Wader populations and macrozoobenthos in a changing estuary: the Oosterschelde

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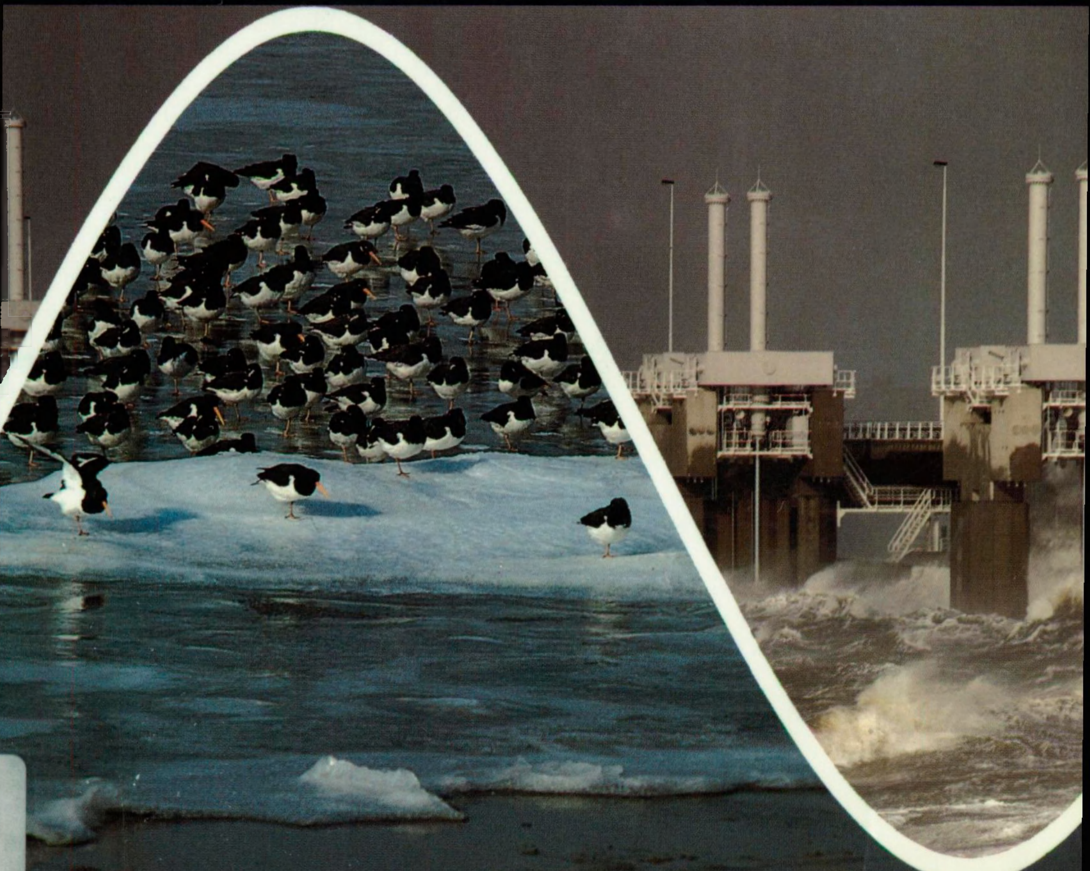

Patrick Meire

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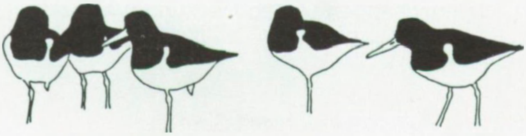

Steltloper populaties en macrozoöbenthos in een veranderend estuarium:
de Oosterschelde (Nl.)

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To many people who live and work around estuaries it is the unceasing ebb and flow of the tides and the constantly changing light and seasons that contribute strongly to their attraction. (Davidson *et al.*, 1991).

Chapter 1

INTRODUCTION

1. Wetland habitat loss: a widespread and major environmental problem.

One of the major environmental problems in the twentieth century is, beyond doubt, the loss of natural habitats. Large areas are disappearing altogether at an ever increasing rate and the remaining sites are often fragmented and further subject to habitat degradation due to many causes, one of them being pollution (e.g., Jones, 1987). This has resulted in many plant and animal species becoming extinct. The population size of others declined dramatically leading to extinction, if no conservation measures will be taken. Only some species could take advantage of the human activities. Their range expanded and their population size increased, sometimes turning the species into a pest species.

Not all habitats, however, disappear at a similar rate. Due to their high productivity and their location near to the sea, wetlands in general and estuaries in particular have suffered large losses.

Estuaries are inlets of the sea reaching into a river valley as far as the upper limit of tidal rise (Fairbridge, 1980). Due to the tides and the mixing of fresh- and seawater the estuarine environment is characterized by many different gradients. The salinity varies from less than 0.5‰ to about 35‰. Together with salinity the concentrations of many other chemical components in the water column, such as nutrients, change. Exposition towards waves and current velocities vary greatly between sites. Fine sedimentary deposits, or muds, are a highly characteristic feature of estuaries, but depending on the current speed and the source of the sediments, gradients from very fluid mud layers to coarse sand banks occur. On top of this, many of the gradients fluctuate during a tidal cycle and/or seasonal. All these make estuaries very dynamic ecosystems. These gradients in environmental parameters are reflected in clear zonations of organisms. (e.g., Wolff, 1973; McLusky, 1981; Day *et al.*, 1989; Davidson *et al.*, 1991).

Estuaries also represent ecosystems with a very high biological productivity due to the continual input, trapping and recycling of sediments and nutrients coming both from the river and the sea (e.g., McLusky, 1981; Day *et al.*, 1989). The biological productivity results in their economic importance for shellfish fisheries and as nursery grounds for commercial fish (e.g., Day *et al.*, 1989).

The large food supply is also exploited by birds. Especially waders and waterfowl can occur in very large numbers and have therefore since long attracted the special attention of ornithologists (e.g., Prater, 1981). The occurrence of birds in estuaries is shortly described here, focused on the situation of the Dutch Delta area.

The most important groups of birds occurring in the estuaries of the Delta area (Oosterschelde and Westerschelde) are ducks, waders, geese, gulls and terns and grebes etc. Approximately 80 species occur regularly

(Saeys & Baptist, 1977; Meininger *et al.*, 1984, 1985, 1988; Meire *et al.*, 1989; Stuart *et al.*, 1990). For all these species estuaries are of vital importance in one or several stages in the birds' life cycle.

Although for some species like the Avocet (*Recurvirostra avosetta*), plovers and terns estuaries are important breeding areas (Meininger, 1991; 1992) the majority of birds is present outside the breeding season. Peak numbers of 300000 and 110000 waterbirds may be present in the Oosterschelde and Westerschelde respectively during winter. The majority of these birds are waders (both *Scolopacidae* and *Charadriidae*) that are nearly entirely dependent on intertidal areas outside the breeding season.

Fig. 1 summarizes the origins and destinations of birds occurring in the Delta. Birds breeding in the boreal, subarctic and arctic zone of Europe, Asia, Greenland and even North America migrate southward after the breeding season, some species as far as the West coast of Africa, and even South Africa. This annual migration routes of populations of waders and waterfowl between the breeding and wintering quarters, including the stopover areas, is known as the East Atlantic Flyway (Smit & Piersma, 1989). Within this flyway the Delta area is, next to the Wadden Sea and several British estuaries, very

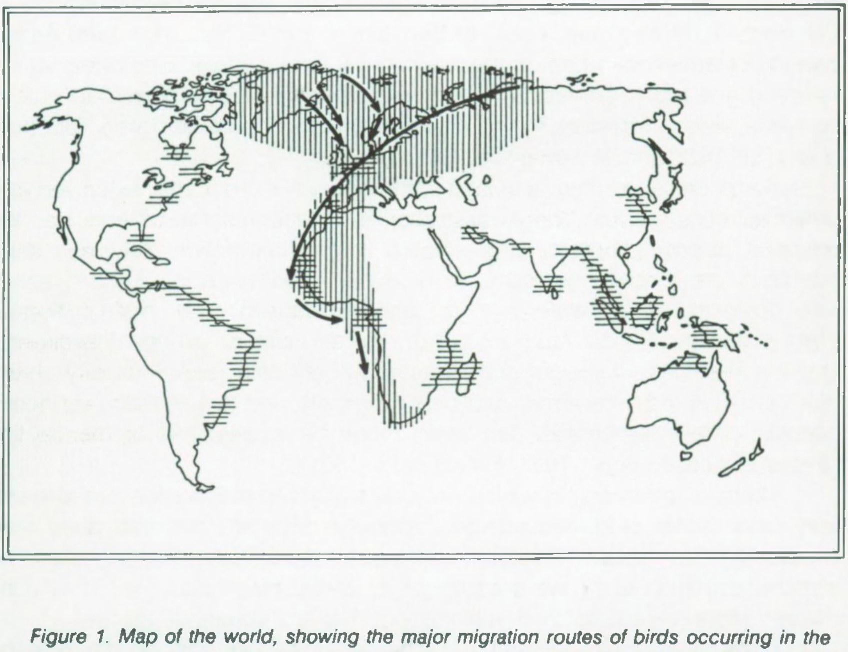

Figure 1. Map of the world, showing the major migration routes of birds occurring in the Delta area. (Horizontal hatching: major intertidal areas; vertical hatching: the East Atlantic flyway).

important either as a refueling site on migration between the breeding areas and the wintering grounds (in spring and autumn), or as a wintering site. The tidal areas of Western Europe acts as a turntable in the large scale movements of birds, which immediately stresses the international importance of tidal areas such as in the Delta.

The estuarine environment, although very rare (less than 0.01% of the earth surface) is severely threatened by different forms of human activities, one of the most important being reclamation (Smit *et al.*, 1987; Davidson *et al.*, 1991).

Land-claim on estuaries and coasts has been practiced since at least Roman times. However since about 1000 à 1100 the enclosure of saltmarshes became very widespread. These agricultural land-claims have been progressive and account for much of the overall estuarine habitat loss. More recent intertidal land-claims have been for a wider variety of industrial and port-related, urban, safety and recreational purposes. For British estuaries it seems typical that they have lost between a quarter and half of their intertidal habitats over the last 150-200 years (Davidson *et al.*, 1991) or 0.2-0.7% per year. Coastal wetlands along the United States coasts suffered a loss of 0.2% per year, from the fifties this even increased to 0.5% per year, similar to the British data (Gosselink & Baumann, 1980). Also on the European continent much intertidal area is lost. In e.g., the Seine estuary the intertidal surface declined from over 13000 ha in the middle of the 19th century to less than 3100 ha at present (Pieters *et al.*, 1991). In the international Wadden Sea large areas were reclaimed, the most spectacular being the closure of the "Zuiderzee" in 1932, but also more recently the "Lauwerszee", and a large area at the Danish/German border were reclaimed.

Some decades ago the land-claim originated from the extension of human activities out from the existing shoreline. These encroachments had in general a disproportionately large impact on the upper tidal flats and salt marshes. More recently the claims covered the whole range of intertidal shore levels down to the low-water mark or below (Davidson *et al.*, 1991). These claims have substantial and long-term indirect effects on the remaining estuarine habitats, through their reduction of tidal prism and hence modification of tidal currents, sediment transport and the location of tidal channels. These processes can even more be accelerated by dredging activities (Davidson *et al.*, 1991, Pieters *et al.*, 1991).

Intertidal areas are, however, not only subject to reclamation but also to many other facets of human activities. Although physically the area does not disappear, a collapse in the benthic populations due to pollution, different forms of recreation etc. have a similar effect as habitat reclamation. They are however more reversible than reclamation. For a throughout discussion of these different forms of human estuarine activities we refer to Langslow, (1981); Senner & Howe, (1984); Smit *et al.*, (1987) and Davidson *et al.* (1991).

2. Effects of estuarine habitat loss on waders

The loss of intertidal habitats, so important for birds, has stimulated a lot of research. However, although the effect of habitat loss on wader numbers and populations was a major subject in many studies (see e.g., Evans & Dugan, 1984; Goss-Custard, 1985; Goss-Custard & Durell, 1990; Evans, 1991; Sutherland & Goss-Custard, 1991; Goss-Custard *et al.*, 1991; Goss-Custard & Yates, 1992), hitherto, only in a limited number of studies data were available to assess the influence of habitat loss or degradation on wader numbers.
Some of these studies will be briefly reviewed here.

2.1 Tees estuary

The intertidal area of the Tees estuary (UK) decreased from about 2400 ha in the beginning of the nineteenth century to some 400 ha in 1973. At that time the South Area of Seal Sands was reclaimed leaving 140 ha if intertidal area in 1974. To estimate the effects of the loss of 260 ha of tidal flats, Evans *et al.* (1979) measured the size of the food resource and the number of birds (or bird-days) each unit of the resource could support. It was predicted that most wader species would have been unable to maintain the same number of bird-days of use of Seal Sands, when restricted to the reduced intertidal zone. The effects varied among shorebird species, but numbers generally declined in the season after reclamation and the percentage decrease was greater than, or equal to the percentage reduction in total feeding area. Next to a reduction in feeding area the birds suffered also a reduction in feeding time. This affected especially smaller species like Dunlin (*Calidris alpina*) and Redshank (*Tringa totanus*) (Evans, 1981). In later winters numbers of some species increased again but this was likely due to interactions between species (Evans, 1981).

2.2 Danish Wadden Sea

In 1980, 1100 ha of salt marsh and mudflats were reclaimed in the south eastern part of the Danish Wadden Sea. Eight out of twelve wader species decreased by 85% in this area and all important duck species by 60%, although some redistribution over a larger area was seen (Laursen *et al.*, 1983). According to Laursen *et al.* (1983) the changes are assumed to be due to shorter feeding time, as the reclamation removed the upper part of the intertidal area. No data on changes in the benthic invertebrates are available.

2.3 Firth of Forth estuary

McLusky *et al.* (1992) reviewed all the available information on intertidal habitat loss in the Firth of Forth estuary. Almost 50% or 2284 ha of the intertidal area present at the beginning of the 19th century has been land-claimed. Losses due to agriculture amount to 23%, for harbour developments to 11% and up to 16% for industrial purposes.

Within the Forth estuary, the effects of the closure of the Valleyfield bay area on birds could be assessed by comparing shorebird numbers (mean counts of the 3 winter months December-February) over five years prior to land-claim with two post land-claim years. This reclamation removed 20% of the birds feeding area. In five species (namely Oystercatcher, *Haematopus ostralegus*; Turnstone, *Arenaria interpres*; Bar-tailed Godwit, *Limosa lapponica*; Knot, *Calidris canutus* and Dunlin, *Calidris alpina*) numbers declined by more than 20% after the reclamation. Numbers of Wigeon (*Anas penelope*) and Redshank (*Tringa totanus*) did not change whereas Shelduck (*Tadorna tadorna*) and Curlew (*Numenius arquata*) numbers increased with 124 and 11% respectively. The changes were statistically significant for Bar-tailed Godwit and Dunlin (Bryant, 1987). No data are available, however, on the benthic food supply, nor is it clear whether the birds moved to adjacent feeding sites.

2.4 Spread of salt-marsh cord grass (Spartina anglica)

A special case of intertidal habitat loss was analysed by Goss-Custard & Moser (1988). In several British estuaries the salt-marsh cord grass (*Spartina anglica*) spread rapidly to form dense stands over large areas of estuarine mudflats. This spread could have similar effects to land-claim developments in that it prevents many waders from feeding in areas they would have used formerly. Dunlin numbers did decline in estuaries where *Spartina* has spread but not in those where the abundance of the plant has remained constant or decreased. Although there need not to be a causal relation between both events, there is a lot of circumstantial evidence that the Dunlins were affected by both the habitat loss and the reduced feeding time, due to the *Spartina* marshes expanding in the upper part of the tidal zone. The results also suggest that most birds displaced from estuaries where *Spartina* has spread have not yet been able to reestablish themselves elsewhere in Britain or in some other countries within the wintering range of Dunlin. Nor have Dunlin numbers increased in estuaries where *Spartina* has declined through natural die-back.

The major problem in this paper is that no information at all is available on the food supply of the birds. The rates of change in some estuaries were so high, almost 4000 birds per year over 8 years, so that nearly the entire population collapsed (e.g., from 20000 to less than 2000 in the Ribble, from 35000 to less than 5000 in Lindisfarne etc.). If this change in numbers should be due only to the spread of *Spartina* other species should have declined as well, which was not the case.

2.5 Clyde estuary

A special case of habitat loss is documented by Furness *et al.* (1986) for the Clyde estuary. Between the early seventies and the early eighties, major improvements were made to the sewage treatments works, resulting in an important reduction of the BOD and an increase of oxygen levels in the water of the estuary. Although the diversity of the macrobenthos did increase substantially (from 1-3 species per station in 1967-69 to 8-12 species per station in 1976-77) the densities of *Corophium* and *Nereis*, the major prey of the birds, did decrease. This could be attributed either to the reduced amount of organic matter in the estuary or to the increased predation of juvenile Flounders, *Platicthys flesus*, which returned to the estuary as the oxygen conditions improved. The decreased food availability was the cause for the quite dramatic decline of the numbers of Redshank, Dunlin and Lapwing (Furness *et al.*, 1986). From ringing recoveries there is no indication that the birds moved to other estuaries.

2.6 Plymouth Bay (USA)

Another special case of habitat loss is disturbance. Based on a long-term date set, Pfister *et al.*, (1992) found that species like Red Knot (*Calidris canutus*) and Short-billed Dowitcher (*Limnodromus griseus*) using the heavily disturbed front side of the beach declined more than the back-beach species, the decline being more pronounced than at other less disturbed places and more than the overall eastern North American population. No information on possible changes in the food supply is available however.

2.7 Conclusions

Although each of these studies mentioned are extremely valuable, they all show some shortcomings. Either the time series before and/or after the impact is short, -there are no data on the benthic food supply, -there is no information on where the displaced birds went to. Therefore firm conclusions cannot always be drawn. This clearly indicates that there is a need for further research into the effects of habitat loss on birds.

3. Estuarine habitat loss in the Dutch Delta area

In the Delta area of South West Netherland a substantial part of the intertidal area disappeared. After the disastrous storm flood of 1953, the Dutch government approved the so called "Delta Law" that foresaw in the closure of all estuaries with the exception of the Westerschelde and the Nieuwe Waterweg that are extremely important as shipping ways to the harbours of Antwerpen and Rotterdam (Knoester, 1984).

The different phases of these large coastal engineering works are summarized in Table 1 and Fig. 2. The smaller estuaries were closed first, and the experience obtained was used to construct ever larger dams.

Already in 1958 the storm surge barrier on the "Hollandse IJssel" was built. By the construction of the "Zandkreekdam" in 1960 and the "Veerse Gatdam" in 1961 the first sea arm, "Het Veerse Gat" was closed, and the brackish "Veerse Meer" was created. In 1969, due to the construction of the "Volkerak dam", the connection between the Oosterschelde, Krammer-Volkerak and the Rijn and Maas was restricted by the Volkerak locks. This

Table 1. Intertidal habitat loss in the Delta area of SW. Netherlands. For each estuary the closure dates of the different dams is given together with an estimate of the total intertidal surface before the start of the Delta plan and the surface lost. (*) For the Westerschelde the loss of intertidal area since 1958, due to land reclamation is given (Pieters et al., 1991).

estuary	dams	year	Surface	lost
Veerse Gat	Veerse Dam	1960		
	Zandkreekdam	1961	1500	1500
Haringvliet/Hollands Diep/Biesbosch	Volkerakdam	1970		
	Haringvlietdam	1971	3000	3000
Grevelingen	Grevelingendam	1965		
	Brouwersdam	1971	5500	5500
Oosterschelde	Markiezaatskade	1983	1410	1410
	Oesterdam	1986		
	Storm surge barrier	1986	12290	925
	Philipsdam	1987	3300	3300
Westerschelde	(*)		10600	2100
Total			37600	17735

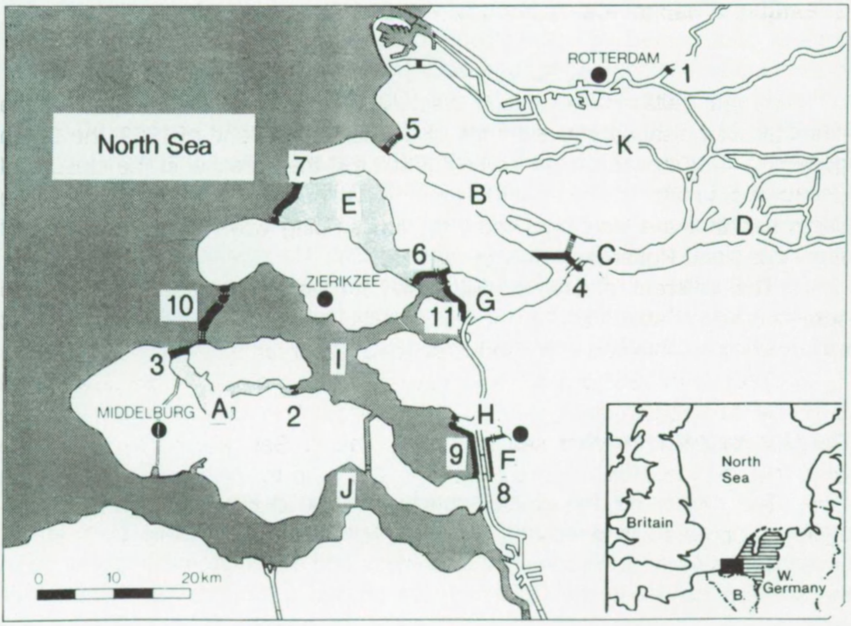

Figure 2. Map of the Delta area with the location of the different dams, estuaries and lakes. (1: storm surge barrier on the Hollandse IJssel; 2: Zandkreekdam; 3: Veerse Gatdam; 4: Volkerakdam; 5: Haringvlietdam; 6: Grevelingendam; 7: Brouwersdam; 8: Markiezaatskade; 9: Oesterdam; 10: storm surge barrier; 11: Philipsdam; A: Veerse Meer; B: Haringvliet; C: Hollands Diep; D: Biesbosch; E: Grevelingen; F: Markiezaat; G: Volkerakmeer; H: Zoommeer; I: Oosterschelde; J: Westerschelde; K: Oude Maas). The tidal areas are shaded in dark gray, the saline lakes in light gray and the fresh water lakes are given in white.

caused major changes in the Oosterschelde, the most important being an important increase in salinity. The "Haringvliet", "Hollands Diep" and "Biesbosch" were cut of from the sea by the construction of the "Haringvlietdam" in 1971. A very small tidal amplitude remains due to the "Oude Maas" which is still open. The water in the whole area became fresh. With the closure of the Haringvliet, the largest fresh water intertidal area in Europe, the "Biesbosch" was lost. Only along the "Zeeschelde" in Belgium and the "Oude Maas" this rare habitat is still present. The next estuary that was closed is the Grevelingen. The connection with the Krammer-Volkerak was closed already in 1965 by the "Grevelingendam" and the "Brouwersdam", finished in 1971, closed the estuary from the sea, turning it into a salt water lake.

The effects of the closures of Veerse Gat and Haringvliet on birds are not well documented. After the closure of the Grevelingen, an estuary adjacent to the Oosterschelde, wader numbers increased substantially in the Krammer-Volkerak, the northern branch of the Oosterschelde (Leewis *et al.*, 1984; Meininger *et al.*, 1984) and numbers of Oystercatchers and Bar-tailed Godwits increased abruptly on a large tidal flat in the mouth of the Oosterschelde (Van Latesteijn & Lambeck, 1986; Lambeck *et al.*, 1989). There is no evidence that wader numbers in the whole Delta area of South-West Netherlands decreased after the closure of the estuaries Veerse Gat, Haringvliet and Grevelingen (Saeijs & Baptist, 1977; Leewis *et al.*, 1984; Meininger *et al.*, 1984). However next to a loss of intertidal habitat many other factors in the area changed as well, making it difficult to interpret these data.

The Oosterschelde works

The closure of the Oosterschelde, with an 8 km long dam, through channels up to 50 m deep had to be the final step of the Delta plan. In the seventies, however, environmental awareness and the economic importance of the shellfish culture in the Oosterschelde caused a long lasting debate over whether or not the Oosterschelde should be closed or not (Stuurgroep Oosterschelde, 1982). Finally, the government decided in 1976 to build a storm surge barrier instead of a closed barrage in the mouth of the Oosterschelde. This is supposed to be a compromise between safety, economy and environment.

The storm surge barrier itself consists of 65 pylons in the three channels that connect the Oosterschelde with the North Sea. Large gates are suspended between the pylons (Fig. 3). They are normally raised well above the high water level. In this way the estuary remains under the influence of the tides. During storm floods, when the water level is expected to rise above 3m NAP (Dutch ordnance level), the gates are lowered, closing the estuary from the sea. In addition to the storm surge barrier additional dams more inland were built. In 1983 the "Markiezaatskade" was built, closing the Markiezaat. This was followed by the closure of the Oesterdam in 1986 and the Philipsdam in 1987. Behind these dams, the Volkerak/Zoommeer was created. These secondary dams were necessary first because the connection between the Schelde and the Rijn ("de Schelde-Rijn verbinding") had to be in a tideless environment according to a treaty between Belgium and The Netherlands and second because reducing the total surface of the estuary increased the tidal amplitude in the remaining part (Knoester *et al.*, 1984).

The construction of the storm surge barrier and the secondary dams caused important changes in the Oosterschelde. For more details about both the coastal engineering works and the effects on the system we refer to Smaal & Boeije (1991) and Nienhuis & Smaal, (1993). Here we shortly summarize the

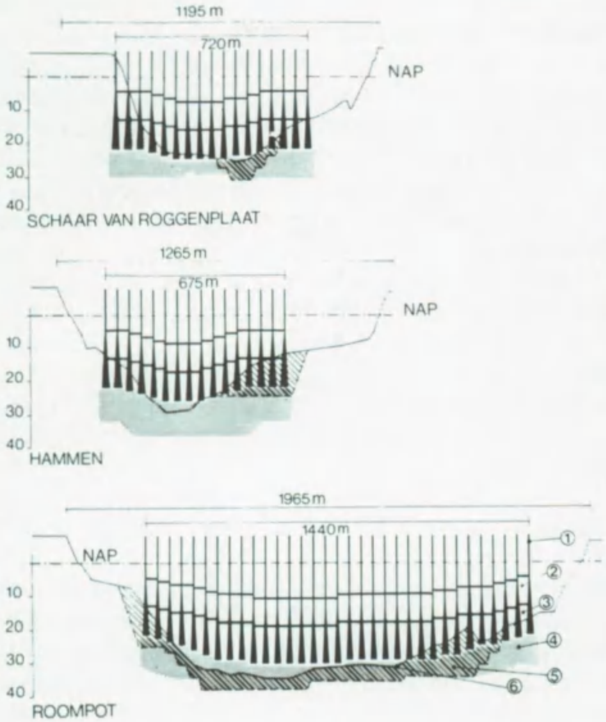

Figure 3a. Schematic view of the storm surge barrier. A cross section of the three channels in the mouth of the Oosterschelde with the position of the different pylons (1). The base of each pylon is embedded in stones (3). The pylons are connected with a lower concrete bar (2). The original profile of the channel (6) and the zone in which the sediment was changed (4 and 5) are also plotted.

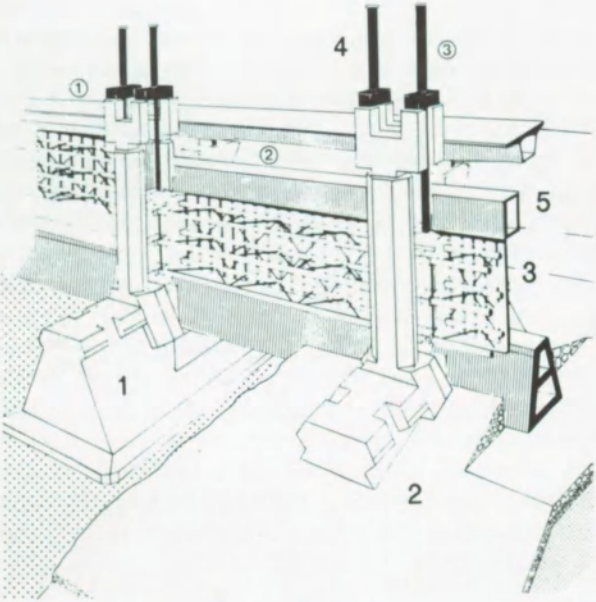

Figure 3b. Schematic view of the storm surge barrier. Detail of two pylons (1), embedded in stones (2). The gates (3) can be moved by the hydraulic system (4) between the upper (5) and lower bar (6) to close the barrier. Under normal conditions the barrier is open.

main changes that are relevant for this study. The total intertidal surface of the Oosterschelde was reduced from 17000 ha to 11365 ha. This loss of habitat is caused by three different factors: -closure of the Markiezaat (in 1983); -closure of the Krammer/Volkerak/Eendracht in 1987; -loss due to reduction in tidal amplitude. Indeed due to an important reduction of the cross section of the mouth of the estuary (from 80000 m^2 to 17550 m^2) the tidal volume was reduced from 1240 to $880*10^6$ m^3 leading to a reduction of the tidal amplitude from 3.7 m to 3.25 m. Current speed dropped on average by 30-40%, in the northern branch of the estuary by 70%. Once the cross section of the estuary mouth was reduced to 35000 m^2 in the middle of 1985, the tidal amplitude started to decline from 3.7m to 2.4m in April 1986. In April 1987, after the closure of the Philipsdam, the tidal amplitude increased again to its final value of 3.25m. The changed hydrodynamics of the estuary resulted in geomorphological changes, the most significant, at least for this study, being a general erosion.

An environmental impact study

To study the effects of the construction of the storm surge barrier in the mouth of the Oosterschelde and the construction of the compartmentalization dams on the ecosystem a comprehensive research program was started by Rijkswaterstaat, Tidal Waters Division in cooperation with several universities and research institutes. The results are summarized in Smaal & Boeije (1991) and a special volume of the journal Hydrobiologia will be published end 1993 with papers covering all the different facets of the research program (Nienhuis & Smaal, 1993). Within this overall research program, a comprehensive study of macrozoobenthos and bird populations was included. Part of the results of that project forms the basis for this thesis. This project was carried out in close cooperation between Rijkswaterstaat, Tidal Waters Division (RWS), the Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology (the former Delta Institute for Hydrobiological Research) (NIOO-CEMO) and the Laboratory of Animal Ecology, Zoogeography and Nature Conservation of the University of Gent (UG). In a later stage the Institute of Nature Conservation (Ministry of the Flemish community) became also involved in the project. The macrozoobenthos was studied by both RWS (Jon Coosen), NIOO-CEMO (Johan Craeymeersch) and UG. The research on birds was divided into three major topics: bird counts; ringing and condition; feeding ecology. The counts of waterbirds were organized by RWS (first by Henk Baptist, followed by Peter Meininger). Ringing and measurements of the condition of birds was done by NIOO-CEMO (Rob Lambeck) in close cooperation with RWS (Peter Meininger; Eric Marteijn). Studies on feeding ecology were coordinated by UG. In the course of the years, many people were involved within this project.

4. Aim of this thesis

The loss of intertidal habitat due to the construction of a storm surge barrier in the mouth of the Oosterschelde and the compartmentalization dams more inland was the immediate cause for the studies presented in this thesis.

Indeed, the works in the Oosterschelde can be seen as a unique opportunity or experiment to study the effects of habitat loss on waterbird populations. The aims of this thesis are therefore:

1) to describe both the waterbird populations (especially waders) and their main food source, the macrozoobenthos, before, during and after the environmental changes;

2) to describe the feeding behaviour of waders and to analyse the relationship between wader populations and their food supply: did this change in response to the habitat loss?;

3) to get more insight into the question whether or not the carrying capacity of the Oosterschelde was reached.

The theoretical background, used as a guideline for this study, and the research program carried out to achieve the postulated aims are elaborated in the next section, together with the outline of this thesis.

5. Conceptual model and outline of this thesis

One way of thinking about the effects of habitat loss is to formulate the question in terms of the ability of estuaries to support birds, i.e., in terms of their carrying capacity (Evans & Dugan, 1984; Goss-Custard & Durell, 1984). The term carrying capacity is, however, a very vague term that has been used in many different ways (Dhondt, 1988), so we cannot use it without clearly defining what we mean by the term. In this thesis the definition by Goss-Custard (1985), Goss-Custard & Durell (1990) and Sutherland & Goss-Custard (1991) is used: the carrying capacity of a particular area within a species range during the non-breeding season is the density at which the addition of one further bird would result in another either starving or leaving that locality to seek a better feeding area. When this point is reached, no net increase in bird density can take place, and the carrying capacity would have been reached.

If in the Oosterschelde the carrying capacity was not yet reached, we can predict that all birds feeding previously in the area could be accommodated for in the remaining tidal areas after the completion of the coastal engineering works. If true, average densities of waders should increase. In the pre-barrier period about 182000 waders were present in the

Oosterschelde and Krammer/Volkerak (Schekkerman *et al.*, 1993) on 17000 ha of intertidal flats or 10.7 birds/ha. Assuming they will all feed on the remaining 11365 ha the density should increase to 16 birds/ha or 49%. Depending on the species the increase would vary between 37 and 57% (Meire & Kuijken, 1987). If carrying capacity was already reached before the habitat loss occurred we predict that bird densities should remain constant and the total population should decrease.

This hypothesis is simple to state, but as bird densities are influenced by many different factors, these must be studied as well. In order to concentrate the thoughts a simple conceptual model was described by Meire and Kuijken (1984) incorporating several factors which, in our opinion, influence the occurrence and distribution of waders in an estuary. It is in several respects similar to a framework of resource systems elaborated by Wiens (1984). He defines a resource as an environmental factor that is directly used by an organism and that may potentially influence individual fitness.

The model is given in Fig. 4 and discussed here, mainly to give insight in the research program carried out in the Oosterschelde and in the organization of this thesis. The number of the chapter dealing with a certain aspect of the model is indicated on the figure.

The research was carried out on two levels of scale: a large scale covering the whole of Oosterschelde estuary and a small scale covering one tidal flat, the Slikken van Vianen. For a detailed description of the Oosterschelde we refer to Smaal & Boeije (1991), for the Slikken van Vianen to Meire & Kuijken (1987; chapter 4 of this thesis). Although in some chapters data on several species of waterbirds are given, the work presented in this thesis deals mainly with waders.

The number of birds (N) returning from the breeding areas and arriving at a particular estuary, varies from year to year depending on breeding success, mortality during migration and local conditions.

> *To detect any possible trend or change in total numbers of waterbirds it was necessary to measure the total number of birds present. This is done for both the Slikken van Vianen and the whole of the Oosterschelde. In chapter 4, numbers and pattern of occurrence of waders at the Slikken van Vianen, before the environmental changes, is described. A comparison between both the number of waders on Vianen before and after the environmental changes and between Vianen and the whole of the Oosterschelde is made in chapter 5. Finally, in chapter 6, the waterbird counts from the whole of the Oosterschelde are analysed and the trends are compared to the population trends of the species in order to distinguish between local and global patterns of change.*

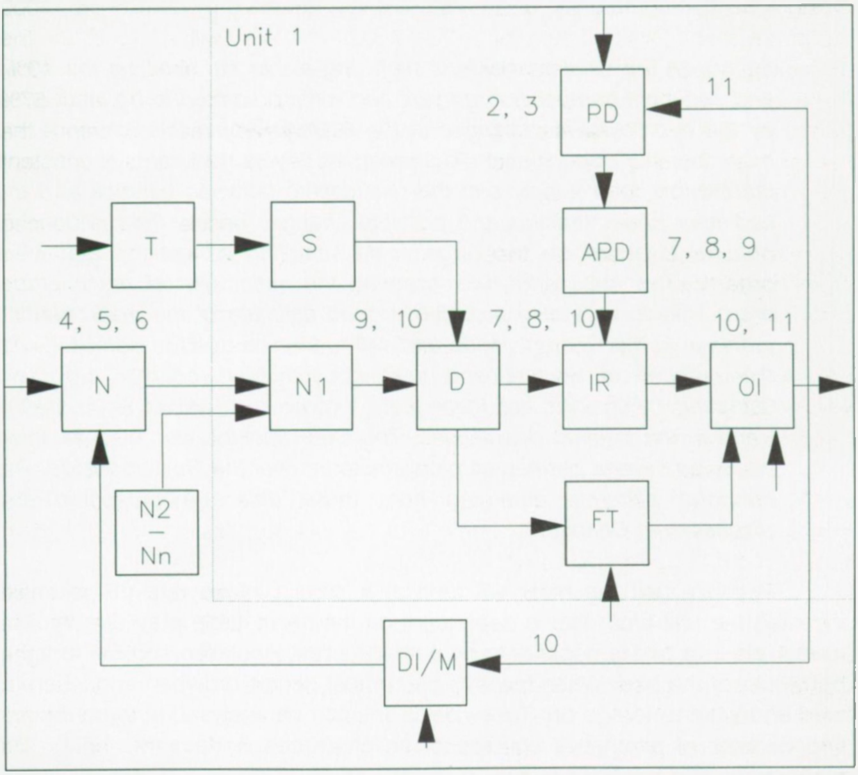

Figure 4. Conceptual model of the factors influencing the occurrence of waders in an estuary. (N: total number of birds present; N1: number of birds in unit 1 (benthic community of area with a given prey density); N2-Nn: number of birds in units 2-n; D: density of birds; IR: Intake rate; OI: overall intake rate; T: tidal conditions; S: surface of the feeding area; PD: prey density; HPD: harvestable prey density; FT: feeding time; DI: dispersal; M: mortality). The numbers refer to the chapter in this thesis were data on that subject are dealt with.

Both within and between estuaries the birds are confronted with a food supply (macrozoobenthos) that varies considerably from place to place. The patchiness in the distribution of most macrobenthic invertebrates, the food supply for most wader species, in the intertidal zone is well known (e.g., Meire *et al.*, 1989). Species composition, density, body size and flesh content of prey vary along three major estuarine environmental gradients: salinity, level on the shore and sediment composition. The feeding grounds of waders can therefore be viewed as a series of units, each unit being a benthic community, or an area having a certain prey density etc.

> *Salinity in the Oosterschelde is high and stable but level on the shore and sediment composition do vary and were predicted to be influenced by the hydrodynamic changes in the estuary. Would this influence the macrobenthic populations? To answer this it was necessary to measure the benthic food supply and the relationship between benthos and the sediment characteristics and possible changes herein. This is done in chapter 2 based on two large scale sampling campaigns that were organized in 1985 and 1989 covering the major part of the intertidal area. This surveys also provided a good estimate of the macrobenthic biomass in the Oosterschelde and will further be used to compare with the number of waders and their consumption (chapter 11). Two sampling campaigns are inadequate, however, to detect any possible trend in the benthic populations. Therefore benthos was also sampled yearly on several permanent plots scattered over the Oosterschelde. The temporal patterns, emerging from these data are presented and discussed in Chapter 3.*

Within a unit the birds will feed at a certain intake rate (IR, biomass ingested per unit time) that is dependent on the harvestable prey density. The intake rate of a bird is dependent on both the prey population and the foraging behaviour of the bird. When feeding, birds must decide on when and where to feed and what to forage on. These decisions can be analysed in terms of cost and benefits of alternative courses of action (Krebs & Kacelnik, 1991). The rationale behind the first generation of Optimal Foraging Theory models is that animals are designed to take these decisions that maximize the net rate of energy intake, which is assumed to correlate with fitness. These Optimal Foraging models could provide the theoretical background to understand the observed patterns of prey selection, to estimate the IR of the birds, given a certain prey population (important for modelling purposes) and to get a better insight into what should be regarded as the prey population for this species.

> *As it was not feasible to study in detail all wader species, the Oystercatcher (Haematopus ostralegus) was chosen for detailed studies on foraging behaviour. The reasons are manifold. It is the most common species in the Oosterschelde and it feeds on large easily visible prey. Do the Oystercatchers select the most profitable prey? In chapter 7, the selection of mussels by Oystercatchers is analysed within the framework of Optimal Foraging Theory. The emerging pattern of prey selection was further analysed by an experimental approach in chapter 8.*

Each unit is characterized by a prey population, but not all individuals will be available to the predator (Fig. 5). Indeed, a part of the prey population

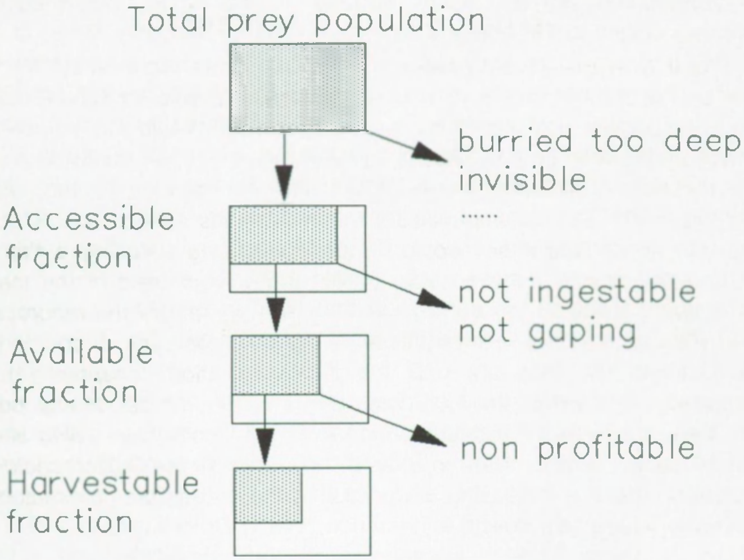

Figure 5. Different fractions of the total prey population and the fraction that is harvestable to the predator.

may be inaccessible to birds for several reasons. Some species can be buried too deep so the birds cannot reach them (Reading & McGrorty, 1978; Zwarts & Wanink, 1984; Richardson, 1985; Zwarts, 1986; Zwarts & Wanink, 1989). Mussels may be one on top of the other so they are not visible anymore (Meire, 1991; this thesis). The remaining part of the prey population is the accessible fraction. Of this fraction some individuals may be too large to be ingested by the bird (especially for birds swallowing the prey whole), or else show behavioural or morphological patterns that make them unavailable. Of the available part of the prey population, birds may actively select some individuals. There can be a large difference between the prey population present and the harvestable population (see Zwarts *et al.*, 1992; Meire, 1993). Measuring this harvestable fraction is therefore very important but first of all it must become clear what determines whether a prey is harvestable or not. Here a good understanding of the foraging behaviour is important.

> *Based on the analysis of prey selection it was possible to get an estimate of the fraction of the prey population that is available. This is summarized in chapter 7, 8 and 9.*

The distribution of individuals between these units can be thought of as two counteracting forces. Firstly, because of the higher intake attainable, individuals collect in the areas of high prey density. Secondly, when at higher densities of competitors, they suffer a reduced intake due to interference (see further). The manner in which birds distribute themselves taking into account both prey density and interference can be considered especially using the concept of the Ideal Free or Despotic Distribution (IFD/IDD) (Fretwell & Lucas, 1970; Fretwell, 1972; Sutherland & Parker, 1985; Bernstein *et al.*, 1991; Milinski & Parker, 1991). This concept assumes individuals are ideal, in that they move to the site where their intake would be the highest, and that they are free and able to move readily between sites (unlike say sessile or territorial species). This concept leads to the conclusion that birds in the different sites should obtain the same intake - if the intake is higher in one site, then individuals should move into that site until the increased interference removes the discrepancy. If however the individuals are unequal, are not free to move to other sites, the birds will distribute themselves but the average intake will differ between sites. Intake rate is indeed not only dependent on the prey population. There is increasing evidence that the density of waders itself may reduce the intake rate due to interference (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987). Interference is the immediate and reversible depression of IR with increasing bird density. In depletion, intake rate decreases as bird density rises because the food is removed. This change is irreversible (Goss-Custard, 1980).

Therefore, the number of birds (N1) that feeds in unit 1 is determined by N, by the number of birds feeding in other units (N2-Nn) by the density of birds already present and by the prey populations. Obviously other factors such as predation risks, distance from roosting sites, sediment characteristics etc. also might influence the distribution of the birds. The available surface of feeding area in a unit is a function of the state of the tide (T) or human factors (disturbance, habitat loss etc.). Together with N1, this determines the bird density (D) within a unit.

> *The distribution of birds over the food gradient was studied in detail on the Slikken van Vianen. Both the temporal and spatial patterns in distribution were studied. This is dealt with in chapter 9 and 10 where the question whether or not the relation between Oystercatcher densities and their prey densities (cockles and mussels) changed after the loss of intertidal habitat is central.*

The overall intake (OI) of the animals within a unit is the intake rate times the feeding time (FT). The maximum feeding time in a unit is determined by the tidal rhythm and the topography of the area. It also can be dependent on the bird density. Indeed there is some evidence that the density of waders has a negative influence on the time they are feeding (Koene, 1978; Meire, 1987). The OI that a bird can achieve during one tidal cycle (either in one or in more units) will determine its condition and will act as a negative feedback on the density. This can work either by dispersal (DI) or mortality (M). The total amount of food taken in a unit has an influence on the prey density (depletion).

The interaction between IR, FT and OI could be studied in October 1986, during the closure of the Oesterdam, when the storm surge barrier was temporarily closed, reducing strongly the available feeding time for the birds. These results are summarized in chapter 10.
If the benthic consumption is high compared to the food supply is analysed in chapter 11.

How can OI, the crucial parameter in the whole model, be influenced by habitat loss? Several of the parameters in the model are likely to be influenced by the construction of the storm surge barrier. The hydrodynamic changes will result in a smaller surface of intertidal area (influencing density) and the reduced tidal amplitude will affect feeding time. Below mid tidal level it will decrease, above it will increase. The changed conditions in the estuary also can have an effect on prey densities and hence available prey densities. This can affect the IR, which is likely to decrease due to interference that is the effect of increased densities. Together with a reduction of feeding time this is likely to affect OI. This can have an effect on mortality which in turn affects population size.

In the epilogue the results are summarized and the value of this simple conceptual model as a framework for studying the effects of habitat loss on birds is evaluated.

The chapters of this thesis are prepared as individual publications, some of which are already published, others accepted or submitted. This approach leads inevitable to some overlap between the chapters in e.g., material and methods and some paragraphs of the introduction and discussion. There is however no overlap in the data and results of each of the chapters.

Not all the reports and papers resulting from our work on benthos and birds in the Oosterschelde are included in this thesis. These references are included in the appendix on the reference list below.

References

Bernstein, C., J. R. Krebs & A. Kacelnik, 1991. Distribution of birds amongst habitats: theory and relevance to conservation. In C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons (Eds), Bird population studies. Relevance to conservation and management. Oxford University Press, Oxford: 317-345.

Bryant, D. M., 1987. Wading birds and wildfowl of the estuary and Firth of Forth, Scotland. Proc. Roy. Soc., Edinburgh 93B: 509-520.

Day, J. W., C. A. S. Hall, W. M. Kemp & A. Yanez-Arancibia, 1989. Estuarine Ecology. Wiley, New York.

Davidson, N. C., D. d'A. Laffoley, J. P. Doody, L. S. Way, J. Gordon, R. Key, C. M. Drake, M. W. Pienkoswki, R. Mitchell & K. L. Duff., 1991. Nature conservation and estuaries in Great Britain. Nature Conservancy Council, Peterborough.

Dhondt, A. A., 1988. Carrying capacity: a confusing concept. Acta Oecologia 9: 337-346.

Ens, B. & J. D. Goss-Custard, 1984. Interference among Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. J. anim. Ecol. 53: 217-231.

Evans, P. R., 1981. Reclamation of intertidal land: some effects on Shelduck and wader populations in the Tees estuary. Verh. Orn. Ges. Bayern 23: 147-168.

Evans, P. R., 1991. Introductionary remarks: habitat loss-effects on shorebirds populations. Acta XX Congr. Int. Ornithol.: 2197-2198.

Evans, P. R. & P. J. Dugan, 1984. Coastal birds: numbers in relation to food resources. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 8-28.

Evans, P. R., D. M. Herdson, P. J. Knights & M. W. Pienkowski, 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. Oecologia 41: 183-206.

Fairbridge, R. W., 1980. The estuary: its definition and geodynamic role. In E. Olaussen & I. Cato (Eds), Chemistry and biogeochemistry of estuaries. Wiley, New York: 1-35.

Furness, R. W., H. Galbraith, I. P. Gibson & N. B. Metcalfe, 1986. Recent changes in numbers of waders on the Clyde estuary, and their significance for conservation. Proc. Roy. Soc., Edinburgh 90: 171-184.

Fretwell, S. D., 1972. Populations in a seasonal environment. Princeton University Press, Princeton.

Fretwell, S. D. & H. L. Jr. Lucas, 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta biotheoretica 19: 16-36.

Goss-Custard, J. D., 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J. D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford: 169-188.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1984. Feeding ecology, winter mortality and the population dynamics of Oystercatchers on the Exe estuary. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 190-208.

Goss-Custard, J. D. & S. E. A. Durell Le V. Dit, 1987. Age-related effects in Oystercatchers *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*. III. The effect of interference on overall intake rate. J. anim. Ecol. 56: 549-558.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis, 132: 273-289.

Goss-Custard, J. D. & M. E. Moser, 1988. Rates of change in the numbers of Dunlin, *Calidris alpina*, wintering in British estuaries in relation to the spread of *Spartina anglica*. J. appl. Ecol. 25: 95-109.

Goss-Custard, J. D. & M. G. Yates, 1992. Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the Wash. J. appl. Ecol. 28: 330-340.

Goss-Custard, J. D., R. M. Warwick, R. Kirby, S. McGrorty, R. T. Clarke, B. Pearson, W. E. Rispin, S. E. A. Le V. Dit Durell & R. J. Rose, 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn estuary. J. appl. Ecol. 28: 1004-1026.

Gosselink, J. G. & R. H. Baumann, 1980. Wetland inventories: Wetland losses along the United States coasts. Z. Geomorphol. N.F. Suppl. 34: 173-187.

Jones, G. E., 1987. The conservation of ecosystems and species. Croom Helm, London.

Knoester, M., 1984. Introduction to the Delta cases studies. Wat. Sci. Tech. 16: 1-9.

Knoester, M., J. Visser, B. A. Bannink, C. J. Colijn & W. P. A. Broeders, 1984. The Eastern Scheldt project. Wat. Sci. tech. 16: 51-77.

Koene, P., 1978. De Scholekster: aantalseffecten op de voedselopname. Msc. Thesis, Zoologisch Laboratorium, University of Groningen.

Krebs, J. R. & A. Kacelnik, 1991. Decision-making. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology: an evolutionary approach. Sinauer Associates, Sunderland, MA: 105-136.

Lambeck, R. H. D., A. J. J. Sandee & L. De Wolf, 1989. Long-term patterns in the wader usage of an intertidal flat in the Oosterschelde (SW Netherlands) and the impact of the closure of an adjacent estuary. J. appl. Ecol. 26: 419-431.

Langslow, D. R., 1981. The conservation of intertidal areas in Britain. Wader Study Group Bull. 31: 18-22.

Laursen, K., I. Gram & L. J. Alberto, 1983. Short-term effect of reclamation on numbers and distribution of waterfowl at Hojer, Danish Wadden Sea. Proc. Third Nordic Congr. Ornithol. 1981: 97-118.

Leeuwis, R. J., H. J. M. Baptist & P. L. Meininger, 1984. The Dutch delta area. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 253-260.

McLusky, D. S., 1981. The estuarine ecosystem. Blackie, Glasgow.

McLusky, D. S., D. M. Bryant & M. Elliot, 1992. The impact of land-claim on macrobenthos, fish and shorebirds on the Forth Estuary, eastern Scotland. Aquatic Conservation: marine and freshwater ecosystems 2: 211-222.

Meininger, P. L., 1991. Populaties van enkele soorten broedvogels in het Deltagebied in 1990 met een samenvatting van twaalf jaar monitoring. Rijkswaterstaat, DGW, Nota GWAO-91.082, Middelburg,

Meininger, P. L., 1992. Kustbroedvogels en de Oosterscheldewerken. De Levende Natuur 93: 153-158.

Meininger, P. L. & A. M. M. Van Haperen, 1988. Vogeltellingen in het zuidelijk deltagebied in 1984/85 - 1986/87. Rijkswaterstaat, Nota GWAO-88.1010, Middelburg.

