Yet, by the end of the subsequent growing season, these same prey are too large to be ingested and/or live at a depth that puts them out of reach of the birds' bills. *Macoma balthica* is a major prey for Knot, because (1) its annual spatfall is less erratic than in the other bivalve species, and (2) it grows more slowly and each cohort is therefore available as food for Knot for at least three years. Knot feed in flocks which roam over the feeding area, but they are more often observed in food-rich than in food-poor areas. A similar relationship between bird and food densities was found in one locality, when the annual numbers of Knot were compared with the yearly variation in food supply. Since the numbers of Knot in the whole area were the same over many years, the birds were apparently able to find other feeding areas when the local food supply was low, i.e. the food supply harvestable by Knot (prey not too small, not too large and not too deep) was less than about 4 g ash-free dry weight m^{-2}. Knot arrive in the study area at the end of July and leave after only a few weeks *en route* to Africa. They depart before a serious decline in the harvestable prey biomass takes place, which results from a decrease in the body condition of individual prey and an increase in the fraction of the prey which burrows out of the reach of the Knot's bill.

Introduction

In late summer, when waders arrive in the Wadden Sea from their arctic breeding areas, they face a fluctuating food supply which implies adjustment of diet and aggravates the problem of how to locate reliable food resources. This unpredictability is caused by annual variation in the densities of the approximately twenty species of prey living in the intertidal flats (Beukema *et al.* 1978, Beukema 1979, 1982, 1989). Indeed, the variation in amount of food harvestable by the various wader species may be even greater than appears from a consideration of the annual total biomass of the prey. Generally, waders only consume part of the prey because they usually ignore the smaller size classes, while the larger prey are too large to be swallowed and/or live too deep in the sediments to be caught (Zwarts & Wanink 1984, Piersma 1987). For instance, Knot *Calidris canutus* feeding on *Macoma balthica* ignore prey less than 9 mm long and cannot swallow prey longer than 16 mm, while prey are unaccessible when buried more than 2 to 3 cm below the surface. The remaining fraction is defined as harvestable prey (Fig. 1; Zwarts & Blomert 1992).

Furthermore, food density is highly variable spatially, and there are many areas where prey are so sparse that the birds are not actually able to feed on them. Just like prey that are buried too deep to reach, such low-density areas cannot be regarded as part of the bird's food supply. Because of these reasons, regarding the entire prey biomass as the food for a wader species will usually give highly inflated results.

After arrival from their Siberian breeding areas, Knot of the subspecies concerned, *Calidris canutus canutus*, remain some weeks in the Wadden Sea to prepare for a long-distance flight which takes them to

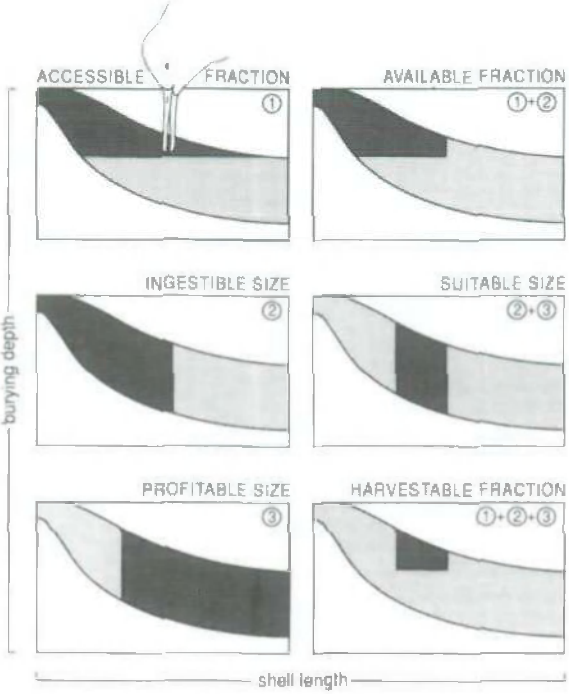


Fig. 1. Terms used in this paper to define different fractions of benthic prey of Knot *Calidris canutus*. Shaded areas: depth below the surface where the prey occur. Dark shading: prey which are (1) accessible, (2) ingestible or (3) profitable for Knot. Available prey are accessible and ingestible. Prey of suitable size are ingestible and profitable. Harvestable prey are accessible, ingestible and profitable.

their tropical wintering grounds (Piersma *et al.* 1990, 1991). The present report describes, on the basis of a decade of sampling, annual and seasonal variations in the harvestable food supply for Knot. The data were used to investigate: (1) standing crop level of the harvestable food supply below which the birds cease to exploit an area (prey harvestable by Knot are, by definition, available as well as profitable (Fig. 1; Zwarts & Blomert 1992)); (2) whether this threshold, or minimum acceptance level, is set by the relation between the harvestable food supply and the rate at which food can be taken; (3) whether Knot remain in the Wadden Sea until their harvestable food supply reaches this level of minimum acceptance and so becomes too low, or whether instead they depart regardless of food supply.

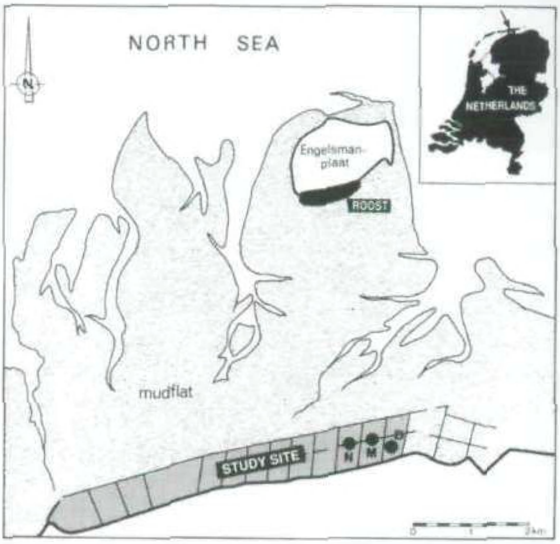


Fig. 2. Study area in the eastern part of the Dutch Wadden Sea. The area, shaded grey, was intersected with brushwood groynes. Detailed observations of Knot and their food supply were made on 146 plots of 0.1 ha (sites N and M). Burying depth of bivalves was measured at site D, and sometimes at sites N and M.

Methods

The study was done between 1976 and 1986 in the eastern part of the Dutch Wadden Sea on intertidal mudflats along the Frisian coast (53°25′ N, 6°04′ E; Fig. 2). The remains of brushwood groynes made several decades before to enhance sedimentation were used as markers bordering 53 sites which varied in size between 6 and 26 ha. The total surface area of these 53 sites was 396 ha (Fig. 2). The elevation of this area varied between 50 cm above and 30 cm below mean sea level, which corresponds to average emersion times of 62% and 39% of the tidal cycle (12 h 25 min), respectively. The substrate was muddy, with the clay content (< 2 μm) being 2 to 20% (Zwarts 1988b). Waders were counted in the study area at low tide from the top of the sea wall (9 m high), usually twice a month, over the period 1977 to 1985. All the Knot from the study area roosted on the island Engelsmanplaat, along with birds feeding on tidal flats further offshore. Roosting birds were counted by local wardens several times a week during summer.

Two sites (N and M in Fig. 2) were selected for more detailed observations: 146 plots of 0.1 ha were pegged out and two towers built to observe the waders. The feeding densities were determined by counting waders in the plots every 30 min over the entire low water period. Sites N and M were situated just below mean sea level; the clay content of the substrate was 4 to 5%.

Core samples of the macrozoobenthos (1/56 m^2) were sieved through a 1 mm screen. A detailed description of the procedures used to determine the ash-free dry weight (AFDW) is given elsewhere (Zwarts 1991). Samples were taken at equally spaced intervals (200 m) along 27 transects over the entire study area in August during four years (1977 to 1980). Also, 73 or 292 cores were collected from site N almost every month over the period 1980 to 1986.

During the same seven years, burying depth of *Macoma* was determined once or twice a month at nearby site D, and sometimes on site N or M; the techniques used are described in Zwarts & Wanink (1989). To maintain a sample size of at least 100 depth measurements for each of the fortnightly periods, the calculations related to all specimens 10 to 23 mm in length, although Knot only selected the size classes smaller than 16 mm (Zwarts & Blomert 1992). Since there was no relationship between size and burying depth for animals larger than 10 mm, the inclusion of larger individuals did not influence the trends shown.

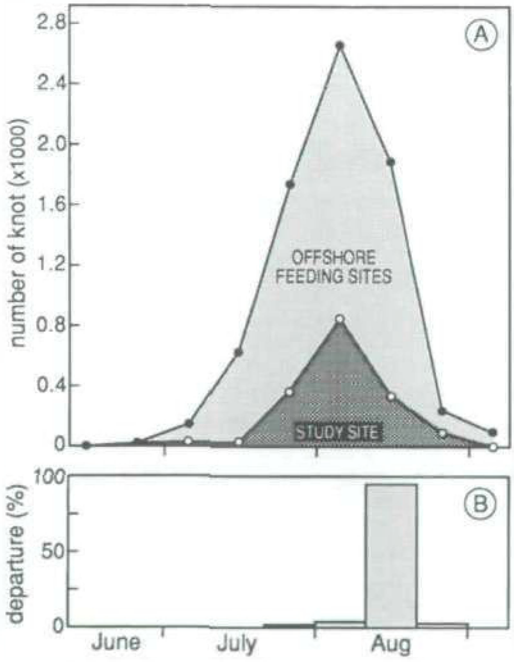


Fig. 3. *Calidris canutus*. **A.** Average number of Knot present on the roost at high tide in the period 1976 to 1990 (190 counts done by the wardens; compiled by Lenze Hofstee) and in the study area at low tide (65 counts from 1977 to 1985). **B.** Timing of departure from the eastern part of the Dutch Wadden Sea between 1964 and 1988; n = 3465 birds.

Growth of the bivalves was estimated from their length frequency distributions in the monthly samples, using the Bhattacharya method for separating cohorts (MPA module of the Compleat ELEFAN software package, version 1.0; Gayanilo *et al.* 1988).

Results

Numbers of Knot

The majority of Knot arrive in the study area around 1 August, and most have left the area by three weeks later (Fig. 3). The timing of departure can be ascertained because, when Knot start a long distance flight, they become noisy and nervous and then disappear in a southwesterly direction (Piersma *et al.* 1990). From this, we know that the Knot leave the area by mid-August (Fig. 3B), which coincides well with the decrease in numbers recorded on the feeding and roosting areas (Fig. 3A).

Annual food supply

The main prey for Knot in the Wadden Sea are bivalves and snails (Boere & Smit 1981, Nehls 1992, Zwarts & Blomert 1992, Piersma *et al.* 1993b). In contrast to *Macoma* and *Mya*, annual variation in the total biomass of *Mytilus* and *Cerastoderma* in site N was very large (Table 1). Though the fluctuations were damped when these species were taken together, the lowest total biomass was still only half of the highest (Table 1). The average biomass of the five bivalve species taken together at site N was 73 g AFDW m^{-2}, which is high compared with the average of 13 to 23 g AFDW m^{-2} over the entire Dutch Wadden Sea (Beukema 1976, 1978, 1989). The total biomass of *Mytilus* was low, but all the other species, especially *Scrobicularia plana*, reached an extremely high

Table 1. Annual variation in the biomass of prey species of Knot *Calidris canutus* (g AFDW m^{-2}) at site N in August of 1977 to 1986. Average, lowest and highest biomass are given. RSD: relative standard deviation (SD as percentage of the mean).

Species	*Average, g*	*Range, g*	*RSD, %*
Macoma	17.22	7.4- 34.5	46.6
Cerastoderma	20.66	0- 62.3	107.2
Mya	13.20	7.0- 23.7	38.6
Scrobicularia	20.23	8.1- 46.3	86.5
Mytilus	1.45	0- 7.9	186.6
Total	73.26	52.8-111.0	26.6

Table 2. Annual variation in the biomass within the range of size classes harvestable by Knot *Calidris canutus* (g AFDW m^{-2}; without depth restriction) at site N in August of 1977 to 1986. Range of harvestable size classes are taken from Zwarts & Blomert (1992). Average, lowest and highest biomass harvestable by Knot are given. RSD: relative standard deviation (SD as percentage of the mean).

Species	*Size range, mm*	*Average, g*	*Range, g*	*RSD, %*
Macoma	6-16	7.81	3.9-14.9	44.0
Cerastoderma	5-12	1.25	0- 6.6	155.7
Mya	7-17	0.33	0- 1.3	153.4
Scrobicularia	7-14	0.14	0- 1.4	300.0
Mytilus	5-20	0.33	0- 2.6	237.9
Total		9.86	3.9-17.7	45.9

biomass. The biomass of these species did not deviate much, however, from the values found in other, similarly sheltered areas with mixed substrate, situated at or just above mean sea level (Beukema 1976, Zwarts 1988b).

Knot do not swallow large prey and they ignore the small size classes (Zwarts & Blomert 1992). Table 2 gives the range of size classes harvestable by Knot and the corresponding biomass for these size classes at site N. A comparison of Tables 1 & 2 reveals that only a small fraction of the total biomass fell within the range of size classes harvestable by Knot. The exception was *Macoma*, for which, on average, 44% of the total biomass may be considered as harvestable by Knot. Moreover, of all the potential prey species, the annual variation in harvestable biomass is least in *Macoma*.

The large annual variation in total food supply was caused by the erratic occurrence of summer recruitment and winter mortality (Beukema *et al.* 1978, Beukema 1979, 1982, Beukema & Essink 1986, Desprez *et al.* 1991, Ducrotoy *et al.* 1991, Essink *et al.* 1991, Jones & Park 1991, Obert & Michaelis 1991). There were also large differences among species in annual growth rate and mortality (Fig. 4). *Cerastoderma* grew rapidly but the majority died within two or three years. There was recruitment in this species during seven of the ten years, but the only substantial cohort originated in 1984. No spatfall of any significance occurred in *Scrobicularia* during the ten years after 1976, when a strong year class was recruited (see also Essink *et al.* 1991). Many of these animals were still alive in 1983 and 1984. In *Mya* as well, there was heavy spatfall during only one of the ten years, viz. 1979. Recruitment was variable in *Macoma*, but the variation was not as large as in the other species: in six of the ten years there was recruitment, with a considerable spatfall occurring in three of them.

Food of Knot

After the first growing season, *Mya* reached a size of 5 to 10 mm and grew to about 25 mm by the end of their second summer (Figs. 4 & 5). This means that the majority of the first-year animals were ignored by Knot since they were too small and therefore unprofitable, while by the end of the next growing season they had become too large to be swallowed. For the same reason, only the largest *Cerastoderma* and *Mytilus* in their first year and the most slowly growing individuals in their second year were potential prey for Knot. However, Knot were able to feed on *Macoma* over a much longer period, as it took a cohort of this species four years to pass through the 'window of predation' (Figs. 4 & 5).

The potential importance of *Macoma* as prey is also clear from Fig. 6, which shows the annual variation in biomass of the size classes harvestable by Knot. The other prey contributed, on average, only 21% of this biomass (Table 2). *Scrobicularia*, though one of the two most important prey in terms of total biomass (Table 1), was of interest for Knot only in the year before the observations began, and not at all over the next

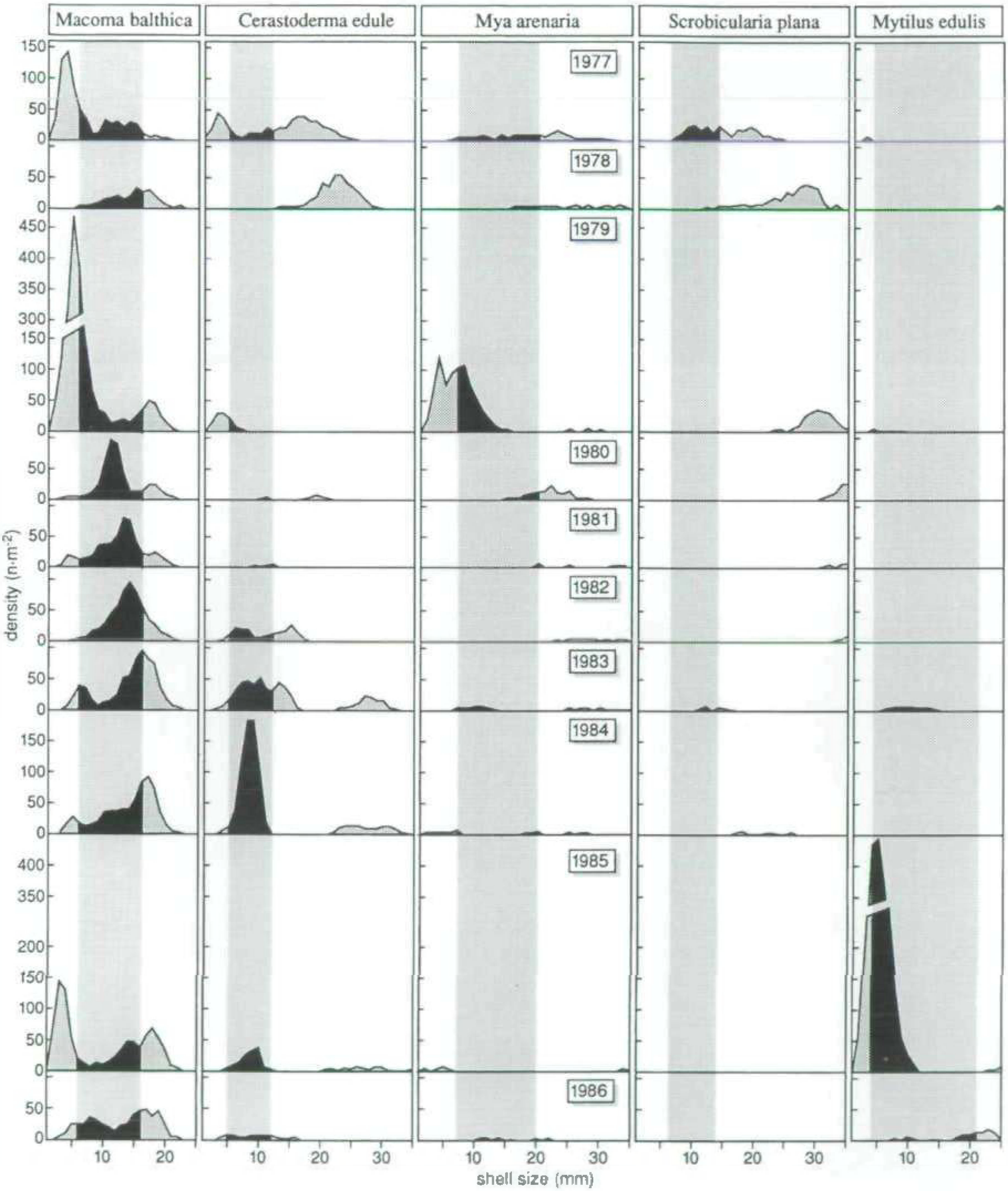
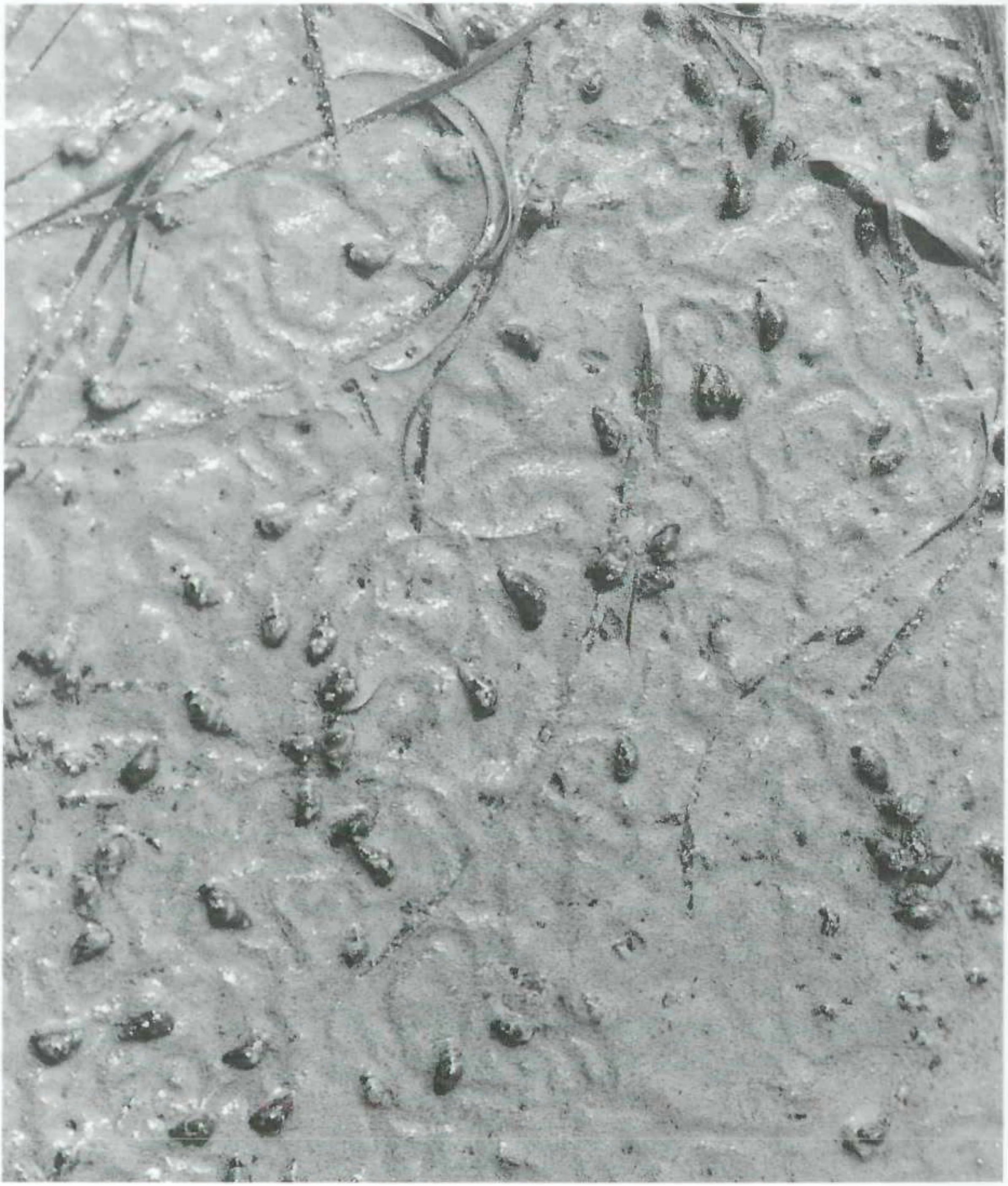


Fig. 4. Density (n m^{-2}) of five bivalve species at site N in August during ten years (1977 to 1986). The size classes harvestable by Knot *Calidris canutus* (i.e. not too small to be unprofitable or too large to be ingestible or accessible) are indicated by vertical grey bars (from Zwarts & Blomert 1992). Data for 1977 are not directly comparable with the following years since the samples were taken from a larger area.



The Mud Snail may occur in huge densities at the substrate and hence seems to be an easy prey for Knot. Knot prefer, however, medium-sized, thin-shelled bivalves.

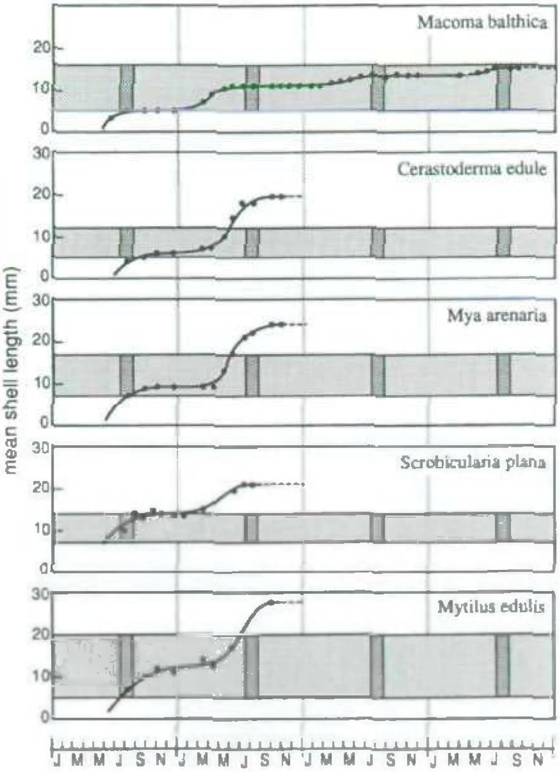


Fig. 5. Growth of five bivalve species at site N after spatfall in summer 1979 (1983 for *Scrobicularia plana*). The size classes vulnerable to predation by Knot (see Table 2) are indicated (horizontal grey field), as well as the period during which Knot were present (vertical grey bars). Average sizes were calculated from the length frequency distributions in the monthly samples (see 'Methods').

ten years. The contribution of the 1979 year class of *Macoma* to the biomass harvestable by Knot is evident: the harvestable food supply was highest after four growing seasons and decreased thereafter because an increasing proportion had passed the critical size threshold of 16 mm.

On some occasions, *Macoma* was the only prey species harvestable by Knot for example in late summer of 1981 and 1983. Though *Cerastoderma* were available in 1983, Knot ignored them, perhaps due to the thick shell (Zwarts & Blomert 1992). *Macoma* must therefore have been the staple food for Knot that passed through the study area in late summer, unless the Mud Snail *Peringia ulvae* was taken as an alternative. This species usually occurred at densities of 40 000 to 50 000 m^{-2}, though the summer of 1979 was an exception, when only low densities of 1000 m^{-2} occurred (Zwarts 1988b). However, direct observations and faecal analysis showed that *Peringia* were not taken in 1979, 1981, 1983 or 1985, even though they were abundant in three of the four years. In fact, the majority of *Peringia* in the study area were too small (< 2 mm) to be profitable food items for Knot (Zwarts & Blomert 1992). The distribution pattern of Knot over the feeding area was another indication that Knot did not feed on *Peringia*. This prey was superabundant at the sites situated above mean sea level and in areas where the clay content of the substrate was above 10% (Zwarts 1988b). However, Knot ignored these areas and were usually found on sites below mean sea level where the clay content of the substrate was less than 3%. This resulted in a negative relationship between density of Knot and that of *Peringia*. Considering all this information together, the conclusion is that *Macoma* was the main, and sometimes the only, prey for Knot in the study area. For that reason, local and seasonal variations only in *Macoma* are described below.

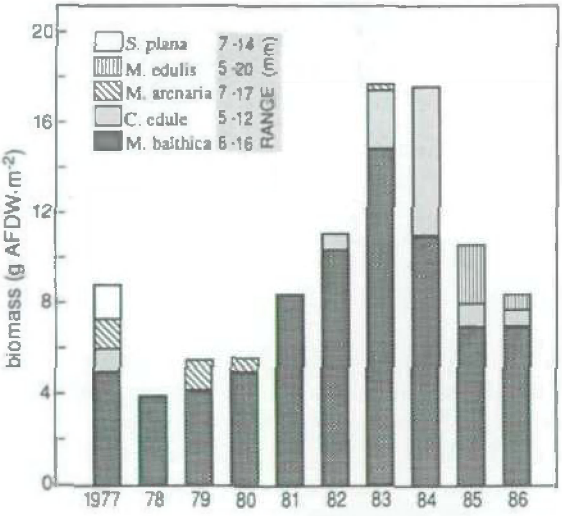


Fig. 6. Biomass (g AFDW m^{-2}) of five bivalve species at site N in August from 1977 to 1986. A selection has been made for the range of size classes harvestable by Knot *Calidris canutus* (see Table 2). No correction has been made for depth distribution of the prey.

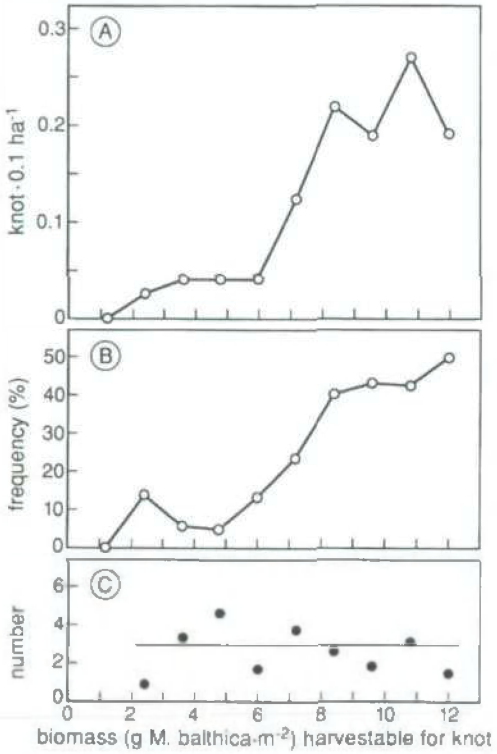


Fig. 7. *Calidris canutus*. Aggregative response of Knot in relation to spatial variations in the harvestable food supply (g AFDW m^{-2} of *Macoma* 6 to 16 mm long living in the upper 2 cm of the substrate; 60% of the prey were found in the upper 2 cm). The data refer to 146 plots of 0.1 ha at sites N and M from July to September 1981; 1095 samples of 1/56 m^2 were taken. **A.** Average feeding density, calculated over 67 counts made during seven low-water periods. **B.** Frequency of occurrence (percent of low-water periods during which one or more Knot were counted). **C.** Average number (number of Knot seen in a plot when the number of Knot was ≥ 1).

Knot return to sites with a high food supply

The distribution of Knot over the feeding area in relation to the density of their harvestable prey was investigated in late summer 1981. The biomass harvestable by Knot varied between 2 and 12 g AFDW m^{-2}, and the density of Knot increased with food supply over this range (Fig. 7A). Such an aggregative response of predators to spatial variations in prey density can be divided into two components: the frequency with which the predators occur and the numbers present on any one occasion. In the case of Knot (Fig. 7A), the response was not determined by the numbers of birds present at any one time (Fig. 7C), but by the frequency with which they occurred in a plot (Fig. 7B).

This was perhaps to be expected, in view of the observation that Knot almost always fed in flocks which were always on the move, even on a scale of less than an hour. They moved readily from one locality to another, probably continuously seeking the most rewarding place (Goss-Custard 1970b, Gerritsen *et al.* 1983). Knot found the best parts of the feeding area by ignoring, or rapidly traversing, marginal areas (Fig. 7B).

Annual food supply and number of Knot

Macoma did not grow between July and November (Fig. 5) and there was no decrease in densities during these months (Zwarts *et al.* 1996h). Nonetheless, the food supply harvestable by Knot decreased over the period, for two reasons. Firstly, the biomass of individual prey, or their condition, decreased by 20 to 30%, although this seasonal trend was small in comparison with annual differences (Fig. 8). Secondly, the proportion of *Macoma* living in the upper two cm of the substrate, and thus within reach of the bill of Knot, de-

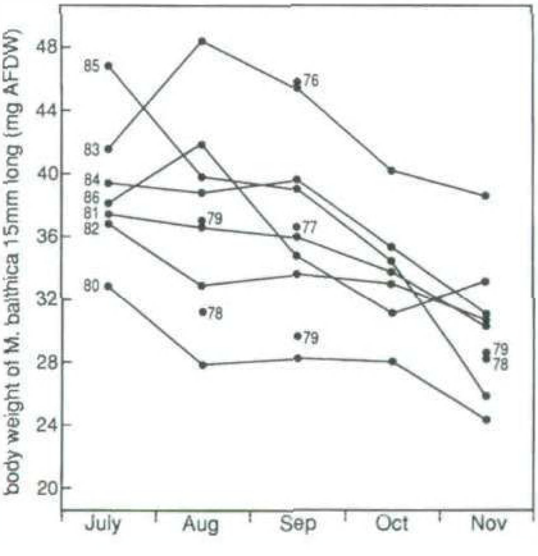


Fig. 8. *Macoma*. Body weight (mg AFDW) of individuals 15 mm long in the study area during late summer and autumn between 1976 and 1986 (based on Zwarts 1991).

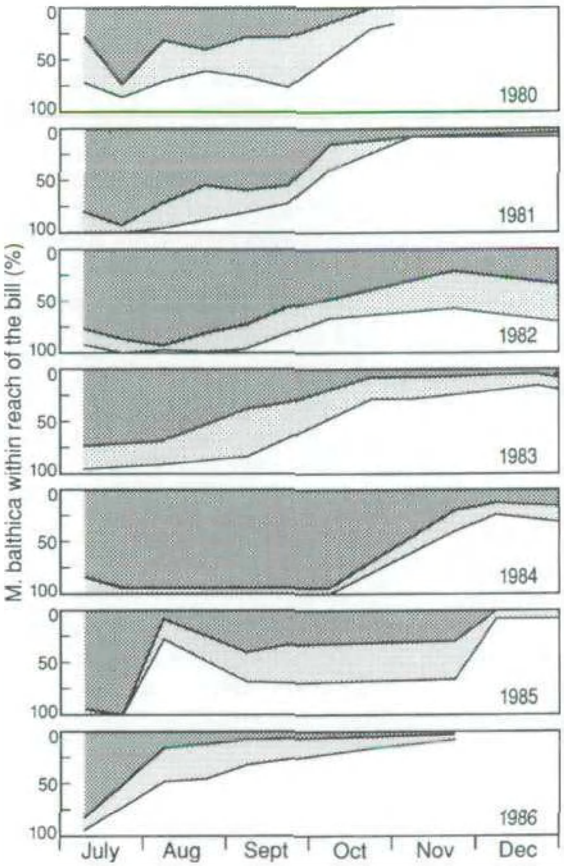


Fig. 9. Proportion of *Macoma* accessible to Knot *Calidris canutus*, i.e. prey living in the upper 2 cm (dark shading) and upper 3 cm (dark + light shading) of the substrate; measurements taken in the study area from 1980 to 1986 (based on Zwarts & Wanink 1989).

creased during the season (Fig. 9). However, there were also considerable differences among years in depth distribution. In 1984, the majority of prey remained within reach of the bill until October, whereas in 1980 and 1986, *Macoma* were beyond reach of the bill from August onwards. The accessible fraction therefore decreased gradually over the course of the season, but 1985 was an exception since *Macoma* lived at a greater depth in August than in September.

