

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

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## ABSTRACT

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<sup>-1</sup> AFDW. In *Scrobicularia plana* and *Mya arenaria*, but not in *Macoma balthica*, the energy density is 10% lower in winter than in summer.
- (2) Depending on the species, 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 *M. balthica*, *S. plana*, *M. arenaria*, *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 *C. edule* and *M. arenaria*, but the four other species live at most shallow depth in early summer and most deeply in midwinter. 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 *M. balthica*, 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 3-6°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.

## 1. 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 descrip-

tion 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

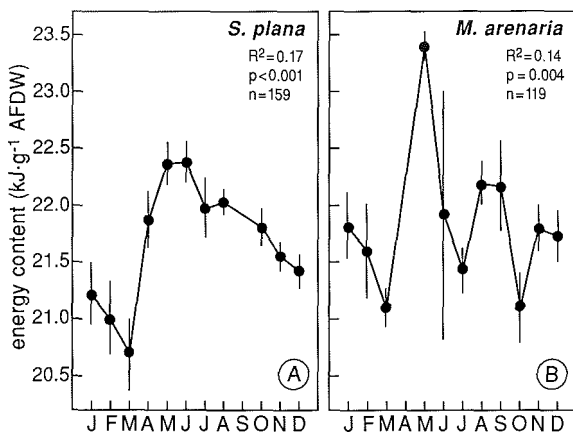


Fig. 1. Seasonal variation in the energy density ( $\text{kJ}\cdot\text{g}^{-1}\text{AFDW} \pm \text{SE}$ ) of *Scrobicularia plana* and *Mya arenaria*. Results of one-way analyses of variance are given.

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, 1979; 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, 1979; CHAMBERS & MILNE, 1979; ZWARTS, 1991). Seasonal variation in the burying depth of benthic animals has been studied by READING & MCGRORTY (1978) and ESSELINK & ZWARTS

(1989).

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 shorebird 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.

## 2. 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 of Friesland ( $53^{\circ}25' \text{N}$ ,  $6^{\circ}04' \text{E}$ ), 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 5-6% clay (fraction  $<2 \mu\text{m}$ ).

Seventy-three or 292 sediment cores (15 cm  $\varnothing$ , 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 1980-1986. We used a corer ( $\varnothing$  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 *N. diversicolor* and *A. marina* 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  $\text{CaCO}_3$ .

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

### 3. RESULTS

#### 3.1. 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 *S. plana* also varied between the years (ZWARTS & WANINK, 1991). These seasonal differences were significant (see Fig. 1), but they amounted to no more than 2 kJ, or 10%.

Although previous studies had found no seasonal variation in the energy density of all three species (*M. balthica*: GILBERT, 1973; BEUKEMA & DE BRUIN, 1979; CHAMBERS & MILNE, 1979; *S. plana*: HUGHES, 1970b; and *M. arenaria*: 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, 1979; PIETERS *et al.*, 1980; PEKKARINEN, 1983; DARE & EDWARDS, 1975; DE VOOYS, 1975; MAYES & HOWIE, 1985). Gametes alone may add at least 20% to the body weight (e.g. DE WILDE & BERGHUIS,

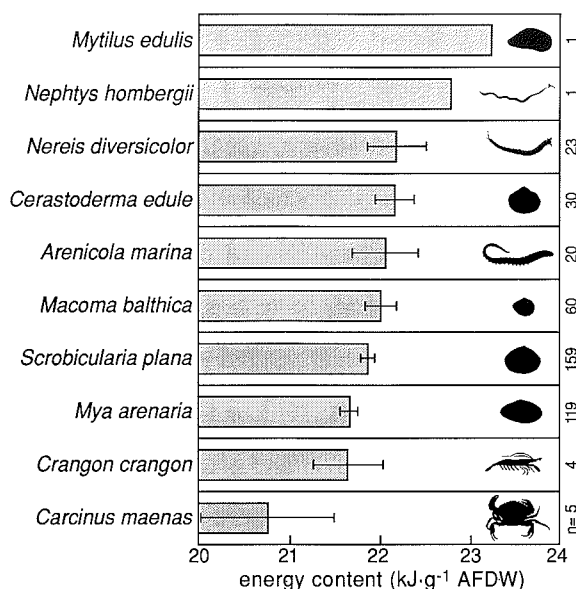


Fig. 2. Average energy density ( $\text{kJ}\cdot\text{g}^{-1}$  AFDW  $\pm$  SE) of ten invertebrates; number of measurements are indicated. According to a one-way analysis of variance, the species differ significantly:  $R^2 = 0.05$ ;  $p = 0.027$ ;  $n = 423$ ).

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 *M. balthica* would raise the energy density of females and lower it for males, since the energy density of eggs was  $24.7 \text{ kJ}\cdot\text{g}^{-1}$  and of sperm  $18.9 \text{ kJ}\cdot\text{g}^{-1}$ , 3 kJ above and below the average energy value of *M. balthica* flesh, respectively. At the population level, it is thus unlikely that gametogenesis would cause the energy value of an average *M. balthica* to vary seasonally as long as the sex ratio approximates 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 *M. edulis* ( $22.2 \text{ kJ}\cdot\text{g}^{-1}$  AFDW), *N. diversicolor* ( $21.8 \text{ kJ}\cdot\text{g}^{-1}$ ), the edible cockle *Cerastoderma edule* ( $20.6 \text{ kJ}\cdot\text{g}^{-1}$ ) and *M. balthica* ( $20.0 \text{ kJ}\cdot\text{g}^{-1}$ ). 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 *M. edulis* of  $23.3 \text{ kJ}\cdot\text{g}^{-1}$ , very close to the value given in Fig. 2. The energy density measured by BAYNE & WORRALL (1980) was slightly higher ( $24 \text{ kJ}\cdot\text{g}^{-1}$ , assuming that ash-content was 10%), but HEPPLESTON (1971) found a slightly lower value:  $22.6 \text{ kJ}\cdot\text{g}^{-1}$ . The average value we found for *M. balthica* is halfway between those given by CHAMBERS & MILNE (1979) ( $20.0 \text{ kJ}\cdot\text{g}^{-1}$ ) and BEUKEMA & DE BRUIN (1979) ( $22.9 \text{ kJ}\cdot\text{g}^{-1}$ ). The published values for other bivalves are also similar to ours. Thus, SWENNEN (1976) found  $21.7 \text{ kJ}\cdot\text{g}^{-1}$  for *C. edule*, HUGHES (1970b)  $21.4 \text{ kJ}\cdot\text{g}^{-1}$  for *S. plana*, and EDWARDS & HUEBNER (1977) and WINTHER & GRAY (1985) found 20.8 and  $21.7 \text{ kJ}\cdot\text{g}^{-1}$ , respectively, for *M. arenaria*.

Although a correction of  $0.3 \text{ kJ}\cdot\text{g}^{-1}$  was made for the endothermic reaction of  $\text{CaCO}_3$  (see Methods), the energy density of *C. maenas* 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  $23 \text{ kJ}\cdot\text{g}^{-1}$  in moulting *C. maenas* 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  $20.2 \text{ kJ}\cdot\text{g}^{-1}$ .

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 *C. volutator* is less than that of bivalves, partly because its fat content is only 1.7% (NAPOLITANO & ACKMAN, 1989) compared with around 10% in the bivalves *Tellina tenuis* (ANSELL & TREVALLION, 1967), *M. edulis* (DARE & EDWARDS, 1975) and *M. balthica* (BEUKEMA & DE BRUIN, 1979). Fat content also varies regionally within a species; for example, the fat content of *M. balthica* 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  $22.7 \text{ kJ}\cdot\text{g}^{-1}$  for many invertebrate species from the Canadian Arctic. BREY *et al.* (1988) arrived at a mean of  $23 \text{ kJ}\cdot\text{g}^{-1}$  for invertebrates from the Baltic Sea. In contrast, this study found a mean of  $21.8 \text{ kJ}\cdot\text{g}^{-1}$  for the Wadden Sea, while DAUVIN & JONCOURT (1989) found a value of only  $20.5 \text{ kJ}\cdot\text{g}^{-1}$  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.

### 3.2. 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): *M. balthica*, *S. plana*, *M. arenaria* and *C. edule* of similar size contained, in May and June, 1.7 to 2.1 times as much flesh as in February-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 *M. edulis* as also found by BAYNE & WORRALL (1980), CRAEYMEERSCH *et al.* (1986) and CAYFORD & GOSS-CUSTARD (1990). The regression equation for *C. maenas* closely resembled that already published by KLEIN BRETELER (1975). The equation for *C. volutator* was

TABLE 1

Exponential relationships 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:  $\ln(\text{mg AFDW})$  against  $\ln(\text{mm})$ , 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.

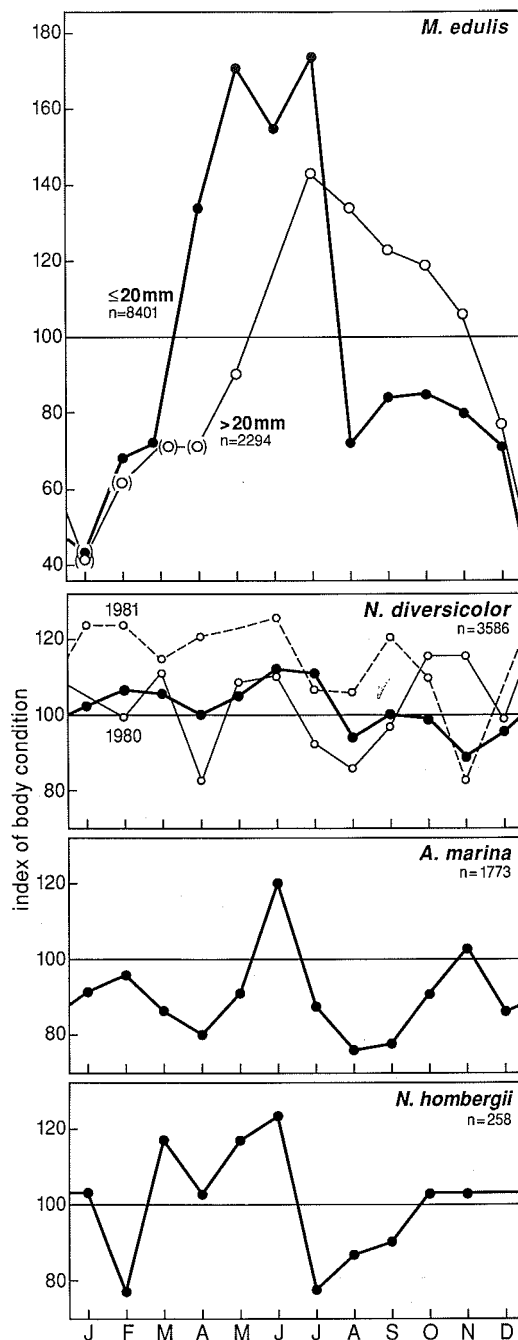
species	a	b	r	n	k	range
<i>Mytilus edulis</i>	-4.596	2.840	0.995	10756	67	2-75 mm
<i>Nephtys hombergii</i>	-0.183	2.017	0.962	263	14	2-12 cm
<i>Nereis diversicolor</i>	-0.898	2.208	0.996	3586	22	1-13 cm
<i>Arenicola marina</i>	+1.198	2.334	0.992	1831	13	1-13 cm
<i>Carcinus maenas</i>	-2.925	2.871	0.998	772	49	2-60 mm
<i>Corophium volutator</i>	-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 are also shown for two separate years in *Nereis diversicolor* to show the year-to-year variation in body condition.

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 standardization 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 *M. edulis* 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 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 *N. diversicolor* (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–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–April (DALES, 1951; OLIVE & GARWOOD, 1981),



compared with April–May in the Wadden Sea (ESSINK *et al.*, 1985) and May in southern Sweden (MÖLLER, 1985).

In accordance with DE WILDE & BERGHUIS (1979), *A. marina* 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-November (FARKE & BERGHUIS, 1979; DE WILDE & BERGHUIS, 1979), which probably explains the low body weight in autumn.

As in *N. diversicolor* and *A. marina*, 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; OYENKAN, 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 *C. maenas*. Possible seasonal changes in the condition of *C. volutator* could not be explored since this species was only collected in summer. However, BOATES & SMITH (1979) report a decrease in body condition of *C. volutator* after spring.

To conclude, the seasonal changes in body condition are caused by weight changes in reproductive and in other body tissues. In *M. balthica*, *M. arenaria* and *C. edule*, 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 *S. plana*, *M. edulis* 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.

### 3.3. 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 *M. balthica* (shell length 1-25 mm) varied between 7 and 66 g·m<sup>-2</sup> (Fig. 4a). This species occurred at a density of 200-300·m<sup>-2</sup> in 1977-1979, but density increased to nearly 2000·m<sup>-2</sup> 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<sup>-2</sup>, the lowest level ever observed in the area. But subsequently, as the animals grew, biomass increased and the year class 1979 dominated total *M. balthica* biomass for several years, because the meagre spatfalls in 1981, 1983, 1984 amounted to less than 100·m<sup>-2</sup>. The 1985 spatfall (500 spat·m<sup>-2</sup>) was the first large one in six years.

The biomass of *S. plana* (shell length 4-50 mm) was high (40-70 g·m<sup>-2</sup>) in 1979-1982 (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 *M. arenaria* (shell length 1-103 mm) (Fig. 4c) was dominated by two year classes: 1976 (from which 250 animals·m<sup>-2</sup> were still present in autumn 1977) and 1979 (800 spat·m<sup>-2</sup> in August). There were only 30 spat·m<sup>-2</sup> 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 5-6 years old.

The biomass of *C. edule* (shell length 1-41 mm) varied between 0 and 73 g·m<sup>-2</sup> (Fig. 4d) while its numerical density varied between 0 and 1550 m<sup>-2</sup>. Spatfall occurred in 1976, 1979 and in five successive years: 1982-1986. However, spat density in August was only about 100·m<sup>-2</sup> in three of these years (1979, 1985 and 1986) and about 500·m<sup>-2</sup> in 1982 and 1983. We found 1400 spat·m<sup>-2</sup> 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<sup>-2</sup>. *C. edule* 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 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).