Meininger, P. L., H. J. M. Baptist & G. J. Slob, 1984. Vogel-tellingen in het Deltagebied in 1975/1976 - 1979/1980. Rijkswaterstaat Deltadienst, Middelburg & Staatsbosbeheer Zeeland, Nota DDMI-84.23, Goes.

Meininger, P. L., H. J. M. Baptist and G. J. Slob. 1985. Vogeltellingen in het Zuidelijk Deltagebied in 1980/81 - 1983/84. Rijkswaterstaat, Nota DGWM 85.001, Middelburg.

Meire, P. M., 1987. Foraging behaviour of some wintering waders: prey selection and habitat distribution. In A. C. Kamil, J. R. Krebs & H. R. Pulliam (eds), Foraging behavior. Plenum Press, New York: 215-237.

Meire, P. M., 1991. Effects of a substantial reduction in intertidal area on numbers and densities of waders. Acta XX Congr. Int. Ornithol. : 2219-2227.

Meire, P., 1993. The impact of bird predation on marine and estuarine bivalve populations: a selective review of patterns and underlying causes. In R. Dame (Ed.), Bivalve filter feeders and marine ecosystem processes. Nato Advanced Research Workshop, Springer Verlag, New York: in press.

Meire, P. & E. Kuijken, 1984 : Barrage schemes - Predicting the effects of changes in tidal amplitude on wader populations. In P. R. Evans, H. Hafner & P. L'Hermite (eds), Shorebirds and large Waterbirds Conservation. Commission of the European Communities, Brussel: 79-89.

Meire, P. M. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, The Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77: 283-311.

Meire, P., J. Dereu, J. Van Der Meer & D. Develter, 1989. Aggregation of some benthic invertebrates: theoretical and practical considerations. Hydrobiologia. 175: 137-148.

Meire, P. M., J. Seys, T. Ysebaert, P. I. Meininger & H. J. M. Baptist, 1989. A changing Delta: effects of large coastal engineering works on feeding ecological relationships as illustrated by waterbirds. In J. C. Hooghart & C. W. S. Posthumus (eds), Hydro-ecological relations in the Delta waters of the South-West Netherlands. Lakerveld B.V., the Hague: 109-143.

Milinski, M. & G. A. Parker, 1991. Competition for resources. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology. Blackwell, Oxford: 137-168.

Nienhuis, P. & A. C. Smaal, 1993. The Oosterschelde estuary: case study of a changing estuary. Hydrobiologia: in press.

Pfister, C., B. A. Harrington & M. Lavine, 1992. The impact of human disturbance on shorebirds at a migration staging area. Biol. Cons. 60: 115-126.

Pieters, T., C. Storm, V. T. Walhout & T. Ysebaert, 1991. Het Schelde estuarium, méér dan een vaarweg. Rijkswaterstaat, Nota GWWS-91.081, Middelburg.

Prater, A.J., 1981. Estuary birds of Britain and Ireland. T. & A.D. Poyser, Calton.

Reading, C. J. & S. McGrorty, 1978. Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. Estuar. coast. mar. Sci. 6: 135-144.

Richardson, H., 1985. Availability of buried littleneck clams (*Venerupis japonica*) to Northwestern crows (*Corvus corone*). J. anim. Ecol. 54: 443-457.

Saeijs, H. L. F & J. M. Baptist, 1977. Vogels in de Deltawerken van Zuidwest-Nederland, overzicht simultaantellingen 1972 t/m 1976. RWS, nota DDMI 77.34, Middelburg.

Schekkerman, H., P. L. Meininger & P. M. Meire, 1993. Changes in the waterbird populations of the Oosterschelde, SW. Netherlands, as a result of large scale coastal engineering works. Hydrobiologia: in press.

Senner, S. E. & M. A. Howe, 1984. The conservation of Nearctic shorebirds. In J. Burger & B. L. Olla (Eds), Shorebirds, breeding behaviour and populations. Plenum Press, New York, 379-422.

Smaal, A. C. & R. C. Boeije, 1991. Veilig getij, de effecten van de waterbouwkundige werken op het getijdemilieu van de Oosterschelde. Rijkwaterstaat, Nota WS 91.088, Middelburg.

Smit, C. J. & T. Piersma, 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In H. Boyd & J.-Y. Pirot (Eds), Flyways and reserve networks for water birds. IWRB Special Publication No. 9: 24-63.

Smit, C. J., R. H. D. Lambeck & W. J. Wolff, 1987. Threats to coastal wintering and staging areas of waders. In N. C. Davidson & M.W. Pienkowski (Eds), The conservation of international flyway populations of waders. Wader study group Bull. 49 suppl./IWRB Special publ. 7: 105-113.

Stuart, J. J., P. L. Meininger & P. M. Meire, 1990. Watervogels van de Westerschelde. Rijksuniversiteit Gent, Nota WWE nr. 14., Gent, Rijkswaterstaat, Nota WAO 89.1010, Middelburg.

Stuurgroep Oosterschelde, 1982. Beleidsplan voor de Oosterschelde, SGO, Middelburg.

Sutherland, W. J. & J. D. Goss-Custard, 1991. Predicting the consequences of habitat loss on shorebird populations. Acta X Congr. Int. Ornithol.: 2199-2207.

Sutherland, W. J. & G. A. Parker, 1985. The distribution of unequal competitors. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology: Ecological Consequences of Adaptive Behaviour Blackwell, Oxford: 255-274.

Van Latesteijn, H. C. & R. H. D. Lambeck, 1986. The analysis of monitoring data with the aid of time-series analysis. Envir. Monit. Ass. 7: 287-297.

Wiens, J., 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In D. R. Strong, D. Simberloff, G. Abele & A.B. Thistle (Eds), Ecological communities. Conceptual issues and the evidence. Princeton University Press, Princeton: 439-457.

Wolff, W. J., 1973. The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the Rivers Rhine, Meuse and Scheldt. Zool. Verh., Leiden 126: 1-242.

Zwarts, L., 1986. Burying depth of the benthic bivalve *Scrobicularia plana* (Da Costa) in relation to siphon-cropping. J. exp. mar. Biol. Ecol. 101: 25-39.

Zwarts, L. & J. Wanink, 1984. How Oystercatchers and Curlew successively deplete clams. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 69-83.

Zwarts, L. & J. Wanink, 1989. Siphon size and burying depth in deposit- and suspension feeding benthic bivalves. Mar. Biol. 100: 227-240.

Zwarts, L., A.-M. Blomert & J. H. Wanink, 1992. Annual and seasonal variation in the food supply harvestable for Knot *Calidris canutus* staging in the Wadden Sea in late summer. Mar. Ecol. Prog. Ser. 83: 128-139.

Appendix

References of reports and papers dealing based on our research on macrozoobenthos and birds in the Oosterschelde that are not included in this thesis.

Baptist, H. J. M. & P. Meire, 1981. Wader research in the Delta of the South West Netherlands. Wader Study Group Bull. 31: 26- 28.

Baptist, H. J. M., F. Colijn, E. C. L. Marteijn, P. L. Meininger, P. M. Meire & F. Twisk, 1988. Gevleugeld onderzoek, watervogels in veranderende watersystemen. Rijkswaterstaat, Middelburg, DIHO, Yerseke, Rijksuniversiteit Gent, Gent.

Coosen, J., P. Meire & A. Van Den Dool, 1988. Kartering bodemdieren intergetijdengebieden Oosterschelde. Rapport BALANS 1988-15; Rijkswaterstaat, DGW, Middelburg, KNAW, DIHO, Yerseke.

Coosen, J., J. Seys, P. M. Meire & J. Craeymeersch, 1993. Effect of geomorphological and hydrodynamical changes in the intertidal areas of the Oosterschelde estuary (SW-Netherlands) on distribution, density and biomass of some common macrobenthic species. *Hydrobia ulvae, Arenicola marina, Scoloplos armiger, Bathyporeia pilosa* and *Spio* spec. Hydrobiologia: in press.

Coosen, J., F. Twisk, M. W. M. van der Tol, R. H. D. Lambeck, M. Van Stralen & P. M. Meire, 1993b. Stock assessment of cockles (*Cerastoderma edule*) in the Oosterschelde and factors determining it in 1980-1990. Hydrobiologia: in press.

Craeymeersch, J., P. Herman & P. Meire, 1986. Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S.W. Netherlands). Hydrobiologia 133: 107- 115.

Dereu, J. & P. Meire, 1985. Ruimtelijke distributie van het macrozoöbenthos op de Slikken van Vianen : fundamentele en practische beschouwingen. Project Vogel (Rijkswaterstaat) Verslag No. 1, Rijksuniversiteit Gent, Gent.

Meire, P., 1987. Foraging behaviour of some wintering waders: prey-selection and habitat distribution. In A. Kamil, J. Krebs, R. Pulliam (eds), Foraging Behavior. Plenum Press, New York: 215-238.

Meire, P., 1993. The impact of bird predation on marine and estuarine bivalve populations: a selective review of patterns and underlying causes. In R. Dame (Ed.), Bivalve filter feeders and marine ecosystem processes. Nato Advanced Research Workshop, Springer Verlag, New York: in press.

Meire, P. & J. Coosen, 1985. Benthos and bird communities in a changing estuary. In R. Van Grieken & R. Wollast (eds), Progress in Belgian Oceanographic Research. Antwerpen, University of Antwerp Press, Antwerpen: 292-303.

Meire, P. & J. Dereu, 1987. Een ekologisch profiel van een hooggelegen slibarm slik op de Slikken van Vianen (Oosterschelde, NL). Project Vogel (Rijkswaterstaat) Verslag No. 2, Rijksuniversiteit Gent, Gent.

Meire, P. & J. Dereu, 1990: Use of the Abundance/biomass comparison method for detecting environmental stress: some considerations based on intertidal macrozoobenthos and bird communities. Journal applied Ecology 26: 210-223.

Meire, P. & E. Kuijken, 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. In P. R. Evans, J. D. Goss-Custard & W. Hale (eds), Coastal Waders and Waterfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. & E. Kuijken, 1984. Barrage schemes - Predicting the effects of changes in tidal amplitude on wader populations. In P. R. Evans, H. Hafner & P. L'Hermite (eds), Shorebirds and large Waterbirds Conservation. Commission of the European Communities, Brussel: 79-89.

Meire, P. & J. Seys, 1989. Benthos en pollutie op de slikken van Vianen. Rapport WWE nr. 8, Rijksuniversiteit Gent, Gent.

Meire, P., J. Dereu, J. Van Der Meer & D. Develter, 1989. Aggregation of some benthic invertebrates: theoretical and practical considerations. Hydrobiologia 175: 137-148.

Meire, P., J. Seys, T. Ysebaert & J. Coosen. 1991. Comparing macrobenthic distribution and community structure between two estuaries in SW-Netherland. In M. Elliot & J. P. Ducrotoy (Eds), Estuaries and Coasts: spatial and temporal intercomparisons. Olson & Olson, Fredensborg: 221-230.

Meire, P., J. Seys, T. Ysebaert, P. Meininger & H. Baptist, 1989. A changing Delta: effects of large coastal engineering works on feeding ecological relationships as illustrated by waterbirds. In J. C. Hooghart & C. W. S. Posthumus (eds), Hydro-ecological relations in the Delta Waters of the South-West Netherlands. TNO Committee on hydrological Research. The Hague: 109-146.

Meire, P., J. Buijs, J. Seys, E. Stikvoort, F. Twisk, D. De Jong, 1992. Macrozoobenthos in de Oosterschelde in het najaar 1989: een situering van de gegevens. Rapport RUG-WWE no 30, RUG; DIHO; RWS-DGW en Instituut voor Natuurbehoud.

Meire, P., J. Buijs, J. Van Der Meer, A. Van Den Dool, A. Engelberts, F. Twisk, E. Stikvoort, D. De Jong, R. Lambeck & J. Polderman, 1991. Macrozoobenthos in de Oosterschelde in het najaar 1985: een situering van de gegevens. Rapport RUG-WWE no 27, RUG; DIHO; RWS-DGW en Instituut voor Natuurbehoud.

Schekkerman, H., P. L. Meininger & P. M. Meire, 1992. Watervogels en de Oosterscheldewerken. De Levende Natuur 93: 147-151.

Seys, J. & Meire, P., 1989. Biomassa- en densiteitsverloop van macrozoobenthos in de Oosterschelde: 1983-1988. Rapport RUG-WWE nr. 7, Rijksuniversiteit Gent, Gent.

Seys, J., P. Meire & J. Coosen, 1993b. Macrobenthic populations in the Oosterschelde before, during and after major coastal engineering works. Rapport RUG-WWE, Gent: in press.

Seys, J., P. M. Meire, J. Coosen & J. Craeymeersch, 1993a. Macrozoöbenthos op acht stations in de Oosterschelde 1983-1989: presentatie data. Rapport RUG-WWE: in press.

Seys, J., P. Meire, J. Coosen & J. Craeymeersch, 1993c. Long-term changes in the macrobenthic fauna at eight intertidal permanent stations in the Oosterschelde estuary - effects of the construction of the storm surge barrier: some preliminary results. Proceedings ECSA20-Hull sept 1990: in press.

Smaal, A. C., M. Knoester, P. Nienhuis & P. Meire, 1991. Changes in the Oosterschelde ecosystem induced by the Delta works. In M. Elliot & J. P. Ducrotoy (Eds), Estuaries and Coasts: spatial and temporal intercomparisons. Olson & Olson, Fredensborg: 375-384.

Chapter 2

SPATIAL AND TEMPORAL PATTERNS OF INTERTIDAL MACROBENTHIC POPULATIONS IN THE OOSTERSCHELDE: ARE THEY INFLUENCED BY THE CONSTRUCTION OF THE STORM SURGE BARRIER?

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ABSTRACT

The construction of a storm surge barrier in the mouth of the Oosterschelde caused important hydrodynamical and morphological changes that could influence the macrobenthic populations. This paper is the first in a series of five all dealing with the effects of the storm surge barrier on macrozoobenthos and analyses the spatial and temporal distribution of macrozoobenthos in the Oosterschelde and its relationship with some environmental parameters, based on two large scale sampling campaigns, one before and one after the completion of the barrier.

The sediment of the sampling stations was fine, well sorted sand, with an average mud content of about 2.5%. Only in the Krabbenkreek the sediment was coarser in 1989. The tidal elevation of the sampling sites decreased significantly in 1989.

The density of macrozoobenthos was significantly lower, the biomass higher in 1989. The density was dominated by deposit feeders, the biomass by filter feeders. The difference in biomass between both years was mainly due to a substantial increase of the biomass of filter feeders in 1989. The number of species per station was significantly smaller in 1989 than in 1985. Between 1985 and 1989, frequency of occurrence decreased in 34 versus 13 which increased, density increased in 13 species and decreased in 34 species, biomass increased in 18 species and decreased in 29 species.

Based on TWINSPAN several clusters of stations, each with a different faunal composition, were identified. These clusters did not form distinct zones on the tidal flats but were dispersed widely.

The relationship between density and biomass of different trophic groups and the mud content of the sediment and the depth was analysed. This relationship sometimes differed clearly between years. The correlation coefficient of a multiple regression between density and biomass of individual species and environmental factors, although significant in most cases, was very low, indicating that only a small proportion of the species variability was explained. The relationship between benthos and environmental factors was further analysed by canonical correlation analysis and multivariate discriminant analysis that gave different results for the 1985 and 1989 data. This is probably due to the broad tolerance of the species to the range of the environmental variables found in our study area. From a TWINSPAN of the density data of 1985 and 1989 together we could conclude that, although the environmental parameters in a group of stations, showing a large faunal similarity in one year, did not change, the faunal composition did. This indicates that faunal changes are not necessarily linked to changes in the measured environmental parameters.

In the discussion the different factors affecting macrobenthic populations are situated and it is suggested that the macrobenthic populations

are probably more towards the nonequilibrium end of the continuum between nonequilibrium and equilibrium communities as defined by Wiens (1984).

Although the impact of the construction of the barrier on the macrobenthic community seems at present to be rather small this does not mean that on the long-term there will be no effect.

INTRODUCTION.

In the estuarine ecosystem, macrozoobenthos is an important group both in terms of species richness, abundance or biomass and in the estuarine food chain. The different species can be divided into several trophic groups (e.g., Fauchald & Jumars, 1979). Filter feeders as mussels (*Mytilus edulis*) and cockles (*Cerastoderma edule*) consume a substantial part of the primary production (Prins & Smaal, 1993). Deposit feeders, the majority of the species, largely rely on organic material on or within the sediment. Some species (e.g., *Nephtys hombergii*) are predators or scavengers. The macrozoobenthic invertebrates, in their turn, are an important food source for fish and birds (Meire *et al.*, 1993), cockles and mussels are also consumed by men (Van Stralen & Dijkema, 1993).

Several studies indicate that macrozoobenthic populations show large variations both in space and time (see e.g., papers in Elliot & Ducrotoy, 1991). Long-term studies provide a good basis for unraveling the underlying causes of this temporal variability (e.g., Dörjes *et al.*, 1986; Desprez *et al.*, 1986; Beukema, 1989), whereas large scale surveys aim to analyse factors causing spatial variation (e.g., Warwick *et al.*, 1991). Man-induced changes of the environment (pollution, coastal engineering works etc.) offer an interesting opportunity to study the factors influencing the occurrence of macrobenthic populations given a carefully designed monitoring scheme before and after the changes. The construction of a storm surge barrier in the Oosterschelde was such an event. This paper is the first in a series of five papers all dealing with the effects of the storm surge barrier on macrozoobenthos. Seys *et al.* (1993) describe the temporal pattern of some overall parameters of the benthic populations (density, biomass and species composition). Coosen *et al.* (1993a) focus on the temporal pattern, distribution and habitat preference of some individual species. The cockle and mussel populations of the Oosterschelde are treated separately (Coosen *et al.*, 1993b; Van Stralen & Dijkema, 1993).

This paper analyses the spatial and temporal distribution of macrozoobenthos in the Oosterschelde and the relationship between macrozoobenthos and some environmental parameters, based on two large scale sampling campaigns, one before and one after the completion of the barrier. To what extent the benthic populations depend upon the measured environmental variables and whether or not this relationship was similar in both campaigns is the central question of this paper. In the discussion we try to situate the macrobenthic populations in the nonequilibrium-equilibrium continuum concept of Wiens (1984).

MATERIAL AND METHODS

Database

For a general description of the Oosterschelde and the engineering works we refer to Nienhuis & Smaal (1993).

For the study of the macrozoobenthos we had access to three different databases, two which were focused on temporal patterns (Seys *et al*., 1993; Coosen *et al*., 1993a) and one on spatial patterns. The "**Interecos**" campaign aimed at a description of the large scale spatial distribution before and after the construction of the barrier and formed the basis for this paper. In August 1985 and 1989, each time a total of 305 locations were sampled, on three different intertidal flats of the Oosterschelde (Fig. 1). At each location 10 samples were taken with a core (4.5 cm diameter) to a depth of 10 cm. All samples were fixed in the field with 40% neutralized formaline and sieved in the laboratory on a 1 mm mesh sieve. All organisms were picked out after staining with Rose Bengale for at least 24 h, and identified to the species level when possible. Additionally 5 samples with a core of 15 cm diameter were taken to a depth of 30 cm. These samples were sieved in the field on a 3 mm mesh sieve and the animals fixed in 7% neutral formaline. The data from the large cores were used to estimate the abundance of three species: *Arenicola marina, Mya arenaria* and *Mytilus edulis*. The first two are known to occur much deeper than 10 cm. Mussels were not well sampled by the small cores due to their size. Data for all other species came from the small cores. Ash free dry weight (AFDW) is the weight after drying for 3 days at 72°C, minus the weight after burning at 520°C for 3.5 hours.

The 305 sampling sites were distributed over different, predefined strata according to a stratified random sampling strategy (Van Der Meer *et al*., 1989). Averages and confidence intervals were calculated accordingly. In both years the same sites were sampled, however in 1989, 5 stations could not be sampled, so all comparisons are based on 300 sites.

At each site several environmental parameters were measured: median grain size, sorting coefficient (both measured in φ units), mud content (% of sediment smaller than 53μ), tidal elevation (further called depth) bulk density (g/cm$_3$), chlorophyl content (μg/g), moisture content (%) and vegetation cover

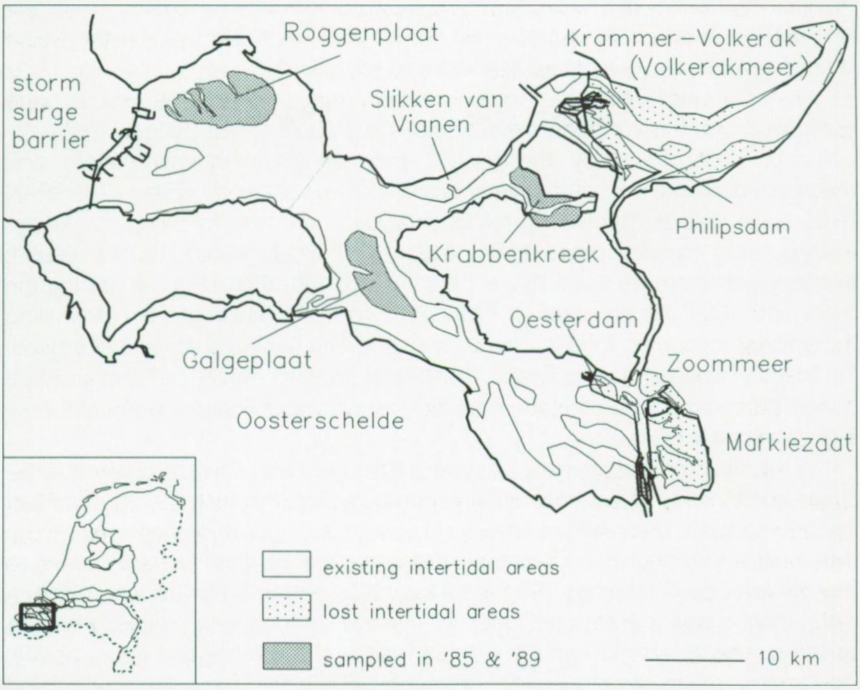


Figure 1. Map of the Oosterschelde with the location of the storm surge barrier, the secondary dams and the intertidal area that were sampled.

(seaweeds and Eelgrass). For more details about the measurement of these parameters we refer to Ten Brinke *et al.* (1993) and De Jong *et al.*, (1993).

The identification of the species was not exactly similar in the two years. Species of genera, difficult to identify, as *Polydora, Nereis, Micropthalmus* etc. were not identified to species level in 1985. In order to compare both years the different species of these genera were lumped to the genus level in the 1989 database. In that way we retained 47 taxa that could be compared between years.

Analyses

The different species were classified into different trophic groups based on Fauchald & Jumars (1976) (for more details see Meire *et al.*, 1991a, b). The mud content of the sediment and depth were grouped in 7 and 12 classes respectively (0-1%; 1-2%; 2-3%; 3-4%; 4-5%; 5-10% and >10% for mud and NAP-2.0- -1.75m; -1.75- -1.5m; ... NAP 1 - 1.25m for depth)(NAP is the Dutch ordnance level and is situated at about mid tidal level).

As in both years the same stations were sampled, the results were compared with the Wilcoxon matched-pairs Signed rank test (Siegel, 1956).

In order to study the relation between sediment parameters and macrozoobenthos we used several types of multivariate analysis. TWINSPAN (Hill, 1979) was performed on the original data, with the following cut levels: analysis with density data: 0, 64, 512, 1028, 4112, 16440, 65792, 99999; analysis with biomass data: 0, 0.5, 1, 5, 10, 25, 100, 9999. For comparing the 1985 and 1989 density data, a TWINSPAN analysis was run after eliminating the species occurring in less than 25 stations. The same cut levels were used. To identify whether the different TWINSPAN clusters could be distinguished based on sediment parameters, a multiple discriminant analysis was used (see e.g., Weston, 1988).

Multivariate discriminant analysis (MDA) was also used to determine the linear combination of environmental parameters discriminating the 20 dominant benthic species. Discriminant analysis is viewed as a good method for defining the multidimensional habitat characteristics of the benthic fauna in order to identify species differences (Flint & Kalke, 1986; James & McCulloch, 1990). A data matrix was constructed with 20 sample groups each representing a species and 8 abiotic variables (mud content, median grain size, sorting coefficient, depth, bulk density, chlorophyl content, vegetation cover and moisture content) (only the 20 most abundant species were used in the analysis). The number of cases per sample group (or the number of observations per species) varied between 22 and 267. Only the stations where the abundance of the species was higher than the overall average were used.

The relation between sediment characteristics and benthos was further analysed by canonical correlation analysis (CCA). The analysis was similar to that described by Van Der Meer (1991), who did the analysis on the 1985 data. The same analysis was done for 1989 and for both years together. For the MDA and CCA the data were transformed according to Van Der Meer (1991).

To perform a multiple regression on both the 1985 and the 1989 data, the data of each year were converted to Z-scores and then combined in order to eliminate between year variation. Of all environmental variables both the original value and its square was used, as a quadratic function was expected.

SYSTAT (Wilkinson, 1988) was used for all statistical analyses.

Table 1. Sediment parameters of the sampling sites. The mean and Standard Error of the parameters in both years with the Z-value and associated probability of the Wilcoxon matched pairs signed rank test (D) are given for the whole dataset and for the three flats separately (OS Oosterschelde; RP Roggenplaat; GP Galgeplaat; KB Krabbenkreek).

Changes in sediment parameters									
Parameter		OS (N=300)		RP (N=120)		GP (N=110)		KB (N=75)	
Depth	85	-0.14	0.03	-0.12	0.05	-0.32	0.04	0.07	0.07
	89	-0.24	0.03	-0.19	0.05	-0.60	0.04	0.18	0.07
	D	-7.15	<0.001	-4.04	<0.001	-8.87	<0.001	5.75	<0.001
Mud	85	2.63	0.21	2.25	0.36	1.77	0.19	4.47	0.52
	89	2.47	0.33	3.39	0.73	1.13	0.1	2.85	0.61
	D	-6.32	<0.001	0.35	ns	-5.47	<0.001	-5.97	<0.001
Med	85	2.78	0.014	2.63	0.03	2.86	0.02	2.89	0.03
	89	2.75	0.015	2.61	0.02	2.82	0.02	2.85	0.03
	D	-5.62	<0.001	-3.14	<0.01	-3.56	<0.001	-3.23	<0.01
Sort	85	0.42	0.005	0.42	0.009	0.40	0.006	0.44	0.01
	89	0.40	0.003	0.40	0.005	0.40	0.005	0.40	0.01
	D	-3.69	<0.001	-3.32	<0.01	0.82	ns	-3.75	<0.001

RESULTS

I. Ecological parameters

The means of some important environmental parameters on the sampling sites are given in Table 1. The sediment in both campaigns can be characterized as fine, well sorted sand. Median grain size varied between 2.18 and 3.45 φ with a mean of 2.78 φ in 1985 and between 2.17 and 3.52 φ with a mean of 2.75 φ units in 1989. The mud content varied between 0 % and 21.4 and 44.9% in 1985 and 1989 respectively, with mean values of 2.6 and 2.4%. Differences between flats existed: the Krabbenkreek was muddier than the other two. The significant decrease in mud content, median grain size and sorting coefficient between 1985 and 1989 (Table 1) was widespread over the stations but the absolute value of the decrease was very small. Only the changes in the Krabbenkreek can be considered as meaningful (Ten Brinke *et al.*, 1993). The variability of most sediment parameters, especially median grain size was very low (coefficient of variation 8.8 and 9.6 % in 1985 and 1989).

The tidal elevation of the sampling sites varied between NAP -1.6 and +1.2 m in both years with means of NAP -0.14 and NAP -0.24 in respectively 1985 and 1989. The decrease in 1989 was significant (Table 1).

A description of the vegetation on the intertidal flats is given by De Jong *et al.*, 1993.

2. Characteristics and spatial distribution of the macrozoobenthos of the Oosterschelde in 1985 and 1989.

2.1 General parameters (Density, biomass and species composition)

The density of macrozoobenthos varied between 630 and 138,150 in 1985, between 480 and 71,600 individuals/m^2 in 1989 (Fig. 2a). It was

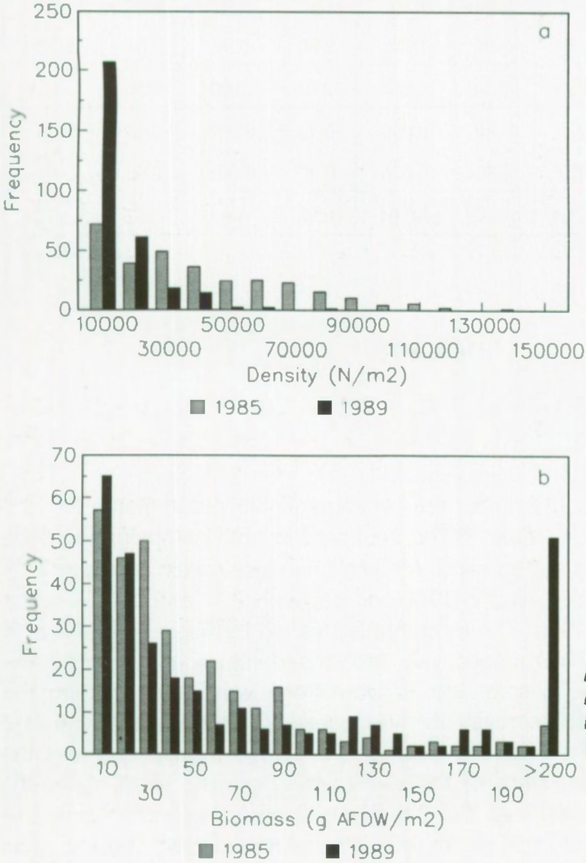


Figure 2. Frequency distribution of density (a) and biomass (b) in 1985 and 1989.

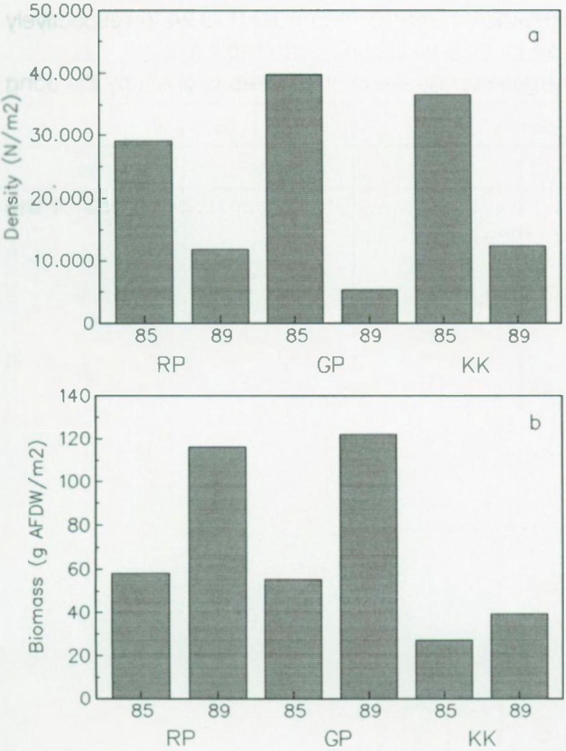


Figure 3. Average density (a) and biomass (b) of macrozoobenthos in 1985 and 1989 at three intertidal flats. (RP Roggenplaat; GP Galgeplaat; KK Krabbenkreek)

significantly lower in 1989 (Wilcoxon matched-pairs Signed-rank test Z=-13.6, N=300, p<0.001). The majority of sites had densities lower than 30,000 individuals/m^2. Differences in densities between tidal flats existed, but densities were in the same order of magnitude (Fig. 3a). The biomass varied between .43 and 343 in 1985 and .23 and 864.9 g AFDW/m^2 in 1989 (Fig. 2b) and was, contrary to the density, higher in 1989 (Wilcoxon matched-pairs Signed-rank test Z=-5.15, N=300, p<0.001). In most stations biomass was lower than 100 g AFDW/m^2. Remarkable was the large number of stations in 1989 with biomass values of more than 200 g AFDW/m^2. Biomass was lowest in the Krabbenkreek in both years (Fig. 3b). The spatial variability of density and biomass was very high. The coefficient of variation for density, biomass and different trophic groups is given in Table 2.

The density was dominated by deposit feeders, mainly surface deposit feeders (Fig. 4a), the biomass by filter feeders, especially on the Roggen- and Galgeplaat (Fig. 4b). The difference in biomass between both years was

Table 2. Coefficient of variation of density and biomass of different trophic groups in both 1985 and 1989. (DF: burrowing deposit feeders; SDF: surface deposit feeders; SF: suspension feeders; O: omnivores and predators).

Spatial variability of the macrozoobenthos of the Oosterschelde				
	Density		Biomass	
group	1985	1989	1985	1989
Total	79.4	109.0	110.1	132.3
DF	135.4	119.5	78.7	78.0
SDF	96.4	172.4	116.8	126.0
SF	126.6	121.8	145.3	150.9
O	106.4	386.3	214.9	184

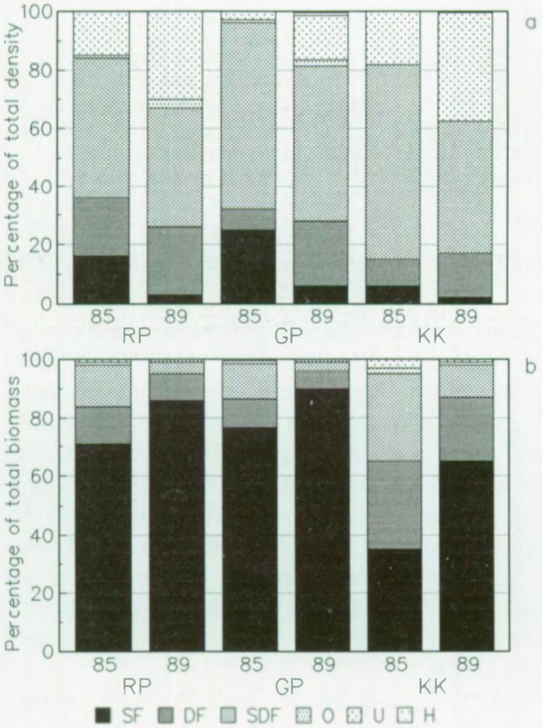


Figure 4. The proportion of different trophic groups in the total density (a) and biomass (b) in both 1985 and 1989 on each of the three tidal flats. (RP Roggenplaat; GP Galgeplaat; KK Krabbenkreek) (SF suspension feeders; DF burrowing deposit feeders; SDF surface deposit feeders; O omnivores; U unknown; H herbivores).

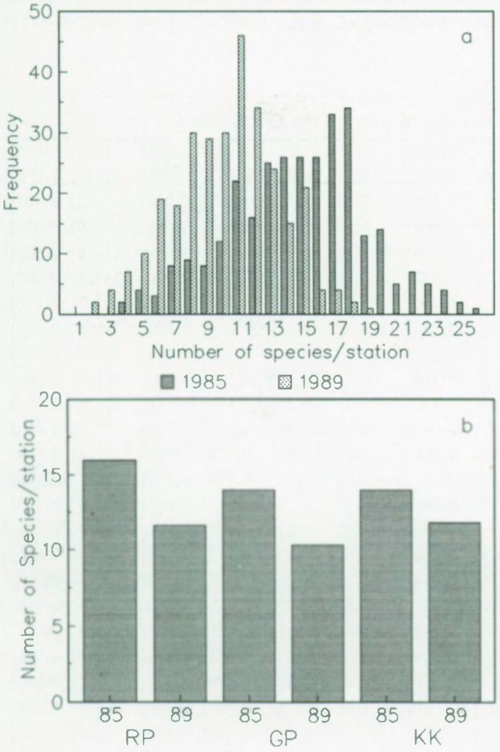


Figure 5. Frequency distribution of the number of species per station in 1985 and 1989 (a) and the average number of species per station in 1985 and 1989 on each of the three tidal flats (b). (RP Roggenplaat; GP Galgeplaat; KK Krabbenkreek)

mainly due to a substantial increase of the biomass of filter feeders in 1989 (Fig. 4b).

The total number of species found was 65, namely 32 polychaetes, 14 crustacea, 16 molluscs, 2 echinoderms and 1 nemertinea and did nearly differ between both campaigns. Only a few species were found in only one year. Remarkable was the appearance of *Ensis directus*, an American species that is colonizing European waters since 1979 (Essink, 1988) (see also Seys *et al.*, 1993). The number of species per station is given in Fig. 5a and was significantly smaller in 1989 than in 1985 (Wilcoxon matched-pairs Signed-rank test Z=-5.15, N=300, p<0.001). Differences between flats were small (Fig. 5b).

2.2 Individual species

In Table 3 the frequency of occurrence, mean density and mean biomass of the individual species is given for both sampling years together with the results of the Wilcoxon matched pairs Signed-rank test. Frequency of

Table 3: frequency of occurrence of different species and wilcoxon. (F = Frequency; B =Biomass [g AFDW/m2]; D = Density [number/m2]; P = significance of the Wilcoxon matched pairs signed rank test

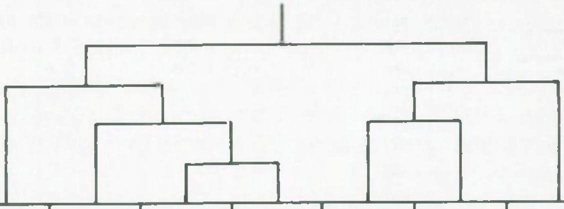
	1985			1989			Difference [1985-1989]				
Species	F	B	D	F	B	D	F	B	P	D	P
Ampharete acutifrons	5.9	.027	14.0	1.6	0.003	1.3	4.2	0.025	0.001	12.6	0.001
Anaitides mucosa	57	.121	164.5	42.6	0.066	60.4	14.3	0.055	0.004	104.0	0.000
Arenicola marina	79.3	.418	36.6	81.6	6.839	27.4	-2.3	-2.421	0.000	9.2	0.003
Aricidea sp.	2.2	.001	5.7	.6	0.000	0.6	1.6	0.001	0.046	5.0	0.074
Bathyporeia sp.	43.6	.078	373.2	23	0.075	513.3	20.6	0.003	0.004	-140.0	0.002
Capitella capitata	73.1	.146	1089.9	56.6	0.033	226.2	16.4	0.113	0.000	863.6	0.000
Carcinus maenas	35.7	.286	47.2	7.3	0.104	5.5	28.4	0.182	0.000	41.7	0.000
Cerastoderma edule	86.2	.402	5565.2	66.6	77.117	259.5	19.5	-51.714	0.000	5305.6	0.000
Corophium sp.	45.9	.060	368.4	35.6	0.037	172.1	10.2	0.023	0.006	196.2	0.000
Crangon crangon	40.9	.079	63.9	14.6	0.124	14.0	26.3	-0.045	0.000	49.9	0.000
Crepidula sp.	.3	.001	0.4	1.6	0.010	1.3	-1.3	-0.009	0.172	-0.9	0.279
Eteone sp.	62.6	.056	114.0	30.6	0.020	37.0	31.9	0.037	0.000	77.0	0.000
Eumida sanguinea	.9	.000	0.6	3.3	0.003	6.8	-2.3	-0.003	0.005	-6.2	0.014
Eurydice sp.	.9	.000	1.1	1.6	0.001	1.8	-.6	-0.000	0.499	-0.7	0.726
Gammarus sp.	5.2	.006	6.4	11.3	0.047	105.0	-6	-0.041	0.029	-98.6	0.001
Harmothoe sp.	.6	.005	0.9	2.3	0.002	1.8	-1.6	0.003	0.441	-0.9	0.126
Heteromastus filiformis	64.2	.693	1622.7	43.3	0.383	132.4	20.9	0.311	0.000	1490.3	0.000
Hydrobia ulvae	84.9	.218	13998.9	32.6	0.844	1058.3	152.2	2.374	0.000	2940.6	0.000
Lanice conchilega	12.1	.105	34.9	25.6	0.548	71.0	-13.	-0.443	0.000	-36.0	0.000
Lepidochitona cinerea	5.2	.026	8.1	1.3	0.002	1.8	3.9	0.024	0.007	6.3	0.010
Littorina littorea	9.5	.394	67.8	.3	0.001	0.4	9.1	0.393	0.000	67.3	0.000
Macoma balthica	86.8	.125	727.1	65	2.224	120.4	21.8	-0.099	0.979	606.7	0.000
Magelona papillicornis	6.2	.007	5.2	2.6	0.010	2.0	3.5	-0.003	0.345	3.2	0.031
Malacoceros sp.	3.2	.002	8.4	2.6	0.002	11.2	.6	0.000	0.683	-2.7	0.776
Melita sp.	.9	.001	2.2	3	0.004	8.0	-2	-0.003	0.041	-5.7	0.066
Microphthalmus sp.	2.2	.002	1.5	10.6	0.002	17.4	-8.3	-0.001	0.002	-15.8	0.000
Mya arenaria	31.1	.131	17.3	5	0.271	2.5	26.1	0.860	0.000	14.7	0.000
Mysella bidentata	7.8	.004	8.5	5	0.004	4.5	2.8	-0.000	0.792	3.9	0.151
Mytilus edulis	19.3	.485	55.7	5.6	7.258	5.5	13.6	-0.773	0.023	50.1	0.000
Nemertinae sp.	8.1	.014	9.1	4.3	0.008	4.5	3.8	0.006	0.442	4.5	0.098
Nephtys sp.	53.1	.267	76.8	56.6	0.633	58.1	-3.5	-0.366	0.000	18.6	0.032
Nereis sp.	63.9	.573	424.9	57.3	0.828	235.6	6.6	-0.255	0.242	189.2	0.000
Oligochaeta	78	.403	3771.4	69.6	0.223	2790.5	8.3	0.180	0.000	980.8	0.000
Ophelia sp.	3.6	.003	17.1	1.3	0.001	8.0	2.2	0.002	0.084	9.1	0.094
Polydora sp.	29.1	.055	222.9	19.3	0.014	36.0	9.8	0.041	0.000	186.8	0.000
Pygospio elegans	89.5	.299	2955.3	64.6	0.093	724.5	24.8	0.207	0.000	2230.7	0.000
Retusa sp.	34.4	.019	58.9	10.3	0.003	11.2	25.1	0.016	0.000	47.7	0.000
Scoloplos armiger	90.4	.092	808.9	87.3	0.886	1357.2	3.1	0.207	0.067	-548.3	0.004
Scolelepis sp.	8.1	.025	30.5	2	0.012	1.8	6.1	0.012	0.001	28.7	0.000
Scrobicularia plana	11.4	.860	13.1	10.3	0.258	12.4	1.1	0.602	0.043	0.7	0.392
Spiophanes bombyx	17.3	.042	57.3	16.6	0.021	30.8	.7	0.021	0.578	26.5	0.019
Spio filicornis	31.8	.022	157.5	57.3	0.089	662.2	-25.	-0.066	0.000	-504.7	0.000
Spisula sp.	3.6	.003	9.7	.3	0.000	0.2	3.2	0.003	0.008	9.4	0.007
Streptosyllis sp.	2.9	.005	22.6	.6	0.000	0.4	2.2	0.005	0.018	22.2	0.018
Tellina sp.	3.9	.061	5.2	5.6	0.024	5.0	-1.7	0.037	0.216	0.1	0.933
Tharyx marioni	60.3	.278	1623.3	47	0.151	818.3	13.3	0.127	0.000	804.9	0.000
Urothoe sp.	14.4	.011	37.9	17.3	0.013	43.6	-2.9	-0.002	0.056	-5.7	0.171

occurrence decreased in most species (34 versus 13 which increased). Density increased in 13 species and decreased in 34 species, the change being significant in 8 and 28 species respectively. Biomass increased in 18 species, decreased in 29 species, the change being significant in 11 and 22 species respectively.

Details of the distribution of each individual species are given by Meire *et al*. (1991a, b) and the relationship with environmental parameters in Seys *et al*. (1992). The distribution of some individual species is discussed in detail by Coosen *et al*. (1993a) and Seys *et al*. (1993).

2.3 Communities

In order to investigate whether different faunal groupings ('communities') could be detected, a classification method (TWINSPAN) was run on the density and biomass data for both years. This resulted in several clusters of stations, each characterized by some typical species. As an example the results of the analysis of the 1985 biomass data are summarized in Fig. 6a. Seven station clusters could be delineated. The first division separated stations with high biomass, density and number of species per sample from the others. Cluster 1 consists of stations situated on musselbeds. They are characterised by a high density, biomass and number of species. Besides mussels, some typical species are *Littorina littorea*, *Lepidochiton cinereus* and *Lanice conchilega*. In the stations of cluster 2 species like *Arenicola marina, Heteromastus filiformis, Hydrobia ulvae, Mya arenaria, Tharyx marioni, Nereis sp.* and Oligochaetes have high biomass values. The



Cluster	1	2	3	4	5	6	7
Nr. of samples	18	45	44	124	42	18	14
Density	54.130	55340	53.190	33.190	5.235	12.930	9.390
Biomass	148.2	61.7	86.6	37.8	9.7	31.0	2.3
Nr. of species	23	17	17	15	9	13	5

Figure 6a. Dendrogram of the TWINSPAN divisions based on the biomass data of 1985. The number of samples, density (N/m^2), biomass (g AFDW/m^2) and the total number of species per cluster are plotted.

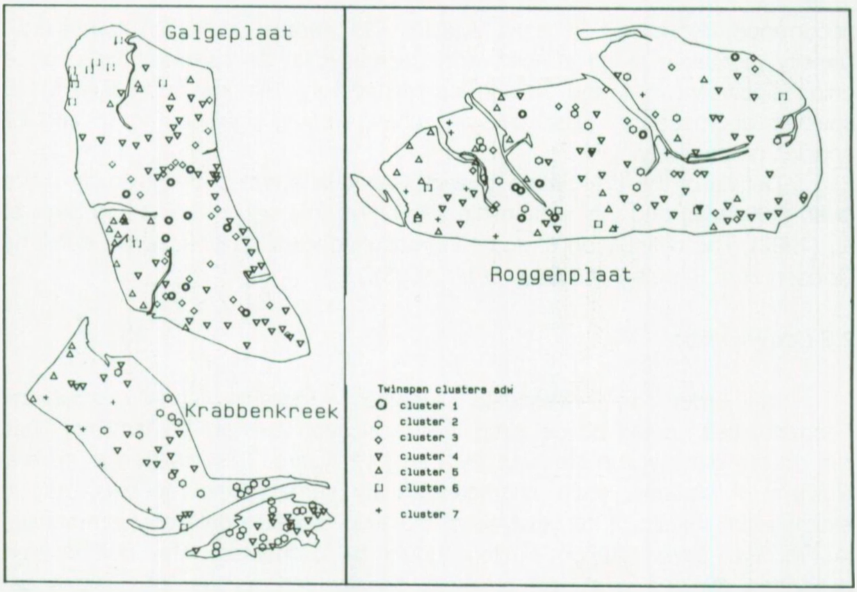


Figure 6b. Map showing the spatial pattern of the different TWINSPAN clusters based on the biomass data of 1985.

species composition of cluster 3 is more or less similar to the former cluster but biomass of many species is much lower except for cockles, whose average biomass is highest in this cluster. In cluster 4 density, biomass and diversity is also lower, especially for species like *Heteromastus filiformis, Macoma balthica.* In clusters 5, 6 and 7 density, biomass and diversity are lower. The stations from cluster 7 consist mainly of *Bathyporeia sp.* This species is also characteristic for clusters 5 and 6. However, in the latter clusters some other species are abundant as well: *A. marina* in cluster 5 and *C. edule* in cluster 6.

The spatial distribution of these clusters is shown in Fig. 6b. Almost all clusters were found on each of the three intertidal flats. They did not form distinct zones but were dispersed over the intertidal area. The clustering of stations based on density or biomass differed within one year as well as between years but the general pattern was similar to the one described above.

3. Relation between macrozoobenthos and environmental parameters.

The average values of total density and biomass, and of the most important trophic groups, are plotted as a function of the different mud and

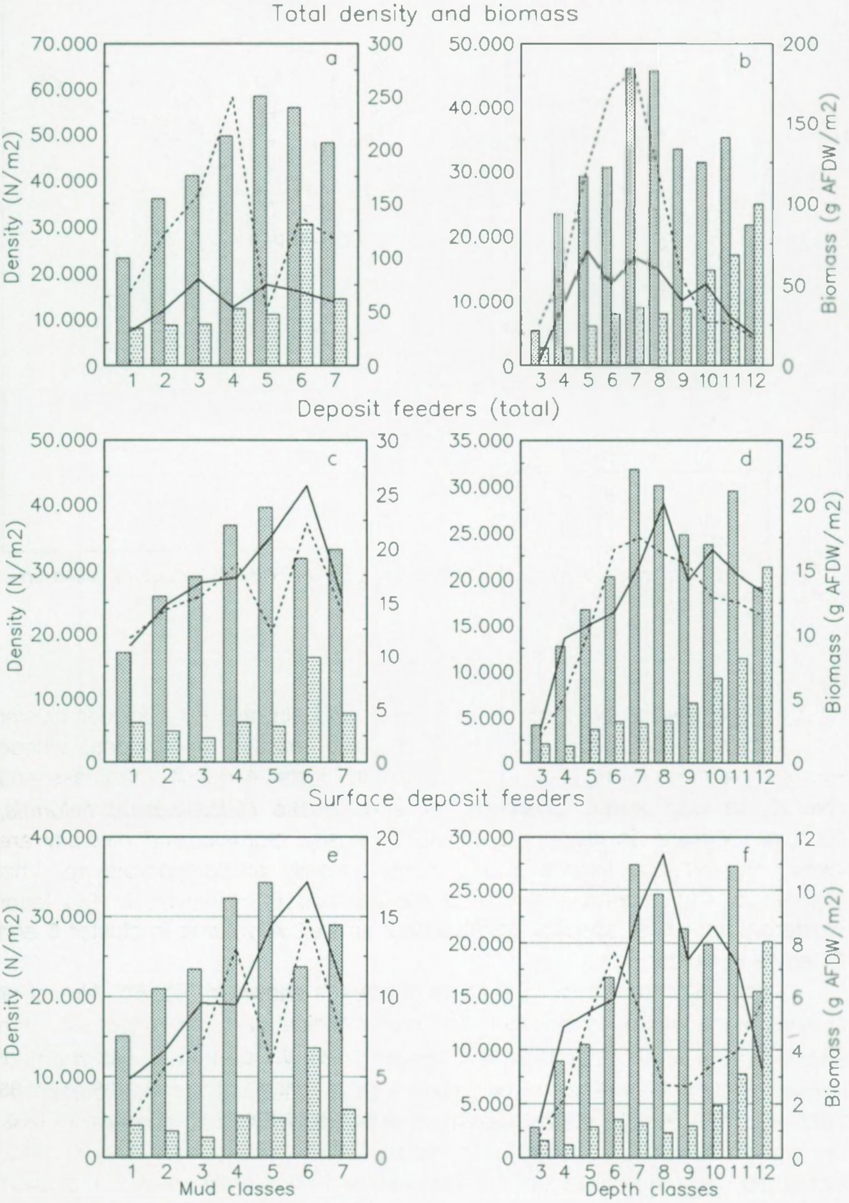


Figure 7. Density and biomass of all macrozoobenthic animals (a-b) and of the most important trophic groups (c-j) as a function of mud content of the sediment and depth (tidal elevation). (for the definition of the mud and depth classes see text)

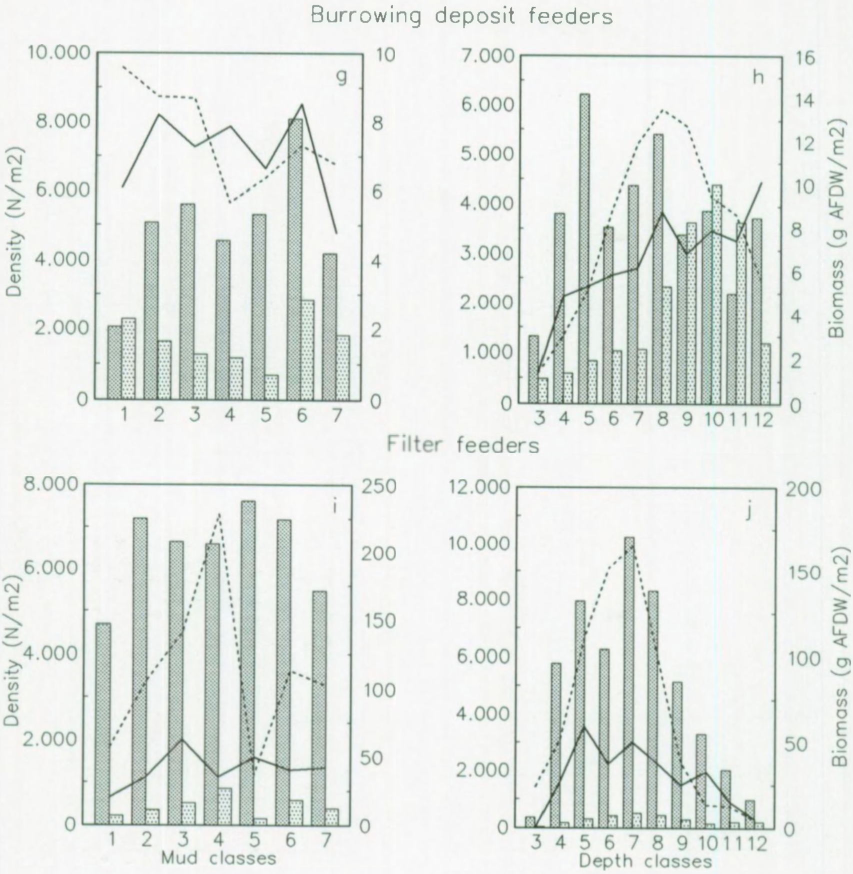


Figure 7, continued.

depth classes in Fig. 7. In 1989, the highest biomass values occurred at or just below mid-tidal level (Fig. 7b), a pattern less pronounced but also present in 1985. In 1989 density clearly increased with tidal elevation, whereas in 1985 the highest densities occurred near mid tidal-level. Density, especially in 1985, increased with mud content of the sediment and decreased again at high mud content (Fig. 7a). Biomass, in 1989, was maximal at intermediate mud content.