Figure 10 shows the decrease in biomass of *Macoma* harvestable by Knot. This figure combines the measurements of prey density (Fig. 4), prey weight (Fig. 8) and the proportion of prey actually within reach of Knot (Fig. 9). Figure 10 also shows when Knot occurred in the study site in the different years. It is evident that the numbers of Knot feeding were closely related to the annual variation in biomass of *Macoma* harvestable by Knot.

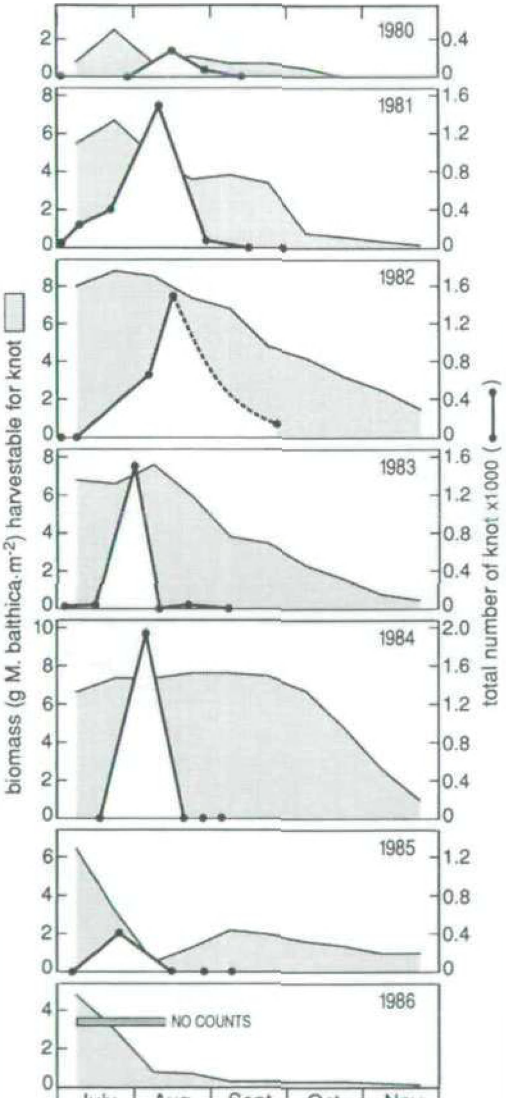


Fig. 10. Biomass of *Macoma* (g AFDW m^{-2} of individuals 6 to 16 mm long living in the upper 2 cm) harvestable by Knot *Calidris canutus* at site N, and occurrence of Knot in the study area during late summer and autumn of 1980 to 1986.

Discussion

Response of Knot to spatial variation in their harvestable food supply

Knot most often visited plots with abundant *Macoma* (Fig. 7B), presumably because their rate of food intake was highest in these areas. The relation between prey density and the rate at which probing Knot encounter *Macoma* (Fig. 11A) can be used to estimate intake rates over the wide range of prey densities found in the field. The predicted intake rate is derived from three variables: encounter rate with prey, handling time and amount of flesh in *Macoma* of each size class (Zwarts & Blomert 1992). The predicted intake rate rises sharply with prey density (Fig. 11B). The two measurements of intake rates actually made correspond well with the predicted values (Fig. 11A), as did the intake rates of Knot feeding on a variable density of *Macoma* in semi-captive conditions (Piersma pers. comm.). Piersma found that intake rate reached a plateau of 2 mg AFDW s^{-1} when *Macoma* occurred at the extremely high biomass of more than 40 g AFDW m^{-2}. Since the harvestable biomass of *Macoma* normally varies from 0 to 10 g AFDW m^{-2}, it would always be worthwhile for Knot to search for sites with the densest food supply. From this, we conclude that choice of site must be one of the most crucial feeding decisions made by Knot, because it has such a direct and large effect on intake rate.

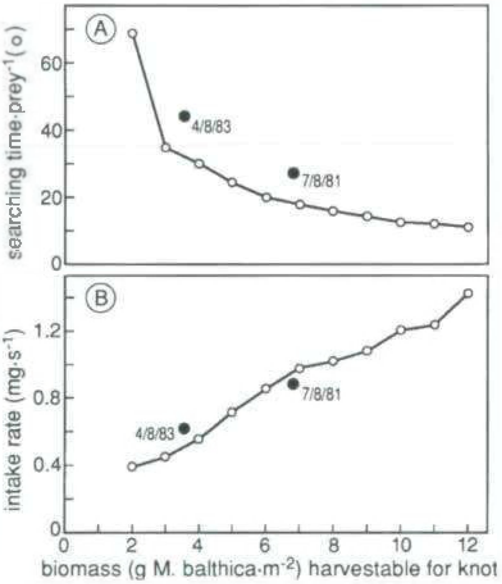


Fig. 11. *Calidris canutus*. **A.** Searching time per prey (s) and **B.** intake rate (mg AFDW s^{-1}) as a function of the harvestable biomass (g AFDW m^{-2} of *Macoma* 6 to 16 mm long living in the upper 2 cm). The biomass data correspond to the 1981 data shown in Fig. 7. The two field measurements on feeding Knot (●) were taken in August 1981 (Zwarts unpubl.) and August 1983 (Zwarts & Blomert 1992). The line in A is the inverse of the encounter rate, as derived from the random touch model (Figs. 10 to 12 in Zwarts & Blomert 1992). The line in B is based on predictions derived from a model with three variables: handling time, encounter rate and flesh content per size class (Fig. 14 in Zwarts & Blomert 1992).

In late summer 1981, when *Macoma* were abundant, Knot avoided sites where the biomass of harvestable *Macoma* was less than 6 to 7 g AFDW m^{-2} (Fig. 7). This means that sites with an intake rate of less than 0.7 mg AFDW s^{-1} were under-used and that the majority of Knot fed on sites where they could maintain an intake rate of more than 1 mg AFDW s^{-1}. The following section discusses whether Knot used the same decision rule to choose between feeding areas in years other than 1981, when *Macoma* were less abundant.

Response of Knot to annual variation in their harvestable food supply

Knot hardly fed in the study area in two years when the biomass of harvestable *Macoma* was less than 4 g AFDW m^{-2}, but did so extensively in the other four years, when prey were abundant (Fig. 12). However, the numbers of Knot at the roost did not vary, apart from the exceptionally low number counted in 1981 (Fig. 12). Therefore, Knot did not leave this part of the Wadden Sea when the harvestable food supply in the study area was very low, but instead must have found other feeding sites in the immediate vicinity. Two questions are therefore discussed below: (1) What decision rule is used by Knot when they exploit *Macoma*? (2) Are there years in which Knot arriving in the Wadden Sea find insufficient food?

When plotted on an annual scale, Knot scarcely fed on *Macoma* when the harvestable food supply was below about 4 g AFDW m^{-2} (Fig. 12), much lower than the apparent acceptance threshold in 1981 (Fig. 7). It seems, therefore, that the acceptance threshold is not fixed, but goes down when there is not much food available. There must, however, be a lower limit below which exploitation of the food resources is not worthwhile. At thermo-neutrality, Knot (119 g body weight) use about 10 g dry flesh (AFDW) day^{-1} to maintain their body weight at a constant level (Klaassen *et al.* 1990, Zwarts *et al.* 1990, Piersma *et al.* 1994). With the feeding areas being exposed for 12 h day^{-1}, and assuming similar feeding rates at night as during the day, the average intake rate must be at least 0.23 mg AFDW s^{-1} if the birds are to survive. Such an intake rate requires a harvestable prey density of 2 g AFDW of *Macoma* m^{-2} (Fig. 11B). This intake rate is not sufficient, however, for Knot preparing for their long-distance flight to Africa, when they have to double their daily consumption to build up their body reserves at the required rate of 3 to 4% day^{-1} (Klaassen *et al.* 1990). Since the feeding time cannot be increased, migrant Knot must at least double their intake rate when they stay in the Wadden Sea. This implies that migrant Knot would feed only at sites which provide an intake rate of at least 0.4 mg AFDW s^{-1}. This further implies that the harvestable food supply of *Macoma* would have to be at least 3 g AFDW m^{-2} (Fig. 11B), as indeed was found to be the case (Fig. 12).

In years when Knot did not exploit the study site itself because the food supply was too low, the total numbers counted on the roost remained quite normal (Fig. 12). Apparently, they were able to switch to other feeding sites further offshore. In summer 1979, when there had been a heavy spatfall of *Mya* and *Macoma* on the high shore (Fig. 4), the lower sandflats were completely covered by *Mytilus* spat. This may have provided a rich food supply for Knot in 1979, but certainly did so in 1980 when the *Macoma* in the study area were sparse. This rich food supply was not available in 1981, when all the 1979 Mussels had grown past the upper size threshold of 20 mm. Indeed no Knot fed that year on the lower shore, since all the birds were concentrated on the higher mudflats in the study area (Fig. 12).

This example shows that Knot may switch from one site to another, according to the prey species taken. However, even when Knot feed on just one prey species, their distributions would be expected to vary from year to year. There is a very large difference between the growth rates of bivalve species, being high on the low sandflats and very low on the high mudflats.

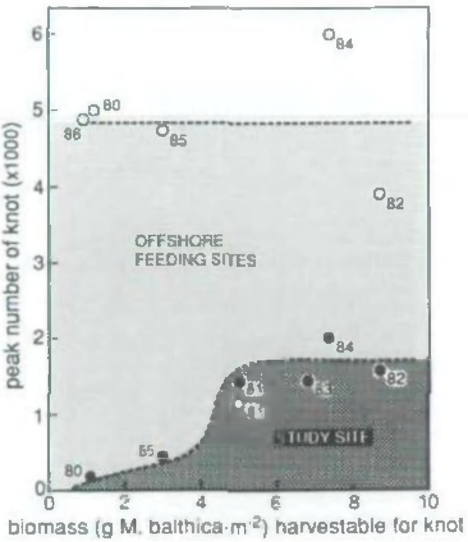


Fig. 12. *Calidris canutus*. Highest numbers of Knot in late summer on the roost at high tide (○) and at the study site at low tide (●) as a function of the prey biomass harvestable by Knot at the study area (g AFDW m^{-2} of *Macoma* 6 to 16 mm long living in the upper 2 cm of the substrate; same data as Fig. 10). No counts were made on the roost in 1983 and at the study site in 1986.

Cerastoderma near the low water mark may, during the first growing season, grow past the upper threshold of 12 mm taken by Knot, while Cockles at the higher shore levels may require three growing seasons to attain the same size (e.g. Cole 1956, Jones 1979, Sanchez-Salazar *et al.* 1987). In *Mytilus*, the upper size threshold of 20 mm may be reached in one to seven years (e.g. Seed 1968). Similar differences in growth rates, although not as large, were found in all bivalve species on the tidal flats in the present study area (Zwarts 1988b). As a consequence, Knot may exploit, for instance, a particular year class of *Macoma* on the lower shore where the larger specimens occur, but then, in subsequent years when these prey have grown too large, switch to sites where the growth rate is lower.

The largest variations in harvestable food supply over the years are primarily determined by the occurrence of severe winters and high spatfall in the following summer (Beukema 1982). Hence there are some years with high spatfall in the benthic species but many other years when reproduction is poor in all species. Thus, there is a corresponding overall pattern of recruitment in different parts of the Wadden Sea (Beukema & Essink 1986). Fortunately for Knot,various species go through the predation window in different years after such a boom summer has occurred (Fig. 5), and this effect is enlarged by the locally varying growth rates. Consequently, Knot may exploit, over a period of five or six years, a food supply that came into existence during a single summer of heavy spatfall, such as occurred in 1940, 1963, 1979 and 1987 (Beukema 1976, 1982, 1989). The data collected (Fig. 10) show that there are years during which the food supply is too low for the migrant Knot to be able to feed, at least on a local level. It is necessary to repeat the measurements described here on a larger scale to find out how often the food supply in the Wadden Sea is insufficient for ensuring the intake rate required by Knot to build up migratory body reserves. Our prediction is that such poor years will hardly ever occur. Flocks of Knot roam easily over feeding areas with a total surface of tens of km^2 and it seems unlikely that good sites would not be found within such a large area, given the local variations in the food supply and the possibilities for Knot to exploit different prey species (Nehls 1992). When another wader, Oystercatcher *Haematopus ostralegus*, lost its major food supply (Mussels) during a study period of ten years, the species remained in the area and switched to Cockles, *Macoma* and the Ragworm *Nereis diversicolor* (Zwarts & Drent 1981). No change in numbers of Oystercatchers at the roost could be discerned during the episode.

Knot depart before their food supply deteriorates

There is a large difference among years in the rate of seasonal decrease in the food supply that is actually accessible to Knot (Fig. 10). It might therefore be expected that the timing of migration would be delayed in years when *Macoma* were scarce, yet there is little annual variation in the timing of departure (Fig. 10). The roost counts showed that Knot leave the area each year around mid-August, about three weeks after their arrival. The migration strategy of Knot is apparently to leave the Wadden Sea as soon as possible, bearing in mind that meteorological conditions must be conducive to long-distance migration. Though the abundance of the accessible food supply is rather unpredictable, there is a clear trend for the food supply to deteriorate during the course of late summer (Figs. 8 to 10). We suggest that the Siberian Knot which arrive in the Wadden Sea around 1 August start building up their migration reserves immediately so that they can leave the area as quickly as possible and before the deterioration in the food supply accelerates. A study of the feeding ecology of the subspecies breeding on Greenland and in Canada, which spends the winter in the Wadden Sea and elsewhere in NW. Europe (Dick *et al.* 1976, Roselaar 1983), accordingly would be extremely interesting: how do these Knot manage to survive under conditions the Siberian Knot seem to be anxious to avoid (Piersma *et al.* 1991)?

Chapter 14

SEASONAL TREND IN BURROW DEPTH AND TIDAL VARIATION IN FEEDING ACTIVITY OF *NEREIS DIVERSICOLOR*

Peter Esselink & Leo Zwarts

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SEASONAL TREND IN BURROW DEPTH AND TIDAL VARIATION IN FEEDING ACTIVITY OF *NEREIS DIVERSICOLOR*

Ragworms *Nereis diversicolor* live in burrows which, if deeper than 5 to 10 cm, offer a safe refuge from most of their predators. Burrow depth must be c. 15 cm before they live out of reach of all predators. Burrow depth increases with body size, levelling off at c. 15 cm, when the depth refuge is reached. Worms live at greater depths in sand than in mud, but this effect disappears if worms with identical body condition (expressed as deviation from mean body weight for a given body length) are compared. Seasonal variation in burrow depth is correlated with sea temperature and to a lesser extent with day length and body condition. Feeding worms are present near or at the surface. Filter feeding occurs in the first 2 h after exposure (at least if a water film still remains at the surface) and surface feeding begins after that. The total time spent at the surface does not exceed an average of 50 seconds per tidal cycle. Feeding must be an extremely risky activity, because predators readily catch most *Nereis* while present near or at the surface.

Introduction

Although the estuarine polychaete *Nereis diversicolor* (O. F. Müller) lives in semi-permanent burrows which provide refuge from predators, they are nevertheless eaten by many predators, particularly wading birds (Zwarts & Esselink 1989). The deeper the burrow, the lower the predation risk, since most predators move over the surface and have to dig or probe in the substrate to find a worm. Predation pressure by other benthic animals seems to be low. The distribution of *Nereis diversicolor* barely overlaps those of 2 potential benthic predators, *Nereis virens* and *Nephtys hombergii* (Wolff 1973, Kristensen 1984, Zwarts 1988b), and moreover the latter species is only able to take the smallest *Nereis* (Davey & George 1986).

Nereis diversicolor can avoid predators by remaining deep in their burrows, but while feeding, predation risk is increased. The species has a wide range of food size, from macrozoobenthos to microfauna and diatoms, but it also takes organic debris (Goerke 1971, Reise 1979, Witte & de Wilde 1979). A wide array of different feeding techniques is used: filter feeding (Harley 1950, 1953, Goerke 1966, 1971), deposit feeding (Linke 1939, Goerke 1971, Reise 1979, Cram & Evans 1980), scavenging (Vader 1964, Muus 1967, Green 1968, Goerke 1971, this paper) and predation on other macrozoobenthos (Reise 1979, Witte & de Wilde 1979, Ratcliffe *et al.* 1981, Ronn *et al.* 1988). The last 3 techniques have in common that the worm usually emerges from the burrow to feed at the surface. It is then an easy prey, being both detectable and accessible to predators. A filter-feeding worm spends about half of its feeding time near the surface, viz. during the construction of the mucous net and during the consumption of this net after irrigation (Harley 1953, Goerke 1966). During filtering (also known as mucous-bag feeding), a worm is thus accessible to most of its predators, but how risky filtering is depends on detectability.

In this paper, we analyse some factors determining burrow depth in *Nereis* and discuss its importance for avoidance of predators. Further we present data on surface feeding and filter feeding and discuss the increased predation risks associated with both feeding methods.

Methods

Study area

Research was carried out on the intertidal flats along the Frisian coast (1980 to 1985) and in the Dollart (1985), both situated in the eastern part of the Dutch Wadden Sea. The salinity is 25 to 30‰ S along the Frisian coast and fluctuates between 1 and 10‰ S in the southern part of the Dollart. The tidal range in the 2 areas is 1.6 to 2.5 m and 2.0 to 3.5 m, respectively. Most study plots were situated just below mean sea level. The clay content (< 2 µm) was determined for the upper 25 cm of the sediment as weight fraction of the dried sample.

Table 1. *Nereis diversicolor*. Relative body length when preserved in alcohol and formalin as compared to measurements of worms still alive (= 100% ; maximal length of worms creeping along a ruler in sea water).

	% ± *SD*	*n*
Alcohol	77.8 ± 10.1	431
Formalin	68.1 ± 17.7	63

Burrow depth

Sediment cores, taken with a sampler (Ø 15 cm, 40 cm deep), were solid enough to remain standing on an improvised table after the sampler was lifted. Cores were placed horizontally with the top against an upright shelf and broken sideways. The burrows of *Nereis* were easy to locate, because they were surrounded by a light coloured oxidation layer and their inner wall looks smooth or even mucous (Linke 1939, Vader 1964). Most of the burrows had the shape of a U, less often a J and occasionally a Y. The worms were usually found in the deepest part of their burrow, sometimes doubled up. Burrow depth was measured to the nearest 0.5 cm, as the distance between the surface and the deepest point of the burrow. A pin was used to correct for a possible loss of the upper layer of the substrate, usually not more than 0.5 cm (Zwarts 1986, Zwarts & Wanink 1989).

Nereis < 3 cm appeared to be missed frequently with the method described above. The depth of these small worms was measured with another technique on 2 sampling occasions: the upper 4 cm of the sediment core was cut into slices of 1 cm, which were sieved separately on a 225 µm sieve.

Body length, body weight and body condition

The length of *Nereis* was measured in 3 ways: (1) the maximal length of a worm creeping along a ruler in seawater, (2) length of worms preserved in 60% alcohol and (3) length of worms stored in 10 to 20% formalin. The length of worms killed in alcohol or formalin was adjusted to the size of living worms (Table 1). The length of broken worms was estimated from the relation between the width of the tenth segment and the length of intact worms (Fig. 1).

Ash-free dry weight (AFDW) was determined after the worms were dried at least 24 h at 70 °C and subsequently ignited 2 h at 550 °C. Only freshly collected animals were selected, since there was a considerable reduction of AFDW when *Nereis* were stored in formalin or alcohol (Zwarts 1988b). Body condition is defined as the deviation from expected body weight, which was derived from the allometric relationship between body length and AFDW as determined per sampling programme.

Feeding behaviour

The activity pattern of *Nereis* in the field and in the laboratory was studied in September and October 1981 and 1985.

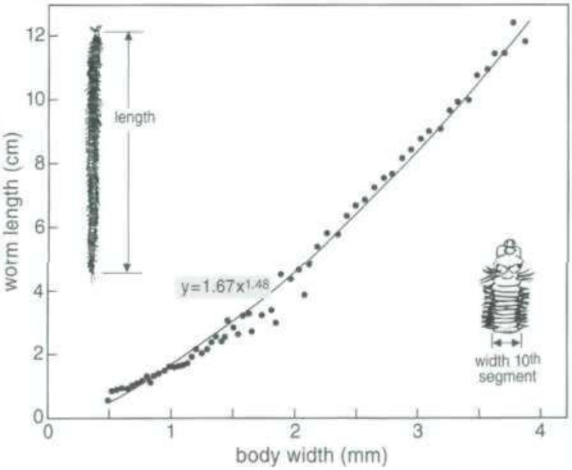

Fig. 1. *Nereis diversicolor*. Body length as a function of body width. The calculated relation was used to estimate the length of broken worms. Results of the regression analysis: $R^2 = 96.7\%$, $p < 0.001$, n = 1014.

Table 2. Results of a 2-way analysis of variance to test the effect of body size and clay content on burrow depth during summer (n = 2383; same data as Fig. 2).

Source of variation	R^2, %	*p*
Main effects	53.0	0.001
body length	33.5	0.001
clay content	6.4	0.001
Two-way interaction	0.7	0.001

Field observations: Worm activity at the surface was observed continuously in 16 plots of 73 cm² during 5 low water periods. Observations were made from a plank bridge to prevent disturbance of the worms. Two categories of activity were distinguished (Goerke 1971, Evans & Rogers 1978, Cram & Evans 1980): 1) 'Surface feeding', when at least the head was out of the burrow. The time spent at the surface was measured to the nearest second. 2) 'Inactive', when no worm was visible in a burrow entrance. The density and size frequency of the worms in the plots were determined afterwards with the core sampler.

Aquarium observations: An aquarium was filled with 15 cm of mud and divided into 12 compartments (10 × 25 cm) with the aid of fine-mesh wire-netting. Each compartment contained 1 worm of 7 to 10 cm length. Tides were simulated by alternately pumping a water column of 15 cm into and out of the aquarium at intervals of 6 h. The worm's food supply was undoubtedly low as the aquarium was poorly lit and the sea water was changed only once a week. Worm activity was recorded by observing the surface of one compartment continuously for 12 periods of 30 minutes and measuring the time spent at the surface ('surface activity'; as in the field situation) and the time spent on 'burrow activity', as determined by air-bubbling, visible water currents or fluctuating water levels in one or both entries of the burrow, without the worm being seen (Twisk 1986). Burrow activity, which was not distinguished in the field, included filter feeding, irrigating for respiration and also crawling and turning round in the burrow (see Evans & Rogers (1978) for a detailed description).

Analysis

SPSS (Nie *et al.* 1975) was used for all statistical analyses. The depth measurements throughout the year are shown per month, but where taken together per season, 'summer' and 'winter' are defined as the periods 16 May-30 September and 15 November-31 March respectively; 'spring' and 'autumn' are the two intervening 6 week periods.

Results

Burrow depth in relation to body length, substrate and season

Nereis lived in burrows 1-29 cm deep (Fig. 2). Average burrow depth increased with worm size but tended to

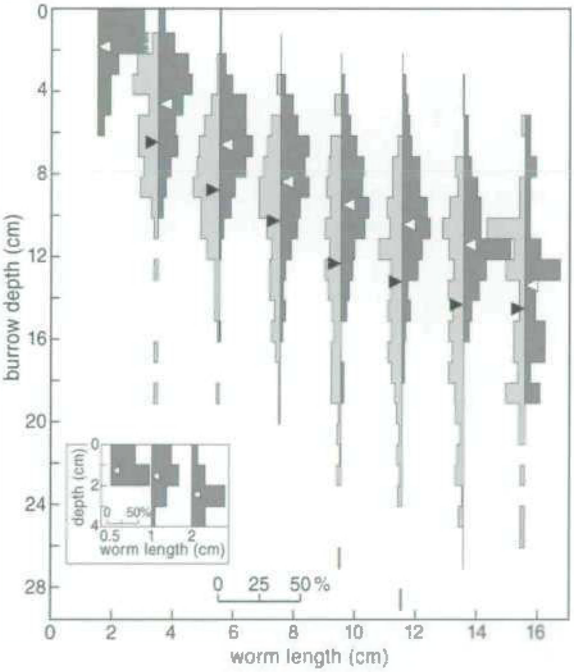

Fig. 2. *Nereis diversicolor*. Burrow depth in relation to body size in mud (clay content ≥ 6%, n = 1496) (black; white arrow indicates the mean burrow depth per size class) and sand (clay content ≤ 5%, n = 887) (grey; black arrow indicates the mean burrow depth per size class), 16 May to 30 September. See Table 2 for statistical analysis. Inset shows depths of 54 worms in mud measured with the slice technique (see Methods).

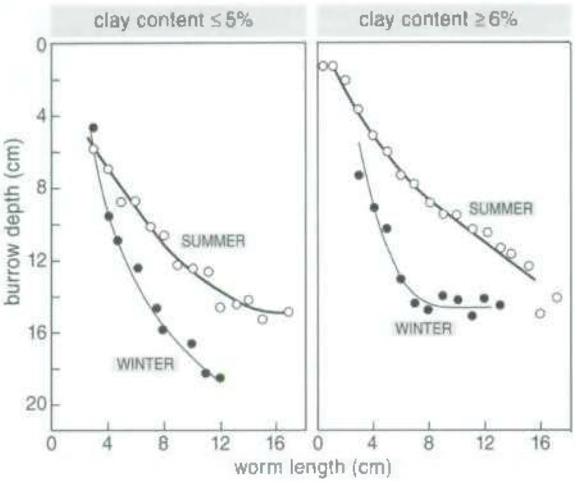

Fig. 3. *Nereis diversicolor.* Burrow depth as a function of body length during summer and winter in sand (left panel; n = 887 and 49, respectively) and mud (right panel; n = 1496 and 293, respectively). The lines are based on third degree polynomials. See Table 3 for statistical analyses.

Table 3. Results of two 2-way analyses of variance to test the effect of body size and season on burrow depth in sand and mud (same data as Fig. 3).

	Clay content			
	≤ 5%		*≥ 6%*	
	n = 936		*n = 1789*	
Source of variation	*R^2, %*	*p*	*R^2, %*	*p*
Main effects	28.2	0.001	63.0	0.001
body size	25.8	0.001	40.2	0.001
season	4.0	0.001	16.9	0.001
Two-way interaction	1.0	0.261	0.8	0.001

level off for the larger size classes. There was a large variation in burrow depths for worms of the same size: *Nereis* > 10 cm were usually found at a depth of 10 to 14 cm, but some lived in shallow burrows of only 3 to 4 cm, whereas others had burrows as deep as 24 to 29 cm.

Worms of < 3 cm were found predominantly in the upper 2 to 3 cm. The majority of 0.5 cm worms lived in burrows of 1 to 2 cm. Size classes measured with the slice and core techniques show similar depths (Fig. 2 inset). According to Dales (1950) and Dales & Kennedy (1954) larvae are present in the parent burrow or in the upper layer of the substrate, whereas worms of 4 mm are already able to construct their own U-shaped tubes. We found worms of this size class within the upper 2 cm in late summer (Fig. 2) and in October even in the upper 4 cm (Esselink & van Belkum unpubl.).

Worms of a similar size buried deeper in sand than in mud (Fig. 2; Table 2). The difference is 2 to 3 cm and is almost independent of worm size. Worms buried more deeply in winter than in summer, in sand as well as in mud (sediments with a clay content of ≤ 5% and ≥ 6% respectively) (Fig. 3; Table 3). Small worms increased their depth about 2 cm and the larger ones by about 5 cm in winter as compared with summer.

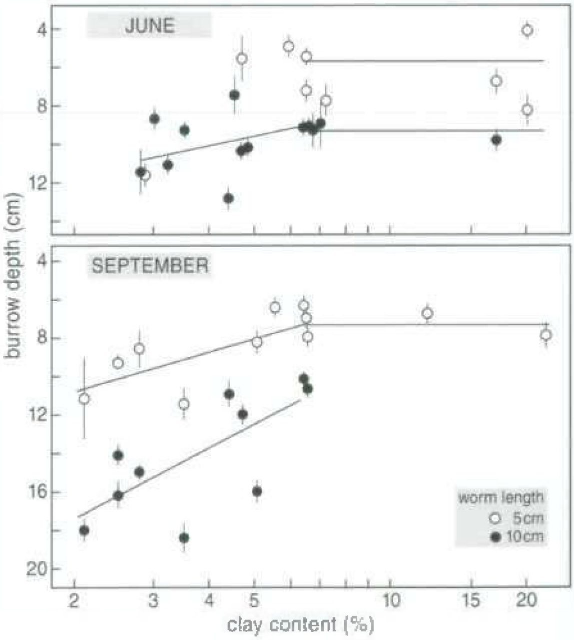

Fig. 4. *Nereis diversicolor.* Burrow depth (mean ± SE) in relation to clay content of the sediment for worms of 5 (4 to 6) and 10 (7 to 14) cm in June (n = 1138 and 51, respectively) and in September (n = 642 and 189, respectively). Mean depth is given for substrate with clay content ≥ 6%. Since there is an increase of depth with size within the selected ranges (Fig. 2), a correction was made to transform the depth measurements of worms of 4 to 6 and 7 to 14 cm to the burrow depth of a standard worm of 5 and 10 cm, respectively.

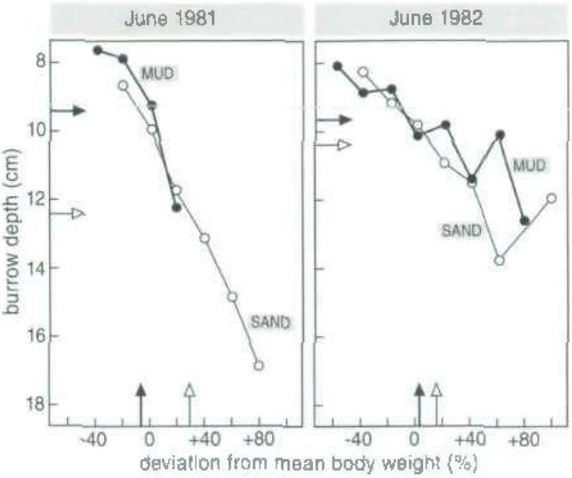

Fig. 5. *Nereis diversicolor.* Burrow depth of worms of 10 (7 to 14) cm living in mud (●) and sand (○) as function of body condition in 2 sampling programmes. Mean burrow depth and mean body condition in mud and sand are indicated by black and white arrows, respectively. A correction has been made, as in Fig. 4, to adjust for the size effect on depth. See Table 4 for statistical analysis.

Figure 4 shows the relationship between clay content and burrow depth. Burrow depth appeared to remain constant if the clay content increased from 6 to 20%. However, in sediments with a clay content of ≤ 5% (defined above as sand) burrow depth increased when clay content decreased from 5 to 2%. *Nereis* are not found in sediments where the clay content is well under 1% (Zwarts 1988b). The relationship between clay content and burrow depth in the sandy sediments was more pronounced in September than in June (Fig. 4). The effect of clay content on burrow depth cannot be attributed to other measured variables, such as elevation (or emersion time).

Burrow depth and body condition

The large variation in burrow depth for individuals of the same size (Fig. 2) can be explained partly by a difference in body condition (Fig. 5). The body weight of deep-living *Nereis* was on average 2 to 3 times greater than that of individuals of the same size class with shallow burrows. Apparently, worms in good condition are able to maintain deeper burrows.

It is known that body condition varies throughout the year and also differs for worms found along the tidal gradient (Chambers & Milne 1975b, Esselink *et al.* 1989). Figure 5 shows that the body condition of worms living in sand was 10 to 35% higher than that of individuals sampled in mud. The effect of clay content on burrow depth, as described in the previous section, disappears completely in 3 out of 4 sampling programmes if body condition is taken into account (Table 4). The deeper burrows found in sandy sediments might thus be explained by the average difference in body weight between individuals inhabiting sandy and muddy sediments.

There is also a positive relationship between body condition and burrow depth when worms within a same season are compared, but this effect appears to be independent of the seasonal variation in depth (Fig. 6, Table 5).

Table 4. *Results of four 2-way analyses of variance to test the effect of body condition and clay content on burrow depth in 4 sampling programmes (data for June and July shown in Fig. 5). Since body condition is related to clay content, the total variance explained by the 2 main effects can be larger than the sum of the variances unique to each of the separate factors.*

Source of variation	*Nov. 1980* *n* = 55		*April 1981* *n* = 67		*June 1981* *n* = 91		*July 1982* *n* = 299	
	R^2, %	*p*	R^2, %	*p*	R^2, %	*p*	R^2, %	*p*
Main effects	36.0	0.001	27.2	0.001	54.2	0.001	11.9	0.001
condition	8.0	0.002	25.0	0.001	2.0	0.001	10.4	0.000
clay content	7.5	0.020	4.4	0.055	0.0	0.876	0.7	0.118
Two-way interaction	0.2	0.734	3.7	0.206	0.4	0.718	2.3	0.190

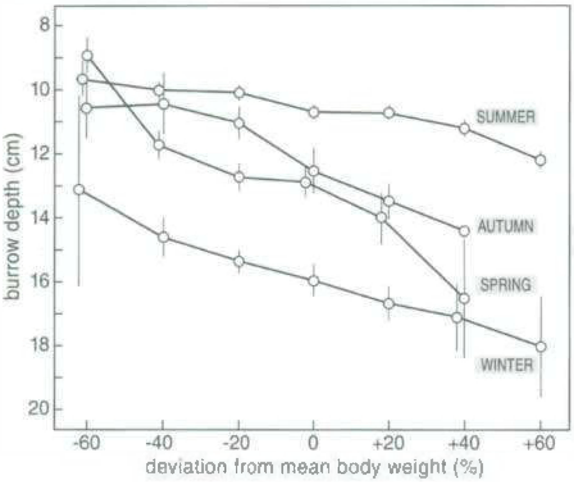

Fig. 6. *Nereis diversicolor*. Burrow depth (mean ± SE) of worms of 10 (7 to 14) cm as a function of body condition in 4 seasons (n = 2247); sites with different clay content are taken together. As in Figs. 4 and 5 a correction was made to adjust for the size effect on depth. See Table 5 for statistical analysis.

Burrow depth in relation to season and temperature

There was a great difference in burrow depth between summer and winter for all size classes (Fig. 3). Figure 7 shows the burrow depth of *Nereis* of 10 cm over a number of years. There is a large similarity between the years: burrow depth was maximal in January or February, followed by a decrease of 2 cm per month until the minimal depth was reached in June or July. Then, in late summer, burrow depth gradually began to increase again with an acceleration after October.