*M. edulis* (shell length 1-54 mm) was rarely found before 1983. Subsequently, there were three spatfalls with 45, 400 and 2000 spat·m<sup>-2</sup> 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 *N. diversicolor* (1-22 cm) varied between 1 and 14 g·m<sup>-2</sup> (Fig. 4f). The biomass was high in the autumn following a successful settlement of juveniles, as occurred in the summers of 1979,



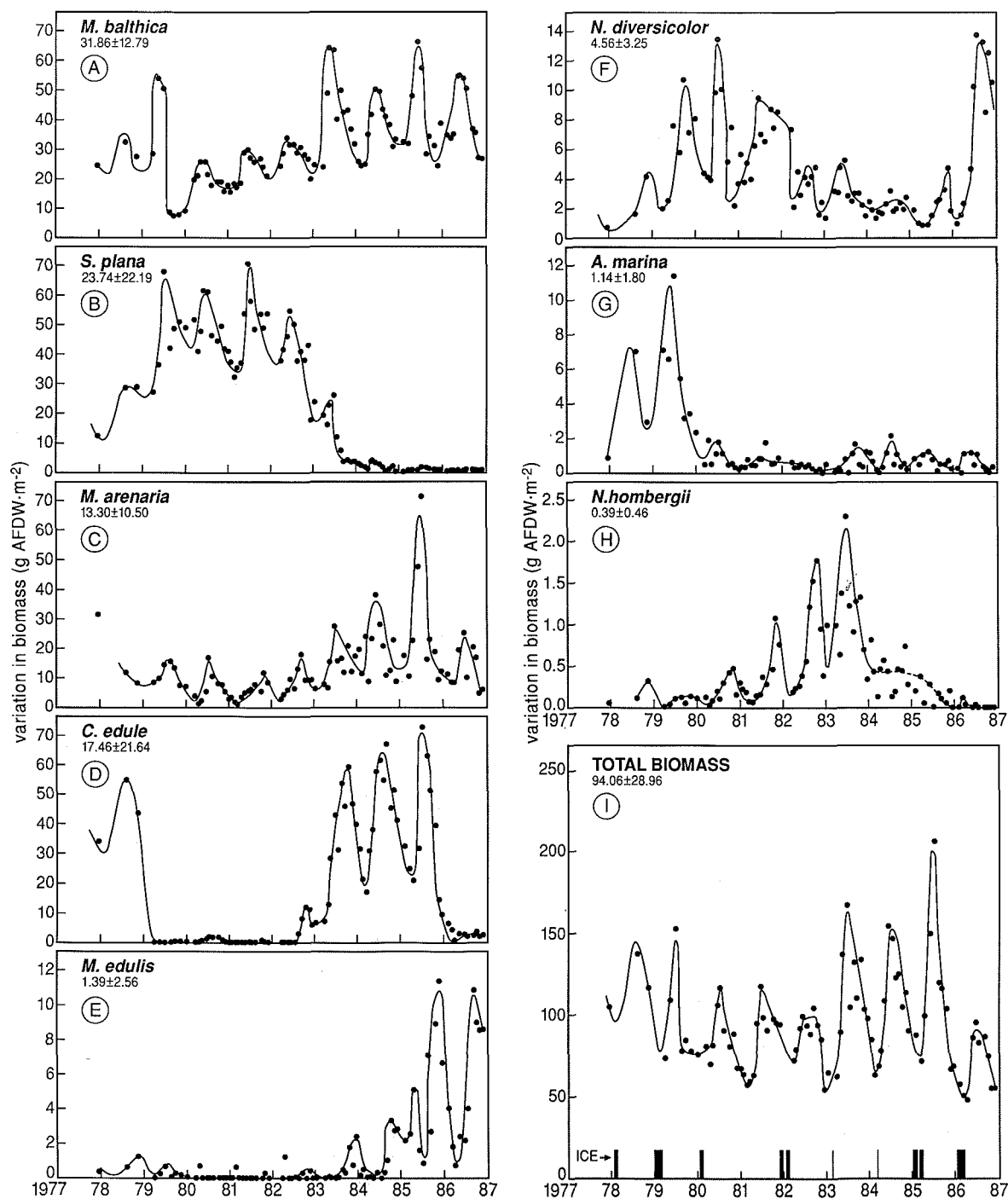


Fig. 4. Variation in the biomass (g AFDW·m<sup>-2</sup>) of five bivalve and three worm species, and in the total biomass of all species during nine years; mean ± SD, calculated over 84 sampling periods, is given; ice periods are indicated in the panel i.

1980, 1981 and 1986 when still 300-350 worms·m<sup>-2</sup> were found to be present in August.

There was recruitment of *A. marina* only in 1978 when 30 juveniles·m<sup>-2</sup> were found. The biomass curve (Fig. 4g) refers to members of this cohort being 2-7 cm long in 1978 and 5-10 cm in 1979. The species was found only incidentally in later years.

*N. hombergii* (1-12 cm) occurred at densities of 0-40 worms·m<sup>-2</sup>, equivalent to 0-2 g·m<sup>-2</sup> in biomass terms (Fig. 4h). The biomass reached, as in *N. diversicolor*, 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, *M. balthica*, *S. plana*, *M. arenaria* and *C. edule* contributed the lion's share to the total biomass of the macrozoobenthos (Fig. 4i). The highest biomass was about 70 g AFDW·m<sup>-2</sup> for each of these species, which is several times as much as the average biomass per species calculated over all sampling dates. *C. edule* and *S. plana* were absent in several years, and *M. arenaria* also occurred at only very low densities in some years. The variability in biomass of *M. balthica* was less extreme, as was also the case for *N. diversicolor*.

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<sup>-2</sup>, averaged over all sampling dates) was rare, except in 1980 when its biomass was over 1 g·m<sup>-2</sup>. *C. maenas* (0.12 g·m<sup>-2</sup>) occurred in late summer at a density of 5-15 specimens·m<sup>-2</sup>. *C. volutator* was only found in 1977, with 270 individuals·m<sup>-2</sup> and a biomass of 0.2 g·m<sup>-2</sup>. *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, *H. ulvae* occurred at high densities of 10 to 20 thousand snails·m<sup>-2</sup>. But as most of the snails were juveniles, the total biomass was not high, varying between 2 and 5 g·m<sup>-2</sup>. Together with *H. filiformis* and *S. armiger* the values for *H. ulvae* have not been included in Fig. 4i. On average, the resulting underestimation must have been about 5-10 g·m<sup>-2</sup>.

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 *N. diversicolor* 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

*C. volutator* 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 *C. volutator* 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. *S. plana* is rare in the Dutch Wadden Sea, but common along the Frisian mainland coast, while the reverse is the case in *A. marina*. The intertidal substrate along the Frisian coast consists of mud and muddy sand, whereas 85% of tidal flats of the Wadden Sea is 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, 1983; ZWARTS, 1988b). Nevertheless, it is remarkable that *C. volutator*, 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 *C. edule* and *A. marina* prevented settlement of *C. volutator* (JENSEN, 1985; FLACH, 1992), and probably the high densities of *C. edule* and *S. plana* 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. *C. edule*, but rather small in *M. balthica* (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, *C. edule* and *M. edulis* 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, *M. arenaria* 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). *M. balthica* 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 *M. balthica*. 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 *C. edule*, *N. hombergii* and *L. conchilega*, 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).

### 3.4. SEASONAL VARIATION IN TOTAL BIOMASS PER SPECIES

Fig. 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 on the basis of the preceding and the following month. *M. balthica* (Fig. 5a) reached their maximum biomass in May-June, *S. plana*, *M. arenaria* and *A. marina* (Fig. 5b, c and h) in June, *C. edule* and *N. diversicolor* (Fig. 5d and f) in June-October, and *M. edulis* and *N. hombergii* (Fig. 5e and g) even later. The biomass remained at about the same level during the winter half of the year in *M. balthica* and *S. plana*, while it decreased during these months in *C. edule*, *N. diversicolor* and *N. hombergii*. 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 *S. plana* and *M. balthica* (1.6 and 1.8x, respectively), but considerably higher in *N. diversicolor* (2.6x), *M. arenaria* (2.9x) and *C. edule* (3.3x). 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 *S. plana* and *M. balthica*, however, the ratio highest/lowest biomass was about as large as the ratio highest/lowest condition, implying that in these species 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 *M. balthica*, *S. plana* and *M. arenaria* (Figs 4 and 5; fig. 8 of ZWARTS, 1991). However, *C. edule* reached the highest biomass in July-September, at a time when the average body condition had already decreased by 30%. This is also true for *M. edulis* 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

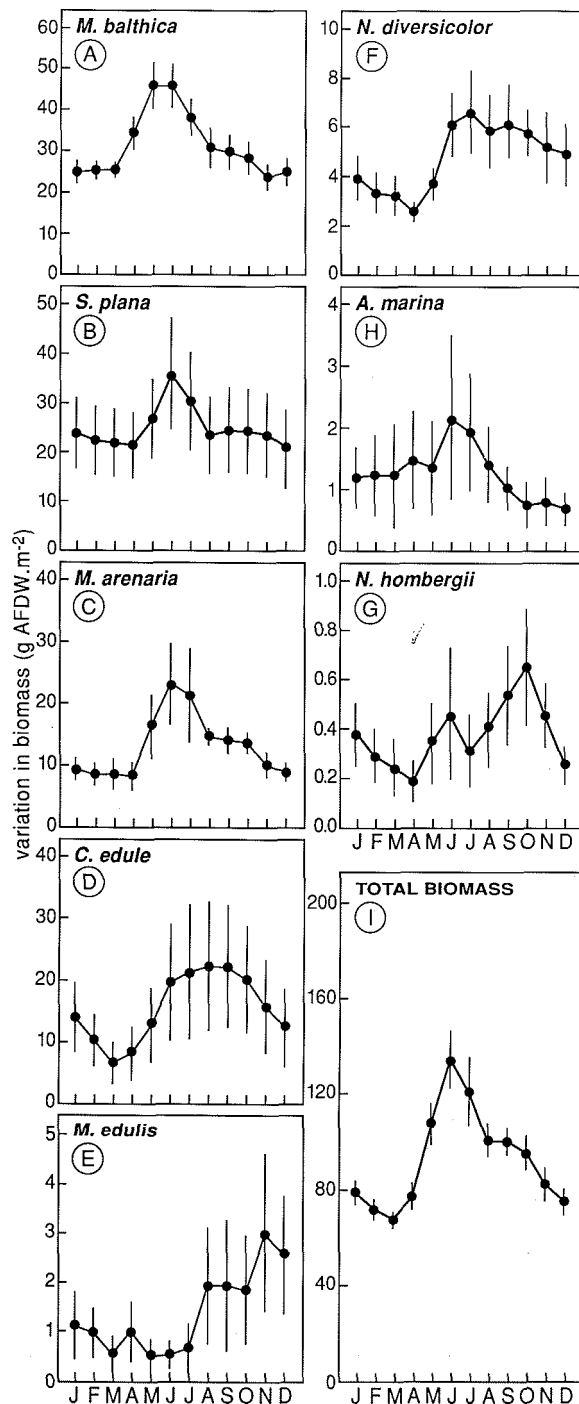


Fig. 5. Seasonal variation in the biomass (g AFDW·m<sup>-2</sup> ± SE) of five bivalve and three worm species, and in the total biomass of all species, calculated for eight years, 1979-1986.

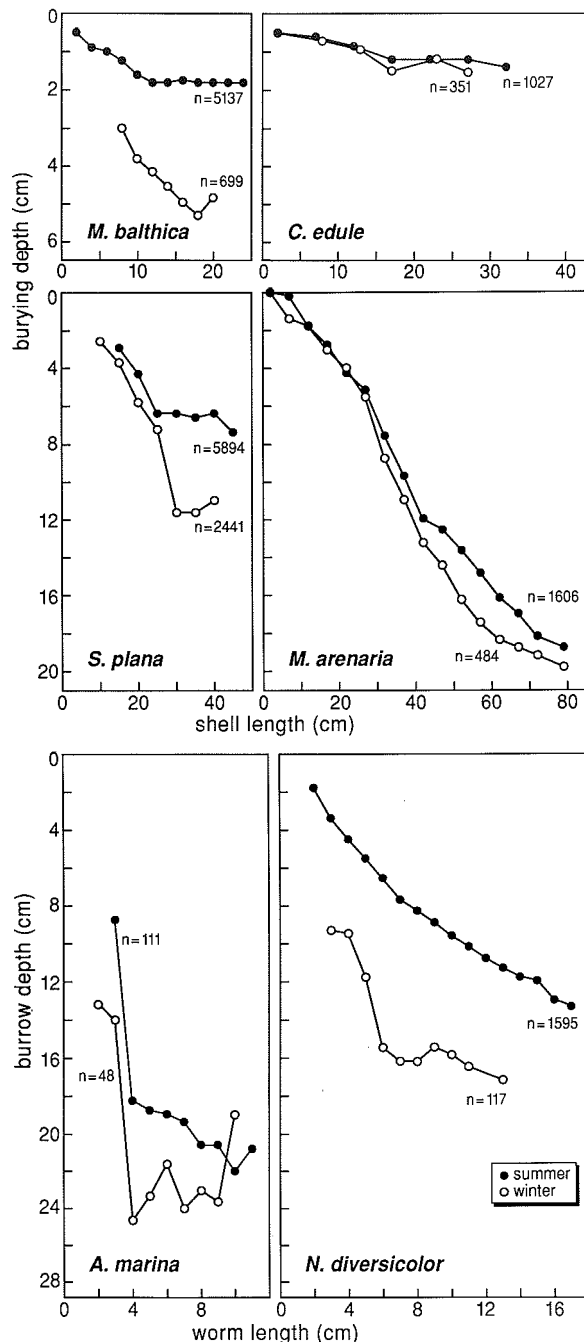


Fig. 6. Burying depth as a function of body size in summer and winter in six benthic species. Winter refers to the period December - February in *Macoma balthica*, December-April in *Arenicola marina*, and December - February in the four other species. Summer refers to the months June - August, except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

continued to grow at a higher rate than the flesh, apparently causing flesh weights at a given length to stop increasing or even to start decreasing. Shell growth continued for longer periods in summer and autumn in *M. edulis* and *C. edule* 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 *M. edulis* and *C. edule* than in *M. balthica* and *M. arenaria*, the biomass peak of the former two species fell even later than in the other bivalve species.

### 3.5. 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 *M. balthica*, *S. plana*, *C. edule* and *M. arenaria*, and the burrow depth of *N. diversicolor* and *A. marina*. 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 *N. diversicolor* and *A. marina* 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 10-20 mm for *M. balthica*, 30-40 mm for *S. plana*, 30-50 mm for *M. arenaria*, 10-35 mm for *C. edule*, 7-14 cm in *N. diversicolor* and 4-11 cm in *A. marina*. 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 *A. marina* 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 *A. marina* in sand are as deep as in mud.