In both years, the biomass of all deposit feeders clearly increased with increasing mud content of the sediment, except at the highest values (Fig. 7c). The density pattern was less clear. The biomass of all deposit feeders also

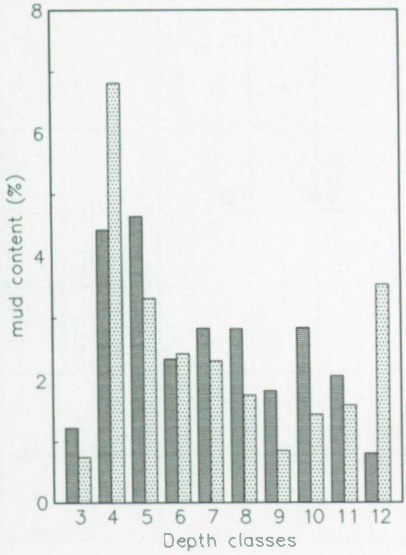


Figure 8. Mud content of the sediment at different tidal elevations in both 1985 and 1989. (for the definition of the depth classes see text)

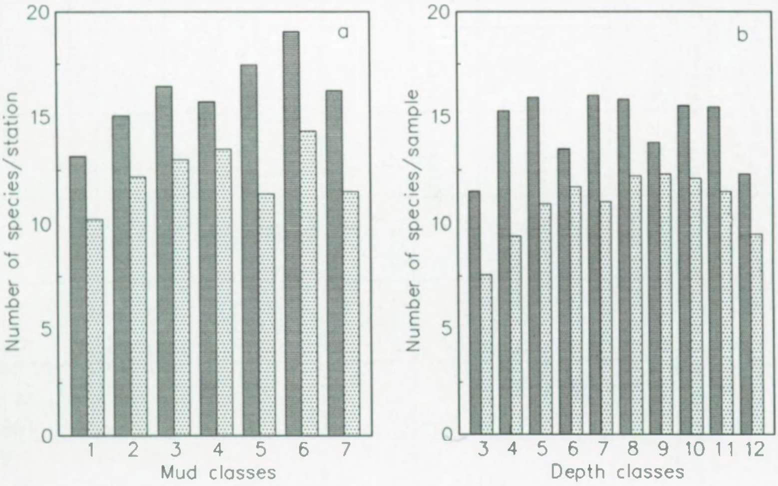


Figure 9. Average number of species per sample in relation to tidal elevation (a) and mud content of the sediment (b). (for the definition of the mud and depth classes see text)

*Table 4: Results of a stepwise multiple regression analysis based on the data of 1985 and 1989. The standardized regressions coefficients for all variables in the model together with the coefficient of determination are given. (D Density; B Biomass; Dep Depth; Mud Mud content of the sediment; Med Median grain size; Sort Sorting coefficient; Oxl depth of oxygenated layer; Vege vegetation cover; *2 square of variable)*

Species	D/B	Year	Dep	Dep*2	Mud	Mud*2	Med	Med*2	Sort	Sort*2	Oxl	Oxl*2	Vege	Vege*2	R2
Arenicola marina	D		0.202	-0.165		0.097					-0.08		0.069		0.109
	B			-0.283					-0.153		-0.092				
Aniatides sp.	D						0.159								0.017
	B			-0.069						0.060					0.005*
Bathyporeia sp.	D		0.241	0.122				-0.119			0.631	-0.314			0.178
	B		0.272	0.130				-0.148	-0.598	0.538	0.311				0.203
Capitella capitata	D		-0.150	-0.086					0.080						0.021
	B				0.682	-0.480		-0.126		-0.172				0.073	0.039
Cerastoderma edule	D		-0.230	-0.228			0.189								0.097
	B		-0.256	-0.259									0.064		0.071
Corophium sp.	D		0.445	0.271			0.140		-0.060						0.160
	B		0.448	0.253				0.139	-0.061						0.162
Heteromastus filiformis	D		-0.099	-0.082	0.444	-0.304		0.126	0.554	-0.571					0.098
	B				0.790	-0.518		0.125						0.122	0.272
Hydrobia ulvae	D		0.208				0.450		-0.081						
	B		0.257				0.381						0.477	-0.414	0.235
Lanice conchilega	D	-0.060	-0.197			-0.084								0.361	0.167
	B	-0.071	-0.202					-0.061						0.330	0.148

Species	D/B	Year	Dep	Dep*2	Mud	Mud*2	Med	Med*2	Sort	Sort*2	Oxl	Oxl*2	Vege	Vege*2	R2
Macoma balthica	D		-0.068	-0.162	0.368	-0.373	0.124						0.086		0.098
	B		-0.122	-0.177					0.734	-0.661			-0.219	0.396	0.081
Mya arenaria	D				0.125				0.099						0.035
	B						0.144	0.468	-0.390						0.030
Nepthys hombergii	D		-0.398		-0.331	0.142			0.168				-0.353	0.241	0.180
	B		-0.236	-0.077	-0.104										0.045
Nereis sp.	D	0.086	0.215	-0.089	0.671	-0.409		-0.168					-0.379	0.197	0.129
	B		0.082	-0.117	0.527	-0.225		-0.226					-0.148		0.087
Oligochaeta	D	0.083	0.125	-0.069	0.842	-0.641	0.123		0.690	-0.663					0.236
	B	0.073	0.086	-0.095	0.694	-0.492		0.091							0.155
Pygospio elegans	D		0.378	0.221				-0.065							0.116
	B		0.331	0.179				-0.074	0.070						0.088
Scoloplos armiger	D		0.346	0.115				-0.095				-0.078			
	B		0.316				-0.171				-0.069				0.133
Scrobicularia plana	D				0.929	-0.702			1.071	-1.187				-0.110	0.129
	B							0.138	0.850	-0.752					0.044
Spio sp.	D		-0.124				-0.253		-0.612	0.543			-0.068		0.096
	B						-0.227	-0.430	0.373						0.058
Tharyx marioni	D						0.124		0.225						0.076
	B		0.711	-0.595									-0.252	0.366	0.120

increased towards the upper part of the intertidal area (Fig. 7d). The biomass of surface deposit feeders showed a marked difference in the distribution in relation to depth between years (Fig. 7f). Compared to the mud content of the sediment in the same depth classes (Fig. 8) it is obvious that where the biomass of surface deposit feeders was lower in 1989 there was also a decrease in the mud content of the sediment. This pattern does not hold for the burrowing deposit feeders (Fig. 7h).

Suspension feeders were not clearly related to the mud content (Fig. 7i) but showed highest values of both density and biomass in the lower part (round and below NAP) of the intertidal area (Fig. 7j).

The number of species per sample increased somewhat with the mud content (Fig. 9a). With depth there was no clear pattern (Fig. 9b).

Table 5: Results of a Canonical correlation analysis on density data of 1985 and 1989 separateley and together (Med, Median grain size).

Canonical correlation analysis macrozoobenthos								
	1985				1989			
Wilks' Lambda	0.044 F=4.926, df=207,2266 p<0.001				0.026 F=5.846, df=207,2232 p <0.001			
Canonical correlations	Axis	1	2	3	Axis	1	2	3
		0.853	0.794	0.611		0.869	0.794	0.541
Intra-set correlations		1	2	3		1	2	3
	mud	0.783	-0.065	0.413	depth	0.979	0.026	-0.0.53
	depth	0.123	0.832	-0.454	mud	-0.157	0.769	0.403
	med	0.763	-0.139	0.231	med	-0.081	0.757	-0.339

	1985-1989			
Wilks' Lambda	0.046 F=0.046, DF=207,4748 p<0.001			
Canonical correlations	Axis	1	2	3
		0.833	0.76	0.539
Intra-set correlations		1	2	3
	depth	0.695	0.639	-0.027
	mud	0.381	-0.679	-0.558
	med	0.365	-0.651	-0.321

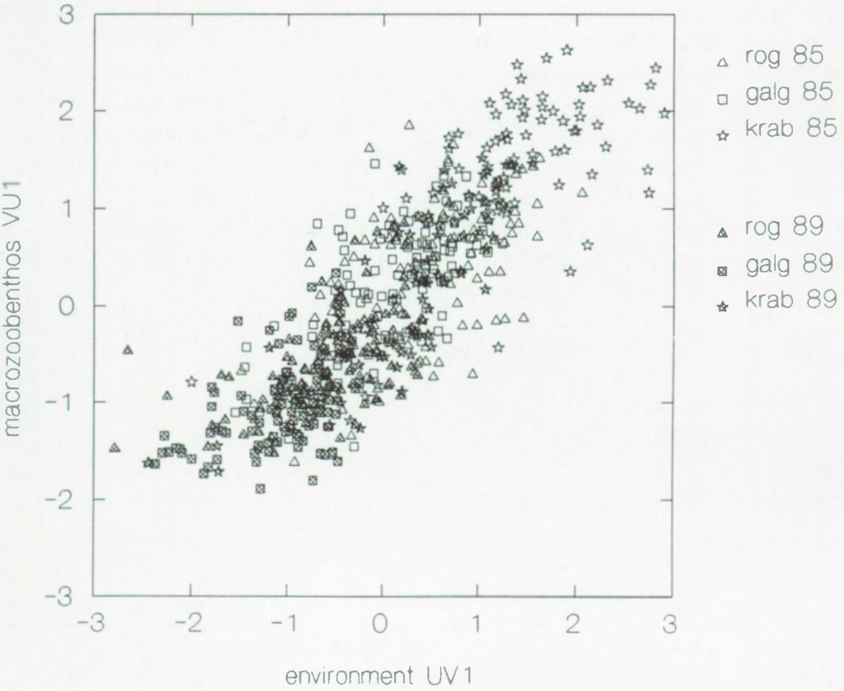


Figure 10. Plot of the first (standardized) canonical variable environment (UV1) against macrobenthos (VU1). (rog: Roggenplaat; galg: Galgeplaat; krab: Krabbenkreek).

A stepwise multiple regression was applied to further analyse these relations (Table 4). The dummy variable year was significant for three species, indicating that the relation between distribution and environmental variables was different between both years. Depth and/or its square was the most commonly selected environmental parameter. For most species, the results for density or biomass are often in agreement, although some clear differences exist as e.g., for *T. marioni*. The multiple correlation coefficient is however in nearly all cases very low, indicating that only a small proportion of the species variability is explained.

To gain more insight into the overall relationship between the distribution of the species and the environmental variables a canonical correlation analysis was performed separately on the data of both individual years and of all data (see also Van Der Meer, 1991). The canonical correlation coefficients, the canonical coefficients and the intra-set correlations are given in Table 5. A clear linear relationship between macrobenthos and environmental variables

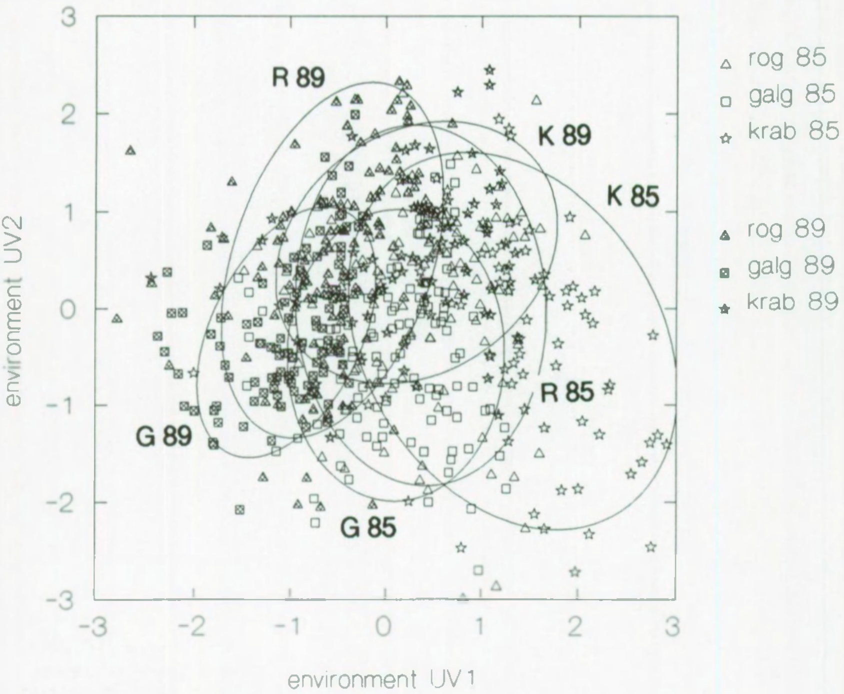


Figure 11. Plot of the first two canonical variables (UV1 and UV2) plotted against each other. For each intertidal area the 80% confidence ellips for each year is given. (rog, R: Roggenplaat; galg, G: Galgeplaat; krab, K: Krabbenkreek).

emerged (Fig. 10). From both the canonical coefficients and the intraset correlations it is obvious that in 1985 the first canonical environmental axis was related to the sediment characteristics, mainly mud content and median grain size. The second axis was related to depth. In 1989 the first canonical environmental axis was related to depth, the second axis to mud content and median grain size. The same holds for the analysis of both years. On the second axis however all variables had high coefficients. The results of this analysis are also summarized in Fig. 11. From the confidence ellipses it is clear that the major shift between years occurred along the first axis which is related to depth. This agrees with the major change in this environmental variable.

The importance of depth and mud content of the sediment is also reflected in the TWINSPAN analysis, described before. Fig. 12 shows that the mud content of the sediment was highest in the first two clusters, lower in

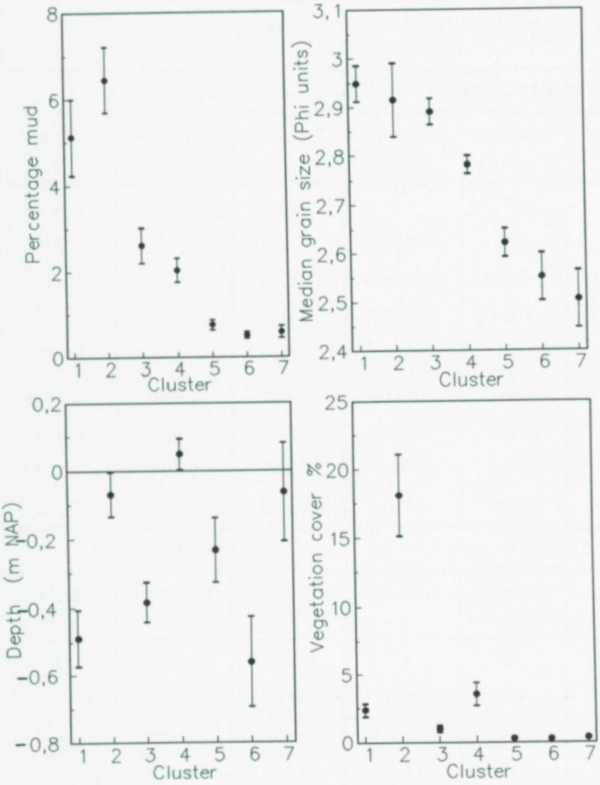


Figure 12. Average value (± SE) of some environmental parameters per TWINSPAN cluster based on the analysis of the biomass data of 1985.

cluster 3 and 4 and very low in the cluster 5 to 7. Median grain size also decreased from cluster 1 to 7. Depth differed between clusters but no clear pattern is obvious. Vegetation mainly occurred in clusters 2.

To test whether the different clusters, as defined by TWINSPAN, could be distinguished based on the environmental parameters measured, a Multivariate Discriminant Analysis (MDA) was performed. The different TWINSPAN clusters were the groups and the sediment parameters (mud content, median grain size, sorting coefficient), depth and vegetation cover the discriminating variables. The results are given in Table 6. The discriminant functions differ quite substantially between both years. The results of the analysis on the 1989 density and biomass data are very similar, depth being the most important factor on axis one, vegetation cover on axis 2 and median grain size on axis 3. The results of the analysis of the 1985 samples are different for density and biomass. Based on the obtained discriminant functions, each station was again classified. 49, 65, 46 and 61% of the stations were classified in the

Table 6. Results of a Multivariate Discriminant Analysis. For each TWINSPAN (on biomass or density data of 1985 or 1989) the analysis was run. Each TWINSPAN cluster was a group and the discriminating variables were the measured environmental variables.

	BIOMASS 1985			BIOMASS 1989		
	Function 1	Function 2	Function 3	Function 1	Function 2	Function 3
df	30	20	12	25	16	9
X 2	212	98	50	387	134	20
p	<0.001	<0.001	<0.001	<0.001	<0.001	<0.05
canonical cor	0.566	0.387	0.367	0.762	0.569	0.247
mud	0.992	0.06	0.09	0.084	0.026	0.058
med	0.181	0.363	-0.901	0.028	0.301	-0.970
depth	0.346	-0.794	-0.505	0.926	0.383	0.131
sort	-0.331	0.153	0.114	0.165	0.488	0.131
vegetation	0.245	-0.263	0.701	-0.445	0.764	0.257
	DENSITY 1985			DENSITY 1989		
	Function 1	Function 2	Function 3	Function 1	Function 2	Function 3
df	20	12	6	20	12	6
X 2	169	61	20	393	107	35
p	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
canonical cor	0.552	0.361	0.233	0.791	0.469	0.334
mud	0.475	-0.393	0.567	0.320	-0.123	0.083
med	0.495	-0.699	-0.381	-0.237	0.335	0.807
depth	0.582	0.370	-0.017	1.001	0.228	-0.095
sort	0.306	-0.260	0.506	0.145	0.607	0.144
vegetation	0.632	0.350	-0.074	-0.270	0.729	-0.527

correct TWINSPAN cluster for density 1985, 1989, and biomass 1985, 1989 respectively. These results indicate that the measured environmental parameters explained only partly the distribution of the species.

The previous finding could result from a broad tolerance of the species to the environmental variables. Therefore we tried to estimate "the habitat" of each species by means of a MDA. The results for both years are summarized in Table 7. The first two discriminant functions were highly significant in differentiating between species according to the chi-square test. In 1985 the

Table 7. Results of a Multivariate Discriminant Aanalysis to discriminate between species based on environmental parameters. For explanation see text.

1985		
	Discriminant function 1	Discriminant function 2
Degrees of freedom	152	126
Chi-square test for significance of the discriminant function	330.8	183.9
P	<0.001	<0.001
Canonical correlation	0.203	0.187
Standardized discriminant function coefficients		
mud(%)	0.738	-0.426
median grain size	0.533	-0.550
depth	0.371	0.724
sorting coef.	-0.455	-0.270

1989			
	Discriminant function 1	Discriminant function 2	Discriminant function 3
Degrees of freedom	152	126	102
Chi-square test for significance of the discriminant function	644.4	279.4	122.6
P	<0.001	<0.001	<0.1
Canonical correlation	0.353	0.236	0.138
Standardized discriminant function coefficients			
mud (%)	0.186	0.512	0.138
median grain size	0.200	0.729	-0.500
depth	-0.937	0.297	0.051
sorting coef.	0.206	0.483	0.124

predominant environmental variable on DF1 was the mud content of the sediment on DF2 the depth. In 1989 depth was the predominant environmental variable on DF1 and median grain size and mud content on DF2. In Fig. 13 the 95% confidence ellipses for the species discriminant scores are plotted for the 1985 data showing a very large overlap between species. Although some species are clearly segregated in the discriminant space most of them are overlapping very much.

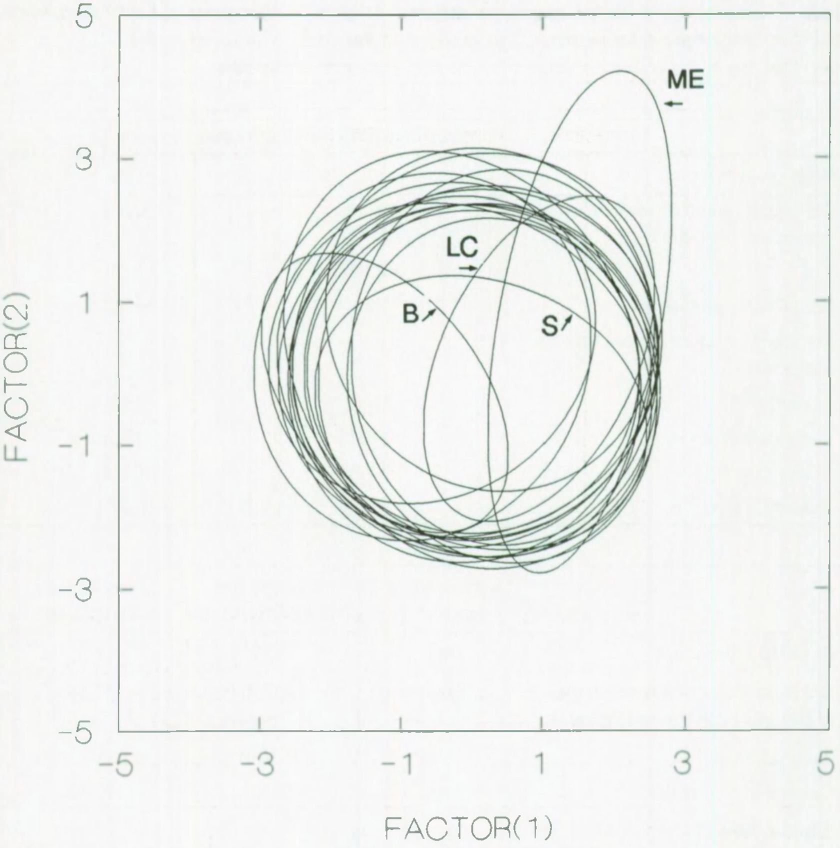


Figure 13. Ninety-five percent confidence ellipses around the mean scores on discriminant functions (axis) 1 and 2 of the 20 most common macrobenthic species (based on a MDA on the density data of 1989). The ellipses of some species are indicated (ME, Mytilus edulis; LC, Lanice conchilega; S, Spio sp.; B; Bathyporeia sp.).

4. Change of the benthic community between 1985 and 1989

The previous results indicate clear differences between both sampling periods. Density and biomass did change significantly and the effect of different environmental parameters varied between years. To get an idea of the overall changes in the benthic community a TWINSPAN on the density data of all stations in both 1985 and 1989 was carried out. The results are summarized in Table 8. Seven different clusters were retained for further

Table 8. Results of TWINSPAN analysis of the density of macrozoobenthos of 1985 and 1989. For each cluster the total number of stations, and the number from each sampling year is given together with the averag value of some environmental parameters.

Characteristics of the different TWINSPAN groups							
Cluster	1	2	3	4	5	6	7
N of stations	47	97	137	100	131	82	11
85 stations	1	92	47	99	54	9	3
89 stations	46	5	90	1	77	73	8
Depth	-.69	-.29	.13	-.02	-.17	-.73	.57
med	2.87	2.88	2.81	2.84	2.58	2.68	2.6
mud	5.2	5.01	2.9	2	0.69	1.2	0.42
vegetation	32	7	4	4	0.8	9	0.3

Table 9: Evolution of some stations from 1985 to 1989 in the TWINSPAN. The first row and colum give the TWINSPAN group. Row 2 consists of all stations whose 1985 data were classified in group 2. The columns show to what TWINSPAN group these stations belonged to in 1989 (of the 92 stations of 1985 belonging to group 2, in 1989, 30 belonged to group 1, 4 to group 2 etc.) The same is given for the plots belonging in 1985 to group 3 and 4.

	Cluster 1989						
Cluster 1985	1	2	3	4	5	6	7
2	30	4	31	0	16	10	0
3	0	0	19	0	18	0	0
4	11	0	34	1	25	26	0

analysis, cluster 7 having only 11 stations. Four of the remaining six clusters consists almost exclusively of samples from one year, two clusters had samples from both years. Average values of environmental parameters per cluster are also given in Table 8. To get more insight into the changes, Table 9 shows to what TWINSPAN cluster the 1985 and 1989 data of each station belonged to. It is clear that the 1989 data of stations, whose 1985 data clustered together into 1 cluster, are found in several clusters. This means that stations with a large faunal similarity in one year evolved in different ways, thereby reducing faunal similarity. This could be due to the fact that the environmental parameters of the stations that form one cluster in 1985

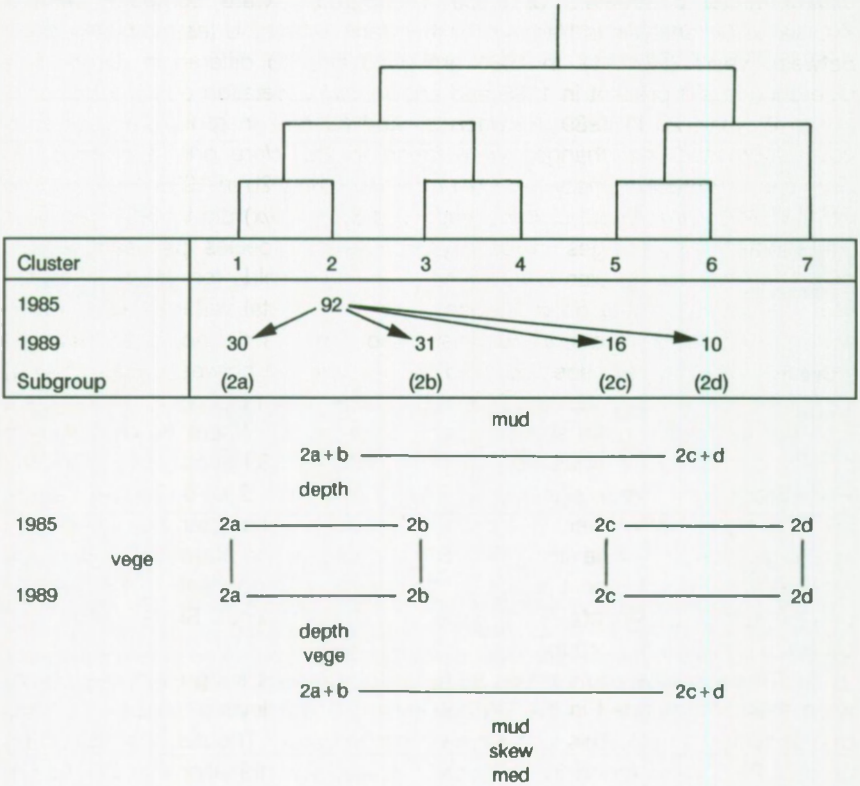


Figure 14. Dendrogram of a TWINSPAN on density data of both 1985 and 1989 together with an analysis of what happened in 1989 to the stations whose 1985 data clustered together in cluster 2. The 1989 data of these stations were found in 4 different clusters and labelled as subgroup 2a-2d. The environmental variables that differed significantly between these subgroups both within and between years are indicated. For further explanation see text.

changed in different ways; in 1985 the stations could have all a similar sediment but by 1989 the sediment in these stations could have changed in different ways, e.g., some stations becoming more sandy, others more muddy. To check this possibility we investigate what happened to the stations belonging in 1985 to cluster 2. Cluster 2 consists of 97 stations, 92 of them being sampled in 1985. The 1989 data of these 92 stations are found in TWINSPAN cluster 1, 3, 5 and 6 (30, 31, 16 and 10 stations respectively)(Table 9). These four subgroups of stations are called group 2a to 2d. The environmental parameters of these 4 subgroups were compared with a Kruskal Wallis analysis of Variance or the Mann Withney U test both within and between years (Fig. 14). In 1985 group 2a and 2b differed in depth. This difference is still present in 1989 and additionally vegetation cover is higher in group 2a than 2b in 1989. Between 85 and 89 only in group 2a vegetation cover increased, no changes were found in 2b. Were only 1 species (*H. filiformis*) differed in density between groups 2a and 2b in 1985 4 species (*A. marina, Gammarus* spec, *L. conchilega* and *S. bombyx*) did in 1989. Between years significant changes in density, number of species per sample and density of several species were found. The same holds for group 2c and d with the exception that no differences in environmental variables were found within and between years. Within years also densities did not differ, between years it did for several species. Mud content differed between group 2(a+b) and group 2(c+d) in 1985. In 1989 both groups differ not only in mud content but also in median grain size and sorting coefficient. Where no difference in density of individual species were found in 1985, in 1989 density of *H. filiformis* and Oligochaeta were significantly higher in group 2(a+b), density of *S. filicornis* significantly lower. This change in sediment characteristics is reflected in a larger faunal change since TWINSPAN cluster 5 and 6 are separated at an early stage from cluster 1 to 4. *H. filiformis* and Oligochaeta are known to prefer muddier sediments, *S. filicornis* coarser sediments. Similar results are obtained for the other groups.

These results could be an artifact if the different subgroups (e.g., 2a-d) were already separated in the TWINSPAN at a lower level of division than the one considered here. This was however not the case. The stations making up groups 2a-d were found in completely different combinations in the further subdivisions of cluster 2. The same is true for the other clusters.

From this analysis we can conclude that, although the environmental parameters in a group of stations, showing a large faunal similarity in one year, did not change, the faunal composition did. This indicates that faunal changes are not necessarily linked to changes in the measured environmental parameters.

DISCUSSION

1. Observed changes in environmental parameters and benthos

1.1 Changes in environmental parameters

The coastal engineering works caused some important hydrodynamical changes in the Oosterschelde estuary (Vroon, 1993), influencing the morphology of the estuary (Mulder & Louters, 1993; Ten Brinke *et al.*, 1993), and the sediment composition of the tidal flats. On average, sediments became coarser with a lower mud content. According to Ten Brinke *et al.*, (1993) the observed changes on the Roggen- and Galgeplaat can not be seen independent of the natural seasonal variation in these parameters. Only on the Krabbenkreek the changes in sediment composition could be attributed to the construction of the storm surge barrier.

The erosion and hence the decrease in depth of the tidal flats is significant all over the Oosterschelde (Philippart, 1991; Mulder & Louters, 1993). Height of a site in se, is of no importance to benthic animals but the emersion period is, which is of course function of the height (e.g., Hummel *et al.*, 1993). Due to the reduced tidal amplitude, above mid tidal level the immersion period decreased, below it increased. Thus major changes in emersion time occurred only in the upper and lower part of the tidal zone. In between, the changes in emersion time due to the construction of the barrier are small, especially compared to the effects wind may have on the tides.

It can be concluded that on average the site characteristics (sediment and emersion) did not change markedly and that the range of observed values is similar before and after the construction of the barrier.

In the watercolumn important changes occurred. The current speed is, at most sites, reduced by 30 to 40%, in the northern branch even by 70% (Vroon, 1993). Due to the manipulation of the barrier the wave attack on the tidal flats, especially during storms, increased in the zone NAP +0.5 m to NAP -1.0 m up to 30%. Primary productivity remained constant (Wetsteyn & Kromkamp, 1993).

1.2 Changes in benthic populations

Between both years significant differences in density, biomass and number of species per sample were found. Density and biomass of some species remained fairly constant while those of others changed dramatically. Comparing different years, the major benthic communities ranging from very muddy musselbeds with a high number of species to very sandy sites with a limited number of species (see Meire & Kuijken, 1984) remained present. However, within these larger habitats, we see important between year variability in the relative abundance of species etc.. The top dominant species within each community varies largely and the Canberra dissimilarity index for one study plot between two successive years amounts to about 60-70%, both for density or biomass of species (Meire unpublished data).

Based on the analyses presented above we want to investigate whether these changes are related to the environmental changes in the Oosterschelde or to other factors. We will firstly focus on the relation between the benthic invertebrates and sediment characteristics, afterwards on other environmental factors.

2. Environmental parameters influencing benthic populations.

2.1 Relations with sediment parameters

The different methods used to describe the relationship between the distribution of benthic invertebrates and environmental parameters, all clearly indicated the importance of depth and sediment characteristics, especially mud content. This is in agreement with earlier studies showing that depth and mud content of the sediment are very important factors influencing benthic populations (e.g., Beukema, 1976; Dankers & Beukema, 1981; Gray, 1974). However, the analyses indicate that, although these parameters clearly influence the benthic invertebrates, the coupling between the species and these variables seems to be rather loose. The coefficients of determination of the multiple regression analyses are all very low (most lower than 0.1!) and the classification of stations by MDA showed a large degree of error. The relative importance of the different parameters also differed between years. In most analyses mud content is the dominant parameter in 1985, depth in 1989. As the range of both parameters was the same in both years the reason for this difference is not clear. The MDA results on the species classification shows a very large overlap between most species. These results contrast with those presented by Flint & Kalke (1986). In a similar analysis they found a very clear separation of most benthic species in the discriminant space. The difference probably can be explained by the fact that the range of sediment parameters in our study is very small, relative to the tolerance of the different species. This is corroborated by the TWINSPAN of both years. If the change in sediment parameters of a station is rather large, then species composition changes in a predictable way. These results indicate the importance of the sediment parameters but also indicate that they are insufficient to explain the observed patterns and that other factors are important in structuring benthos populations.

2.2 Relations with other environmental parameters

Next to sediment parameters the most important environmental variables influencing benthic populations are weather conditions. Severe winters are known to have a very important impact on benthic populations. Several species as *Nephtys hombergii, Lanice conchilega* etc. are very sensitive to frost (Beukema, 1985) and their populations are likely to be decimated in severe winters. Additionally several species (*Arenicola marina;* most bivalves) are known to have very successful spatfalls after a severe winter (Beukema, 1985).

Comparison of the data presented in this paper with the long term patterns observed in the Oosterschelde indicates that the density of most species peaked in 1985 (Seys *et al.*, 1993; Coosen *et al.*, 1993a). This was probably a respons to the very severe winter 1984/85 in which a high mortality of benthos occurred. In the 1985 samples, large numbers of small individuals (juveniles) were found. The cockle population collapsed resulting in low values for the total biomass, but high numbers of spat. After the severe winter of 1986/87 also much cockle spat was found. In 1989 these second year cockles made up an important part of the biomass (Coosen *et al.*, 1993a). The decrease in density and the increase in biomass do therefore not indicate long term trends but fluctuations around a long term mean, that did not seem to change until 1989, three seasons after the completion of the barrier (Seys *et al.*, 1993). The difference between years found in this study are therefore more likely to be caused by the weather conditions than by changes in sediment parameters.

3. Structure of the benthic communities: abiotic versus biotic control of populations.

3.1 Biotic control

In general, the structure of macrobenthic communities and the concomitant processes have been studied intensively during the last decade; some of the evidence has recently been reviewed by Wilson (1991). Although both inter- and intraspecific competition occurs on tidal flats (e.g., Bonsdorff *et al.*, 1986; see Wilson, 1991 for review), predation is thought to be the most important form of biotic interaction (Reise, 1985; Wilson, 1991). Ambrose (1984) proposed a three level interactive model for soft-sediment marine systems, the first level being epibenthic predators (birds, fish, crabs and shrimps), the second being predatory infauna (mainly polychaetes like *Nereis diversicolor* and *Nephtys hombergii*) and the non-predatory infauna as third level. The importance of epibenthic predators is well known (Baird *et al.*, 1985; Meire *et al.*, 1993; Reise, 1985; Sanchez-Salazar *et al.*, 1987). The importance of infauna predators is only recognized since a decade and recently reviewed by Ambrose (1991). Estimates of feeding rates indicate that many predatory taxa have the potential to reduce the size of prey populations. Based on manipulative field experiments it was demonstrated that infaunal predators have indeed a significant effect on infaunal densities and affect the spatial and temporal distribution of their prey.

3.2 Abiotic control

Severe winters have an important direct effect on benthos as many individuals may die. They have also very important indirect effects (Kneib, 1991). Severe winters can be considered as a natural predator removal experiment (Reise, 1985): some predators are killed, others arrive later in spring on the flats. This can have pronounced effects. The increase of *Scoloplos armiger* after a severe winter, when *Nephtys hombergii*, its main predator, is decimated is a clear example (Coosen *et al.*, 1993a; Beukema, 1987). After a severe winter the water temperature needs more time to increase, causing juvenile crabs and shrimps, important predators of (juvenile) benthos, to move up the flats significantly later (Beukema 1985). At that time many juvenile benthos species are large enough to escape predation, and can survive, giving rise to high density populations. If large enough, they will then be prey of larger epibenthic predators as fish and birds, most of which are able to switch easily between different prey species.

4. Macrobenthos as a non-equilibrium community.

Lying at the foundation of contemporary views of community patterns and the processes producing them is the presumption that these systems are at or close to equilibrium (by equilibrium is meant the stability or "steadiness" of the community components) (Wiens, 1984). They are ecologically saturated, resource limited and governed by biotic interactions, especially competition. Fluctuations in natural communities are attributed to variations in resource levels which are closely tracked by members of the community. Several predictions can be made on ecomorphological patterns, diet niche relationships, patterns of habitat occupancy etc.

Estuarine benthic populations seem however not to be in any readily definable equilibrium. Species vary rather independently of one another (Beukema & Essink, 1986; Elliot & Ducrotoy, 1991; Coosen *et al.*, 1993a); the community seems not to be saturated. Several exotic species became established without any or small observable effect on native species. Examples are *Crepidula fornicata, Crassostrea sp.* and *Ensis directus*. The polychaete *Tharyx marioni* became established in the Wadden Sea in the early 1970's and is at present one of the most abundant species. No clear effect on other species was noticed (Reise, 1985). Also no clear effects of the introduction of *Marenzellaria viridis* on other species were found (Essink, pers. comm). Intertidal benthic populations also do not appear to be resource-limited very often. Biomass of suspension feeders varies between years with several orders of magnitude, their food supply (phytoplankton) does not (e.g., Wetsteyn & Kromkamp, 1993). A low biomass of cockles do not coincide with low values of primary production, suggesting, at that time, they will probably not be resource limited. Food supply for deposit feeders is difficult to measure but in predator exclusion experiments densities of several deposit feeders can increase substantially, which could indicate they are not resource limited (Reise, 1985). This is however in contrast to the results by Beukema & Cadee (1986) who attribute an increase in macrobenthic populations in the Wadden Sea to eutrophication. Infauna predation is also important in determining the observed patterns. Diet overlap occurs in many species (Ambrose, 1991) and the results presented above indicate there is a large overlap in habitat preference between species. Predation is probably more important than competition, which seems to occur more widely within than between species (Reise, 1985; Wilson, 1991).

Loose community structuring can be expected in highly variable or harsh environments. Under such conditions, resource levels and environmental conditions may at times be severely constraining. Such "ecological crunches" (e.g., severe winters) may act in a major way to determine the ecological adaptations of species and the observed patterns of community composition. Much of the time the environment may be more benign and resource levels essentially non-limiting. Under these conditions populations and communities may be freed of close direct biotic or even abiotic control and vary in manners that erode the clean patterns expected from equilibrium theory (Wiens, 1984). These communities are non-equilibrium communities. They should be characterized by a general "decoupling" of close biotic interactions, and the species should respond to environmental variations largely independent of one another. Habitats may not be fully saturated with individuals and species may be under represented. Populations and communities may be more strongly influenced by abiotic agents than by the imposition of ceilings on resource abundance, and population dynamics may be governed by effects that are largely independent of density. Collectively these factors produce communities that are only loosely structured, and clear consistent patterns may be largely lacking (Wiens, 1984). Equilibrium and nonequilibrium community structure are not discrete states of ecological communities, but are the opposite ends of a continuum (Wiens, 1984). The results presented in this paper, together with the evidence presented in the discussion, in our opinion, indicates that intertidal macrobenthic populations should be considered rather as nonequilibrium communities. Boecklen & Price (1991) came to the same conclusion for a population of sawflies on arrayo willow.

On the tidal flats different broad habitat types can be distinguished as muddy musselbeds and more exposed sites characterized by sandy sediments and large ribble marks. Most species, however, have a large tolerance for sediment parameters, especially relative to the range found in our study area. Within the range of conditions within specific habitats, e.g., musselbeds, most species can occur. Which species occur and in wich densities is probably mainly determined by differences in settlement and subsequent predation. Differences in settlement are caused by variations in the number of offspring produced by the adults and, to a large extent, by the settlement conditions. The timing of settlement in relation to other species and especially to the invasion of the flats by shorecrabs will determine the population. This means that within each major habitat many different combinations of dominant species are possible. If the environmental parameters change drastically then a more pronounced change in benthic composition occurs. Within a habitat the benthic system can be seen in neighbourhood stability (Gray, 1977). The existence of many stable points could be seen as a consequence of the nonequilibrium community.

5. Conclusion

Although the impact of the construction of the barrier on the macrobenthic community seems at present to be rather small. This does not mean that on the long term there will be no effect. During 1985/1986 when the reduction in tidal amplitude was more pronounced (see Nienhuis & Smaal, 1993), clear effects on benthos were found in the upper part of the intertidal area, where the emersion time decreased drastically (Craeymeersch *et al.*, 1988; Seys *et al.*, in press). Furthermore it is possible that the important changes in the water column will have an effect on the transport or settlement of larvae, and the transport of food to the bottom. This was not studied until now. Also the availability of benthos as food for birds may decrease (Meire *et al.*, 1993). The expected long term change in the erosion-sedimentation equilibrium might over time have a pronounced effect on the whole ecosystem.

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REFERENCES

Ambrose, W.G., 1984. Role of predatory infauna in structuring soft-bottom communities. Mar. Ecol. Prog. Ser. 17: 109-115.

Ambrose, W.G. Jr., 1991. Are infaunal predators important in structuring marine soft-bottom communities?. Am. Zool. 31: 849-860.

Baird, D., P. R. Evans, H. Milne & N. W. Pienkowski, 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanogr. Mar. Biol. annu. Rev. 23: 573-597.

Beukema, J. J., 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.

Beukema, J. J., 1985. Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea. In J. S. Gray & M. E. Christiansen (Eds), Marine Biology of Polar regions and effects of stress on marine organisms. Wiley & Sons, New York: 351-361

Beukema, J. J., 1987. Influence of the predatory polychaete *Nephtys hombergii* on the abundance of other polychaetes. Mar. Ecol. Prog. Ser. 40: 95-101.

Beukema, J., 1989. Long-term changes in macrobenthic abundance on the tidal flats of the Western Wadden Sea. Helgoländer Meeresunters. 43: 405-415.

Beukema, J. J. & G. C. Cadee, 1986. Zoobenthos responses to eutrophication of the Dutch Wadden Sea. Ophelia 26: 65-76.

Beukeman, J. J. & K. Essink, 1986. Common patterns in the fluctuations of macrobenthic species living at the different places on tidal flats in the Wadden Sea. Hydrobiologia 142: 199-207.

Boecklen, W. J. & P. W. Price, 1991. Nonequilibrium community structure of sawflies on arroya willow. Oecologia 85: 483-491.

Bonsdorff, E., J. Mattila, C. Rönn & C-S. Oosterman, 1986. Multidimensional interactions in shallow soft-bottom ecosystems: testing the competitive exclusion principle. Ophelia Suppl. 4: 37-44.

Coosen, J., J. Seys, P. Meire, 1993a. Effects of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde on distribution, density and biomass of some common macrobenthic species: *Spio martinensis* (Mesnil), *Hydrobia ulvae* (Pennant), *Arenicola marina* (L.), *Scoloplos armiger* (Muller) and *Bathyporeia*. Hydrobiologia: in press.

Coosen, J., F. Twisk, M. W. M. Van der Tol, R. H. D. Lambeck, M. Van Stralen & P. M. Meire, 1993b. Stock assessment of cockles (*Cerastoderma edule*) in the Oosterschelde and factors determining it in 1980-1990. Hydrobiologia: in press.

Craeymeersch, J. A., J. Coosen & A. Van den Dool, 1988. rendanalyse van densiteit- en biomassawaarden van bodemdieren in het getijdengebied in de Oosterschelde (1983-1986). Rapporten en Verslagen 1988-7, DIHO, Yerseke.

Dankers, N. & J. J. Beukema, 1981. Distributional patterns of macrozoobenthic species in relation to some environmental factors. In N. Dankers, H. Kühl & W. J. Wolff (Eds), Invertebrates of the Wadden Sea. Balkema, Rotterdam: 4/69-4/103.

De Jong, D. J., P. H. Nienhuis & B. J. Kater, 1993. Microphytobenthos in the Oosterschelde (NL), 1981-1990; Consequences of a changed tidal regime. Hydrobiologia: in press.

Desprez, M., J-P. Ducrotoy & B. Sylvand, 1986. Fluctuations naturelles et évolution artificielle des biocénoces macrozoobenthiques intertidales de trois estuaires des côtes françaises de la Manche. Hydobiologia 142: 217-232.

Dörjes, J., H. Michaelis & B. Rhode, 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). Hydrobiologia 142: 217-232.

Elliot, M. & J. P. Ducrotoy, 1991. Estuaries and Coasts: spatial and temporal intercomparisons. Olson & Olson, International Symposium Series, Fredensborg.

Essink, K., 1988. Recent introduction of North American marine invertebrates in the North Sea and the Baltic Sea. Rijkswaterstaat, Dienst Getijdewateren, Notitie GWAO-88.2240, Haren.

Fauchald, K. & P. A. Jumars, 1979. The diet of worms. A study of polychaete feeding guilds. Oceanogr. Mar. Biol. annu. Rev. 17: 193-284.

Flint, R. W. & R. D. Kalke, 1986. Niche characterisation of dominant estuarine benthic species. Estuar. coast. shelf Sci. 22: 657-674.

Gray, J. S., 1974. Animal-sediment relationships. Oceanogr. Mari. Biol.: an annu. Rev. 12: 223-161.

Gray, J. S., 1977. The stability of benthic ecosystems. Helgoländer wiss. Meeresunters. 30: 427-444.

Hill, M. O, 1979. TWINSPAN, a fortran program for arraging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca; N.Y.

Hummel, H., A. W. Fortuin, R. H. Bogaards, A. Meijboom & L. De Wolf, 1993. The effects of prolonged emersion and submersin by tidal manipulation on marine macrobenthos. Hydrobiologia: in press.

James, F. C. & C. E. McCulloch, 1990. Multivariate analysis in ecology and systematics: panacea or pandora's box? Annu. Rev. Ecol. Syst. 21: 129-166.

Kneib, R. T., 1991. Indirect effects in experimental studies of marine soft-sediment communities. Am. Zool. 31: 874-885.

Meire, P. M. & E. Kuijken, 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. M., H. Schekkerman & P. L. Meininger, 1993. Consumption by waterbirds in the Oosterschelde, SW Netherlands, in relation to carrying capacity and the benthic invertebrate community. Hydrobiologia: in press.

Meire, P. M., J. Buijs, J. Seys, F. Twisk, E. Stikvoort, D. De Jong, 1991b. Macrozoobenthos in de Oosterschelde in het najaar 1989: een situering van de gegevens. Rapport RUG-WWE nr. 30, Universiteit Gent, Gent.

Meire, P. M., J. Buijs, J. Van Der Meer, A. Van Den Dool, A. Engelberts, F. Twisk, E. Stikvoort, D. De Jong, R. H. D. Lambeck & J. Polderman, 1991a. Macrozoobenthos in de Oosterschelde in het najaar 1985: een situering van de gegevens. Rapport RUG-WWE nr. 27, Universiteit Gent, Gent.

Mulder, J. P. M. & T. Louters, 1993. Changes in basin geomorphology after implementation of the Oosterschelde project. Hydrobiologia: in press.

Nienhuis, P. & A. Smaal, 1993. General Introduction. Hydrobiologia: in press.

Philipart, M. E., 1991. Bodemligging Oosterschelde: de invloed van de werken. Rapport 1991-12, Geografisch Instituut Rijksuniversiteit Utrecht, Utrecht.

Prins, T. & A. Smaal, 1993. The role of benthic suspension feeders: activity, turnover, feedback. Hydrobiologia: in press.

Reise, K., 1985. Tidal Flat Ecology: an experimental approach to species interactions. Springer-Verlag, Berlin.

Sanchez-Salazar, M. E., C. L. griffiths & R. Seed, 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible Cockle, *Cerastoderma edule*. Estuar. coast. Shelf. Sci. 25: 245-260.

Seys, J. & P. Meire, 1992. Long-term fluctuations (1979-1989) of the intertidal macrozoobenthos in the Oosterschelde: before, during and after the construction of the storm surge barrier. Rapport WWE nr. 33, Universiteit Gent, Gent.

Seys, J. J., P. M. Meire, J. Coosen & J. A. Craeymeersch, 1993. Long-term changes (1979-89) in the intertidal macrozoobenthos of the Oosterschelde estuary: are patterns in total density, biomass and diversity induced by the construction of the storm surge barrier? Hydrobiologia: in press.

Seys, J. J., P. M. Meire, J. Coosen, J. A. Craeymeersch, R. H. D. Lambeck, A. Van den Dool, in press. The intertidal macrozoobenthos in the Oosterschelde before, during and after the construction of the storm surge barrier: some preliminary results. In N. V. Jones (Ed.), The changing coastline: in press.

Siegel, S., 1956. Nonparametric Statistics for the behavioural sciences. MacGraw-Hill, Tokyo.

Ten Brinke, W. B. M., J. Dronkers & J. P. M. Mulder, 1993. Fine sediments in the Oosterschelde estuary before and after partial closure. Hydrobiologia: in press.

Van Der Meer, J., 1991. Exploring macrobenthos-environment relationship by canonical correlation analysis. J. exp. mar. Biol. Ecol. 148: 105-120.

Van Der Meer, J., A. Van Den Dool, A. Engelberts, D. De Jong, R. H. D. Lambeck & J. Polderman, 1989. Het macrozoöbenthos van enkele intergetijdengebieden in de Oosterschelde. Resultaten van een inventarisatie in de nazomer van 1985. GWAO 89.307, Rijkswaterstaat, Middelburg.

Van Stralen, M. & R. Dijkema, 1993. Standing stock, growth and mortality of cultivated mussels. Hydrobiologia: in press.

Vroon, J., 1993. Hydrodynamic characteristics of the Oosterschelde over the last decades. Hydrobiologia: in press.

Warwick, R. M., J. D. Goss-Custard, R. Kirby, C. L. George, N. D. Pope & A. A. Rowden, 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn estuary different? J. appl. Ecol. 28: 1004-1026.

Weston, D. P., 1988. Macrobenthos-sediment relationships on the continental shelf of Cape Hatteras, North Carolina. Continental Shelf Res. 8: 267-286.

Wetsteyn, L. P. J. M. & J. Kromkamp, 1993. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (NL) before, during and after a large-scale coastal engineering project (1980-1990). Hydrobiologia: in press.

Wiens, J., 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In D. R. Strong, D. Simberloff, L. G. Abele & A. B. Thistle (Eds), Ecological communities. Conceptual issues and the evidence. Princeton University Press, Princeton: 439-457.

Wilkinson, L., 1988. SYSTAT, the system for statistics. SYSTAT, Evanstin, Illinois.

Wilson, W. H., 1991. Competition and predation in marine soft-sediment communities. Annu. Rev. Ecol. Syst. 21: 221-241.