Table 5. Results of a 2-way analysis of variance to test the effect of body condition and season on burrow depth (n = 2247; same data as Fig. 6).

Source of variation	R^2, %	p
Main effects	29.5	0.001
season	27.1	0.001
condition	3.5	0.001
Two-way interaction	0.9	0.242

Variations in burrow depth throughout the year correspond with day length, but there is a better correlation between depth and sea water temperature (Fig. 7). Figure 8 shows a curvilinear relationship between sea water temperature and burrow depth. Burrow depth appears to depend on temperature, independent of the time of year; an analysis of covariance (not shown) confirmed this.

All burrows were found in the upper 30 cm, even in winter, and since a core sampler of 40 cm was used, the possibility of deeper burrows was eliminated. The fact that burrow depth correlates well with sea water temperature (Figs. 7 and 8) suggests that low temperatures stimulate *Nereis* to deepen their burrows. The only time we observed remarkable digging activity by

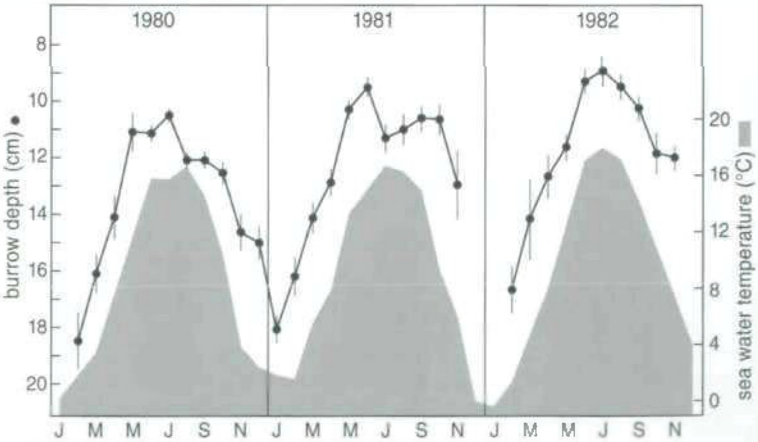

Fig. 7. *Nereis diversicolor*. Seasonal variation in burrow depth (mean ± SE) of worms of 10 cm (7 to 14 cm, with transformation as in Fig. 4), living in mud (clay content ≥ 6%). Sea water temperatures on the sampling dates are taken from the series of daily measurements of Rijkswaterstaat at Holwerd.

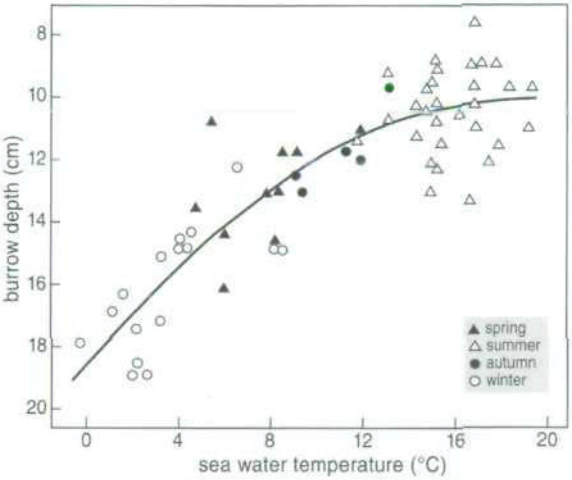

Fig. 8. *Nereis diversicolor*. Burrow depth of worms of 10 cm, living in mud (clay content ≥ 6%), as a function of sea water temperature, given separately for the 4 seasons (61 sampling days from 1980 to 1985). Line based on second degree polynomial ($R^2 = 77.6\%$, $p < 0.001$, $n = 61$).

Nereis was after a sudden drop in temperature (to below 0 °C) in October, when the burrows were deepened by an average of 2 cm.

Linke (1939) and Beukema (1979 and pers. comm.) found very deep burrows of c. 40 cm in the Wadden Sea after a cold spell during which the upper layer of the mud was frozen. Muus (1967) measured the burrow depth of *Nereis* in Nivå Bay, Denmark. The winter temperature there is lower than in the Wadden Sea, and in February he indeed found most large worms at a depth of 40 cm and some even at 50 to 60 cm. The depth distribution in summer does not differ between Nivå Bay (0 to 20 cm, Muus 1967) and the Wadden Sea (5 to 25 cm, according to Thamdrup (1935) and this study (Fig. 2).

Feeding behaviour in the field

We spent 5 low water periods during daylight in the field recording the activity of *Nereis*. No activity at all was observed during 2 days in September on a tidal flat with a mixed substrate (clay content 5%), though the worm density was high (95 worms m^{-2}) and the mud temperature not low (19 °C). The surface activity varied significantly from day to day as well as during the low water period on a mudflat where the clay content amounted to 25% (Fig. 9). Worms appeared at the surface there at an average of 2.4, 0.7 and 0 times during 3 low water periods in September and October (Fig. 9A). This variation might be attributed to mud temperature, which averaged 20, 17 and 11 °C, respectively. The mean duration of the surface bouts also varied between days; on the first day it was 17.6 s and 11 days later it was 27.3 s (Fig. 9B).

For both days there was a similar tidal trend in the frequency with which *Nereis* appeared at the surface, as well as in the duration of the surface bouts. Almost no worms came to the surface during the first 2 h after the mudflat emerged. The peak frequency occurred in the third hour with a gradual decline afterwards. The frequency was again very low during the last 1 to 2 h that the mudflat was exposed. In contrast to the frequency, the duration of the surface bouts increased during the course of the emersion period (Fig. 9B). The length of the surface bouts ranged from 0.5 to 14 s during the first 2 h after emersion and 50% lasted less than 4 s. This is in great contrast to the last 2 h of the emersion time, when only 40% of the bouts were less than 15 s and c. 20% of the feeding bouts exceeded 60 s. A similar tidal trend in the feeding behaviour was measured in May (Twisk 1986), but the overall level of activity was higher than in late summer.

Nereis spent 0.1 to 0.2% of the emersion phase at the surface (Fig. 9C), i.e. an average of 25 to 50 s per individual worm. There was, however, a large variation in the time individuals spent on the surface. It was estimated that half the worms remained in their burrow on the first day of observation, while others spent 300 s and more at the surface.

Feeding behaviour in an aquarium

Nereis were never observed at the surface during high water. Worms appeared 6 times per hour at the surface during low water conditions (12 half hours of continuous observation), which is 15 to 50 times the frequency in the field (Fig. 9A). The average bout length (63.7 s, n = 36) was c. 7× longer in the aquarium than in the field (Fig. 9B). Consequently much more time was spent at the surface in the aquarium (Fig. 10A) than in the field situation, possibly because in the aquarium the food concentration in the water was much lower. A total feeding time of c. 20% during the low water pe-

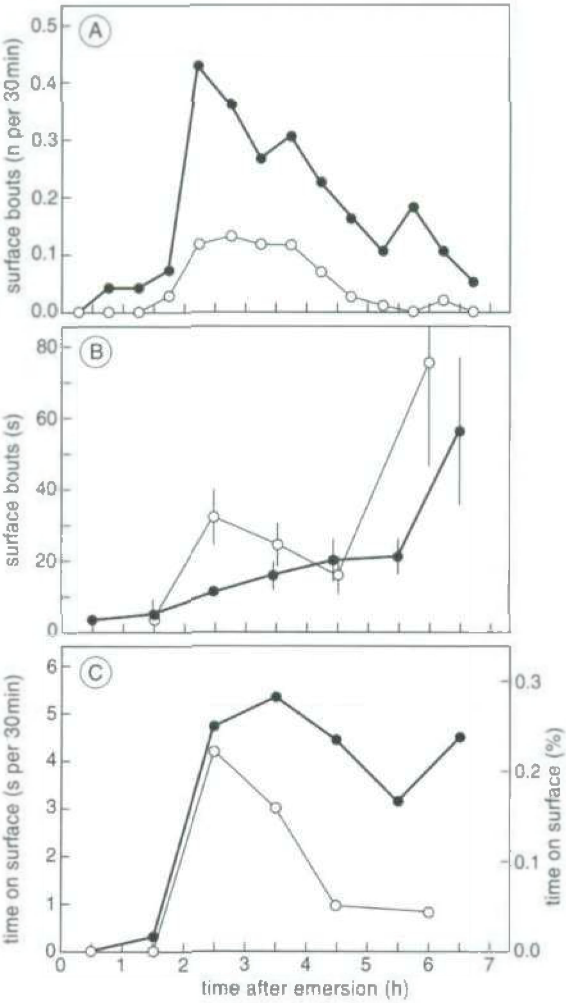

Fig. 9. *Nereis diversicolor*. Surface activity on a muddy intertidal flat after emersion on 9 September (●) and 22 September (○). **A.** Frequency with which worms ≥ 3 cm were observed at the surface (freq. = no. of observations/mean density; it was assumed that worms < 3 cm were not detected). **B.** Duration of the surface bouts (mean ± SE). **C.** Surface activity as percentage of the time budget (freq. h^{-1} × duration of surface bout).

riod of 6 h is c. 10 times more than that measured by Twisk (1986) in a more natural experimental setting.

The surface activity was, as in the field situation, minimal during the first 2 h after exposure, but the burrow activity was then at its maximum (c. 20%). The time spent on burrow activity decreased during the low water period, whereas surface activity increased, resulting in an almost constant level of observed activity during the entire exposure time. This pattern of activity changed completely after a slurry of shelled and minced *Scrobicularia plana* was poured over the mud shortly after emersion (Fig. 10B). *Nereis* came to the surface immediately to scavenge on the pieces of meat, which they took down into their burrows. The worms spent most of their time at the surface during the first 3 h of this experiment. It is unlikely that the decrease in activity after 3 h was caused by a depletion of the food supply because of the large quantity of slurry used in the experiment. Possibly the worms became satiated.

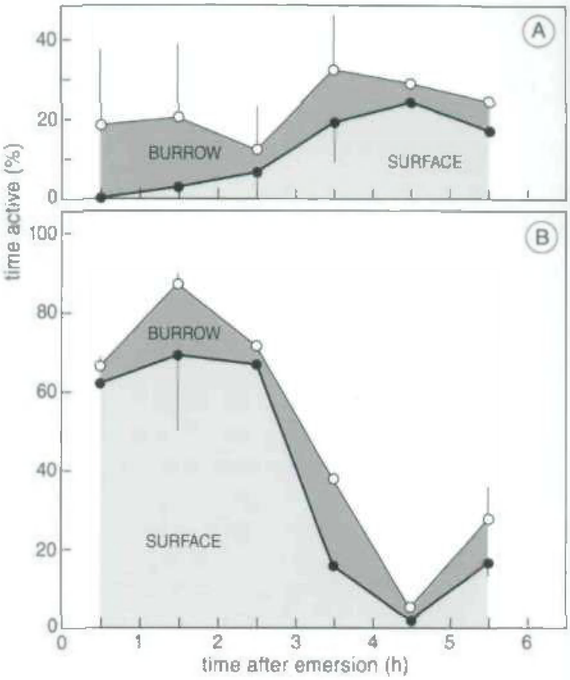

Fig. 10. *Nereis diversicolor*. Time-budget in an aquarium after exposure; active at surface (light area) and in burrow (dark). **A.** Control; **B.** Feeding experiment when a slurry of minced *Scrobicularia plana* was poured over the substrate just after emersion. Standard errors computed per half hour periods (n = 12).

There was no burrow activity when there was no water left at the surface (Fig. 11), as also found by Twisk (1986). The observation that burrow activity was maximal if the overlying water layer was thin, might be explained by the increasing food concentra-

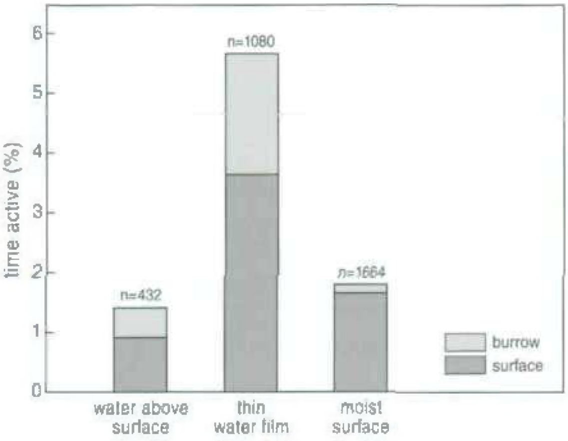

Fig. 11. *Nereis diversicolor*. Activity in an aquarium in relation to water level after exposure, based on activity counts every 10 min (n = counts × worms in aquarium).

tion when the depth of the water column decreased, but we cannot exclude the possibility that the burrow activity became more visible. The method used to quantify the activity data in Fig. 11 apparently led to an underestimation compared with the time-budget study (Fig. 10A). This does not, however, change the relative differences in activity as caused by water level.

Discussion

Burrow depth and size

Burrow depth of *Nereis* increased with size (Figs. 2 and 3). However, within each size class there was a large variation in burrow depth. A part of this variation can be attributed to body condition: worms with a relatively heavy body weight have deeper burrows than worms in poor condition (Figs. 5 and 6). The difference in burrow depths of worms living in sand and mud (Figs. 2 to 4) might also be explained by systematic differences in body condition for worms living in sand and mud (Fig. 5). There is no reason to assume that deep burrows cause enhanced body condition, so the reverse seems more likely: worms with a poor condition are apparently not able to dig and/or maintain a deep burrow. In bivalves it was also found that individuals with a better body condition increase their burying depth, achieving a decrease in their predation risk (Zwarts 1986, Zwarts & Wanink 1989).

Burrow depth and predation risk

When the tidal cycle is simulated in a laboratory, worms remain deep in their burrows and perform no surface activity during immersion (Vader 1964, this paper). If this is also the case in the field, depth would determine accessibility to shrimp and fish feeding when the tidal flats are flooded. Shrimp *Crangon cran-*

It is necessary to sit quietly for many hours to know how often Ragworms come to the surface to feed during the low water period.

gon and fish (e.g. *Potamoschistus microps* and *Platichthys flesus*) do not dig deeply and must capture *Nereis* from near or at the surface. The larger the shrimp the larger the worm taken, to a maximum of 3 cm (Pihl & Rosenberg 1984). *P. microps* are able to kill and eat an adult *Nereis*, but mainly take the smallest worms in the field (Muus 1967). There is no information available on size selection by Flounder *P. flesus*, but since they make feeding holes of only a few cm (Summers 1980), a restriction to the smaller size classes is to be expected. *Nereis*, however, are an unimportant prey for *P. flesus* or Plaice *Pleuronectus platessa* in the Wadden Sea (de Vlas 1979a), in contrast to the situation elsewhere (Muus 1967, Pihl 1982). Baird & Milne (1981) calculated that in the Ythan estuary (Scotland), for example, 60% of the total production of *Nereis* was consumed by predators, of which 1/3 was taken by flatfish and the other 2/3 by three bird species: Shelduck *Tadorna tadorna*, Redshank *Tringa totanus* and Oystercatcher *Haematopus ostralegus*.

Nereis present at the surface during low water retreat quickly when disturbed (Linke 1939, Vader 1964, own obs.). The frequency distribution of burrow depth, as given for the different size classes (Fig. 2) can therefore be used to calculate accessibility to predators which dig or probe to a certain depth.

The maximum probing depth of waders, as determined by bill length, varies from 3 cm (Dunlin *Calidris alpina*, Grey Plover *Pluvialis squatarola*) to 15 or 16 cm (female Curlew *Numenius arquata*). In winter all burrows of *Nereis* ≥ 5 cm in body length are deeper than 4 cm, thus greater than the bill length of Dunlin or Grey Plover (Fig. 12A). The first species indeed selects *Nereis* ≤ 4 cm in winter (Worrall 1984). Kersten & Piersma (1984) found that Grey Plover took 2.5 and 5 worm min^{-1} in May and September, respectively, and calculated that Grey Plovers had to take worms of 5 to 7 cm, the most common size class present in the mud, to meet their energy demands. Evans *et al.* (1979) observed that most Grey Plovers wintering in the Tees estuary (NE. England) took the larger *Nereis*. Grey Plovers must, therefore, rely on worms present in or at the burrow entrance. This must also be the case with most other short-billed wader and gull species. Observations on the feeding behaviour of the Black-headed Gull *Larus ridibundus* (Curtis *et al.*

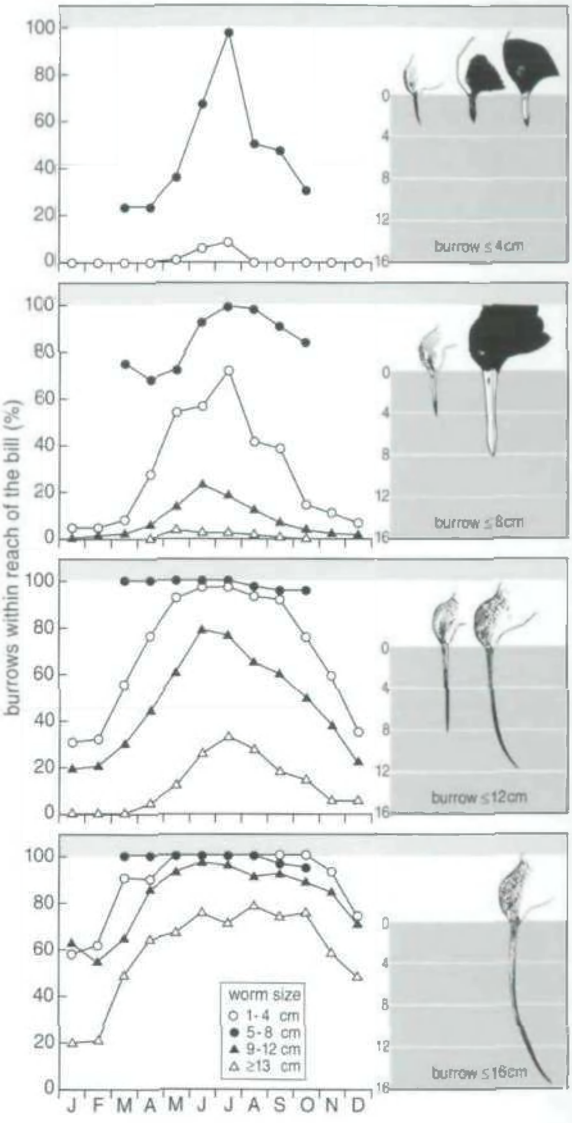

Fig. 12. *Nereis diversicolor*. Annual variation in the accessibility of 4 size classes of *Nereis* to predators with different bill lengths, as calculated from the frequency distribution of the burrow depths in mud (Figs. 2 and 3). The panels show from top to bottom the accessible fraction in the range 0 to 4 cm (within reach of e.g. Dunlin, Grey Plover and Black-headed Gull), 0 to 8 cm (within reach of e.g. Redshank and Oystercatcher), 0 to 12 cm (within reach of ♀♀ Bar-tailed Godwit and ♂♂ Curlew) and 0 to 16 cm (within reach of ♀♀ Curlew).

1985) and Curlew (Zwarts & Esselink 1989) show that these birds take most *Nereis* from the surface.

Avocets *Recurvirostra avosetta* sweep their bill through the upper layer of the surface and nevertheless take large *Nereis* (Tjallingii 1969, Engelmoer & Blomert 1985). The intake rate of Avocets in the course of the emersion period closely resembles the tidal trends in surface feeding of *Nereis* as shown in Fig. 9 (own obs.). In winter Redshank (bill length 4 cm) prey on worms larger than 4 cm (Goss-Custard 1969, 1977a, 1977b), which would be unavailable if they remained deep in their burrows (Fig. 12B).

Most worms caught by Curlews are ≥ 9 cm. The fraction of this size class accessible to a probing male Curlew (bill length 12 cm) is 80% in summer against 20% in winter (Fig. 12C). In summer Curlews feed on worms which are extracted from the burrows, while in winter nearly all worms are taken from the surface. Female Curlews are the only predators which are able to probe to a depth of 13 to 16 cm (Fig. 12D). Worms below this danger line are out of reach of all their predators.

Apparently, the majority of the waders take worms from the surface. Most of these predators have no choice, since the burrow depth exceeds their bill length. Figure 3 shows that burrow depth increases with worm size but that the depth levels off as soon as worms reach a critical depth below the maximal probing depth. The same has also been found in estuarine bivalves (Zwarts & Wanink 1989). A simple explanation for this might be excessive predation pressure on all accessible worms. The creaming-off effect of predators taking worms from shallow burrows was studied with an exclosure experiment set up in July; after 2 months a difference in average depth was apparent (worms inside the exclosure burrowed on average 0.5 cm shallower). This difference (although not statistically significant on account of small sample sizes) suggests that the critical depth of 12 to 15 cm is partly caused by a selective predation on shallow-living worms.

Seasonal variation in burrow depth

There are 3 possible explanations for the seasonal variation in burrow depth (Fig. 7): predation pressure, temperature and feeding method.

Assuming that the selection of burrow depth has evolved so as to minimize predation risk, it is to be expected that a seasonal variation in predation pressure will correspond with a similar trend in burrow depth. It is indeed true that worms live at a minimal depth from May to mid July when most deep-probing predators (Curlew, Oystercatcher and Bar-tailed Godwit) are absent, but the burrows remain shallow after these waders return in July and are present in maximum numbers in August/September. Seasonal depth variation is thus not governed by predation pressure alone.

Temperature seems to be of overriding importance. In summer, mud temperature decreases with depth but the reverse is true when the surface temperature is c. 0 °C (de Wilde & Berghuis 1979a, Zwarts unpubl.). A deeper burrow in winter might therefore be an adaptation to escape low temperatures. Worms do indeed increase their depth at an average rate of 0.6 cm for a sea temperature drop of 1 °C, at least below c. 15 °C (Fig. 8). The digging activity of the worms after a frost in October, mentioned earlier in the text, can be interpreted as a direct effect of temperature on burrow depth. This observation also shows that the worms' adjustment of burrow depth is not continuous, but erratic.

A third seasonal effect might be prompted by the use of different feeding techniques. If the worm obtains all its food from the surface, the burrow is solely a refuge from predators and an adverse climate. During filter feeding, however, the burrow also serves as an irrigation channel. Irrigation is an energy-demanding feeding technique (Kristensen 1981), but these costs are minimized if the burrow depth is reduced. It is therefore likely that, other things being equal, filter feeders burrow less deep than surface-feeding worms. This effect is likely to be found only if filter feeding occurs predominantly at high sea water temperature, given the close relationship found between temperature and burrow depth. Though detailed information is lacking, it is true that filter feeding is rare in winter and very common in summer (Goerke 1971).

One can thus conclude that temperature is an important factor determining the seasonal variation in burrow depth. The possibility that filter feeding is more profitable if the burrow depth is reduced and that seasonal variation in the significance of filter feeding might effect the observed trends in burrow depth deserves further research.

Feeding and prey risk

The choice of *Nereis* to filter feed from the overlying water, to leave the burrow to feed at the surface, or to remain inactive in the burrow, depends on the trade-off between gain of energy and avoidance of predation. Though *Nereis* is one of the best studied estuarine zoobenthic species, it is still impossible to describe this decision-making in a quantitative way, although some qualitative predictions can be made.

Nereis respond immediately to a change in their food supply (Fig. 10), which suggests that they evaluate the current yield from filtering or surface feeding. The food supply in water and on the surface-layer is different for worms living in mud and in sand. The surface layer contains more food on a mudflat than on a sandflat (Newell 1979), whereas filter feeding on muddy shores is probably less profitable or even impossible, because *Nereis* probably meet the same problem as other filter feeders, viz. the relatively low concentration of food particles among all suspended material. More suspension feeding and less deposit feeding can therefore be expected if *Nereis* living in sand are compared with those in mud. Our field observations indeed suggest that surface feeding is common in mud and absent on sandflats.

Filter feeding makes no sense when the food supply in the water is too low. The food supply is maximal in summer and minimal in winter, but this variation is much larger in the water than in the upper surface of the substrate (Colijn 1982, Hummel 1985a), so it is to be expected that filter feeding disappears during the winter. Goerke (1971) indeed observed little filter feeding in winter, whereas it was very common in summer.

Filter feeding is impossible if no water remains at the surface (Twisk 1986), whereas surface feeding can occur regardless of the stage of the tidal cycle. However, worms exposed to a tidal regime do not feed at the surface during immersion (Vader 1964, this paper), probably to escape the high risk of being taken by fish, shrimps and crabs.

Filter feeding is not without danger because predators probably see the burrow entrances or even the water current or fluctuating water level at the entrance to the burrow (Twisk 1986). Moreover, filter-feeding *Nereis* spend about half their time close to the surface, viz. during the construction of the mucous net and during the consumption of this net after irrigation (Harley 1953, Goerke 1966). Surface feeding is the most dangerous feeding technique, however, because the worm is very conspicuous and easy to catch. The likelihood of its escape from an approaching predator depends on how quickly it can retreat into the lower part of its burrow.

The time spent by *Nereis* at the surface is very limited. Figure 9C shows it was only 0.1 to 0.2% during low water in September and 0% during 2 other low water periods, also during late summer.

Birds feeding on exposed tidal flats take more worms from the surface than from burrows (Zwarts & Esselink 1989), which means that the predation risk during surface feeding must be extremely high compared with a situation in which the worms remain in their burrows. Thus worms obtaining all their food from the surface (e.g. worms in soft mud) are exposed to a greater predation risk than worms which solely filter feed (e.g. worms in sand). The low body condition of worms in mud (Fig. 5) and the reduced growth in mud as compared with sand (Zwarts 1988b) might therefore be the consequences of the counterbalancing of the enhanced predation risk.

The feeding rate (energy intake s^{-1}) must be very high during surface bouts, compared with the feeding rate during filter feeding. The difference in energy gain between both techniques is even greater if one takes into account that the feeding costs of filtering are high (Kristensen 1981). Nevertheless, surface feeding is, in our view, a supplement to filter feeding, because of the very high predation risk it entails. Worms feed at the surface in 3 circumstances in which filter feeding is unprofitable or impossible: (1) during that phase of a tidal cycle when filter feeding is made impossible by lack of water on the surface (Fig. 11), (2) in winter when the low concentration of food in suspension makes filter feeding unprofitable, (3) on muddy shores where the relatively low amount of food in the suspended material makes filtering less profitable.

The density of *Nereis* actually available to predators thus depends not only on the depth of their burrows but also on their own choice of feeding methods (Zwarts & Esselink 1989).

Chapter 15

VERSATILITY OF MALE CURLEWS *NUMENIUS ARQUATA* PREYING UPON *NEREIS DIVERSICOLOR*: DEPLOYING CONTRASTING CAPTURE MODES DEPENDENT ON PREY AVAILABILITY

Leo Zwarts & Peter Esselink

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VERSATILITY OF MALE CURLEWS *NUMENIUS ARQUATA* PREYING UPON *NEREIS DIVERSICOLOR*: DEPLOYING CONTRASTING CAPTURE MODES DEPENDENT ON PREY AVAILABILITY

Curlews *Numenius arquata* use 2 methods to capture Ragworms *Nereis diversicolor*: they search for worms at the surface, which are taken with a single peck (called N_{peck}) and/or they search for visual cues, such as burrow entrances, and probe deep to extract the worm from the burrow (called N_{probe}). It is argued that male Curlews select predominantly active worms, which are either grazing at the surface (N_{peck}) or are filter feeding within their burrows (N_{probe} and sometimes N_{peck}). Profitability (mg s^{-1} handling) increases with worm length and is greater for N_{peck}, because of its shorter handling time, than for N_{probe}. Worms of both prey types $\leq$ c. 6 cm are ignored, since profitability is below the intake rate (mg s^{-1} feeding). During low water there is a shift from N_{probe} to N_{peck}, which can be explained by changes in feeding behaviour of the worms. N_{probe}, common in summer, disappears during autumn due to the increase of burrow depth (with the corresponding decrease of worms accessible as N_{probe}), and to a reduction in filter feeding of the worm, which means that fewer traces are visible. Curlew search rate increases if, relatively, many prey are of the N_{peck} type. There appears to be a trade-off between search rate and probability of detection of conspicuous N_{peck} and cryptic N_{probe}. No evidence was found that Curlews ignore one prey type and selectively search for the other. We conclude that (1) unprofitable prey sizes are ignored, (2) the greater part of the profitable prey are not available, being hidden in the substrate and mostly not accessible even when detectable, (3) Curlews continuously readjust their capture technique to changes in the available food supply.

Introduction

The density of available prey is a major factor determining the feeding behaviour of a predator, but because prey availability cannot usually be measured adequately, absolute prey density is usually measured instead. The implicit assumption is that the proportion of available prey does not differ spatially or temporally. This study shows that there is a very large variation in the fraction of a burrow-dwelling prey species, Ragworm *Nereis diversicolor*, which is actually available to a wading bird, Curlew *Numenius arquata*. The feeding behaviour of the bird can even be described as a continuous adjustment to changes in the available food supply (Wanink & Zwarts 1985).

Ragworm is a major prey for estuarine wader species throughout its range on the intertidal mudflats along the coast of Europe and NW. Africa. Analyses of faeces, pellets and gizzards of waders in different areas and also direct observations on prey selection shows that this species is one of the main prey of about 15 wader species and the dominant prey of at least 5 waders: Avocet *Recurvirostra avosetta*, Grey Plover *Pluvialis squatarola*, Curlew Sandpiper *Calidris ferruginea*, Bar-tailed Godwit *Limosa lapponica* (particularly ♀♀) and Curlew (particularly ♂♂) (Höfmann & Hoerschelmann 1969, Zwarts 1974, Goss-Custard et al. 1977b, Evans *et al.* 1979, Ens & Zwarts 1980a, Townshend 1981, Kersten & Piersma 1984, Worrall 1984).

The species is an important prey for birds because it is common, profitable and detectable as well as accessible. It is a common species with a wide distribution over estuarine flats where it can occur in high densities: 500-500 000 juveniles m^{-2} in summer and 50-200 adults m^{-2} (1+ year) (Linke 1939, Dales 1950, Smidt 1951, Muus 1967, Wolff 1973, Chambers & Milne 1975b, Beukema 1976, Essink 1978, Dankers & Beukema 1984). It is a profitable prey for waders and the Black-headed Gull *Larus ridibundus* (Goss-Custard 1977a, Curtis *et al.* 1985, this study) since it can be handled rapidly, whereas the flesh weight is high compared with most other common estuarine worm species (Beukema 1976). It is also a detectable and accessible prey, especially easy to capture during grazing excursions at the surface around its burrow. A worm which filters food from the overlying water spends half of its time near one of the entrances of its burrow (Harley 1953, Goerke 1966) and thus also within reach of most waders' bills. When disturbed at or near the surface, however, a Ragworm retreats quickly to the bottom of its burrow (Vader 1964). A small fraction of worms then remains accessible for 3 long-billed waders: Oystercatcher *Haematopus ostralegus* (bill length 6 to 8 cm), Bar-tailed Godwit (bill 7 to 10 cm) and Curlew (bill 10 to 16 cm). The Curlew, however, is the only wader able to capture *Nereis* in their burrows throughout the year (Esselink & Zwarts 1989).

The fraction of worms accessible to a probing wader can be calculated if its bill length and the depths of the burrows are known (Fig. 12 in Esselink & Zwarts 1989). However, if the same wader preys on surface-feeding worms, the frequency with which the worms emerge from their burrows provides a more relevant measure of prey accessibility (Fig. 9 in Esselink & Zwarts 1989). The accessibility of *Nereis* to waders is thus complex to quantify.

This paper deals with Curlews feeding on *Nereis*. There is a remarkable difference in the feeding of individual Curlews, even when specializing on this prey. This variation is greatly reduced when birds with the same bill length are compared. All data presented here pertain to male Curlews (bill 10 to 12.5 cm); the problem of individual variation will be treated elsewhere.

We distinguish 2 methods of prey capture: (1) worms which are taken from the surface or the entrance of the burrow are classified as N_{peck}, (2) worms taken from the depths of the burrow are referred as N_{probe}.

This paper focuses on 2 questions:

- can size selection be explained by the profitability and availability (thus accessibility and detectability) of the different size classes of *Nereis*?
- how does a Curlew cope with variations in prey accessibility within a tidal cycle and during the course of the year?

Methods

Study area

The study was carried out on intertidal flats along the Frisian coast, Dutch Wadden Sea (53° 25′ N, 6° 04′ E) from 1979 to 1982 inclusive. Most data were collected in late summer. Four observation towers were erected, around which 274 plots of 0.1 ha and 85 plots of 0.06 ha were pegged out, and each year 400 to 800 small plots of 25 m^2 were staked out 10 to 200 m from one of the towers.

The larger part of the study area was situated between 10 and 30 cm below mean sea level, which corresponds to an emersion period of 37 to 43% per tidal cycle. The clay content (< 2 μm), determined for the upper 25 cm of the substrate, varied between 0.8 and 10.8%, but at most sites it was 4 to 5% with a median grain size of 95 μm (excluding the fraction < 16 μm) (Zwarts 1988b). Water level in a nearby creek and mud temperature at a depth of 2 to 3 cm were measured continuously.

Curlews

There were 3000 Curlews present in the study area between July and April; 250 of these birds were marked individually with 2 colour rings. This paper is based upon work done on 24 colour-banded and 28 unbanded Curlews which, because of their territorial behaviour and consequent extreme site fidelity, could be recognized individually (Ens & Zwarts 1980b). About 10% of the observations concern birds which were not identified as individuals. Bill length of marked birds was known and it was estimated for the unbanded ones. The estimation error -as determined for the marked birds- was small and usually ≤ 1 cm, thus < 10% (Ens & Zwarts 1980a and unpublished).

Individual Curlews were observed continuously, usually during the entire low water period, by 2 persons using a zoom-telescope (magnification 15 to 60×) and a mirror-telescope (40×). The following data were noted or registered on tape: (1) plot coordinates, (2) type of prey taken, (3) prey size (using bill

Table 1. *Numenius arquata.* Search rate predicted by the 'grid method' (explanation in the text) compared to the search rate as derived from the product of pace length (as measured from the prints in the mud) and pace frequency. All data were collected for one Curlew observed an entire low water period.