There was little or no seasonal variation in the burying depths of *M. arenaria* and of *C. edule*, 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 *M. balthica* in the Wash, eastern England, that was similar to the trend shown in Fig. 7 and suggests that depth is governed by day length and not by temperature. We also found that depth increased after June, when the seawater temperature continued to increase for two months, and decreased again after December, when the temperature continued to decrease for two months. The seasonal varia-

tion of the burying depth of *M. balthica* (Fig. 7a) was thus synchronized 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 seawater temperature ( $r = -0.79$ ). As in *M. balthica*, *S. plana* burrowed more deeply from July onwards, but in contrast to *M. balthica*, they remained at their winter depth until April. Hence, the average depth of *S. plana* was better correlated with temperature ( $r = -0.93$ ) than with day length ( $r = -0.85$ ). This was also true for *A. marina*:  $r = -0.81$  for depth against day length, while  $r = -0.53$  for depth against temperature. The two correlations were equal in the case of *N. diversicolor* (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 *M. balthica*, *S. plana* and *N. diversicolor* within separate months. The 126 sampling dates were divided per month into 7 classes of seawater 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 *M. balthica*, *S. plana* and *N. diversicolor*, 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 seawater temperature in March and April, so temperature was obviously not a trigger for *M. balthica*, *S. plana* and *N. diversicolor* 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 *N. diversicolor* 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-February period revealed no relation between seawater temperature in the range from  $-1$  to  $+6^\circ\text{C}$  and the burying depth of *M.*

*balthica*, *S. plana* and *N. diversicolor*. In contrast, ESSELINK & ZWARTS (1989) concluded that in winter *N. diversicolor* live in deeper burrows at lower temperatures. However, their winter period referred to the longer period of 15 November-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.

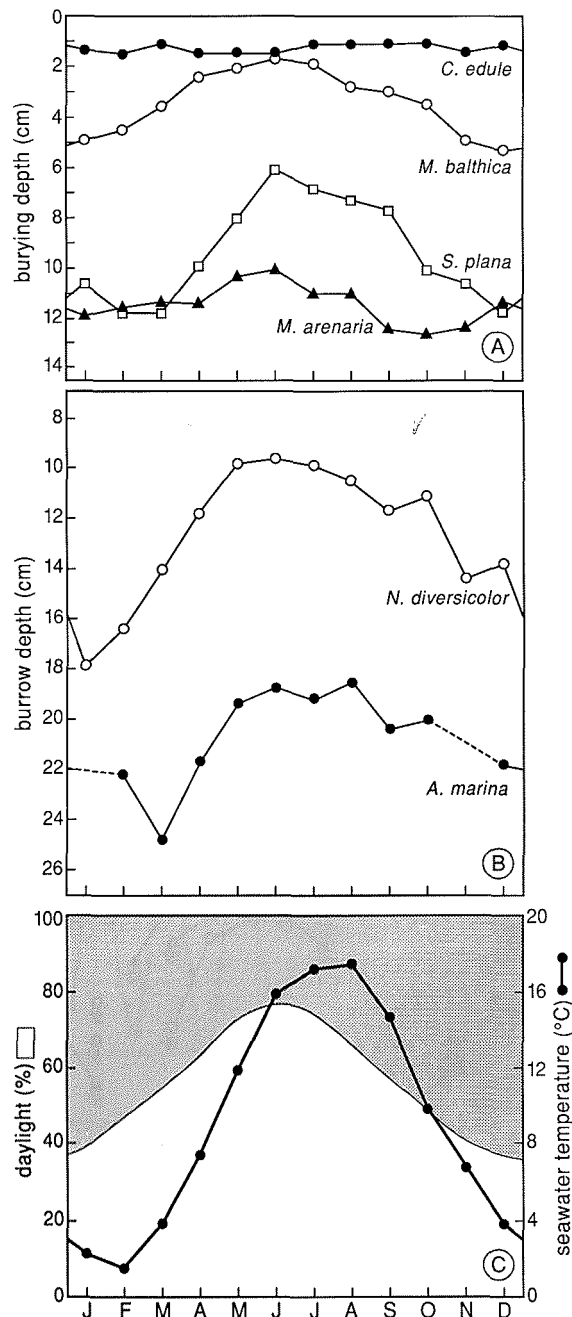


Fig. 7. Seasonal variation in (a) burying depth of *Cerastoderma edule* (10-35 mm;  $n = 1802$ ), *Macoma balthica* (10-20 mm;  $n = 12124$ ), *Scrobicularia plana* (30-50 mm;  $n = 14305$ ) and *Mya arenaria* (30-50 mm;  $n = 1396$ ), (b) burrow depth of *Nereis diversicolor* (7-14 cm;  $n = 1946$ ) 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 *C. edule* of 20 mm, *M. balthica* of 15 mm, *S. plana* of 35 mm, *M. arenaria* of 40 mm, *N. diversicolor* of 10 cm and *A. marina* of 8 cm. The depth measurements are averaged for seven years (1980 - 1986) and sea water temperature for 15 years (1972 - 1986).

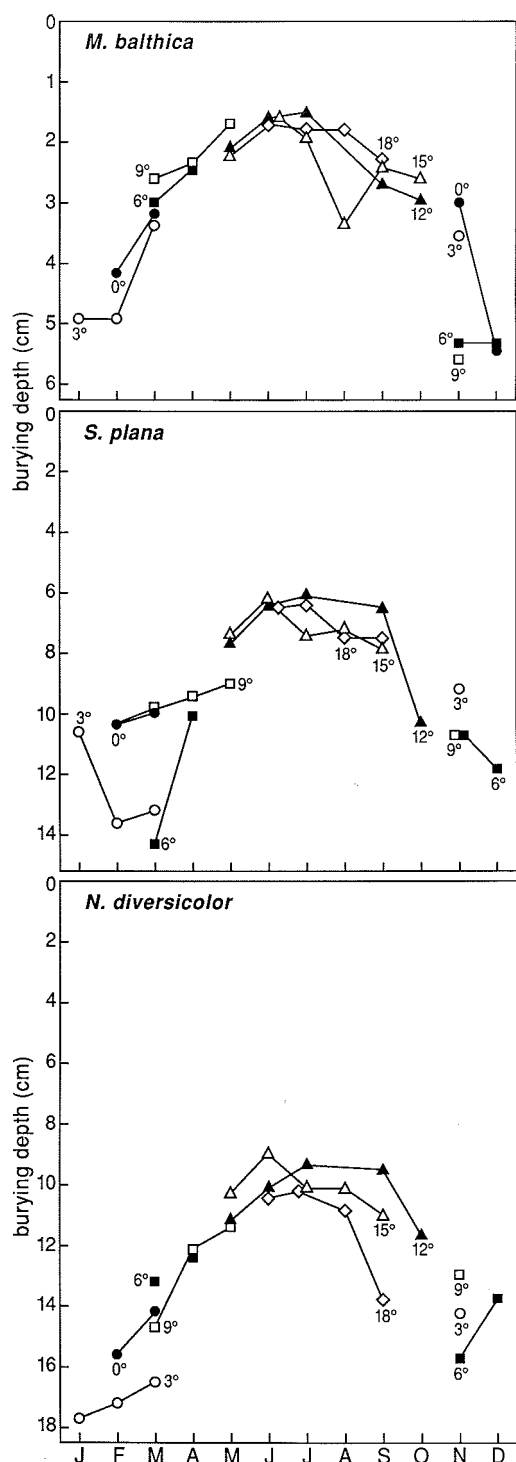


Fig. 8. Burying depth of *Macoma balthica* (15 mm) and *Scrobicularia plana* (35 mm) and burrow depth of *Nereis diversicolor* (10 cm) during the course of the year, split up for seven categories of sea water temperature. The graphs are based on the same data as in Fig. 7.

Nonetheless, it remains likely that *N. diversicolor* 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, *N. diversicolor* 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 *N. diversicolor* remains a distinct possibility.

There were large differences in the burying depths between the eight winter and seven summer periods studied (Fig. 9). *M. balthica* lived at depths of only 3-4 cm in the winters of 1982/83 and 1984/85, but at depths of 6-7 cm in the winters of 1979/80, 1980/81 and 1986/87. The summer depth of *M. balthica* also varied between years by between 1 and 2 cm. *S. plana* reached a winter depth of 12-14 cm in the first three winters when the strong year class of 1976 was still abundant, but not subsequently as the population collapsed. Again, *N. diversicolor* lived at greater depths in the first three winters than in the last five. Fig. 9 confirms that these variations in depth were not associated with seawater 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 *M. balthica* and *S. plana* was not regulated by changes in temperature. This was also true for *N. diversicolor*, 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 *M. balthica* and *S. plana* can be attributed partly to variation in siphon weight and also that the difference in depth between winters depends on the size of the siphon.

### 3.6. SEASONAL VARIATION IN THE ACCESSIBLE FRACTION OF *M. BALTHICA* AND *S. PLANA*

Figs 7-9 show the average seasonal variation in the burying depth of *M. balthica*, *S. plana* and *N. diversicolor*. 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 *M. balthica*) and in Fig. 11 (the upper 2, 4, 6, 8 cm, and below 8 cm for *S. plana*).

The data for *S. plana* 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 *N. diversicolor* 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 the Discussion.

## 4. DISCUSSION

## 4.1. 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 of 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 prey density causes an increase in the search time per prey and may therefore reduce the intake rate (GOSS-CUSTARD, 1970a, 1977c; HULSCHER, 1976; GOSS-CUSTARD *et al.*, 1977b; 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 to only 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, *C. edule* 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 *M. balthica*, *S. plana*, *M. arenaria* and *N. diversicolor*, species 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. Intake rates of oystercatchers have been measured in 90 studies, compiled by ZWARTS *et al.* (in press). Intake rates vary between 1 and 4 mg·s<sup>-1</sup>, 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 summarized in Table 2 are split up per month, the intake rate of oystercatchers appears to peak in midsummer, then to decrease until midwinter, 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

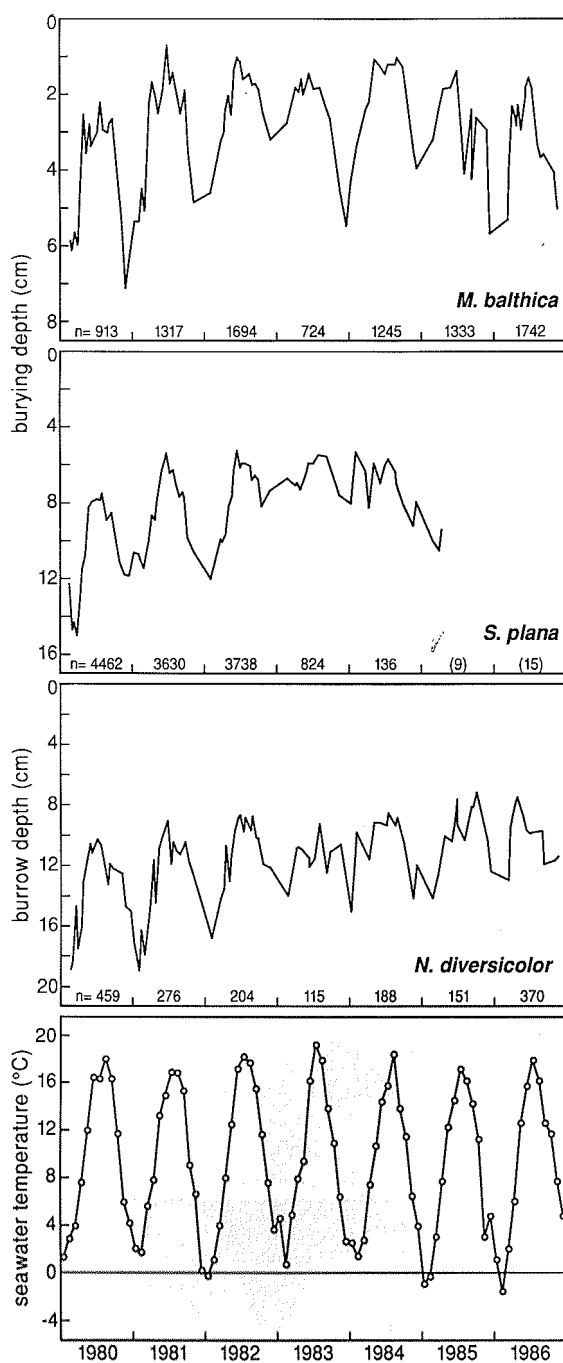


Fig. 9. Burying depth of *Macoma balthica* (15 mm) and *Scrobicularia plana* (35 mm) and burrow depth of *Nereis diversicolor* (10 cm) at each sampling date during the course of seven years; sample size in each year is indicated. The lower panel shows the average sea water temperature per month.

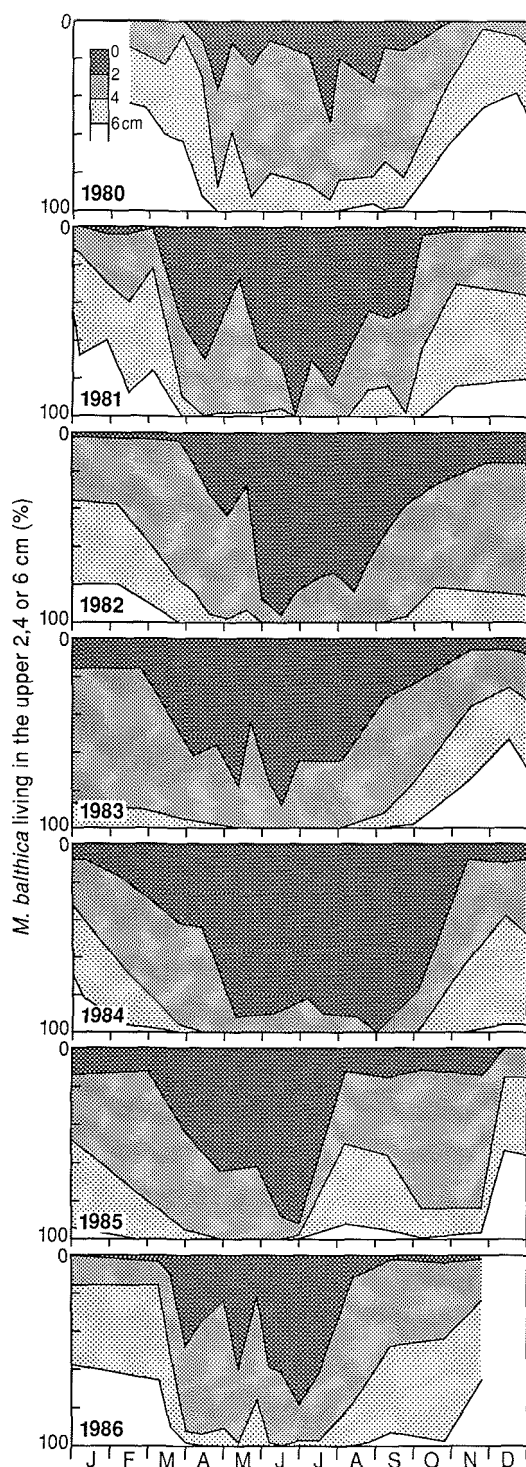


Fig. 10. Seasonal variation in the accessibility of *Macoma balthica* (15 mm) over 7 years. The proportion of the population living in the upper 2, 4 and 6 cm is shown.