Chapter 3

LONG-TERM CHANGES (1979-89) IN THE INTERTIDAL MACROZOOBENTHOS OF THE OOSTERSCHELDE ESTUARY: ARE PATTERNS IN TOTAL DENSITY, BIOMASS AND DIVERSITY INDUCED BY THE CONSTRUCTION OF THE STORM SURGE BARRIER ?

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ABSTRACT

To evaluate the effects of the construction of a storm surge barrier in the Oosterschelde, long-term patterns (1979-89) in abundance and biomass of the intertidal macrozoobenthos were studied at 14 permanent stations. Additionally, data of a large-scale survey in late summer 1985 and 1989 were analysed. In this paper, patterns in general parameters are discussed.

Late summer values of total biomass, total density, species richness, diversity and abundance- and biomass ratio show no overall significant trend during the study period. The changes in the hydrodynamics and the morphology of the Oosterschelde after the completion of the storm surge barrier do not seem to have influenced the normal patterns in benthic populations. The observed patterns are determined by the occurrence of severe versus mild winters, rather than by hydrodynamic changes caused by the construction of the barrier. Low biomasses, high densities (particularly of opportunistic species) and higher "stress-values" (abundance- and biomass ratio) in 1985(-87) indicate a temporal disturbance by severe winter weather. At the elevated COST-station 27, total biomass decreased sharply in 1985, due to a short-term increase in exposure time, caused by the manipulation of the storm surge barrier.

INTRODUCTION

When the decision was made to build a storm surge barrier in the mouth of the Oosterschelde estuary, an ecological monitoring program was developed to assess the impact of these engineering works. The interest in biomonitoring programs has been widely recognized. This seems to be part of a maturation process in ecology, resulting from the need for integration on a larger temporal and spatial scale (Reise, 1989). The recent success of ecological monitoring has different reasons. First of all, it improves our understanding of natural patterns and processes; by statistical modelling, long-term data sets can be used to assess the appropriateness of sampling schedules (spatial and temporal) and as a predictor of future trends (Coull, 1986; Gray & Christie, 1983). Secondly, departures from a common pattern may indicate local effects of pollutants or other factors of disturbance (Gray & Christie, 1983; Beukema & Essink, 1986). It is a necessary precondition for translating the principle of anticipatory action into practical policy (Reise, 1989). With an increasing anthropogenic impact on the natural environment, the development of biomonitoring studies is necessary.

Because of the crucial importance of the intertidal macrozoobenthos in

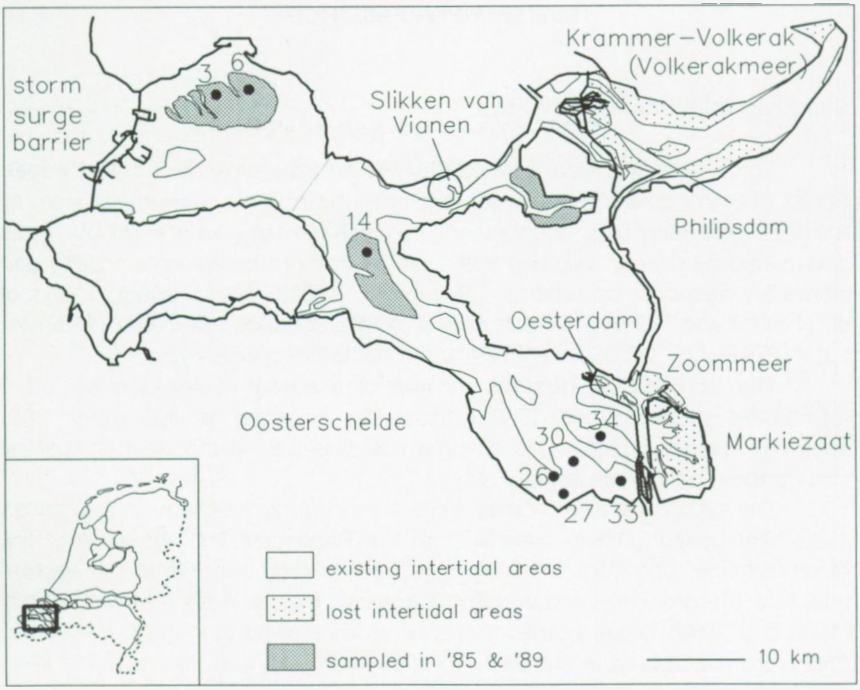


Figure 1. Study area and sampling stations of macrozoobenthos. The 8 COST-stations (3,6,14,26,27,30,33 and 34) are spread over the Oosterschelde intertidal flats, the 6 VIANEN-stations are enclosed by a circle. The three tidal flats sampled during the INTERECOS-surveys 1985 and 1989 (resp. 305 and 300 sampling points) are shaded.

the food-web of the intertidal system (as consumers of plankton, detritus; as prey for higher trophic levels: birds, fish), intensive studies on this group were started as part of the monitoring program in the Oosterschelde (Nienhuis & Smaal, 1993).

In this paper, trends and patterns of some general characteristics (total biomass, density, species richness, diversity, abundance - and biomass ratio) of the macrozoobenthos at 14 permanent stations during the period 1979-89 and at 300 stations in late summer 1985 and 1989 are presented and the effects of the changed environmental conditions in the Oosterschelde (cf. Nienhuis & Smaal, 1993) on the macrozoobenthic system is discussed. Structural aspects and changes in the distribution and biomass of some important macrobenthic species are treated respectively in Meire *et al.* (1993) and Coosen *et al.* (1993).

MATERIAL AND METHODS

Sampling methods and -stations.

Three data-sets were available for the analysis presented in this paper. For all of them, core-samples were taken and sieved on a 1mm-mesh size. All animals were identified, counted and the ash-free dry weight (AFDW) was determined by drying, weighing and ashing. For more details on sampling and laboratory methods, we refer to ^{1} Meire *et al.* (1991a; 1991b; 1993), ^{2} Seys *et al.* (1993b) and ^{2} Craeymeersch *et al.* (1988) and ^{3} Meire et Dereu (1989) for the INTERECOS-^{1}, COST-^{2} and VIANEN-^{3} dataset respectively.

The INTERECOS data-set consists of a survey in late summer 1985 (pre-barrier situation) and 1989 (post-barrier situation) at 305 (resp. 300) sampling stations distributed over three tidal flats, i.e., in the western, central and northern part of the estuary (Fig.1).

The COST data-set comes from a monitoring program in the period 1983-1989 based on two stations from the Roggenplaat in the west of the Oosterschelde, one from the Galgeplaat (central part) and five at the eastern tidal flats (Verdronken Land van Zuid-Beveland; Fig. 1). Samples were initially (1983 and 1984) taken 4 times a year, and twice since then (1985-1989). No data were available from station 14 in 1983 and 1986, from station 26 in 1988 and from station 30 in 1985-1986 (Table 1). For two of the stations (3 and 27), all species were picked out and identified; for the other six stations, only data for the 11 biomass-dominant species (*Arenicola marina* L., *Cerastoderma edule* L., *Heteromastus filiformis* Claparède, *Hydrobia ulvae* Pennant, *Lanice conchilega* Pallas, *Macoma balthica* L., *Mya arenaria* L., *Nephtys hombergi* Savigny, *Nereis diversicolor* O.F. Müller, *Scoloplos armiger* O.F. Müller and *Scrobicularia plana* Da Costa) were available. For these stations, 'total biomass' means the sum of biomass of these 11 species. Total density, species richness, diversity, and abundance- and biomass ratio were not calculated for these stations.

The VIANEN-dataset comes from a monitoring program at 6 stations on the "Slikken van Vianen" (Meire & Dereu, 1989), a tidal flat in the northern branch of the Oosterschelde (Fig. 1). Samples were taken annually in late summer 1981, 1982 and 1984-1989. Samples of late summer 1979 were taken at station 60,10 and 13.

This paper is primarily based on late summer data from the COST- and VIANEN-set, supplemented with INTERECOS-data where necessary. For data on seasonal variability, we refer to Coosen *et al.* (1993) and Seys *et al.* (1993a,b,c). For some stations, data from one or more years are missing. Therefore not all stations could be used in all statistical analyses. Three different combinations of permanent stations were used for analysis (Table 1). The fewer stations are included in the combination the more year data are

Table 1. Available data on abiotic characteristics of the CV0-stations in the period 1979-1990 (TL= tidal level; MGS= median grain size (in φ units); SC= silt (< 53 μ) content). The classification of stations in the CV0, CV1 and CV2 groups is also indicated. (V=VIANEN, C=COST data set)

CV2		▨	▨	▨	▨	▨	▨
CV1		▨	▨	▨	▨	▨	▨
CV0		▨	▨	▨	▨	▨	▨
Location		V	V	V	V	V	V
Variable/ station	year	10	22	60	13	32	39
TL (MTL+cm)	79	-81		-70	-41		
	84	-78	-78	-82	-51	+63	-10
	85	-68	-69	-78	-57	+59	-13
	86	-92	-94	-98	-80	+43	-18
	87	-91	-94	-97	-79	+42	-18
	88	-93	-88	-85	-72	+47	-15
	89	-97	-92	-88	-83	+42	-19
	90	-97	-94	-90	-96	+42	-20
MGS (φ units)	79	3.17		3.17	3.07		
	81	2.91	2.99	2.89	2.66	3.02	2.83
	84	2.85	2.76	2.95	2.88	2.94	2.96
	85	2.92	2.87	2.84	2.78	2.95	2.89
	86	2.73	2.69	2.69	2.84	2.97	2.93
	87	2.75	2.82	2.74	2.78	2.89	2.95
	88	2.50	2.53	2.55	2.80	2.63	2.61
SC (%)	79	8.5		9.2	3.9		
	81	7.6	16.6	6.0	7.0	5.0	6.0
	84	4.5	4.0	10.0	11.0	4.0	7.0
	85	5.7	5.6	5.2	4.5	3.2	6.2
	86	5.6	7.0	5.1	13.6	5.3	5.2
	87	2.0	2.8	2.5	2.8	0.8	5.6
	88	3.4	1.54	3.2	4.7	2.1	2.3

Table 1 continued

CV2		▬	▬						
CV1		▬	▬	▬	▬	▬			
CV0		▬	▬	▬	▬	▬	▬	▬	▬
Location		C	C	C	C	C	C	C	C
Variable/ station	year	3	27	6	33	34	14	26	30
TL (MTL+cm)	83	+36	+110	+50	+60	-35	-50	-50	-70
	85					-50			-25
	89			+40		-50	+0	-25	-40
	90	+25		+40				-50	
MGS (φ units)	83	2.65	3.39	2.74	3.47	3.04	3.00	3.09	3.12
	87	2.50	3.03						
	89	2.31	3.22	2.48	3.26	2.73	2.31	2.85	2.82
SC (%)	83	4.8	3.9	0.5	12.0	0.7	1.2	2.2	0.5
	87	2.8	7.6						
	89	0.9	2.7	0.1	7.8	0.4	0.3	2.1	1.1

available. The CV0-combination includes data from all 14 COST/VIANEN-stations. The COST-stations 14, 26 and 30, of which less than 7 late summer data are available are omitted in the CV1-combination. The COST-stations with incomplete data on smaller species (all COST-stations except 3 and 27) were excluded from combination CV2. Calculations of total density, species richness, diversity and abundance - and biomass ratio's were done only with the CV2 combination.

Data-analysis

Biomass was expressed as g ash free dry weight (AFDW) m^{-2} and density as number of individuals m^{-2}. The abundance ratio, Abundance/number of species (A/S), and biomass ratio, Biomass/abundance (B/A) were used as "stress-indicators" (Gray *et al.*, 1988). For the division into feeding guilds, we refer to Seys *et al.* (1993c). Species richness and diversity was expressed as Hill-indices N_0 - N_2 (Hill, 1973).

Since the time series available, is short and contains gaps for most stations no statistical time series analysis could be performed on the data. To detect if any long term change was present in the data a simple non-parametrical test, the Spearman's rank correlation, was calculated. This test enables us to detect gradual increases or decreases in the selected variables during the study-period, but can not reveal any other pattern.

A Detrended Correspondence Analysis (Hill, 1979) on density and biomass data of all (314) INTERECOS-, COST- and VIANEN sampling stations in 1989, was performed with all species present in more than 5 samples.

Environmental changes in the Oosterschelde

For a detailed description of the Oosterschelde and the engineering works we refer to Nienhuis & Smaal (1993). The major changes are shortly summarized. Hydrodynamic changes started medio 1985 and resulted, after the completion of the storm surge barrier (October 1986) and the compartmentalization dams (Oesterdam, October 1986; Philipsdam, April 1987) in a reduction of the tidal range (-13%); current velocities were reduced by 30% in the western sector and 70% in the northern sector; tidal volume decreased by 28%, mean fresh water input was 64% less and nitrogen input decreased by 58%. Water residence time increased by 100% and chlorinity by 14%. Primary production has slightly increased (+5%) whereas zooplankton is now much more abundant (+60%). In the period end 1986 - April 1987, the tidal reduction was more pronounced, caused by the manipulation of the storm surge barrier for the completion of the compartmentalization dams. This resulted in significantly longer exposure periods in the upper part and significantly longer immersion periods on the lower part of the intertidal areas (see Nienhuis & Smaal, 1993; Seys *et al.*, 1993c).

Table 2. Mean biomass, density and number of species from the different data sets in 1985 and 1989 (I INTERECOS, CV0, CV1 and CV2 see Table 1).

Parameter	Data set	1985 Mean	1989 Mean
Biomass	I	49.3	99.3
(g AFDW m^{-2})	CVO	48.3	88.2
	CV1	52.5	105.8
	CV2	64.1	134.2
Density	I	34715	9673
(numbers m^{-2})	CV2	31838	15254
number of species	I		65
	CV2		57

RESULTS

1. Representativity of the monitoring stations.

The representativity of the COST/VIANEN monitoring stations for the Oosterschelde can be tested by comparing the 1985 and 1989 COST/VIANEN data with the results of the two large scale surveys (INTERECOS) made in both years. The results are summarized in Table 2. The biomass estimates are in close agreement in both years. The biomass of the CV2 combination is higher as the proportion of sampling stations on musselbeds is rather high in this group. The densities are also very comparable, although in 1989 they are higher in the monitoring stations than in the INTERECOS set. In the INTERECOS-survey 1989, 65 species were found. It is not possible to compare this value with the results of 1985 since not all organisms were identified to species level in the INTERECOS survey 1985. In all CV2 stations 57 species were found.

To see whether the benthic communities found at the monitoring

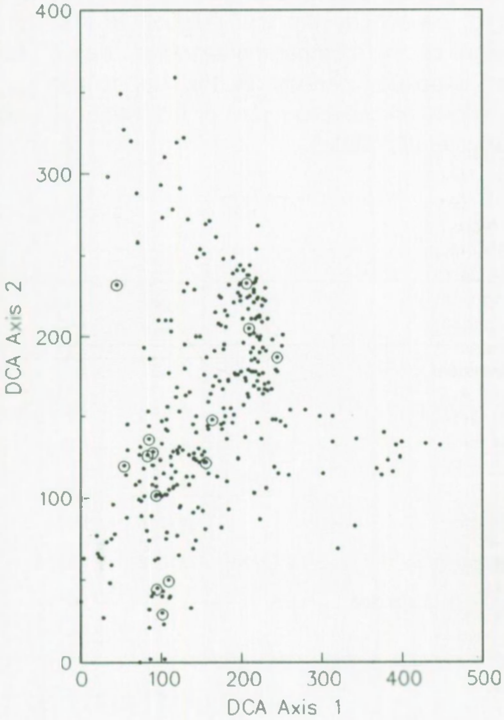
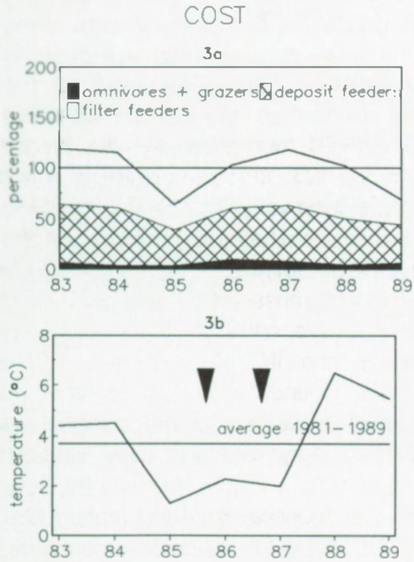


Figure 2. Detrended Correspondance Analysis on the density data of the INTERECOS- and COST/VIANEN-stations in late Summer 1989 (314 stations). Stations are presented according to their position on the first and second DCA-axis. The CV-stations are encircled.



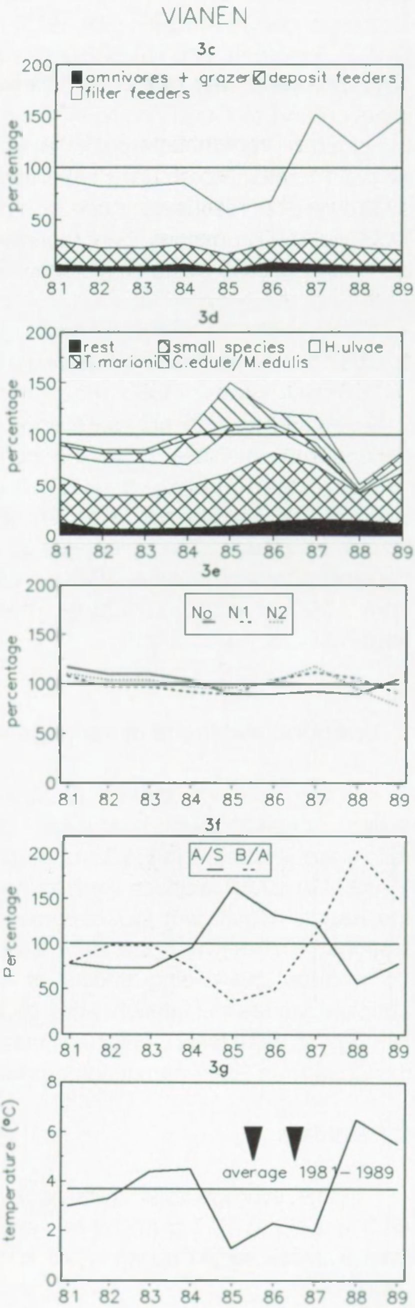


Figure 3. Change in total biomass (3a,c), total density (3d), diversity (N_0,N_1 and N_2)(3e) and abundance- (A/S) and biomass ratio (B/A)(3f) at 8 COST-, resp. 6 VIANEN-stations in the period 1983-1989, resp. 1981-1989. Values are converted to percentages of the long-term average, i.e. the average of the whole study period. For the COST-stations, total biomass is the biomass of the 11 biomass-dominant species and density, diversity and A/S, B/A are not calculated (not all species sorted at 6 of the 8 stations). The 'small species' in 3d are: Anaitides spec., Bathyporeia spec., Boccardia redeki, Capitella capitata, Corophium spec., Eteone spec., Heteromastus filiformis, Oligochaeta, Polydora spec. and Pygospio elegans. In 3b,g, the average winter air temperature (average of mean monthly temperature December-February) and the period of maximal manipulation of the storm surge barrier (arrows) are indicated.

stations are representative for the Oosterschelde a Detrended Correspondence Analysis (Hill, 1979) both on density and biomass data of the COST-, VIANEN-, and INTERECOS stations of late summer 1989 was done. In both analyses the first two DCA-axes were responsible for most of the variation and all COST/VIANEN monitoring stations are very well spread within the cloud of INTERECOS points as shown in Fig. 2 for the density data. Nearly all main benthic community types found in the INTERECOS-set (Meire *et al.*, 1993) were represented by one or more monitoring stations. The results of the COST/VIANEN stations can therefore be used for further analysis of the temporal patterns of the Oosterschelde macrozoobenthos.

2. Changes in environmental parameters

Available data on some environmental parameters of the stations are summarized in Table 1. In the period 1979-83, all stations were situated between Mean Tidal Level (MTL) -80cm and MTL +110cm. In 1988-89, nine stations had eroded with 5-30 cm, while at three stations sedimentation (25-50cm) occurred. The sediments at all COST/VIANEN-stations, except one, became coarser between 1979-83 and 1987-89: median grain size changed from 2.65-3.47 φ to 2.31-3.26 φ, while the range in silt-content (< 53μ) shifted from 0.5-16.6% to 0.1-7.8%.

3. Temporal variations in some general parameters

The temporal pattern of total biomass, biomass of different feeding guilds, density, species richness, diversity and abundance- and biomass ratio's are illustrated in Fig.3. As most of the patterns observed in the different VIANEN or COST-stations were found to be significantly concordant (based on the Kendall Coefficient of Concordance), average values for the six VIANEN-stations (1979-89) and the eight COST-stations were used to produce Fig. 3. To exclude overruleing effects of some individual stations in the figures, absolute values per station were transformed to percentage of the long-term average at this station, before different stations were combined. The results of the Spearman Rank correlation coefficient are summarized in Table 3 and 4.

3.1 Biomass

The average total biomass in the INTERECOS-stations changed from 49.3 in 1985 to 99.3 g AFDW m^{-2} and 1989 respectively. For the CV0-stations, total biomass varied between 5.5 and 531 g AFDW m^{-2} with an overall mean value of 76.2 g (Table 5). The highest values occur at the VIANEN-musselbed stations 10,22 & 60 (Table 5).

*Table 3a. Trends in total biomass (TB), biomass excluding C.edule/ M.edulis (TE) and biomass of feeding guilds (FF=filter feeders; DF= deposit feeders; OP= omnivores/predators; GR= grazers) at the CV1-stations. The Spearman Rank correlation coefficients are based on late summer values 1979-1989 (station 60,10,13), 1981-1989 (station 22,32,39) or 1983-1989 (station 3,6) (N= number of cases; * $p < 0.05$; ** $p < 0.01$; ns= not significant).*

station	N	TB		TE		FF		DF		OP		GR	
C3	7	-0.679	ns	-0.750	ns	-0.679	ns	-0.357	ns	-0.750	ns	+0.099	ns
C6	7	-0.821	*	-0.786	*	-0.714	ns	-0.786	*	+0.179	ns	+0.408	ns
C27	7	-0.571	ns	-0.571	ns	+0.107	ns	-0.500	ns	+0.321	ns	+0.089	ns
C33	7	+0.143	ns	+0.071	ns	-0.000	ns	+0.214	ns	-0.143	ns	+0.408	ns
C34	7	+0.107	ns	+0.214	ns	+0.179	ns	+0.143	ns	+0.321	ns	+0.450	ns
V60	9	-0.133	ns	-0.333	ns	-0.133	ns	-0.400	ns	-0.400	ns	+0.367	ns
V10	9	+0.150	ns	+0.033	ns	+0.150	ns	+0.183	ns	+0.233	ns	+0.500	ns
V13	9	+0.950	**	+0.583	ns	+0.950	**	+0.433	ns	+0.283	ns	+0.800	*
V22	8	-0.381	ns	-0.690	ns	-0.333	ns	-0.952	**	-0.119	ns	+0.071	ns
V32	8	+0.667	ns	-0.000	ns	-0.714	ns	-0.167	ns	+0.571	ns	+0.910	**
V39	8	+0.667	ns	-0.190	ns	-0.667	ns	-0.286	ns	-0.310	ns	+0.333	ns

*Table 3b. Trends in total density (DT), density excluding C.edule/ M.edulis (DE) and diversity (Hill numbers N_0,N_1,N_2) at the CV2-stations. The Spearman Rank correlation coefficients calculated for these variables are based on available late summer values of the period 1979-1989 (stations 60,10,13,22,32,39) or 1983-1989 (stations 3,27) (N= number of cases; * $p < 0.05$; ** $p < 0.01$; ns= not significant).*

station	N	DT		DE		N0		N1		N2	
C3	7	-0.786	*	-0.857	*	-0.673	ns	+0.321	ns	+0.321	ns
C27	7	-0.857	*	-0.857	*	-0.611	ns	+0.536	ns	+0.429	ns
V60	9	+0.017	ns	-0.033	ns	-0.600	ns	-0.533	ns	-0.517	ns
V10	9	+0.267	ns	+0.333	ns	-0.641	ns	-0.883	**	-0.817	*
V13	9	+0.650	ns	+0.600	ns	-0.025	ns	-0.283	ns	-0.250	ns
V22	8	-0.524	ns	-0.524	ns	+0.036	ns	+0.714	ns	+0.286	ns
V32	8	-0.571	ns	-0.690	ns	-0.626	ns	+0.881	**	+0.786	*
V39	8	-0.429	ns	-0.476	ns	-0.182	ns	-0.190	ns	-0.595	ns

*Table 4. Trends in abundance ratio (A/S) and biomass ratio (B/A) at the CV2-stations. The Spearman Rank correlation coefficients calculated for these variables are based on available late summer values of the period 1979-1989 (station 60,10,13,22,32,39) or 1983-1989 (station 3,27)(N= number of cases; * $p < 0.05$; ** $p < 0.01$; ns= not significant).*

station	N	A/S		B/A	
3	7	-0.857	*	+0.357	ns
27	7	-0.893	**	+0.714	ns
60	9	+0.533	ns	-0.283	ns
10	9	+0.333	ns	-0.233	ns
13	9	+0.683	*	+0.750	*
22	8	-0.571	ns	+0.286	ns
32	8	-0.357	ns	+0.643	ns
39	8	-0.500	ns	+0.690	ns

Total biomass is dominated by the taxonomically diverse group of deposit feeders and the filter feeders, essentially comprised of *C. edule* and *M. edulis*. Particularly this last group fluctuated rather strongly, with low values in 1985-86 (Fig. 3) and high values in 1987-89 especially at the VIANEN-stations (Fig. 3). The low values are due to mass mortality after the severe winter 1984/85 - 1985/86, the high values to the abundant spatfall, especially of *C. edule*, after the severe winters and their subsequent survival. Without *C. edule* and *M. edulis*, an overall mean biomass of only 19.3 g AFDW m^{-2} was found with a much smaller range (8.54 - 28.93 g AFDW m^{-2}). In the INTERECOS-surveys 1985 and 1989 biomass without *C. edule* and *M. edulis* was 17.0 and 14.9 g AFDW m^{-2} respectively. The temporal pattern of biomass excluding *C. edule* and *M. edulis*, is rather stable, with slightly lower values in 1985, mainly due to a decrease of deposit feeders and omnivores/ predators.

No significant trend was found at 9 of the 11 CV1 stations (Table 3a). The positive trend at station 13 (due to a reestablishment of filter feeders - in casu *C. edule* - in the second half of the study period) disappeared if *C. edule* and *M. edulis* were omitted. The decrease in biomass at station 6 resulted from a lower biomass of deposit feeders. Also station 22 had lower biomasses of deposit feeders at the end of the study period (Table 3b). Although no overall trend in total biomass was found at station 13 and 39, the grazers, which were of minor importance for total biomass, showed a negative trend.

3.2 Density

The average density at the INTERECOS stations in 1985 was 34715 m^{-2} (29094 m^{-2} excluding *C. edule/M. edulis*), while in 1989 much lower values were found (resp. 9673 and 9409 m^{-2}). The average value for the CV2-stations in the period 1984-89 was 21426 m^{-2} (without *C. edule* and *M. edulis*: 19317 m^{-2}). The absolute values of total density were quite different between these stations: they ranged from 6058 m^{-2} at station 13 to 38256 m^{-2} at station 39 (Table 5).

No significant trend was found in 6 of the 8 CV2 stations, a decrease in 2 stations (Table 3b). Peak values (=more than average) were found in 1985-87 (Fig. 3b). These values are caused by an increase in the abundance of (small) *C. edule/M. edulis* and of a number of other small species (*Anaitides mucosa, Bathyporeia pilosa/sarsi, Boccardia redeki, Capitella capitata, Corophium volutator/arenarium, Eteone longa, Heteromastus filiformis, Oligochaeta, Polydora ligni, Pygospio elegans*). For all these invertebrates, 1988 showed low abundances. Two species with high densities in the first half of the study period (*Tharyx marioni* and *Hydrobia ulvae*) became less common after 1985-86. The overall density of the other species was more or less stable.

3.3 Diversity

In the INTERECOS-survey 1989, 65 species were found. Although it was not possible to compare this value with the results of 1985 (not all organisms were identified to species level in the INTERECOS survey 1985), no species seemed to have (dis)appeared. For all CV2 stations an average value of 22 species per station was found, with a range of 18-26 species (Table 5).

The number of species (N_0) did not change significantly in the study period (Table 3b). The species richness N_0 and the Hill-indices of diversity N_1 and N_2 (Hill, 1973) were rather constant over time, with a small increase in 1987 (Fig. 3e). No significant trend was found for N_1 and N_2 at six CV2-stations, a negative significant trend at station 10 and a positive, significant trend at station 32. The negative sign of R_s for N_0, in contrast with positive R_s-values for N_1 & N_2 at station 32 illustrated the different rationale behind these Hill numbers. While there was apparently no significant change in the total number of species (N_0), a significant decrease in numbers of *H. ulvae* (cf. Coosen *et al.*, 1993) had increased the (N_2)-diversity (expressed as the reciprocal of the probability to take two individuals of the same species, if one samples at random and without replacement).

Table 5. Average late summer values (1984-1989) of total biomass (TB), total density (TD) and diversity (DI) indices N_0, N_1 and N_2 at the CV0-stations (including overall average), compared to total biomass and -density values of all INTERECOS-samples 1985 and 1989 (IE). For total biomass and -density, "all" means all species included, "excl" means all species excluding C. edule and M. edulis.

	station	V10	V22	V60	V13	C30	C26	C14	C34	V39
TB	all	184.0	134.7	218.5	88.9	16.4	48.4	43.9	48.7	79.9
	excl	27.6	28.9	27.7	8.5	12.2	14.7	17.9	13.6	21.5
TD	all	19741	25643	32143	6058					38256
	excl	15300	25187	28109	3979					34504
DI	N_0	25	26	26	18					22
	N_1	6.78	4.64	5.57	7.40					4.82
	N_2	4.28	2.47	3.34	4.95					3.10

	station	C3	C6	V32	C33	C27	mean CV0	IE 1985	IE 1989
TB	all	102.3	27.2	27.7	30.4	15.4	76.2	49.3	99.3
	excl	24.8	16.6	16.8	23.5	15.2	19.3	17.0	14.9
TD	all	8033		16884		24651	21426	34715	9673
	excl	6415		16497		24547	19317	29094	9409
DI	N_0	24		18		18	22		65
	N_1	8.69		3.14		3.25			
	N_2	6.14		1.93		2.18			

3.4 Abundance/Number of species - Biomass/abundance ratio's

Except for station 13, none of the CV2-stations had increasing A/S values over the study period 1979-89 (Table 4). At stations 3 & 27, A/S decreased significantly, because of lower numbers of *H. ulvae* in the second half of the study period. The biomass ratio B/A showed an increasing trend at station 13, due to significant higher biomasses in the second half of the study period. Lowest values were observed in 1985-86 (less than 50% of the long-term average), and high values (above average) in the period 1987-89. The abundance ratio showed an opposite pattern (Fig.3f).

DISCUSSION

The monitoring plots on the Slikken van Vianen were selected to represent the major macrobenthic habitats. The selection of the six stations was based on a larger number of plots that were sampled in previous years (Meire & Dereu, 1989). The selection of the COST stations is based on a large scale mapping of the major macrobenthic habitats of the Oosterschelde (Coosen *et al.*, 1988). The good resemblance between the results of the monitoring stations in late summer 1985 and 1989 and the INTERECOS large scale surveys indicate that the results from the monitoring stations can be seen as representative for the Oosterschelde. Also the changes in the environmental parameters of the different monitoring stations are similar to the observed changes in the rest of the Oosterschelde (Mulder & Louters, 1993; Ten Brinke *et al.*, 1993).

The biomass of the Oosterschelde intertidal macrozoobenthos is high, compared to other Dutch estuaries and brackish lakes: in the Dutch Wadden Sea, a very productive area, a year-average biomass of 38.5 g AFDW m^{-2} (28.1 g AFDW m^{-2}, excluding *C. edule/M. edulis*) was found in 1987 (Beukema, 1989). Corrected for the differing sampling period (biomass in late summer is about 20% higher than year-average biomass; Beukema, 1974) and the incalculation of organic matter in bivalve shells (measured by not removing the flesh from the shell in our study compared to Beukema, 1989) (biomass 17% higher if organic matter in shells is included: Beukema, 1974), a late summer biomass of 54 g AFDW m^{-2} for the Dutch Wadden Sea can be calculated. This value is intermediate between the biomass of the INTERECOS-surveys 1985 (49.3 g AFDW m^{-2}) and 1989 (99.3 g AFDW m^{-2}) and lower than the overall CV0-biomass for the period 1984-89 (76.2 g AFDW m^{-2}). In the marine part of the estuaries the Westerschelde and the Eems, lower values have been found: in 1987, a late summer biomass of 33 g AFDW m^{-2} was observed in the Westerschelde and 22 g AFDW m^{-2} in the Eems (Meire *et al.*, 1991c). Wolff & De Wolf (1977) found an average of 37.5 g AFDW m^{-2} for the Grevelingen estuary in September, with minima of 12.2 g AFDW m^{-2} in December. Lower biomasses were also found in the saline lake Grevelingen (24.8-38.6 g AFDW m^{-2} in spring 1985-1989: Fortuin & Altena, 1990) and in the brackish Lake Veere (22.2 g AFDW m^{-2} in late summer 1987: Seys & Meire, 1988).

The general characteristics of the macrobenthic system in the Oosterschelde did not yet change markedly after the construction of the storm surge barrier. Notwithstanding some variation, especially in the period 1985-1987, no overall increasing or decreasing trends in biomass, density, species richness, diversity, abundance- or biomass ratio were observed. These results suggest that hydrodynamical (Vroon, 1993) and sedimentological (Ten Brinke *et al.*, 1993) changes in the Oosterschelde after the completion of the storm surge barrier (Nienhuis & Smaal, 1993) had, by now, only a small effect on the general characteristics of the benthic fauna, compared to the impact of natural phenomena, like the occurrence of severe winters.

In most long-term data-sets (Wadden Sea: Beukema, 1989; Essink & Beukema, 1986; Dörjes *et al.*, 1986; Reise *et al.*, 1989; Northumberland coast: Buchanan & Moore, 1986; Scottish lochs: Pearson *et al.*, 1986; Baie de Morlaix: Dauvin & Ibanez, 1986; Ibanez & Dauvin, 1988; Baltic Sea: Rosenberg & Loo, 1988; Cederwall & Elmgren, 1980; Persson, 1987; Joseffson & Widbom, 1988) there is quite a large natural seasonal and year to year variation. This makes it often difficult to separate these fluctuations from effects of gradual man-induced changes in the system, particularly because species react in different ways. Only when the system is affected abruptly and severely (heavy pollution: Dauvin & Ibanez, 1986; Pearson *et al.*, 1986; complete closure of an estuary: Lambeck, 1981; dredging activities: Lopez-Jamar *et al.*, 1986), general parameters of the macrozoobenthic community react clearly upon these changes. In two Scottish lochs, Pearson *et al.* (1986) found the organic input from a paper mill to determine the major changes in total density and biomass. However, this input was on average 4-14 times larger than the natural carbon input from planktonic sources. Neither the changes in the sediments of the Oosterschelde nor the change in primary production were so drastic (Wetsteyn & Kromkamp, 1993) although the plankton communities did change (Bakker *et al.*, 1993).

It was shown that the most pronounced changes in some general parameters of the benthic system occurred in 1985(-87). This can result from effects of the first (1984-1985) of three successive severe winters (Fig. 3g), but also from the major hydrodynamic changes, started medio 1985. If hydrodynamic changes would have an effect on the general characteristics of the Oosterschelde macrozoobenthos, we would expect a gradual change after 1985 when the hydrodynamic changes occurred. Although the time series is rather short no other long-term trend was observed before or after the changes. Secondly, at the COST-stations low biomass- and density values were found already in spring 1985 (Seys *et al.*, 1993b; Craeymeersch *et al.*, 1988), i.e., before the major hydrodynamic changes. Moreover, different species known as winter sensitive collapsed immediately after the winter 1984-1985 and/or 1985-1986, 1986-1987 (Coosen *et al.*, 1993; Seys *et al.*, 1993b). Indeed a closer examination of the long-term pattern of 24 important species in the data-set (Seys *et al.*, 1993c) revealed that 20 species were directly or indirectly affected by the severe winter periods: the populations of winter-sensitive species, such as *C. edule, L. conchilega, S. plana* and *N. hombergii*, were decimated during one or more of the severe winters 1984-85, 1985-86 and 1986-87. *C. edule* and some other large species (*A. marina, M. balthica*) may have a good recruitment after severe winters, while others (*S. armiger, H. filiformis*) can benefit from the high mortality in the populations of one of their predators: *N. hombergii* (Beukema, 1989). In the Oosterschelde, there was a good spatfall of *C. edule* after the winter 1984-1985 and *S. armiger* did indeed increase significantly in numbers where *N. hombergii* was decimated (Smaal *et al.*, 1991; Coosen *et al.*, 1993; Seys *et al.*, 1993c). A group of small species with a large ecological spectrum and a short generation time, was particularly abundant immediately after the severe winters 1984-85 and 1985-86. Since these opportunists can recolonize empty niches in any "stress" situation (after pollution, dredging, severe winters,...) they are often used as "stress" indicators. The rationale behind the use of the biomass ratio B/A and the abundance ratio A/S (Gray *et al.*, 1988) is based on this mass occurrence of opportunists following any kind of disturbance. In the Oosterschelde, maximal "stress" values (high A/S, low B/A) were concentrated in 1985, i.e. after the first severe winter (1984/85).

Although there were no clear effects of hydrodynamic changes in the Oosterschelde on the general characteristics of the benthic system, some changes could be observed if we looked in more detail. On a small spatial scale, some stations were clearly influenced by the hydrodynamic changes. At one elevated COST-station (station 27: NAP+110cm), total biomass, total density and the abundance of individual species declined sharply between late summer 1986 and spring 1987, due to a considerable temporal decrease in inundation time (Coosen *et al.*, 1993; Seys *et al.*, 1993b). At this tidal level the mudflat was exposed for several successive days, due to the manipulation of the barrier. Experimentally it was demonstrated that most estuarine organisms show a considerable mortality after four days of exposure (Hummel *et al.*, 1993).

Although by now there is not much evidence of major changes in the macrozoobenthic populations of the Oosterschelde, this does not mean that on the long run there will be no effects. Indeed changed hydrodynamic conditions may have an impact on the distribution of larvae, on the sedimentation of food particles to the bottom etc. Furthermore the clear erosion of the intertidal flats (Mulder & Louters, 1993) will in the end certainly have an impact on the total benthic populations. Therefore it is of crucial importance to continue the monitoring of the benthic populations in order to detect the long term effect of the construction of the storm surge barrier on the benthos.

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REFERENCES

Bakker, C., P. M. J. Herman & M. Vink, 1993. A new trend in the evolution of the phytoplankton community after the construction of the storm surge barrier in the Oosterschelde (SW Netherlands) (1982-1990). Hydrobiologia: in press.

Beukema, J. J., 1974. Seasonal changes in the biomass of the macrobenthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 94-107.

Beukema, J. J., 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. Helgoländer Meeresunters. 43: 405-415.

Beukema, J. J. & K. Essink, 1986. Common patterns in the fluctuations of macrozoobenthic species living at different places on tidal flats in the Wadden Sea. Hydrobiologia 142: 199-207.

Buchanan, J. B. & J. J. Moore, 1986. Long-term studies at a benthic station off the coast of Northumberland. Hydrobiologia 142: 121-127.

Cederwall, H. & R. Elmgren, 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. Ophelia suppl. 1: 287-304.

Coosen, J., P. Meire & A. Van Den Dool, 1988. Kartering bodemdieren intergetijdengebieden Oosterschelde. Rapport Balans 1988-15. RWS, Middelburg, KNAW-DIHO, Yerseke.

Coosen, J., J. Seys, P. M. Meire & J. Craeymeersch, 1993. Effect of geomorphological and hydrodynamical changes in the intertidal areas of the Oosterschelde estuary (SW-Netherlands) on distribution, density and biomass of some common macrobenthic species: *Hydrobia ulvae, Arenicola marina, Scoloplos armiger, Bathyporeia pilosa* and *Spio* spec. Hydrobiologia: in press.

Coull, B. C., 1986. Long-term variability of meiobenthos: value, synopsis, hypothesis generation and predictive modelling. Hydrobiologia 142: 271-279.

Craeymeersch, J. A., J. Coosen & A. van den Dool, 1988. Trendanalyse van densiteit- en biomassawaarden van bodemdieren in het getijdengebied van de Oosterschelde (1983-1986). Rapporten en verslagen DIHO 1988-7, Yerseke.

Dauvin, J-C. & F. Ibanez, 1986. Variations à long-terme (1977-1985) du peuplement des sables fins de la Pierre Noire (baie de Morlaix, Manche occidentale): analyse statistique de l'évolution structurale. Hydrobiologia 142: 171-186.

Dörjes, J., H. Michaelis & B. Rhode, 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). Hydrobiologia 142: 217-232.

Essink, K. & J. J. Beukema, 1986. Long-term changes in intertidal flat macrozoobenthos as an indicator of stress by organic pollution. Hydrobiologia 142: 209-215.

Fortuin, A. W. & H. C. Altena, 1990. Macrozoöbenthos in het Grevelingenmeer: bestandsopname in voorjaar 1989. Rapporten en verslagen DIHO, Yerseke, 1990-15.

Gray, J. S. & H. Christie, 1983. Predicting long-term changes in marine benthic communities. Mar. Ecol. Progr. Ser. 13: 87-94.

Gray, J. S., M. Aschan, M. R. Carr, K. R. Clarke, R. H. Green, T. H. Pearson, R. Rosenberg & R. M. Warwick, 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. Mar. Ecol. Prog. Ser. 46: 151-165.

Hill, M. O., 1973. Diversity and eveness: a unifying notation and its consequences. Ecology 54: 427-432.

Hill, M. O., 1979. DECORANA - A Fortran program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University Ithaca, New York.

Hummel, H., A. W. Fortuin, R. H. Bogaards, A. Meijboom & L. de Wolf, 1993. The effects of prolonged emersion and submersion by tidal manipulation on marine macrobenthos. Hydrobiologia: in press.

Ibanez, F. & J-C. Dauvin, 1988. Long-term changes (1977 to 1987) in a muddy fine sand *Abra alba - Melinna palmata* community from the Western English Channel: multivariate time-series analysis. Mar. Ecol. Progr. Ser. 49: 65-81.

Joseffson, A. B. & B. Widbom, 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. Mar. Biol. 100: 31-40.

Lambeck, R. H. D., 1981. Effects of closure of the Grevelingen estuary on survival and development of macrozoobenthos. In N. V. Jones & W. J. Wolff (eds), Feeding and survival strategies of estuarine organisms. Plenum Publishing Corporation: 153-158.

Lopez-Jamar, E., G. Gonzalez & J. Mejuto, 1986. Temporal changes of community structure and biomass in two subtidal macroinfaunal assemblages in La Coruna bay, NW Spain. Hydrobiologia 142: 137-150.

Meire, P. M. & J. Dereu, 1989. Use of the Abundance/Biomass Comparison method for detecting environmental stress: some considerations based on intertidal macrobenthos and bird communities. J. appl. Ecol. 27: 210-223.

Meire, P. M., J. Seys, J. Buys & J. Coosen, 1993. Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm surge barrier ? Hydrobiologia: in press.

Meire, P. M., J. Seys, T. J. Ysebaert & J. Coosen, 1991c. A comparison of the macrobenthic distribution and community structure between two estuaries in SW Netherlands. In M. Elliott & J-P. Ducrotoy (eds), Estuaries and Coasts: Spatial and Temporal Intercomparisons, Proc. ECSA 19 Symposium. Olsen & Olsen, Fredensborg: 221-230.

Meire, P. M., J. Buys, J. Seys, F. Twisk, E. Stikvoort & D. De Jong, 1991b. Macrozoöbenthos in de Oosterschelde in het najaar van 1989: een situering van de gegevens. Rapport RUG-WWE nr. 30, Gent; RWS, Middelburg; DIHO, Yerseke.

Meire, P. M., J. Buys, J. Van Der Meer, A. Van Den Dool, A. Engelberts, F. Twisk, E. Stikvoort, D. De Jong, R. H. D. Lambeck & J. Polderman, 1991a. Macrozoobenthos in de Oosterschelde in het najaar 1985. een situering van de gegevens. Rapport RUG-WWE nr. 27, Gent; RWS, Middelburg, DIHO, Yerseke.

Mulder, J. P. M. & T. Louters, 1993. Changes in basin geomorphology after the implementation of the Oosterschelde project. Hydrobiologia: in press.

Nienhuis, P. H. & A. C. Smaal, 1993. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction. Hydrobiologia: in press.

Pearson, T. H., G. Duncan & J. Nuttall, 1986. Long term changes in the benthic communities of Loch Linnhe and Loch Eil (Scotland). Hydrobiologia 142: 113-119.

Persson, L-E., 1987. Baltic eutrophication: a contribution to the discussion. Ophelia 27 (1): 31-42.

Reise, K., 1989. Monitoring the Wadden Sea - an introduction. Helgoländer Meeresunters. 43: 259-262.

Reise, K., E. Herre & M. Sturm, 1989. Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. Helgoländer Meeresunters. 43: 417-433.

Rosenberg, R. & L-O. Loo, 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, Western Sweden. Ophelia 29 (3): 213-225.

Seys, J. & P. M. Meire, 1988. Macrozoobenthos van het Veerse Meer. Rapport RUG-WWE nr. 4, Gent.

Seys, J., P. Meire & J. Coosen, 1993b. Macrobenthic populations in the Oosterschelde before, during and after major coastal engineering works. Rapport RUG-WWE, Gent: in press.

Seys, J., P. M. Meire, J. Coosen & J. Craeymeersch, 1993a. Macrozoöbenthos op acht stations in de Oosterschelde 1983-1989: presentatie data. Rapport RUG-WWE: in press.

Seys, J., P. Meire, J. Coosen & J. Craeymeersch, 1993c. Long-term changes in the macrobenthic fauna at eight intertidal permanent stations in the Oosterschelde estuary - effects of the construction of the storm surge barrier: some preliminary results. Proceedings ECSA-Hull Sept. 1990: in press.

Smaal, A. C., M. Knoester, P. Nienhuis & P. M. Meire, 1991. Changes in the Oosterschelde ecosystem induced by the Delta works. In M. Elliott & J-P. Ducrotoy (eds), Estuaries and Coasts: Spatial and Temporal Intercomparisons, Proc. ECSA 19 Symposium. Olsen & Olsen, Fredensborg: 375-384.

Ten Brinke, W. B. M., J. Dronkers & J. P. M. Mulder, 1993. Fine sediments in the Oosterschelde tidal basin before and after partial closure. Hydrobiologia: in press.

Vroon, J., 1993. Hydrodynamical characteristics of the Oosterschelde over the last decades. Hydrobiologia: in press.

Wetsteijn, L. P. J. M. & J. Kromkamp, 1993. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (NL) before, during and after a large-scale coastal engineering project (1980-1990). Hydrobiologia: in press.

Wolff, W. J. & L. De Wolf, 1977. Biomass and production of zoobenthos in the Grevelingen estuary, The Netherlands. Estuar. coast. mar. Sci. 5: 1-24.

Chapter 4

A DESCRIPTION OF THE HABITAT AND WADER POPULATIONS OF THE SLIKKEN VAN VIANEN (OOSTERSCHELDE NL.) BEFORE MAJOR ENVIRONMENTAL CHANGES AND SOME PREDICTIONS ON EXPECTED CHANGES.

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ABSTRACT

The Oosterschelde is a major estuary in the Delta area of S.W. Netherlands and is of great importance for wintering waders. Coastal engineering works will however reduce the available surface of tidal flats with 36%. This paper describes the study area and the pattern of occurrence of waders on the "Slikken van Vianen", a tidal flat in the Oosterschelde. For 11 important wader species the data are situated against the background of the migration pattern of the species and the average occurrence as well as the within and between year variation is given. In the discussion several factors contributing to the observed variations in numbers are discussed and the influence of the reduction in tidal area is assessed. As there is increasing evidence that in the profitable feeding sites density is regulated by density related behaviour it is likely that the wader populations will decline substantially in the Oosterschelde.

INTRODUCTION

From 1979 onwards, the ecology of waders on the "Slikken van Vianen", a tidal flat in the Oosterschelde (The Netherlands) (Fig. 1), has been studied for two main reasons. First, notwithstanding growing interest in the ways predators may affect the population dynamics of their prey (May, 1981) and in Optimal Foraging Theory (Krebs & McCleery, 1984), few related field studies have been done until now. Secondly, the future of estuarine feeding areas of waders is threatened all over the world by e.g., barrage building, reclamation, pollution etc. (Langslow, 1981; Prater, 1981).

Studies of food relationships may help in assessing the importance of winterfood supplies and density related behaviour in affecting the size of populations in these changing environments. This knowledge can subsequently be used for conservation and management purposes especially in the Oosterschelde where the construction of a storm surge barrier reduces the available feeding area for waders by ca. 36%.

Large numbers of waders breed in arctic and cool climatic zones of the Palearctic region. Outside the breeding season birds following the East-Atlantic flyway are dependent for food on intertidal areas along the European and West-African coasts, with relatively small number of areas being important in terms of numbers. The main sites are the Wadden Sea, the Banc d'Arguin (Mauritania), the Delta area (The Netherlands), Morecambe Bay and the Wash (Great Britain) (Altenburg *et al.*, 1983; Prater, 1981; Saeys & Baptist, 1980; Smit, 1981; 1984).

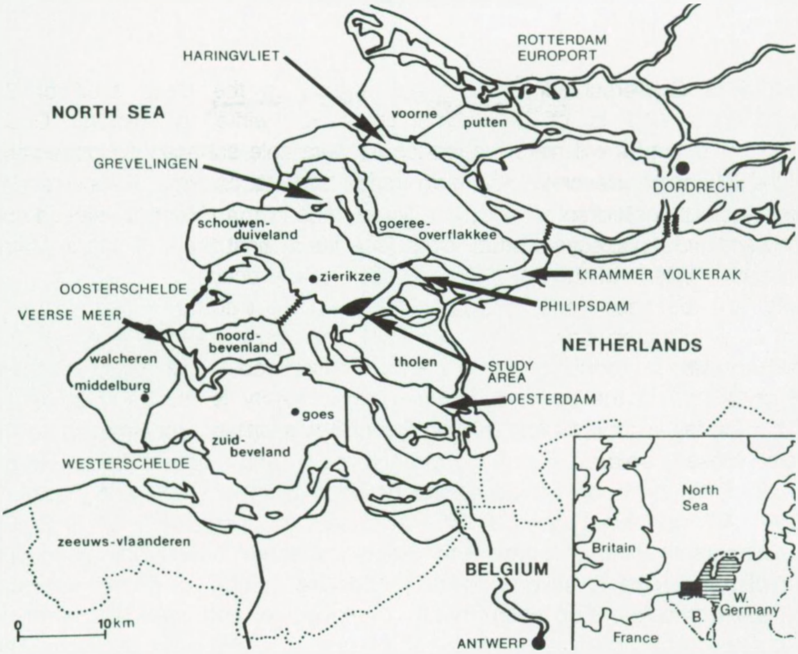

Figure 1. Map of the Delta area and location of the 'Slikken van Vianen'.

Individual shorebirds of many species do not stay during the whole non breeding season in a single area but move between sites sometimes separated by thousands of kilometers. Thus, the importance of an area can not only be assessed by the maximum number of birds present but also by the number of birds using the area (turnover) for refuelling (Pienkowski, 1984). In these refuelling sites birds rapidly gain weight by the accumulation of fat which enables them to proceed their migration. Although little information on this matter is published, recent research in the Delta (Marteyn, pers. comm.) indicates the Oosterschelde plays an important role as a refuelling and moulting area as well.

In this paper we describe some abiotic and biotic features of our study area, as well as the expected abiotic changes in the estuary. The pattern of occurrence (numbers and fluctuations) of waders in the study area is given in detail and compared with the patterns described for the Delta area as a whole (Meininger *et al.*, 1984), and for other important sites. This can be used as a reference to compare with the situation after the completion of the storm surge barrier. Subsequently some predictions are made on the expected changes in wader populations after the construction of the barrier and secondary dams.