Search rate	*Mean ± SE*	*n*
Grid method (cm s^{-1})	22.6 ± 0.02	180
Pace rate × pace length (cm s^{-1})	22.3 ± 25.2	
pace rate (pace s^{-1})	1.8 ± 0.02	63
pace length (cm)	13.6 ± 0.68	20

length or size of colour ring as a reference), (4) duration of 4 types of activity to the nearest second: handling time (the Curlew catches and swallows a prey; if handling is preceded by probing this is always a part of the handling time); probing time (the Curlew probes a greater part of its bill into the substrate without finding a prey); searching time (feeding time without probing and handling; single pecks (duration < 1 s) are considered as part of the searching time); non-feeding time (preening, resting and aggression, but kleptoparasitism is considered as part of the feeding time).

Additional information was collected for Curlews feeding within the grid of 5×5 m plots around the hides, viz. the habitat from which the prey was taken (water film or dry surface) and coverage by water film (estimated from the tower as % of the surface in the 5×5 m plot visited).

All observations were pooled in 3 min periods. The analyses for this paper are confined to 3 min periods during which < 20% of the total biomass of prey taken by male Curlews (bill length ≤ 12.5 mm) consisted of prey other than *Nereis*. After these 2 restrictions a total feeding time of 6335 min was left for analysis.

The search rate was estimated by measuring the pace frequency (time to make 50 steps during searching) and pace length (from prints in the mud). The search rate of Curlews feeding within the grid of 5×5 m plots could be estimated from the path length as predicted with the grid method (Reddingius *et al.* 1983). The path length equals the number of grid crossings multiplied by π/4 times the side length of the plots (in our case 5 m). On one day both methods of measuring search rate were used simultaneously and showed corresponding results (Table 1).

The estimation of worm size by most observers differed little: 39% of the worms taken by a Curlew were

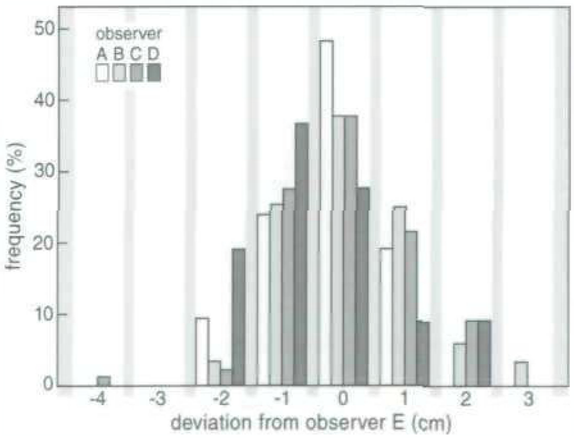

Fig. 1. Comparison between observers who estimated lengths of *Nereis diversicolor* taken by a Curlew. Frequency distributions show agreement of 4 different observers (A: n = 32; B: n = 32; C: n = 56; D: n = 11) with observer E. Most worms were 9 to 14 cm.

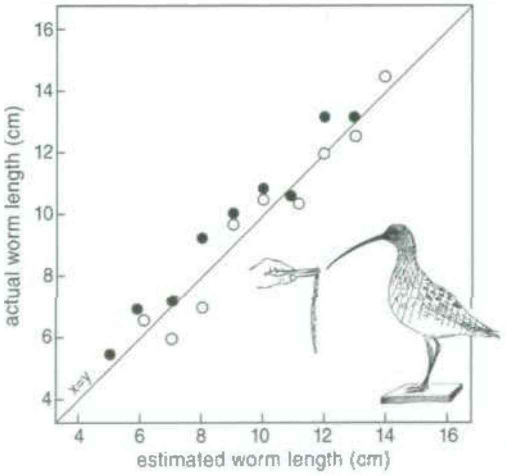

Fig. 2. *Nereis diversicolor.* Worm size measured in the laboratory (maximal length of creeping worms, see Esselink & Zwarts 1989) as a function of estimated worm size, averaged for 5 observers using a telescope at a distance of 100 m. Worms were held near the bill of 2 stuffed Curlews (○: bill length 11.7 cm, n = 136 and ●: 14.7 cm, n = 74).

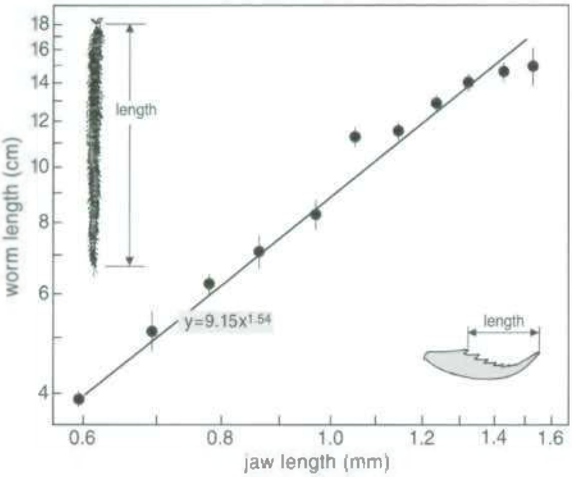

Fig. 3. *Nereis diversicolor*. Worm length (cm ± SE) as a function of jaw length: September 1981. The regression is highly significant ($R^2 = 82.2\%$, $p < 0.001$, $n = 288$).

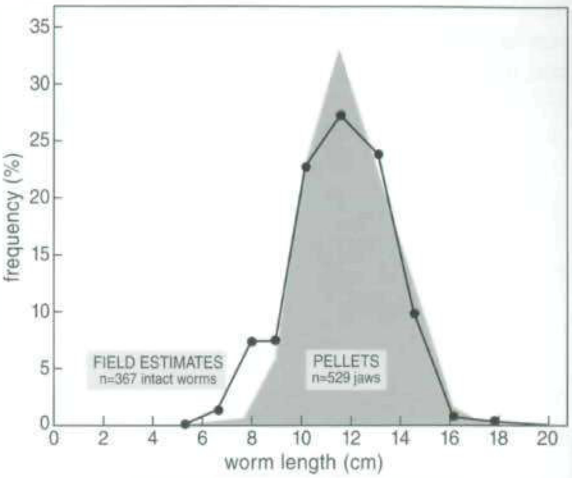

Fig. 4. *Numenius arquata* feeding on *Nereis diversicolor*. Check on field estimates of worm length by analysis of pellets (Fig. 3). Four pellets were produced by individual Curlews which had been observed during entire low water periods in September 1981.

estimated by 2 persons as having exactly the same length and 48% differed 1 cm only (Fig. 1). Size estimates were adjusted to take into account the small differences between observers. The field estimates were calibrated with the measurements in the laboratory by holding living worms near the bill of stuffed Curlews during sessions comparable to the situation in the field (at the same distance and using the same telescopes). The field estimates are on average 0.5 cm below the measurements in the laboratory (Fig. 2).

Pellet analysis gave another check on the estimated prey sizes. Four times we collected a pellet which was regurgitated by individuals observed during an entire low water period in late summer 1981. The jaws of *Nereis* give a good prediction of worm length (Fig. 3). There is a close agreement between the frequency distribution of worm sizes as estimated in the field and as derived from the pellets (Fig. 4).

Prey

The methods used to determine length, weight, burrow depth and feeding activity of *Nereis* are described in Esselink and Zwarts (1989). A core sampler (15 cm Ø, 40 cm deep) was used to determine worm density. The core was sieved through a 1-mm sieve in plenty of sea water. Although the smaller worms were not always retained on the 1-mm sieve, no worms > 6 cm were missed (Table 2), which means that the size classes selected by Curlews were sampled accurately (Table 2 and Fig. 8A).

Analysis

SPSS (Nie *et al.* 1975) was used for all statistical analyses.

Results

Prey handling

Two types of prey capture were distinguished: (1)

Table 2. *Nereis diversicolor*. Fraction of worms passing the 1-mm sieve, but retained on a 0.5-mm sieve; from Blomert (unpubl.). It is likely that small worms pass the 0.5-mm sieve, so that an even larger number of the smaller worms are missed when the 1-mm sieve is used.

Size (cm)	1	2	3	4	5	6	7	> 7
n	2302	1217	378	98	60	57	44	325
Passing (%)	84	75	59	31	22	4	2	0

N_{peck}, *Nereis* taken in a rapid, single peck from the surface or the entrance of the burrow, (2) N_{probe}, *Nereis* which a Curlew obtains after probing, sometimes as deep as its eyes. N_{probe} concerns a worm which tries to escape by remaining at the bottom of its burrow or by creeping towards the other corridor of the generally U-shaped burrows. Curlews were often seen to probe alternately in both entrances. Probing Curlews could also sometimes suddenly 'freeze' and remain motionless for 10 to 60 s, apparently waiting for an upward movement of *Nereis*.

N_{peck} lasted 2 to 7 s, usually 4 s, while N_{probe} took on average nearly 3 times as long (Fig. 5). The longest handling time of N_{probe} ever observed was 128 s. The handling of an N_{peck} included catching and swallowing of the prey, but it took more time if the worm is washed in a nearby tidal pool. The major time-component of N_{probe} was the probing preceding the eating. The handling time of a broken worm was an average of 2 s longer for N_{peck} and 6 s for N_{probe}. Broken worms from which one fragment was eaten did not require more time than intact worms, but the handling time increased if the worm was extracted from the mud as 2 or more pieces. N_{probe} worms broke more often than N_{peck} worms (Figs. 5 and 6A), probably because a worm present in its burrow can offer more resistance and/or is less easy to seize firmly than a worm on the surface.

Only 5% of the worms of the N_{peck} type taken from a 'dry' surface broke as compared to c. 30% of those taken from an area covered by water (Fig. 6A). That is one reason we assume that an N_{peck} from a dry surface is captured when extended from the burrow, while prey

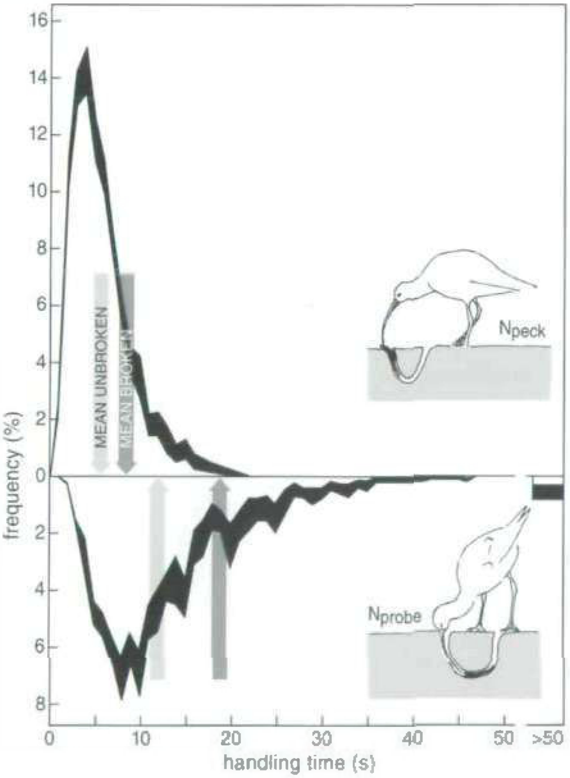

Fig. 5. *Numenius arquata* feeding on *Nereis diversicolor*. Frequency distribution of handling times for worms taken from the surface or entrance of burrow (N_{peck}) or deeply from burrow (N_{probe}). Broken worms (black area) took significantly more time than intact worms (open area) (N_{peck}: $R^2 = 8.8\%$, $p < 0.001$, $n = 6230$; N_{probe}: $R^2 = 9.8\%$, $p < 0.001$, $n = 2519$). An N_{probe} takes more time than an N_{peck} ($R^2 = 28.9\%$, $p < 0.001$, $n = 8749$).

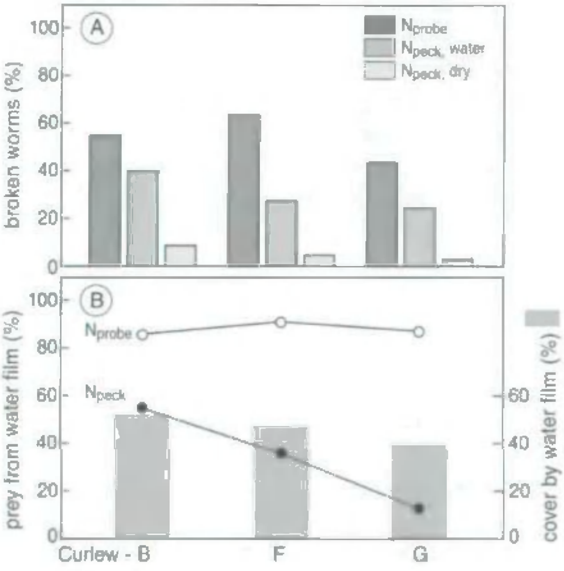

Fig. 6. *Numenius arquata*. **A.** Percent of broken worms taken by 3 Curlews in late summer: Curlews B (n = 521), F (n = 1405) and G (n = 567). **B.** Percent of N_{peck} (●) and N_{probe} (○) taken from mud covered by water film for the Curlews B, F and G; same data as in upper panel. Histograms show average coverage by water film in the 3 Curlew territories.

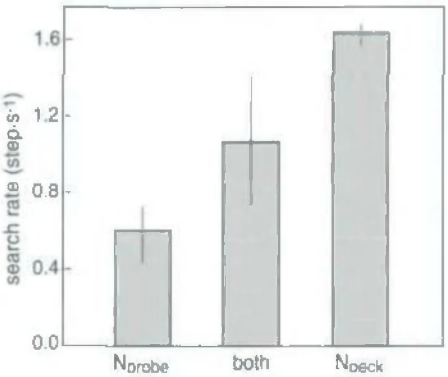

Fig. 7. *Numenius arquata*. Search rate (step s^{-1}) if all prey within a 3 minute period were N_{peck}, N_{probe}, or a mixture of both. Differences are significant ($R^2 = 64.2\%$, $p < 0.001$, $n = 66$). All data are from male Curlews in late summer 1981.

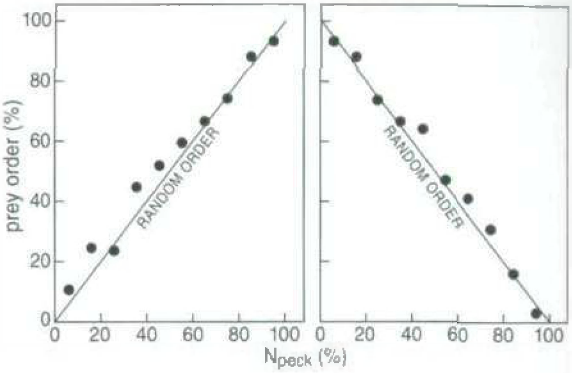

Fig. 8. *Numenius arquata* feeding on *Nereis diversicolor*. Probability that 2 N_{peck} (left panel) or 2 N_{probe} (right panel) will follow each other, as a function of percent of prey being N_{peck} during a 30 minute feeding period; each graph based upon 2409 prey. Diagonals show the expectation if the sequence is random.

taken from a water film also include filter-feeding worms present in the entrance of a burrow.

Searching

A Curlew selecting N_{peck} walked 3 times as fast as a bird taking N_{probe} (Fig. 7). Prey of the N_{peck} type are either on the surface or in the burrow entrance and thus easy to see. The high search rate is thus probably a way to increase the encounter rate with potential prey. A Curlew selecting N_{probe} does not probe continuously in order to find worms within reach. On the contrary, it scans the surface carefully, apparently to detect tracks left by *Nereis*. This is probably the reason the bird has to walk slowly. There is evidence, however, that a Curlew searching for N_{probe} does not simply sample each burrow detected: 80 to 100% of all N_{probe} were taken from burrows covered by a water film. Since the average water cover amounted to only 40 to 50%, Curlews predominantly selected N_{probe} from a substrate covered by water, whereas they took N_{peck} relatively more often from a dry surface (Fig. 6B). We know from our own observations that *Nereis* burrows are easily visible on the dry surface and it therefore seems unlikely that better detectability of the burrow itself is the reason why Curlews take more N_{probe} from mud covered by water.

A Curlew can select purely N_{peck} or N_{probe} for hours, but more often the two types of prey capture were mixed. N_{probe} rarely occurred by itself in long runs. If all days of observation are split into 30 min periods, solely N_{peck} or N_{probe} are found in 28% and 5% of the periods, respectively; 67% is thus mixed. Sequence analysis within these mixed 30 min periods shows that Curlews do not ignore one capture type during feeding, for the order in which both prey types occurred appears to be at random (Fig. 8).

Size selection

The size frequency distribution of *Nereis* is bimodal for each late summer in the 3 years of observation (Fig. 9A). There is one large peak at 3 to 5 cm and another, lower and less pronounced, for the size class 9 to 12 cm. The first peak represents juveniles which have become large enough to be retained on the 1-mm sieve. The density of the 0-group in late summer is at least twice as large as indicated in Fig. 9A, due to smaller worms being missed (Table 2).

Whatever the density of juvenile worms, Curlews ignored them completely (Fig. 9B). Most worms taken from the surface were 10 to 15 cm and the same size classes formed the majority of N_{probe}. The average size of N_{probe} and N_{peck} was exactly the same, 10.8 cm. Worms present in the mud, as well as prey captured, were larger in 1979 than in both other years.

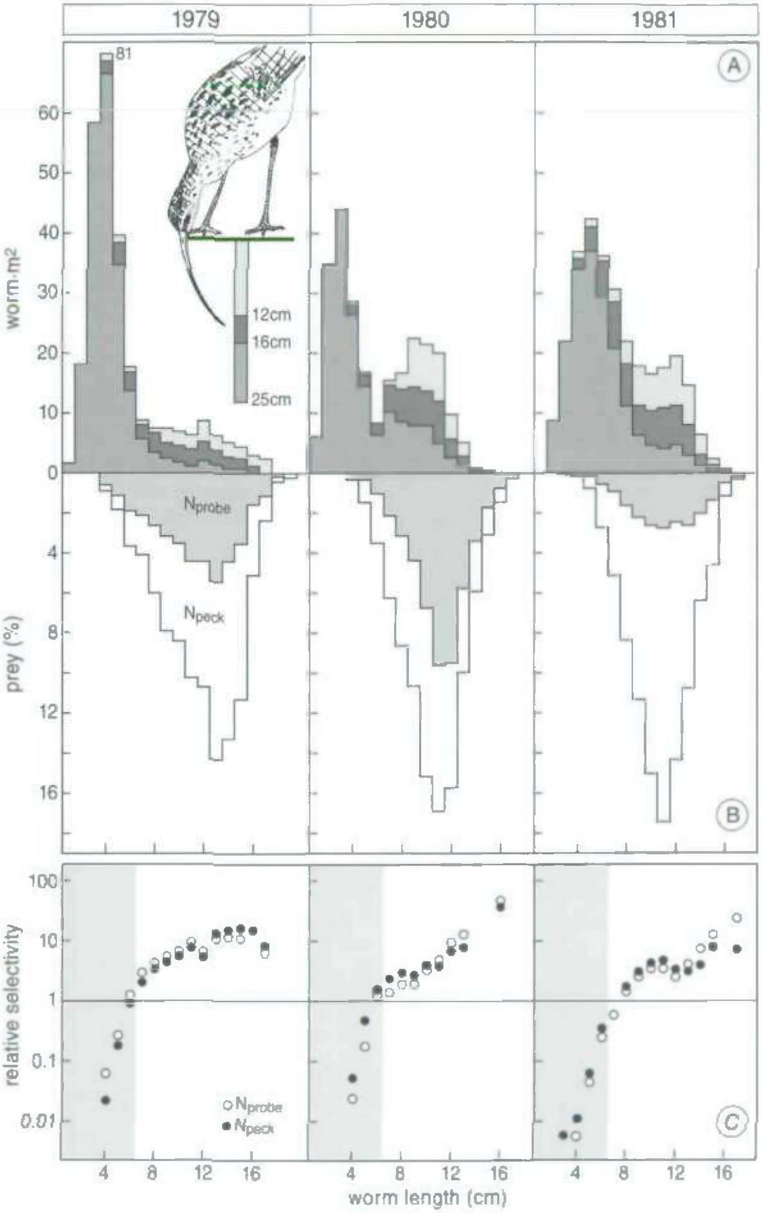

Fig. 9. *Numenius arquata* feeding on *Nereis diversicolor*. **A.** Density m^{-2} of worms per cm class in the study area during 3 late summers. Each frequency distribution is based upon c. 600 core samples of $^1/_{56}$ m^2. The known depth distribution per size class in sandy substrate during summer (Fig. 2 in Esselink & Zwarts 1989) has been used to calculate the density in the upper 12 and 16 cm. **B.** Size frequency distribution of intact worms taken by male Curlews in July to September in 1979 (n = 1292), 1980 (n = 1489) and 1981 (n = 2658); N_{probe} (grey) and N_{peck} (open). Graphs based upon running means calculated for 3 classes. **C.** Relative selectivity for N_{peck} (●) and N_{probe} (○) given as ratio between prey taken and prey present in the substrate (see 2 upper panels); prey ≤ 6 cm (shaded area) are under-represented.

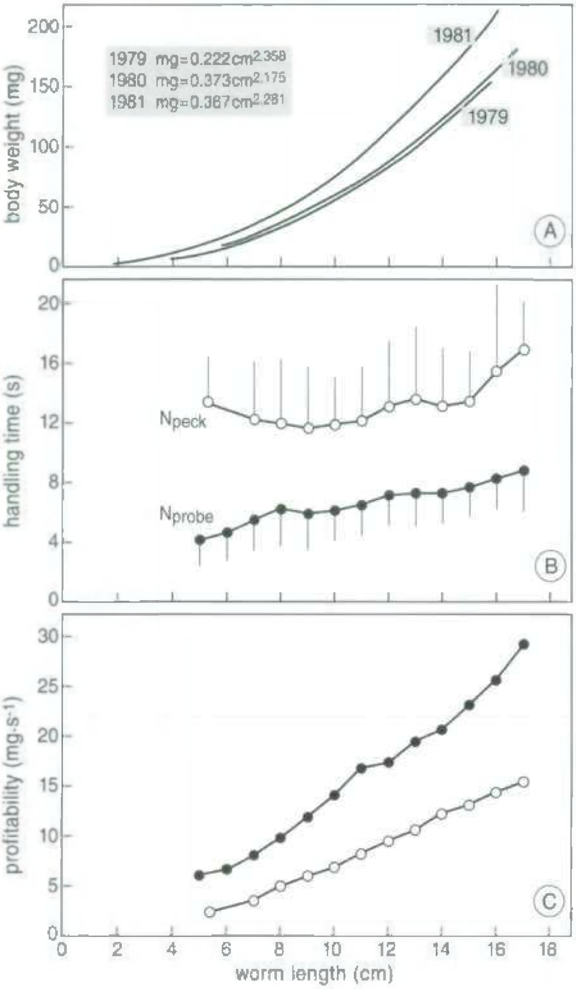

Fig 10. *Numenius arquata* feeding on *Nereis diversicolor*. **A.** Body weight (mg AFDW) of worms as a function of their length in September during 3 years. The allometric relations are given ($R^2 >$ 99.9%, $p < 0.001$, n = 1682 (1979), 1219 (1980) and 783 (1981)). **B.** Handling time (means ± SD) of non-broken prey taken by male Curlews as a function of worm length for N_{peck} (●) and N_{probe} (○); n varies between 6 and 907; total n = 7173 prey. **C.** Profitability (mg AFDW s^{-1} handling ± SE) of intact prey as a function of worm length for N_{peck} (●) and N_{probe} (○). Same data as B.

The relative size selection can be calculated by dividing per size class 'proportion taken' (Fig. 9B) by 'proportion present' (Fig. 9A, after a correction is made for small worms passing the 1-mm sieve: Table 2). The selection curves (Fig. 9C) are similar for the 3 years. Predation risk was very low for *Nereis* ≤ 6 cm and maximal for the larger worms.

The size frequency distributions of intact (Fig. 9B) and broken worms differ: most broken worms were 6 to 11 cm and appeared, on average, 2 cm shorter than non-broken ones. A broken worm taken as one piece is by definition a fragment, but if more pieces are taken it is often unclear whether the entire worm has been eaten. If prey were broken, the length of each piece was estimated separately and summed. There is no reason to believe that small worms break more frequently, so we assume that the mean size of broken and intact worms is in fact the same and that the 2 cm difference equals the uneaten fragment in broken worms.

The profitability of *Nereis* depends on its size as well as whether the prey is taken as N_{peck} or as N_{probe}. Ash-free dry weights of worms of 5 and 16 cm differ 13-fold (Fig. 10A). The handling time of N_{peck} merely doubles within that range and is virtually independent of size for N_{probe} (Fig. 10B). Hence the yield per handling time increases with size (Fig. 10C).

The flesh content of a broken worm can be estimated by converting length into weight in the same way as in the intact prey. This will, however, usually give a large underestimation: for instance, a broken worm of 6 cm being the half of a worm of 12 cm weighs 2.4 times as much as a worm of 6 cm. Since we assume that broken and intact worms have on average the same length, we have calculated the weight of broken worms as the quotient of the prey length and mean prey length (10.8 cm) multiplied by the weight of a 10.8 cm worm. The adjusted profitability of N_{peck} and N_{probe} declines by 7% and 12% respectively, if the broken worms are included in the calculations (Table 3). The profitability is still lower if it is taken into account that a Curlew probing without success cannot search for other prey in the meantime. This 'wasted time' has to be added to the successful handling times, by which the average profitability of N_{probe} decreases again by 28% (Table 3).

Seasonal variation

Sightings of individually marked Curlews showed that most of them remained in the study area from their arrival in July until their departure in April (Ens & Zwarts 1980a). During this time their food supply

Table 3. *Numenius arquata* feeding on *Nereis*. Handling time (mean ± SD) and profitability (mean ± SD) for N_{peck} and N_{probe}, calculated for intact worms, broken + intact worms and for N_{probe} also broken + intact worms, unsuccessful probing time inclusive.

	Handling time *(s)*	*Profitability* *(mg AFDW s^{-1})*	*n*
N_{peck}			
intact	5.49 ± 3.09	20.46 ± 15.04	5341
all (broken + intact)	5.91 ± 3.50	19.11 ± 14.71	6230
N_{probe}			
intact	12.31 ± 7.77	8.78 ± 6.41	1832
all (broken + intact)	14.11 ± 9.37	7.73 ± 5.99	2519
all (probing inclusive)	19.56	5.58	2519

changed drastically. The proportion of large *Nereis* (≥ 13 cm) with burrows within the reach of a male's bill decreased from 35% in July to 5% in November and 0% during the winter (Fig. 11A). The accessible fraction of smaller worms (9 to 12 cm, therefore just above the lower acceptance level) decreased in the same period from nearly 80% to 20%.

Searching in the N_{probe} mode makes no sense if burrow depths exceed the bill length, and indeed N_{probe} nearly disappeared during the course of the autumn (Fig. 11B). A part of this loss was compensated by a higher intake of N_{peck}, but the total intake of *Nereis* decreased by c. 45% during the autumn (Fig. 11B).

It is to be expected that the average size of N_{probe} shortened during the autumn because the average size of worms remaining within reach of the bill decreased

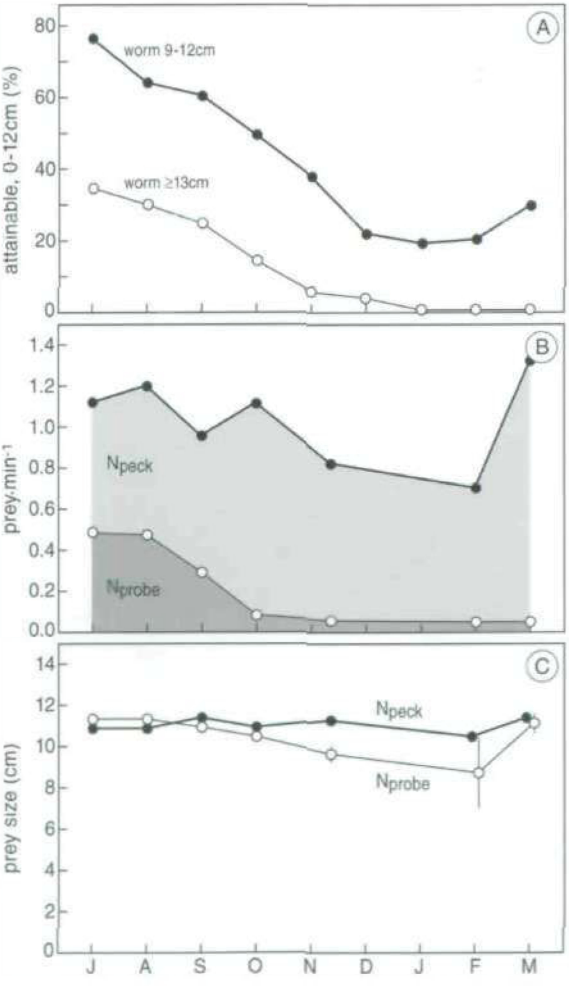

Fig. 11. *Numenius arquata* feeding on *Nereis diversicolor*. **A.** Percentage of worms present in burrows in the upper 12 cm of the substrate for 2 size classes (9 to 12 cm ●) and ≥ 13 cm (○)) from July to March (data from Esselink & Zwarts 1989). **B.** Prey min^{-1} feeding for N_{peck} (light) and N_{probe} (dark) during the course of the year. Means per month are calculated for each year separately and averaged after that. Each month is based upon several low water periods and at least 350 min of feeding, except February (2 days and 157 min). The one day in December was lumped with November. Results of two 1-way analyses of variance (based upon a total feeding time of 6335 min): N_{peck}: $R^2 = 2.8\%$, $p < 0.001$; N_{probe}: $R^2 = 24.3\%$, $p < 0.001$. **C.** Worm length (mean ± SE) of N_{peck} (●) and N_{probe} (○) during the course of the year.

too (Fig. 11A). Indeed, the average size of N_{probe} decreased 1 cm from July to winter. No significant trend was found in N_{peck}: on average its size remained the same during the course of the year (Fig. 11C).

Substrate temperature had no effect on the feeding rate of Curlews in summer or autumn, when the temperature lay between 2 and 24 °C. This seems to be different for February and March, because temperature has a highly significant effect on feeding rate, which increased from 0.6 to 1.8 prey min^{-1} with a rise in mud temperature from 1 to 8 °C. However, this effect was not found within any single day, so it is unlikely that substrate temperature has a direct short-term effect on prey availability.

About 25% of N_{probe} broke during summer and more than 50% in winter (Fig. 12A). The most likely explanation is the greater burrow depth in winter, making it more difficult for a Curlew to grasp the prey well. The increase in handling time in the same period from 15 to 20 s can partly be attributed to the increased proportion of broken worms (Fig. 12B), but the effect is still present for intact worms, indicating that depth itself causes an increase in handling time.

In contrast to N_{probe}, the proportion of broken N_{peck} decreased from 25% in summer to 10% in winter (Fig. 12A). Also, the average handling time declined from 8 s in July to 5 s in October, remaining at the same level afterwards (Fig. 12B). This decline cannot be explained by a decrease in broken worms, since the trend was the same for unbroken worms. The decrease in handling time as well as in the proportion of broken N_{peck} indicates that *Nereis* became easier to capture later in the season, which is the consequence of a seasonal shift in the feeding behaviour of *Nereis*, as will be discussed later.

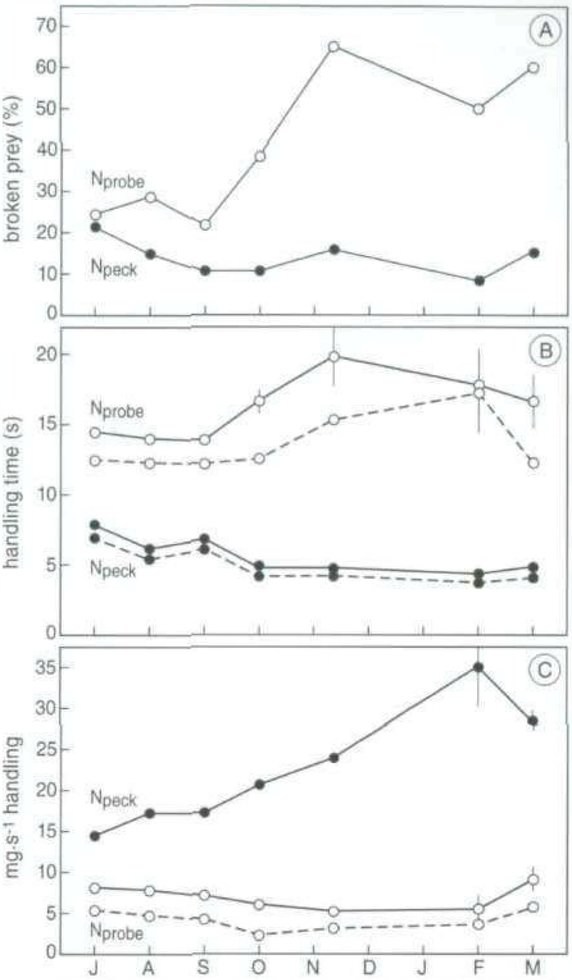

Fig. 12. *Numenius arquata* feeding on *Nereis diversicolor*. **A.** Percentage broken N_{peck} (●) and N_{probe} (○) during the course of the year. Total is 8749 worms, with at least 400 per month, except February (n = 136). **B.** Handling time (means ± SE) of N_{peck} (●: $R^2 = 7.2\%$, $p < 0.001$; n = 6230) and N_{probe} (○: $R^2 = 0.8\%$, $p < 0.01$, n = 2519) during the course of the year. Handling time of non-broken worms is indicated with dashed lines. **C.** Profitability (mg s^{-1} handling) of N_{peck} (●: $R^2 = 9.2\%$, $p < 0.001$, n = 6230) and N_{probe} (○: $R^2 = 1.0\%$, $p < 0.001$, n = 2519) during the course of the year, dashed line shows the profitability of N_{probe}, including unsuccessful probing time.