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 *M. balthica* and *S. plana* decline (Figs 10 and 11). ZWARTS & WANINK (1991) show that the seasonal 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 *S. plana* 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 *N. diversicolor*. The consequence is that only lean prey are accessible in winter and that oystercatchers feeding on *S. plana*, 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 cited 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 *S. plana* and *M. arenaria* 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.

#### 4.2. 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 *M. balthica*, *S. plana* and *M. arenaria*, 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 *S. plana* 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 *M. balthica* or *S. plana* probe their 7.5-cm-long bill on average 3-4 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).

Three studies have exactly determined the depth at which prey are taken: sanderlings preying on three crustacean species, curlews, *Numenius arquata*, feeding on *M. arenaria* and oystercatchers on *S. plana*. 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 *M. arenaria*. When a prey is found, they pull up the

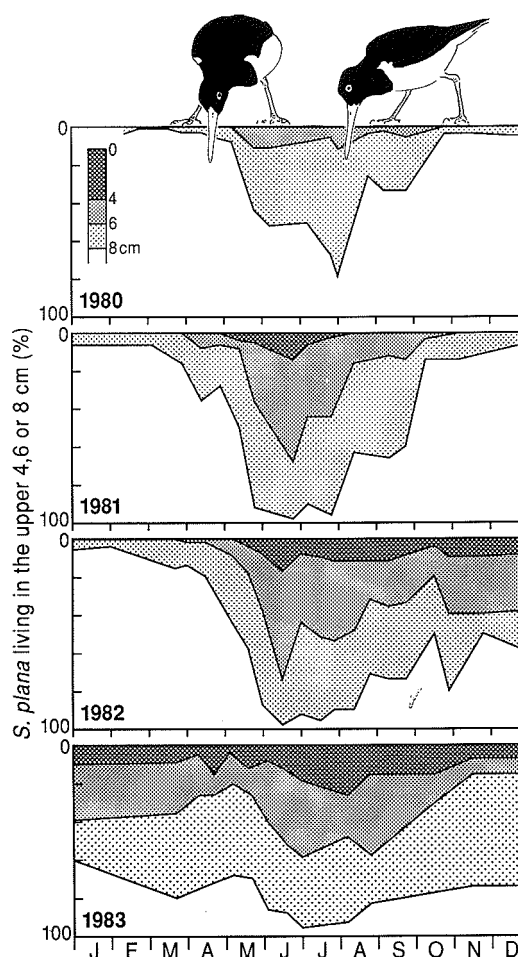


TABLE 2

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  $s^{-1}$ )  $\pm$  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 ( $R^2 = 0.04$ ;  $p = .58$ ).

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

Fig. 11. Seasonal variation in the accessibility of *Scrobicularia plana* (35 mm) over 4 years. The proportion of the population living in the upper 2, 4, 6 and 8 cm is shown.

siphon and eat *in situ* the remaining flesh from the gaping shell. ZWARTS & WANINK (1984) located *M. arenaria* 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 *S. plana* 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 6-11) 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 *M. balthica* 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 *M. balthica* 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), *S. plana* 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, *Calidris alba*, 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 *M. balthica* from the upper 2-3 cm of the substrate. The seasonal variation in the accessible fraction of *M. balthica* is very large for knot, much greater than for oystercatchers (Fig. 10; READING & MCGRORTY, 1978). The accessibility of *M. balthica* 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 *C. volutator* 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.

*A. marina* live in burrows 20-25 cm deep (Figs 6 and 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 *A. marina* defecate about once per hour and cast production takes some seconds, worms expose themselves to predation for about one thousandth of the low water period. Curlews run to catch a defecating worm at distances of 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 *U. tangeri* is easier to measure when Whimbrels wait motionless above a burrow for the emergence of a crab. In this case it is sufficient to determine the waiting time.

Like *U. tangeri*, *C. volutator* retreat down their burrows when a wader walks over the mud (GOSS-CUSTARD, 1970b). *C. volutator* occur in densities of many thousands per m<sup>2</sup>. Even if 99.9% of them retreat into their burrows, enough remain accessible to allow a slowly-walking bird to feed on them without the need to make dashes or to wait for emerging prey. However, since *C. volutator* only return to the surface 5-10 minutes after a disturbance, birds feeding at high densities may severely depress the accessible fraction of the prey (GOSS-CUSTARD, 1970b, 1976).

When disturbed, *N. diversicolor* also retreat down their burrows, where they are safe from waders with short bills. Curlews use two methods for preying on *N. diversicolor*. 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 and 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 *M. edulis* and *C. edule* and so take them in a fast rate (ZWARTS & DRENT, 1981; SWENNEN *et al.*, 1983). *C. volutator* 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 *C. volutator* to follow the tide edge. In contrast, waders feeding on surface-feeding *N. diversicolor* 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 *N. diversicolor* at low tide take alternative prey as the tide ebbs (DE VLAS *et al.*, 1994) 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 (*C. edule*, *M. arenaria* and *M. edulis*), larger in bivalves with a seasonal variation in burying depth (*M. balthica* and *S. plana*), and very large in invertebrates that emerge from their burrows to defecate (*A. marina*) or to feed (*N. diversicolor*, *C. volutator*).

#### 4.3. 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 *C. edule* (HULSCHER, 1976) and *M. balthica* (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 *M. balthica* when all the surface clues on the mud surface had been erased experimentally (HULSCHER, 1982). The burrow entrance of *N. diversicolor* 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 star-like feeding tracks around their burrow. Curlews searching for *N. diversicolor* do not probe at random, but look systematically for these small tracks. Siphon holes of *M. arenaria* can be very conspicuous, especially in muddy substrate (LINKE, 1939: photos 50-52). Curlews probably know the size of *M. arenaria* 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. *A. marina* defecating within 2 m of a curlew are accessible, but not detectable if the cast is produced behind the bird. METCALFE (1985)

found that *C. volutator* was taken at a smaller distance by lapwing *Vanellus vanellus*, than *N. diversicolor* 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, *C. volutator* may have been less accessible than *N. diversicolor*, because they retreated more quickly into their burrows than *N. diversicolor*. Second, the *C. volutator* were smaller and less profitable than *N. diversicolor* and so perhaps less worth 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 *C. volutator*, which appear to be easily detectable at the surface and search more slowly for the less visible surface tracks of *N. diversicolor* (GOSS-CUSTARD, 1977a, 1977b). Search rate may also vary within one type of prey, depending on its detectability, as four studies have shown. First, semipalmated sandpipers, *Calidris pusilla*, walk faster when they feed on *C. volutator* 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 *M. arenaria* 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. obs.). Third, oystercatchers that stab into *M. edulis* 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 *N. diversicolor* 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).

#### 4.4. THE INGESTIBLE AND DIGESTIBLE PREY FRACTION

Curlews eating large *M. arenaria* take some minutes to pull up the siphon and consume the flesh piece-meal from the shell (ZWARTS & WANINK, 1984). Curlews also dismember large *C. maenas* 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 *C. edule* 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 *M. balthica* up to 16 mm long, *M. arenaria* up to 17 mm long, *S. plana* up to 19 mm long and *M. edulis* 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 and 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.

#### 4.5. 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: *M. edulis* (ZWARTS & DRENT, 1981; ENS, 1982; SUTHERLAND & ENS, 1987; MEIRE & ERVYNCK, 1986; CAYFORD & GOSS-CUSTARD, 1990), *M. balthica* (HULSCHER, 1982), *C. edule* (SUTHERLAND, 1982a) and *M. arenaria* (ZWARTS & WANINK, 1984), in redshank preying on *N. diversicolor* (GOSS-CUSTARD, 1977b), in curlews feeding on *M. arenaria* (ZWARTS & WANINK, 1984), *N. diversicolor* (ZWARTS & ESSELINK, 1989) and *U. tangeri* (ZWARTS, 1985), in whimbrels feeding on *U. tangeri* (ZWARTS, 1985) and in knot feeding on *M. balthica* (ZWARTS & BLOMERT, 1992). These studies show that birds are more selective than predicted by theory, because barely profitable prey was 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 g) 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:

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

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 generalized lower prey-size acceptance threshold. Accepting that the profitability ( $\text{mg}\cdot\text{s}^{-1}$  handling) must at least be equal to the intake rate ( $\text{mg}\cdot\text{s}^{-1}$  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.

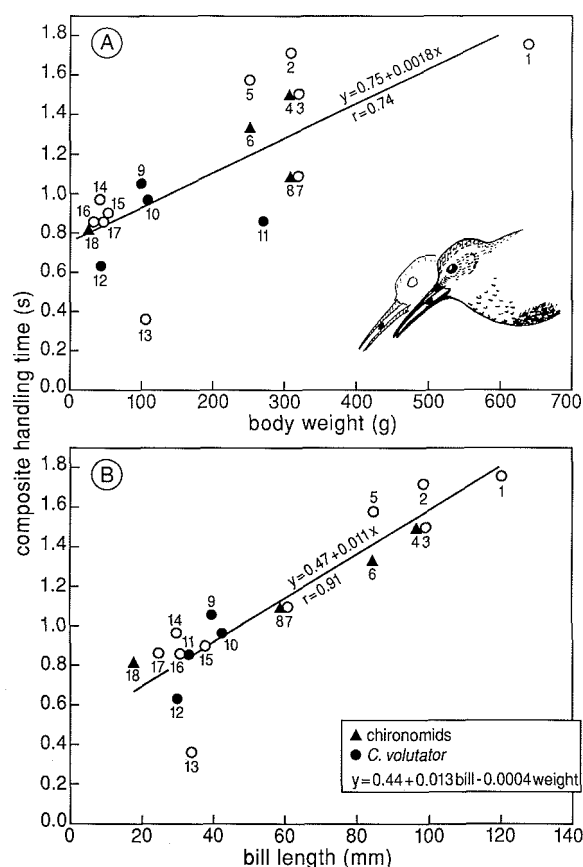
Waders can take up to 40-160 small prey per min when feeding rapidly at one spot so that they hardly spend any time searching for prey. The minimum time to take a prey then varies between 0.4 and 1.5 s. Film and video analyses showed that the time taken to transport a small prey up the bill to the gape 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) 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) distinguish 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 s which was then followed by the time to return the bill to the surface, the down time of 0.12 sec. The total handling time was 0.69 sec, 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 sec, 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 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*, *C. volutator* and *H. ulvae*, 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.).

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 - 9 and 11). In all other cases, we took the highest 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 *N. diversicolor* 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 *C. volutator* 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	<i>Corbicula fluminalis</i>	van der Kamp & Zwarts, unpubl.
2	Black-tailed Godwit	rice grain	Zwarts, unpubl.
3	Black-tailed Godwit	<i>Corbicula fluminalis</i>	van der Kamp & Zwarts, unpubl.
4	Black-tailed Godwit	chironomid larvae	DIRKSEN <i>et al.</i> , 1992; SZÉKELY & BAMBERGER, 1992
5	Bar-tailed Godwit	artificial pellets	Blomert & Zwarts, unpubl.
6	Bar-tailed Godwit	chironomid larvae	DIRKSEN <i>et al.</i> , 1992
7	Avocet	<i>N. diversicolor</i>	Blomert & Engelman, unpubl.
8	Avocet	chironomid larvae	DIRKSEN <i>et al.</i> , 1992
9	Young Avocet	<i>C. volutator</i>	ENGELMOER & BLOMERT, 1985
10	Redshank	<i>C. volutator</i>	GOSS-CUSTARD, 1969
11	Black-headed Gull	<i>C. volutator</i>	DE VRIES, 1969
12	Dunlin	<i>C. volutator</i>	VAN DER VOET, 1967
13	Knot	<i>H. ulvae</i>	Piersma <i>et al.</i> , in prep.
14	Dunlin	<i>Artemia salina</i>	VERKUIL <i>et al.</i> , 1993
15	Curlew Sandpiper	<i>Artemia salina</i>	VERKUIL <i>et al.</i> , 1993
16	Broad-billed Sandpiper	<i>Artemia salina</i>	VERKUIL <i>et al.</i> , 1993
17	Sanderling	isopods	MYERS <i>et al.</i> , 1980
18	Semipalmated Sandpiper	chironomid larvae	ASHKENAZIE & SAFRIEL, 1979



Also bar-tailed godwits, *Limosa lapponica*, spent 20% more time in handling an artificial pellet of twice the wet weight of a chironomid larvae (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 (*C. volutator* 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  $1.25 \cdot s^{-1}$  is required. According to equation (2) the average intake rate would be  $0.07 \text{ mg} \cdot s^{-1}$ . Thus, the minimum weight of acceptable prey would be  $0.07 / 1.25 = 0.05 \text{ mg}$ . 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  $2.6 \text{ s} \cdot \text{prey}^{-1}$  or  $23 \text{ prey} \cdot \text{min}^{-1}$ . With a body weight of 900 g and an intake rate of  $2.56 \text{ mg} \cdot s^{-1}$ , the smallest acceptable prey for curlew should therefore weigh 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:

$$\text{minimum prey weight (mg dry flesh)} = 0.0012 W^{1.20} \quad (3)$$

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 stint. 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 *C. edule* 8 mm long and weighing 3.3 mg (MEIRE, 1994b), but usually they feed on prey of 20 to 800 mg (ZWARTS *et al.*, in press). The prey selected by curlews weigh 100 to 300 mg (ENS *et al.*, 1990) and are taken at an average rate of  $1 \text{ prey} \cdot \text{min}^{-1}$ . There are, however, two prey that weigh less. Both are taken at a high rate for curlews: siphons of *S. plana* (5–10 mg) up to  $9 \cdot \text{min}^{-1}$  and juvenile *C. maenas* (40 mg) up to  $7.4 \text{ prey} \cdot \text{min}^{-1}$  (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, *C. volutator*. Fig. 13 shows the relation between size and weight in *C. volutator* (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 *C. volutator* (GRATTO *et al.*, 1984); (*C. volutator* > 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 *C. volutator* 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 *C. volutator* 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 *C. volutator* (CURTIS *et al.*, 1985). They have a short bill in comparison to waders with a similar body weight and handle their prey quickly (Fig. 12); unfortunately no data are available on their size selection. *C. volutator* 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 *N. diversicolor* (ENGELMOER & BLOMERT, 1985) as would also be predicted. Adult avocets (320 g) do not take

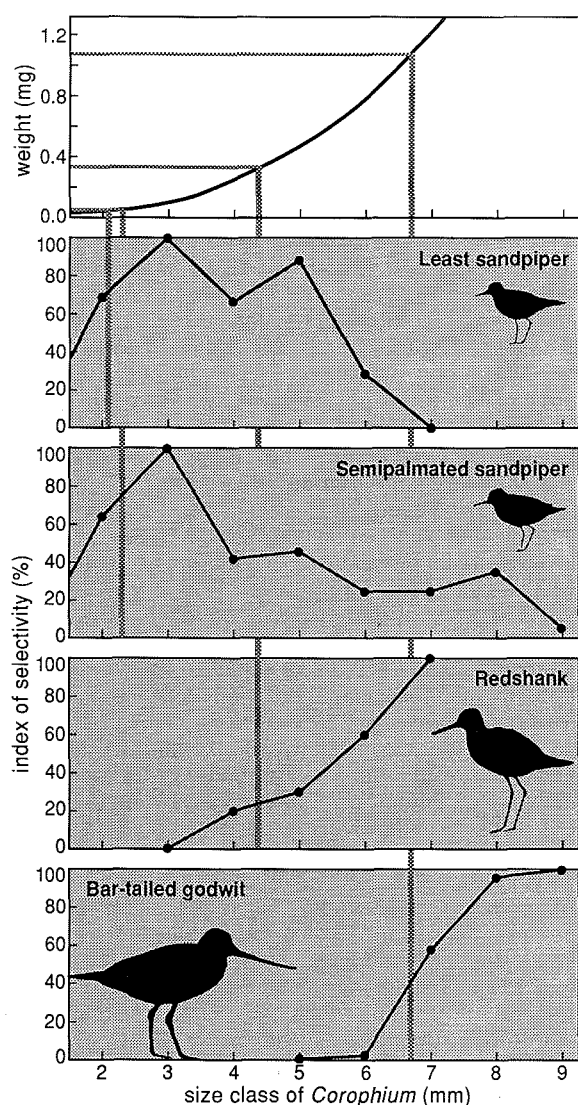


Fig. 13. The relation between weight and size in *Corophium volutator* (from Table 1) and the observed size selection by four wader species. The horizontal lines in the upper graph indicate the expected lower weight threshold according to equation (3) (see text) and the vertical lines show the corresponding 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.