MATERIAL AND METHODS

Habitat description

A map of the several habitat types was plotted based on observations in the field, a geomorphological map (made by Ir. Buysrogge, Rijkswaterstaat), false color photographs and additional data of a macrofauna sampling program in 14 permanent study plots (see Meire & Kuijken, 1984a,b; Meire & Coosen, 1985) .

Bird counts

During high tide birds, having fed on the mudflats, concentrate on "high water roosts", situated mainly on the salt marsh and adjacent fields. Here we counted the birds on 60 occasions between October 1976 and September 1982. An additional number of 42 counts by observers of the 'Delta department of Rijkswaterstaat' and 'Staatsbosbeheer' have kindly been put to our disposal. Due to several circumstances the number of counts is unequal for each species. For each month the average and standard error was calculated, when several counts for one month of a year were available. These averages were used for calculating the overall mean.

For comparison data of the Wadden Sea are taken from Smit & Wolff (1981), and for the British Isles from Prater (1981). For estimation of the total population sizes of birds using the East Atlantic flyway we followed Altenburg *et al.* (1983). All references to "total population sizes" refer to these numbers.

In the species account, only the facts necessary to understand the pattern of occurrence are given. More information can be found in Cramp & Simmons (1983), and Glutz *et al.* (1975; 1977).

Predictions

To assess the impact of the expected environmental changes on the wader populations we used the counts of the Oosterschelde and Krammer-Volkerak (Fig.1) given in Meininger *et al.* (1984; 1985). Only those months in which both areas were entirely counted are used (circa 40 counts, differing between species, spread equally over the 12 months). Assuming birds are uniformly spread over the tidal flats, the density of waders in each month was calculated for both areas by dividing numbers of birds by the surface (being 14310 and 2570 ha. of tidal flats respectively for Oosterschelde and Krammer-Volkerak). Further the assumption was made that after the closure of the Philipsdam all birds now using the Krammer-Volkerak will move to the remaining tidal area of the Oosterschelde and no emigration of birds previously using the Oosterschelde will occur. So "new" expected densities in each month were calculated by dividing the number of birds in the Oosterschelde plus the number of birds in the Krammer-Volkerak by 10900 being the expected area of tidal flats in the Oosterschelde after the completion of civil engineering works.

RESULTS

1. The Oosterschelde: recent evolution.

The "Delta area" in the southwest Netherlands (Fig. 1) consists of six estuaries. In february 1953 a disastrous storm flood killed nearly 2000 people and innumerable cattle. As a result the "Delta law" was accepted by the Dutch Government in 1956. This implied the closure of four of the six estuaries. Three of them are closed already. First lake Veere was created in 1961, followed by the Haringvliet in 1970 and lake Grevelingen in 1971. The Oosterschelde is a very large estuary (overall size 45000 ha) and the last to be dammed up. Increasing pressure from economic (fisheries) and environmental considerations resulted in a change of the original plans. As a compromise between safety and nature conservation, a storm surge barrier is now under construction in the mouth of the estuary. This barrier consists of 66 pillars between which slides are put up. Thus normally, the estuary remains under the influence of the tides, but it can be closed in case of danger of inundation. Next to the barrier two secondary dams are build more inland (Philipsdam and Oesterdam, Fig. 1). Behind these, two fresh water lakes (Markiezaatsmeer and Zoommeer) will be created. All this will change the hydrodynamic properties of the estuary.

The construction itself causes a reduction in the cross-section of the estuary from 80000 to 14000 m^2. This decreases the tidal amplitude from 3.5 to 3.1 m. (near Yerseke). Because a smaller tidal volume is involved, current velocities will also decrease in the whole area on average by one third, except in the immediate surrounding of the barrier. This might result in increased sedimentation if sufficient material is still carried by the water. The average chlorinity is expected to remain high and constant (average 16.5 gr. Cl^- /l.). The intertidal area will decrease from 17000 to 10900 ha because of the reduction of tidal amplitude and the construction of the secondary dams. The decrease of tidal amplitude will also influence the time of inundation: below mid-tidal level, tidal flats will be exposed for a shorter time, and above mid-tidal level for a longer time than previously. All these changes will have profound influences on the environmental conditions, and these in turn, on plants and animals (for details see Anonymus, 1986).

2. Description of the study area.

The area called "Slikken van Vianen" situated south of Schouwen-Duiveland (Fig. 1) is approximately five kilometers in length and divided in two parts by a creek leading to a small harbour with a breaking yard; The largest width at low water is approximately 1500 meter. A small saltmarsh of ca. 30 ha. developed along a part of the seawall. The tidal surface of the area is 510 ha., 285 of which are situated above NAP (Nieuw Amsterdams Peil, Dutch Ordnance Level, which is about mid tidal level).

2.1. Geological build up.

The following description is a summary based upon Bij de Vaate (1976), Van der Sluijs *et al*. (1965) and Wilderom (1964).

The pleistocene sedimentary deposits are mainly sandy and form the basis for the Holocene layers. An improvement of the climate in the beginning of the Holocene, associated with an increase of the sea-level, resulted in the formation of peat (called "basisveen") from 10000 BP onwards. Because of a further increase in sea-level the area flooded and the sedimentary layers of Calais were deposited. This consists of fine sand with some clay layers. After the sea retreated, a new layer of peat ("Hollandveen") of approximately 1 meter was formed between 4300 BP and 1700 BP. This has been covered since by the sedimentary deposits of Duinkerke, which mainly consists of fine sand locally with small clay layers.

The circumscription of the area to the north (landward) came about by gradual reclaiming of saltmarshes, started well before 1300. Most dikes were build by 1400. The last polder was reclaimed in 1645 and definite lining towards land was achieved. The shape of the tidal flats did not change much over the last hundred years. Only the western part gradually diminished. In comparison with most other intertidal areas of the Delta, the "Slikken van Vianen" remained relatively stable since the 17th century.

2.2. Abiotic components.

2.2.1 Water.

Data collected near the study area by "Rijkswaterstaat Deltadienst" in a weekly monitoring scheme were kindly put to our disposal. For the most important parameters, average values, minima, maxima and coefficients of variation are given in Table 1 for the period 1976-1980.

The salinity is on the average 29.3 gr/l showing relatively small fluctuations and without vertical stratification. According to the Venice system

Table 1. Some abiotic parameters of the water near the 'Slikken van Vianen'

	Mean	C.V.
Temperature (°C)	10.94	5.36
Oxygen saturation (%)	99	10
pH	8.07	0.17
Suspended matter (mg/l)	23.6	13.1
Visibility (dm)	17	10
Clorinity (mg/l)	16.40	9.32
Salinity (gr/l)	29,29	1.55

the area is situated in the polyhaline part of the estuary. This high and constant salinity has profound influences on the macrobenthic communities.

From the other factors listed in Table 1 it can be seen that the Oosterschelde is virtually unpolluted.

Air and water temperature shows seasonal variations with minima in January-February and maxima in July-August. Water temperature may be respectively 5°C less or more than in the adjacent North Sea.

The current velocities in the main tidal channels are peaking at 108 cm/sec during ebb and at 121 cm/sec during flood. However, there must be large differences in current velocities above different parts of the mudflats, but no data are available.

2.2.2 Sediment and geomorphology.

The sediment of 14 study plots consists of very well to less well sorted muddy sand. According to Wolff (1973a) there is a correlation between grain size and depth in areas with no or only slight wave action. This trend was not found in our data (R_s = 0.205, n=14, ns), however depth was correlated with the sorting coefficient (R_s = -0.66, n=14, $P<0.01$) indicating that higher in the intertidal zone the sediments are better sorted. This is possible because less time is available for sedimentation so only a narrow range of particles is reaching the bottom.

The amount of silt ($<53\mu$) is normally < 10% and of organic matter between 0.23 and 0.77%. As deposition of organic detritus may be expected in areas with calm water, a positive correlation between median grain size of the sediment and its percentage of organic matter may be expected (Wolff, 1973a). Elgershuizen *et al.* (1982), pointed out that a correlation between % silt and % organic matter would normally be stronger. We indeed find a correlation between % silt and % organic matter (R_s = 0.793, n=14, $p<0.001$) but not between median grain size and % organic matter (R_s = 0.2, n=14, ns).

Our data show that the soil composition at the Slikken van Vianen is very similar to that of other tidal flats of the Oosterschelde (Elgershuizen *et al.*, 1982).

In some places we find accumulations of empty shells (mainly of *Cerastoderma edule*) 1 meter high, several meters wide and over hundred meters long.

Tides.

The tides of the Delta area belong to the semi-diurnal type with high and low water twice a day. The tidal range is on average 3.5 meter. Between spring and neap tides the difference is most pronounced at high water levels. These can differ 80-90 cm in contrast to the low water levels which differ only between 30-50cm.

3. Habitat description.

On tidal flats a zonation of benthic species occurs, depending mainly on sediment composition (e.g., Anderson, 1972; Wolff, 1973a). This results in different macrofauna communities, which have been analyzed elsewhere (Meire and Kuijken, 1984a,b; Meire and Coosen, 1985). As changes in abiotic factors are likely to affect the presence and extend of these biocoenoses it is important to describe their present distribution, since this will affect the wader

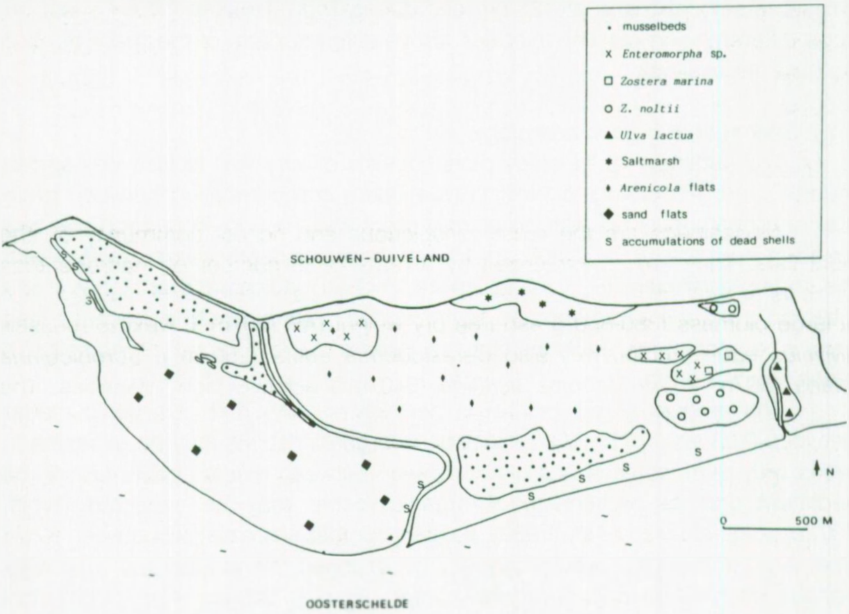

Figure 2. Map of the Slikken van Vianen with the major habitats.

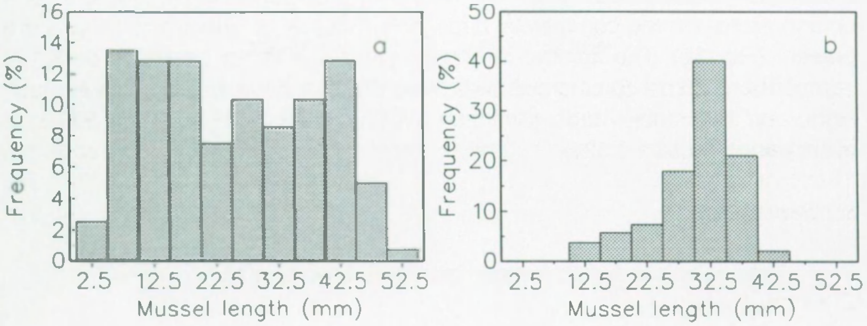

Figure 3. Length-frequency distributions of mussels on a stable (a) and a commercial musselbed (b).

populations. A brief description of the habitat types on the "Slikken van Vianen" is given together with a map of their distribution (Fig. 2). The biocoenoses are easily recognized in the field and a map for the whole Oosterschelde is in preparation (Coosen & Meire, in prep.). The densities given between brackets are the maxima found in the studyplots within these habitats. It should be stressed that considerable variation in densities between years can occur.

3.1 Musselbeds (60 ha).

Musselbeds are the most conspicuous and richest community on the tidal flats. They are characterized by a remarkable number of macrobenthos species (20 Annelida, 8 Crustacea and 8 Mollusca species found already), and a large biomass (380-860 g ash free dry weight (AFDW)/m^2). Next to mussels (*Mytilus edulis*) (1500/m^2) also *Cerastoderma edule* (250/m^2), *Scrobicularia plana* (50/m^2) and *Macoma balthica* (540/m^2) achieve high densities. The mussels are often covered by barnacles (*Balanus balanoides*, *B. crenatus*, *Elminius modestus*).

Oligochaeta are very abundant (8000/m^2) as well as the Polychaetes *Heteromastus filiformis* (5000/m^2), *Capitella capitata* (6000/m^2), *Lanice conchilega* (1200/m^2), *Tharyx marioni* (200/m^2). Other important species, reaching densities of a few hundred individuals per m^2 are *Nereis diversicolor*, *N. succinea*, *Nepthys hombergii* and *Ampharete acutifrons*.

Most musselbeds are commercially exploited and the mussel fisheries can have pronounced influence on the beds. Some are fished very often (once every one or two years) and called here "commercial beds" while others are never or only very infrequently harvested (once in ten years and called here "stable musselbeds"). The differences are obvious. On stable musselbeds, mussels of all sizes occur (Fig. 3a), since they grow for a long time and spat is able to settle. On the commercial beds, only mussels of limited size ranges are present (Fig. 3b). The number of benthic species is larger on stable beds, 36 compared to 25 on commercial beds. Also the diversity and evenness is much higher on the stable beds (Shannon Weaver diversity H 2.09 - 1.539 and evenness H' 0.658 - 0.321).

3.2 Sandy Flats

Within the sandy flats we can distinguish two types:

3.2.1 Arenicola flats (200 ha).

The fauna of this habitat, occurring mainly above N.A.P is characterized by *Arenicola marina*. Its burrowing activity and casts are very typical. Although occurring in low densities (50/m^2) it is dominant in terms of biomass (30 g AFDW/m^2). Other important species are *C. edule* (600/m^2), *M. balthica* (400/m^2), *Hydrobia ulvae* (5000/m^2), *Scoloplos armiger* (1500/m^2) and *N. hombergii* (100/m^2).

3.2.2 Sand Flats (175 ha).

These sandy areas with pronounced microrelief and ripplemarks, occurring mainly below NAP, have a very poor fauna. Some *C. edule* (70/m^2) and *M. balthica* (20/m^2) are found as well as *N. hombergii* (50/m^2), *S. armiger* (300/m^2) and *A. marina* (15/m^2). The amphipod *Bathyporeia pilosa* reaches quite high densities (350/m^2).

3.3 Muddy flats (40 ha).

On some places, spread over the study area, the sediment consists of muddy sand. The fauna is similar to that on musselbeds except that it lacks mussels.

Together with the *Arenicola* flats they are sometimes covered by eelgrass (*Zostera marina, Z. noltii*) and algae (*Enteromorpha* sp., *Ulva lactua*). Annual variations in the extend of the area covered by eelgrass and especially by *Enteromorpha* sp. are considerable. During winter, this vegetation cover gradually decreases, mainly as a result of waterfowl grazing (*Anas penelope, Branta bernicla, Cygnus bewickii*).

Table 2. Numbers of waders at the Slikken van Vianen. For each species: average, maximum, standard error and number of counts/month are given.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Haematopus ostralegus												
mean	4309	3639	2887	1778	469	284	579	2766	4208	3926	3911	4105
max.	6920	5300	4650	4850	509	530	680	4000	6210	7451	7039	6704
SE	851	523	508	663	21	82	48	351	628	935	876	766
N	6	5	6	6	4	4	4	5	5	6	6	6
Charadrius hiaticula												
Mean	0.1	2	9	9	9	3	4	53	86	5	0	0
max	1	8	42	24	14	4	7	107	150	120	0	0
SE	0.1	1	7	4	3	1	2	18	16	3	0	0
N	6	6	6	6	4	4	4	5	6	6	6	6
Charadrius alexandrinus												
mean	0	0	4	10	1	0.1	26	66	20	1	0	0
max.	0	0	26	40	3	1	65	130	52	5	0	6
SE	0	0	4	6	1	0.2	14	26	9	1	0	0
N	6	6	6	6	4	4	5	5	6	7	6	6
Pluvialis squatarola												
mean	102	196	190	267	324	43	5	111	372	298	293	244
max.	210	370	350	480	414	148	15	160	610	730	534	304
SE	36	52	47	49	32	35	3	13	55	109	89	29
N	6	6	6	6	4	4	4	5	6	6	6	4
Calidris canutus												
mean	953	2059	538	149	95	15	0	89	294	229	602	1150
max.	3050	9000	2100	420	250	62	0	150	640	410	1700	6100
SE	518	1412	313	73	58	15	0	37	103	75	259	993
N	6	6	6	5	4	4	5	5	5	6	6	6
Calidris alpina												
mean	1380	1590	2125	1839	1017	48	296	1795	2372	2670	1920	1530
max.	3400	2500	3200	2750	1500	145	780	2400	4000	4000	2450	4000
SE	466	221	288	298	258	34	164	297	397	594	367	536
N	6	6	6	6	4	4	4	5	6	5	6	5
Limosa lapponica												
mean	500	720	656	632	725	114	173	614	1066	1054	514	1112
max.	1217	1280	1240	1135	1480	270	250	903	1980	1430	1467	2060
SE	181	204	168	174	281	52	58	82	218	123	249	471
N	6	5	6	6	4	4	4	5	6	5	5	4
Numenius arquata												
mean	159	173	204	104	30	39	443	357	383	271	100	99
max.	308	470	403	146	51	78	720	524	560	600	172	199
SE	61	61	44	17	10	13	104	51	48	97	19	34
N	6	6	6	6	4	4	4	5	6	5	6	6
Tringa erythropus												
mean	0	0	0.2	2	11	6	44	71	30	36	2	0
max.	0	0	1	5	15	12	100	125	150	120	10	
SE	0	0	0.2	1	4	6	25	25	30	23	2	
N	6	6	5	5	2	2	4	5	5	6	6	
Tringa totanus												
mean	114	107	79	97	31	30	191	113	181	136	97	133
max.	420	355	240	184	74	48	315	140	288	284	150	376
SE	65	50	32	21	15	10	63	10	39	46	13	59
N	6	6	6	6	4	4	3	5	4	5	5	6
Arenaria interpres												
mean	149	62	91	123	126	23	64	75	175	125	91	111
max.	432	180	204	228	220	82	143	168	360	300	245	232
SE	63	25	27	24	41	30	23	28	46	42	33	33
N	6	6	6	6	4	4	5	5	5	6	6	6

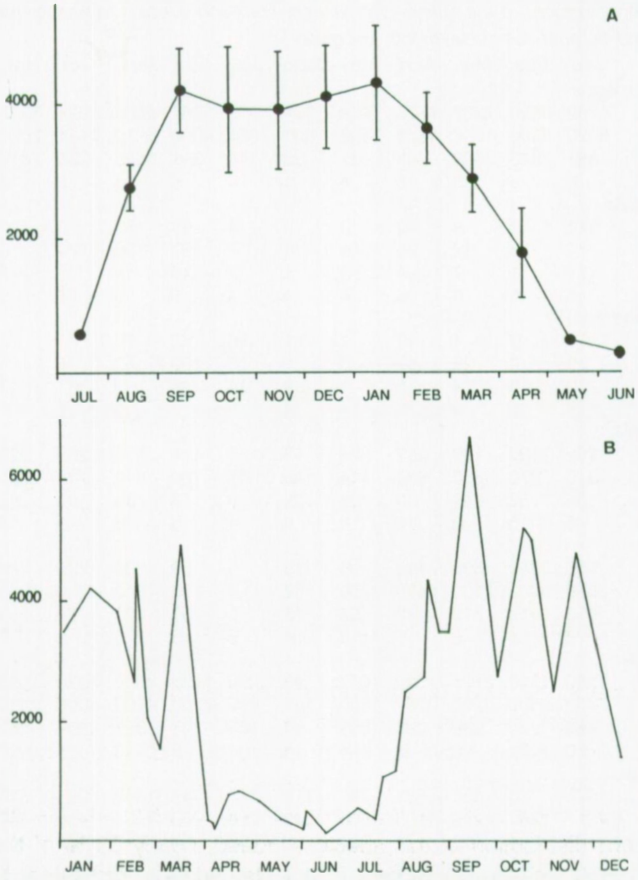

Figure 4. Pattern of occurrence of Oystercatchers at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

4. Occurrence of waders

All data are summarized in Table 2 which gives for each species the monthly mean, standard error (SE), maximum and number of counts. Mean and SE per month are plotted in Fig. 4a to 14a. To illustrate within year variation all counts (39) of 1981 are given in Fig. 4b to 14b.

4.1 Oystercatcher (*Haematopus ostralegus* LINNAEUS) Fig.4

The Oystercatcher is the most abundant species in the Oosterschelde

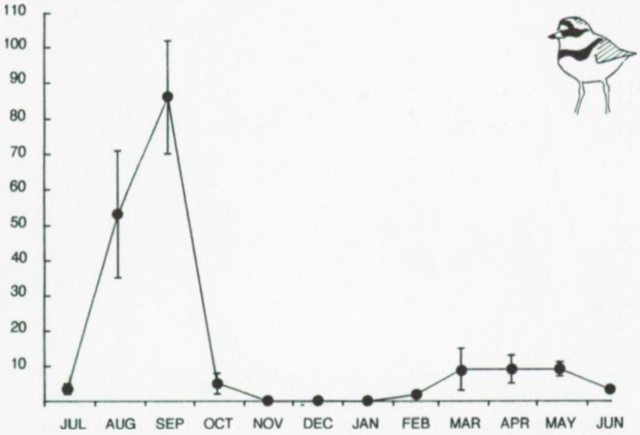

Figure 5. Pattern of occurrence of Ringed Plovers at the "Slikken van Vianen". Average and standard error per month of the period October 1976 - September 1982 are plotted.

(up to 10000 may be present in midwinter), as well as on the "Slikken van Vianen". Between May and July only a few hundred, mainly immature, birds are present in the study area. By the end of July their number increases until September and then remains quite stable. Depending on the weather conditions the birds start to leave for the breeding grounds in February. Then the number declines towards the summer level in May. This pattern is very similar in the whole Delta area, the Wadden Sea and England and fits very well with the northern distribution of this species. Indeed, nearly 85 % of the total population (715800 individuals) winters in the Netherlands and Great Britain. This pattern is also quite constant from year to year as well as within one year. During severe weather, when ice is present in the Wadden Sea, an influx of birds can occur in the Delta area (Meininger *et al.*, 1984).

4.2 Ringed Plover (*Charadrius hiaticula* LINNEAUS) Fig. 5

The Ringed Plover is numerically not very important on the "Slikken van Vianen". The species is more abundant on the more sandy parts of the estuary (Meininger *et al.*, 1984). In September a maximum of some 3200 birds occurs in the Oosterschelde (Meininger *et al.*, 1984). The birds at the "Slikken van Vianen" mainly arrive in August, reaching a peak in September, after which they leave quickly for the wintering grounds along the coast of France, the Iberian peninsula, NW. and W. Africa (Cramp & Simmons, 1983). Nearly 200000 birds are wintering in Africa and only some 25000 along the European coast. During spring migration only small numbers are present between March

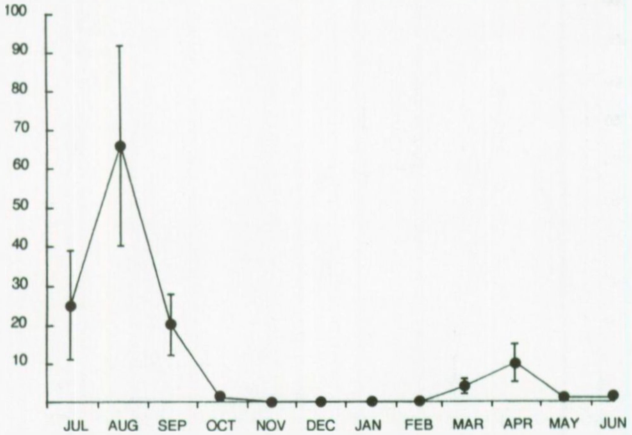

Figure 6. Pattern of occurrence of Kentish Plovers at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 are plotted.

and May, however the turnover may be greater. This pattern is similar to that of the whole Delta area and the Wadden Sea. This species is difficult to count as it often has it high water roosts inland on arable land. Therefore numbers given for our study area are minima.

4.3 Kentish Plover (*Charadrius alexandrinus* LINNAEUS) Fig.6

Both in our study area and in the whole Delta, Kentish Plover reaches its peak numbers in August. Up to 2600 birds may be present in the Delta, but only one hundred at the "Slikken van Vianen". Small numbers are present during spring migration. The Kentish Plover mainly winters along the Mediterranean and the North African coasts, where 30000 birds of the total population (35000) occur (Altenburg *et al.*, 1983).

4.4 Grey Plover (*Pluvialis squatarola* LINNAEUS) Fig. 7

The wintering area of the Grey Plover ranges from the North Sea coasts towards the coastal lagoons of South Africa, whereby males are mainly wintering in Europe and females in Africa (Cramp & Simmons, 1983). About one third of the population (153000) is wintering in Europe (Meininger *et al.*, 1984). In the Wadden Sea and Oosterschelde peak numbers occur during autumn and spring passage. In the Wadden Sea, however, the difference between the peak numbers and the winter numbers is more marked than in the Oosterschelde (5000 - 3000). The pattern on the "Slikken van Vianen" fits exactly with that of the Oosterschelde. The variation in numbers can differ

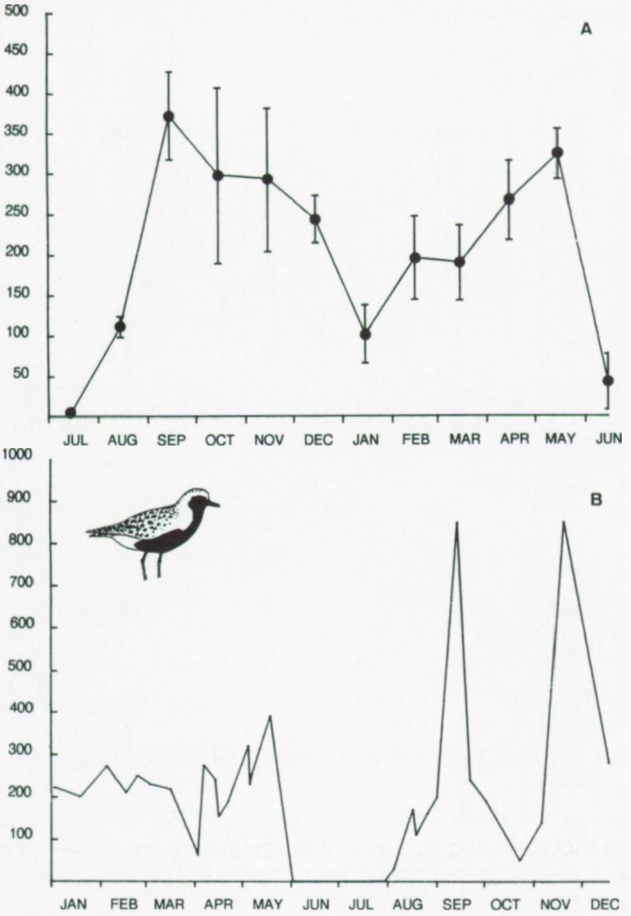

Figure 7. Pattern of occurrence of Grey Plovers at the 'Slikken van Vianen'. Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

considerably within one year (Fig. 7b) or between years (see large SE in Fig. 7a).

4.5 ***Knot*** (*Calidris canutus* LINNAEUS) Fig. 8

Knots occurring in Western Europe belong to two subspecies. The nominate form (*C. c. canutus*) breeding in central Siberia migrates through Europe to the West and South African moulting and wintering areas. Those breeding in the Canadian high-arctic islands and in northern Greenland (*C. c.*

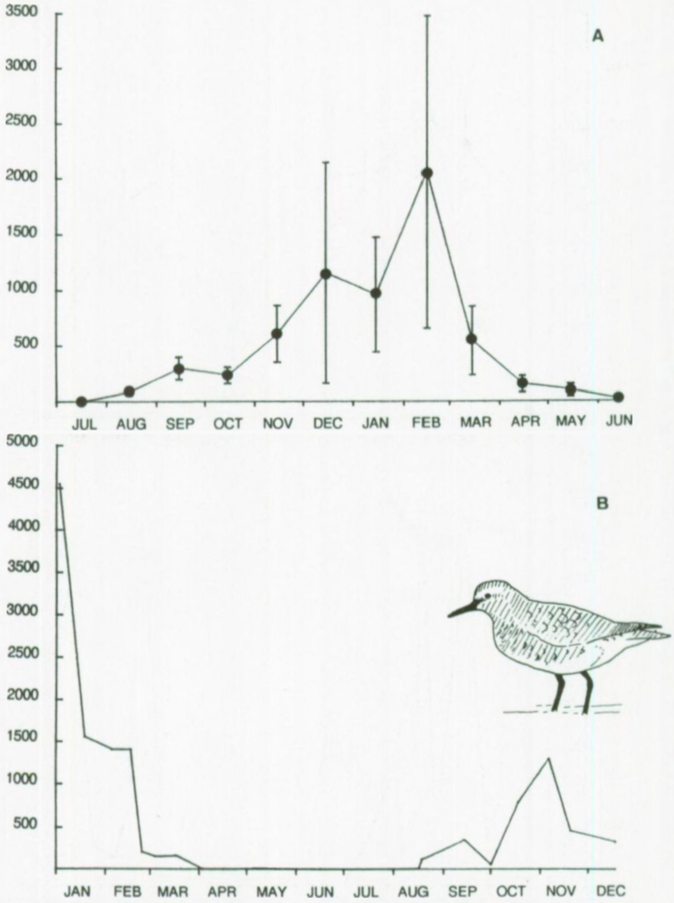

Figure 8. Pattern of occurrence of Knots at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

islandica) winter in West-Europe, mainly on the British Isles (Dick *et al.*, 1987). The total population of both subspecies is estimated at 750000 individuals.

In the Wadden Sea peak numbers are present in September. Numbers of Knots in the Oosterschelde increase steadily from July till December (15000) and drop in April-May. This pattern is however very different in the Western and Eastern part of the estuary. In the Western part the species reaches its peak numbers in September-October whereas in the Eastern part maximum numbers are counted between December and February (Wolff, 1973b; Leewis *et al.*, 1984; Meininger *et al.*, 1984). Whether this difference is due to the

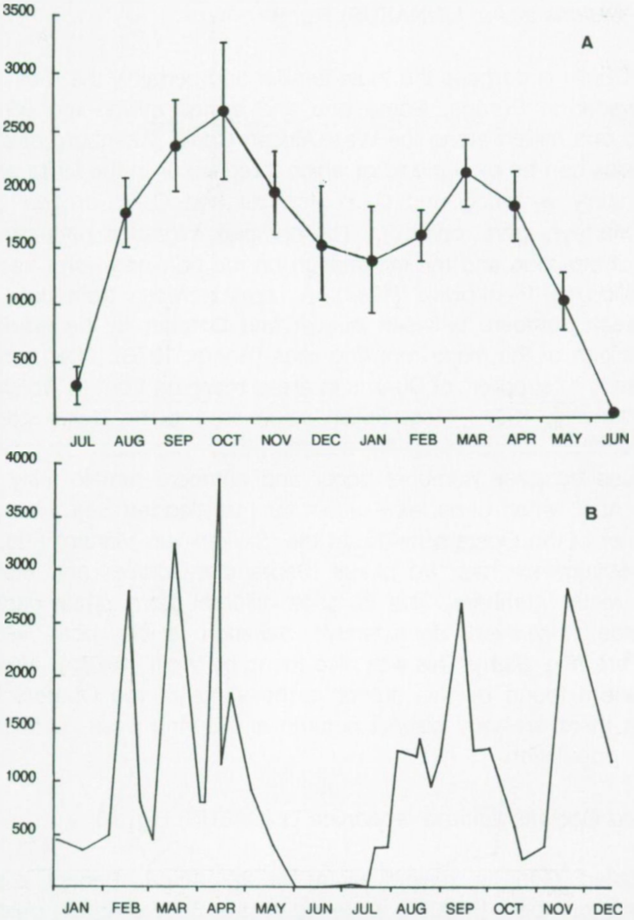

Figure 9. Pattern of occurrence of Dunlins at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

occurrence of the two subspecies is unknown. Fig. 8a shows that the patterns of occurrence at the "Slikken van Vianen" is similar to the Eastern (inland) part of the estuary. Both the within and between year variation is considerable (see large SE Fig. 8a, b). This is also true for numbers in the whole Delta, and might result from movements between West European estuaries (Cramp & Simons, 1983).

4.6 Dunlin (*Calidris alpina* LINNAEUS) Fig. 9

The Dunlin is perhaps the most familiar and certainly the most common estuarine wader in Europe. Some one and a half million are wintering in Europe and one million along the West African Coast (Altenburg *et al.*, 1983). Six subspecies can be recognized of which three occur in the Delta area: *C. c. alpina* is mainly wintering and *C. c. schinzii* and *C. c. arctica* occur on migration (Marteyn, pers. comm.). The complex migration patterns received quite a lot of attention and the information on the nominate form has recently been compiled by Pienkowski (1984). A rapid increase from July onwards results in peak numbers between August and October in the Wadden Sea, when this is one of the major moulting sites (Boere, 1976). After moulting the Wadden Sea is a "supplier" of Dunlins to areas reaching from N. Scotland to S. Iberia (Pienkowski, 1984). Most British estuaries and the Delta area have a wintering function for Dunlins. In autumn, they are both "suppliers" and "recipients" so no peak numbers occur and numbers remain fairly constant until March-April, when birds leave again for the Wadden Sea. Up to 90 000 Dunlins winter in the Oosterschelde. At the "Slikken van Vianen" (Fig. 9a), the pattern of occurrence has two peaks (September-October and March-April) and lower winter numbers. This is quite different from other parts of the Oosterschelde. However, considerable variation exists both within and between years (Fig. 9a,b). This was also found by Wolff (1973b). Although the average pattern found by this author is the same of the Oosterschelde, in some years there are very distinct autumn and spring peak numbers and a small winter population.

4.7 Bar-tailed Godwits (*Limosa lapponica* LINNAEUS) Fig. 10

Bar-tailed Godwits mainly winter in W. Africa. Recent expeditions revealed large numbers (540000) wintering on the Banc d'Arguin (Altenburg *et al.*, 1983). Nearly three quarters of the population wintering in Europe (100000) occur in Britain, with peak numbers occurring between November and February. In the Wadden Sea and the Delta area, however, peak numbers occur during autumn and spring migration. In the Oosterschelde two peaks can be distinguished in autumn: the first in August, probably consisting of birds heading immediately to W. Africa to moult, the second one in October presumably birds which have moulted in the Wadden Sea (Meininger *et al.*, 1984). Those peaks are clearly apparent in our study area in 1981 (Fig. 10b). The average occurrence however shows peak numbers in September-October and again in December, but from the large SE in Fig. 10a one should notice that the occurrence of Bar-tailed Godwits is very variable. This was also found on the Roggenplaat, another tidal flat of the Oosterschelde (Wolff, 1973b). In April-May some spring passage occurs. This pattern found at the "Slikken van Vianen" resembles closely that of the Oosterschelde, and contrasts with that of

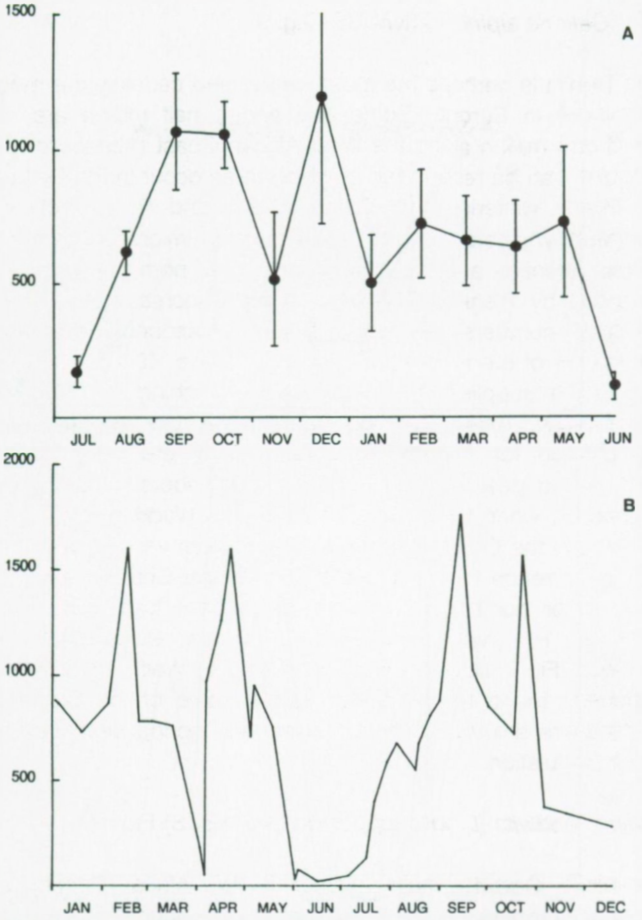

Figure 10. Pattern of occurrence of Bar-tailed Godwits at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

the Krammer-Volkerak, where numbers remain low throughout the year except in May when up to 6000 birds can be present.

4.8 ***Curlew*** (*Numenius arquata* LINNAEUS) Fig. 11

Most Curlews spend the winter period in Europe (400000 out of the 428000). The overall pattern of occurrence is very similar for the Wadden Sea, the British Isles and the Delta area. As they start to leave the breeding grounds in western and eastern Europe in late June and early July, large

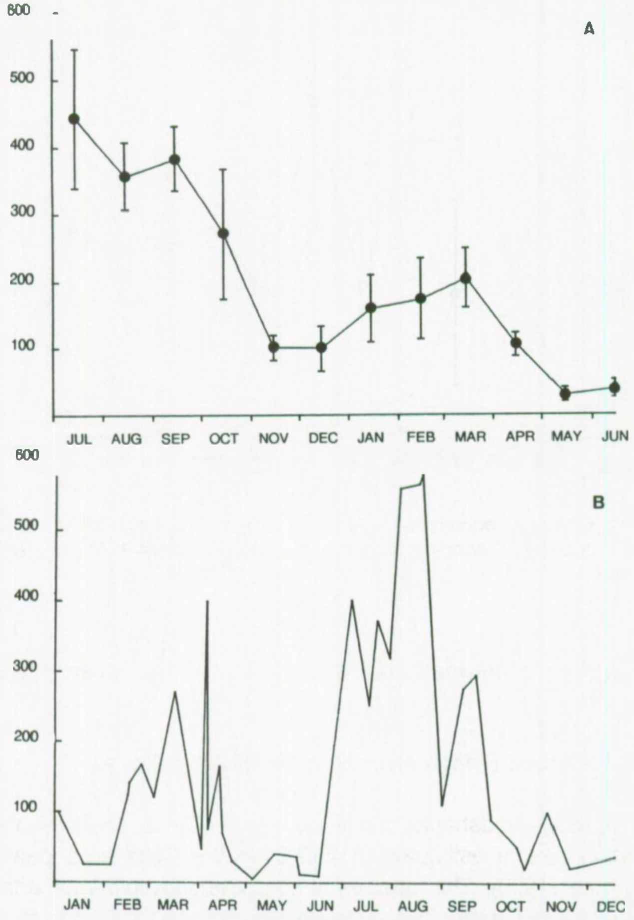

Figure 11. Pattern of occurrence of Curlews at the "slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

numbers are already present in July and peak numbers occur in August, September. From October onwards numbers start to decline to a minimum in midwinter. This partly coincides with an increase more inland. It has been suggested that mainly short-billed males are foraging inland (Ens & Zwarts, 1980; Townsend, 1981) This is explained by the fact that their main prey, the Ragworm (*Nereis diversicolor*), is buried deeper in the sediment and small Shorecrabs (*Carcinus maenas*) are absent during winter. In spring numbers increase slightly towards March and then drop to a very low summer level. This pattern fits very well with the overall pattern of the Delta area. The

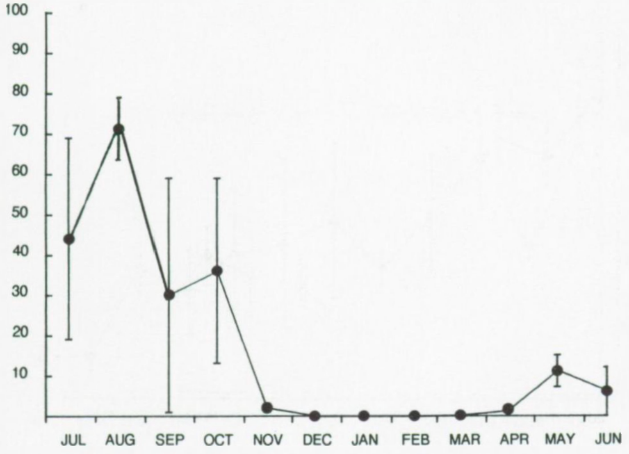

Figure 12. Pattern of occurrence of Spotted Redshanks at the "slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) are plotted.

variation in numbers between counts (Fig. 11b) and between years is rather small.

4.9 Spotted Redshank (*Tringa erythropus* LINNAEUS) Fig. 12

The Spotted Redshanks mainly winter in Africa, south of the Sahara. The population size is estimated at 26000. In the Delta area peak numbers occur in August (1500). This species is nearly absent in winter and in spring only few birds are seen. This species is difficult to count as it has its high-water roosts inland along small creeks. Average numbers in Vianen are given in Fig. 12. The pattern is similar to the Delta, but numbers are certainly underestimated.

4.10 Redshank (*Tringa totanus* LINNAEUS) Fig. 13

The Redshank is a more southerly breeding bird. Nearly 400000 birds winter in W. Europe and W. Africa. In W. Europe the numbers are generally peaking in July shortly after the breeding period. From August on a nearly continuous decline in numbers occur. The pattern at the "Slikken van Vianen" (Fig. 13a) corresponds well with that of the Oosterschelde, where on average 4000 birds are present in July and numbers decline to 1000 the next June. In 1981 (Fig. 13b) the decline from July onwards is very neat but it is possible that in March-April there was a migration peak. This occurs probably in many

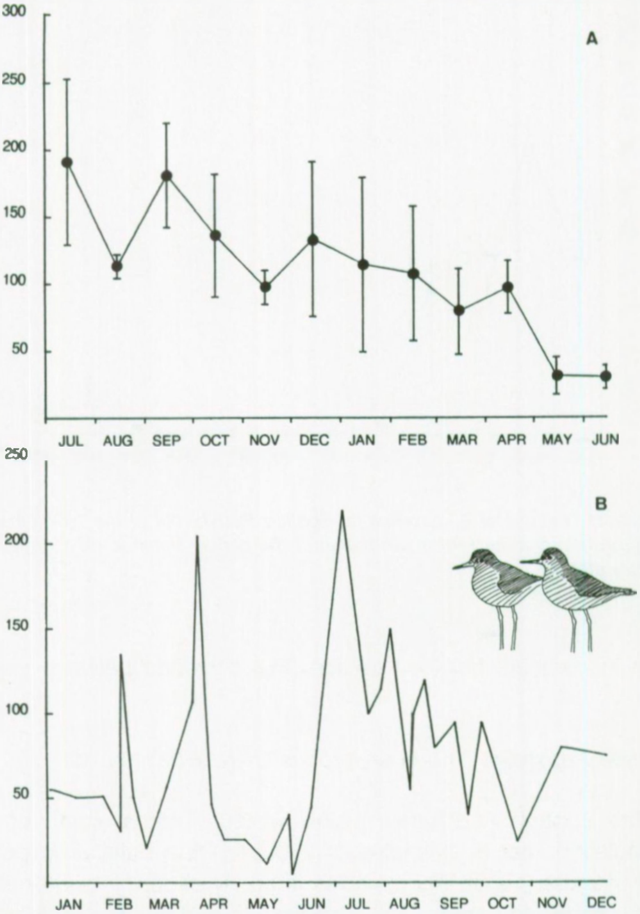

Figure 13. Pattern of occurrence of Redshanks at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (a) and each count of 1981 (B) are plotted.

parts of the Delta but birds may stay only for a short time (Marteijn, pers. comm.). From September onwards the continental birds (*T. t. totanus*) are gradually replaced by Icelandic birds (*T. t. robusta*). The proportion of each subspecies in winter is unknown but most probably the Icelandic birds dominate (Marteijn, pers. comm.).

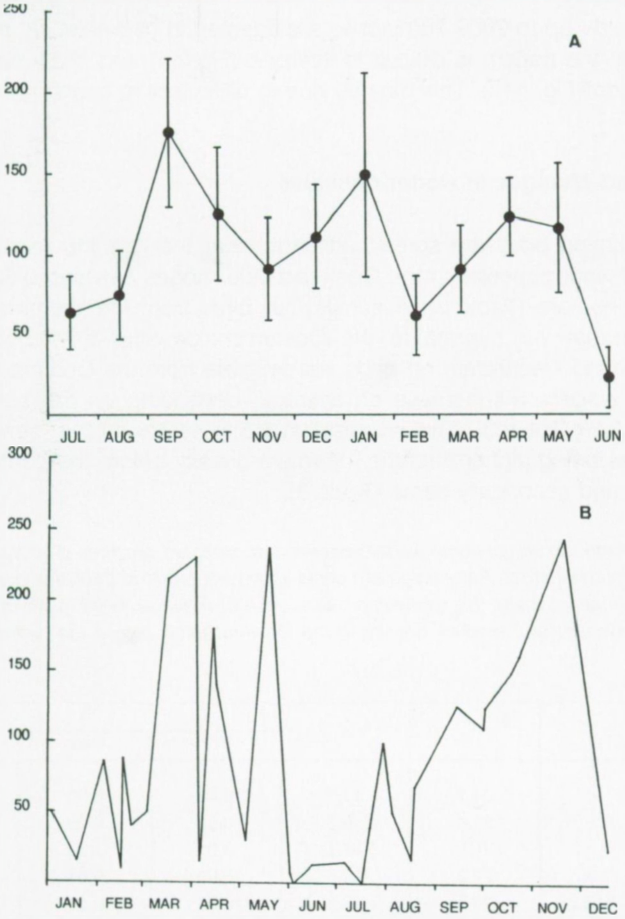

Figure 14. Pattern of occurrence of Turnstones at the "Slikken van Vianen". Average and standard error per month of the period October 1979 - September 1982 (A) and each count of 1981 (B) are plotted.

4.11 Turnstone (*Arenaria interpres* LINNAEUS) Fig. 14

Wintering Turnstones can be found all over the world. About 75.000 birds are wintering in Europe and W. Africa. In NW. Europe it concerns the nominate race which breeds in north-eastern Canada and Greenland. Breeding birds from Northern Europe (namely Finland) occur only on passage to West Africa. In the Wadden Sea numbers peak in spring and autumn whereas in the Delta, Great Britain and along the Belgian coast (Becuwe, 1973) numbers also increase very rapidly in August but remain fairly constant till April-May. In the

Oosterschelde up to 2000 Turnstones are counted in midwinter. At the "Slikken van Vianen" the pattern is difficult to interpret (Fig. 14) and show strong within year variation (Fig. 14a). This may be due to difficulties in counting these birds.

5. Expected changes in wader densities

Assuming birds are spread uniformly over the flats the median density of different wader species in the Oosterschelde ranges between 0.32 and 4.37 birds per hectare (Table 3). Assuming all birds from the Krammer-Volkerak and Markiezaat will migrate to the Oosterschelde after the closure of the Philipsdam and Oesterdam no birds will emigrate from the Oosterschelde the density of waders will increase on average, depending on the species, with 37.1 to 57.3 % (Table 3). This will result in 9.3 to 44.7% of the "new" densities of a species being higher than the maximum density before the construction of the barrier and secondary dams (Table 3).

Table 3. Average density of some wader species and expected changes after the completion of the storm surge barrier. Percentage of counts which will result in densities higher than the previous maximum density (for explanation see text) (1); Average % increase in density (2); minimum, maximum and median density in the Oosterschelde before the reduction in tidal area (3).

Species	1	2	3		
			min.	max.	median
Oystercatcher	44,7	41,7	0,46	6,96	4,37
Grey Plover	21,4	56,3	0,03	0,70	0,32
Knot	9,3	37,1	0,01	1,54	0,56
Dunlin	27,2	52,5	0,09	5,61	1,97
Bar-tailed Godwit	20,5	47,2	0,02	0,84	0,32
Curlew	15,0	50,5	0,02	1,14	0,35

DISCUSSION

Waders are threatened all over their winter quarters by a considerable loss of tidal habitats, and hence the question: "what is the influence of these coastal engineering works on wader numbers?" received quite a lot of attention in recent years (see Goss-Custard, 1985 for review). However until now only in a limited number of studies enough data were available to assess the influence of coastal engineering works on wader numbers (Evans, 1981; Evans *et al.*, 1979; Joyes *et al.*, 1976; Laursen, 1983; Van Latesteijn &

Lambeck, 1986).

To document the future changes of bird densities in the Oosterschelde it is necessary to have a description of the present situation for comparison. As bird numbers primarily depend on the available habitats and their extent (Meire & Kuijken, 1984b), a first step is to characterize these habitats and map their distribution. On the basis of macrofauna and sediment features it was possible to determine several habitat-types which all differ in species composition and densities of waders (Meire & Kuijken, 1984a; Meire & Coosen, 1985). Changes in the hydrodynamical characteristics of the estuary will influence the occurrence of habitat types and hence the distribution and number of waders. Therefore to document the expected changes the distribution and extent of these different areas for our study area and for the whole Oosterschelde (Coosen & Meire, in prep.) is mapped.

Wader numbers can fluctuate strongly both within or between years. Several factors can cause these variations. A first obvious one is the accuracy of the counts. Recently Kersten *et al.* (1981), Smit (1984) and Rappoldt *et al.* (1985) analyzed the accuracy of shorebird counts. It is useful to distinguish between errors originating from counting one group and from counting an area. The average coefficient of variation (CV) from counts of a group is ca. 20% independent of group size (Kersten *et al.*, 1981). When counting an area the CV declines with group size. Indeed a few birds are easily overlooked, whereas the larger groups are always counted. This is important in our case: uncommon species such as Ringed or Kentish Plover or Spotted Redshank may be easily overlooked, especially as they roost regularly on arable land. By adding up the results of several single groups the stochastic error on counts is rather small (5 à 10%) for numerous species. The systematic error, being the difference between the actual number of birds and the number counted is estimated in the range of 0 to 20% and is almost always an underestimation (Rappoldt *et al.*, 1985). As no large differences in errors between species and seasons occur it is justified to compare the results between years (Rappoldt *et al.*, 1985) and we can assume most of the observed variation is not due to counting errors.

Variation in numbers within a year also can be due to migration or to dispersion within the estuary. For instance, the several peaks of Dunlin in the spring of 1981 (Fig. 11b) and the peaks of Bar-tailed Godwits (Fig. 12b) might be caused by movements of flocks between several high water roosts or may represent different groups migrating quickly through the area. Indeed Symonds *et al.* (1984) found that in the Firth of Forth waders could be divided into two groups: Grey Plover, Turnstone, Oystercatcher and Redshank tended to stay within the same part of the estuary throughout the winter whereas Bar-tailed Godwit, Dunlin and Knots ranged more widely. Between year variation can be caused by either differences in overall population size (partly depending on the breeding success), or by differences in available food, weather conditions or the availability of other more attractive (more food) areas (even within the estuary).

The pattern of occurrence of waders at the "Slikken van Vianen" given in this paper is very similar to that of the total Oosterschelde but not to that of the Krammer-Volkerak, notwithstanding its location in between the two. Also Coosen & Van Den Dool (1983) classified the "Slikken van Vianen", based on abiotic features and macrozoobenthos-communities, within the Oosterschelde, and found neat differences with the flats of the Krammer-Volkerak. The salinity is lower in the Krammer-Volkerak.