Although we could not observe whether N_{peck} was taken from the entrance of the burrow or from the surface, we are convinced that all prey of the N_{peck} type in winter are taken from the surface whereas this is probably not always the case in summer. The handling time is reduced to seizing and swallowing if *Nereis* is taken from the surface, but if the prey is extracted from the burrow it has more opportunity to retreat, resulting in a longer handling time and a higher proportion of broken worms. Two explanations for both effects are conceivable. Either the proportion of worms taken from the surface increases during the season or substrate temperature might influence the rapidity with which a worm can retreat into its burrow. According to our analyses, however, temperature has no direct effect on

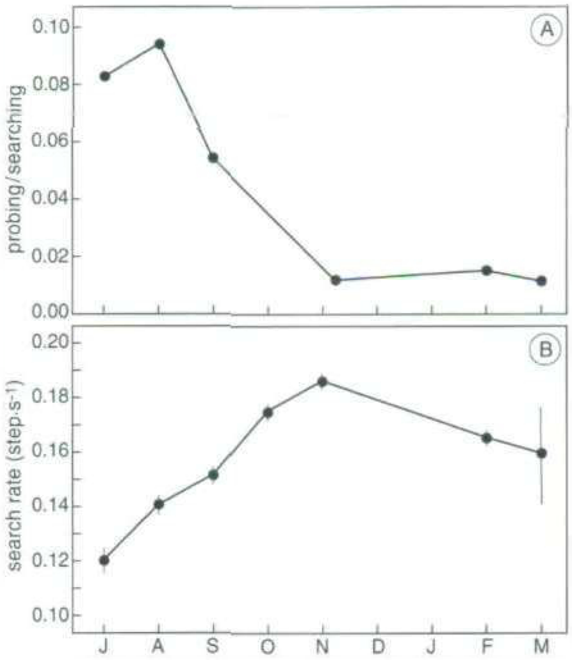

Fig. 13. *Numenius arquata.* **A.** Probing time as ratio of searching time during the course of the year. Same data as in Fig. 11B. **B.** Search rate (step s^{-1} ± SE) during the course of the year ($R^2 = 17.4\%$, $p < 0.001$, $n = 585$).

handling time nor on the proportion of broken worms, so we favour the first explanation.

The profitability of N_{probe} decreased during the course of the season (Fig. 12C) because handling time increased (Fig. 12B), more prey broke (Fig. 12A) and prey size decreased. If probing time is taken into account as 'negative handling time' the prey value is still lower (Fig. 12C). Meanwhile, profitability of N_{peck} increased because all effects work the other way around: less prey broke, handling time decreased and prey size remained constant.

The disappearance of N_{probe} during the autumn correlates with a change in the searching behaviour: there was less probing (Fig. 13A) and an increase in the search rate (Fig. 13B). However, if unsuccessful probing is considered in relation to the total handling time of N_{probe}, there was a relative increase: in July 38 s was spent probing for each 100 s handling N_{probe} and this ratio rose gradually to 62 s per 100 s handling in October.

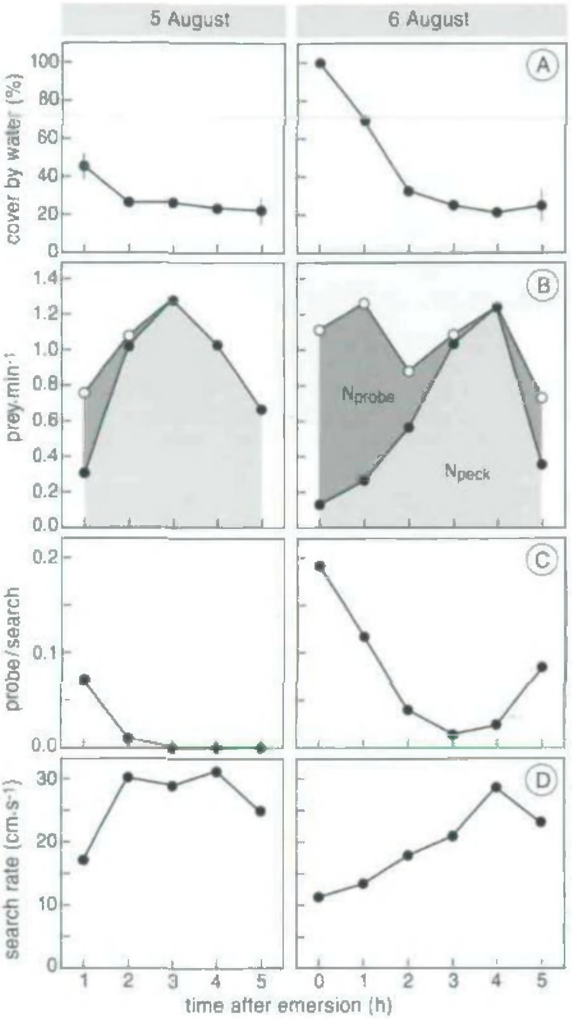

Fig. 14. *Numenius arquata.* Water film and feeding behaviour of Curlew F on 5 and 6 August 1981 during the course of the low water period. **A.** Coverage by water film (mean ± SE) in 5×5 m plots visited light. **B.** Prey min^{-1} feeding for N_{peck} (light) and N_{probe} (dark). **C.** Probing time as ratio of searching time. **D.** Search rate (cm s^{-1}) as derived from the number of grid crossings (Table 1).

Tidal trends

Individual Curlews were observed during 40 entire low water periods of 4 to 7 h. There were large differences from day to day, but in general the intake of N_{probe} was maximal during ebbing tide and sometimes

Table 4. *Numenius arquata*. Feeding behaviour of Curlew F in its feeding territory during a day when a slurry of meat was spread out over the mud in order to increase surface feeding of *Nereis diversicolor* (experiment on 12 September 1981; 168 worms captured) compared to 3 preceding low water periods ('control'; 393 worms captured; SE calculated over the means of the 3 observation periods).

	Control	*Experiment*	*Difference*
Feeding rate (*Nereis* min^{-1})	0.86 ± 0.05	1.02	+ 19 %
Feeding rate(N_{peck} min^{-1})	0.79 ± 0.07	0.99	+ 25 %
Feeding rate(N_{probe} min^{-1})	0.07 ± 0.03	0.03	– 57 %
Broken worms (%)	16.6 ± 7.1	2.2	– 87 %
Search rate (cm s^{-1})	18.4 ± 0.8	17.7	– 4 %

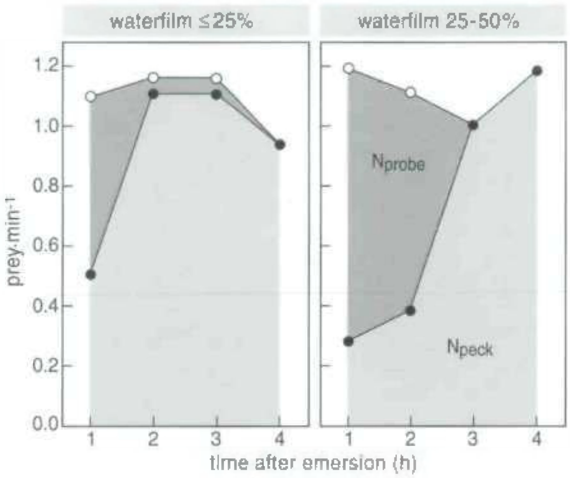

Fig. 15. *Numenius arquata*. Prey min^{-1} feeding for N_{peck} (light) and N_{probe} (dark) during the course of the low water period in 5×5 m plots where coverage by water film during a visit of Curlew F was < 25% (left panel) or 25 to 50% (right panel). Same data as Fig. 14; both days combined. Two-way analyses of variance show that time after exposure and to a lesser degree water film itself have significant effects on the intake rate; also the interaction is significant (N_{peck}: total $R^2 = 39.6\%$, $p < 0.001$, $n = 458$ min; N_{probe}: total $R^2 = 17.8\%$, $p < 0.001$, $n = 458$ min).

again during the flood, whereas N_{peck} was usually taken at low water. The daily variation, shown for 2 days in Fig. 14B, can partly be explained by the water film which remains at the surface (Fig. 14A). Cover by water film decreases gradually after exposure, but wind-force and wind-direction cause a large variation in the decrease in coverage by water film during receding tide.

The feeding rate of N_{peck} generally reached a peak 3 to 4 h after emersion. The rate at which a Curlew took N_{peck} coincided with the frequency at which *Nereis* occurred at the surface during the course of the exposure period (Fig. 9 in Esselink & Zwarts 1989).

N_{probe} dominated during ebbing tide. The rate at which the water film disappeared seemed to determine the feeding rate of N_{probe}, but on many days N_{probe} was limited to the first 2 h of the low water period, even at sites where the water cover remained high for a longer time (Fig. 15). The occurrence of N_{probe} corresponded with our observations on filter feeding by *Nereis*, which is also limited to surfaces covered by a water film during the first 2 h after exposure (Figs. 10 and 11 in Esselink & Zwarts 1989).

Behaviour of Curlew after experimentally raised prey accessibility

We were able to elicit surface activity of *Nereis* in the laboratory by spreading out minced meat over the mud surface (Fig. 10B in Esselink & Zwarts 1989). The same experiment was repeated in the field. A 50 m hose was used to bring 30 l of a slurry of minced meat from the observation tower to the feeding territory of Curlew F just after the exposure of the mudflat. It was not possible to quantify the surface activity of the worms, but if the effect were the same as in the laboratory, it was to be expected that the Curlew would take more worms from the surface and less from the burrows. The slurry which spread out over an area of c. 5 m × 20 m had a clear effect on the feeding behaviour of the Curlew, which spent a remarkable amount of its feeding time near the end of the hose. Comparison with a control situation was possible, since the bird was also observed during 3 preceding low water periods (Table 4). The feeding rate on the experimental day was 19% above the average in the control situation, which was achieved by a 25% increase of N_{peck}. Hardly any worm broke during the experiment, which also suggests that Curlew F was able to seize *Nereis* easily from the surface.

Discussion

Prey availability

The distinction between N_{peck} (prey detected at the surface) and N_{probe} (prey taken from its burrow after a track reveals its presence in the mud) is not an absolute one. On the one hand, a Curlew might detect a surface-feeding worm but be too late to catch it and subsequently try to catch the prey in its burrow. If that were to occur often, no large deviation would be found in the frequency with which both prey types are taken from dry and wet surfaces. As this difference, however, is very large (Fig. 6B), it is unlikely that prey of the N_{probe} type are often detected as surface-feeding worms. On the other hand, worms present close to the entrance might be taken just in a single peck and be classified as N_{peck}. It is reasonable to assume that this kind of prey breaks more often than worms taken at the surface. Indeed c. 5% of N_{peck} from a dry surface broke as compared to c. 30% if this prey type is taken from a substrate covered by water (Fig. 6A), indicating that the latter category also includes at least some filter-feeding worms. We assume that this problem of interpretation is more likely in summer (when filtering is common) than in winter (when filter feeding is rare), since the handling time of N_{peck} and the proportion of broken N_{peck} decreased from late summer to winter (Fig. 12). In other words, all worms of the N_{probe} type are presumably captured when filter feeding, while N_{peck} are surface-feeding and sometimes filter-feeding worms.

In this section we will estimate the density of available prey, if a Curlew selects solely worms of the N_{peck} or N_{probe} variety. *Nereis* occur with a total density of at least 200 to 400 m^{-2} in the study area during late summer (Fig. 9A, Table 2), but the density relevant for Curlews is reduced to c. 100 m^{-2} on average, since prey < 7 cm are ignored.

The density of worms available as N_{peck} depends mainly on the surface activity of *Nereis*. Surface activity was measured during 5 field days in September and October (Esselink & Zwarts 1989). Not a single worm was recorded during 3 low water periods, while during the other 2 low water periods, surface activity took up only 0.1 to 0.2% of the time. This means that a Curlew can expect not more than 1 worm at the surface per 5 or 10 m^2 at any one time. Moreover, the density of surface-feeding worms actually accessible to feeding Curlews is even lower since *Nereis* retreat quickly into their burrows if they detect any visible stimulus or vibration in the substrate (Linke 1939, Vader 1964, own observations).

Because of this anti-predator reaction, the frequency at which worms appear at the surface is probably a more relevant measure of prey availability than

A 50 m hose was used to bring 30 l of a slurry of minced meat from the observation tower to the feeding territory of a curlew. The photo shows the preparations at receding tide, before the arrival of the bird.

total time spent at the surface. The minimal N_{peck} feeding rate directly after emersion and the maximal intake c. 3 h later, observed for an individual Curlew (Fig. 14B), agree with the frequency of *Nereis* surface bouts observed during the low water period (Fig. 9 and Esselink & Zwarts 1989). In late summer, *Nereis* emerged not more than 1 to 4 times per 300 min from their burrows (Esselink & Zwarts 1989). If the prey density is 100 m^{-2}, the search rate is 25 cm s^{-1}, and assuming a field of view of 1 (or 2?) m, one might expect that a Curlew has to walk 10 to 50 m (or 5 to 25 m?) before a worm is found. We know that a Curlew in late summer has to cover a distance of 12.5 to 25 m per N_{peck} taken, given the measured search rate (25 cm s^{-1}) and search time (50 to 100 s) per prey. It is thus likely that all prey encountered are captured, certainly if it is taken into account that some worms retreat quickly into their burrow if a Curlew approaches.

The highest feeding rate was measured in the second half of March, when the search time per N_{peck} was half as long as in late summer (Fig. 11B). We suppose that the surface activity of *Nereis* in spring is high (as found by Twisk 1986) because of the bloom of benthic algae caused at that period by a combination of irradiation and temperature (Colijn & de Jonge 1984), whereas at the same time the concentration of food in the overlying water is still too low to make filter feeding worthwhile. A high feeding rate during sunny periods in spring was also observed in Oystercatchers feeding on *Nereis* (Ens pers. comm.) and Brent Geese *Branta bernicla* (Drent & van Eerden pers. comm.). We conclude that the tidal as well as the seasonal variation in feeding rate of N_{peck} can largely be explained by the frequency at which the worms appear at the surface.

The accessibility of worms caught as N_{probe} depends on the burrow depth In late summer 60% of *Nereis* ≥ 7 cm had burrows beyond the reach of male Curlews, reducing the density of accessible prey to 40 worms m^{-2}. Such a density is apparently too low to probe at random, so a Curlew searches on the surface for detectable prey. In late summer 60% of all probes were unsuccessful, which is equivalent to the proportion of burrows too deep for male Curlews. *Nereis* cannot be detected if there is no visible entrance to the burrow. An entrance formed by an active worm may disappear again (Evans 1987) and therefore inactive worms usually have no holes at the surface. Worms filter feeding are, upon close observation, detectable: their burrows are always visible, and there is either a water current, or other traces of activity, within the burrow entrance (Twisk 1986, Esselink & Zwarts 1989). Filter feeding cannot occur on dry surfaces and is generally restricted to the first 2 h of the exposure time (Twisk 1986, Esselink & Zwarts 1989). N_{probe} indeed tended to be taken from substrate covered by water film, especially towards the beginning of the emersion time (Figs. 14 and 15). The N_{probe} type disappeared for 2 reasons during the course of the autumn. First, the worms spend less time filter feeding, so that fewer worms are detectable. Second, fewer worms remain accessible because of the increase in burrow depth (Fig. 11A).

Detection and recognition of profitable prey

Curlews feeding on *Nereis* usually select the larger worms. Worms of 12 cm occurred, for example, 5 times more often in the diet than worms of 6 cm (Fig. 9B). The selection of larger worms is more pronounced if one takes into account the density of all prey sizes (Fig. 9A). Worms of 12 cm were then taken 8 times more often than worms of 6 cm (Fig. 9C).

The selection curves in Fig. 9C are similar for the 3 years and there is also no difference between selectivity for N_{probe} and N_{peck}. The selectivity is calculated by dividing the frequency of prey sizes taken by the frequency of prey sizes present in the substrate. This does not say much, however, about the active selection for size when the accessible fraction is not the same for all size classes. Such information is lacking for N_{peck}, but because the depth distribution for each size class is known this can be used to calculate the selection of accessible prey of the N_{probe} type. Worms which belong to the prey sizes which are ignored have burrows within reach of the bill, but the larger the worms the greater the fraction with burrows deeper than the bill length (Fig. 16A). The selection of larger N_{probe} becomes thus more pronounced, taking into account the accessibility of the worms (Fig. 16B): worms of 12 cm are now selected 23 times more often than the size class 6 cm.

Optimal foraging theory can assist us in explaining why small worms are not taken. A predator maximizing its intake rate has to ignore all prey for which the

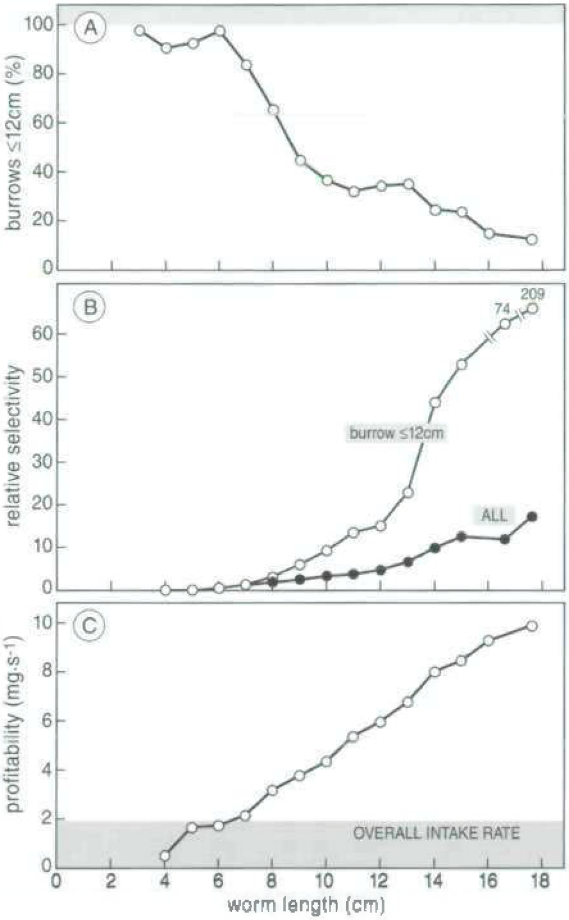

Fig. 16. *Numenius arquata* feeding on *Nereis diversicolor*. **A.** Accessibility of N_{probe} worms (percent of burrows found in the upper 12 cm of the substrate; clay content ≤ 5%) as a function of worm length during late summer (same data as Fig. 2 in Esselink & Zwarts 1989). **B.** Relative size selection on N_{probe} as a function of worm length in late summer, averaged for the 3 years (same data as Fig. 9C). Lower graph shows the selectivity without taking into account the increase of burrow depths with size. Upper graph takes into account the relative number of worms found in the upper 12 cm of the substrate (Fig. 16A). **C.** Profitability (mg s^{-1} handling) of N_{probe}, including broken worms and probing time (cf. Table 3) as a function of worm length. Intake rate (mg s^{-1} feeding) is indicated.

energy gain during handling is below the general intake rate during feeding and has to take each profitable prey encountered, i.e. prey for which mg s^{-1} handling is above mg s^{-1} feeding (Hughes 1980, Krebs *et al.* 1983).

The profitability of N_{peck} and N_{probe} increases with size because although Curlews handle small worms relatively rapidly, this is not fast enough given the small amount of flesh taken (Fig. 10). The prey value curves, shown in Fig. 10C, concern intact prey only. The profitability decreases 9% for N_{peck} and 12% for N_{probe} if broken prey are included and again 28% for N_{probe} if all unsuccessful probing times are reckoned as handling times (Table 3). The adjusted profitabilities of N_{probe} (Fig. 16C) are thus 36% below the prey values for intact worms and successful probes only (Fig. 10C).

The intake rate of male Curlews in late summer and autumn was, according to our data, 1.9 mg s^{-1} feeding on average. The profitability of all size classes of N_{peck} is above this lower limit: the yield of an N_{peck} of 5 cm is 5 mg s^{-1}, and making an extrapolation downward worms of 4 cm should still be profitable, but in fact they are not taken.

For all size classes N_{probe} is less profitable than N_{peck}. The rare $N_{probe} \leq 6$ cm is below the predicted lower limit and 2.2 mg s^{-1} for an N_{probe} of 7 cm is just above the intake rate of 1.9 mg s^{-1} (Fig. 16C). According to the simple optimal diet equation there should be a step change in the selectivity at a worm of c. 7 cm. As in many other empirical studies (Krebs *et al.* 1983), this is not the case - rather there is a gradual increase of selectivity with size.

One of the assumptions of the classical optimal diet model is that predators know the energy value of all encountered prey, whereas it is more realistic to suppose that predators can only estimate prey values and thus must make mistakes (Rechten *et al.* 1983). A Curlew which detects a worm at the surface must derive its size from the prey width, since usually only a part of the body emerges from the burrow. N_{probe} is extracted from the substrate. Its size can be estimated only from the width of the entrance of the burrow. Although we have not quantified the relationship between width of the corridor and worm length, we are convinced that there is a close relationship, also because body width and body length are well correlated

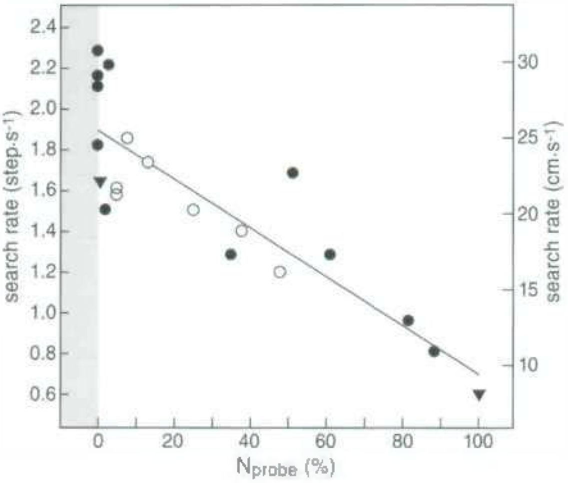

Fig. 17. *Numenius arquata* feeding on *Nereis diversicolor*. Search rate as a function of the relative occurrence of Nprobe (percent of worms being Nprobe) ($R^2 = 76.2\%$, $p < 0.01$; $n = 20$). Data from Fig. 7 (□), Fig. 11B combined with 13B (○) and, Fig. 14B combined with 14D (●).

(Esselink & Zwarts 1989). The width of the corridor offers a good prediction of the size of the bivalve *Mya arenaria* (Zwarts & Wanink 1989), but if the width of the corridor is measured at the surface instead of halfway, the accuracy decreases considerably, as some of the tubes are funnel-shaped and others straight (Zwarts unpublished). If the same applies for *Nereis*, it will not be easy for a Curlew to deduce worm length and thus prey value from the size of holes at the surface of the substrate.

We conclude that Curlews select larger worms because they are the most profitable. Deviations from the expected step change in size selection might be explained by the misidentification of prey size. An alternative explanation is that small prey are simply less detectable.

Optimal search rate

An increase in search rate raises the encounter rate with prey but the number of prey overlooked may increase so much that the net profit will be lower. The trade-off between search rate and probability of detection depends on the conspicuousness of the prey. This idea has been worked out in a model (Gendron & Staddon 1983) which has been tested with prey with a different crypticity (Gendron 1986).

A Curlew searching for *Nereis* has to deal with 2 types of prey which both demand a specific search rate. Capturing prey from the burrows can be considered as the situation of maximal crypsis. The Curlew walks slowly at 6 to 10 cm s^{-1} (Figs. 7, 13B, 14D, Table 1). Its posture is hunched forward with the bill just above the surface. On the other hand, the search rate increases by a factor of 3 if all prey are of the N_{peck} mode. Still larger is the difference in area searched per unit time, since the search path, although this has not been quantified, must also be much wider. A Curlew searching for N_{peck} walks upright and appears to detect worms at a distance of 1 to 2 m.

Though searching for N_{peck} and N_{probe} requires a different search technique, there is no evidence that Curlews ignore one type of prey and concentrate on the other. Both prey types occur together, and if only one prey type is taken, this can be explained by the behaviour of the prey. If the prey types are mixed, the order in which they are taken is completely random (Fig. 8), which also suggests that feeding Curlews do not ignore one of the 2 prey types.

Curlews taking a mixture of N_{probe} and N_{peck} have an intermediate search rate (Fig. 7). A shift from one prey type to the other is accompanied by a change in the search rate within a tidal cycle (Fig. 14) as well as over the year (Figs. 11B and 13B). The data from these figures have been summarized in Fig. 17. One can conclude from this that Curlews continuously adjust their search rate to the ratio of N_{probe} and N_{peck} currently experienced. If a Curlew, for instance, expects a few *Nereis* at the surface, and detects many visible burrows, it will decrease its search rate. If a worm then appears at the surface within the restricted field of view of the bird, it will of course be taken, for N_{peck} is always a profitable prey. On the other hand, if many worms are at the surface and a Curlew has quickened its pace to increase the encounter rate with N_{peck}, many potential N_{probe} will not be detected, but if the bird catches sight of a potential N_{probe}, there is no reason to ignore it since it remains a profitable prey.

The general conclusion is that a feeding Curlew which maximizes its intake rate while searching for *Nereis* has to decide continuously how to anticipate changes in the behaviour of its prey.

Chapter 16

HOW OYSTERCATCHERS AND CURLEWS SUCCESSIVELY DEPLETE CLAMS

Leo Zwarts & Jan Wanink

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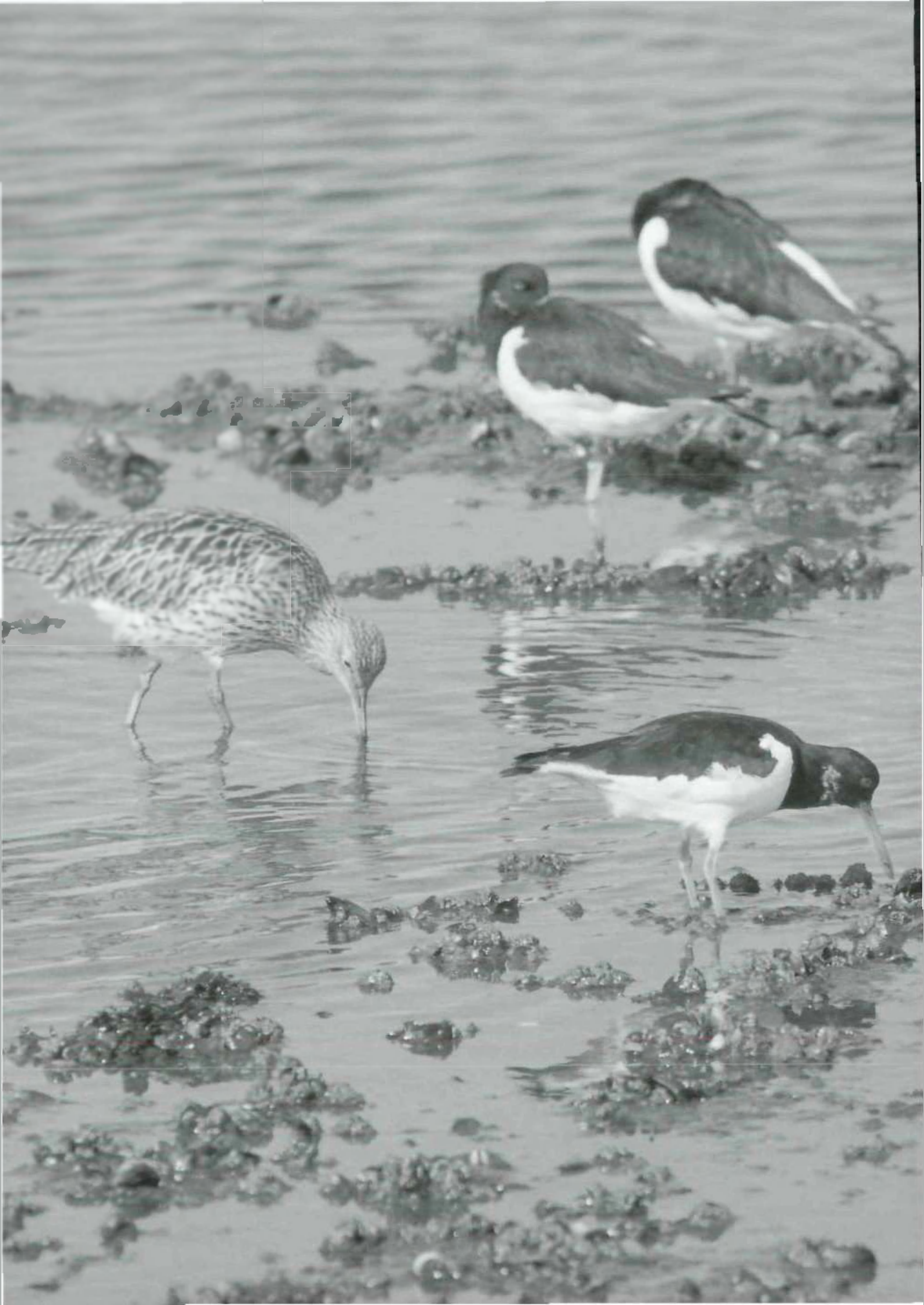


HOW OYSTERCATCHERS AND CURLEWS SUCCESSIVELY DEPLETE CLAMS

Oystercatchers and Curlews ignore prey which are unprofitable, i.e. those of which the handling efficiency is below the intake rate during feeding (handling + searching) as predicted by optimal foraging theory. The predation risk is maximal for clams *Mya arenaria* which are about 1 cm above the lower acceptance threshold. Bigger clams are taken less often since they live out of reach of the bill. Given a size class, clams which are buried less deep have a greater risk of being taken. The resource partitioning between both bird species is quite complete in the natural situation. Manipulation of the food stock, by planting big clams at a shallow depth, elicited interference between Curlews and Oystercatchers, which normally is very rare. Male Curlews take a few clams only, whilst it is a main prey for the females. It is suggested that because males have a shorter bill than females, the proportion of accessible clams above the lower acceptable size limit is too small. Oystercatchers deplete the clams in the winter following the second growing season. After this the Curlew females exert a heavy predation pressure on the remaining clams.

Introduction

The leading problem tackled in most studies of the feeding ecology of coastal wading birds is to what degree the food supply on the intertidal flats is a limiting factor for the bird populations (see review by Goss-Custard 1980). Their food supply -mainly macrobenthic animals living in the substrate- is highly variable from season to season and also from year to year. The study by Beukema (Beukema *et al.* 1978, Beukema 1979) of the intertidal flats of the Balgzand (western Wadden Sea) shows that the spatfall of important shorebird prey species like the clam *Mya arenaria*, the Mussel *Mytilus edulis* and the Cockle *Cerastoderma edule* is very erratic. Their survival over the winter period also varies from year to year.

The variability in prey density is even larger if we take into account the fluctuations in the numbers of prey which are likely to be taken by the different wading birds; some of the prey are ignored because they are too small to be profitable, whereas others lie too deep in the substrate and are out of the reach of the waders' bills (Reading & McGrorty 1978).

We summarize in this chapter some results of current research on colour-banded birds feeding on the mudflats along the Frisian coast, near the village of Moddergat. We will explain why Oystercatchers *Haematopus ostralegus* and Curlews *Numenius arquata* feeding on clams select different size and depth classes and will show that both bird species combine to deplete the food stocks in the course of 2 or 3 years.

Selection of the profitable clams

Not all prey accessible to birds are in fact taken. For example, Herring Gulls *Larus argentatus* ignore Shore Crabs *Carcinus maenas* below c. 20 mm carapace width, whilst the rejection threshold for the Curlew is c. 10 mm, and for the Redshank *Tringa totanus* and Greenshank *Tringa nebularia* it is still lower (c. 5 mm) (Zwarts 1981). It was suggested by MacArthur & Pianka (1966) that the lower acceptance threshold was chosen by the bird in such a way that a maximal intake rate was ensured. Prediction of the lower limit for Oystercatchers feeding on Mussels was correct (Zwarts & Drent 1981), and the data Hulscher (1982) for Oystercatchers preying upon *Macoma balthica* also support

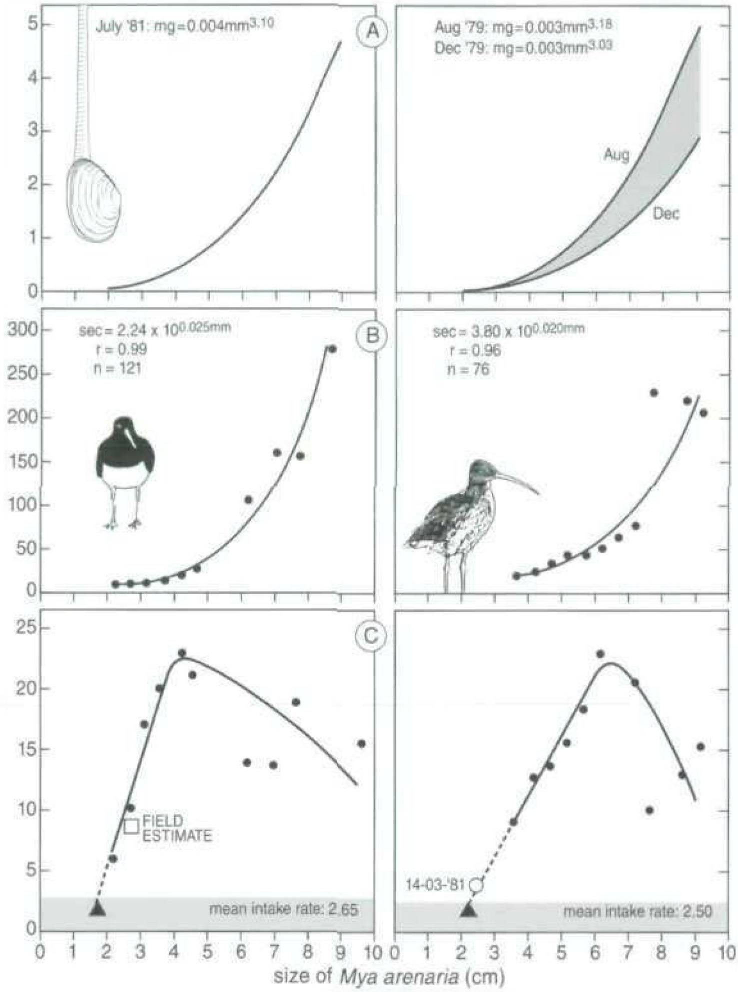


Fig. 1. A. Weight (g ash-free dry weight) of clam *Mya arenaria* in relation to its size. **B.** Handling time for clams of different size classes by a captive Oystercatcher (left) and a free-living Curlew (right). **C.** Yield (mg ash-free dry weight) per second of handling time of clams of different size classes. For the Oystercatcher (left) this was determined in July 1981, whereas the handling efficiency of the Curlew (right) was derived from measurements in different months (August-November; 1978 and 1979 combined). The lines have been drawn by eye. The lower acceptance threshold for clam size (solid triangle) is determined by the point where the extrapolated line meets the level of mean feeding rate (in the left panel the intake rate of free-living Oystercatchers was used; Jan B. Hulscher unpubl.). The open square and the open circle are discussed in the text. Note: the data from the Oystercatcher concern an experimental situation where all clams were present just below the surface, whilst the Curlew data were collected on the mudflats, where the big clams are living at greater depth (see Fig. 3). If depth itself has an effect on the handling efficiency, which seems likely, the slope for both species cannot be compared directly.

the rule: the observed lower limit taken, of c. 11 mm shell length, is near the expected acceptance threshold.