*C. volutator* 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 *C. volutator* and *H. ulvae*. 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<sup>-1</sup> (BUXTON & YOUNG, 1981), much faster than waders.

Waders that take *C. volutator* 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 *C. volutator* from the surface and do not probe for them, though they are accessible to most wader species in burrows 3–5 cm deep (MEADOWS, 1964; JENSEN & KRISTENSEN, 1990). If it is assumed that the handling time is twice as long for a redshank probing for *C. volutator* 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 *H. ulvae* 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 *S. plana*, 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. 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 conditions are known to be accessible can be ignored 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 their diet as their intake rate goes down. For example, as prey density declines, oystercatchers accept all the *C. edule* encountered and not only the open ones that can be handled quickly (HULSCHER, 1976). Redshank and oystercatchers include the smaller size classes in their

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.

diet as prey density declines (GOSS-CUSTARD 1977b, 1977c; ZWARTS & DRENT, 1981) and, as mentioned, oystercatchers eat the less profitable *S. plana* lying at a greater depth.

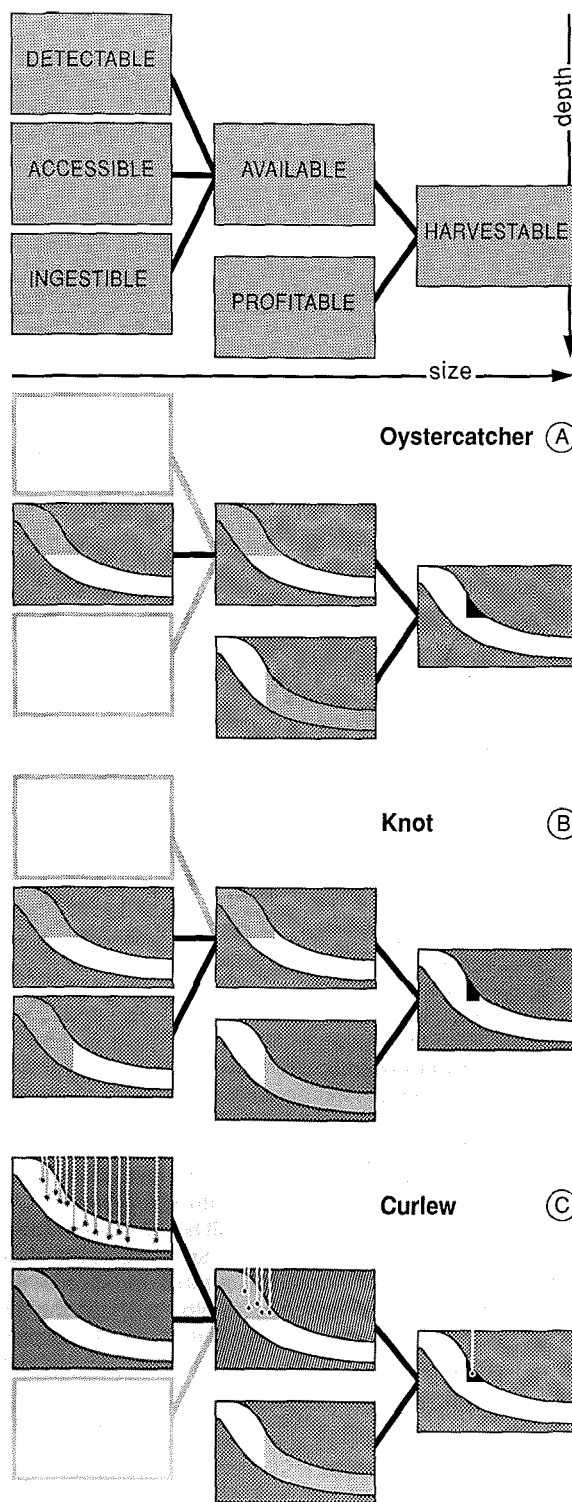
The profitability of prey may vary systematically between individual birds. HULSCHER (1982) showed that oystercatchers with blunt bills need more time to handle *M. balthica* than birds with pointed bills. Similarly, SUTHERLAND & ENS (1987) found that an oystercatcher with a chisel-shaped bill was faster at stabbing *M. edulis* than a bird with a blunt bill, while it was the 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 *C. edule* as did Wanink (unpubl.) and Hulscher (unpubl.) for oystercatchers eating *S. plana* and *M. arenaria*, respectively, and Piersma *et al.* (in prep.) for knot eating *M. balthica*. 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 take prey of at least 10-20 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.

#### 4.6. THE HARVESTABLE PREY FRACTION

The information given in the above 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 6.5-8.5 cm) take the majority of *M. balthica* and *S. plana* 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.*, 1994; ZWARTS *et al.*, in press). *M. balthica* smaller than 10 mm and *S. plana* smaller than 13 mm are always ignored because they are unprofitable (HULSCHER, 1982; ZWARTS *et al.*, in press). 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 *M. balthica* less than 15 mm long and *S. plana* smaller than 25 mm long (ZWARTS *et al.*, in press). The harvestable fraction is thus highly variable for two reasons. First, the depth distribution and prey biomass fluctuate seasonally 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). *M. balthica* is a preferred prey for knot, but they ignore the size classes smaller than 10 mm long and reject *M. balthica* 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 *M. balthica* over ten years varied between 6 and 35 g·m<sup>-2</sup>, with an average of 17.7 g·m<sup>-2</sup> (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 6-35 g·m<sup>-2</sup> in the total biomass of *M. balthica* was small compared to those of other benthic species (BEUKEMA *et al.*, 1993), the standard deviation of 8.6 g·m<sup>-2</sup> being only 49% of the mean (17.7 g·m<sup>-2</sup>). The relative standard deviation (RSD) for suitable biomass (6-16 mm long) was 44% and thus lower than that for the total biomass. The annual variation in the fraction of *M. balthica* 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 bio-

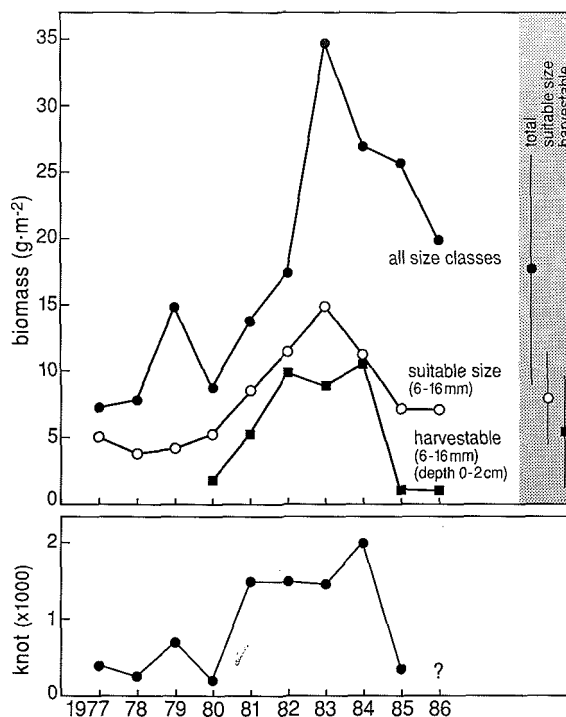


Fig. 15. The biomass of *Macoma balthica* in August 1977 - 1986, given for all size classes ('total'), for only the specimens in the range 6-16 mm ('suitable size') and for animals of 6-16 mm living in the upper 2 cm of the substrate ('harvestable'). The grey field gives the averages  $\pm$  SD. The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

mass of *M. balthica* 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 *M. balthica* 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. Fig. 14c illustrates the relatively simple situation of a curlew searching for the siphon holes of *M. arenaria*. This prey is harvestable if it lives within reach of the bill (13-16 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 10-13 cm) never feed on *M. arenaria*, while it is the main prey for the females (bill length 13-16 cm) in areas where the prey species occurs (ZWARTS & WANINK, 1984). The detectable fraction also varies considerably. Siphon holes arise when *M. arenaria* extend their siphon to the surface for suspension feeding. *M. arenaria* 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 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 selections 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 *M. balthica* 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 *M. edulis* 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,

1994a). 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 *M. balthica*. Possibly knot select prey to maximize the energy processing rate in the gut, since *M. balthica* 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 curlew determines the harvestable fraction of large *N. diversicolor* and of medium-sized *M. arenaria*. Yet ENS & ZWARTS (1980, unpubl.) found that, among curlews feeding in the same area, individuals with a similar bill length took either *N. diversicolor*, or *M. arenaria*, 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, 1991; 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.

#### 4.7. 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 and 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 *C. volutator* did not emerge from their burrows when the mud temperature was below 6°C and that redshank then switched to less preferred prey, *N. diversicolor* and *M. balthica*, these still being available. Similarly, SMITH (1975) showed that when the temperature of the substrate dropped below 3°C, *A. marina* 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 and 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-October. The birds took *M. balthica* and *S. plana* on a mudflat and *M. edulis* on a nearby mussel bed. The females with bill lengths of 7.5-8.5 cm, took twice as many *S. plana* as *M. balthica*. In contrast, *S. plana* occurred in the diet of the males (bill length 6.5-7.5 cm) as much as *M. balthica*. 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 *S. plana* to *M. balthica* in late summer, since the density of accessible prey would drop much more in *S. plana* than in *M. balthica* (Figs 7, 10 and 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 *S. plana* and *M. balthica* 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 *M. edulis* provided a higher intake than *S. plana* and *M. balthica*.

-(2) The majority of *S. plana* 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 of Schiermonnikoog in winter, found that birds taking *S. plana* 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 *S. plana*, increasing from 0.2 to 1 prey·min<sup>-1</sup> within the range of 100 to 600·m<sup>-2</sup> at which *S. plana* occurred. The majority of these prey lived at 4 to 7 cm below the surface. *M. balthica* of suitable size occurred in the area at a density of 70 to 120 prey·m<sup>-2</sup>, but were hardly taken. They were accessible, but *S. plana* were preferred above the smaller *M. balthica* because of their greater profitability.

-(3) *M. balthica*, and to a lesser degree *N. diversicolor*, were the major prey of oystercatchers on the mudflats near Schiermonnikoog in spring and summer (BUNSKOEKE *et al.*, 1994). *N. diversicolor* were taken less during receding tide than during low tide, the reverse being the case for *M. balthica* (DE VLAS *et al.*, 1994). This change in diet may be wholly attributed to a shift in the feeding behaviour of *N. diversicolor* 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 *M. balthica* to *N. diversicolor* (BUNSKOEKE *et al.*, 1994) during the summer. *M. balthica* 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 *M. balthica* from June onwards (BEUKEMA & DE BRUIN, 1979; ZWARTS, 1991), made them less profitable. Indeed, the intake rate of oystercatchers feeding on *M. balthica* decreased from May-June to August (BUNSKOEKE *et al.*, 1994).

-(4) BOATES & GOSS-CUSTARD (1989) studied oystercatchers wintering in the Exe estuary, Southwest England. They observed a switch in October from *N. diversicolor* to *S. plana*. There was hardly any change in the body condition of *S. plana* during the winter, but a large decline in that of *N. diversicolor* 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 *S. plana* c. 25 mm long in early winter but specimens of 30-35 mm length in early spring. This may indicate that *S. plana*, 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 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 *S. plana* became more profitable than *N. diversicolor*.

-(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 *N. diversicolor*. The worms taken in winter were small (1-3 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 *N. diversicolor* 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. *H. ulvae* were an important alternative prey in midwinter. *M. balthica* were less important; the length classes 5-7.5 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 *M. balthica*, 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.*, in prep.) took only *M. balthica* in August, but in September and October switched to two other prey that were still found at, or just beneath, the surface, *H. ulvae* and *C. edule*, and returned to *M. balthica* 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 *M. balthica* to *N. diversicolor* in midsummer and from *N. diversicolor* to *S. plana* 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. *M. balthica* 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 *M. balthica*, its mortality is lower in winter than in summer (BEUKEMA, 1993).