If total population sizes remain constant. This will result in an increased density within the remaining sites. Higher densities cause a higher food consumption and there is some evidence that Oystercatchers feeding on musselbeds consume already a large part of the production (Craeymeersch *et al.*, 1986). Increasingly however research indicates that due to density-related behaviour there might be an upper limit to the numbers in an area. This results in a sequential filling of decreasingly profitable feeding sites, as numbers arriving increase in autumn (Zwarts, 1976; Goss-Custard, 1977; Meire & Kuijken, 1984a). Subdominant birds are excluded from the best feeding sites (Ens & Goss-Custard, 1984) and Swennen (1984) showed that birds feeding on less profitable feeding sites are more likely to die if the situation get worse. If more birds are forced into these poorer feeding sites mortality probably will increase and Goss-Custard (1980) showed that even a slight increase in density-dependent mortality might reduce the breeding populations quite substantially. Based on the unrealistic assumption that waders are spread uniformly over the flats the densities would increase quit substantially. Assuming now that the density on the preferred feeding sites will not increase an even higher increase in density in the less profitable feeding sites is expected. This is in our opinion not possible. From this it is obvious that the loss of intertidal area in the Oosterschelde may have a serious effect on wader populations.

In the light of all the possible causes of variation it will however be quite difficult to detect the changes in wader populations in the Oosterschelde Even more it may even take several years before a new equilibrium both of prey and bird populations is reached. Therefore it will be necessary to continue counts on a regular basis for several years before it will be possible to describe the changes. If changes in wader populations occur it will be necessary to compare this to the presence and distribution of habitat type and foraging behaviour before they can be explained properly.

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REFERENCES

Altenburg, W., M. Engelmoer, R. Mes & T. Piersma, 1983. Recensement des Limicoles et autres *Oiseaux Aquatiques au Banc d'Arguin, Mauretanie. Le Gerfaut 73: 243-264.*

Anderson, S. S., 1972. The ecology of Morecambe Bay II. Intertidal invertebrates and factors affecting their distribution. J. appl. Ecol. 9: 161-178.

Anonymous, 1986. Te verwachten ontwikkelingen in het Oosterscheldebekken na 1987. Nota GWAO-86.106, Rijkswaterstaat, Middelburg.

Becuwe, M., 1973. Een ecologische interpretatie van het seizoenale talrijkheidspatroon van de Steenloper, (*Arenaria interpres*), in Belgie. De Giervalk 63: 281-290.

Bij de Vaate, S. J., 1976. De bodemkundige gesteldheid van de Slikken van Vianen. RIJP 1976-258 Bbw, RIJP, Lelystad.

Boere, G. C., 1976. The significance of the Dutch Waddenzee in the annual life cycle of arctic, subarctic and boreal waders. Part I. The significance as a moulting area. Ardea 64: 210-291.

Coosen, J. & A. Van Den Dool, 1983. Macrozoöbenthos van het Krammer-Keeten-Volkerak estuarium. Verspreiding der soorten, aantallen en biomassa in relatie met het zoutgehalte: eindrapportage "Zachtsub". Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke.

Craeymeersch, J., P. 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.

Cramp, S. & K. E. L. Simmons, 1983. The birds of the Western Palearctic, Vol III. Oxford University Press, Oxford.

Dick, W. J. A., T. Piersma & P. Prokosch, 1987. Spring migration of the Siberian Knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project. Ornis Scandinavica 18: 5-16.

Elgershuizen, J., R. Misdorp & O. Oenema, 1982. De verspreiding van de mediane korrelgrootte, slib en de organische stof in de bodem van de Oosterschelde. Een compilatie van bestaande gegevens tot drie kaarten. RWS-notitie 82-259, Rijkswaterstaat, Middelburg.

Ens, B. J. & J. D. Goss-Custard, 1984. Interference among Oystercatchers, *Haematopus ostralegus* L., feeding on mussels, *Mytilus edulis* L., on the Exe estuary. J. anim. Ecol. 53: 217-232.

Ens, B. & L. Zwarts, 1980. Wulpen op het wad van Moddergat. Watervogels 5: 108-120.

Evans, P. R., 1981. Reclamation of intertidal land: some effects on Shelduck and wader populations in the Tees estuary. Verh. Orn. Ges. Bayern 23: 147-168.

Evans, P. R., D. M. Herdson, P. J. Knights & M. W. Pienkowski, 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. Oecologia 41: 183-206.

Glutz von Blotzheim, V. N., K. M. Bauer & E. Bezzel, 1975. Handbuch der Vogel Mitteleuropas, 6. Akademische Verlagsgesellschaft, Wiesbaden.

Glutz von Blotzheim, V. N., K. M. Bauer & E. Bezzel, 1977. Handbuch der Vogel Mitteleuropas, 7. Akademische Verlaggesellschaft, Wiesbaden.

Goss-Custard, J. D., 1977. 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., 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J. D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology: Ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford: 169-188.

Joyes, A., P. J. Knight, R. T. Leah & M. W. Pienkowski, 1976. The blockage of the Oued Chebelka estuary and its effects on the avifauna. Bull. Inst. Sci. 1: 39-47.

Kersten, M., K. Rappoldt & C. Smit, 1981. Over de nauwkeurigheid van wadvogeltellingen. Limosa 54: 37-46.

Krebs, J. R. & R. McCleery, 1984. Optimization in Behavioural Ecology. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford: 91-121.

Langslow, D. R., 1981. The conservation of intertidal areas in Britain. Wader Study Group Bull. 31: 18-22.

Laursen, K., I. Gram & L. J. Alberto, 1983. Short-term effect of reclamation on numbers and distribution of waterfowl at Hojer, Danish Wadden Sea. In J. Fjeldsa & H. Meltofte (eds), Proceedings of the third Nordic congress of Ornithology. Dansk Ornitologisk Forening- Zoologisk Museum, Kobenhavn: 97-118.

Leewis, R. J., H. J. M. Baptist & P. L. Meininger, 1984. The Dutch Delta Area. In P.R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal Waders and Wildfowl in Winter. Cambridge University Press, Cambridge: 253-260.

May, R. H., 1981. Theoretical Ecology: Principles and Applications. Blackwell Scientific Publications, Oxford.

Meininger, P. L., H. J. M. Baptist & G. J. Slob, 1984. Vogeltellingen in het Deltagebied in 1975/76 - 1979/80. RWS nota DDMI-84.23, Rijkswaterstaat, Middelburg.

Meininger, P. L., H. J. M. Baptist & G. J. Slob, 1985. Vogeltellingen in het Zuidelijk Deltagebied in 1980/81 - 1983/84. Nota DGWM 85.001, Rijkswaterstaat, Middelburg.

Meire, P. M. & J. Coosen, 1985. Benthos and bird communities in a changing estuary. In R. Van Grieken & R. Wollast (eds), Progress in Belgian Oceanographic Research. University of Antwerp Press, Antwerp: 292-303.

Meire, P. M. & E. Kuijken, 1984a. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, The Netherlands. In P. R. Evans, J.D. Goss-Custard & W. G. Hale (eds), Coastal waders and Wildfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. M. & E. Kuijken. 1984b. Barrage schemes-predicting the effects of changes in tidal amplitude on wader populations. In P. R. Evans, H. Hafner & P. L'Hermite (eds), Shorebirds and large Waterbirds Conservation. Commission of the European Communities, Brussels: 79-88.

Pienkowski, M. W., 1984. Identification of relative importance of sites by studies of movement and population turnover. In P. R. Evans , H. Hafner & P. L'Hermite (eds), Shorebirds and large Waterbirds Conservation. Commission of the European Communities, Brussels: 52-67.

Prater, A. J., 1981. Estuary birds of Britain and Ireland. T. Calton & A. Poyser, Calton.

Rappoldt, C., M. Kertsen & C. Smit, 1985. Errors in large-scale shorebirds counts. Ardea 73: 13-24.

Saeys, H. L. F. & H. J. M. Baptist, 1980. Coastal engineering and European wintering wetland birds. Biol. Cons. 17: 63-83.

Smit, C. J., 1981. The importance of the Wadden Sea for estuarine birds. In C.J. Smit & W.J. Wolff (eds), Birds of the Wadden Sea. Balkema, Rotterdam: 280-289.

Smit, C. J., 1984. Identification of important sites for waders by coordinated counts. In P.R. Evans, H. Hafner and P. L'Hermite (eds), Shorebirds and large Waterbirds conservation. Commission of the European Communities, Brussels: 43-51.

Smit, C. J. & W. J. Wolff, 1981. Birds of the Wadden Sea. Balkema, Rotterdam.

Swennen, C., 1984. Differences in quality of roosting flocks of oystercatchers. In P.R. Evans, J.D. Goss-Custard and W.G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 177-189.

Symonds, F. L., D. R. Langslow & M. W. Pienkowski, 1984. Movements of wintering shorebirds within the Firth of Forth: species differences in usage of an intertidal complex. Biol. Cons. 29: 187-215.

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 (eds), Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 261-274.

Van der Sluijs, P., G. G. Steur & I. Ovaa, 1965. De bodem van Zeeland. Stichting voor bodemkartering, Wageningen.

Van Latesteijn, H. C. & R. H. D. Lambeck, 1986. The analysis of monitoring data with the aid of time-series analysis. Envir. Monit. Ass. 7: 287-297.

Wilderom, M. H., 1964. Tussen afsluitdijken en deltawerken II, Noord Zeeland. Kups Repro, Meppel.

Wolff, W. J., 1973a. The estuary as a habitat. Zool. Verh. 126, Leiden.

Wolff, W. J., 1973b. Resultaat van vijf jaar steltlopertellingen op Schouwen. Limosa 46: 21-41.

Zwarts, L., 1976. Density related processes in feeding dispersion and feeding activity of teal (*Anas crecca*). Ardea 64: 192-209.

Chapter 5

CHANGES IN WADER POPULATIONS AT THE SLIKKEN VAN VIANEN (OOSTERSCHELDE NL.) AFTER MAJOR ENVIRONMENTAL CHANGES (1976-1990).

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ABSTRACT

The Oosterschelde is a major estuary in the Delta area of the SW Netherlands and is of great importance for wintering waders. Coastal engineering works changed the hydroynamical characteristics of the estuary and reduced the available surface of tidal flats by 36%. The effects of these works on some environmental parameters and the distribution of major habitats on the "Slikken van Vianen", a small tidal flat in the Oosterschelde were found to be similar to those of the Oosterschelde as a whole. This paper further describes the effects of this overall habitat reduction on the occurrence of 12 species of waders on the Slikken van Vianen. Number of bird-days decreased in 8 species and increased in 4, maximum numbers increased in 8 species and decreased in 4. The changes detected at the Slikken van Vianen correlate well with those found for the Oosterschelde as a whole. It is concluded that local carrying capacity was reached and that, with the exception of Bar-tailed Godwits, no birds from the lost intertidal areas were accommodated at the Slikken van Vianen.

INTRODUCTION

Loss and degradation of habitats is one of the major environmental problems. Among others, estuarine and other intertidal habitats all over the world have been severely affected by habitat loss. Being wintering grounds and migration stops for millions of waders and waterfowl, intertidal habitats received much attention from ornithologists and ecologists. A major subject in many studies was the effect of habitat loss on wader numbers and populations (see Evans & Dugan, 1984; Goss-Custard, 1985; Goss-Custard & Durell, 1990; Evans, 1991; Sutherland & Goss-Custard, 1991 for reviews). However, hitherto, only in a limited number of studies data were available to assess the influence of coastal engineering works on wader numbers (Evans, 1981; Evans *et al.*, 1979; Joyes *et al.*, 1976; Laursen, 1983, Van Latesteijn & Lambeck, 1986; Lambeck *et al.*, 1989).

In the Delta area of the SW Netherlands the total area of intertidal flats decreased between 1958 and 1987 from nearly 40 km^2 to less than 20 km^2 due to the closure of several estuaries and other large coastal engineering works. The effects of the closures of Veerse Gat (1961) and Haringvliet (1971) on birds are not well documented. Indeed, the first complete bird counts in the whole Delta area date from August 1966 and January 1967 (Wolff, 1967), followed by eight others between 1972 and 1975 (Saeys & Baptist, 1977), giving some insight in the effects of the closure of the Grevelingen (1971)

(Leewis *et al.*, 1984). On a smaller scale, Van Latesteijn & Lambeck (1986) and Lambeck *et al.* (1989) documented the effects of the closure of the Grevelingen estuary on wader numbers at the Roggenplaat, a major intertidal flat in the adjacent Oosterschelde. From the season 1975/76 onwards monthly counts of all tidal areas are available with the exception of the seasons 1983/84 - 1984/85 (Meininger *et al.*, 1984; 1985; Meininger & Van Haperen, 1988). This time series could be used to assess the impact of the construction of a storm surge barrier in the mouth of the Oosterschelde and the closure of the Markiezaat (1983), Zoommeer and Krammer-Volkerak (1987) (Schekkerman *et al.*, 1993).

If the birds, previously feeding on the intertidal area lost after the closure of the Oesterdam and Philipsdam, could be accommodated for in the remaining tidal part of the estuary, total bird numbers would remain stable, but densities should increase. If, however, the carrying capacity was already reached, we would expect the bird densities not to increase and hence total number of birds to decrease. Carrying capacity is defined here as the density at which the addition of any further birds would result in other birds dying or leaving the area because they fail to achieve adequate intake rates (Sutherland & Goss-Custard, 1991).

The Slikken van Vianen is a small intertidal area in the northern branch of the Oosterschelde, near the Krammer-Volkerak. On this mudflat, both benthos and birds were studied in detail since 1979 (see e.g., Meire & Kuijken, 1987). In this paper we investigate whether or not the bird numbers on this mudflat changed in respons to the coastal engineering works in general and especially to the loss of intertidal habitat. The environmental changes and the occurrence of different habitat types at the study area are briefly described. For the twelve most common wader species the seasonal pattern, maximum numbers and number of bird-days is given and compared between the pre- and the post-barrier situation. The results are also compared to those for the Oosterschelde as a whole (Schekkerman *et al.*, 1993) to investigate the representativity of the results obtained in a small study area.

MATERIAL AND METHODS

Study area and environmental parameters

The "Slikken van Vianen" is a tidal flat of ca 510 ha, bordering the south-east coast of Schouwen-Duiveland (see Meire & Kuijken (1987) for a detailed description of the study area). Within six permanent plots, scattered over this tidal flat, sediment characteristics, macrozoobenthos and birds were monitored between 1979 and 1990. In this paper only sediment characteristics (median grain size, sorting coefficient and percentage silt < 53μ), measured by standard methods (Dyer, 1979) on samples collected each autumn are used. The height of each plot was measured and expressed in cm NAP, the Dutch ordnance level. For the data on macrozoobenthos we refer to Coosen *et al.* (1993a) and Seys *et al.* (1993).

Bird counts

During high tide, waders, which feed during low tide on the mudflats of the Slikken van Vianen, concentrate on "high tide roosts", mainly on the salt marsh and on adjacent fields. Here waders were counted on 282 occasions between October 1976 and June 1990.

Although several species of ducks and geese (e.g., Wigeon, *Anas penelope*, Pintail, *A. acuta*, Shelduck, *Tadorna tadorna*, Brent Goose, *Branta bernicla* and Bewick's Swan, *Cygnus columbianus*) are present in rather large numbers during migration or in winter, counts of these species are less complete. This paper, therefore, deals only with twelve regularly occurring wader species, being: Oystercatcher (*Haematopus ostralegus* LINNAEUS); Ringed Plover (*Charadrius hiaticula* LINNEAUS); Kentish Plover (*Charadrius alexandrinus* LINNAEUS); Grey Plover (*Pluvialis squatarola* LINNAEUS); Knot (*Calidris canutus* LINNAEUS); Dunlin (*Calidris alpina* LINNAEUS); Bar-tailed Godwit (*Limosa lapponica* LINNAEUS); Curlew (*Numenius arquata* LINNAEUS); Spotted Redshank (*Tringa erythropus* LINNAEUS); Redshank (*Tringa totanus* LINNAEUS); Greenshank (*Tringa nebularia* LINNAEUS); Turnstone (*Arenaria interpres* LINNAEUS).

Due to several circumstances the number of counts is not equal for all species. When several counts for one specific month were available, the mean was calculated. The number of bird-days for each species per season (seasons running from July through June) was calculated by summing the average monthly counts and multiplying by 30. Due to some incomplete counts, bird-days could not be calculated for each season.

To compare the pre- and post-barrier situation the data for five seasons in the pre-barrier period (1978/79 - 1982/83) and three seasons in the post-barrier period (1987/88 - 1989/90) were used. Based on the monthly averages, the overall monthly mean per period was calculated to describe the seasonal pattern of occurrence. Differences in means between periods were tested using Student's t statistic. In view of the large variability of bird numbers and the short study periods, a significance level of 10% has been used (see also Schekkerman *et al.*, 1993).

The results from our study area are compared with the data from the whole Oosterschelde estuary compiled by Meininger *et al.* (1984; 1985) and Meininger & Van Haperen (1988).

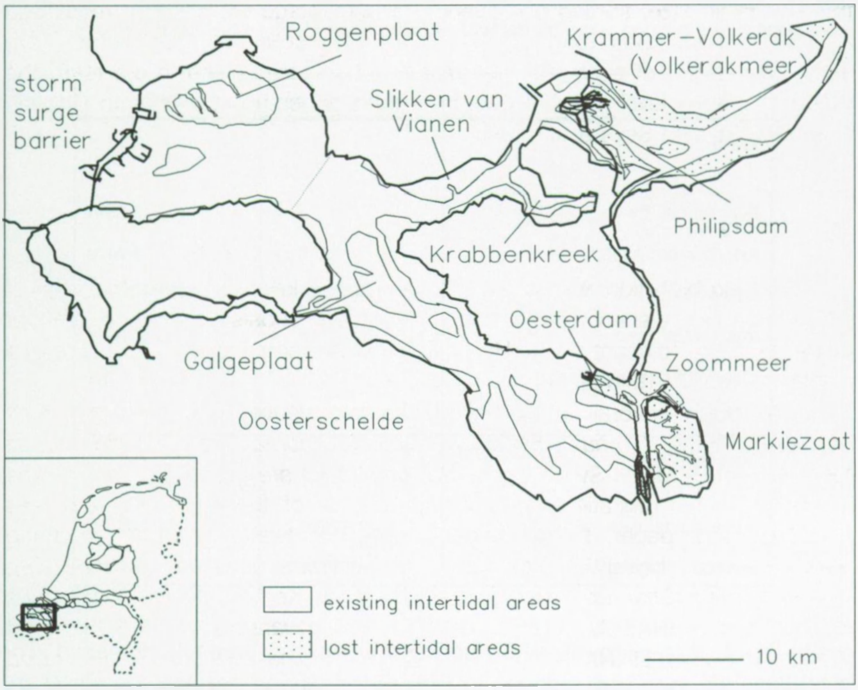


Figure 1: The Oosterschelde with the position of the "Slikken van Vianen", the storm surge barrier and the secondary dams.

RESULTS

Environmental changes in the Oosterschelde

The construction of a storm surge barrier in the mouth of the estuary was completed in 1987. This construction consists of 65 pylons between which large doors can be lowered when the water-level is expected to rise above a certain initial level. This construction reduced the cross section of the estuary mouth by 80%. In addition, secondary dams have been built more inland, closing off "Zoommeer", "Markiezaat" and "Krammer-Volkerak" (Fig. 1). These constructions caused profound changes in the estuary. The effects on some environmental parameters are summarized in Table 1. The tidal amplitude and current speed decreased, salinity of the water remained more or less constant, but increased in the northern branch of the estuary. Due to a smaller fresh

Table 1. Changes in some environmental parameters of the Oosterschelde estuary due to the construction of the storm surge barrier and two secondary dams (after Smaal & Boeije, 1991).

	before	after
Water:		
tidal amplitude	3.7 m	3.25m
max current speed	1.5 m/s	1 m/s
tidal volume	$1240*10^6$ m^3	$880*10^6$ m^3
fresh water load	70 m^3/s	25 m^3/s
chlorinity (western part)	16.9 g/l	17.1 g/l
Intertidal area:		
surface tidal flats	17000 ha	11365 ha
surface saltmarshes	1725 ha	643 ha

water input, nutrient levels decreased and water transparency increased. The total intertidal area was reduced to 64% of the original surface. Details of the coastal engineering works and changes in the ecosystem are summarized in Smaal *et al.* (1991) and are dealt with in detail in the papers compiled by Nienhuis & Smaal (1993).

Changes in environmental parameters and habitat distribution at the Slikken van Vianen.

The available sediment parameters and tidal elevation in six permanent study plots are given in Table 2. The sediment can be characterized as fine sand with a low percentage of silt. Although the sediment was more or less stable during the study period there was a trend of a decreasing percentage silt. In most plots some erosion occurred in recent years. The intertidal surface of the Slikken van Vianen decreased by about 25% due to the reduction in tidal amplitude.

Based on an average tidal curve of 1985 and 1989 the exposure time of sites situated between -1.00 and 0.75 m NAP decreased with 48 minutes from 3h 36 min to 2h 48 min. Sites between 0.75 and 1.00 m NAP are exposed 18 min longer (from 9h 24 min to 9h 42 min). Near NAP (mid-tidal level) no changes occurred.

Table 2. Available data on abiotic characteristics of six plots in the period 1979-1989 (Height= tidal level expressed in cm NAP; MGS= median grain size in φ units; silt= fraction of the sediment < 53 μ).

PLOT	VARIABLE	79	81	82	84	85	86	87	88	89
6	height	-70			-82	-78	-98	-97	-85	-88
	MGS	3.17	2.89	2.89	2.95	2.84	2.69	2.74	2.55	
	silt	9.2	6.0		10.0	5.2	5.1	2.5	3.2	
10	height	-81			-78	-68	-92	-91	-93	-97
	MGS	3.17	2.91	2.91	2.85	2.92	2.73	2.75	2.5	
	silt	8.5	7.6		4.5	5.7	5.6	2.0	3.4	
13	height	-41			-51	-57	-80	-79	-72	-83
	MGS	3.07	2.66	2.66	2.88	2.78	2.84	2.78	2.80	
	silt	3.9	7.0		11.0	4.5	13.6	2.8	4.7	
22	height	-			-78	-69	-94	-94	-88	-92
	MGS	-	2.99	2.99	2.76	2.87	2.69	2.82	2.53	
	silt	-	16.6		4.0	5.6	7.0	2.8	1.54	
32	height	-			63	59	43	42	47	42
	MGS	-	3.02	3.02	2.94	2.95	2.97	2.89	2.63	
	silt	-	5.0		4.0	3.2	5.3	0.8	2.1	
39	height	-			-10	-13	-18	-18	-15	-19
	MGS	-	2.83	2.83	2.96	2.89	2.93	2.95	2.61	
	silt	-	6.0		7.0	6.2	5.2	5.6		

During the entire study period, the distribution of the various biocoenoses at the Slikken van Vianen remained more or less similar to that described by Meire & Kuijken (1984a; 1987). Major changes occurred in the distribution of eelgrass (*Zostera marina, Z. noltii*). Although Eelgrass cover varies considerably between years (De Jong, 1989), in recent years the coverage on the Slikken van Vianen has been much lower than in previous years. In 1977 the coverage of Eelgrass amounted to about 140 ha or some 25 ton ash free dry weight (ADW). In 1984 the area covered dropped to 9 ha, in 1989 it increased slightly upto 14 ha but the biomass further decreased: 2.8 ton in 1984 and 1.5 ton in 1989 (D. De Jong, pers. comm.).

The area of musselbeds remained approximately the same but the mussel-cover on the beds decreased significantly (Fig. 2). The biomass of mussels decreased to a minimum in 1986, but the biomass of cockles increased, especially in the period 1987-1989 both on the musselbeds

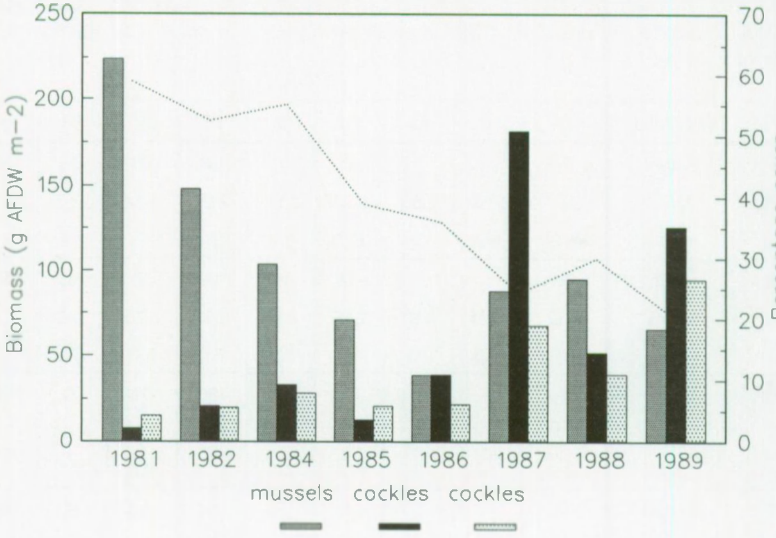


Figure 2. Average autumn biomass (g AFDW/m2) of cockles and mussels in the plots on musselbeds (first and second bar) and in the other plots (third bar) on the Slikken van Vianen between 1981 and 1989. The line represents the average mussel cover on the musselbeds.

and outside the musselbeds (Fig. 2). Data on macrozoobenthos of the Slikken van Vianen have been summarized by Seys *et al.* (1993), Coosen *et al.* (1993a) and Meire *et al.* (in prep.). Notwithstanding some large variations, late summer values of total biomass, total density, species richness, diversity and abundance- and biomass ratio showed no overall significant trend during the study period.

Wader populations in Vianen compared to the Oosterschelde

The composition of the wader community at the Slikken van Vianen is given in Figure 3. Nearly half of the total number of "bird-days" was made up by Oystercatcher, followed by Dunlin and Bar-tailed Godwit. These three species together made up more than 75% of all bird-days on the Slikken van Vianen. In the post-barrier period Bar-tailed Godwits became the second most important species, Dunlin third. The Oosterschelde as a whole shows a very similar pattern (Fig. 3): proportionally Oystercatcher, Grey Plover, Curlew and Redshank are somewhat more abundant, Bar-tailed Godwits less abundant,

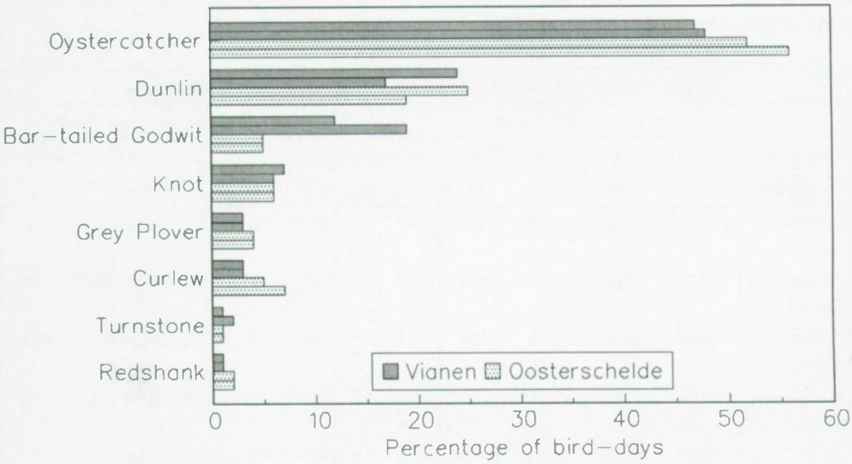


Figure 3. Percentage of the total number of bird-days of each species for both the Slikken van Vianen and the whole Oosterschelde. The upper bar is the pre-, the lower bar the post-barrier situation.

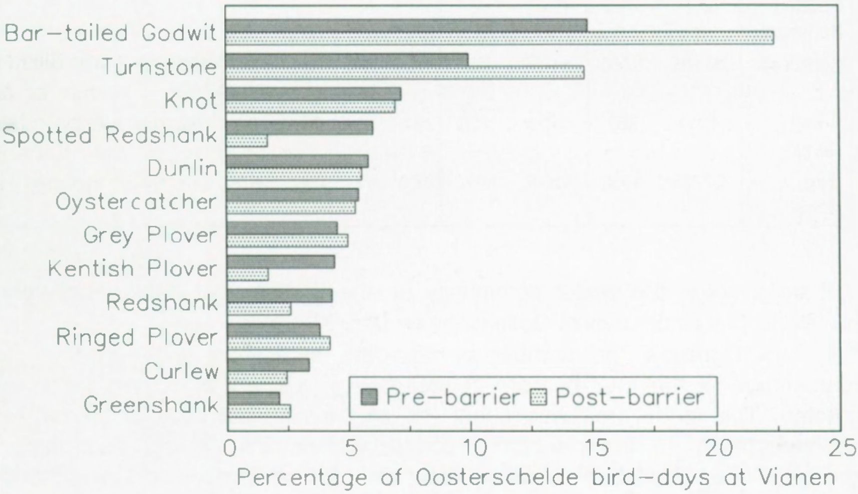


Figure 4. Percentage of total number of bird-days in the Oosterschelde spent on the Slikken van Vianen for several species.

Table 3. Changes in bird-days and maximum number of twelve wader species on the Slikken van Vianen in the pre- and post-barrier period. The average (x), standard deviation (se), percentage change (%) and significance (P, student t-test) are given.

Wader populations on the Slikken van Vianen, pre- and post barrier												
	Bird-days						Maximum counts per season					
Species	1978-1983		1987-1990		difference		1978-1983		1987-1990		difference	
	x	se	x	se	%	p	x	se	x	se	%	p
Oyster-catcher	1076151	115845	1012231	53680	-5.9	ns	8174	1289	9030	2064	10.5	ns
Ringed Plover	4255	713	5600	437	31.5	ns	128	24	175	68	36.7	ns
Kentish Plover	2836	1229	623	188	-78.0	ns	80	25	22	13	-72.5	0.09
Grey Plover	77133	5559	71343	4778	-7.5	ns	618	78	636	120	2.9	ns
Knot	5332	848.7	4395	1086.7	-17.5	ns	4370	1256	4380	626	0.2	ns
Dunlin	548471	95933	359195	15104	-34.5	ns	3500	306	2733	33	-21.9	0.06
Bar-tailed Godwit	267960	25304	400806	17636	49.6	0.008	1964	189	3000	230	66.5	0.021
Curlew	70031	5210	54249	5599	-22.5	0.09	659	123	665	131	0.9	ns
Spotted Redshank	6341	1860	2035	931	-67.9	ns	158	35	71	17	-55.1	0.07
Redshank	31105	4760	14139	723	-54.5	0.036	282	39	153	3	-45.7	0.03
Green-shank	1011	387	1261	186	24.6	ns	35	9	42	5	20.0	ns
Turn-stone	32733	4553	41840	8023	27.8	ns	266	40	310	97	16.5	ns

but on average the wader community on the Slikken van Vianen was very similar to that of the overall Oosterschelde (Fig. 3).

In Figure 4 the number of bird-days in Vianen, expressed as a percentage of the total number of bird-days in the whole Oosterschelde is plotted. The study area was about 3% of the intertidal area of the entire Oosterschelde. In the pre-barrier period, Greenshank, in the post-barrier period, Curlew, Redshank, Spotted Redshank, Kentish Plover and Greenshank were less abundant than could be expected on the basis of the size of the intertidal area of the Slikken van Vianen.

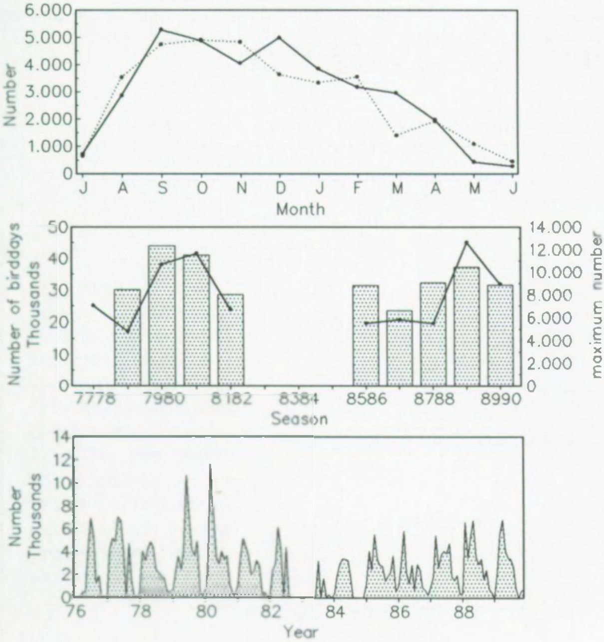
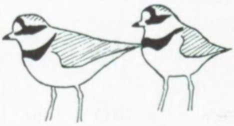


Figure 5. Pattern of occurrence of Oystercatcher on the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).



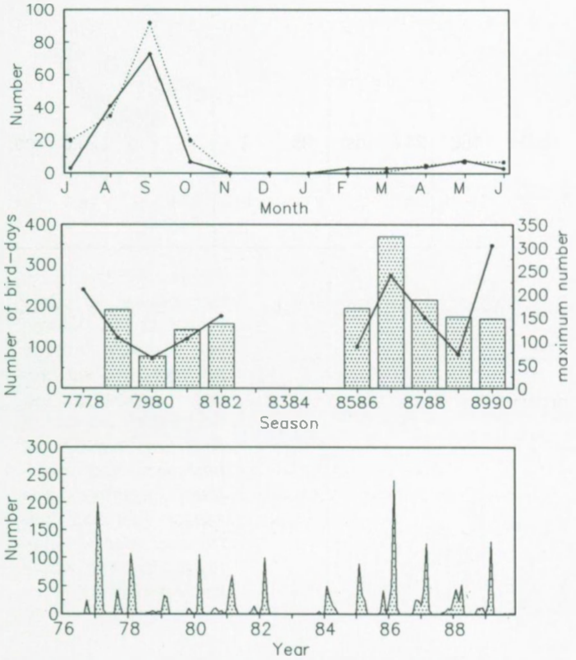


Figure 6. Pattern of occurrence of Ringed Plover at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

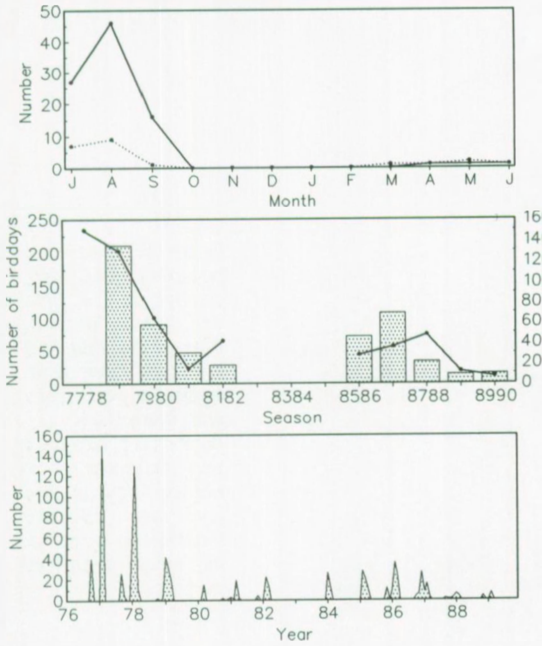


Figure 7. Pattern of occurrence of Kentish Plover at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

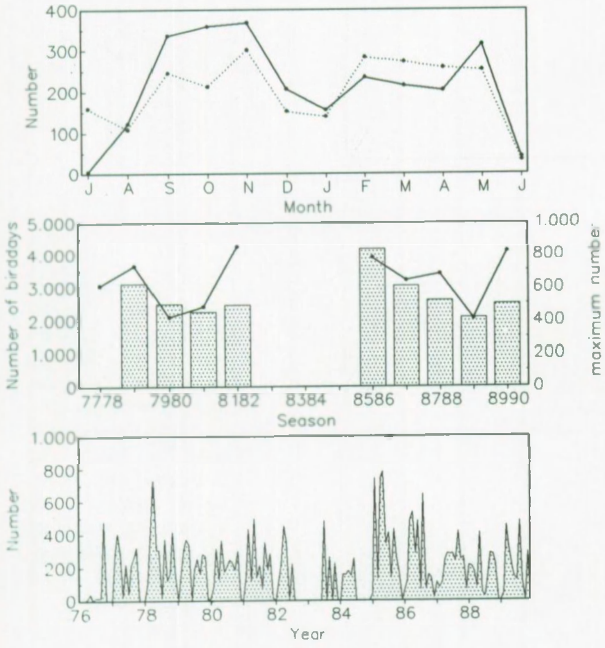


Figure 8. Pattern of occurrence of Grey Plover at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

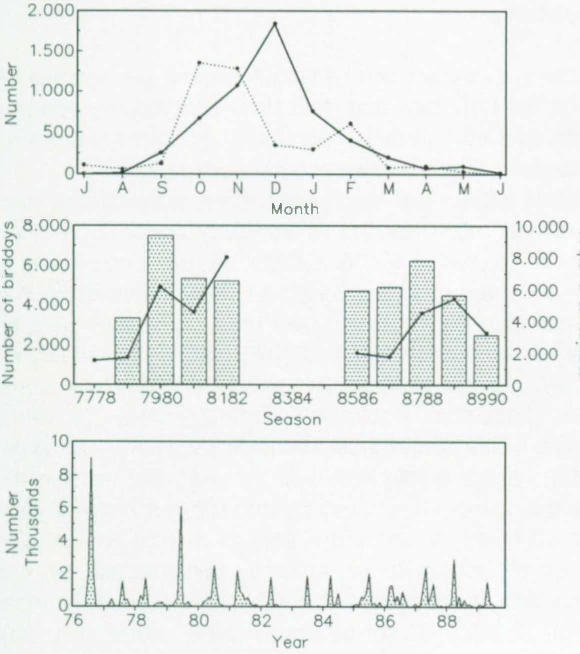


Figure 9. Pattern of occurrence of Knot at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of birddays and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

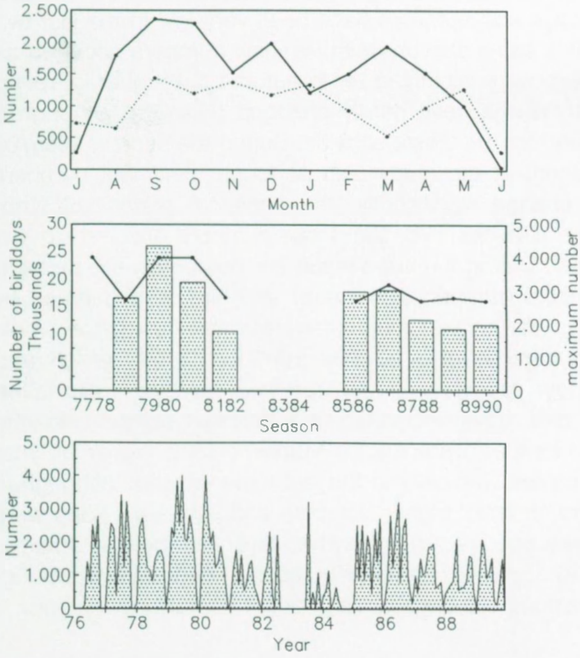


Figure 10. Pattern of occurrence of Dunlin at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of birddays and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

Changes in wader populations

The average number of bird-days and seasonal maxima per species on the Slikken van Vianen for both the pre- and post barrier period are summarized in Table 3. For eight species bird-days decreased, for four it increased. Maximum numbers decreased in four and increased in eight species.

The average seasonal pattern pre- and post-barrier, maxima and bird-days and average number per month for the whole study period have been plotted for each species in Figures 5 to 16. Details on the occurrence of waders at the study area are given by Meire & Kuijken (1987). **Oystercatcher** numbers and bird days remained fairly constant over the study period (Fig. 5). Numbers were somewhat lower between 1983 and 1986 and increased slightly since 1987. The seasonal pattern was similar, although there are some indications that in winter (December - January) numbers were somewhat lower, a trend that was clear in the overall Oosterschelde (Schekkerman *et al.*, 1993). Number of bird-days varied a little from year to year, but were in the same order of magnitude during the whole study period. **Ringed Plovers** were mainly seen on autumn migration, a consistent pattern on the Slikken van Vianen (Fig. 6a). Numbers increased in autumn, in contrast to the Oosterschelde where especially in spring higher numbers were seen. Number of bird-days was very high in 1986/87, but otherwise rather stable (Fig. 6b). **Kentish Plover**, an autumn migrant, maximum numbers decreased significantly, the drop in bird-days was large but not significant. From Figure 7b,c it is clear that bird-days and numbers have been very low in the last two seasons. In the early 1980s some seasons with very low numbers occurred as well. **Grey Plover** numbers were slightly lower in autumn but higher in spring (Fig. 8a). Bird-days and maxima have hardly changed (Fig. 8b), although a decreasing trend was found for the Oosterschelde. During the season 1985/86 large numbers were present at the study site. Although maximum numbers and bird-days did not change significantly, the seasonal pattern of **Knot** showed some remarkable changes (Fig. 9a). Peak numbers occurred in late autumn instead of in winter. During the last season low numbers were present (Fig. 9 b,c). **Dunlin** numbers dropped significantly and bird-days declined by more than one third. Fig. 10a shows numbers were lower during the whole season. The decreasing trend is also obvious from Fig. 10b,c, which also show that values were low especially in the last three seasons. **Bar-tailed Godwit** numbers and bird days increased significantly, contrary to the Oosterschelde were no changes were found. Numbers were higher all year round (Fig. 11a). This increase was clear in the last three seasons although in the seasons 1985/86 and 1986/87 higher numbers and bird-day values were seen (Fig. 11b,c). **Curlews** occurred in somewhat lower numbers in autumn, resulting in a significant ($0.1>p>0.05$) smaller number of bird-days. From Fig. 12b,c no clear trend is obvious. Although not significant (maximum numbers;

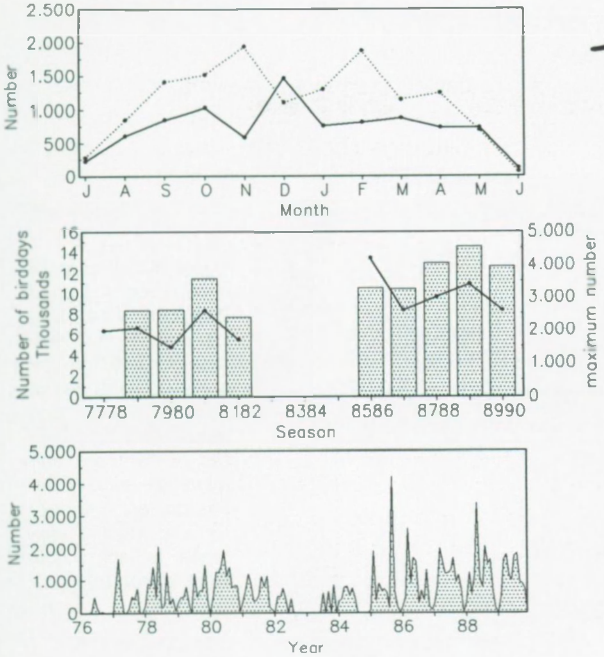


Figure 11. Pattern of occurrence of Bar-tailed Godwits at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

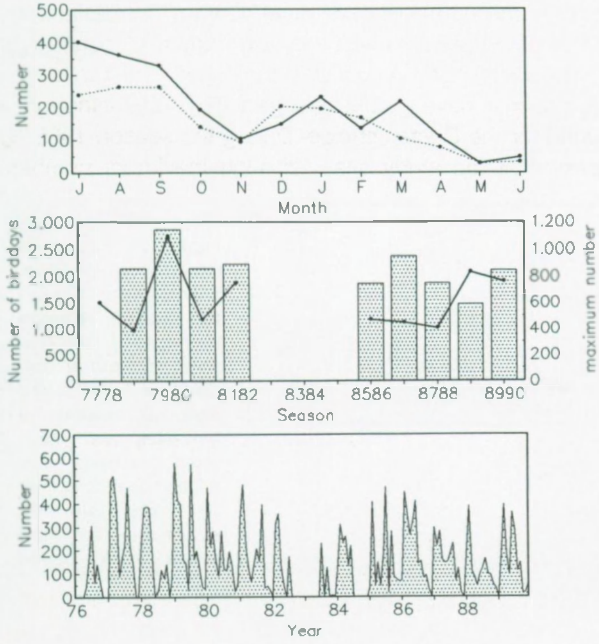


Figure 12. Pattern of occurrence of Curlew at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

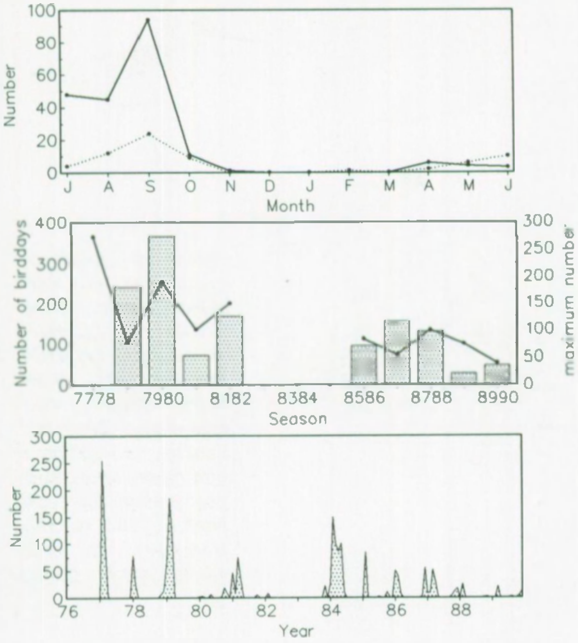
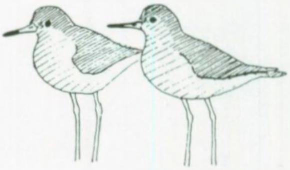


Figure 13. Pattern of occurrence of Spotted Redshank at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).



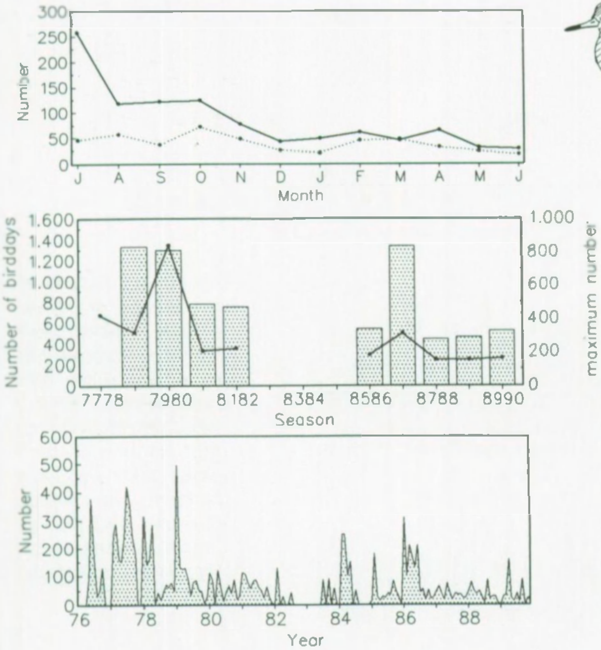


Figure 14. Pattern of occurrence of Redshank at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

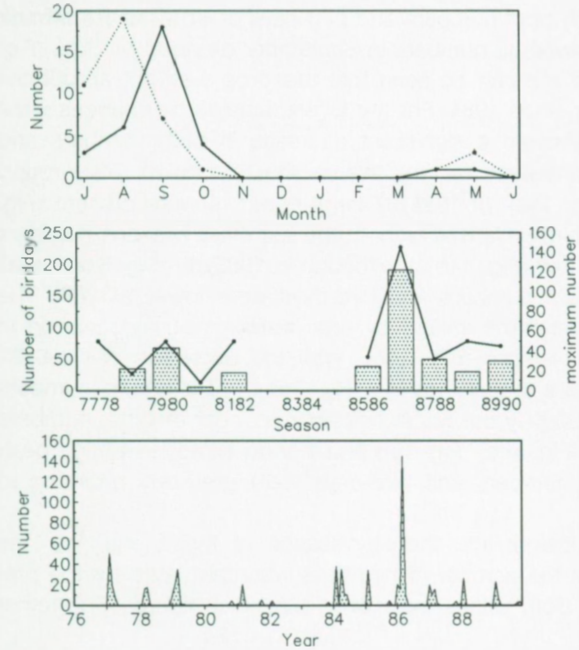
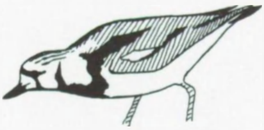


Figure 15. Pattern of occurrence of Greenshank at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).



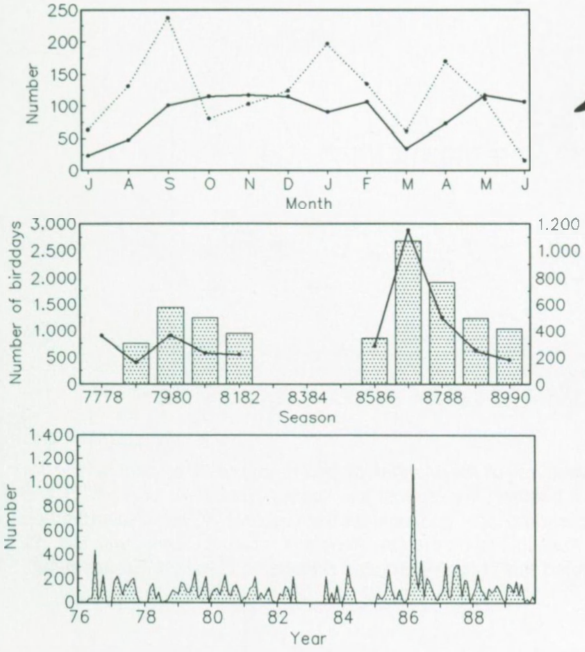


Figure 16. Pattern of occurrence of Turnstone at the "Slikken van Vianen". Average per month in the pre- and post-barrier period (solid and dotted line) (a), number of bird-days and maximum number per season (bar and line) (b) and monthly averages for the whole study period (c).

0.1>p>0.05; see Table 3) both numbers and bird-days of **Spotted Redshank** decreased dramatically. Average numbers in September dropped by 80% (Fig. 13a). From Fig. 13b and c it can be seen that this drop was not abrupt but occurred rather gradually since 1984. For the Oosterschelde no changes were found. The **Redshank** showed a significant decrease in both numbers and bird-days, a pattern consistent for the whole Oosterschelde. Year-round numbers were lower (Fig. 14a). In 1986/87 large numbers were present (Fig. 14c) and the number of bird-days was high. In the last three seasons numbers and bird-days were very low (Fig. 14b,c), although in 1985/86 they were small as well. In the early 1980s numbers and bird-days were lower as well. The seasonal pattern of **Greenshank** shifted by one month, maxima occurred in August instead of in September (Fig. 15a). With the exception of 1986/87 numbers and bird-days are low and stable (Fig. 15b,c). **Turnstone** numbers and bird-days increased slightly but not significantly. In most months, numbers were on average higher (Fig. 16a). Fig. 16b and c show however a huge peak in 1986/87, after which numbers and bird-days were gradually returning to their normal levels.

To get a better insight into the significance of these changes, the coefficient of variation on the number of bird-days was calculated for the pre- and post-barrier period. Both values have been plotted in figure 17 together

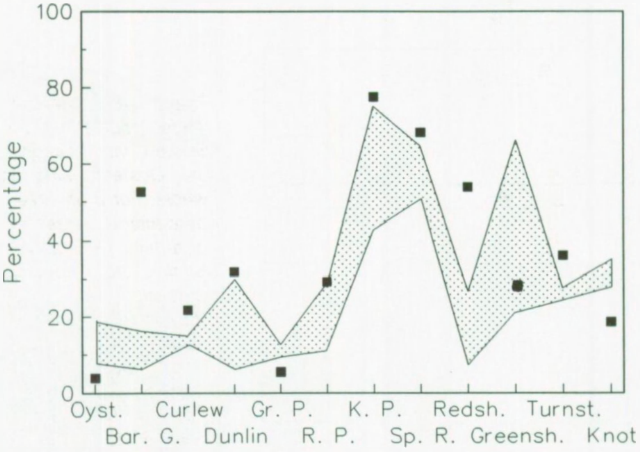


Figure 17: Coefficient of variation of the number of bird-days pre- and post-barrier for each species (the distance between the highest and lowest coefficient is shaded) and percentage difference in bird-days pre- and post-barrier (square). (Oyst. Oystercatcher; Gr. P. Grey Plover; K. P. Kentish Plover; Redsh. Redshank; Turnst. Turnstone; Bar. G. Bar-tailed Godwit; R. P. Ringed Plover; Sp. R. Spotted Redshank; Greensh. Greenshank).

with the percentage change in bird-days between the pre- and post-barrier period (see Table 3). The change in bird-days for Bar-tailed Godwit and Redshank was clearly higher than between year variability and significant differences were found. This was also true for the Curlew. For the other species the difference was smaller than between year variation or only slightly more, not resulting in significant differences. For some species the changes in maximum number are significant, whereas changes in bird-days are not (Table 3). Only for Curlew maximum numbers did not decrease, bird-days did.