The applicability of this rule to our study of waders feeding on the clam *Mya arenaria* can be investigated by comparing the handling efficiency (mg ingested per second of handling) of each size class of prey with the overall intake rate (mg ingested per second of feeding), where feeding = searching + handling. Optimal foraging theory predicts that prey sizes for which the handling efficiency is below the average rate of food intake should be ignored (see Krebs 1978 for a general review of the topic).

We observed that Oystercatchers feeding on clams did not take shells below a certain size. Since it is difficult to measure the prey size exactly in a field situation, we decided to capture some Oystercatchers and offered them clams of different size classes in controlled experiments, as Hulscher had done with *Macoma balthica*.

In one of the experiments an Oystercatcher fed on clams of different size classes buried in the substrate, all at the same depth, just below the surface. The yield per second of handling time appeared to be maximal for shell of 40-45 mm (Fig. 1).

Hulscher and his students made a series of observations in October and November 1980 on free-living Oystercatchers feeding on clams in our study area. They measured the handling of about 3000 prey and collected the fresh shells recently opened by Oystercatchers. They found that clams of 15-40 mm (average 28.2 mm) were taken (Fig. 2: left panel). But in contrast to the captive bird, the free-living Oystercatchers

We were able to locate the clams seen to be taken in relation to a grid of thousands of numbered poles, separated from each other by 2.5 m.

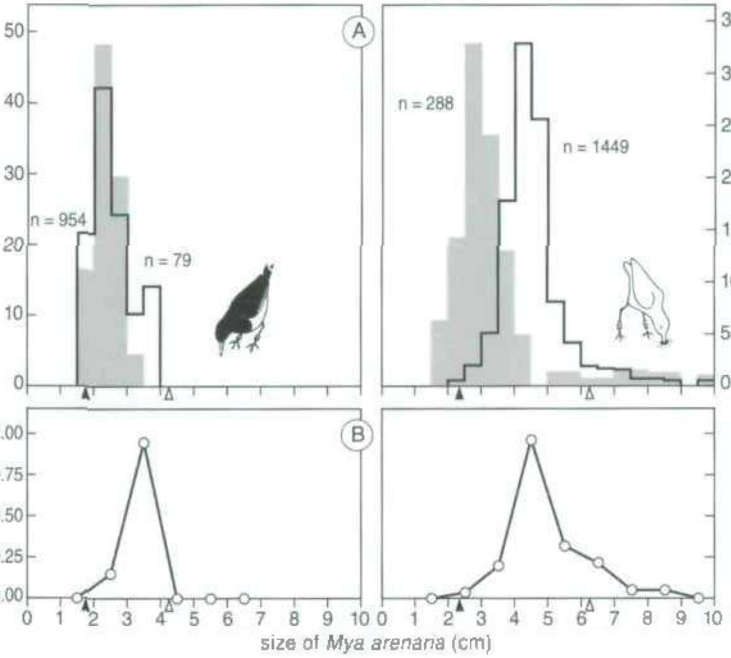


Fig. 2. A. Size selection by Oystercatcher (left) and Curlew (right), preying on clams (% frequency distribution per 5 mm class; sample size indicated). Clams eaten by free-living Oystercatchers in October-November 1980 or Curlews in August-December 1978 are compared to the clam population on offer in the Moddergat area for Oystercatchers and in the Nes area for Curlews. The right panel shows the prey selection by a single colour-banded Curlew (20Y); the size has been derived from the known relationship between handling time and weight (and thus size) of the clams. **B.** Risk to a clam of being taken, relative to the maximal predation risk of a single size class. The maximal risk is set to 1 (Oystercatcher: clam size 3-4 cm; Curlew: clam size 4-5 cm). The relative risk is derived from the data given in the upper panel. The solid triangle denotes the predicted lower limit and the open triangle the most profitable size class (see Fig. 1).

did not take all the flesh from the shells. In many cases they pulled out the siphon, together with the greater part of the body, in one jerk. On average 22% of the flesh remained in the shell and the flesh taken averaged 51 mg ash-free dry weight. The mean handling time was 5.82 s, so the average yield during handling was 8.74 mg/s (open square in Fig. 1C). This field estimate is quite close to the performance curve of the captive Oystercatcher.

Since free-living Oystercatchers devote 30.3% of their feeding time to handling the clams (the other 69.7% being spent in searching for prey), the average rate of intake of biomass amounted to 0.303 × 8.74 = 2.65 mg/s (shaded block in Fig. 1C). The theory predicts that all prey sizes yielding a lower rate of biomass intake would be ignored. The smallest clam given to the captive bird was 22 mm. The handling efficiency for this is still above the predicted lower threshold. For clams between 20 and 40 mm there is a linear relationship between yield and shell size. Extrapolating the line downwards, we would expect that clams of 17.3 mm and smaller should be rejected, which fits well with the observed threshold in the free-living Oystercatchers (Fig. 2).

The clam is also an important prey for Curlews, but the threshold size required for acceptance is higher. For this species we measured the profitability of different shell sizes for free-living Curlews. It was easy to measure the handling time but impossible to estimate directly the size of the shells taken, because a Curlew pulls the siphon and pieces of flesh out of the shell, from below the mud surface. It was possible, however, to locate the clams after they had been eaten, for a Curlew makes a small crater while handling the prey. We were able to locate the clams seen to be taken in relation to a grid of thousands of numbered poles, separated from each other by a few metres on the feeding area. After an observation period, during which we timed the handling of the clams being eaten and noted their positions, we searched the different craters. To calculate the yield for the Curlews, the flesh which remained in the shell was weighed and subtracted from an estimated total flesh weight, derived from a weight/length relationship. Figure 1 shows the handling time and the profitability as a function of the shell size for a single colour-banded Curlew (called 20Y), which fortunately fed near one of our observation towers and has done so for five years. As Fig. 1

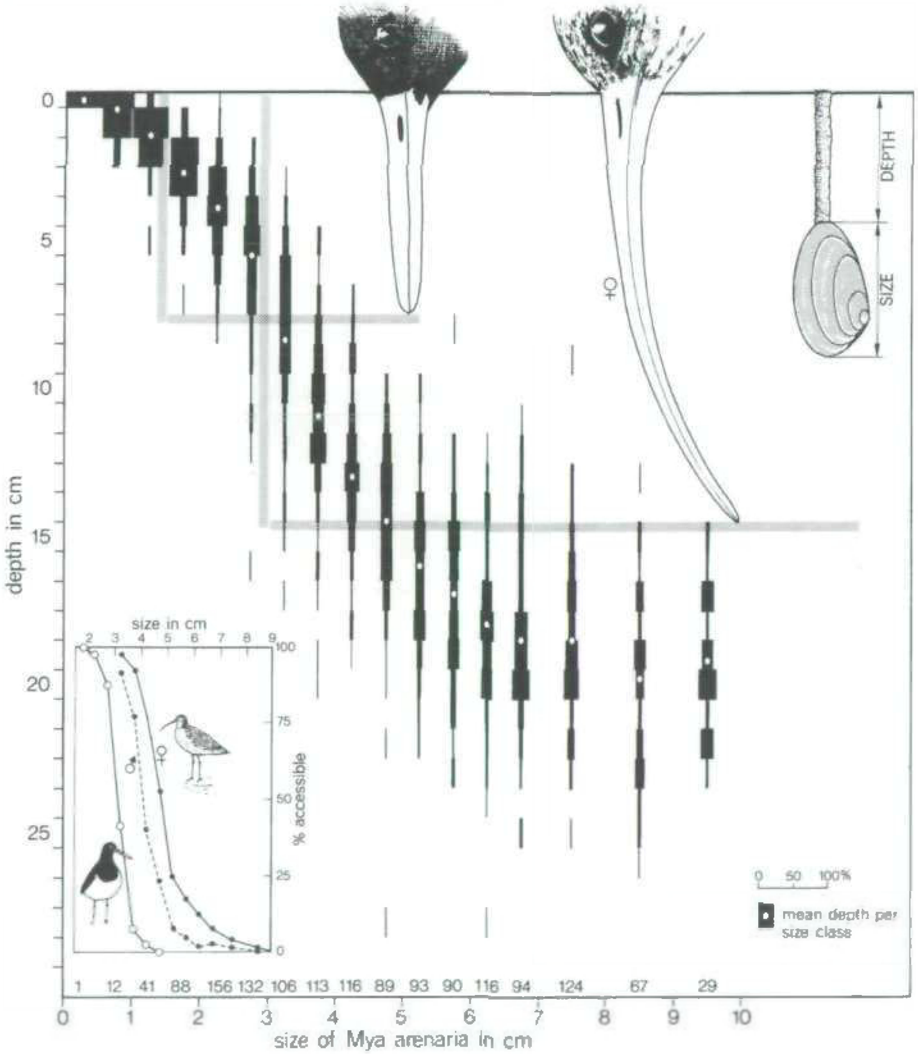


Fig. 3. Frequency distribution of depth of clams per size class (0-4, 5-9 mm, etc.). The mean and the number of clams dug out are indicated. With the aid of grey bars the part of the clams being taken by Oystercatchers and Curlews are shown. The inset figure shows the accessible percentage per size class for Oystercatchers (upper 7 cm of the substrate), and for male and female Curlews (upper 12 and 14 cm, respectively).

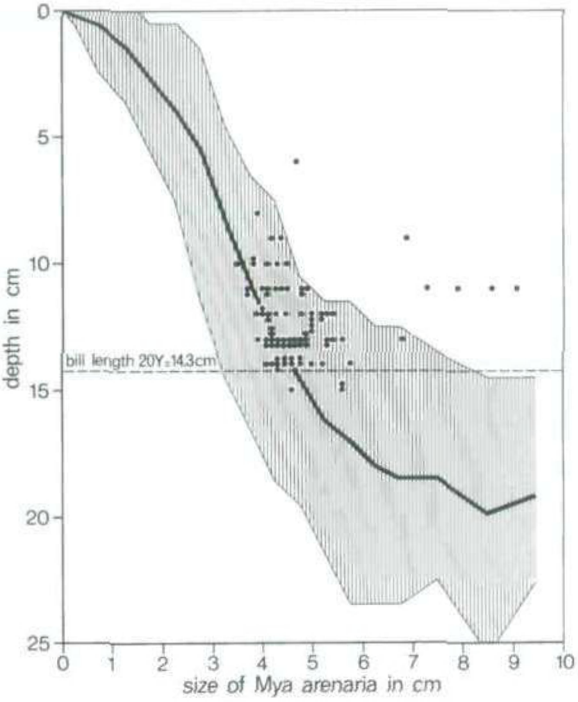


Fig. 4. Depth of clams on offer in relation to their size, and depth of 84 clams taken by the colour-banded Curlew 20Y (dots). The grey field shows the depth range at which 95% of the clams are living (based on the same data as in Fig. 3).

shows, large clams appear to be more profitable than small ones. Most clams taken by the bird were indeed large (Fig. 2A). The risk to a clam of being taken was maximal if it measured 4-5 cm (Fig. 2B), but the risk to the most common clam size present (2-3 cm) was 130 times less.

From Fig. 1C it can be seen that clams below 23.6 mm length would be unprofitable for this bird. In March 1981, when large clams were very rare, we observed that the marked bird took some small prey but since we could not locate the clams which were taken, their exact size was unknown. Assuming these were solely second-year clams, which averaged 25 mm in size at that time, the bird would have obtained 4.14 mg/s handling time (indicted with an open circle in Fig. 1C), which is just above the rejection threshold.

Certain other colour-banded Curlews also took clams of about 25 mm, or even smaller, but in those cases the birds swallowed the clam whole, including the shell. The handling time was very short: 3.41 s (n = 252) for two Curlews observed in November 1980; hence they obtained quite a high yield of 9.2 mg/s handling time. Eating clams in this way may have disadvantages, however, for is was observed predominantly in periods when big clams were very rare (the winter of 1977-78 and of 1980-81), and even in those lean winters most of the colour-banded Curlews for which clams were the main prey never swallowed the small ones. Perhaps they would have caused a 'digestive bottleneck' (Kenward & Sibly 1978).

The accessible fraction of the profitable clams

The data on the yields of food from different sizes explain why Oystercatchers take smaller sizes than Curlews, but cannot help us to understand why the Oystercatchers on the mudflats do not attack successfully those clams of over 4 cm and why Curlew 20Y took relatively few clams above 6 cm (Fig. 2). These upper limits are in fact determined by the proportion of the different size classes within the reach of the bills of the two waders.

To investigate the depth distribution of the clams in each size class, we used a circular corer (of surface area 176 cm^2) pushed 40 cm into the substrate. After breaking open the core, it is possible to measure accurately the distance between the mud surface and the upper tip of the bivalves. From these measurements it appeared (Fig. 3) that an Oystercatcher cannot find clams of more than 4 cm in length in the upper 7 cm of the substrate (the bill length of an Oystercatcher) and that the greater part of the shell above 7 cm length are out of the reach of the female Curlew (bill length 14 cm). Even fewer are accessible to a male (bill length 12 cm) (Fig. 3, inset).

Most clams taken by the marked Curlew lived, given their size, at remarkably shallow depths (Fig. 4). Nearly all were buried above the mean depth of their respective size classes. The bird managed to find the very rare clams of more than 6 cm length which lived at atypically shallow depths, only 8-14 cm below the mud surface.

In the summer of 1979 we manipulated the food supply in the former feeding territory of the marked

Curlew, by burying some hundreds of big clams just below the surface of the intertidal flats. As an unexpected but interesting result, an Oystercatcher started to prey on the big clams and vigorously defended the site, with success, not only against congeners but also against Curlews. It did so for a couple of days, during which this single bird completely depleted the planted population of prey. This kind of behaviour was never observed in 'natural' situations. Interactions between Oystercatchers and Curlews are normally quite rare.

In the natural situation, it is very unlikely that there is direct competition between Oystercatcher and

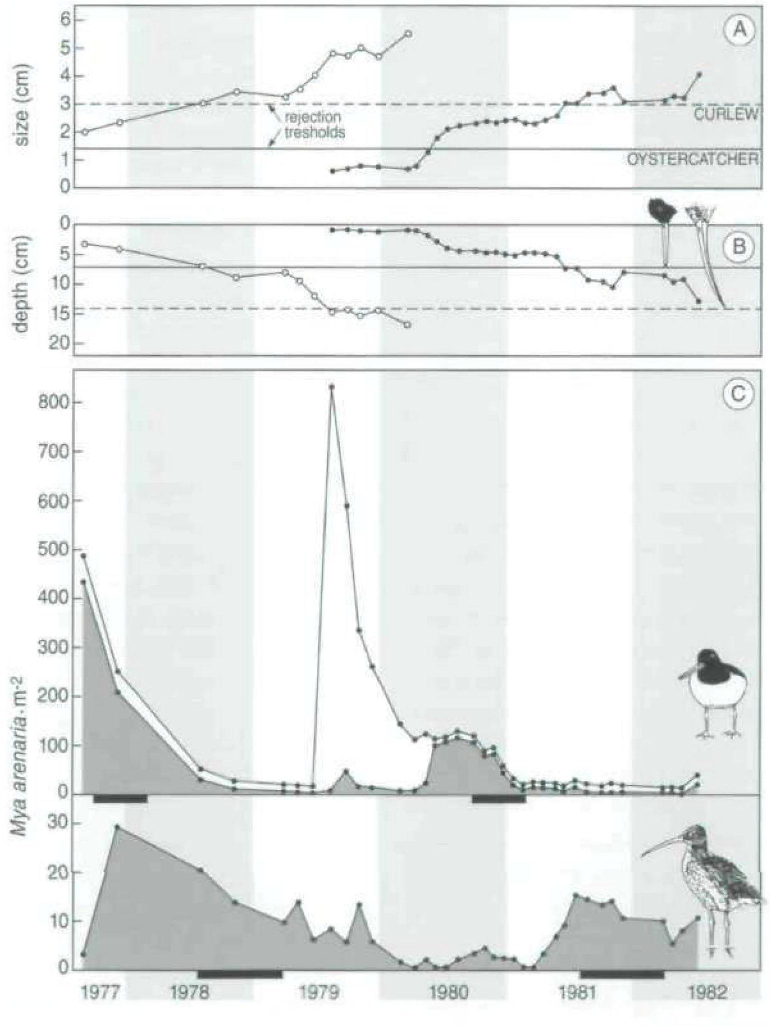


Fig. 5. **A.** Average size of two cohorts of clams of which the spatfall took place in 1976 (open circles) and 1979 (solid circles) in the Nes area (Frisian coast); rejection threshold for both bird species is indicated. **B.** Average depth of two cohorts of which the spatfall took place in 1976 (open circles) and 1979 (solid circles); bill length (and thus maximal prey depth) for both bird species is given. **C.** Density of clams/m^2 since 1977 in the Nes area (number of two cohorts together). Upper panel shows total density and density of clams vulnerable to predution by Oystercatchers (clam size ≥ 15 mm, depth ≤ 7 cm, see Fig. 3). Lower panel gives density of potential prey for Curlews (size ≥ 30 mm, depth ≤ 14 cm, see Fig. 3). Note the different scale used for both bird species. Main exploitation periods (as derived from bird counts and observations on prey selection) are indicated by black bars along the x-axis.

Curlew when they both feed on clams, because of the small overlap between the prey sizes which are available as well as profitable for both bird species (Fig. 3). Since Curlews select larger clams than Oystercatchers, there is a segregation in time if the two species are to feed on clams from the same year of spatfall.

However, this potential partitioning of resources does not tell us anything quantitatively about competition for food between the species. Oystercatchers might deplete the clam stock completely before the shells have reached the size at which they can be harvested profitably by Curlews.

Depletion of the food stock

Since we started our sampling programme of the macrobenthic fauna in 1977, there has been one successful spatfall of clam (1979); the previous one was in 1976.

Spatfall occurs during the summer. First-winter clams reach a size of c. 8 mm and are thus still too small to be utilized by Oystercatchers. During the second growing season most animals pass the lower acceptance threshold for Oystercatchers, but not until the next year do they become profitable for Curlews (Fig. 5A). During the growth of the shell, clams bury deeper. The size-depth relationship (Fig. 3), can be used to derive the average depth of each cohort (Fig. 5B), but also allows calculation for all sampling date of the numbers of clams above the lower acceptance size threshold and which are accessible to both bird species (Fig. 5C). Good years for clam-eating Oystercatchers (the winters of 1977-78 and 1980-81) precede the rich years for Curlews (the winters of 1978-79 and 1981-82).

The predation pressure by Oystercatchers and Curlews appears to be high enough to explain the greater part of the loss of clams after the second growing season.

In October and November 1980 all Oystercatchers present on the mudflats preyed upon clams. From the work of Hulscher we know that the average intake was 3.63 clams/min (n = 870 min). Because the water level was measured continuously, we know that the mudflats were exposed for 15 900 min in daylight during these two months and for 21 500 min at night. During daytime low-water periods, Oystercatchers fed for 88% of the time that the flats were exposed, at a density of 1.26 birds/ha. Combining these data, we calculate that in two months the Oystercatchers took 6.4 clams/m^2 by day. Bird counts were made also at night, with infra-red binoculars, and from this it is known that Oystercatchers remained to feed at night, but their feeding rate could not be measured. Assuming the same feeding rate as by day, the total predation in October and November amounted to 15.1 clams/m^2.

If the birds which were present during the rest of the winter continued to feed on clams and did not switch to the only alternative prey available, *Macoma balthica*, the resultant predation pressure in the period 1 October 1980 to 1 March 1981 could be estimated at 20 clams/m^2 by day only, or 49 clams/m^2 in total if the predation rate by night was the same as by day. This value is a minimum, since we have omitted one bird count which took place just after a cold spell, during which the mudflats were frozen and many Oystercatchers fed on dying bivalves. During this period the density rose to 30 birds/ha, 20 times as high as the average density that winter. This situation lasted for between 3 and 5 days. In that short period as many as 20 clams/m^2 might have been eaten if the birds had achieved the same feeding rate as in autumn.

Between 1 October 1980 and 1 March 1981 there was a decrease from 110 to 20 clams/m^2 (Fig. 5C). At maximum, Oystercatchers took 69 of the 90 clams/m^2 which disappeared. A smaller proportion were eaten by Common Gulls *Larus canus*, present after the cold spell, and by some of the Curlews which started to swallow the small clams.

No detailed observations are available for the winter of 1977-78 when the density of preferred size classes was much higher but also decreased dramatically during the winter (Fig. 5C). Counts of birds on the feeding area are available, however, and we also know that clams were the main (and perhaps the only) prey taken because we found many clams recently opened by Oystercatchers. The average Oystercatcher density in the winter of 1977-78 was 5.1 times as high as in the winter of 1980-81. Assuming the same intake rate by the birds, the predation pressure in the period October-March would have been 351 clams/m^2, assuming equally heavy predation by day and by night. The decrease which was found -from 440 to 120 clams/m^2- was in fact below the estimated impact of the Oystercatchers.

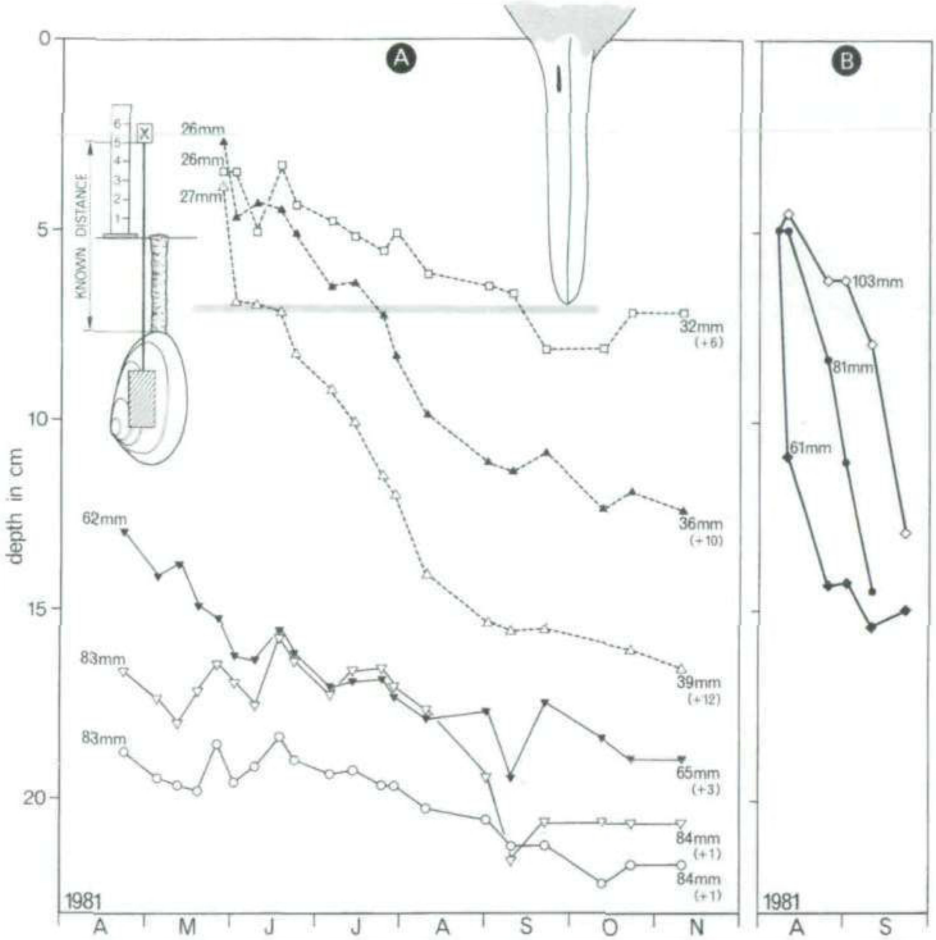


Fig. 6. A. Depth of six individual clams on an intertidal flat between April and November 1981, measured with the aid of a thin nylon thread attached on the shell. Size was determined in April and November. Maximal probing depth for Oystercatchers is given. Note the relationship between size increment in the three second-year clams and the vulnerable period. **B.** Changes in depth of three clams planted at a shallow depth, to show that big clams have not lost the ability to burrow.

The predation pressure by Curlew is more difficult to measure, since there is a large variation in the food choice of different individuals. The majority of male Curlews, for instance, never take clams, nor do some of the females. The best data at hand concern the predation by the marked female 20Y within her territory. The density of the accessible clams of the preferred size classes amounted to 8 clams/m^2 in July 1978. In the next nine months, she took at maximum about half of the food stock in her territory of 6000 m^2.

Discussion: prey risk and depth

The mortality rate of the clam decreases with age (Brousseau 1978). It is well documented that Plaice exert heavy predation on the spat of the clam (Schmidt 1951, de Vlas 1979a). In our study area bird predation on the spat is quite low. Knot *Calidris canutus* take them, but this wading bird was usually rather rare in our area.

The data presented above show that the lower acceptance threshold for the birds is determined by the yield in relation to handling time, whilst the upper threshold is set by the decreasing proportion of the clams of the larger classes living within the reach of the bill. Amongst the accessible clams there is a relatively heavy predation on the larger size classes, which are the most profitable prey. Oystercatchers take many clams of 3-4 cm in length, although most clams of that size class lie at depths beyond the Oystercatchers' bill. Clearly an essential part of the life strategy of the clam should be to grow a long siphon as quickly as possible so that it can live at a safe depth as soon as possible. The fact that the siphon weight of a small clam amounts to 50% of its total body weight, compared to 30% in large clams, attests to this. The selection by 20Y of clams which live at shallower depths than average for their respective size classes (Fig. 4), indicates that there is a lower risk to prey living at greater depths. The same has been found by Myers *et al.* (1980) in experiments with crustacean prey of Sanderlings *Calidris alba.*

Oystercatchers start to feed on clams during the bivalve's second growing season as they pass the lower size limit of about 17 mm. A year after that, most clams live beyond the reach of the bill of the Oystercatcher. How long individual clams are vulnerable to predation by Oystercatchers depends on the growing-burrowing rate, which is highly variable. A period of some weeks of months only has been indicated (Fig. 6A). However, the differences between individual clams are so great that the cohort remains exploitable for a year (Fig. 5). Curlews have a longer period in which to take clams which still live within the reach of their bills, but by selecting only clams above 3 cm in length, they suffer a considerable reduction in the density of available prey. The numbers of clams which are buried just out of reach of the Curlew's bill after they pass the acceptable size threshold is rather great. The biomass of preferred sizes of clams able to be reached by male Curlews with bills of 11-12 cm is only about half of that accessible to females (bill sizes 14-16 cm). This is probably one of the reasons why most males do not feed on clams, whilst most females do.

Clams which live below the reach of the Curlew's bill (a maximum of 16 cm) are out of danger. Measurements of the depth of individual clams (Fig. 6) show that there is no short-term variation in their living depth. Yet it is possible that very big clams become accessible to avian predators if the upper layer of the substrate has been eroded. Continuous measurements made on the variation in absolute height of the intertidal flats show that after heavy storms erosion of about 10 cm may occur. On the other hand, big clams are able to bury themselves again. In contrast to what is generally believed, big clams planted just below the mud surface are able to burrow c. 5 cm within a few days (Fig. 6B).

We are convinced that precise measurements on the accessible fraction of that part of the food supply which can be harvested profitably are necessary to understand the predator-prey relationship. Nature is complex, however. On most intertidal flats and also in our study area, wading birds seldom meet a one-prey situation. Normally, in attempts to maximize their rate of biomass intake, birds can decide what prey to take and thus where to go. In autumn 1980, for instance, most Oystercatchers did not remain on the mudflats, but switched to nearby cockle and mussel beds, which came into existence after the heavy spatfall of the year before. Switching was profitable because the intake rate on the mudflats, where the clam was the only prey, was lower than on the cockle beds (Hulscher unpubl.) and on the mussel banks (Zwarts & Drent 1981). Switching by short-billed male Curlews from mudflat-feeding to meadow-feeding in winter is another example (Townshend 1981). The substantial differences between the prey choice of individual colour-banded Curlews in our study area (B. Ens & L. Zwarts unpublished) show that feeding decisions have to be studied even on the level of individual birds. Switching on the part of the individual predator to more profitable prey is thus another factor determining the predation risk to alternative prey. This makes us again aware of how much work still has to be done before it is possible to ascertain the role of food as a limiting factor for the large number of wading birds feeding on the intertidal flats.

SAMENVATTING

SAMENVATTING

Voorgeschiedenis

In 1960 verscheen een dun boekje onder de titel "Een inleidend onderzoek naar de relatie tussen wadvogels en bodemfauna". Het was een verslag van veldwerk dat in de zomers van 1956 en 1957 op Vlieland had plaatsgevonden. Nooit eerder, ook niet elders in de wereld, was er een poging gedaan om precies te meten wat tot dusver niet te meten leek: de gigantische aantallen steltlopers die zich met afgaand water verspreidden over immense wadvlakten om zich te voeden met kokkels, nonnetjes, wadpieren en andere bodemdieren die al even ontelbaar leken. Het bleek echter heel goed mogelijk om de vogels te tellen. Bovendien kon de dichtheid van prooidieren worden berekend door op een gestandaardiseerde manier monsters van het wad te nemen en die uit te spoelen over een fijnmazige zeef.

We zijn nu bijna 40 jaar verder. De Waddenzee is intussen één van de best onderzochte natuurgebieden ter wereld, afgaande op het aantal publicaties dat de laatste decennia is verschenen. De onderzoeksmethoden zijn grotendeels dezelfde gebleven. Nog steeds worden wadmonsters uitgezeefd en nog steeds wordt geteld hoeveel prooien wadvogels eten. Veel van dit werk kwam voort uit een gemeenschappelijke motivatie. De onderzoekers hoopten door nauwkeurige meting van het voedselaanbod van bodemdieren en de voedselopname door vogels een belangrijke vraag te kunnen beantwoorden: wordt het aantal steltlopers op de NW-Europese wadgebieden beperkt door wat het wad heeft te bieden?

De vraag is niet alleen theoretisch interessant, maar ook ingegeven door bezorgdheid. Overal gingen en gaan immers wadgebieden verloren. Wat kunnen de gevolgen zijn voor de miljoenen vogels die vanuit een enorm gebied, reikend van Oost-Canada tot diep in Siberië, naar de Waddenzee komen?

Het schatten van de draagkracht: is er genoeg voedsel?

Is er genoeg voedsel voor de vogels in de Waddenzee? Stel het geval dat de helft van de Waddenzee zou verdwijnen. Er zijn twee mogelijkheden, met allerlei gradaties er tussen in. In het ene extreme geval, kunnen alle vogels terecht in het overgebleven deel. Er is per vogel weliswaar minder ruimte (de 'dichtheid' van de vogels is groter geworden), maar er is voor elke vogel genoeg voedsel te vinden. De 'draagkracht' van de Waddenzee was in de oorspronkelijke situatie blijkbaar nog niet bereikt. In het andere extreme geval blijft de dichtheid van de vogels gelijk en zijn de verdwenen vogels dood gegaan of naar een ander voedselgebied vertrokken. In dit geval weten we zeker dat de draagkracht was bereikt. Is het nu mogelijk om te voorspellen wat er gebeurt met de vogels als een voedselgebied gedeeltelijk verdwijnt?

Het is in de loop van de jaren duidelijk geworden dat het moeilijk is om deze vraag te beantwoorden. Ten eerste varieert het voedselaanbod van jaar op jaar. Het is niet voldoende om te weten hoe groot het gemiddelde aanbod van bodemdieren is. We moeten vooral weten hoe vaak het voedselaanbod op het wad erg klein is en hoe de vogels daar op reageren. Ten tweede zijn wadvogels niet de enige consumenten van bodemdieren. Vissen, krabben en garnalen eten voor een deel dezelfde prooien, dus de consumptie van deze diergroepen moet eveneens bekend zijn. Maar zelfs als we weten dat alle roofvijanden samen jaarlijks 30 of 80% van alle bodemdieren weg zouden eten, is dat moeilijk te interpreteren zolang we niet weten hoe snel bodemdieren groeien en verschillende generaties elkaar opvolgen. Het is daarom nodig om de produktie van de bodemdieren te meten en zó vaak te monsteren dat groei en sterfte van de diverse jaarklassen nauwkeurig kan worden bepaald. Maar ook dan zijn we er niet.

Krabben, garnalen en vissen eten, evenals sommige vogels, delen van bodemdieren (zoals staarten en sifo's) die weer kunnen aangroeien. Dit moet allemaal worden verdisconteerd in de berekening van de produktie en de consumptie.