#### 4.8. 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 Northwestern 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 Northwestern 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.*, 1977b). 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

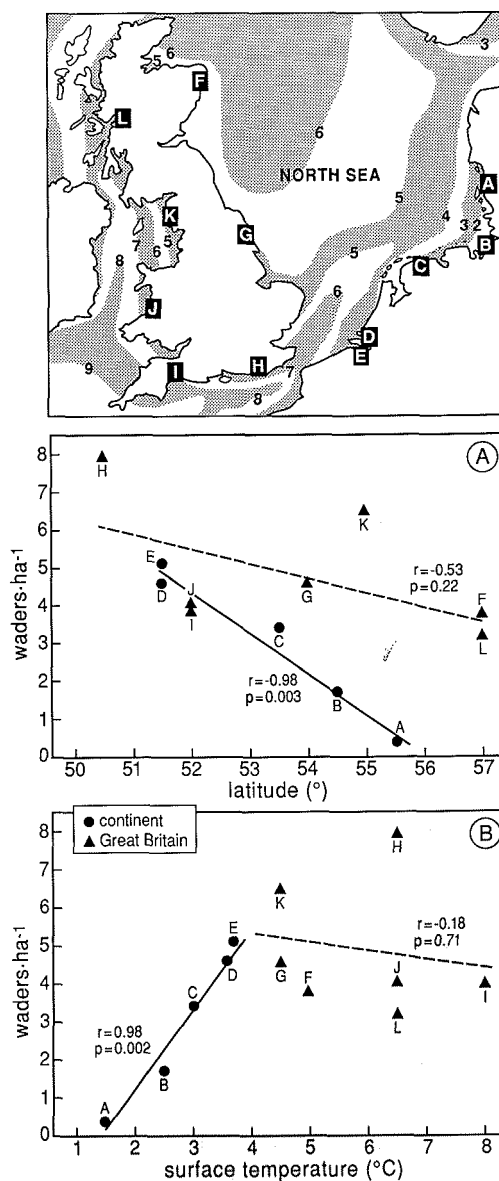


Fig. 16. Wader densities (birds·ha<sup>-1</sup> intertidal flat) in NW Europe in winter as a function of (a) latitude and (b) surface temperatures; the map gives the average temperatures in February, based on BÖHNECKE & DIETRICH (1951) and ANONYMUS (1962). The letters in the graphs correspond with the 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).

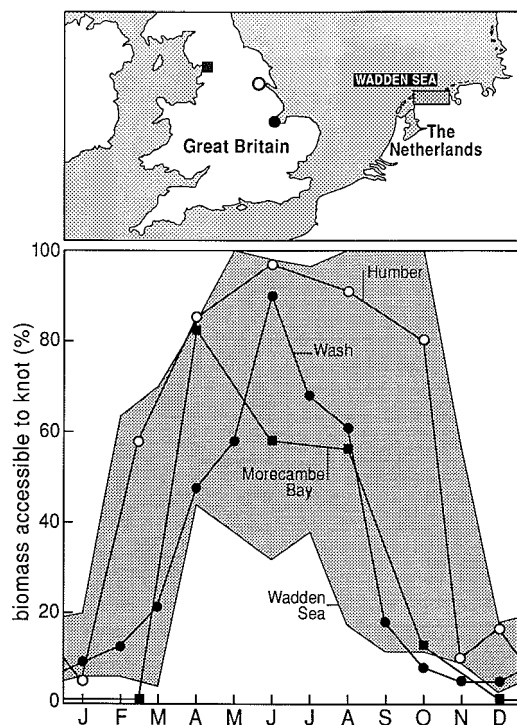


Fig. 17. Seasonal variation in the fraction of the biomass of *Macoma balthica* harvestable by knot in the Wash (READING & MCGRORTY, 1978), Humber (RATCLIFFE *et al.*, 1981; EVANS, 1988), Morecambe Bay (EVANS, 1988) and along the Frisian coast (highest and lowest values found in seven years). READING & MCGRORTY (1978), EVANS (1988) and RATCLIFFE *et al.* (1981) made slices in the sediment core and counted the number of *M. balthica* per depth category. Accessible to knot are *M. balthica* found in the slices 0 - 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.

Sea is visited by hundreds of thousands of migrant waders in spring and Scotland, Northwestern 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, 1983a; PROKOSCH, 1988).

The average surface temperature in February is 1.5°C in the northern and eastern parts of the Wadden Sea and 7-8°C along the English and French coasts (Fig. 16). The tidal flats in the Danish, German and eastern part of the Dutch Wadden Sea 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 & PERSMA, 1987; WIERSMA & PERSMA, in press). 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, 1983b; ZWARTS *et al.*, 1990a; MEININGER *et al.*, 1991; PERSMA, in press). 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, variations in the 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, *C. crangon*, (BEUKEMA, 1992), shore crab, *C. 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 Northwestern 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).

It is unknown whether the depth distribution in winter differs geographically, but the burying depth of *M. balthica* has been measured in six different places in Northwestern Europe. Unfortunately, the depth measurements in the Ythan estuary, Scotland (CHAMBERS & MILNE, 1975) 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 *M. balthica* (9-13 mm) living in the upper 2.5 cm. All studies found that 40-100% 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, *M. edulis* and *H. ulvae*, or continue to feed on *M. balthica* (EVANS, 1979, 1988). Indeed, for knot wintering in Morecambe Bay, *M. balthica* 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 *M. balthica* 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 Northwestern 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 *C. volutator* (GOSS-CUSTARD, 1969; see also MEADOWS & RUAGH, 1981), *H. ulvae* (BRYANT & LENG, 1975), *A. marina* (SMITH, 1975; CADÉE, 1976) and *S. armiger* (PIENKOWSKI, 1983a and b). Some bivalves feed less at low temperature (e.g. HUMMEL, 1985), 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 of PIERSMA, in press).

-(4) The body condition of prey is 30-60% lower in winter than in summer. As a result more prey per unit time have to be eaten in winter to obtain a given

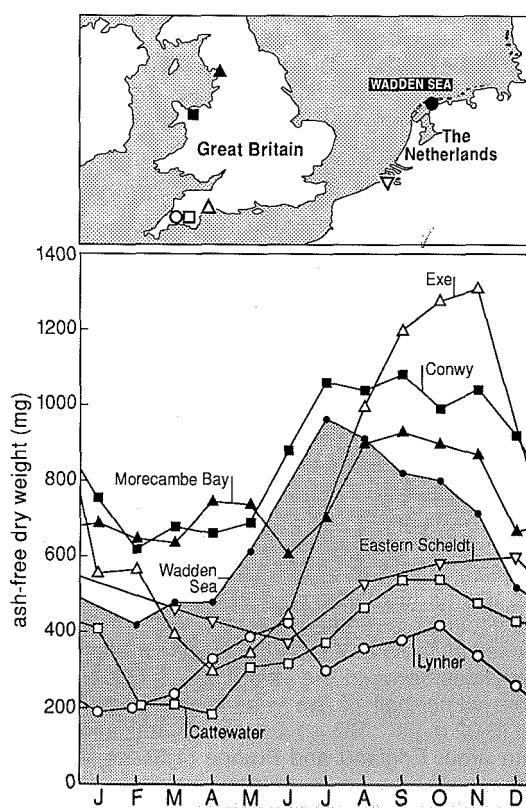


Fig. 18. Variation in body weight (AFDW, mg) of *Mytilus edulis* 50 mm long in seven areas. Sources: Exe (CAYFORD & GOSS-CUSTARD, 1990), Conwy (DARE & EDWARDS, 1975; averages for three years), Morecambe Bay (DARE, 1975; averages for three years; correction has been made for weight loss due to formalin (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 & Catteewater (BAYNE & WORRALL, 1980; weights are of mussels 6 cm long; these were transformed to those of 5 cm using regressions given in their paper).

intake rate. 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 *M. balthica*, *S. plana*, *M. arenaria* and *C. edule* during winter (figs 13-16 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 *M. edulis* (DARE, 1975; DARE & EDWARDS, 1975; this study; Fig. 3). Fig. 18 compares the seasonal variation in the average flesh weight of *M. edulis* 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 *M. edulis* (e.g. emersion time). The eastern Dutch Wadden Sea is the only site where the body condition diminishes from midsummer to midwinter. 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 oystercatcher in winter, we re-analysed the data summarized 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 ( $2.02 \text{ mg} \cdot \text{s}^{-1}$ ; SD = 1.04;  $n = 13$ ) and in the Dutch Delta area, England and France ( $1.91 \text{ mg} \cdot \text{s}^{-1}$ ; 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 *M. edulis*, the flesh 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 seawater 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: *M. balthica* and *S. plana* lose more body weight in mild winters than in

cold ones (ZWARTS, 1991). Moreover, there are incidental occasions in winter, usually associated with a large drop in temperature, when the benthic food becomes highly available to birds. *A. marina* and *N. diversicolor* 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 *C. edule* 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, *N. diversicolor* 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 *N. diversicolor* achieve their highest intake rates in late winter, and not in summer or autumn (ZWARTS & ESSELINK, 1989). The surface feeding by *N. diversicolor* also gives redshank the opportunity to switch to *N. diversicolor* at low mud temperatures when the surface activity of the preferred prey *C. volutator* 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 year-to-year differences may be expected in the profitability of the prey and in the fraction available to waders.

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## 5. REFERENCES

- ANSELL, A.D. & A. TREVALLION, 1967. Studies on *Tellina tenuis* Da Costa I. Seasonal growth and biochemical cycle.—J. exp. mar. Biol. Ecol. 1: 220-235.
- ANONYMUS, 1962. Mean monthly temperature and salinity of the surface layer of the North Sea and adjacent waders from 1905 to 1954. Conseil Explor. Mer Service Hydrogr. Charlottenlund Slot.

- ASHKENAZIE, S. & U.N. SAFRIEL, 1979. Time-energy budget of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska.—*Ecology* **60**: 783-799.
- BAIRD, R.H., 1966. Factors affecting the growth and condition of mussels (*Mytilus edulis* L.).—*Fish. Invest.*, Lond., Ser. II, **25**(2): 1-33.
- BARNES, R.S.K., 1986. Daily activity rhythms in the intertidal gastropod *Hydrobia ulvae* (Pennant).—*Estuar. coast. Shelf Sci.* **22**: 325-334.
- BARTELS-HARDEGE, H.D. & E. ZEECK, 1990. Reproductive behaviour of *Nereis diversicolor* (Annelida: Polychaeta).—*Mar. Biol.* **106**: 409-412.
- BAYNE, B.L. & C.M. Worrall, 1980. Growth and production of mussels *Mytilus edulis* from two populations.—*Mar. Ecol. Prog. Ser.* **3**: 317-328.
- BEUKEMA, J.J., 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea.—*Neth. J. Sea Res.* **8**: 94-107.
- , 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea.—*Neth. J. Sea Res.* **10**: 236-261.
- , 1979. Biomass and species richness of the macro-benthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter.—*Neth. J. Sea Res.* **13**: 203-223.
- , 1980. Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: I. the tellinid bivalve *Macoma balthica*.—*Neth. J. Sea Res.* **14**: 323-338.
- , 1982a. Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: II. the edible cockle, *Cerastoderma edule*.—*Neth. J. Sea Res.* **15**: 391-405.
- , 1982b. Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea.—*Neth. J. Sea Res.* **16**: 37-45.
- , 1985. Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea. In: J.S. GRAY & M.E. CHRISTIANSEN. *Marine biology of polar regions and effects of stress on marine organisms*. John Wiley, Chichester: 351-361.
- , 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Wadden Sea.—*Helgoländer Meeresunters.* **43**: 405-415.
- , 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters.—*J. exp. mar. Biol. Ecol.* **153**: 97-113.
- , 1992. Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters.—*Mar. Ecol. Prog. Ser.* **83**: 157-165.
- , 1993. Increased mortality in alternative bivalve prey during a period when the tidal flats of the Dutch Wadden Sea were devoid of mussels.—*Neth. J. Sea Res.* **31**: 395-406.
- BEUKEMA, J.J. & J. DE VLAS, 1979. Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea.—*Neth. J. Sea Res.* **13**: 331-353.
- BEUKEMA, J.J. & W. DE BRUIN, 1979. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea.—*Neth. J. Sea Res.* **11**: 42-55.
- BEUKEMA, J.J., K. ESSINK, H. MICHAELIS & L. ZWARTS, 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds?—*Neth. J. Sea Res.* **31**: 319-330.
- BIRKLUND, J., 1977. Biomass, growth and production of the amphipod *Corophium insidiosum* Crawford, and preliminary notes on *Corophium volutator* (Pallas).—*Ophelia* **16**: 187-203.
- BLOMERT, A-M., M. ENGELMOER & D. LOGEMANN, 1983. Voedsel-ecologie van de scholekster op het Friese wad. Report Rijkdienst IJsselmeerpolders, Lelystad.
- BOATES, J.S. & J.D. GOSS-CUSTARD, 1989. Foraging behaviour of oystercatchers *Haematopus ostralegus* during a diet switch from worms *Nereis diversicolor* to clams *Scrobicularia plana*.—*Can. J. Zool.* **67**: 2225-2231.
- , 1992. Foraging behaviour of oystercatchers *Haematopus ostralegus* specializing on different species of prey. *Can. J. Zool.* **70**: 2398-2404.
- BOATES, J.S. & P.C. SMITH, 1979. Length-weight relationships, energy content and the effects of predation on *Corophium volutator* (Pallas) (Crustacea: Amphipoda).—*Proc. Nova Scotia Inst. Sci.* **29**: 489-499.
- , 1989. Crawling behaviour of the amphipod *Corophium volutator* and foraging by semipalmated sandpipers, *Calidris pusilla*.—*Can. J. Zool.* **67**: 457-462.
- BÖHNECKE, G. & G. DIETRICH, 1951. Monatskarten der Oberflächentemperatur für die Nord- und Ostsee und die angrenzenden Gewässer. Deutsches Hydrographisches Institut, Hamburg.
- BREY, T., H. RUMOHR & S. ANKAR, 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy.—*J. exp. mar. Biol. Ecol.* **117**: 271-278.
- BRYANT, D.M. & J. LENG, 1975. Feeding distribution and behaviour of shelduck in relation to food supply.—*Wildfowl* **26**: 20-30.
- BUNSKOEKE, E.J., B.J. ENS, J.B. HULSCHER & S. DE VLAS, 1994. Prey choice of the oystercatcher *Haematopus ostralegus* during the breeding season.—*Ardea*, in press.
- BUXTON, N.E. & C.M. YOUNG, 1981. The food of the shelduck in north-east Scotland.—*Bird Study* **28**: 41-48.
- CADÉE, G.C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea.—*Neth. J. Sea Res.* **10**: 440-460.
- CAYFORD, J.T. & J.D. GOSS-CUSTARD, 1990. Seasonal changes in the size selection of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*: an optimality approach.—*Anim. Behav.* **40**: 609-624.
- CHAMBERS, M.R. & H. MILNE, 1975. The production of *Macoma balthica* (L.) in the Ythan estuary.—*Estuar. coast. Mar. Sci.* **3**: 443-455.
- , 1979. Seasonal variation in the condition of some intertidal invertebrates of the Ythan estuary, Scotland.—*Estuar. coast. mar. Sci.* **8**: 411-419.
- CRAEYMEERSCH, J.A., P.M.J. HERMAN & P.M. MEIRE, 1986. Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S.W. Netherlands).—*Hydrobiologia* **133**: 107-115.
- CURTIS, D.J., C.G. GALBRAITH, J.C. SMYTH & D.B.A. THOMPSON, 1985. Seasonal variations in prey selection by estuarine black-headed gulls (*Larus ridibundus*).—*Estuar. coast. Shelf Sci.* **21**: 75-90.
- DAAN, S. & P. KOENE, 1981. On the timing of foraging flights by oystercatchers, *Haematopus ostralegus*, on tidal flats.—*Neth. J. Sea Res.* **15**: 1-22.
- DALES, R.P., 1951. An annual history of a population of