The changes observed in the study area are compared to the changes in the Oosterschelde as a whole in Figure 18. Without the Spotted Redshank, which declined dramatically at Vianen, but increased in the whole of the Oosterschelde, a significant correlation was found between the changes on the Slikken van Vianen and for the Oosterschelde as a whole ($r^2=0.76$, $n=11$, $p<0.01$).

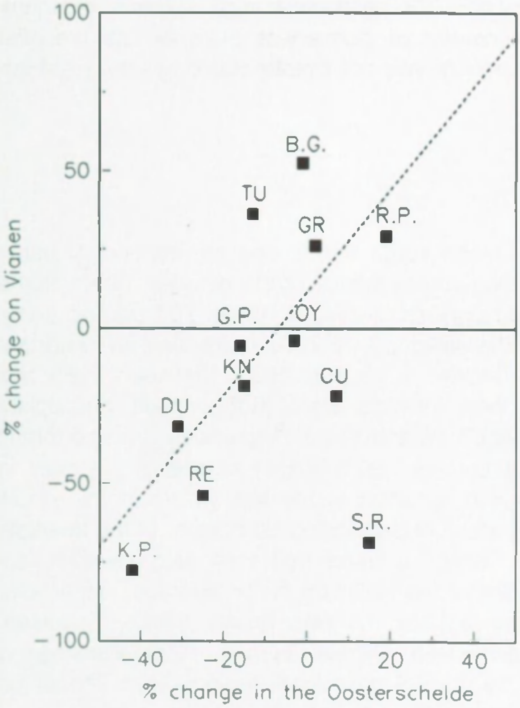


Figure 18: Changes in wader populations on the Slikken van Vianen and the Oosterschelde as a whole. For both areas the percentage change in bird-days pre- and post-barrier per species is plotted. (K.P. kentish Plover; RE Redshank; DU Dunlin; KN Knot; G.P. Grey Plover; OY Oystercatcher; CU Curlew; S.R. Spotted Redshank; R.P. Ringed Plover; GR Greenshank; TU Turnstone; B.G. Bar-tailed Godwit).

DISCUSSION

Changes in bird numbers can be caused by several factors such as changes in the overall population size, changes in the local abiotic environment or the local food supply, changes in other areas etc. Also methodological aspects like inaccuracies in the counting method can introduce variability in the dataset. To interpret the changes in bird numbers situated above these different possibilities are discussed.

It is well known that bird counts are subject to some error (see e.g., Kersten *et al.*, 1981; Rappoldt *et al.*, 1985). It is, however, very unlikely that the results presented in this paper are due to inaccuracies in the counting method. The counting errors in this study probably will be rather small as all the counts were done by only a few people, each very familiar with the area. Furthermore, the errors will be random and hence not influence the trends observed (Lambeck *et al.*, 1989). Observed changes are therefore expected to be caused by other factors. Furthermore some observed trends could be checked by observations at low tide. The decrease in e.g., Spotted Redshank was also apparent from the counts of permanent plots on the mudflat indicating that the decline in numbers was not due to counting errors at high water.

Environmental changes

The construction of the storm surge barrier and the secondary dams caused profound changes in the hydrodynamics of the estuary. Tidal volume and current velocities decreased significantly (Vroon, 1993). This caused some geomorphological changes in the estuary. In general there was an important erosion of the intertidal area (Mulder & Louters, 1993). Between 1985 and 1989 the average height of 3 large intertidal areas (Roggenplaat, Galgeplaat and Krabbekreek) decreased with 7, 28 and 11 cm respectively, a trend that is believed to continue (Mulder & Louters, 1993). Within several of the plots in our study area, erosion was also apparent in the last years. In the whole Oosterschelde there was also a trend of decreasing silt content of the intertidal sediments (ten Brinke *et al.*, 1993), a trend that was also seen in our permanent plots. The silt content of the sediment is, on average, rather low. The changed hydrodynamics affected also the water quality. Salinity increased, nutrient loads and turbidity decreased (Bakker & Vink, 1993; Wetsteijn & Kroonkamp, 1993). All these parameters have however no direct impact on wader populations, but can indirectly influence their distribution.

For birds feeding in the intertidal zone, the major environmental change in the Oosterschelde estuary was the loss of intertidal habitat due 1) to the closure of the Krammer-Volkerak and Markiezaat - Zoommeer (5800 ha) and

2) to the reduction in tidal amplitude and the erosion of the remaining tidal flats (630 ha)(Mulder and Louters, 1993). On the Slikken van Vianen the intertidal area decreased by some 25%, somewhat less than the Oosterschelde as a whole. Next to the loss of feeding grounds the reduction of the tidal amplitude from 3.7 to 3.25 m (Vroon, 1993) changed the available feeding time. There is an increased exposure time above mean tidal level and a decreased exposure time below mean tidal level (Meire & Kuijken, 1984b). The combination of erosion and reduced exposure time below mean tidal level will reduce the availability of the intertidal area for birds (Mulder & Louters, 1993; Meire *et al.*, 1993a).

Biotic changes

The macrozoobenthos populations did not yet show any clear change (Meire *et al.*, 1993b; Seys *et al.*, 1993) although the mudsnail (*Hydrobia ulvae*) decreased dramatically in the Oosterschelde (Coosen *et al.*, 1993a) and cockles had no successful recruitment in recent years (1987-1990) (Coosen *et al.*, 1993b). Long-term changes in wader numbers at the Slikken van Vianen are therefore probably not caused by changes in macrozoobenthos. Between year variation could however be caused by differences in benthic biomass.

If all birds feeding previously in the Krammer Volkerak and Markiezaat area are accounted for in the "new Oosterschelde" total bird numbers should remain constant but densities at the low water feeding areas would have increased up to 50% (Meire & Kuijken, 1987). For the whole Oosterschelde total wader numbers in midwinter decreased with more than 50.000 individuals and densities decreased from 16.8 to 15.8 birds/ha (Schekkerman *et al.*, 1993). Bird-days decreased significantly for Avocet, Kentish Plover, Grey Plover, Dunlin and Redshank. Winter, autumn and spring numbers of most species decreased significantly, only Spotted Redshank numbers in spring increased significantly (Schekkerman *et al.*, 1993). On the Slikken van Vianen only for Bar-tailed Godwit a significant increase in bird-days and maximum numbers was found, decreases were found in four species (Kentish Plover, Dunlin, Curlew and Redshank). With the exception of the Spotted Redshank there is a good agreement between the changes on the Slikken van Vianen and the Oosterschelde as a whole.

These changes in bird numbers could be the result of the overall population changes of the species. Therefore the results for the Oosterschelde and the Slikken van Vianen are compared with trends found in other areas (Table 4). The overall populations of four species increased: Oystercatcher, Ringed Plover, Grey Plover and Bar-tailed Godwit. In contrast to these overall population trends, Oystercatcher and Bar-tailed Godwit numbers remained stable in the Oosterschelde, Grey Plovers decreased and Ringed Plovers followed the overall increase, although not significant.

Table 4. Comparison of changes in wader populations on the Slikken van Vianen (this study), the Oosterschelde (Schekkerman et al., 1993), the British Isles (Kirby et al., 1990) and the Western Palearctic (Smit & Piersma, 1989). For the Slikken van Vianen and the Oosterschelde the difference in bird-days (in %) between the pre- and post barrier seasons are given, for the British Isles the population index (see Kirby et al., 1990).

Population trends in wader populations				
	Slikken van Vianen	Ooster-schelde	British Isles	Western Palearctic
Oystercatcher	-5.9	-3	32	increase
Ringed plover	31.5	19	8	increase
Kentish plover	-78.0	-42		decline
Grey plover	-7.5	-16	95	increase
Knot	-17.5	-15	18	decline
Dunlin	-34.5	-31	8	decline
Bar-tailed godwit	49.6	-1	-25	increase
Curlew	-22.5	7	15	stable
Spotted redshank	-67.9	15		?
Redshank	-54.5	-25	35	decline
Greenshank	24.6	2		?
Turnstone	27.8	-13	35	stable

Within the Oosterschelde there must have been a redistribution of Bar-tailed Godwits. The increase in Vianen may have been due partly to an influx of birds from the Krammer-Volkerak. There the species occurred mainly during spring migration in early May, but during the winter season several hundreds of birds were present. From Fig. 13b and c a rather steep increase in numbers from the season 1987/88 can be seen suggesting indeed birds from the Krammer-Volkerak moved in. Lambeck *et al.* (1989) also found an influx of Bar-tailed Godwits in the Oosterschelde after the closure of the Grevelingen. Oystercatchers, of which up to 10000 were present in the Krammer-Volkerak, did not show any increase, although in autumn 1987 very high numbers were counted at a few occasions. Lambeck (1991) showed that of the birds, colour ringed in the Oosterschelde between 1984-87, 67% were still present in the Delta area in the winter of 1989/90 whereas for the birds of the Krammer-Volkerak this was only 40%, a significant difference. This indicates the birds wintering in the Krammer-Volkerak did not move in large numbers to the remaining Oosterschelde.

The overall population of four species declined: Kentish Plover, Dunlin, Knot and Redshank. All these species showed also a decrease in both our study area as well as in the whole Oosterschelde. Turnstone and Curlew populations are stable, but population trends on the Slikken van Vianen are contrary to those of the Oosterschelde.

This information can lead us to the conclusion that all waders previously occurring in the Slikken van Vianen could not be accommodated in the remaining part of the estuary, a strong indication that the carrying capacity had been reached, at least for these species occurring in important numbers (see also Schekkerman *et al.*, 1993; Meire *et al.*, 1993a).

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REFERENCES

Bakker, C. & M. Vink, 1993. Suspended matter, nutrients and phytoplankton biomass before and after the construction of the storm surge barrier in the Oosterschelde (SW Netherlands)(1982-1990). Hydrobiologia: in press.

Coosen, J., J. Seys, P. M. Meire & J. Craeymeersch, 1993a. Effect of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde on distribution, density and biomass of some common macrobenthic species. Hydrobiologia: in press.

Coosen, J., F. Twisk, M. W. M. Van Der Tol, R. H. D. Lambeck, M. Van Stralen & P. M. Meire, 1993b. Spatfall, growth and biomass of the cockle (*Cerastoderma edule* L.) in the Oosterschelde (1980-1990). Hydrobiologia: in press.

De Jong, D. J., 1989. Wieren en weiden in de Oosterschelde. Rapport Rijkswaterstaat, Dienst Getijdenwateren Den Haag/Middelburg en Meetkundige Dienst Delft.

Evans, P. R., 1981. Reclamation of intertidal land: some effects on Shelduck and wader populations in the Tees estuary. Verh. Orn. Ges. Bayern 23: 147-168.

Evans, P. R., 1991. Introductory remarks: Habitat loss - effects on shorebird populations. Acta XX Congr. Int. Ornith.: 2197-2198.

Evans, P. R. & P. J. Dugan, 1984. Coastal birds: numbers in relation to food resources. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 8-28.

Evans, P. R., D. M. Herdson, P. J. Knights & M. W. Pienkowski, 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. Oecologia 41: 183-206.

Goss-Custard, J. D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology: Ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford: 169-157.

Goss-Custard, J. D. & S. E. A. Le V. dit Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Joyes, A., P. J. Knight, R. T. Leah & M. W. Pienkowski, 1976. The blockage of the Oued Chebeika estuary and its effects on the avifauna. Bull. Inst. Sci. 1: 39-47.

Kersten, M., K. Rappoldt & C. Smit, 1981. Over de nauwkeurigheid van wadvogeltellingen. Limosa 54: 37-46.

Kirby, J. S., R. J. Waters & R. P. Prys-Jones, 1990. Wildfowl and wader counts 1989-90. Wildfowl & Wetlands Trust, Slimbridge.

Lambeck, R. H. D., 1991. Changes in abundance, distribution and mortality of wintering Oystercatchers after habitat loss in the Delta area, SW Netherlands. Acta XX Congr. Int. Ornithol. 2208-2218.

Lambeck, R. H. D., A. J. J. Sandee & L. De Wolf, 1989. Long-term patterns in the wader usage of an intertidal flat in the Oosterschelde (SW Netherlands) and the impact of the closure of an adjacent estuary. J. appl. Ecol. 26: 419-431.

Laursen, K., I. Gram & L. J. Alberto, 1983. Short-term effect of reclamation on numbers and distribution of waterfowl at Hojer, Danish Wadden Sea. In J. Fjeldsa & H. Meltofte (eds), Proceedings of the third Nordic congress of Ornithology, Dansk Ornitologisk Forening- Zoologisk Museum, Kobenhavn: 97-118.

Leewis, R. J., H. J. M. Baptist & P. L. Meininger, 1984. The Dutch Delta Area. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal Waders and Wildfowl in winter. Cambridge University Press, Cambridge: 253-260.

Meininger, P. L. & A. M. M. Van Haperen, 1988. Vogeltellingen in het zuidelijk deltagebied in 1984/85 - 1986/87. Nota GWAO-88.1010, Rijkswaterstaat, Middelburg.

Meininger, P. L., H. J. M. Baptist & G. J. Slob, 1984. Vogeltellingen in het Deltagebied in 1975/76 - 1979/80. RWS Nota DDMI-84.23, Rijkswaterstaat, Middelburg.

Meininger, P. L., H. J. M. Baptist & G. J. Slob, 1985. Vogeltellingen in het Zuidelijk Deltagebied in 1980/81 - 1983/84. Nota DGWM 85.001, Rijkswaterstaat, Middelburg.

Meire, P. M. & E. Kuijken, 1984a. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, The Netherlands. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and Wildfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. M. & E. Kuijken. 1984b. Barrage schemes-predicting the effects of changes in tidal amplitude on wader populations. In P. R. Evans, H. Hafner & P. L'Hermite (eds), Shorebirds and large Waterbirds Conservation. Commission of the European Communities, Brussels: 79-88.

Meire, P. M. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, The Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77: 283-311.

Meire, P. M., H. Schekkerman & P. L. Meininger, 1993a. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary. Hydrobiologia: in press.

Meire, P. M., J. Seys, J. Buijs & J. Coosen, 1993b. Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm surge barrier? Hydrobiologia: in press.

Mulder J. P. M. & T. Louters, 1993. Changes in basin geomorphology after implementation of the Oosterschelde project. Hydrobiologia: in press.

Nienhuis, P. & A. C. Smaal, 1993. The Oosterschelde estuary: a case study of a changing estuary. Hydrobiologia: in press.

Rappoldt, C., M. Kertsen & C. Smit, 1985. Errors in large-scale shorebirds counts. Ardea 73: 13-24.

Saeys, H. L. F. and H. J. M. Baptist, 1977. Watervogels in de veranderende Delta van Zuidwest-Nederland. Limosa 50: 98-113.

Schekkerman, H., P. L. Meininger & P. M. Meire, 1993. Changes in the waterbird populations of the Oosterschelde, SW. Netherlands, as a result of large scale coastal engineering works. Hydrobiologia: in press.

Seys, J., P. M. Meire, J. Coosen & J. Craeymeersch, 1993. Long-term changes (1979-89) in the intertidal macrozoobenthos of the Oosterschelde estuary: are patterns in total density, biomass and diversity induced by the construction of the storm surge barrier? Hydrobiologia: in press.

Smaal, A. C. & R. Boeije, 1991. Veilig getij. Nota GWWS 91.088/ AX 91.091. Rijkswaterstaat, Middelburg.

Smaal, A. C., M. Knoester, P. H. Nienhuis & P. M. Meire, 1991. Changes in the Oosterschelde ecosystem induced by the Delta works. In M. Elliot & Ducrotoy (Eds), Estuaries and Coasts: spatial and temporal intercomparisons. Olson & Olson, Fredensborg: 375-384.

Smit, C. J. & T. Piersma, 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In H. Boyd & J.-Y. Pirot (eds), Flyways and reserve networks for water birds. IWRB spec. publication n° 9, Slimbridge: 24-63.

Sutherland, W. J. & J. D. Goss-Custard, 1991. Predicting the consequences of habitat loss on shorebird populations. Acta XX Congr. int. Ornithol.: 2199-2207.

Ten Brinke, W. B. M., J. Dronkers & J. P. M. Mulder, 1993. Fine sediments in the Oosterschelde tidal basin before and after partial closure. Hydrobiologia: in press.

Van Latesteijn, H. C. & R. H. D. Lambeck, 1986. The analysis of monitoring data with the aid of time-series analysis. Envir. Monit. Ass. 7: 287-297.

Vroon, J., 1993. Hydrodynamic characteristics of the Oosterschelde over the last decades. Hydrobiologia: in press.

Wetsteijn, L. P. & J. Kroonkamp, 1993. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (NL) before, during and after a large coastal engineering project (1980-1990). hydrobiologia: in press.

Wolff, W. J., 1967. Watervogeltellingen in het gehele Nederlandse Deltagebied. Limosa 40: 216-225.

Chapter 6

CHANGES IN THE WATERBIRD POPULATIONS OF THE OOSTERSCHELDE, SW. NETHERLANDS, AS A RESULT OF LARGE SCALE COASTAL ENGINEERING WORKS.

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ABSTRACT

Between 1982 and 1987, the construction of a storm surge barrier and two secondary dams in the eastern and northern parts of the Oosterschelde/Krammer-Volkerak area resulted in the loss of 33% of the 170 km² of intertidal area in the estuary. Consequences for non-breeding waterbirds were evaluated on the basis of monthly high-tide counts during five seasons before and three seasons after the construction period.

In the entire Oosterschelde/Krammer-Volkerak area, numbers of wintering waders decreased but those of ducks increased. Peak numbers and total number of bird-days changed little, but the seasonal pattern shifted from a midwinter maximum to a peak in autumn.

In the Oosterschelde (excluding the Krammer-Volkerak), where 17% of the tidal flats disappeared, species feeding mainly on open water remained stable or increased. Species dependent on intertidal areas for foraging (mainly waders and dabbling ducks) generally decreased. Total density of intertidal foragers decreased slightly. In most intertidal species, the Oosterschelde wintering population showed a stronger decrease, or smaller increase, than was shown during the same period by numbers in Britain and Ireland which were taken as an index of the total W-European winter populations. Changes varied considerably between species, and were correlated with their distribution within the estuary. Species concentrated in the eastern sector, where most habitat loss occurred, declined more than species with a more westerly distribution.

Results indicate that intertidal foragers forced to move from the enclosed parts of the estuary were not generally able to settle into the remaining intertidal areas. Both dispersal to adjacent areas (mainly by dabbling ducks) and mortality during severe winter weather (in some wader species) may have contributed to the declines. Populations of intertidal foragers apparently were (and consequently still are) close to carrying capacity, and further changes in capacity, as foreseen from geomorphological changes still under way in the estuary, are likely to be reflected in bird populations.

Numbers of waders moulting in the Oosterschelde in late summer declined strongly compared to numbers in other seasons. Increased disturbance due to recreational activities may have played a role during this time of the year.

INTRODUCTION

Estuarine habitats throughout the world are affected by human activities like fisheries, disturbance, pollution, manipulations of the tidal regime and reclamation (Smit *et al.*, 1987). In many cases, such activities reduce the suitability of the habitat for birds, through a decrease in the feeding area or the food stocks available, or through a reduction in potential feeding time. Besides effects on bird populations on a local scale, such events may also affect total population size, although our present knowledge of the population dynamics of most species is not yet sufficient for a quantitative evaluation (Goss-Custard, 1980, 1981, Goss-Custard & Durell, 1990, Sutherland & Goss-Custard, 1991).

An impact of loss of habitat or feeding time on local waterbird populations can only be expected if bird numbers are close to carrying capacity in the area concerned (Goss-Custard, 1977, 1985). Here, carrying capacity is defined as the density at which the addition of any further birds would result in other birds dying or leaving the area because they fail to achieve adequate intake rates as a result of increased interference and/or depletion of prey stocks (Goss-Custard, 1985, Sutherland & Goss-Custard, 1991). Whether or not this critical density is reached or approached in estuarine areas used by waterbirds has important implications for nature conservation and management.

One possible approach to this issue is to study the impact of habitat loss on bird numbers in estuarine areas. If bird numbers were close to carrying capacity before the habitat changes, one would expect *1)* that numbers decline after habitat loss, *2)* that this decline is a local event unrelated to changes in total population size, and *3)* that differing responses of individual species can be understood in view of their distribution and/or diet. So far, few case studies of estuarine habitat loss have been reported. Evans *et al.* (1979) and Evans (1981) described the impact of reclamation of part of the Tees estuary, Britain, on waders and Shelduck, showing some reductions in numbers. Laursen *et al.* (1983) documented the effects of the reclamation of 11 km² of salt marsh and tidal flats in the Danish and German Wadden Sea. A local redistribution of birds was found, but an impact on numbers on a larger scale was not clear.

This paper describes changes in numbers and species composition of non-breeding waders and other waterbirds coinciding with loss of one third of 170 km² of intertidal area in the Oosterschelde/Krammer-Volkerak, SW. Netherlands, in 1982-1987. This area is one of the major wintering haunts for estuarine birds in western Europe, in addition to being an important staging and moulting site in spring and autumn (Leewis *et al.*, 1984, Meininger & van Swelm, 1989). Lambeck *et al.* (1989) showed that numbers of some wader species on a tidal flat in the Oosterschelde increased abruptly after the closure of the nearby Grevelingen estuary in 1971, which suggested that carrying capacity had not been reached at that moment (but see discussion). Further increases in wader numbers on the estuary have occurred afterwards, and densities on the Oosterschelde in the period shortly before the engineering works were among the highest in western Europe. Were all waders using the intertidal areas lost in 1982-1987 to have moved to the remaining feeding areas in the Oosterschelde, this would have resulted in a 49% increase in overall densities. Meire & Kuijken (1984) predicted this to be unlikely.

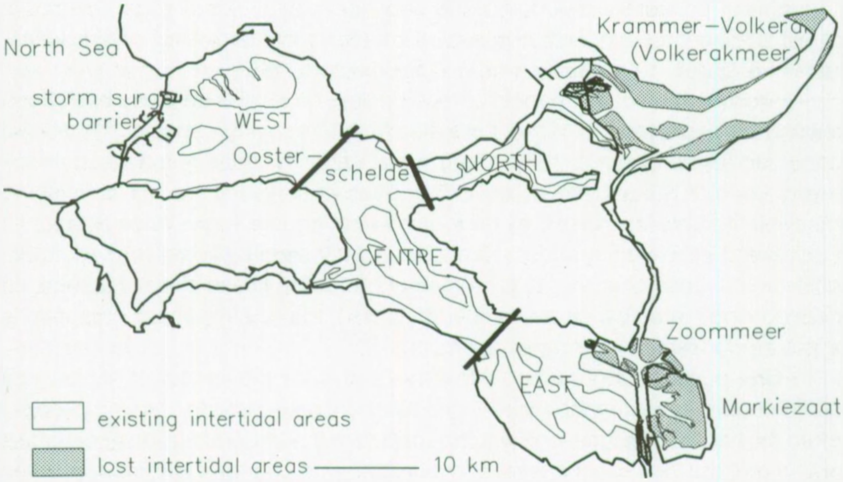

Figure 1. Map of the Oosterschelde/Krammer-Volkerak estuary showing location of coastal engineering works, lost and remaining intertidal areas and boundaries of sectors defined within the area.

METHODS

Study area

The Oosterschelde/Krammer-Volkerak was the main estuarine area in the Delta region of the SW-Netherlands, with a total area of 452 km² and 170 km² of intertidal flats prior to the coastal engineering project. Between 1982 and 1986, a storm surge barrier was built in the mouth of the estuary (Fig. 1), causing a considerable reduction of the tidal volume. In order to retain a sufficient tidal amplitude, two compartmentalization dams were completed in the eastern part in 1986-1987, reducing the volume of water accommodated within the estuary. The areas behind the dams, including 50 km² of intertidal flats (about 30% of the former intertidal area), became freshwater lakes: the present Zoommeer/Markiezaat and Volkerakmeer. In addition, 6 km² (3%) of flats was lost in the remaining estuarine part of the Oosterschelde, through a 0.45 m reduction of the tidal range.

The post-barrier intertidal area is 114 km². For a general description of the area's geomorphology and more details on the coastal engineering works see Mulder & Louters (1993), Smaal *et al.*, (1991), and Nienhuis & Smaal (1993).

Changes in total waterbird numbers and species composition are described for the whole Oosterschelde/Krammer-Volkerak area, including the present Volkerakmeer (i.e., the former Krammer-Volkerak), Zoommeer and Markiezaat. Mainly because counts from the Krammer-Volkerak are less complete than from the Oosterschelde, more detailed analyses of changes in bird numbers, bird-days and densities are made for the Oosterschelde only. The latter area excludes the Krammer-Volkerak, but includes for the pre-barrier period the (now closed) Zoommeer/Markiezaat. This apparent inconsistency was necessary because in the pre-barrier period birds feeding in the present Zoommeer/Markiezaat used the same high-tide roosts as birds feeding on adjacent tidal flats that still remain, and thus could not be separated. The coastal engineering works caused a decrease of the area of intertidal flats of 33% for the entire Oosterschelde/Krammer-Volkerak, and of 17% for the Oosterschelde proper.

Within the Oosterschelde, four sectors have been defined: west, centre, east and north (Fig. 1). The boundaries are chosen so that nearly all birds roost at sites in the same sector as their intertidal feeding areas. The area of tidal flats in each of the sectors before the engineering works was 24.5 (18% of the total), 34.8 (25%), 59.4 (44%) and 18.0 km² (13%), respectively. The effect of the engineering works was most pronounced in the eastern sector: 33% of the intertidal area was lost here, compared with 3%, 4%, and 9% in the western, central and northern sectors.

Count data

Monthly censuses of all waterbirds present in the Oosterschelde/Krammer-Volkerak were carried out by teams of professional and amateur ornithologists. Counts in tidal areas were performed during high tide, when birds concentrate on roosts. Count dates were set close to mid-month, but depended on the occurrence of high tide during daylight hours. Counts in different parts of the estuary were spread over a period of about a week around the requested counting dates, but neighbouring roosts between which bird movements were frequent were normally counted on the same day. Counts in non-tidal areas were made from boats and from the shore.

All waterbird species observed were included in the totals for the Oosterschelde/Krammer-Volkerak area. Gulls were only counted before the construction of the coastal engineering works; their numbers are assumed to have remained stable in intertidal areas in this paper. For a more detailed analysis of waterbird numbers in the Oosterschelde proper, 23 species were selected which

*Table 1. Changes in numbers of non-breeding waterbirds in the Oosterschelde. Given are mean (x) and standard deviation (sd) of yearly bird-days, and mean peak numbers in winter, spring and autumn, for the pre-barrier (1978/79-1982/83) and the post-barrier situation (1987/88-1989/90) and changes expressed as % of pre-barrier means (diff). For spring and autumn, months on which figures are based (means of maximum counts within these months) are indicated (autumn: July, August, September, October, November; spring: March, April, MaY). Additional functions: m species undergoes primary moult in Oosterschelde; s important mass gain during spring migration. Significance levels (Student's t): * p<0.10; ** p<0.05; *** p<0.01.*

	bird-days (x1000)					winter				
	1978-82		1987-89			1978-82		1987-89		
species	x	sd	x	sd	diff.	x	sd	x	sd	diff.
Great Crested Grebe	26	27	51	10	+92	90	86	170	47	+89
Cormorant	20	5	146	30	+639***	41	21	260	64	+534**
Brent Goose	1493	497	2299	490	+54*	7999	2770	10950	2383	+37
Shelduck	1001	179	709	151	-29*	7605	1990	3625	803	-52
Wigeon	2020	224	1860	291	-8	15387	4574	13517	5540	-12
Teal	213	26	120	46	-44***	1283	299	622	440	-52**
Pintail	461	164	322	74	-30	5526	1355	2897	183	-48**
Shoveler	213	58	102	43	-52*	1599	778	627	431	-61*
Goldeneye	29	11	60	30	+105	405	162	634	280	+57
Red-breasted Merganser	40	13	38	8	-3	330	158	201	61	-36
Oystercatcher	19810	726	19117	42	-3	98137	10007	75656	9891	-23**
Avocet	155	9	92	20	-41***	153	77	222	204	+45
Ringed Plover	112	20	133	40	+19	51	14	57	29	+12
Kentish Plover	64	9	37	13	-42**	0	-	0	-	-
Grey Plover	1695	98	1432	190	-16*	5875	1287	5892	1157	+0
Knot	2219	369	1895	303	-15	13426	5073	12523	1234	-7
Dunlin	9408	1349	6448	1392	-31**	53322	11652	37295	1126	-30*
Bar-tailed Godwit	1802	331	1788	206	-1	7307	1684	6647	500	-9
Curlew	2086	140	2240	280	+7	8568	1201	7262	278	-15
Spotted Redshank	105	24	121	26	+15	5	4	23	15	-
Redshank	721	102	542	72	-25**	2118	133	1492	73	-30**
Greenshank	48	20	49	8	+2	1	-	2	-	-
Turnstone	328	11	284	43	-13	1347	282	1077	169	-20

Table 1, continued

		autumn						spring				
		1978-82		1987-89				1978-82		1987-89		
species		x	sd	x	sd	diff.		x	sd	x	sd	diff.
Great Crested Grebe	SO	124	166	386	218	+211*	AY	19	17	56	30	+195*
Cormorant	ASO	224	67	1129	205	+404*	MAY	25	12	286	79	1044**
Brent Goose	ON	8143	2607	12561	4149	+54	Ys	3568	1513	5487	927	+54
Shelduck	SO	905	315	1850	1177	+104	Y	1594	245	1155	358	-28*
Wigeon	SON	16931	3741	13873	2451	-18	M	1447	335	2922	1513	+102
Teal	SON	1921	1048	930	321	-52	M	340	92	260	139	-24
Pintail	SON	2735	1158	1669	710	-39	M	505	296	323	71	-36
Shoveler	SON	2046	541	823	173	-60**	MA	393	175	243	243	-38
Goldeneye	ON	103	68	319	239	+210	M	131	125	139	90	+6
Red-breasted Merganser	ON	167	106	360	218	+116	M	229	55	167	55	-27
Oystercatcher	Am	60161	14008	76228	5890	+27	AY	18832	5037	20028	1553	+8
Avocet	Am	427	160	303	306	-29	MA	799	195	437	110	-45
Ringed Plover	ASm	1595	368	1474	753	-8	Ys	317	220	606	272	+91
Kentish Plover	JASm	828	193	598	168	-28	Y	116	68	124	67	+7
Grey Plover	Am	4879	1197	2671	1152	-45*	Ys	6517	1340	6200	775	-5
Knot	Am	5235	2773	3452	1213	-34	Y	2381	1092	2119	1882	-11
Dunlin	Am	10615	2713	4260	1868	-60**	Ys	10315	4868	14431	13639	+40
Bar-tailed Godwit	Am	7878	2718	4471	851	-38	Ys?	7818	792	6999	3323	-10
Curlew	Am	9858	1423	9925	1178	-6	MAs	5320	966	5478	286	+3
Spotted Redshank	ASm	1620	718	1341	352	-17	AYs	68	38	136	26	+100**
Redshank	JAm	3603	808	2393	304	-34*	As?	2252	1016	1203	157	-47
Greenshank	Am	579	313	473	96	-18	AY	20	16	129	102	+545
Turnstone	Am	1354	359	1235	315	-9	Ys	793	274	788	169	-1

are characteristic for estuarine habitats, and occur in the Oosterschelde in significant numbers (Table 1). These species comprise 74-80% of all waterbirds wintering on the Oosterschelde. Scientific names and acronyms for species mentioned in the text and figures are given in an appendix.

Counts during five seasons before (1978/79-1982/83; pre-barrier period) and during three seasons after the construction of the engineering works (1987/88-1989/90; post-barrier period) have been used (seasons running from July through June). Mean numbers per month were calculated for both periods. Bird-days per season were calculated by multiplying the sum of the monthly totals by 30. Three season-related functions of the estuary for waterbirds were distinguished: *1)* wintering (mean maximum in December-February), *2)* spring staging (mean maximum number during the period of spring migration; this period varies per species), and *3)* autumn moulting/staging function (for species which moult in the

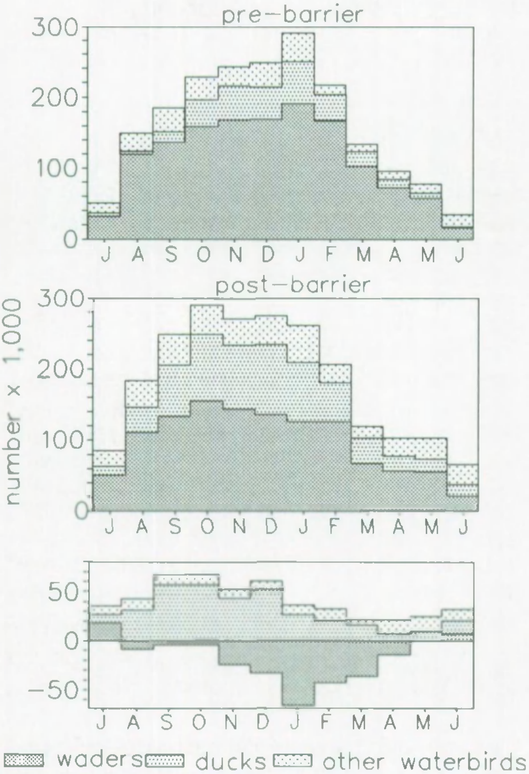

Figure 2. Monthly mean numbers of waterbirds in the Oosterschelde/Krammer-Volkerak area during pre-barrier (upper panel) and post-barrier (middle panel) periods, and changes in numbers between these periods (lower panel).

area, mean number in the month(s) in which the largest proportion of the birds present is in moult (usually August); for others the mean maximum number in the month(s) of autumn migration). Differences in means between periods were tested using Student's t statistic. In view of the large variability of bird numbers and the short study periods, a significance level of 10% has been used.

As an index of total population size to which changes in bird numbers in the Oosterschelde can be compared, population trends in Great Britain and Ireland have been used. Mean indices based on mid-winter counts (Kirby *et al.*, 1990) were calculated for the same periods as the Oosterschelde figures. Although for some species the breeding origin of the birds wintering in the British and Irish estuaries may be partly different from that of the Oosterschelde population, these estuaries are the only areas for which published data allow this approach. Together they hold 40-50% of the total number of waders wintering along the Atlantic coasts of Europe (Smit & Piersma, 1989). For some species (Great Crested Grebe, Cormorant, Kentish Plover), no British indexes were available. For the Brent Goose, the change in total population size is known from yearly counts (28% increase, Madsen *et al*., 1991), and has been used instead of the British index.

RESULTS

Bird numbers and species composition in the Oosterschelde/Krammer-Volkerak

During the pre-barrier period, a mean maximum of 292,000 waterbirds were present in the Oosterschelde/Krammer-Volkerak area in January (Fig. 2). These included 182,000 estuarine waders (65%), 57,000 ducks, geese and swans (19%), 40,000 gulls (14%) and 3,000 other waterbirds (Fig. 3). Eight wader species wintered in numbers exceeding 1,000: Oystercatcher, Grey Plover, Dunlin, Knot, Bar-tailed Godwit, Curlew, Redshank and Turnstone. Ducks and geese were dominated by Barnacle Goose, Brent Goose, Shelduck, Wigeon, Mallard, Pintail and Teal.

In the post-barrier period, mean maximum numbers of waterbirds have hardly changed (Fig. 2). However, the seasonal peak shifted from January to October. The area's significance as a wintering site decreased, but the total number of bird-days per season increased slightly. Changes in the species composition occurred, but only in the Volkerakmeer and Zoommeer/Markiezaat (Fig. 3).

The average number of waders in the entire Oosterschelde/Krammer-Volkerak area in January decreased to 125,000 (31% less), and the number of bird-days of waders decreased by 15% compared to the pre-barrier situation. During the pre-barrier period, only about 8,000 waders wintered in the Krammer-Volkerak, 5% of the total number in the Oosterschelde/Krammer-Volkerak area. Therefore, although 90% of the waders wintering in the Krammer-Volkerak disappeared after the closure of the Philipsdam, their contribution to the decrease in the total Oosterschelde/Krammer-Volkerak area was only 15%, and the majority of the waders which disappeared originated from the Oosterschelde. In spring and autumn, the importance of the Krammer-Volkerak for waders was greater, with 20% and 10% of the total numbers, respectively.

The maximum number of ducks in the Oosterschelde/Krammer-Volkerak area increased from 57,500 to 98,600, mainly in the new freshwater habitats and during autumn; the number of bird-days roughly doubled. Numbers in the Oosterschelde decreased by 21% in January, but increased during autumn. In many duck species post-barrier numbers in the Volkerakmeer and the Markiezaat/Zoommeer exceeded those in the former intertidal areas, but numbers of wintering Shelduck and Pintail were lower than before.

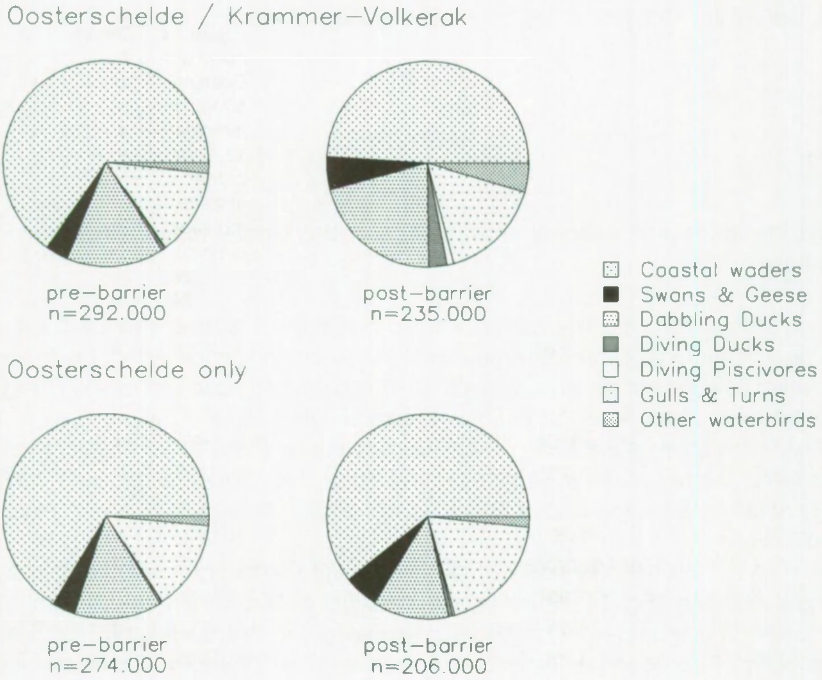

Figure 3. Species composition of waterbirds wintering in the entire Oosterschelde/Krammer-Volkerak area and in the Oosterschelde proper during pre-barrier and post-barrier periods, based on mean January numbers. Note that gulls were not counted in the post-barrier period, but were assumed to have remained stable in numbers in the intertidal areas.

Bird numbers and densities in the Oosterschelde

Table 1 summarizes changes in the use of the Oosterschelde proper (pre-barrier situation including present Zoommeer/Markiezaat) for 23 characteristic waterbird species. Significant ($p<0.1$) changes in the total annual number of bird-days have occurred in ten species: an increase in Cormorant and Brent Goose, and decreases in Shelduck, Teal, Shoveler, Avocet, Kentish Plover, Grey Plover, Dunlin, and Redshank. Non-significant (although considerable, i.e., 25% or more) changes occurred in Great Crested Grebe and Goldeneye (increase) and Pintail (decrease).

The average winter maximum of Cormorant showed a significant increase, those of Teal, Pintail, Shoveler, Oystercatcher, Dunlin and Redshank a significant

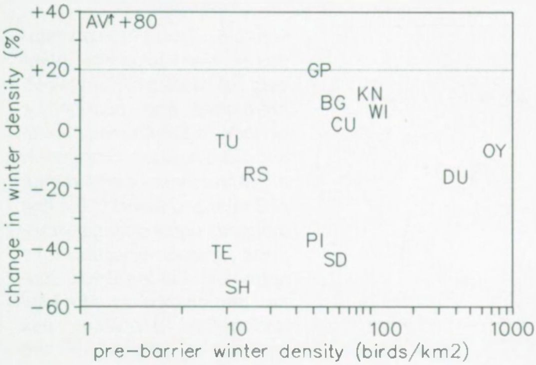

Figure 4. Changes in mean winter density in the Oosterschelde of waterbirds foraging in the intertidal areas, expressed as % deviation from pre-barrier density. The broken line marks the density increase necessary to accomodate all birds displaced from Zoommeer/Markiezaat. Acronyms identify species (see appendix for clarification).

decrease. Non-significant changes exceeding 25% occurred in Great Crested Grebe and Avocet (increase), and in Shelduck and Red-breasted Merganser (decrease).

Significant increases in autumn were found in Great-crested Grebe and Cormorant, significant decreases in Shoveler, Grey Plover, Dunlin and Redshank. A 25% or stronger decrease in average number during the wing moult period occurred in Avocet, Kentish Plover, Grey Plover, Knot, Dunlin, Bar-tailed Godwit and Redshank, although most of these changes are statistically not significant.

In spring, few significant changes were found: increases in Great Crested Grebe, Cormorant and Spotted Redshank, and a decrease in Shelduck. Notable non-significant changes (>25%) were found in Brent Goose, Wigeon, Ringed Plover, Dunlin (increase) and in Avocet (decrease).

With the exception of the Avocet, which is very scarce in winter, and the Grey Plover, none of the species foraging in intertidal areas (see appendix) showed the 20% or more increase in winter density that would be necessary to compensate for the area of intertidal flats lost (Fig. 4). In contrast, densities of several species showed a considerable decline. The total midwinter density of intertidal foragers declined by 8% from 16.2 to 14.9 birds/ha.

Changes in the Oosterschelde in relation to total population size

Figure 5 compares changes in winter numbers in the Oosterschelde with those in Britain and Ireland, taken as an indication of changes in the size of the total W-European winter population. Only four out of 17 species for which British indices were available are 'doing better' in the Oosterschelde, while 13 species are 'doing worse'. When the changes for each species in the Oosterschelde and in Britain and Ireland are used as paired observations in a Wilcoxon matched-pairs signed-ranks test, the Oosterschelde wader population appears to have fared

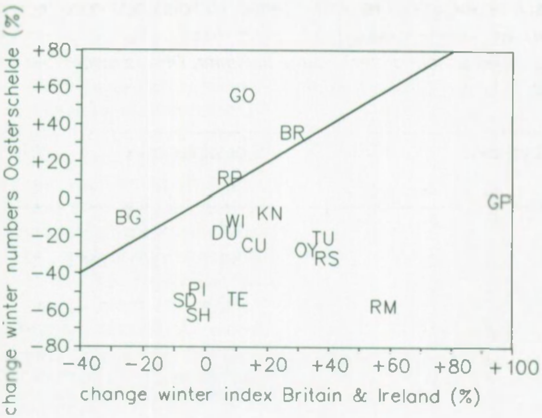

Figure 5. Comparison of changes in mean midwinter numbers of waterbirds between pre-barrier and post-barrier periods in the Oosterschelde and simultaneous changes in midwinter index of abundance in Britain and Ireland. The line indicates equal change. Acronyms identify species (see appendix). For the Brent Goose, the change in the total dark-bellied population has been used instead of the British index.

significantly worse than the British and Irish one (T=22, N=17, p<0.01). The difference is especially apparent in intertidally foraging species: out of eleven strictly intertidal foragers wintering in the Oosterschelde in numbers exceeding 2,000, only the Bar-tailed Godwit showed a more favourable trend in the Oosterschelde than in the British Isles (T=2, N=11, p<0.01).

The increase in the Oosterschelde of Great Crested Grebe and Cormorant, for which no British indexes were available for comparison, coincided with an increase in the W-European winter populations. No recent population estimates are available for the Great Crested Grebe, though it is unlikely that the total population doubled as it did in the Oosterschelde. The European breeding population of Cormorant increased by c. 300% between 1980 and 1988 (Osieck, 1991), whereas Oosterschelde numbers increased by 600%.

Population changes in relation to distribution

The population development of species foraging in the intertidal zone showed considerable variation, ranging from a 52% decline to a +19% increase in bird-days (Table 1). This variation appeared to be related to differences in within-estuary distribution. Sediment composition and macrobenthos vary locally and, modified by preferences for certain substrates or prey types, are reflected in the distribution of the bird species. Consequently, the loss of intertidal areas, which occurred mainly in the easternmost part, did not affect all species to the same extent. Species preferring soft mudflats bordering saltmarshes, which are found mainly in the northern and eastern sectors (e.g., Shelduck, Pintail, Shoveler, Redshank), suffered a considerably larger loss of feeding area than species feeding in the more sandy areas in the western and central parts of the estuary (e.g., Bar-tailed Godwit).

Table 2. Distribution (% of total in each sector) in the pre-barrier period, and distribution-corrected habitat loss (DHL) of some intertidal bird species in the Oosterschelde, based on yearly bird-days and midwinter maxima. For some species absent or very scarce in winter, DHL is calculated on the basis of bird-days only. W west, C centre, E east, N north.

Species	% of bird-days				DHL	% of winter max.				DHL
	W	C	E	N	(%)	W	C	E	N	(%)
Shelduck	10	13	52	25	20	4	13	58	24	22
Wigeon	19	25	32	24	14	23	19	31	26	14
Teal	23	19	26	32	13	27	19	24	30	12
Pintail	2	2	81	15	28	2	3	79	16	28
Shoveler	13	5	68	14	24	13	5	73	9	25
Oystercatcher	25	30	26	18	12	25	31	28	16	13
Avocet	37	8	21	34	11					
Ringed Plover	8	29	28	36	14					
Kentish Plover	21	40	6	34	7					
Grey Plover	18	28	37	16	15	11	31	43	14	17
Knot	32	24	26	18	12	21	22	38	19	16
Dunlin	12	26	47	15	18	11	31	47	10	18
Bar-tailed Godwit	36	28	11	25	8	32	31	8	29	7
Curlew	20	19	44	16	17	18	22	44	16	17
Spotted Redshank	23	33	14	30	9					
Redshank	14	22	46	17	18	12	31	41	16	17
Greenshank	6	25	44	25	18					
Turnstone	22	36	19	22	10	13	35	29	23	13

To evaluate this effect, 'distribution-corrected habitat loss' (DHL) was calculated and compared to changes in population size. For each species, the percentage of the pre-barrier total occurring in each sector of the Oosterschelde was multiplied by the percentage of intertidal area lost in that section. The sum of these terms for the four sections constitutes DHL (Table 2). Thus, a large DHL was calculated for a species mainly occurring in the eastern part of the Oosterschelde, and a small one for species occurring only in small numbers here.

In eleven species of which on average more than 2,000 individuals fed in the intertidal areas of the Oosterschelde during pre-barrier winters, there is a significant relation between DHL and changes in wintering numbers (Fig. 6A). In these eleven species, DHL accounts for 45% of the total variance in the changes (linear regression, $F=8.51$, $p=0.02$). By combining DHL and population changes in the British Isles in a multiple regression analysis, the proportion of variance explained increased to 64% for these species ($F=8.89$, $p=0.01$; % change Oosterschelde = 1.67*(DHL) + 0.28*(% change British index) - 2.55). The

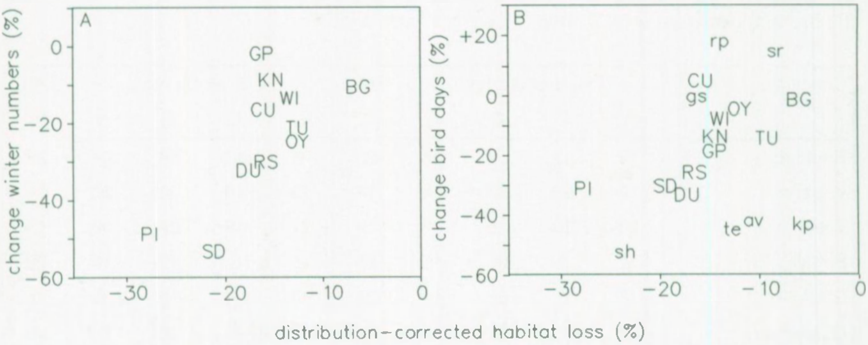

Figure 6. Relationship between distribution-corrected habitat loss (see text) and changes in abundance of waterbirds feeding in the intertidal zone, based on (A) midwinter numbers and (B) total annual bird-days. In A, only species wintering with more than 2,000 individuals are shown; in B these species only are indicated in capitals. Acronyms identify species (see appendix).

relationship also exists when the calculation is based on bird-days. However, species which are common in the Oosterschelde only in autumn and spring (Avocet, Ringed Plover, Kentish Plover, Greenshank and Spotted Redshank), or winter in numbers under 2,000 (Teal, Shoveler), tend to deviate from it (Fig. 6B).

DISCUSSION

General considerations

Waterbird numbers are affected by many factors. There is a considerable variation in numbers between years, partly as a result of wide fluctuations in breeding productivity. In addition, some degree of inaccuracy is inherent to large scale waterbird counts (Rappoldt *et al.*, 1984). Standard deviations are therefore in most cases considerable (Table 1). Differences between means, tested using Student's t, were significant in only relatively few cases, even when using a significance level of 10%. This is partly due to the rather short study periods: five (pre-barrier) and three years (post-barrier). However, environmental planners, management institutions and politicians generally cannot wait for an evaluation of projects such as the Oosterschelde works as long as would be desirable from a statistical point of view.

The pre-barrier period of five seasons included two cold (1978/79 and 1981/82) and three mild winters; the post-barrier period included three successive mild winters. The weather conditions may have affected the numbers of some species which are sensitive to severe winter weather (Meininger *et al*., 1991). The relatively high winter numbers of Avocet and Ringed Plover during the post-barrier period might be explained in this way. However, the weather effect is unlikely to have affected the general patterns observed in this study.

Notwithstanding these additional sources of variation, important changes in waterbird numbers have become apparent in the Oosterschelde. In general, species feeding in open water have increased, while the area became less important for intertidal foragers. Because the latter group is numerically most important, total bird numbers in the estuary declined.

Numbers of migratory birds are not only influenced by circumstances within the study area, but also by factors operating elsewhere. The main external factor to be considered is a change in overall size of the populations using W-European wetlands. A change in total population size may affect bird numbers in a particular area, even when local conditions remain unaltered (e.g., Moser, 1988). However, the comparison of changes in waterbird numbers in the Oosterschelde with those in Britain and Ireland indicated that changes in the Oosterschelde in most species did not merely reflect large scale population trends.

Pelagic foragers: population growth and water transparency

Out of the four species which do not feed in intertidal areas but in open water, Great Crested Grebe, Cormorant and Goldeneye increased in the Oosterschelde, while the Red-breasted Merganser showed a non-significant decrease in winter, but remained stable in bird-days due to a concomitant increase in autumn. Three of these species are piscivorous and locate their prey visually; only the Goldeneye mainly feeds on benthic and epibenthic invertebrates. For the increased species, the total W-European population is also growing, but the rate of increase in the Oosterschelde seems to be higher. It is possible that the increased water transparency within the estuary (Bakker & Vink, 1993, Wetsteijn & Kromkamp, 1993) is an additional explanation for the increase. Mean winter (minimum) water transparency in the eastern sector, measured using a Secchi disc, increased from approximately 0.8 m in 1980-85 to 2.5 m in 1987-90, causing a 30-fold increase in the volume of water in which prey can be detected by pursuit-diving predators (Eriksson, 1985). The water transparency in the eastern sector now approaches that in the nearby brackish-saline lakes Grevelingen and Veerse Meer, which are characterized by an abundance of piscivores (Doornbos, 1984; Meire *et al*., 1989).

Intertidal foragers: carrying capacity of tidal flats

The majority of intertidally foraging species showed a decrease in winter numbers and/or bird-days, which was significant ($p < 0.1$) in Shelduck, Pintail, Teal, Shoveler, Oystercatcher, Avocet, Kentish Plover, Grey Plover, Dunlin, and Redshank. A significant increase was found only in the Brent Goose, which is not strictly intertidal but takes a considerable proportion of its food from agricultural areas. In waders, increasing trends were in no case significant and occurred only in species which occur mainly in spring and autumn and are very scarce in winter (Avocet, Ringed Plover, Spotted Redshank, and Greenshank). For the decreasing species, there are no indications that a similar decline occurred in the total western European populations, except for the Kentish Plover (Jönsson *et al.*, 1990). In addition, several species showed an increase in the British Isles, but not at all, or hardly so, in the Oosterschelde.