Het belang van individuele gedragsmetingen

Hoe noodzakelijk al die berekeningen ook zijn, ze brengen het gevaar met zich mee dat de onderzoeker de natuur steeds meer gaat zien als "een zwarte doos" waaraan wel van alles indirect te meten valt, maar niets valt te zien. Het aardige van wadvogels is nu juist dat er veel is te meten én te zien. Als we bijvoorbeeld naar een scholekster kijken die op het wad loopt, valt ontzettend veel waar te nemen. De vogel loopt rustig over het wad, prikt zijn snavelpunt regelmatig in de grond, soms zelfs tot aan zijn oog in de modder, en haalt nu en dan een prooi omhoog. Dit is allemaal nauwkeurig vast te leggen. Scholeksters eten vervolgens hun prooi leeg en laten de lege schelp achter, zodat we precies kunnen nagaan welke prooien worden gepakt en hoe groot ze zijn. Bovendien is dezelfde monsterbuis waarmee de prooidichtheid wordt gemeten, te gebruiken om nauwkeurig te bepalen hoe ver beneden het wadoppervlak de diverse prooien ingegraven leven. Deze metingen geven inzicht in hoeveel bodemdieren buiten het bereik van de snavel leven en daarmee helemaal geen onderdeel kunnen vormen van het exploiteerbare voedselaanbod. Die onbereikbare fractie is soms heel groot, en moet dus echt worden bepaald als we het voedselaanbod willen meten dat relevant is voor de vogels.

Maar zelfs dan zijn we er niet, omdat niet alle bereikbare prooien van belang zijn voor de vogels. Dezelfde scholekster die zo vaak tevergeefs in de bodem prikt, raakt met zijn snavelpunt voortdurend kleine schelpdieren aan die ondiep leven. Voor deze kleine prooien heeft hij geen belangstelling omdat ze niet lonend zijn om te worden gegeten. Met andere woorden: de kosten van pakken en opeten wegen niet op tegen de energie opbrengst. Het deel van de bereikbare prooien dat wel lonend is, wordt de oogstbare prooifractie genoemd.

Vogels nemen beslissingen

Als een scholekster prooien weigert neemt hij een beslissing. Het inzicht dat dieren beslissingen nemen, en dat we de natuur pas een beetje begrijpen als we die beslissingen kunnen voorspellen, heeft ons denken over de natuur -en dus ook over de relaties tussen wadvogels en bodemfauna- in sterke mate bepaald. Een scholeksters die besluit te gaan foerageren, moet onder andere de volgende beslissingen nemen: welk voedselgebied te kiezen, welke prooisoort te selecteren, hoe diep te prikken, hoe hard te lopen, hoe prooien open te maken en welke grootteklassen binnen het voedselaanbod te negeren. Sommige van deze beslissingen, zoals de keuze van het voedselgebied en soms prooisoort, zijn lange termijn beslissingen, andere (pikdiepte, loopsnelheid) zijn beslissingen op de korte termijn. De beslissingen die worden genomen zijn veelal te voorspellen op basis van relatief simpel rekenwerk. We gaan er daarbij vanuit dat vogels de snelheid waarmee ze voedsel zoeken steeds zo groot mogelijk proberen te maken. Als gebied A een grotere voedselopname garandeert dan gebied B, verwachten we dat een vogel naar A zal vliegen, en pas naar B als de situatie in gebied A slechter is geworden dan in B. De vogel neemt deze lange termijn beslissing om voortaan naar B te vliegen *níét als hij in gebied A een uurtje weinig succes heeft gehad*, maar misschien wèl wanneer hij één, of misschien wel meerdere, dagen in gebied A minder succesvol heeft gefoerageerd. Een voorbeeld van een korte termijn beslissing die een scholekster moet nemen is de wijze waarop een hij een ingegraven schelpdier moet eten: omhooghalen en aan het oppervlak openmaken, of proberen de schelp onder de grond al te openen en leeg te eten. De tijdwinst bedraagt slechts een paar seconden, maar toch zal de vogel kiezen voor de techniek die de snelste is.

Ook prooien nemen beslissingen

Niet alleen roofdieren nemen beslissingen, ook prooien doen dat. Ook zij moeten eten en zullen daarbij afwegingen maken. Een zeeduizendpoot bijvoorbeeld loopt weinig gevaar als hij diep in zijn hol zit, maar zodra hij omhoogkruipt om aan het oppervlak te foerageren, stelt hij zich bloot aan allerlei roofvijanden die zitten te wachten op wormen die uit hun hol komen. Toch moet een worm ook eten en zal hij de volgende afwegingen moeten maken: wanneer moet hij omhoog kruipen en hoe ver kan hij uit zijn hol komen. Als de worm ver uit zijn hol kruipt kan meer voedsel worden gevonden, maar is het risico dat hij zo'n foerageerperiode niet overleeft veel groter. Intuïtief is aan te geven dat bij een grotere voedselbehoefte en/of een kleiner predatierisico de worm vaker en verder uit zijn hol zal kruipen. De laatste jaren zijn modellen ontwikkeld waarmee kwantitatieve voorspellingen kunnen worden gedaan over wat de worm precies zal moeten doen.

Het schatten van de draagkracht: kunnen vogels altijd genoeg voedsel vinden?

Kunnen gedetailleerde metingen aan het gedrag van prooi en predator ons helpen om de draagkracht van het wad voor wadvogels te bepalen? De draagkracht is te definiëren als het aantal vogels dat in een gebied in leven kan blijven. Anders gezegd: als er één vogel bij komt, gaat één andere vogel dood of moet deze emigreren. Vogels sterven of emigreren als ze hun dagelijkse voedselbehoefte niet kunnen dekken. De voedselconsumptie hangt af van twee factoren: de tijd waarin vogels per etmaal kunnen voedsel zoeken en de snelheid waarmee ze voedsel kunnen opnemen. De foerageertijd op het wad wordt bepaald door de getijdebeweging. Deze varieert van dag tot dag, maar is op de lange termijn zeer voorspelbaar. De opnamesnelheid daarentegen wordt bepaald door vaardigheden en eigenschappen van de vogel zelf èn door eigenschappen van de geëxploiteerde prooipopulaties. Om in leven te blijven, moeten vogels hun opnamesnelheid boven een bepaald minimum niveau zien te houden. Zolang alle vogels boven deze ondergrens zitten, wordt het aantal vogels in een gebied niet bepaald door de draagkracht van dat gebied. Als we de draagkracht willen schatten, is het dus essentieel om de opnamesnelheid te meten.

De opnamesnelheid hangt grotendeels af van hoe lonend de prooien zijn en hoe lang de vogels er naar

moeten zoeken. De zoektijd is gerelateerd aan de kans om een prooi te treffen. Deze trefkans wordt op zijn beurt bepaald door de dichtheid en het gedrag van de prooien en hun diepteverspreiding in het substraat. De totale prooidichtheid is weliswaar eenvoudig te bepalen, maar de oogstbare fractie van het voedsel blijft moeilijk te definiëren. Welk deel van het voedselaanbod door de predatoren wordt afgeroomd, heeft tevens te maken met de beslissingen die een predator neemt. We kunnen die keuze proberen te voorspellen door te vergelijken wat de verschillende prooien opleveren. Daarvoor is het nodig om voor diverse prooicategorieën te meten hoe lonend ze zijn en hoe groot hun trefkans is. Als we in staat zouden zijn daarmee de foerageerbeslissingen van de vogels juist te voorspellen, weten we de opnamesnelheid en kunnen we aangeven wanneer het wad niet voldoende heeft te bieden. Veel van de beschreven gedetailleerde waarnemingen zijn verricht met deze gedachte in het achterhoofd.

Opzet van het onderzoek

De basis van het onderzoek waren proefveldjes van 1000 m^2 die op het wad werden uitgezet. Van die veldjes werden de hoogteligging en de bodemgesteldheid bepaald. Vanuit hoge observatietorens werden de vogels in de proefveldjes geteld, overdag met normale kijkers en 's nachts met een infra-rood kijker of een lichtversterker. Hoewel de vogels vaak slechts op enkele tientallen meters van de torens foerageerden, gebruikten we altijd sterke telescopen om hun voedselkeuze en voedselopname nauwkeurig te meten. Daarnaast werd het voedselaanbod in de veldjes bepaald door frequent dichtheid en diepteverspreiding van de bodemdieren te meten. Deze gegevens maakten het mogelijk om de verspreiding van de vogels, hun prooikeuze, de opnamesnelheid en de totale voedselopname te koppelen aan de ruimtelijke variatie in het voor vogels relevante prooiaanbod, dat wil zeggen dat deel van het voedsel dat werkelijk oogstbaar is.

Om deze relaties beter te kunnen onderzoeken, werden de twee grootste steltlopersoorten -scholekster en wulp- gevangen en van kleurringen voorzien. Vanaf dat moment hadden we niet langer te maken met anonieme vogels, maar met individuen die we soms jarenlang konden volgen. Behalve wulpen en scholeksters kwamen nog zo'n tien andere vogelsoorten voedsel zoeken in de proefveldjes. De voedselkeuze van deze soorten werd onderzocht door braakballen en faeces te verzamelen en te analyseren. Prooisoort, prooigrootte en aantal prooien werden vastgesteld aan de hand van goed herkenbare en meetbare fragmenten in de braakballen en faeces. De prooigroottes werden afgeleid uit ijklijnen, gebaseerd op exacte metingen in het laboratorium van specifieke fragmenten van prooien met bekende lengte en gewicht.

Met het veldonderzoek werd begonnen in de zomer van 1976 en het werd beëindigd in december 1986. Al het veldwerk heeft zich geconcentreerd in de Fries-Groningse kuststrook. De gegevens zijn verzameld door een groot team (zie dankwoord). Dit hoofdstuk geeft geen uitputtend overzicht van al het verrichte werk, maar wel een samenvatting van de 16 artikelen die hier zijn opgenomen. Twee hoofdstukken beschrijven de variatie in de voedselvoorraad voor steltlopers als gevolg van variatie in dichtheid, vleesgewicht, leefdiepte en gedrag van hun prooidieren. Vier hoofdstukken gaan over de leefdiepte van de bodemdieren: welke factoren bepalen de leefdiepte en waarom leven niet alle individuen veilig buiten het bereik van de snavel? Eén hoofdstuk beschrijft de activiteit en de ingraafdiepte van de zeeduizendpoot. Nog eens negen hoofdstukken laten zien hoe wadvogels inspelen op de variatie in het voedselaanbod; daarvan gaan er vijf over scholeksters, twee over kanoetstrandlopers, één over wulpen en één over scholeksters en wulpen.

Fluctuaties in de oogstbare voedselvoorraad

Dankzij het uitvoerige bemonsteringsprogramma van Jan Beukema weten we dat in de bodem van de Waddenzee gemiddeld zo'n 20 gram vlees per m^2 bevat. Droog vlees wel te verstaan, zonder water maar ook zonder zout, kalk en substraat. Die 20 gram biomassa is een gemiddelde, want op zeer zandig wad is het tien maal minder en op mosselbanken kan het 50 maal zo groot zijn. Behalve deze ruimtelijke verschillen in voedselaanbod is er ook een variatie in de loop van de tijd. Bodemdieren planten zich 's zomers voort. De nieuwkomers kunnen buitengewoon talrijk zijn, maar

omdat ze nog vrijwel niets wegen, leveren ze pas na minstens een jaar, en bij enkele soorten zelfs na enkele jaren, de grootste bijdrage aan de totale biomassa van een soort, ook al is intussen meer dan 99% van de individuen verdwenen. De voortplanting van de bodemdieren is niet elk jaar even succesvol, met als gevolg een grote variatie in de bijdrage die de verschillende soorten leveren aan de totale biomassa.

De seizoensvariatie in de biomassa is minder grillig dan de verschillen van jaar tot jaar. De bodemdieren groeien in het voorjaar en vroege zomer en verliezen in de rest van het jaar gewicht. Het gevolg is dat de steltlopers die van deze prooien afhankelijk zijn 's winters 1,5 tot 2 maal zoveel prooien moeten vangen van eenzelfde grootte als in de voorzomer, willen ze althans even veel voedsel vergaren. Dit verschil wordt nog groter als de opname zou worden uitgedrukt in energie. Immers, de energie-inhoud is 's winters iets minder dan 's zomers, althans bij enkele schelpensoorten. Van meer belang is evenwel dat 's winters veel bodemdieren buiten het bereik van de snavel leven. Slijkschelpen en nonnetjes graven zich 's winters diep in. Vanaf maart komen ze langzamerhand omhoog om na juni weer dieper te gaan leven. Daarnaast zijn de bodemdieren in de winter bij lage temperaturen minder actief, en daardoor minder beschikbaar als voedselbron. Wormen komen bijvoorbeeld niet naar het oppervlak en schelpdieren houden hun kleppen stevig op elkaar. Tegelijkertijd hebben garnalen en krabben zich teruggetrokken in de diepe geulen. Vandaar dat de Waddenzee veel steltlopersoorten 's winters nauwelijks voedsel biedt. De meeste soorten steltlopers overwinteren er niet, maar gebruiken de Waddenzee als tussenstation in de nazomer op weg van hun noordelijke broedgebied naar warme overwinteringsgebieden, en andersom op de terugtocht in april en mei.

Waarom leven niet alle bodemdieren buiten het bereik van de steltlopersnavel?

Ingegraven schelpdieren lopen een verhoogd risico om door een steltloper te worden gepakt als ze dicht bij de oppervlakte leven. We konden dit experimenteel en met veldmetingen overtuigend aantonen. De vraag is waarom sommige schelpdieren zich blootstellen aan zo'n groot risico.

De sifo is van levensbelang Ingegraven schelpdieren leven verborgen in de bodem en dat geeft hen een eerste bescherming tegen op het oog jagende roofvijanden. Toch zijn ze voor hun eigen voedselvoorziening en zuurstof afhankelijk van het oppervlak. Schelpdieren die ingegraven leven hebben een buis, de sifo, waarmee ze de oppervlak kunnen bereiken en voedsel uit het water kunnen filteren. Typische filteraars zijn de kokkel en de strandgaper. Andere soorten zoals de slijkschelp en het nonnetje, hebben een lange, buigzame sifo waarmee ze voedsel vanaf de bodem kunnen zuigen. Behalve een instroom- hebben deze soorten ook een uitstroomsifo, alleen bij de strandgaper zitten beide buizen in één dikke sifo.

Bij alle soorten vinden we dat grote schelpdieren dieper ingegraven leven dan kleine exemplaren. Het verband is echter niet lineair, maar eerder S-vormig. Alle kleine exemplaren leven ondiep, alle grote dieren diep, maar bij de tussenliggende categorie zien we met toename van de grootte ook een sterke toename van de diepte.

Wanneer het sifogewicht wordt uitgezet tegen de schelplengte vinden we een exponentieel verband. Toch is het sifogewicht geen vast percentage van het totaalgewicht. Kleine exemplaren hebben relatief weinig sifo, daarna neemt het gewicht van de sifo snel toe, om bij de grootste schelpen weer af te nemen. Het lijkt er sterk op dat de investering in de sifo maximaal is in de levensfase waarbij de schelpdieren hun ingraafdiepte het meest vergroten.

Tussen de soorten bestaat een groot verschil in de hoeveelheid weefsel die ze investeren in de instroomsifo. Hoe dieper ze leven, hoe groter relatief het sifogewicht. Vergelijking van enkele soorten laat zien dat per cm diepte 0.6% van het lichaamsgewicht moet worden geïnvesteerd in sifoweefsel. Bij de strandgaper is dit zelfs meer, omdat bij deze soort de in- en uitstroomsifo is samengegroeid tot één buis.

Echte filteraars als kokkel en strandgaper leven het hele jaar op ongeveer dezelfde diepte. Daarentegen leven soorten die voedsel van het oppervlak kunnen afzuigen 's winters dieper ingegraven dan 's zomers. Een mogelijke verklaring hiervoor is dat het stukje sifo dat 's zomers wordt benut om horizontaal over het wad te reiken 's winters wordt gebruikt om dieper te leven. De voedselbehoefte is 's winters immers erg klein.

De sifo is niet van elastiek Deze interpretatie van de gegevens kan alleen juist zijn als er niet te veel rek zit in de sifo. Op het eerste gezicht zou je dat echter niet verwachten, want een sifo lijkt het meeste op een elastisch ventielslangetje. Als de sifo een soort elastiekje zou zijn, hoeft de sifo alleen maar iets te worden uitgerekt om verder over het oppervlakte te reiken, of om dieper onder het oppervlak te kunnen leven. Op diverse manieren werd aannemelijk gemaakt dat dit niet zo is. Zo deden we metingen aan de rek van de sifo, bijvoorbeeld door de foerageerstraal te meten van schelpdieren die we aan een dun touwtje hadden vastgeplakt, waardoor we precies wisten hoe diep ze ingegraven leefden. Bij deze exemplaren was er een redelijk verband tussen de lengte en het gewicht van de sifo. We konden dit verder uitzoeken door ook stukjes van de sifo af te knippen.

Diepte en seizoen De toename van ingraafdiepte met sifogewicht is niet het gehele jaar gelijk. Schelpen met eenzelfde sifogewicht leven 's zomers veel ondieper dan 's winters. Daarvoor zijn twee verklaringen. 's Zomers is hun voedselbehoefte groter en daarnaast durven ze ondieper te leven omdat het prooirisico veel kleiner is door het ontbreken van grote aantallen steltlopers op het wad. Als nonnetjes en slijkschelpen 's winters ondiep leven worden ze snel opgeruimd, maar omdat ze meestal diep leven, is de sterftekans 's winters kleiner dan 's zomers.

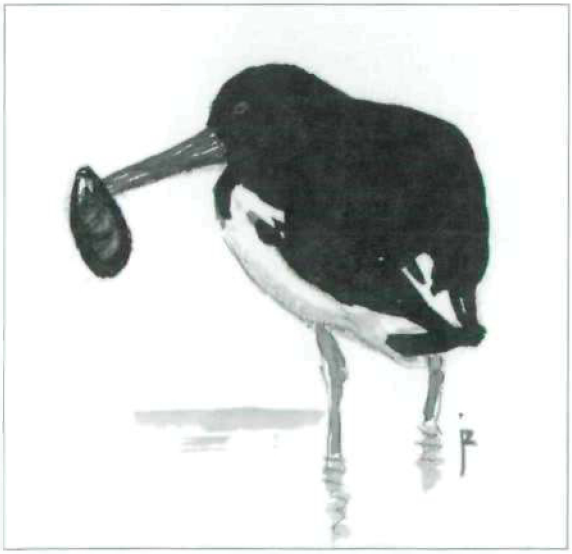
's Zomers leven nonnetjes en slijkschelpen niet alleen ondieper omdat ze meer risico willen en durven te nemen, maar ook omdat hun sifogewicht veel kleiner is. Het geringe sifogewicht kan, zoals reeds door Jaap de Vlas is beschreven, worden verklaard door de begrazing van de sifo door predatoren, en wel door jonge platvissen in voorjaar en later door garnalen, grondels en jonge strandkrabben in de zomer. De schelpen verliezen daarbij zo vaak een stukje van de sifo dat ze niet snel genoeg sifoweefsel kunnen aanmaken. Dit was heel goed aan te tonen door op het wad kleine kooitjes neer te zetten met zulk fijn gaas dat die sifoknabbelaars werden buitengesloten (zie blz. 354). Het resultaat was verbluffend. Binnen twee weken waren de sifo's aanzienlijk zwaarder, leefden de schelpen dieper en was zelfs hun lichaamsgewicht toegenomen. Het steeds opnieuw verliezen van een stukje sifo gaat dus duidelijk ten koste van de lichaamsconditie en dwingt de schelp bovendien omhoog te komen waardoor ze een grotere kans lopen om te worden opgegeten. Samengevat: (1) sifobegrazing verkleint de sifolengte, (2) een kortere sifo leidt tot een geringe leefdiepte, (3) minder diep leven betekent een grotere kans om door een vogel te worden gepakt. De bereikbaarheid van schelpdieren voor de scholekster wordt dus deels gestuurd door sifobegrazing van schol in het voorjaar en van garnaal, grondel en jonge strandkrab in de zomer.

Diepte en conditie Niet alle schelpdieren met een korte sifo leven ondiep. In feite zijn het alleen de schelpdieren met zowel een korte sifo als een laag lichaamsgewicht die dicht onder het oppervlak leven. Dit is een ondersteuning van de gedachte dat de leefdiepte van de schelpen een compromis is tussen twee tegenstrijdige tendensen: ondiep leven om met de sifo over een zo'n groot mogelijk oppervlak voedsel te kunnen opzuigen, òf diep leven en zo min mogelijk kans te lopen om te worden gepakt. Exemplaren met een korte sifo en een grote lichaamsreserve kiezen er voor om een tijdje weinig te eten, maar magere schelpdieren kunnen zich dat niet permiteren, gebruiken daarom hun sifo om voedsel te zoeken en leven dus ondiep en lopen een groter risico om te worden gegeten.

Het feit dat vooral marginale schelpdieren ondiep leven en exemplaren in goede conditie diep ingegraven zitten, heeft natuurlijk zijn weerslag op de steltlopers die van deze prooien leven. Aangezien steltlopers alleen de ondiepe schelpdieren pakken, worden de magere examplaren meer gegeten dan de dikke. De berekende voedselopname wordt dus overschat als er vanuit wordt gegaan dat steltlopers van elke grootteklasse een willekeurige steekproef nemen. De fout is vooral groot als slechts een kleine fractie van de totale prooipopulatie voor de roofvijand beschikbaar komt.

Scholeksters en hun voedselaanbod

Selectie van grote prooien Voedselkeuze en prooiselectie zijn bij de scholekster makkelijk te bestuderen omdat deze vogel de gewoonte heeft schelpdieren open te hakken of te snijden, het vlees op te eten en de onverteerbare schelp achter te laten. Dit geeft onderzoekers een uitgelezen kans om de prooiselectie precies vast te leggen. In de Waddenzee eten scholeksters vooral mossels en kokkels, in mindere mate nonnetjes en strandgapers, en langs de Fries-Groningse kust ook slijkschelpen.

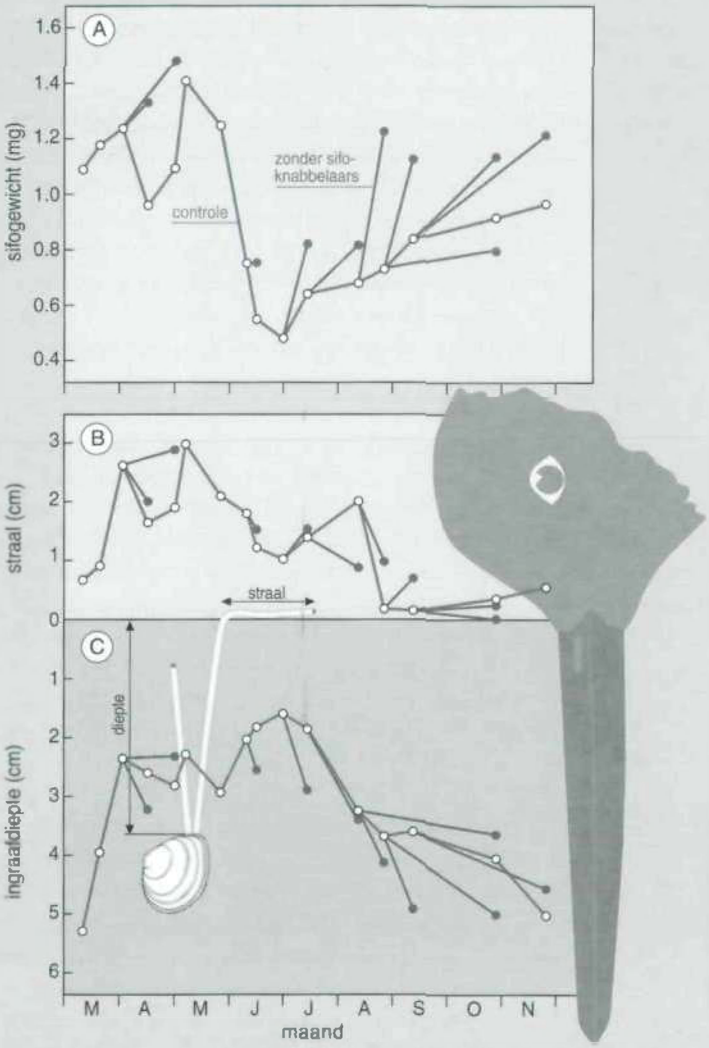


Een vergelijking tussen het aanbod van de prooi en wat scholeksters daarvan eten, laat zien dat bij elke prooisoort de kleinste schelpdieren helemaal niet worden gegeten en de grootste schelpen oververtegenwoordigd zijn in het menu. Dit is voor een deel te verklaren met, zoals Jan Hulscher al heeft aangetoond, de kans om een schelp met de snaveltop te raken. Zoals Hulscher ook liet zien, is dit niet de volledige verklaring. Nonnetjes kleiner dan 10 mm en mossels kleiner dan 20 mm worden door scholeksters genegeerd, zelfs als ze supertalrijk zijn. De verklaring hiervoor is dat het scholeksters relatief zó veel tijd kost om deze, weinig vlees bevattende, schelpen te openen en leeg te eten, dat ze er beter aandoen om zo'n prooi te negeren. De tijd die ze kwijt zouden zijn om hem op te eten, kunnen ze beter besteden om naar een grotere prooi te zoeken. Of een bepaalde prooi wel of niet moet worden gegeten, hangt dus af van de geschatte opnamesnelheid tijdens het eten van die prooi en van de gemiddelde opnamesnelheid die de vogels bereiken tijdens het foerageren. Deze selectieregel heeft tot gevolg dat naarmate lonende prooien ruimer voorradig zijn, de minder lonende prooien in toenemende mate worden genegeerd, met andere woorden: de vogel wordt selectiever. Ook andersom geldt dat als de opnamesnelheid tijdens het foerageren afneemt, prooien die eerst geweigerd werden alsnog in het menu worden opgenomen.

Deze simpele regel kan een groot deel van de waargenomen prooiselectie verklaren. De tijd die nodig is om een grotere prooi te eten neemt weliswaar toe met de grootte van de prooi, maar de toename van de vleesinhoud met grootte neemt nog meer toe. Het gevolg is dat bij alle prooisoorten die de scholekster eet, de grote prooien het meest lonend zijn en kleinere prooien alleen worden gegeten worden als de opnamesnelheid gering is.

Selectie van ondiepe prooien De selectieregel verklaart eveneens waarom scholeksters hun snavel alleen tot hun ogen in de modder stoppen, als de dichtheid van de ingegraven schelpen gering is. Het kost meer

SCHOL, MAAR OOK GARNAAL EN STRANDKRAB HELPEN SCHOLEKSTER



Sifoknabbelaars verminderen de ingraafdiepte van schelpdieren. **A.** Sifogewicht, **B.** foerageerstraal en **C.** ingraafdiepte van nonnetjes (15 mm lang) tussen maart en november 1986. De dikke lijn verbindt de gemiddelde waarden buiten de kooi; de dunne lijnen laten zien wat het effect van de kooi is, als vis, garnaal en krab zijn uitgesloten.

Iedereen kent het nonnetje als een schelp waarmee het strand bezaaid ligt. Als ze nog leven, zitten ze veilig verborgen in het substraat. Ze kunnen ingegraven leven omdat ze een dun buisje hebben, de instroomsifo, waarmee ze zuurstof en voedsel van het oppervlak kunnen halen. De sifo kan nog verder over het wadoppervlak worden uitgerekt om te grazen. In dit geval is de sifo een kant-en-klaar brokje voor predatoren.

Wat gebeurt er met de sifo als een deel ervan wordt weggegeten? Het blijkt dat beperkte sifobegrazing niet dodelijk is voor de eigenaar van de sifo, het is zelfs mogelijk om nieuw sifoweefsel aan te maken. De vraag is of voldoende nieuw weefsel kan worden aangemaakt en of deze regeneratie ten koste gaat van de algehele conditie van het schelpdier.

Om deze vragen te beantwoorden, maakten we van dunne ijzeren buisjes kooien van 1 × 1 meter en 30 cm hoog, waarvan we de bovenkant en de zijkanten bedekten met fijn gaas. We zetten die kooien op het wad, zodat we begrazing door jonge strandkrabben, garnalen en vissen konden verhinderen. Na veertien dagen, en soms langer, vergeleken we de sifogewichten van nonnetjes binnen en buiten de kooi. Zelfs in die korte periode bleken de sifo's van nonnetjes in de kooi zwaarder te zijn geworden. Dat stelde de nonnetjes in staat om zich dieper in te graven. Het bereik

van de uitgerekte sifo over het wadoppervlak hebben we niet rechtstreeks gemeten, maar kon worden afgeleid uit de relatie tussen sifogewicht en sifolengte nadat we de ingraafdiepte er van af hadden getrokken. Zoals de grafiek laat zien, nam de potentiële foerageerstraal toe bij de schelpdieren binnen de kooi. Het eindeloos knabbelen op het uiteinde van de sifo leidt er toe dat de dieren steeds weer nieuw weefsel moeten aanmaken. Dit kost blijkbaar zoveel energie dat het ten koste gaat van de algehele lichaamsconditie. Deze conclusie trekken we tenminste uit het feit dat de dieren binnen de kooien duidelijk zwaarder waren dan daarbuiten.

Heeft het geknabbel op de sifo nog effect op de overlevingskans van de nonnetjes? Als de sifoknabbelaars werden uitgesloten, groeven de nonnetjes zich dieper in. De belangrijkste predator van grote nonnetjes is de scholekster. Deze vogel heeft een snavellengte van 7 tot 8 cm lang en aangezien de vogel in staat is zijn snavel volledig in de modder te drukken, kan de vraag worden gesteld of de waargenomen toename van de ingraafdiepte het risico verkleind om door scholeksters te worden gepakt. Preciese waarnemingen aan de diepteselectie van scholeksters die nonnetjes ontbreken nog steeds, maar er is genoeg indirecte evidentie dat nonnetjes die 4-6 cm onder het wadoppervlak leven door deze vogels worden genegeerd, ook al leven ze nog binnen het bereik van de snavel. De verklaring is dat het een scholekster extra tijd kost om zijn snavel diep in de grond te prikken en om diepliggende prooien te eten. Als een scholekster gedwongen zou worden op diepliggende nonnetjes te foerageren, zou zijn opnamesnelheid altijd erg gering zijn. Om dezelfde reden zijn nonnetjes alleen 's zomers een belangrijke prooi voor scholeksters, want 's winters leven ze te diep om het de moeite waard te maken op ze te foerageren. Vandaar dat zelfs een geringe verkleining van de ingraafdiepte als gevolg van de sifobegrazing de prooien meer lonend maakt voor scholeksters, waarmee het risico groter wordt om door hen te worden gepakt. De conclusie is duidelijk: de sifoknabbelaars maken het de vogels 's zomers makkelijker om op ingraven schelpdieren, zoals het nonnetje, te foerageren, of zoals Rudi Drent onmiddellijk zei toen ik hem voor het eerst de grafieken liet zien: schol helpt scholekster.

tijd om de snavel diep in de grond te prikken, zo ook kost het meer tijd om een prooi te eten die diep zit ingegraven. In een experiment waarin wij een mannetje scholekster lieten voedsel zoeken op een kunstmatige wadbodem, waarin we schelpdieren in verschillende dichtheden en op verschillende dieptes hadden geplaatst, waren we in staat om uit te rekenen welke prooien de scholekster moest kiezen om een zo'n groot mogelijke opname te krijgen. Precies zoals voorspeld pakte de scholekster bij de geringste dichtheden alle prooien die binnen het bereik van de snavel lagen. Bij de grootste prooidichtheid voorspelden we dat de vogel alleen prooien uit de bovenste centimeter zou pakken, maar hij pakte ze uit de bovenste drie cm. Toch bereikte de vogel een grotere opnamesnelheid dan we hadden becijferd op basis van het rekenmodel. De vogel deed het beter dan wij hadden voorspeld, omdat hij behalve diepte nog een tweede selectiecriterium gebruikte waar wij geen metingen aan konden doen: hij pakte alleen nog maar schelpdieren die iets open stonden en waar hij zijn snavel in één keer in kon steken om het vlees te bemachtigen. Dit waren prooien die snel gegeten konden worden en dus zeer lonend waren.

Foerageerbeslissingen Dit experiment liet duidelijk zien dat vogels continu en op allerlei niveau's beslissingen nemen om hun opnamesnelheid te maximaliseren, ook als ze één prooisoort eten en zelfs indien, zoals in dit experiment, prooien even groot zijn. Al enkele tientallen jaren worden in navolging van C. S. Holling veelal eenvoudige modellen gebruikt waarmee het foerageersucces als functie van de prooidichtheid kan worden voorspeld. De modellen blijken in de praktijk niet erg bruikbaar, omdat predatoren niet alle prooien pakken die ze tegenkomen, maar keuzes maken en bij een grotere opnamesnelheid meer prooien zullen weigeren. Het experiment maakte ook duidelijk dat de beslissingen die de predator neemt een niet te onderschatten betekenis hebben voor de individuele overlevingskans van de prooien: diep levende prooien hebben een grotere overlevingskans, vooral bij grotere prooidichtheden.

Consumptie en produktie In hun eerste levensfase zijn de prooien nog te klein om te worden gegeten door een grote steltloper zoals de scholekster. De rol van de scholekster bij het elimineren van de grotere exemplaren is echter zó dominant dat de prooisoorten door te groeien bijna niet kunnen ontsnappen aan de predatie van de scholekster. Om dit verder uit te zoeken werd de maandelijkse groei en sterfte van verschillende schelpensoorten per jaarklasse berekend. In ons onderzoeksgebied langs de Friese waddenkust bedroeg de biomassa van de vijf belangrijkste prooisoorten 80 gram per m^2, dus vier maal zo veel als het gemiddelde voor de Waddenzee. De gemiddelde jaarlijkse produktie was 56 gram per m^2. Daarvan was een deel niet van belang voor de scholekster: 5 gram kwam voor rekening van te kleine prooien, 9 gram voor strandgapers die te diep leefden om gepakt te kunnen worden, en nog eens 9 gram ging voor de scholeksters verloren omdat de prooien massaal dood gingen en al aan het vergaan waren voordat de vogels alles op hadden kunnen eten. Al met al bleef er dus gemiddeld 32 gram per m^2 over voor scholeksters. Hiervan bleken ze 12 gram te consumeren, dus bijna 40%. Wanneer diezelfde berekeningen apart per jaar of per prooisoort werden uitgevoerd, bleek de predatiedruk sterk te variëren. Scholeksters ruimden in een paar maanden tijd 80% van tweedejaars strandgapers op, maar aten jaarlijks slechts een fractie van de slijkschelpen. Ook de verschillen tussen de jaren waren groot. In magere jaren waren er bijna geen scholeksters in het onderzoeksgebied, omdat ze verhuisden naar naburige voedselgebieden die blijkbaar aantrekkelijker waren; predatie door scholeksters stelde dan nauwelijks iets voor. Maar in jaren met een rijk voedselaanbod trok het gebied veel vogels en was de predatiedruk heel groot, zowel absoluut als relatief. De verschillen in predatiedruk tussen de prooisoorten, en tussen de jaren, konden worden verklaard met verschillen in de opnamesnelheid. Hoe groter de opnamesnelheid, hoe meer vogels en hoe groter de gepredeerde fractie van de prooien.