- Nereis diversicolor* O.F. Müller.—Biol. Bull. **101**: 131-137.
- DANKERS, N. & J.J. BEUKEMA, 1983. Distributional patterns of macrozoobenthic species in relation to some environmental factors. In: W.J. WOLFF. Ecology of the Wadden Sea. Balkema, Rotterdam. Vol. 1, Part 4: 69-105.
- DANKERS, N. & M.A. BINSBERGEN, 1984. Zeeduizendpoten (*Nereis diversicolor*) trekken ook.—Levende Natuur **85**: 14-15.
- DARE, P.J., 1975. Settlement, growth and production of the mussel, *Mytilus edulis* L., in Morecambe Bay, England.—Fishery Invest., Lond., Ser. 2, **28**: 1-25.
- DARE, P.J. & D.B. EDWARDS, 1975. Seasonal changes in flesh weight and biochemical composition of mussels (*Mytilus edulis* L.) in the Conwy estuary, North Wales.—J. exp. mar. Biol. Ecol. **18**: 89-97.
- DAUVIN, J. & M. JONCOURT, 1989. Energy values of marine benthic invertebrates from the western English Channel.—J. mar. biol. Ass. U.K. **69**: 589-595.
- DAVIDSON, P.E., 1971. Some foods taken by waders in Morecambe Bay, Lancashire.—Bird Study **18**: 177-186.
- DE GLOPPER, R.J., 1967. Over de bodemgesteldheid van het waddengebied.—Van Zee tot Land **43**. Tjeenk Willink, Zwolle.
- DE LEEUW, J.J. & M.R. VAN EERDEN, 1992. Size selection in diving tufted ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*.—Ardea **80**: 353-362.
- DE VLAS, S., A.J. BUNSKOEKE, B.J. ENS & J.B. HULSCHER, 1994. Tidal changes between *Nereis diversicolor* and *Macoma balthica* as main prey for oystercatcher *Haematopus ostralegus*.—Ardea, in press.
- DE VOOYS, C.G.N., 1975. Glycogen and total lipids in the lugworm (*Arenicola marina*) in relation to reproduction.—Neth. J. Sea Res. **9**: 311-319.
- DE VRIES, G., 1969. Verslag kleine meeuw, in het bijzonder kapmeeuw.—Schierboek **3**: 105-144.
- DE WILDE, P.A.W.J. & E.M. BERGHUIS, 1978. Laboratory experiments on the spawning of *Macoma balthica*; its implication for production research. In: D.S. MCLUSKY & A.J. BERRY. Physiology and behaviour of marine organisms. Pergamon, Oxford: 375-284.
- , 1979. Spawning and gamete production in *Arenicola marina* in the Netherlands, Wadden Sea.—Neth. J. Sea. Res. **13**: 503-511.
- DEKINGA, A. & T. PIERSMA, 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*.—Bird Study **40**: 144-156.
- DIRKSEN, S., M. VAN WOUWE & H. SMIT, 1992. Watervogels in het zoutwatergetijdengebied Ventjagersplaten (Haringsvliet) in relatie tot chironomiden en de waterstand. Report RIZA, Dordrecht.
- DUGAN, P.J., 1981. The importance of nocturnal feeding in shorebirds: a consequence of increased invertebrate prey activity. In: N.V. JONES & W.J. WOLFF. Feeding and survival strategies of estuarine organisms. Plenum Publishing Corporation, London: 251-260.
- DURELL, S.E.A. LE V. DIT, J.D. GOSS-CUSTARD & R.W.G. CALDOW, 1993. Sex-related differences in diet and feeding method in the oystercatcher *Haematopus ostralegus*.—J. Anim. Ecol. **62**: 205-215.
- EDWARDS, D.C. & J.D. HUEBNER, 1977. Feeding and growth rates of *Polinices duplicatus* preying of *Mya arenaria* at Barnstable Harbor, Massachusetts.—Ecology **58**: 1218-1236.
- ENGELMOER, M. & A-M. BLOMERT, 1985. Broedbiologie van de kluut langs de Friese waddenkust seizoen 1983.—RIJP report 1985-39Abw, Lelystad.
- ENGELMOER, M., T. PIERSMA, W. ALTENBURG & R. MES, 1984. The Banc d'Arguin. In: P.R. EVANS, J.D. GOSS-CUSTARD & W.G. HALE, Coastal waders and wildfowl in winter.—Cambridge University Press, Cambridge: 293-310.
- ENS, B.J., 1982. Size selection in mussel-feeding oystercatchers.—Wader Study Group Bull. **34**: 16-20.
- ENS, B.J. & L. ZWARTS, 1980. Wulpen op het wad van Moddergat.—Watervogels **5**: 108-120.
- ENS, B.J., P. ESSELINK & L. ZWARTS, 1990. Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*.—Anim. Behav. **39**: 219-230.
- ESSELINK, P. & L. ZWARTS, 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*.—Mar. Ecol. Prog. Ser. **56**: 243-254.
- ESSINK, K., H.L. KLEEF, W. VISSER & P. TYDEMAN, 1985. Population dynamics of the ragworm *Nereis diversicolor* in the Dollard (Ems estuary) under changing conditions of stress by organic pollution. In: J.S. GRAY & M.E. CHRISTIANSEN. Marine Biology of polar regions and effects of stress on marine organisms: 585-600.
- EVANS, P.R., 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. In: E. NAYLOR & R.G. HARTNOLL. Cyclic phenomena in marine plants and animals. Pergamon Press, New York: 357-366.
- , 1988. Predation of intertidal fauna by shorebirds in relation to time of the day, tide and year. In: G. CHELAZZI & M. VANNINI. Behavioral adaptation to intertidal life. Plenum Press, New York: 65-78.
- EVERARDS, K., 1973. De groei van *Mytilus edulis* L. als functie van de onderdompelingstijd.—NIOZ report 1973-2, Texel.
- FARKE, H. & E.M. BERGHUIS, 1979. Spawning, larval development and migration of *Arenicola marina* under field conditions in the western Wadden Sea.—Neth. J. Sea Res. **13**: 529-535.
- FLACH, E.C., 1992. The influence of four macrozoobenthic species on the abundance of the amphipod *Corophium volutator* on tidal flats in the Wadden Sea.—Neth. J. Sea Res. **29**: 379-394.
- GENDRON, R.P., 1986. Searching for cryptic prey: evidence for optimal search rate and the formation of search images in quail.—Anim. Behav. **34**: 898-912.
- GERRITSEN, A.F.G., 1988. General and specific patterns in foraging acts of sandpipers (*Calidris*). In: A.F.G. GERRITSEN. Feeding techniques and the anatomy of the bill in sandpipers (*Calidris*). Thesis University of Leiden: 91-137.
- GERRITSEN, A.F.G. & A. MEIBOOM, 1986. The role of touch in prey density estimation by *Calidris alba*.—Neth. J. Zool. **36**: 530-562.
- GETTY, T. & H.R. PULLIAM, 1993. Search and prey detection by foraging sparrows.—Ecology **74**: 734-742.
- GILBERT, M.A., 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.).—Biol. Bull. **145**: 119-126.
- GOSS-CUSTARD, J.D., 1969. The winter feeding ecology of the redshank *Tringa totanus*.—Ibis **111**: 338-356.
- , 1970a. The responses of redshank (*Tringa totanus*) to spatial variations in the density of their prey.—J. Anim. Ecol. **39**: 91-113.
- , 1970b. Feeding dispersion in some overwintering



- wading birds. In: J.H. CROOK. Social behaviour in birds and mammals. Academic Press, London : 3-35.
- , 1976. Variation in the dispersion of redshank *Tringa totanus* on their winter feeding grounds.—*Ibis* **118**: 257-263.
- , 1977a. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density.—*J. Anim. Ecol.* **46**: 1-19.
- , 1977b. Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field.—*Anim. Behav.* **25**: 10-29.
- , 1977c. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii).—*J. appl. Ecol.* **14**: 721-739.
- GOSS-CUSTARD, J.D. & S.E.A. LE V. DIT DURELL, 1983. Individual and age differences in the feeding ecology of oystercatchers *Haematopus ostralegus* wintering on the Exe estuary.—*Ibis* **125**: 155-171.
- , 1987. Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. Foraging efficiency and interference.—*J. Anim. Ecol.* **56**: 521-536.
- GOSS-CUSTARD, J.D., R.A. JENYON, R.E. JONES, P.E. NEWBERY & R. LE B. WILLIAMS, 1977a. The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii).—*J. appl. Ecol.* **14**: 701-719.
- GOSS-CUSTARD, J.D., D.G. DAY & R.M. BLINDELL, 1977b. The density of migratory and overwintering redshank *Tringa totanus* (L.) and curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England.—*Estuar. coast. Mar. Sci.* **5**: 497-510.
- GRATTO, G.W., L.H. THOMAS, & C.L. GRATTO, 1984. Some aspects of the foraging ecology of migrant juvenile sandpipers in the outer Bay of Fundy.—*Can. J. Zool.* **62**: 1889-1892.
- HABEKOTTÉ, B., 1987. Scholeksters en slijkgapers.—Student report University of Groningen, Groningen.
- HANCOCK, D.A. & A.E. URQUHART, 1964. Mortalities of edible cockles (*Cardium edule* L.) during the severe winter of 1962-63.—*J. Anim. Ecol.* **33**: 176-178.
- HANCOCK, D.A. & A. FRANKLIN, 1972. Seasonal changes in the condition of the edible cockle (*Cardium edule* L.).—*J. appl. Ecol.* **9**: 567-579.
- HAWKINS, C.M., 1985. Population carbon budgets and the importance of the amphipod *Corophium volutator* in the carbon transfer on a Cumberland Basin mudflat, upper Bay of Fundy, Canada.—*Neth. J. Sea Res.* **19**: 165-176.
- HEPPLESTON, J.B., 1971. The feeding ecology of oystercatchers (*Haematopus ostralegus* L.) in winter in northern Scotland.—*J. Anim. Ecol.* **40**: 651-672.
- HICKLIN, P.W. & P.C. SMITH, 1984. Selection of foraging sites and invertebrates prey by migrant semipalmated sandpipers *Calidris pusilla* (Pallas) in Minas Bay, Bay of Fundy.—*Can. J. Zool.* **62**: 2201-2210.
- HOLTHUIJZEN, Y.A., 1979. Het voedsel van de zwarte ruit *Tringa erythropus* in de Dollard.—*Limosa* **52**: 22-33.
- HUGHES, R.N., 1970a. Population dynamics of the bivalve *Scrobicularia plana* (da Costa) on an intertidal mud-flat in North Wales.—*J. Anim. Ecol.* **39**: 333-356.
- , 1970b. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (Da Costa).—*J. Anim. Ecol.* **39**: 357-379.
- HULSCHER, J.B., 1976. Localisation of cockles (*Cardium edule* L.) in darkness and daylight.—*Ardea* **64**: 292-310.
- , 1982. The oystercatcher as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea.—*Ardea* **70**: 89-152.
- , 1990. Survival of oystercatchers during hard winter weather.—*Ring* **13**: 167-172.
- HULSCHER, J.B. & B.J. ENS, 1991. Somatic modifications of feeding system structures due to feeding on different foods with emphasis on changes in bill shape in oystercatchers.—*Acta XX Congr. Intern. Ornith.*: 889-896.
- HUMMEL, H., 1985. Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea.—*Neth. J. Sea Res.* **19**: 52-76.
- JENSEN, K.T., 1985. The presence of the bivalve *Cerastoderma edule* affects migration, survival and reproduction of the amphipod *Corophium volutator*.—*Mar. Ecol. Prog. Ser.* **25**: 269-277.
- JENSEN, K.T. & L.D. KRISTENSEN, 1990. A field experiment on competition between *Corophium volutator* (Pallas) and *Corophium arenarium* Crawford (Crustacea: Amphipoda): effects on survival, reproduction and recruitment.—*J. exp. mar. Biol. Ecol.* **137**: 1-24.
- JONES, D. & J. CLARE, 1977. Annual and long-term fluctuations in the abundance of fish species inhabiting an intertidal mussel bed in Morecambe Bay, Lancashire.—*Zool. J. Limn. Soc.* **60**: 117-172.
- KERSTEN, M. & T. PIERSMA, 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life.—*Ardea* **75**: 175-187.
- KIRKEGAARD, J.B., 1978. Settling, growth and life span of some polychaetes from Danish waters.—*Meddr. Danm. Fisk.- og Havunders. N.S.* **7**: 447-496.
- KLEIN BRETELER, W.C.M., 1975. Food consumption, growth and energy metabolism of juvenile shore crabs, *Carcinus maenas*.—*Neth. J. Sea Res.* **9**: 255-272.
- KREBS, J.R. & A. KACELNIK, 1991. Decision-making. In: J.R. KREBS & N.B. DAVIES. Behavioural ecology: 105-136. Blackwell, Oxford.
- LINKE, P., 1939. Die Biota des Jadebusenwattes.—*Helgoländer Meeresunters.* **1**: 201-348.
- LITTLE, C. & W. NIX, 1976. The burrowing and floating behaviour of the gastropod *Hydrobia ulvae*.—*Estuar. coast. Mar. Sci.* **4**: 537-544.
- MADSEN, P.B. & K. JENSEN, 1987. Population dynamics of *Macoma balthica* in the Danish Wadden Sea in an organically enriched area.—*Ophelia* **27**: 197-208.
- MATHIVAT-LALLIER, M.H. & C. CAZAUX, 1991. Life-history of *Nephtys hombergii* in Arcachon Bay.—*Estuar. Coast. Shelf. Sci.* **32**: 1-9.
- MAYNES, E. & D.I.D. HOWIE, 1985. Biochemical composition and sediment temperature in relation to the reproductive cycle in the lugworm *Arenicola marina*.—*Neth. J. Sea Res.* **19**: 111-118.
- MEADOWS, P.S., 1964. Experiments on substrate selection by *Corophium volutator* (Pallas): depth selection and population density.—*J. exp. Biol.* **41**: 677-687.
- MEADOWS, P.S. & A.A. RUAGH, 1981. Temperature preferences and activity of *Corophium volutator* (Pallas) in a new choice apparatus.—*Sarsia* **66**: 67-72.
- MEININGER, P.L., A.-M. BLOMERT & E.C.L. MARTEIJN, 1991. Watervogelsterfte in het Deltagebied, ZW-Nederland, gedurende de drie koude winters van 1985, 1986 en

- 1987.—*Limosa* **64**: 89-102.
- MEIRE, P.M., 1994a. Interacation between oystercatchers (*Haematopus ostralegus*) and mussels (*Mytilus edulis*): implications from optimal foraging theory.—*Ardea*, in press.
- , 1994b. Feeding behaviour of oystercatcher during a period of tidal manipulation.—*Ardea*, in press.
- MEIRE, P.M. & A. ERVYNCK, 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*).—*Anim. Behav.* **34**: 1427-1435.
- METCALFE, N.B., 1985. Prey detection by intertidally feeding lapwing.—*Z. Tierpsychol.* **67**: 45-57.
- METTAM, C., 1979. Seasonal changes in populations of *Nereis diversicolor* O.F. Müller from the Severn estuary, U.K. In: E. NAYLOR & R.G. HARTNOLL. Cyclic phenomena in marine plants and animals. Pergamon Press, New York: 123-130.
- MÖLLER, P., 1985. Production and abundance of juvenile *Nereis diversicolor*, and oogenic cycle of adults in shallow waters of western Sweden.—*J. mar. biol. Ass. U.K.* **65**: 603-616.
- MÖLLER, P. & R. ROSENBERG, 1982. Production and abundance of the amphipod *Corophium volutator* on the west coast of Sweden.—*Neth. J. Sea Res.* **16**: 127-140.
- MOURITSEN, K.N. & K.T. JENSEN, 1992. Choise of microhabitat in tactile foraging *Calidris alpina*: the importance of sediment penetrability.—*Mar. Ecol. Prog. Ser.* **85**: 1-8.
- MYERS, J.P. S.L. WILLIAMS & F.A. PTELKA, 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans.—*Can. J. Zool.* **58**: 1564-1574.
- NAPOLITANO, G.E. & R.G. ACKMAN, 1989. Lipids and hydrocarbons in *Corophium volutator* from Minas Basin, Nova Scotia.—*Mar. Biol.* **100**: 333-338.
- NORUSIS, M.J., 1988. SPSS/PC+ V2.0 Base manual. SPSS Inc., Chicago.
- OLIVE, P.J.W. & P.R. GARWOOD, 1981. Gametogenic cycle and population structure of *Nereis (Hediste) diversicolor* and *Nereis (Nereis) pelagica* from north-east England.—*J. mar. biol. Ass. U.K.* **61**: 193-213.
- OLIVE, P.J.W., M.G. BENTLEY, N.H. WRIGHT & P.J. MORGAN, 1985. Reproductive energetics, endocrinology and population dynamics of *Nephtys caeca* and *N. hombergi*.—*Mar. Biol.* **88**: 235-246.
- OYENKAN, J.A., 1986. Population dynamics and secondary production in an estuarine population of *Nephtys hombergii* (Polychaeta: Nephtyidae).—*Mar. Biol.* **93**: 217-223.
- PAINE, R.T., 1966. Endothermy in bomb calorimetry.—*Limnol. Ocean.* **11**: 126-129.
- PEKKARINEN, M. 1983. Seasonal changes in condition and biochemical constituents in the soft part of *Macoma balthica* (Lamellibranchiata) in the Tvärminne brackish water area (Baltic Sea).—*Ann. Zool. Fennici* **20**: 311-322.
- PIENKOWSKI, M.W., 1977. Differences in habitat requirements and distribution pattern of plovers and sandpipers as investigated by studies of feeding behaviour.—*Verh. orn. Ges. Bayern* **23**: 105-124.
- , 1983a. The effects of environmental conditions on feeding rates and prey-selection of shore plovers.—*Ornis Scand.* **14**: 227-238.
- , 1983b. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators.—*Mar. Ecol. Prog. Ser.* **11**: 141-150.
- PIERSMA, T., in press. Energetic constraints on the non-breeding distribution of coastal shorebirds.—*Wader Study Group Bull.*, in press.
- PIERSMA, T., A. KOOLHAAS & A. DEKINGA, 1993a. Interactions between stomach strength and diet choice in shorebirds.—*Auk* **110**: in press.
- PIERSMA, T., R. HOEKSTRA, A. DEKINGA, A. KOOLHAAS, P. WOLF, P. BATTLE & P. WIERSMA, 1993b. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea, in relation to food, friends and foes.—*Neth. J. Sea Res.* **31**: 331-357.
- PIETERS, H., J.H. KLUYTMANS, W. ZURBURG & D.I. ZANDEE, 1979. The influence of seasonal changes on energy metabolism in *Mytilus edulis* (L.). I. Growth rate and biochemical composition in relation to environmental parameters and spawning. In: E. NAYLOR & R.G. HARTNOLL. Cyclic phenomena in marine plants and animals. Pergamon Press, New York: 285-293.
- PIETERS, H., J.H. KLUYTMANS & D.I. ZANDEE, 1980. Tissue composition and reproduction of *Mytilus edulis* in relation to food availability.—*Neth. J. Sea Res.* **14**: 349-361.
- PRATER, A.J., 1972. The ecology of Morecambe Bay III. The food and feeding habits of knot (*Calidris canutus*) in Morecambe Bay.—*J. appl. Ecol.* **9**: 179-194.
- , 1981. Estuary birds of Britain and Ireland. Poyser, Calton.
- PROKOSCH, P., 1988. Das Schleswig-Holsteinische Wattenmeer als Frühjahrs-Aufenthaltsgebiet Arktischer Wattvogel-Populationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*, L. 1758), Knutt (*Calidris canutus*, L. 1758) und Puhlschneppe (*Limosa lapponica*, L. 1758).—*Corax* **12**: 273-442.
- RATCLIFFE, P.J., N.V. JONES & N.J. WALTERS, 1981. The survival of *Macoma balthica* (L.) in mobile sediments. In: N.V. JONES & W.J. WOLFF. Feeding and survival strategies of estuarine organisms. Plenum Publishing Corporation, London: 91-108.
- READING, C.J. & S. MCGRORTY, 1978. Seasonal variation in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds.—*Estuar. coast. mar. Sci.* **6**: 135-144.
- SMIDT, E.L.B., 1951. Animal production in the Danish Wadden Sea.—*Meddr. Danm. Fisk.-og Havunders.* **11**: 1-151.
- SMIT, C., 1982. Wader and waterfowl counts in the international Wadden Sea area: the results of the 1981-1982 season.—*Wader Study Group Bull.* **24**: 135-139.
- , 1983a. The importance of the Wadden Sea for birds. In: W.J. WOLFF. Ecology of the Wadden Sea. Balkema, Rotterdam. Vol. 2 Part 6: 280-289.
- , 1983b. Production of invertebrates and consumption in the Dutch Wadden Sea. In: W.J. WOLFF. Ecology of the Wadden Sea. Balkema, Rotterdam. Vol. 2, Part 6: 290-301.
- SMITH, P.C., 1975. A study of the winter feeding ecology and behaviour of the bar-tailed godwit (*Limosa lapponica*).—Ph.D. thesis, University of Durham.
- SUMMERS, R.W., S. SMITH, M. NICOLL & N.K. ATKINSON, 1990. Tidal and sexual differences in the diet of purple sandpipers *Calidris maritima* in Scotland.—*Bird Study* **37**: 187-194.
- SUTHERLAND, W.J., 1982a. Do oystercatchers select the most profitable cockles?—*Anim. Behav.* **30**: 857-861.
- , 1982b. Spatial variation in the predation of cockles by

- oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality.—*J. Anim. Ecol.* **51**: 491-500.
- SUTHERLAND, W.J. & B.J. ENS, 1987. The criteria determining the selection of mussels *Mytilus edulis* by oystercatchers *Haematopus ostralegus*.—*Behaviour* **103**: 187-202.
- SWENNEN, C., 1971. Het voedsel van de groenpootruiter, *Tringa nebularia* tijdens het verblijf in het Nederlandse Waddenzeegebied.—*Limosa* **44**: 71-83.
- , 1976. Populatie-structuur en voedsel van de eider-eend *Somateria m. mollissima* in de Nederlandse Waddenzee.—*Ardea* **64**: 311-371.
- SWENNEN, C., L.L.M. DE BRUIJN, P. DUIVEN, M.F. LEOPOLD & E.C.L. MARTEIJN, 1983. Differences in bill form of the oystercatcher *Haematopus ostralegus*, a dynamic adaptation to specific foraging techniques.—*Neth. J. Sea Res.* **17**: 57-83.
- SZANIAWSKA, A., 1984. Seasonal changes in weight and energy content in *Crangon crangon* population of Gdansk Bay.—*Ophelia* **3**: 247-251.
- SZÉKELY, T. & Z. BAMBERGER, 1992. Predation of waders (Charadrii) on prey populations: an enclosure experiment.—*J. Anim. Ecol.* **61**: 447-456.
- TOWNSEND, D.J., 1981. The importance of field feeding to the survival of wintering male and female curlews *Numenius arquata* on the Tees estuary. In: N.V. JONES & W.J. WOLFF. Feeding and survival strategies of estuarine organisms. Plenum Publishing Corporation, London: 261-273.
- VADER, W.J.M., 1964. A preliminary investigation into the reactions of the infauna of the tidal fluctuations in water level.—*Neth. J. Sea Res.* **2**: 189-222.
- VAN BEEK, F.A., 1976. Aantallen, groei, productie en voedselopname van de zandgrondel (*P. minutus*) en de wadgrondel (*P. microps*) op het Balgzand.—NIOZ report 1976-9, Texel.
- VAN HEEZIK, Y.M., A.F.C. GERRITSEN & C. SWENNEN, 1983. The influence of chemoreception on the foraging behaviour of two species of sandpiper, *Calidris alba* and *Calidris alpina*.—*Neth. J. Sea Res.* **17**: 47-56.
- VAN DER VEER, H.W., L. PIHL, L. & M.J.N. BERGMAN, 1990. Recruitment mechanisms in North Sea plaice *Pleuronectes platessa*.—*Mar. Ecol. Prog. Ser.* **64**: 1-12.
- VAN DER VEER, H.W., M.J.N. BERGMAN, R. DAPPER & J.I.J. WITTE, 1991. Population dynamics of an intertidal 0-group flounder *Platichthys flesus* population in the western Dutch Wadden Sea.—*Mar. Ecol. Prog. Ser.* **73**: 141-148.
- VAN DER VOET, I., 1967. Voedselgebruik en fourageergedrag van de bonte strandloper (*Calidris alpina* (L.)). NIOZ Report 1968-2, Texel.
- VERKUIL, Y., A. KOOLHAAS & J. VAN DER WINDEN, 1993. Wind effects on prey availability: how northward migrating waders use brackish and hypersaline lagoons in the Sivash, Ukraine.—*Neth. J. Sea Res.* **31**: 359-374.
- VERWEY, J., 1958. Orientation in migrating marine animals and a comparison with that of other migrants.—*Archs néerl. Zool.* **13**: 418-445.
- WACASEY, J.W. & E.G. ATKINSON, 1987. Energy values of marine benthic invertebrates from the Canadian Arctic.—*Mar. Ecol. Prog. Ser.* **39**: 243-250.
- WANINK, J. & L. ZWARTS, 1985. Does an optimally foraging oystercatcher obey the functional response?—*Oecologia (Berl.)* **67**: 98-106.
- WERNER, B., 1956. Über die Winterwanderung von *Arenicola marina* L. (Polychaeta sedentaria).—*Helgoländer Meeresunters.* **5**: 353-378.
- WIERMA, P. & T. PIERSMA, in press. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots.—*Condor*, in press.
- WINTHER, U. & J.S. GRAY, 1985. The biology of *Mya arenaria* (Bivalvia) in the eutrophic inner Oslofjord.—*Sarsia* **70**: 1-9.
- WOLFF, W.J., 1991. The interaction of benthic macrofauna and birds in tidal flat estuaries: a comparison of the Banc d'Arguin, Mauritania, and some estuaries in the Netherlands. In: M. ELLIOTT & J-P. DUCROTOY. Estuaries and coasts: spatial and temporal intercomparisons. Olsen & Olsen, Fredensborg: 299-306.
- WORRALL, D.H., 1984. Diet of the Dunlin *Calidris alpina* in the Severn estuary.—*Bird Study* **31**: 203-212.
- ZEGERS, P.M. & N.D. KWINT, 1992. Vogeltellingen in het Nederlandse deel van het Waddengebied 1979-1990.—SOVON-report 1992/14, SOVON, Beek-Ubbergen.
- ZWARTS, L., 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau.—*Ardea* **73**: 3-12.
- , 1986. Burying depth of the benthic bivalve *Scrobicularia plana* (da Costa) in relation to siphon-cropping.—*J. exp. mar. Biol. Ecol.* **101**: 25-39.
- , 1988a. Numbers and distribution of coastal waders in Guinea-Bissau.—*Ardea* **76**: 42-55.
- , 1988b. De bodemfauna van de Fries-Groningse waddenkust.—*Flevobericht* **294**: 1-191.
- , 1990. Increased prey availability drives premigration hyperphagia in whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time.—*Ardea* **78**: 279-300.
- , 1991. Seasonal variation in body condition of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea.—*Neth. J. Sea Res.* **28**: 231-245.
- ZWARTS, L. & A.M. BLOMERT, 1990. Selectivity of whimbrels feeding on fiddler crabs explained by components specific digestibilities.—*Ardea* **78**: 193-208.
- , 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available.—*Mar. Ecol. Prog. Ser.* **83**: 113-128.
- ZWARTS, L. & R.H. DRENT, 1981. Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In: N.V. JONES & W.J. WOLFF. Feeding and survival strategies of estuarine organisms. Plenum Publishing Corporation, London: 193-216.
- ZWARTS, L. & P. ESSELINK, 1989. Versatility of male curlews (*Numenius arquata*) preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availability.—*Mar. Ecol. Prog. Ser.* **56**: 255-269.
- ZWARTS, L. & J.H. WANINK, 1984. How oystercatchers and curlews successively deplete clams. In: P.R. EVANS, J.D. GOSS-CUSTARD & W.G. HALE. Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 69-83.
- , 1989. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves.—*Mar. Biol.* **100**: 227-240.
- , 1991. The macrobenthos fraction accessible to waders may represent marginal prey.—*Oecologia (Berl.)* **87**: 581-587.

- ZWARTS, L., A-M. BLOMERT, B.J. ENS, R. HUPKES & T.M. VAN SPANJE, 1990a. Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania?—*Ardea* **78**: 39-52.
- ZWARTS, L., A-M. BLOMERT & R. HUPKES, 1990b. Increase of feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania.—*Ardea* **78**: 237-256.
- ZWARTS, L., A-M. BLOMERT & J.H. WANINK, 1992. Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer.—*Mar. Ecol. Prog. Ser.* **83**: 129-139.
- ZWARTS, L., J.T. CAYFORD, J.B. HULSCHER, M. KERSTEN, P.M. MEIRE & P. TRIPLET, in press. Size selection and intake rate in oystercatcher. In: J.D. GOSS-CUSTARD. The behavioural ecology of the oystercatcher. Oxford University Press, Oxford, in press.