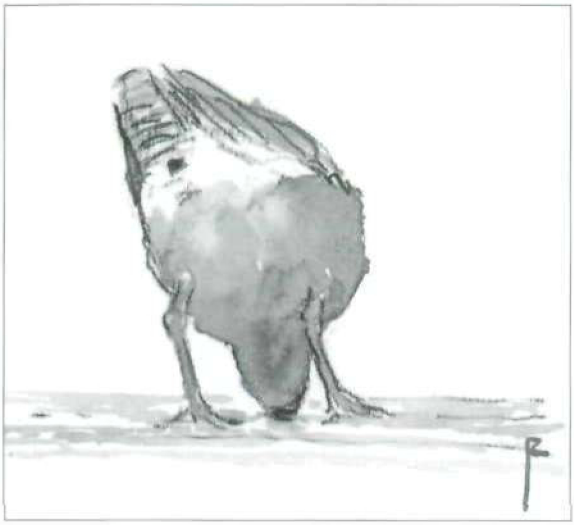
Sterfte van scholeksters bij te weinig voedsel Is er altijd genoeg voedsel voor scholeksters? Niet in ons studiegebied, want in vier van de tien jaar was er, zeker in het winterhalfjaar, nauwelijks iets te halen. De vogels weken uit naar wadplaten die verder uit de kust en lager in de getijzone waren gelegen. We weten niet of de vogels daar genoeg voedsel konden vinden, maar hebben wel een dramatische aanwijzing dat de vogels het toen niet gemakkelijk hebben gehad. Wanneer we de sterfte van de scholeksters vergelijken in vijf milde winters (twee met veel en drie met weinig voedsel) dan was de sterfte in de drie slechte jaren bijna twee maal zo groot als in de twee rijke jaren. De vergelijking is beperkt tot milde winters, omdat de sterfte sterk toeneemt als de wadplaten onder het ijs bedekt raken. Ook als ijswinters onderling worden vergeleken, blijkt het voedselaanbod een groot effect te hebben op de overleving. Gegeven de gestrengheid van de winter van 1986/87 zou een wintersterfte van nog geen 4% onder de adulte vogels kunnen worden verwacht. Dat jaar was het voedselaanbod echter erg klein en de sterfte was er ook naar: 16% van de volwassen vogels overleefde deze extreme winter niet.

Een scholekster heeft 36 g droog vlees per dag nodig. Nu hoeft die limiet niet elke dag te worden gehaald. De vogel heeft namelijk een strategische vetvoorraad. 's Zomers is die voorraad klein, zodat de vogel hoogstens enkele dagen zonder eten kan. Aan het begin van de winter legt een scholekster genoeg vet aan om een of twee weken te kunnen hongeren. Als echter 's winters de dagelijkse voedselopname gedurende langere tijd veel te gering is, kan die vetvoorraad toch te klein blijken te zijn. Terugmeldingen van geringde, dode scholeksters tonen aan dat de belangrijkste doodsoorzaak gebrek aan voedsel is.

Gedwongen verteringspauzes Hoe hard moeten scholeksters werken om een consumptie van 36 g per dag te halen? Als ze alleen op het wad voedsel zoeken, moeten ze al hun voedsel zien te verzamelen in de laagwaterperiode, dat wil zeggen in vijf tot zes uur. Als ze 10 uur per etmaal kunnen voedsel zoeken, moeten ze tijdens het voedsel zoeken een opnamesnelheid zien te halen van 1 mg droog vlees per seconde, maar dan moeten ze zonder enige onderbreking door blijven eten. Pas als ze sneller kunnen eten, blijft er tijd over. Of dat lukt, hangt af van de voedselsituatie. Maar er is nog een andere beperking. Het opgenomen voedsel moet worden verwerkt en, zoals Marcel Kersten heeft laten zien, ligt deze verwerkingssnelheid slechts op 0,66 mg droog vlees per seconde. De scholekster heeft een groot verteringsstelsel en kan 80 g nat vlees, of 12 gram droog vlees, opslaan. Hieruit is precies te berekenen wanneer een scholekster moet stoppen met voedsel zoeken bij een bepaalde opnamesnelheid. Scholeksters hebben meestal een opnamesnelheid van 2 mg per seconde. Bij deze gemiddelde opname zitten de vogels helemaal vol met eten als ze twee uur onafgebroken hebben gefoerageerd. Ze hebben dan de keuze hun opnamesnelheid te verlagen tot het niveau van de verwerkingssnelheid, of te stoppen met foerageren voor een verteringspauze. Scholeksters blijken voor het laatste te opteren.

Hieruit kunnen we concluderen dat de verwerkingssnelheid en de tijd dat ze op het wad terecht kunnen uiteindelijk bepalen hoeveel voedsel maximaal kan worden opgenomen. Een belangrijk gevolg hiervan is dat binnen een laagwaterperiode van zes uur scholeksters nooit meer dan 25 gram kunnen opnemen. Als ze naar de hoogwatervluchtplaats vliegen, hebben ze pas 13 gram verteerd en nemen ze 12 gram mee om tijdens het rusten te verteren. Dit betekent dat ze onmogelijk hun dagelijkse consumptie kunnen halen door slechts tijdens één laagwaterperiode per dag voedsel te zoeken, hoe goed de voedselsituatie ook is.

Is de foerageertijd wel lang genoeg? Op het wad zijn de steltlopers afhankelijk van de getijdebeweging, omdat de waterstand bepaalt of hun voedselgebied wel of niet beschikbaar is. Als een harde noordwestenwind zorgt voor een meter verhoging van de waterstand, blijft er van de normale laagwaterperiode niet veel over. De dagelijkse variatie in de beschikbare foerageertijd hangt in sterke mate af waar de vogels in de getijzone voedsel zoeken. Als ze volledig afhankelijk zijn van mosselbanken die 30 cm beneden NAP liggen, zullen ze vaker te kort komen dan vogels die voedsel zoeken tot bij de kwelderrand, op 30-40 cm boven NAP. De locatie van foerageergebieden verschilt per vogelsoort, maar bij de scholekster ook nog eens van jaar tot jaar. In jaren dat op het hoge wad weinig voedsel is te vinden, leggen scholeksters 's zomers een grotere vetvoorraad aan dan in jaren met genoeg voedsel op het hoge wad. De vogels nemen dus hun voorzorgsmaatregelen als de dagelijks beschikbare foerageertijd regelmatig te kort is. 's Winters zijn scholeksters al zo'n 100 gram zwaarder dan 's zomers maar worden ze niet nog zwaarder als het voedselaanbod kleiner of minder voorspelbaar is. Daardoor zijn de vogels kwetsbaarder, zoals de al genoemde verhoogde wintersterfte bewijst.



Kanoetstrandlopers en hun voedselaanbod

Kanoeten eten geen grote prooien Evenals scholeksters eten kanoetstrandlopers mossels, kokkels, nonnetjes en strandgapers. Er is echter een groot verschil tussen beide soorten. Terwijl scholeksters veel tijd besteden aan het openen van hun prooien en daardoor gebonden zijn aan grote prooien, slikken kanoeten de schelpdieren met schelp en al in. Ze kunnen de schelpen razend snel inslikken, maar de prooien moeten daarna wel in de maag worden gekraakt. Veel schelpdieren zijn voor scholeksters te klein of te diep ingegraven. Voor kanoeten komt er nog een beperking bij: een prooi kan te groot zijn om te worden ingeslikt en is misschien ook nog te sterk om te kunnen worden gekraakt. Als een schelp door het keelgat naar binnen glijdt, bepaalt de maximale omtrek van de schelp of hij nog kan worden ingeslikt. Het grootste nonnetje dat naar binnen kan, is 16 mm lang en heeft een omtrek van 30 mm. Het nonnetje is een vrij bolle schelp. Het is daarom te verwachten dat kanoeten grotere strandgapers kunnen inslikken, omdat deze soort langwerpiger is dan het nonnetje en pas een omtrek van 30 mm bereikt wanneer hij 19 mm lang is. De kokkel is daarentegen ronder dan een nonnetje, met het gevolg dat de omtrek van 30 mm al gehaald wordt door een kokkeltje die 12 mm lang is. Kanoeten aten van diverse schelpsoorten inderdaad alleen de grootteklassen beneden deze limiet.

Oogstbare prooien voor kanoeten De kanoeten werden waargenomen op een plek waar de prooidieren samen een biomassa bereikten van 138 gram per m^2. Daarvan viel 113 gram af omdat deze prooien te groot waren om te worden ingeslikt. Van de resterende 26 gram was 6 gram niet te groot maar zat te diep voor een kanoet, zodat 20 gram per m^2 beschikbaar was. Daarvan was nog eens 4 gram te klein om lonend te zijn, zodat uiteindelijk 16 gram per m^2 oogstbaar bleef voor kanoeten. De kanoeten concentreerden zich geheel op nonnetjes, waarvan slechts 4 gram per m^2 oogstbaar was. Ze negeerden dus 12 gram per m^2, vooral in de vorm van oogstbare kokkeltjes (10 gram per m^2). Toch bereikten de kanoeten een opnamesnelheid die twee maal zo groot was als nodig om hun dagelijkse energiebehoefte te dekken. De metingen werden begin augustus gedaan. De kanoeten waren zich toen aan het voorbereiden om door te vliegen van de Waddenzee naar Afrika. In een paar weken tijd namen ze waarschijnlijk zo'n 40% toe in gewicht. Om dit te bereiken moesten ze inderdaad twee maal zo veel eten als nodig was om in gewicht gelijk te blijven.

Deze waarnemingen roepen een paar vragen op. Waarom concentreerden de kanoeten zich volledig op nonnetjes en negeerden ze de kleine kokkels die ze anders wel eten. Misschien had de voorkeur voor nonnetjes te maken met het feit dat de kokkel een steviger schelp is. Als kanoeten nonnetjes eten krijgen ze vijf maal zoveel kalk als droog vlees binnen, maar als ze kokkels eten is dat tien maal zo veel.

Een andere vraag is of kanoeten in staat zijn om een aanzienlijk deel van de nonnetjes weg te eten. Kanoeten hebben de gewoonte in groepen te foerageren. We vonden dat het aantal kanoeten dat onze proefvakjes bezocht niet afhankelijk was van de dichtheid van de prooien maar dat de vogels op meer dagen in de vakjes werden gezien als de oogstbare biomassa van het nonnetje groter was. Desondanks bleek de predatiedruk op de nonnetjes heel klein te zijn geweest. Dit was voor een groot deel te danken aan het feit dat de kanoeten slechts een paar weken in het gebied aanwezig waren.

De kanoeten arriveerden half juli uit Siberië en waren half augustus al weer vertrokken naar hun Afrikaanse overwinteringsgebieden. Elk jaar is het voor hen weer een verrassing wat voor voedsel ze in de Waddenzee zullen aantreffen. Niet elk jaar zijn er voldoende nonnetjes van 10 tot 15 mm lang. Soms zullen ze genoegen moeten nemen met eerstejaars mossels, kokkels, strandgapers of met wadslakjes. Het is maar goed dat de kanoeten onmiddellijk na de broedtijd naar de Waddenzee vliegen, want als ze een maand later in de Waddenzee zouden aankomen, zouden de foerageeromstandigheden in de meeste jaren nog veel slechter zijn. Nonnetjes verliezen in de nazomer gewicht, maar wat belangrijker is: de fractie die in de bovenste 3-3,5 cm is te vinden neemt vanaf half augustus snel af, en daarmee de oogstbare biomassa. Het zal met vorderende nazomer steeds moeilijker worden om de grote voedselopname te halen die nodig is om de reserves op te bouwen waarmee ze in één ruk 4500 km kunnen vliegen naar hun Afrikaanse overwintersgebieden.

Wulpen en hun voedselaanbod

Prooikeuze Wulpen eten verschillende prooisoorten. In ons gebied waren het vooral strandkrabben, strandgapers, zeeduizendpoten, wadpieren en sifo's van slijkschelpen. Strandkrabben en sifo's werden alleen in de zomermaanden gegeten. Dat is begrijpelijk omdat in het winterhalfjaar strandkrabben ontbreken op de wadplaten, er geen grazende sifo's van slijkschelpen zijn te zien en wadpieren minder vaak aan het oppervlak komen. Strandgapers en zeeduizendpoten blijven dus over als de belangrijkste winterprooien.

De individueel gemerkte wulpen werden enkele jaren intensief gevolgd. Ze waren opvallend plaatstrouw en een deel van de vogels verdedigde zelfs voedselterritoria op het wad. Het was daarom mogelijk om de voedselkeuze van de verschillende individuen gedurende meerdere jaren te volgen. Zo kwamen we te weten dat de meeste wulpen die strandgapers aten nooit zeeduizendpoten aten, en andersom. Op zich is dat vreemd omdat deze prooien in hetzelfde gebied voorkwamen en er regelmatig wulpen op de zelfde plaats door elkaar liepen die één van beide prooien aten. We weten nog niet goed waarom de individuele wulpen zo zijn gespecialiseerd. Misschien is het niet eenvoudig voor een wulp om te leren hoe een prooi moet worden gezocht en beperken veel vogels zich daarom tot het leren vinden van een beperkt aantal prooisoorten. In ieder geval waren jonge wulpen die voor het eerst op het wad verschenen gemakkelijk te herkennen aan de klungelige manier waarop ze prooien aanpakten en naar binnen probeerden te werken. Het is dus goed denkbaar dat er een behoorlijke tijd nodig is om specifieke prooien te leren vangen.

Prooikeuze en snavellengte De keuze of een wulp zich de rest van zijn leven zal richten op de ene of de andere prooi, hangt voor een groot deel af van de snavellengte. De snavellengte van volwassen wulpen varieert tussen 10 en 17 cm. Strandgapers werden vooral gegeten door vogels met lange snavels. Daarentegen aten de kortsnavelige vogels nooit strandgapers. Hoe is dit te verklaren? Het bleek dat de gemiddelde opnamesnelheid toenam met de snavellengte. Dat is logisch omdat snavellengte en gewicht met elkaar zijn gecorreleerd en langsnavelige en dus zware vogels meer voedsel nodig hebben. De langsnavelige vogels die strandgapers aten, haalden gemiddeld een iets grotere opnamesnelheid dan vogels met een even lange snavel die zeeduizendpoten aten. Dit verklaart waarom we zagen dat de langsnavels veel vaker strandgapers aten. De vraag is dan: waarom eten kortsnavels dan geen strandgapers? Dat heeft te maken met het feit dat alleen grote strandgapers lonend zijn om te eten; deze zijn buiten bereik van kortsnavelige wulpen. Wulpen maken deze schelp namelijk niet open maar selecteren schelpdieren die enigszins openstaan. Ze scheuren de sifo los en eten de rest van het vlees uit de schelp. Dit is een tijdrovende klus, en de reden waarom strandgapers onder de 25 mm werden genegeerd en exemplaren van 25-30 mm zelden werden gegeten. De leefdiepte van de strandgaper neemt toe met schelplengte (zie blz. 362). Een wulp met een snavel van 14 cm kan geen prooien eten die groter zijn dan 60 mm. Dat betekent dat een wulp met een korte snavel van 11 cm al geen strandgapers groter dan 50 mm meer kan pakken vanwege de diepte waarop die zitten. De oogstbare biomassa van strandgapers voor een kortsnavelige wulp is zo klein, dat deze vogel zich nooit op strandgapers kan specialiseren. Volledigheidshalve moet daaraan worden toegevoegd dat sommige wulpen wel kleine strandgapers eten door ze -net als kanoeten dat doen- met schelp en al in te slikken. Dat hebben we echter weinig gezien.

Hoe wulpen zeeduizendpoten eten Zeeduizendpoten kunnen op verschillende manieren aan voedsel komen. Ze kunnen boven in hun hol een filterzakje maken, daarna een waterstroom op gang brengen in hun U-vormige hol, net zo lang tot het filterzakje vol met voedsel zit, dat opeten, weer een filterzakje maken, enzovoorts. Deze foerageermethode lijkt veilig omdat de worm in zijn hol blijft, maar wulpen zien aan het oppervlak dat de worm actief is en prikken op goed geluk in een van twee openingen van het hol. Als het mis is, proberen ze vaak de andere holopening. Wanneer wulpen zoeken naar deze foeragerende zeeduizendpoten, moeten ze langzaam lopen, omdat de wormen niet te zien zijn maar slechts subtiele spoortjes. Als wulpen deze techniek gebruiken hebben vogels met lange snavels meer succes dan soortgenoten met een kortere snavel. Ook hier is het weer de toename van de bereikbare fractie die het verschil verklaart.

Wulpen volgen een totaal andere strategie, als ze zoeken naar zeeduizendpoten die buiten het hol, op het wadoppervlak, foerageren. In dat geval gaat het om goed zichtbare prooien, en kunnen de wulpen door snel te lopen meer wormen tegenkomen.

Wanneer zeeduizendpoten beschikbaar zijn als prooi Zeeduizendpoten die in zandig wad leven, komen minder vaak aan het oppervlak dan zeeduizendpoten die in slik leven. Er is ook een seizoensverschil: op de eerste warme voorjaarsdagen verschijnen veel zeeduizendpoten aan het oppervlak, maar 's zomers gebeurt dat veel minder vaak. Ook de tijd ten opzichte van laagwater speelt een rol: zeeduizendpoten komen aan het begin van de laagwaterperiode niet aan het oppervlak, maar in de loop van de laagwaterperiode neemt de graasactiviteit toe.

Het heeft voor een zeeduizendpoot alleen zin te filteren als er water is en er in dat water voedsel zit. Als het wad droog ligt, kan de worm niet filteren, en moet hij wel op het oppervlak grazen als hij door wil gaan met eten. Filteren heeft evenmin zin als het water voedselarm is, zoals aan het eind van de winter. Grazen op het wadoppervlak is dan wèl lonend, omdat op het wad wèl voedsel is te vinden. Dit verklaart de getij- en seizoensvariatie in grazen en filteren. Dat zeeduizendpoten in slik meer grazen dan zeeduizendpoten in zand heeft waarschijnlijk ook te maken met wat grazen en filteren opleveren. In modder heeft filteren meestal weinig zin omdat het water vol zit met slib en in zand heeft grazen minder zin wanneer er op de schone zandkorrels geen voedsel is te vinden.

Hoe wulpen zich aanpassen Wulpen die zeeduizendpoten eten, stemmen hun manier van foerageren af op de frequentie waarmee ze grazende of filterende wormen aantreffen. Aan het begin van de laagwater periode lopen ze langzamer, boren ze vaker, halen ze meer wormen diep uit hun hol, doen ze langer over het eten van een worm en eten ze meer gebroken wormen dan enkele uren later. Dit is allemaal te verklaren met de afname van het aantal filterende wormen (die de vogels uit hun hol moeten halen) en de toename van het aantal grazende wormen (die de vogels van het oppervlak kunnen plukken). We konden dit simpel aantonen. Uit experimenten die we in aquaria hadden gedaan, wisten we dat een beetje vleesbouillon op het wad wormen vaker en langduriger aan de oppervlakte bracht. We kookten daarom 30 liter bouillon en lieten dat vanuit de waarnemingstoren via een 50 m lange tuinslang in het territorium lopen van een wulp die we al dagenlang zeeduizendpoten hadden zien eten. De wulp haalde, in vergelijking met voorafgaande dagen, meer wormen van het oppervlak en minder wormen uit hun hol. De wormen reageerden meteen op het aangevoerde voedsel en de wulp paste zich onmiddellijk aan.

Het foerageergedrag van wulpen die zeeduizendpoten eten, verandert niet alleen binnen een laagwaterperiode maar ook in de loop van het seizoen. Dit is voor een groot deel te verklaren met de boven genoemde verschuiving in het gedrag van de wormen: van filteren in de zomer naar grazen in het vroege voorjaar. Daarnaast speelt de seizoensvariatie in de diepte van het hol een rol. Wulpen eten alleen wormen die groter zijn dan 9 cm, omdat de kleinere niet lonend zijn. Van deze grote wormen leeft 's zomers 60% in de bovenste 12,5 cm van de bodem. Dit daalt tot 10% in december, om pas in maart weer toe te nemen. De wormen hebben dus in de loop van de herfst meer kans om te ontsnappen aan wulpen en dat maakt het voor wulpen minder aantrekkelijk om te proberen wormen uit hun hol te halen. Het gevolg hiervan is dat de opnamesnelheid van wulpen vanaf juli tot diep in de winter geleidelijk afneemt, want hoewel iets meer wormen vanaf het wadoppervlak worden geplukt, worden er veel minder diep uit hun hol gehaald. De grootste opname werd gemeten op een aantal zonnige dagen in maart, toen veel zeeduizendpoten aan het oppervlak waren verschenen.

Het verdelen van het voedselaanbod door de verschillende steltlopersoorten

Er is opvallend weinig overlap in de voedselkeuze van de diverse steltlopersoorten. Ze eten verschillende prooisoorten en als ze dezelfde prooien eten, doen ze dat op verschillende plaatsen of selecteren ze verschillende grootteklassen. In het laatste geval kan de ene soort het voedselaanbod van de andere soort aanzienlijk beïnvloeden. Zilvermeeuwen zijn in staat alle mossels op te ruimen voordat ze de kans hebben gekregen om 25 mm lang te worden, en dus voordat ze groot genoeg zijn om te worden gegeten door scholeksters. Kanoeten eten hoofdzakelijk nonnetjes van 10-15 mm. Scholeksters eten daarentegen de exemplaren die groter zijn. Op dezelfde manier is er weinig overlap in de strandgapers die kanoeten, scholeksters en wulpen eten (zie blz. 362). Die overlap is klein om drie redenen. Ten eerste is de snavel van een wulp twee maal zo lang is als die van een scholekster, en is die op zijn beurt twee maal zo lang als de snavel van een kanoet. De diepteselectie van prooien verschilt dus navenant. Ten tweede hebben alle drie de vogelsoorten te maken kleine prooien die niet lonend zijn. Ten derde kan de kanoet geen grote strandgapers inslikken.

De kleinere predatorsoort beïnvloedt op twee manieren het voedselaanbod van de soort die later aan bod komt: door prooien weg te eten neemt de prooidichtheid af, terwijl tevens de ondiepste exemplaren selectief worden weggegeten; hierdoor verdwijnen de ondiepe, meest lonende prooien.

Het schatten van de draagkracht: wat weten we nu?

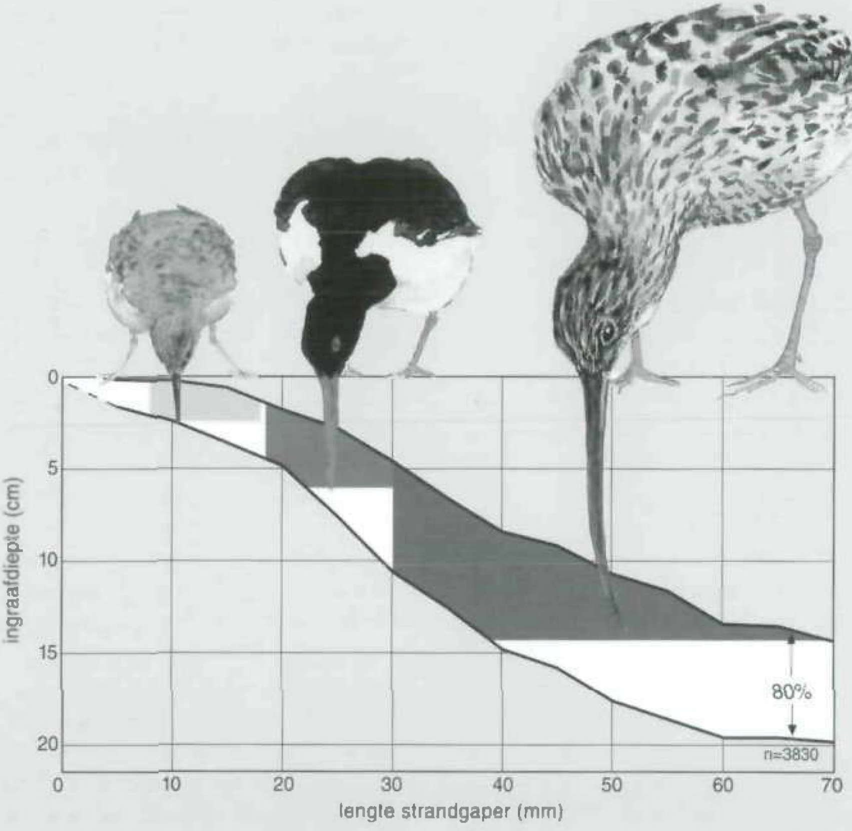
De Deltawerken zijn, als het gaat om het schatten van de draagkracht van een waddengebied voor wadvogels, te beschouwen als een enorm experiment. In de Oosterschelde verdween als gevolg van de aanleg van dammen en de demping van het getijdeverschil eenderde van het getijdegebied. Als die vogels op het resterende wad waren blijven foerageren, zou de dichtheid van de vogels anderhalf keer zo groot zijn geworden. De tellingen wezen echter uit dat er helemaal geen toename was.

De Dollard is het tweede voorbeeld. Tot de jaren zeventig werd hier veenkoloniaal afvalwater geloosd, wat in de afgelopen twintig langzamerhand tot nul is gereduceerd. Dankzij het bemonsteringsprogramma van Karel Essink weten we dat dit gepaard ging met een afname van de zeeduizendpoot in de Dollard. De Vogeltelgroep Dollard heeft gelukkig al die jaren vogeltellingen uitgevoerd en Jouke Prop kon zodoende laten zien dat de vogelsoorten die van deze voedselbron afhankelijk waren, sterk waren afgenomen.

Beide voorbeelden zijn belangrijk omdat ze laten zien dat de vogelaantallen nauw zijn gerelateerd aan wat het wad heeft te bieden. De vraag blijft waaròm de vogels afnamen.

Onderzoek naar de produktie van bodemdieren en de predatiedruk hierop heeft veel opgeleverd, maar blijkt ons nauwelijks te kunnen helpen bij het beantwoorden van de gestelde vraag. Immers, er kan geen conclusie worden verbonden aan de constatering dat de vogels 30 of 80% van de vleesproduktie hebben weggegeten.

WAAROM KANOETSTRANDLOPERS, SCHOLEKSTERS EN WULPEN STRANDGAPERS VAN VERSCHILLEND FORMAAT ETEN



Het levensverhaal van de strandgaper ziet er vrij simpel uit. Ze komen aanvankelijk in zeer grote dichtheid voor, waarna er geen geleidelijke, maar een stapsgewijze afname plaatsvindt. Deze abrupte afnames worden veroorzaakt door bepaalde predatoren die gedurende een korte tijd een zware predatiedruk uitoefenen. Broedjes van een paar maanden oud zijn zo'n 5 mm lang en een gemakkelijke prooi voor strandkrabben en garnalen. Ook kanoetstrandlopers kunnen er op foerageren en daar de hele winter mee doorgaan. Na het volgende groeiseizoen worden de meeste exemplaren in het winterhalfjaar weggegeten door scholeksters en in de twee winters daarna eten wulpen er veel.

Strandkrabben, garnalen en kanoeten pakken alleen eerstejaars strandgapers, omdat ze het daaropvolgende jaar te groot zijn om te worden ingeslikt en te diep ingegraven zitten om bereikbaar te zijn. Als gevolg van een verdere toename in de ingraafdiepte kunnen scholeksters geen strandgapers eten die ouder

zijn dan twee jaar en wulpen geen strandgapers die ouder zijn dan vier jaar. De toename van de ingraafdiepte verklaart waarom de drie vogelsoorten geen grotere strandgapers pakken dan waargenomen.

Waarom negeren scholeksters en wulpen de kleine exemplaren? Theoretisch modellen die er vanuit gaan dat vogels streven naar maximalisering van de opnamesnelheid tijdens het voedsel zoeken, geven de verklaring. Als scholeksters hun foerageeersnelheid maximaliseren, moeten ze de weinig lonende strandgapers van 17 mm en kleiner negeren. Om dezelfde reden zouden wulpen exemplaren onder de 25-30 mm niet mogen pakken. De vogels blijken zich keurig aan deze regel te houden, hoewel ze de prooien net boven deze ondergrens minder pakken dan theoretisch verwacht.

Voor elke predator kan worden gedefinieerd welke fractie van de prooien de moeite waard is om te pakken, niet te groot is om te worden ingeslikt en niet te diep is ingegraven om bereikbaar te zijn. De prooifracties die aan deze drie eisen voldoen, en oogstbaar worden genoemd, verschillen voor de drie vogelsoorten. Hiermee is verklaard waarom de drie soorten op verschillende momenten strandgapers eten en waarom er nauwelijks overlap is in de grootteklassen die ze eten. Voor strandgapers is het zaak om in de eerste vier levensjaren, wanneer ze successievelijk de predatiedruk van kanoet, scholekster en wulp moeten zien te overleven, zich altijd zo diep mogelijk in te graven. Dat kunnen ze echter alleen als ze veel weefsel in hun sifo stoppen. En dat is precies wat ze doen tot wel 45% van hun hele lichaamsgewicht.

De richting waarin de oplossing moet worden gezocht, is hierboven al aangeduid. We moeten proberen om de voedselvoorraad te splitsen in bereikbare, inslikbare, lonende en (voor visueel jagende vogels) zichtbare delen. Door de predatiedruk te relateren aan de oogstbare fractie kan worden aangegeven hoe smal de marges zijn. Een belangrijke stap daarna is de opnamesnelheid in verband te brengen met de dichtheid van de oogstbare prooien, zodat kan worden afgeleid wanneer de voor de vogels relevante prooivoorraad te klein is geworden gegeven de hoeveelheid voedsel die ze dagelijks moeten consumeren binnen de beschikbare foerageertijd. Als de voedselopname van bijvoorbeeld scholeksters afneemt tot 1 mg per seconde, wordt het kritiek voor de vogels en kan een verhoogde mortaliteit worden verwacht.

Om de mortaliteit beter te kunnen voorspellen, is het nodig te analyseren in hoeverre de opnamesnelheid voor individuen verschilt. Dat heeft gedeeltelijk te maken met de morfologie, met name de snavellengte, maar ook met de ervaring van het individu. Bovendien speelt dominantie over soortgenoten in een aantal gevallen een belangrijke rol, zoals is aangetoond voor scholeksters die op mosselbanken foerageren. Scholeksters bereiken daar grote dichtheden, beroven elkaar vaak van zojuist gevonden mossels of maken elkaar het leven anderszins zuur. Sommige vogels zijn de baas over andere vogels. Dankzij die pikorde wordt het voedselaanbod tussen de vogels niet eerlijk verdeeld. Dominante vogels hebben geen last van veel soortgenoten om hen heen, maar bij subdominante vogels gaat de voedselopname sterk naar beneden. Eenzelfde situatie komt waarschijnlijk in extreme mate voor als 's winters de wadplaten bedekt zijn met ijs en de vogels gedwongen zijn op de weinige plekken die nog niet bevroren zijn iets van hun gading te vinden. Vogels foerageren dan heel dicht op elkaar. Het is nog niet gemeten, maar we mogen aannemen dat juist in deze situatie subdominante vogels zwaar hebben te lijden van de beperkte foerageermogelijkheden. Bij scholeksters zijn oude vogels dominant over jonge vogels en mannetjes over vrouwtjes. Het is dan ook geen toeval dat in strenge winters relatief weinig adulte mannetjes de hongerdood sterven.

Wanneer we de variatie in de oogstbare voedselvoorraad vergelijken met de sterfte van de wadvogels blijkt dat in jaren met een geringe oogstbare voedselvoorraad meer vogels doodgaan dan in voedselrijkere jaren. Bovendien blijkt dat de kans om dood te gaan niet gelijk verdeeld is over de leeftijdsklassen en de seksen van de vogels. Zo weten we van scholeksters dat jonge dieren en vrouwtjes een grotere kans hebben om een moeilijk jaar niet te overleven dan mannetjes.

De toename in de sterftekans bij afnemend voedselaanbod in het winter is een duidelijk bewijs dat de draagkracht van het wad voor de vogels, althans in magere jaren, wordt bereikt. Op basis van de gegevens kunnen we maar één conclusie trekken: het wad is weliswaar voor wadvogels een meestal rijk gedekte tafel, maar het aanbod is periodiek zo klein dat het de vogelaantallen beperkt. In ons gelukkig alleen maar denkbeeldige voorbeeld van een halvering van de Waddenzee zullen de aantallen overwinterende wadvogels navenant verminderen.

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Het veldonderzoek heeft tien jaar geduurd en was zeer breed opgezet. Zoiets lukt alleen maar als veel mensen kunnen samenwerken in teamverband.

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was dan ook dankzij de inzet van alle monsternemers dat deze gegevens konden worden verzameld met slechts weinig gaten in de jarenlange meetserie. De meeste bodemfaunamonsters werden gestoken en uitgezeefd door Jan Bronkema, Justinus van Dijk, Sytse van de Meer en de helaas te vroeg overleden Lou Terpstra. Dezelfde mensen, samen met Harm Hoekstra, bouwden de observatietorens, zetten de honderden proefvakjes uit en bepaalden de hoogteligging en de bodemgesteldheid van deze vakjes. De leefdieptes van vele tienduizenden schelpdieren en wormen werden gemeten door Tonny van Dellen en Bert Toxopeus, later ook door Justinus van Dijk en Lou Terpstra. De bodemfaunamonsters werden in het laboratorium uitgezocht door Tonny van Dellen en Bert Toxopeus. In totaal moeten ze de lengtes en de gewichten van honderdduizenden prooien hebben bepaald, en eenzelfde aantal prooifragmenten uit braakballen, faeces en maaginhouden met een binoculair hebben uitgezocht en gemeten. Het asvrij drooggewicht en de energiedichtheid werden bepaald door J. L. Straat. Willem Huizingh hield de administratie van al deze gegevens bij.

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