The fact that most strictly intertidal species decreased after the loss of 17% of the feeding area means that this loss was not compensated by higher bird densities in the remaining part of the Oosterschelde. In fact, overall densities of several species were lower in the post-barrier period than before. In the same way, birds displaced from feeding areas in the adjacent Krammer-Volkerak were unable to settle into the Oosterschelde. The observation that species mainly occurring in the eastern part of the estuary were more affected than others suggests that it was indeed the loss of feeding habitat which caused the decline.

Additional evidence that displaced birds were not generally able to settle into the remaining intertidal areas is presented by Lambeck (1991). Of Oystercatchers colour-marked in the Krammer-Volkerak in 1984-87, only 40% were still present in the Oosterschelde and the nearby Westerschelde in the winter of 1989/90, while this figure was significantly higher (67%) for birds marked in other sectors of the Oosterschelde.

These observations suggest that numbers of the most abundant intertidal foragers were at least close to carrying capacity in the period before the coastal engineering works. Goss-Custard (1985) has pointed out that bird numbers can be said to be strictly at capacity only when every new individual entering the estuary (or every loss of habitat equivalent to one bird's means of living) causes the emigration or death of another bird. Demonstrating that this condition is met is practically impossible in case studies like that described here. It would require an assessment of the proportion of suitable habitat that is lost for each species much more precise than our estimate of DHL. However, reaching carrying capacity should not be considered as an abrupt process, but as the result of a gradually increasing pressure on individuals to look out for alternative settling options. Even before carrying capacity *sensu stricto* is reached, there is a trajectory of bird densities at which adding more birds, or removing part of the habitat, causes *some* birds to emigrate or die. In such cases habitat loss will reduce the number of birds, and the question as to whether or not bird numbers are strictly at capacity becomes academic from a conservation point of view.

Table 3. Numbers and age composition of frost victims found in the total Delta area and in the Oosterschelde after cold spells in the winters of 1985-87, compared to the decrease in mean winter maxima in the Oosterschelde between pre- and post-barrier periods. Data on frost victims from Meininger et al. (1991), Lambeck (1991), and P.L. Meininger (unpubl.).

species	no of victims found		% adults among victims	decrease of winter numbers Oosterschelde	
	Total Delta (A)	Oosterschelde (A)		(B)	A/B (%)
Shelduck	1114	538	-	3980	14-28
Wigeon	53	28	-	1870	1-3
Teal	16	10	-	661	2
Pintail	190	97	-	2629	4-7
Oystercatcher	9811	6500	57%	22481	29-44
Grey Plover	643	424	55%	-17	-
Knot	237	176	67%	903	19-26
Dunlin	604	280	59%	16027	2-4
Bar-tailed Godwit	39	26	57%	660	4-6
Curlew	451	252	71%	1306	19-34
Redshank	792	437	60%	626	70-100
Turnstone	230	169	55%	270	63-85

Possible mechanisms of population decline

The level of pressure at which the local system starts to overflow when carrying capacity is approached and birds start leaving the area is likely to be influenced, in addition to factors affecting feeding efficiency within the estuary, by the presence or absence of alternative areas nearby where additional birds can still be accommodated. In the Oosterschelde, former intertidal feeding areas behind the compartmentalization dams were replaced by freshwater lakes. Extensive shallow areas in these lakes and the development of a saltmarsh-like vegetation on the permanently exposed former tidal flats offered good feeding opportunities for several species of dabbling ducks. This development may help explain why these species showed such drastic declines compared with most waders, and with the area of tidal flats lost. Judging from numbers wintering in the Volkerakmeer and Zoommeer/Markiezaat in the post-barrier period, these lakes may have accommodated the majority of Wigeon, Teal and Shoveler displaced from the lost intertidal areas, but only about half of Pintail and less than 10% of Shelduck.

As an alternative to dispersal, the decrease in bird numbers may have been brought about by mortality. In normal winters, only few dead birds are found in the Oosterschelde area (Meininger, unpubl.). However, during three successive cold winters in 1985-87, a total of 12,900 starved waders and 2,400 dead ducks were found during searches in the whole Delta area (Meininger *et al.*, 1991). Although not all of these belonged to the Oosterschelde population, ringing recoveries suggest that the majority did. Although a large proportion of the frost victims were first-year birds which are likely to have had a lower survival than adults anyway, the numbers of Redshank, Turnstone and Oystercatcher found even within the boundaries of the Oosterschelde were substantial compared with the decrease in wintering numbers (Table 3). For these species, mortality during these severe winters, possibly aggravated by manipulations of the tidal regime during the construction of the coastal engineering works (Lambeck, 1991; Meininger *et al.*, 1991), may have been an important mechanism in (though not a cause of) the decrease. For the other species, this type of mortality was probably unimportant.

A historical comparison

An interesting comparison can be made between the events described here and those following the closure in 1971 of the Grevelingen estuary, 15 km north of the Oosterschelde, which held about 50,000 wintering waders (Wolff, 1967). A sudden increase in the numbers of Oystercatcher and Bar-tailed Godwit using the Roggenplaat, a tidal flat in the western sector of the Oosterschelde, was shown to coincide with this (Van Latesteijn & Lambeck, 1986; Lambeck *et al.*, 1989). Wader numbers in the adjacent Krammer-Volkerak increased substantially, while total numbers in the Delta region as a whole did not clearly decrease (Leewis *et al.*, 1984). Apparently, waders displaced from the Grevelingen feeding areas could be accommodated elsewhere in the Delta. However, it would not be entirely safe to conclude that carrying capacity was not reached in the Oosterschelde/Krammer-Volkerak estuary before that time, since the closure of the Grevelingen brought about important changes. Benthic food stocks and feeding opportunities in the Krammer-Volkerak and part of the Oosterschelde are likely to have increased as a result of the higher salinity and larger tidal amplitude following the closure of the Volkerakdam in 1969. Wolff (1971) showed that diversity of macrobenthos in the Krammer-Volkerak increased substantially. At the same time, mussel cultures became established. A further increase was noted in several waterbird species in the Oosterschelde during the 1970s. However, already during this period some indications were found that bird numbers might be approaching an upper limit, as the seasonal pattern of several species on the Roggenplaat showed a shift from winter towards autumn (Lambeck *et al.*, 1989). This phenomenon was later reflected by numbers of Oystercatchers in the entire estuary (Lambeck, 1991).

Factors determining bird numbers in the estuary

Changes in carrying capacity for intertidal waterbirds in the Oosterschelde estuary could be caused by changes in three local factors, acting singly or in combination: the total surface of intertidal feeding area, the biomass per unit area of available macrobenthos, and the exposure time of tidal flats which limits potential feeding time for birds. Of these, the amount of feeding area has been affected most strongly by the coastal engineering works, and this has reduced both the total amount of food available to birds and the space available for their foraging behaviour.

The importance of benthic biomass and depletion of prey stocks in determining carrying capacity in the Oosterschelde is explored elsewhere in this volume (Meire *et al.*, 1993). The total intertidal macrobenthic biomass per unit area (excluding the strongly fluctuating cockle *Cerastoderma edule* and mussel *Mytilus edulis)* has not changed significantly since 1985 (Seys *et al.*, 1993). For some specialized foragers however, food availability may have changed. For instance, an important decrease in the mudsnail *Hydrobia ulvae* was noted in the central and eastern sectors of the Oosterschelde (Coosen *et al.*, 1993), and may have affected feeding conditions for species like Shelduck (Meininger & Snoek, 1992). Low biomasses of cockles and mussels during the past few years, partly caused by intensive cockle fisheries, are likely to have caused difficulties for Oystercatchers (Lambeck, 1991). The numerical relationship between Oystercatcher feeding densities and that of their main bivalve prey has not changed (Meire, 1991).

The coastal engineering works have affected potential feeding time of intertidal foragers within the remaining part of the Oosterschelde. Changed hydrodynamic conditions (Vroon, 1993) have caused a net transport of sediments from the tidal flats into the gullies (Mulder & Louters, 1993). As a result, an increasing proportion of the intertidal area is situated in the lower reaches of the tidal range, and thus exposed for shorter periods during low tides. This process is aggravated to some extent by a decrease in the tidal amplitude from 3.70 to 3.25 m, which causes intertidal areas above mid-tide level to be exposed for longer, but areas below mid-tide level for shorter periods than before. The result is a decrease of feeding potential (integration of area and time of exposure) of 15-30% on some flats in the western and central sectors between 1984 and 1989. Loss of feeding potential due to this process has been much smaller in the northern and eastern sectors.

It is not clear at present whether, and to what extent, reduced exposure time has affected bird numbers in the Oosterschelde. However, it may have contributed to the inability of the remaining area to accommodate birds displaced from lost feeding areas behind the compartmentalization dams, and of the slightly lower feeding densities in the 'new' estuary. As the morphological changes in the estuary are expected to continue during the next few decades, and to eventually

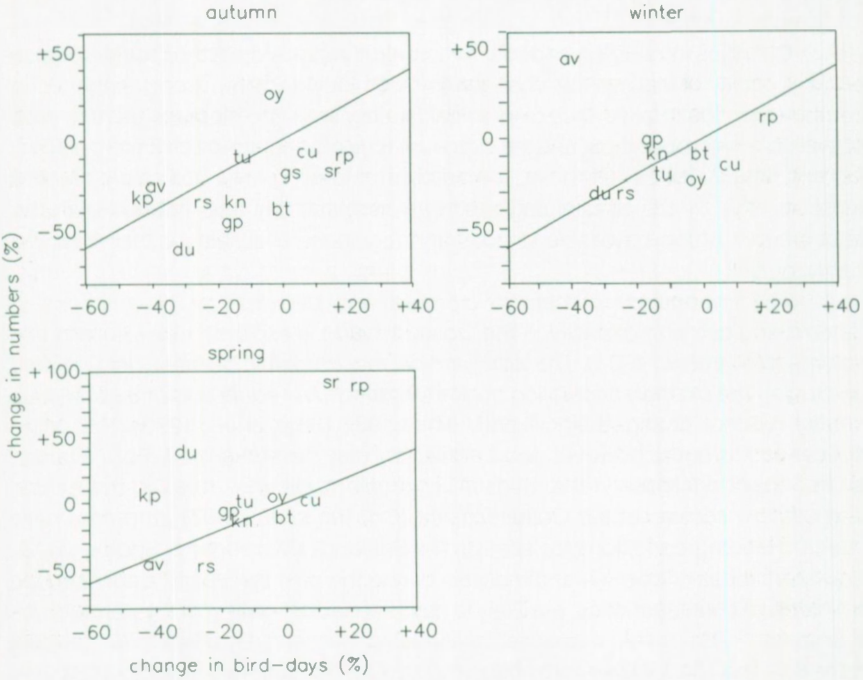

Figure 7. Comparison of changes in season-related functions of the Oosterschelde for waterbirds and changes in the total use of the area (annual number of bird-days). Lines indicate equal change. Acronyms identify species (see appendix).

result in the loss of a further 15% of the intertidal area (Mulder & Louters, 1993), a further decline in intertidal waterbird numbers can be expected.

Decrease in numbers of moulting waders

When the changes in wader numbers are evaluated separately for the three seasons distinguished (autumn, winter, spring), the decrease in numbers wintering is in proportion to the decrease in bird-days (Fig. 7). Changes in numbers during spring are, for some species, much smaller. In contrast, a comparatively strong decline is seen in late summer. This suggests that the Oosterschelde lost part of its significance as a moulting area for waders.

It seems unlikely that a decrease in feeding habitat or food stocks would have a stronger impact on bird numbers in late summer than in winter. Total numbers and energy demand of the birds are relatively low, while the potential daily energy intake is likely to be higher than in winter as a result of higher macrobenthic biomass and production, longer daylight feeding time and higher surface activity of macrobenthic organisms (e.g., Evans, 1976). Since the regulation of bird densities in intertidal areas is likely to act through the possibility of maintaining a balanced energy budget over a period of days or months (Evans, 1976; Goss-Custard, 1985), these factors would be expected to result in a higher carrying capacity of the mudflats in spring and summer than in winter. This presumption is consistent with the observation that the number of Oystercatchers in the Oosterschelde increased during summer and early autumn, while wintering numbers have decreased markedly.

Another indication that factors other than habitat loss have caused the disproportionate decline of moulting waders is the fact that Dunlin and Knot, among the more heavily affected species in late summer, at this time of the year hardly use the eastern sector where most habitat loss occurred (5 and 0% of the total in east). In addition, extensive sampling of macrobenthos in August 1985 and 1989 showed no important changes in benthic biomass in the main moulting area, apart from cockles and mussels (Seys *et al.*, 1993).

The peak of recreational activities in the Oosterschelde (July-August) overlaps with the most important moulting period. Recreation in the Oosterschelde, especially boating and wind-surfing, increased considerably during the past years. For instance, the number of harbour sites for boats increased from 1,200 to 2,100 between 1982 and 1989. In addition, the coastal engineering works made several formerly isolated mudflats easily accessible to people. It is not unlikely that increased disturbance has contributed to the decrease of moulting waders in the Oosterschelde.

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REFERENCES

Bakker, C. & M. Vink, 1993. Suspended matter, nutrients and phytoplankton biomass before and after the construction of the storm surge barrier in the Oosterschelde (SW. Netherlands) (1982-1990). Hydrobiologia: in press.

Coosen, J., J. Seys, P. M. Meire & J. Craeymeersch, 1993. Effect of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde on distribution, density and biomass of some common macrobenthic species. Hydrobiologia: in press.

Doornbos, G., 1984. Piscivorous birds on the saline Lake Grevelingen, The Netherlands: abundance, prey selection and annual food consumption. Neth. J. Sea Res. 18: 457-479.

Evans, P. R., 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. Ardea 64: 117-139.

Evans, P. R., 1981. Reclamation of tidal land: some effects on Shelduck and wader populations in the Tees estuary. Verh. Orn. Ges. Bayern 23: 147-168.

Evans, P. R., D. M. Herdson, P. J. Knights & M. W. Pienkowski, 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. Oecologia 41: 183-206.

Goss-Custard, J. D., 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding ground on wading birds (Charadrii). J. appl. Ecol. 14: 721-739.

Goss-Custard, J. D., 1980. Competition for food and interference amongst waders. Ardea 68: 31-52.

Goss-Custard, J. D., 1981. Role of winter food supplies in the population ecology of common British wading birds. Verh. Orn. Ges. Bayern: 125-146.

Goss-Custard, J. D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (eds), Behavioural ecology - ecological consequences of adaptive behaviour. Blackwell scientific publications, Oxford: 169-188.

Goss-Custard, J. D. & S. E. A. le V.Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Eriksson, M. O. G., 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. Ornis Scand. 16: 1-7.

Jönsson, P. E., P. L. Meininger, R. Schultz & T. Székely, 1990. The WSG Kentish Plover Project. Wader Study Group Bull. 60: 1-3.

Kirby, J. S., R. J. Waters & R. P. Prys-Jones, 1990. Wildfowl and wader counts 1989-90. Wildfowl & Wetlands Trust, Slimbridge.

Lambeck, R. H. D., 1991. Changes in abundance, distribution and mortality of wintering Oystercatchers after habitat loss in the Delta area, SW Netherlands. Acta XX Congr. Int. Ornithol.: 2208-2218.

Lambeck, R. H. D., A. J. J. Sandee & L. de Wolf, 1989. Long-term patterns in the wader usage of an intertidal flat in the Oosterschelde (SW Netherlands) and the impact of the closure of an adjacent estuary. J. appl. Ecol. 26: 419-431.

Laursen, K., I. Gram & L. J. Alberto, 1983. Short-term effect of reclamation on numbers and distribution of waterfowl at Højer, Danish Wadden Sea. Proc. 3rd Nordic Congr. Ornithol. 1981: 97-118.

Leewis, R. J., H. J. M. Baptist & P. L. Meininger, 1984. The Dutch Delta. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 253-260.

Madsen, J., A. St.Joseph & M. O'Brian, 1991. The status of Brent Goose Branta bernicla 1986-89. IWRB Goose Res. Group Bull. 1: 4-7.

Meininger, P. L. & H. Snoek, 1992. Non-breeding Shelduck *Tadorna tadorna* in the SW-Netherlands: effects of habitat changes on distribution, numbers, moulting sites and food. Wildfowl 43: 139-151.

Meininger, P. L. & N. D. Van Swelm, 1989. Biometrisch en ringonderzoek aan steltlopers in de Oosterschelde in het voorjaar van 1984 en 1985. Rijkswaterstaat Dienst Getijdewateren Nota GWAO-89.1009, Middelburg/Oostvoorne.

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., 1991. Effects of a substantial reduction in intertidal area on numbers and densities of waders. Acta XX Congr. Int. Orn.: 2219-2227.

Meire, P. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, The Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77: 283-311.

Meire, P. M., H. Schekkerman & P. L. Meininger, 1993. Consumption by waterbirds in the Oosterschelde estuary, SW. Netherlands, in relation to carrying capacity and the benthic invertebrate community. Hydrobiologia: in press.

Meire, P. M., J. Seys, T. Ysebaert, P. L. Meininger & H. J. M. Baptist, 1989. A changing Delta: effects of large coastal engineering works on feeding ecological relationships as illustrated by waterbirds. In J.C. Hooghart & C.W.S. Posthumus (eds), Hydro-ecological relations in the Delta waters of the South-West Netherlands. TNO/CHO, The Hague: 109-145.

Moser, M. E., 1988. Limits to the numbers of Grey Plovers Pluvialis squatarola wintering on British estuaries: an analysis of long-term population trends. J. appl. Ecol. 25: 473-485.

Mulder, J. P. M. & T. Louters, 1993. Changes in basin geomorphology after implementation of the Oosterschelde project. Hydrobiologia: in press.

Nienhuis, P. H. & A. C. Smaal, 1993. The Oosterschelde estuary: a case study of a changing ecosystem: an introduction. Hydrobiologia: in press.

Osieck, E. R., 1991. Cormorant & man: a conservation view. In M. R. Van Eerden & M. Zijlstra (eds), Proceedings workshop 1989 on Cormorants Phalacrocorax carbo. Rijkswaterstaat Directie Flevoland, Lelystad: 244-247.

Rappoldt, C., M. Kersten & C. Smit, 1984. Errors in large scale shorebird counts. Ardea 73: 13-24.

Seys, J. J., P. M. Meire, J. Coosen & J. Craeymeersch, 1993. Long-term changes in the intertidal macrozoobenthos of the Oosterschelde: are patterns in total density, biomass and diversity induced by the construction of the storm-surge barrier?. Hydrobiologia: in press.

Smaal, A. C., M. Knoester, P. H. Nienhuis & P. M. Meire, 1991. Changes in the Oosterschelde ecosystem induced by the Delta works. In M. Elliott & J.-P. Ducrotoy (eds), Estuaries and coasts: spatial and temporal intercomparisons. ECSA 19 Symposium, Olsen & Olsen, Fredensborg: 375-384.

Smit, C. J. & T. Piersma, 1989. Numbers, midwinter distribution and migration of wader populations using the East-Atlantic Flyway. In H. Boyd & J-Y. Pirot (eds), Flyways and reserve networks for water birds. IWRB Spec. Publ. No. 9, Slimbridge: 24-63.

Smit, C. J., R. H. D. Lambeck & W. J. Wolff, 1987. Threats to coastal wintering and staging areas of waders. In N. C. Davidson & M. W. Pienkowski (eds), The conservation of international flyway populations of waders. Wader Study Group Bull. 49, Suppl.: 105-113.

Sutherland, W. J. & J. D. Goss-Custard, 1991. Predicting the consequences of habitat loss on shorebird populations. Acta XX Congr. Int. Ornithol.: 2199-2207.

Van Latesteijn, H. C., & R. H. D. Lambeck, 1986. The analysis of monitoring data with the aid of time-series analysis. Envir. Monit. Ass. 7: 287-297.

Vroon, J., 1993. Hydrodynamic characteristics of the Oosterschelde over the last decades. Hydrobiologia: in press.

Wetsteijn, L. P. J. M. & J. Kromkamp, 1993. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (NL) before, during and after a large-scale coastal engineering project (1980-1990). Hydrobiologia: in press.

Wolff, W. J., 1967. Watervogeltellingen in het gehele Nederlandse Deltagebied. Limosa 40: 216-225.

Wolff, W. J., 1971. Changes in intertidal benthos communities after an increase in salinity. Thalassia Jugoslavica 7: 429-434.

APPENDIX

Acronyms and scientific names of bird species mentioned in text and figures. Species considered dependent on the intertidal flats for food are marked with an asterisk (*).

-	Great Crested Grebe	*Podiceps cristatus*
-	Cormorant	*Phalacrocorax carbo*
-	Barnacle Goose	*Branta leucopsis*
br	Brent Goose	*Branta bernicla*
sd	*Shelduck	*Tadorna tadorna*
wi	*Wigeon	*Anas penelope*
-	Mallard	*Anas platyrhynchos*
te	*Teal	*Anas crecca*
pi	*Pintail	*Anas acuta*
sh	*Shoveler	*Anas clypeata*
go	Goldeneye	*Bucephala clangula*
rm	Red-breasted Merganser	*Mergus serrator*
oy	*Oystercatcher	*Haematopus ostralegus*
av	*Avocet	*Recurvirostra avosetta*
rp	*Ringed Plover	*Charadrius hiaticula*
sp	*Kentish Plover	*Charadrius alexandrinus*
gp	*Grey Plover	*Pluvialis squatarola*
kn	*Knot	*Calidris canutus*
du	*Dunlin	*Calidris alpina*
bg	*Bar-tailed Godwit	*Limosa lapponica*
cu	*Curlew	*Numenius arquata*
sr	*Spotted Redshank	*Tringa erythropus*
rs	*Redshank	*Tringa totanus*
gs	*Greenshank	*Tringa nebularia*
tu	*Turnstone	*Arenaria interpres*

Chapter 7

ARE OYSTERCATCHERS (*Haematopus ostralegus*) SELECTING THE MOST PROFITABLE MUSSELS (*Mytilus edulis*)?

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ABSTRACT

Size selection by Oystercatchers (*Haematopus ostralegus*) feeding on the edible mussel (*Mytilus edulis*) by hammering the ventral side is analysed and compared with the predictions of an optimal diet model. It is found that the Oystercatchers select mussels between 30 and 45 mm long which are not overgrown by barnacles and which are thin shelled. However, after including waste handling events in both the profitability and the diet model, and estimating the prey population available to the Oystercatchers, a good agreement between the prediction and the data is found. These results are further discussed in the light of optimal foraging theory.

INTRODUCTION

The maintenance of an energy balance sufficient to meet the present needs of an individual and to accumulate energy for the future, is important in the evolutionary success of a genotype. In animals with a close coupling between feeding behaviour and fitness, natural selection should be an important force driving the organization of feeding behaviour, and this can be modelled to show how the animal performs as efficiently as possible. This is the rationale behind optimal foraging theory. This approach has until now been quite successful in explaining several aspects of foraging behaviour (for reviews see Pyke *et al.*, 1977; Krebs, 1978; Krebs *et al.*, 1983; Krebs & McCleery, 1984). However, as pointed out by Krebs *et al.*, (1983), many papers purporting to test optimal foraging models do no more than refer to some qualitative agreement between observations and one or more assumptions of the model. There is a need for more rigorous quantitative tests of the predictive value of the models (e.g., Thompson & Barnard, 1984).

Oystercatchers (*Haematopus ostralegus* L.) occur in winter on estuaries of North-West Europe. Many of them feed on mussels (*Mytilus edulis* L.) which are opened either by hammering a hole through the shell or by stabbing between the intact valves (Norton Griffiths, 1967). Stabbing Oystercatchers usually select the largest mussels present (Norton Griffiths, 1967; Zwarts & Drent, 1981; Ens, 1982) whereas hammering Oystercatchers may not do so, even when a wide range of mussel sizes is present (Drinnan, 1958; Norton Griffiths, 1967; Ens, 1982). The aim of this study was to test whether, by ignoring the largest mussels, hammering Oystercatchers increased their energy gain.

METHODS

The data were collected in August and September 1982 on the Slikken van Vianen, a tidal flat in the Oosterschelde (The Netherlands). Extensive musselbeds occur in this area (for a description, see Meire & Kuijken, 1984) and some hundred to several thousand Oystercatchers use the beds as feeding areas. All observations were made from a hide at approximately 100 m from plots (50 x 100 m) marked out with stakes on the musselbeds. Only birds hammering the mussels through the ventral side of the mussel are considered.

Birds

Throughout the tidal cycle, individual birds were observed for at least 5 min. A focal animal was selected at random and the following recorded.

(1) Pecking.

(2) Handling a prey: pulling a mussel from the substrate, carrying it to a firm place, putting it down, hammering through the shell and swallowing the flesh.

(3) Waste handling: the mussel was attacked but the bird gave up without opening it.

(4) The length of mussels attacked by Oystercatchers: this was measured against bill length, and later converted to mm using a regression line relating estimates to real size. This regression line was obtained from estimates, made by the observers, of mussels of known size which were presented at the bill of a stuffed Oystercatcher under 'field conditions' (using binoculars and the same observation distance).

Sequences of behaviour were recorded on tape and later transferred to a computer. A program written by L. Vanhercke was available to time all events.

Mussels

The study plots were located within the most homogeneous parts of the musselbeds. Fifteen core samples (diameter = 15 cm, surface = 176.7 cm^2) were taken to a depth of 5 cm in each plot and preserved in 7% neutral formalin. Mussels were counted and the length and thickness of the shell at the ventral side (near the posterior adductor muscle) were measured with a vernier calliper to the nearest 0.05 mm. A sample of mussels from each plot was used to determine ash-free dry weight (AFDW), by cutting the flesh free from the shell, drying for 12 h at 110°C, weighing and subsequently incinerating at 550°C for 2 h.

To analyse the aggregation pattern we used the *b* value of the Taylor

Power Law, which states that there is a relation between variance (s^2) and the mean (m) of the form $s^2=am^b$ (Taylor, 1969). Parameter b is an index of dispersion and varies continuously from 0 for a regular distribution to infinity for a highly aggregated one. If b is not significantly greater than 1, we can conclude that the population is not aggregated (Taylor, 1969). The value b (and its 95% confidence interval), was calculated by linear regression of log s^2 on log m. In addition to the data from the five plots discussed here, we used data from four other mussel plots, sampled in the same area at the same time, for this analysis.

Mussels opened by ventral hammerers are easily recognized, and were collected and measured as described above.

All statistical analyses were performed on the University computer (Siemens BS 2000-VS6) using SPSS (Nie *et al.*, 1975).

RESULTS

1. Prey population.

1.1 Density and size distribution

The length frequency distributions of mussels present in the plots were compared with a Kolmogorov-Smirnov two-sample test, and found to be significantly different between all plots except between plots 30 and 31 (Table 1). As mussels smaller than 12.5 mm were not taken by Oystercatchers, the frequency distributions of mussels larger than 12.5 mm were compared in the

*Table 1. H values of the Kolmogorov-Smirnoff two-sample test comparing the frequency distribution of all mussels present (lower left triangle) and mussels >12.5 mm (upper right triangle) between each pair of plots. (*P<0.05; **P<0.01; ***P<0.001).*

	plot				
plot	6	10	18	30	31
6		1.568*	2.106***	4.558***	3.643***
10	2.227***		2.035**	4.528***	3.571***
18	1.891**	2.372***		4.757***	4.302***
30	4.401***	3.420***	5.466***		1.262NS
31	3.993***	2.770***	4.997***	1.322NS	

Table 2. Total density and density for each sizeclass of mussels in each plot. Densities are given as number of mussels per m^2.

	Plot			
Length (mm)	6	10	18	30/31
1-4.9	24	60	26	3
5-9.9	275	326	211	42
10-14.9	170	309	124	49
15-19.9	137	309	90	77
20-24.9	101	183	75	91
25-29.9	129	248	64	537
30-34.9	149	204	67	1612
35-39.9	101	248	252	707
40-44.9	234	313	562	56
45-49.9	210	121	252	3
50-54.9	84	17	52	-
55-55.9	20	-	-	-
Total	1637	2342	1780	3183

same way and resulted in the same significant differences (Table 1). As there was no difference between plots 30 and 31, and the two plots were situated near each other, the data were pooled in all further analyses and are referred to as plot 30. The density of each size-class of mussels in each plot is given in Table 2.

The density of mussels varied between 1637/m^2 in plot 6 and 3183=m^2 in plot 30 and is comparable to that found in other studies (Zwarts & Drent, 1981; Ens, 1982). The mussels in plots 6, 10, and 18 have persisted for several years, so mussels of all size-classes were present. Plots 30 and 31 were situated on a commercial bed where mussels were added and removed regularly, and so contained many mussels of approximately the same size. On all plots, mussels were free of weed cover, but many of them were overgrown by barnacles (*Balanus balanoides*).

1.2 Aggregation

Mussels occur in clumps on the beds and are clearly aggregated. However it is important to know whether the different size-classes of mussels

Table 3. Relation between mussel length and ashfree dry weight for each plot.
** Ln weight (in g) = a+b Ln length (in mm).*

Plot	a*	b*	r	N	P
6	-2.131	2.867	0.960	30	<0.001
10	-3.202	3.146	0.968	20	<0.001
18	-2.683	3.010	0.958	30	<0.001
30/31	-1.998	2.743	0.956	20	<0.001

occur at random within the mussel clumps, or whether different sizes occur in different clumps, since then size selection becomes a patch choice problem. To test this, we calculated the index of aggregation (*b*) from the Taylor Power Law (Taylor, 1969). The values of *b* (+95% confidence interval) are given in Table 4 and show that only the 15-20 mm size-class was significantly aggregated. Therefore, most size-classes are scattered randomly over the mussel clumps.

Table 4. The b values of the Taylor Power Law (± 95% confidence interval), CI for each size-class of mussels.

length (mm)	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
b	0.51	1.08	0.89	1.81	1.10	1.16	1.20	1.11	2.37	1.03	1.42	1.20
CI	0.83	0.51	0.05	0.49	0.33	0.39	0.26	0.24	1.70	0.66	0.57	0.75

1.3 Biomass

As there is no difference in body composition in mussels of different sizes (Dare & Edwards, 1975), we assume that AFDW is a good measure of energy content. The linear relationship between the natural logarithm of mussel length and that of AFDW is given in Table 3. The regression equations differ significantly between the plots (Ancova: $F=5.347$; $df=4,124$; $P<0.001$).

2. Mussel selection by Oystercatchers

2.1 Size-classes preyed upon

The length frequency distributions of mussels present on the bed and those taken by the Oystercatchers are compared in Fig. 1a,b. The distributions differ significantly in all plots whether the entire prey population or only the population above 12.5 mm is considered (Kolmogorov-Smirnov two-sample

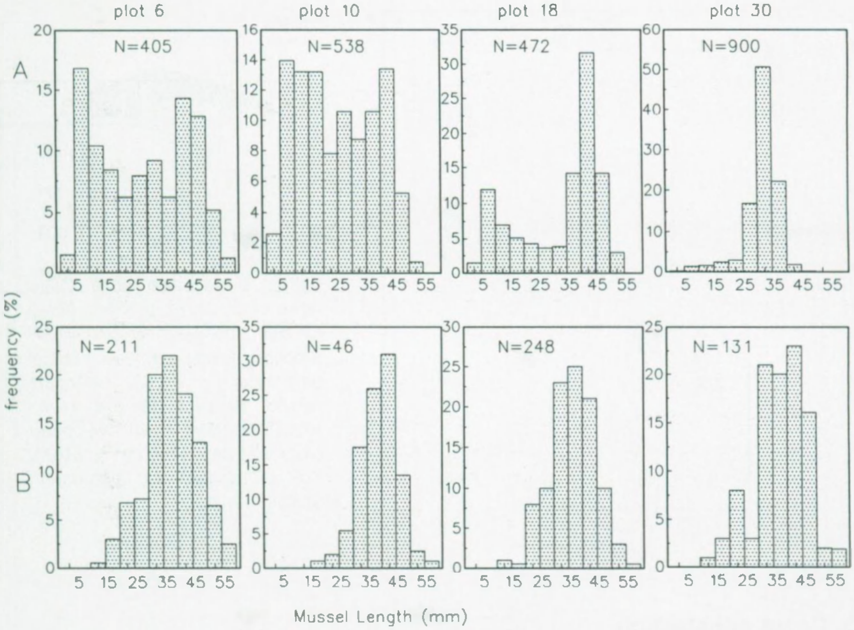


Figure 1. Length frequency distribution of (a) all mussels present and (b) mussels taken by Oystercatchers in four different study plots. The distribution of mussels taken by Oystercatchers consists of mussels both opened and rejected after a waste handling.

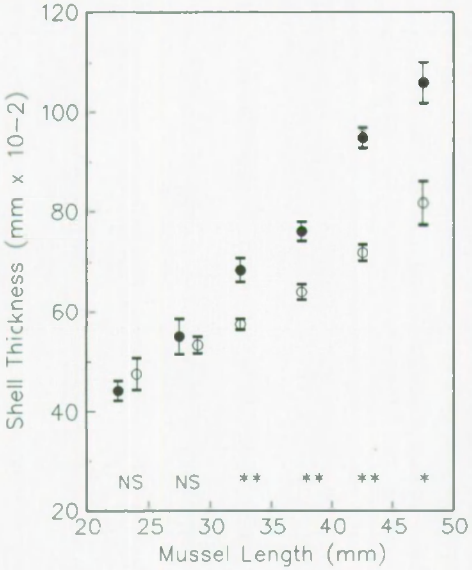
test, all cases *P*<0.001). Oystercatchers tend to select mussels between 30 and 45 mm long.

2.2 Selection for shell thickness

The mean ventral shell thickness of mussels opened by Oystercatchers was less than that of mussels present on the bed. It seems that, the larger the shell, the more choosey the Oystercatchers are for the thinnest ones (Fig. 2), resulting in significant differences (Student *t*-test) for the larger mussels (Fig. 2). This was also found by Durell & Goss-Custard (1984).

2.3 Selection for mussels not overgrown by barnacles

In comparing mussels from the samples with mussels taken by Oystercatchers, it was obvious that the birds seldom ate mussels overgrown by barnacles (see below and Durell & Goss-Custard, 1984).



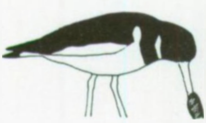


*Figure 2. Average shell thickness of mussels present (filled circles) and opened by Oystercatchers (open circles). Vertical bars give ± 1 SE. Only the results of plot 18 are given since the data from the other plots are very similar. (*P<0.01; **P<0.001; NS not significant; Student t-test.)*

3. Costs of selection

Several costs are associated with this selection of mussels, and will be considered here.

3.1 Handling costs

Handling time (*H*) includes both the time to open the mussel and the time to swallow the flesh and is found to be a linear function of mussel length. There was no difference between plots (Ancova: $F=1.992$; $df=3{,}33$; $P>0.05$), so the data ($N=389$) were pooled and the regression line was calculated on the basis of the average handling time per size-class (H (in s) $=2.027$ x shell length (mm) - 10.80; $r=0.925$; $df=9$, $P<0.01$; Fig. 3). This handling time is short compared with the data given by Ens (1982).

3.2 Waste handling costs

About one-third of the mussels attacked were not opened. After handling the mussel for up to 80 s, the birds resumed their searching behaviour without opening it. The proportion of mussels actually opened was calculated for each size-class and is a decreasing function of size (Fig. 4): *P* (probability of a mussel being opened once taken) = 1.127- 0.016 shell length (in mm); $r=0.826$, $N=10$, $P<0.01$. The waste handling time (WH) was also a linear function of mussel length (Fig. 3) and the regression line was calculated on the basis of

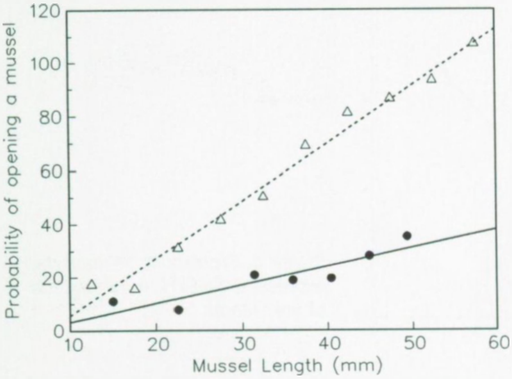


Figure 3. The average handling time (filled circles) and waste handling time (open circles) for each size-class of mussels. The regression lines are y=2.027x - 10.80 and y=0.679x - 4.04 respectively.

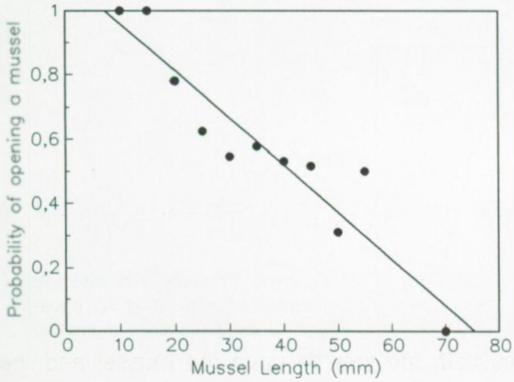


Figure 4. The probability (P) that mussel is opened, after being taken by an Oystercatcher, as a function of mussel length. The regression line (P=1.127-0.016x) is plotted.

the average/size-class (overall $N=129$): WH (in s) = 0.679 x shell length (mm) - 4.04; $r=0.825$; $P<0.05$).

4. Do Oystercatchers Select the Most Profitable Prey?

Once we know the costs and benefits associated with mussel selection we are in a position to calculate an optimal diet and compare this with the data.

4.1 Profitability

Profitability in optimal diet models is defined as the amount of energy (*E*) gained per unit time spent in handling (*E/H*) (e.g., Krebs, 1978). For mussels,

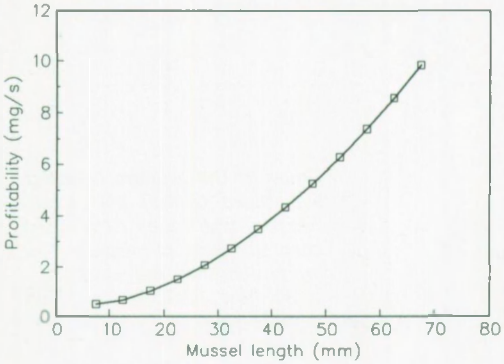


Figure 5. Profitability of mussels, expressed as E/H, as a function of their length.

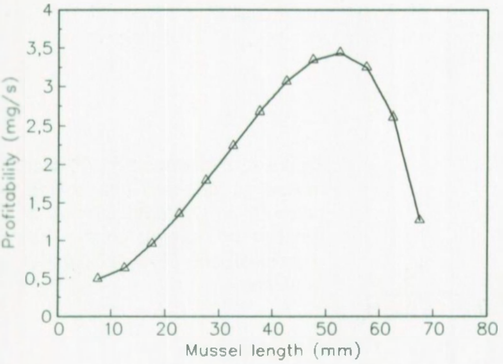


Figure 6. Profitability of mussels (calculated according to equation 1) as a function of mussel length.

we found the profitability increases supraproportionally with mussel length (Fig. 5). However this is not, we feel, the profitability the Oystercatchers are experiencing. Indeed, if they take 10 mussels of 50 mm they can open only about three of them (see Fig. 4). We can account for this in calculating the profitability by using the energy gained after taking N mussels (E_iP_i) and the time spent handling these N mussels (H_iP_i + WH (1 - P_i)), or

Profitability of size-class i=

$$\frac{E_iP_i}{H_iP_i+WH(1-P_i)} \qquad (1)$$

Table 5. Assumptions of the optimal diet model (after Krebs & McCleery, 1984), and their validity in this study.

	Assumption	Valid?
(1)	Prey value is measurable in terms of net energy content or some other comparable simple dimension	Yes
(2)	Handling time is a fixed constraint	Yes
(3)	Handling and searching cannot be done at the same time	Yes
(4)	Prey are recognized instantaneously and with no errors	No
(5)	Prey are encountered sequentially and randomly	Yes
(6)	Energetic costs per s of handling are similar for different prey	Yes
(7)	Predators are designed to maximize rate of energy intake	Yes

The profitability curves now show a peak around 50-55 mm (Fig. 6), but this is still much larger than the average taken (30-45 mm). However, the diet not only depends on the profitability of the prey but also on the density of the different prey types (Charnov, 1976; Krebs, 1978). In order to test the optimal diet model, it is therefore necessary to use a more rigorous formulation.

4.2 The model

The model used is a multi-species version of Hollings' disc equation (Charnov, 1976)

$$\frac{E}{T}=\frac{\Sigma E_i\lambda_i}{1+\Sigma\lambda_i H_i} \tag{2}$$

in which λ_i is the encounter rate for size-class i, and T is the foraging time.

The assumptions of the model and their validity for this study are listed in Table 5. To correct for the fourth assumption, the probability of opening a mussel once taken (P) is included in the same way as was done for the profitability.

$$\frac{E}{T}=\frac{\Sigma E_i\lambda_i P_i}{1+\Sigma\lambda_i(H_i P_i+(1-P_i)WH_i)} \tag{3}$$

4.3 Encounter rate

Before calculating the optimal diet based on equation (3) we only need to know the encounter rate (λ_i) for each prey class. This can be estimated from equation (4) given by Thompson (1983)

$$\lambda_i=1/100\sqrt{(1/d_i)/s} \tag{4}$$

where s is the search speed and d_i the density of size-class i (number of mussels per m^2). On the basis of observations of walking speed and step length (measured on mud flats), the search speed can be estimated at 0.085 m/s (Meire, unpublished data). This is a relative measure of the encounter rate since it does not take any width of the search path into account. For estimating the mussel density, two additional factors must be taken into account. First mussels taken by Oystercatchers are almost free of barnacles (Durell & Coss-Custard, 1984; present study), yet many mussels on the bed are covered extensively by barnacles. The mussels from the samples were therefore redesignated as edible (with no or only a few barnacles) and inedible (for the greater part overgrown by barnacles): the difference was usually very obvious as few mussels with intermediate coverage were present. The percentage of edible mussels varied between plots and particularly with size-class (Table 6).

Second, only thin-shelled mussels are taken (Durell & Goss-Custard, 1984; present study). For each size-class the fraction of mussels available was estimated as the cumulative percentage of mussels occurring within the range of shell thicknesses taken by the Oystercatchers. The density of mussels actually available to the birds was then obtained by subtracting the proportions of mussels overgrown by barnacles and with shells that were too thick. The frequency distributions obtained in this way are given in Fig. 7a. Now it can be seen that Oystercatchers are selecting for the largest mussels of the available population.

Table 6. Percentage of mussels per size-class that are edible for Oystercatchers. (* Not extensively covered by barnacles).*

Length (mm)	Plot			
	6	10	18	30/31
10-14.9	100	100	66	100
15-19.9	100	100	78	100
20-24.9	100	100	100	100
25-29.9	100	94	55	42
30-34.9	100	70	50	44
35-39.9	73	47	30	53
40-44.9	31	30	20	100
45-49.9	36	30	20	-
50-54.9	12	1	25	-
55-59.9	1	-	-	-

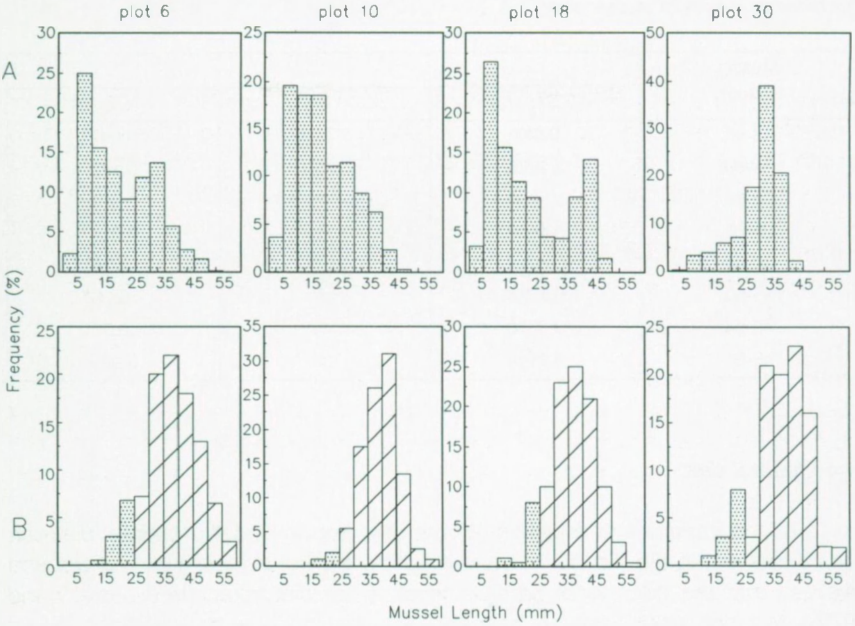


Figure 7. Length frequency distributions of (a) mussels available to Oystercatchers (see text) and (b) mussels taken by Oystercatchers. The hatched bars show the predicted optimal diet.

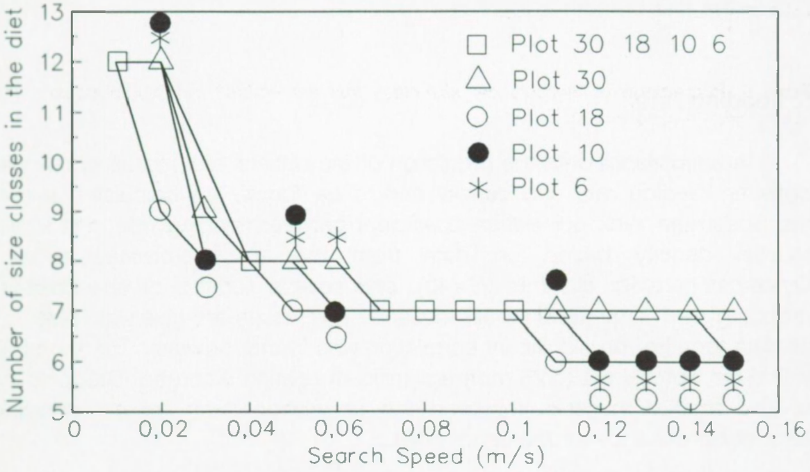


Figure 8. Sensitivity of the model to variations in S (search speed). The number of size-classes in the optimal diet is given as a function of S.

Table 7. Spearman rank correlation coefficients (r_s) between feeding rate and mussel density, for different ranges of mussel size.

Mussel length			
	r_s	N	P
10-60	0.077	40	0.637
15-60	0.2276	36	0.182
20-60	0.3351	32	0.061
25-60	0.4592	28	0.014
30-60	0.6792	24	<0.001
35-60	0.7734	20	<0.001
40-60	0.8576	16	<0.001
45-60	0.7144	12	0.009

4.4 Optimal diet

All the variables of equation (3) are now known and the optimal diet can be calculated. In Fig. 7b the hatched columns are the optimal size-classes and we see that the diet model predicts most of the diet taken (between 90 and 97%). We can ask, however, how sensitive the model is to variations in our estimates of the various factors. Therefore we calculated the number of size-classes in the diet for various values of s (Fig. 8). As s increases, the encounter rate increases and obviously fewer size-classes should be added to the diet. However, for a large range of values near the estimated value of 0.085 the diet breadth is identical.

5. Feeding rate

In accordance with the prediction of the optimal diet model, a correlation between feeding rate and density should be found. We calculated therefore the Spearman rank correlation coefficient between feeding rate and available mussel density based on data from the 10 size-classes taken by Oystercatchers for all plots ($N=40$), and several subsets of size-classes by dropping each time the smallest mussels. The results are given in Table 7. For all data together no significant correlation was found; however, for the mussels within the optimal set (>25 mm) a significant relation emerged. Dropping more of the smaller mussels improved the correlation even more, indicating a stronger preference for the larger ones.

DISCUSSION

Though optimal foraging models have been quite successful in predicting some aspects of foraging behaviour (see review by Krebs *et al.*, 1983); many difficulties remain. Zach & Smith (1981) argue that optimal foraging theory is very useful in simple laboratory experiments but that most feeding problems in the wild are complex, so that in practice it is difficult to define optima. We originally thought that the Oystercatcher-mussel situation would be a simple system, but it is now clear that mussel length selection is not the only factor involved (Durell & Goss-Custard, 1984; present study). Each large size-class should be divided into at least thin- and thick-shelled groups.

Moreover mussels overgrown by barnacles are seldom taken, perhaps because they are not recognized by the Oystercatchers or because the presence of barnacles on the ventral side makes it impossible to hammer the shell. It is also important to incorporate the waste handling times into the model.

Ideally we should be able to predict both selection for shell size and for shell thickness. However because the relation between handling time and shell thickness has not been measured in the field, this is actually impossible. Then if our measures of prey density do not include those prey categories (thick and overgrown shells) that are not actually consumed, we can predict the optimal mussel sizes.

Do our results confirm the optimal diet model? The predictions can be summarized as follows (after Krebs & McCleery, 1984). (1) The highest-ranking prey should never be ignored. (2) Low-ranking prey should be ignored following equation (2) and this exclusion should be all-or-nothing. (3) The exclusion of low-ranking prey does not depend on their own values of λ. From the first prediction it is obvious that prey within the optimal set should be taken proportional to their density (Goss-Custard, 1977; Sutherland, 1982; Thompson & Barnard, 1984). For the optimal size-classes we indeed found a significant correlation between density and feeding rate.

Prediction 2 is violated in most studies, and many explanations have been offered to account for it (discrimination errors, long-term learning, inherent variation in the animal, runs of bad luck, simultaneous encounters, averaging across individuals: Krebs & McCleery, 1984). Oystercatchers in this study also took some prey outside the optimal set though it was only a small proportion of the total (5-10%). The most likely explanation might be that adding sub-optimal size-classes to the diet decreases intake rate only by less than 5% (Fig. 9). In addition, given the enormous variation in handling time and profitability, it is not surprising that some sub-optimal mussels are taken. The fact that the smallest prey are the most abundant, yet very scarce in the diet, is in accordance with prediction 3. The optimal diet is the same in the four plots. Therefore we could not prove that, if the density of more profitable

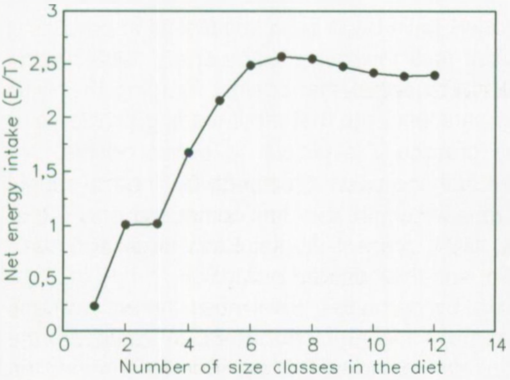


Figure 9. The intake rate (E/T) as a function of the number of size-classes included in the diet. The size classes are ranked according to their profitability. Only data from plot 6 are shown since they are very similar in all other plots.

mussels increased, fewer size-classes would be taken. But overall, the selection for the thin-shelled and most profitable mussels does suggest that Oystercatchers are optimizing their intake rate and, within constraints that must be taken into account, the diet model is successful in predicting diet breadth.

The importance of including additional factors (selection against thick-shelled mussels and mussels overgrown by barnacles) and constraints (waste handling) are obvious when comparing the predictions of equations (2) and (4). On the basis of the original model (equation 2) and the overall densities of mussels present, the optimal diet consists only of mussels larger than 40 mm or between 40 and 80% of the actual diet.

In this paper we discussed some factors that may explain why Oystercatchers do not take the largest mussels. Obviously there are other possible explanations in addition to those considered here.

Larger mussels may be harder to pull from the bed (Norton Griffiths, 1967). Handling time may be greater for larger prey (contradicting assumption 6, Table 5), or large mussels may involve the risk of damaging the bird's bill, but this is very difficult to measure. The risk of having food stolen may increase with mussel size. This is likely and has already been found for other birds (Thompson & Barnard, 1984) but, in our study area, both inter- and intraspecific aggression and robbing is very rare. Parasite infections are almost absent and are not size dependent (Dijkema, pers. comm.). Incorporating any of these factors could improve the fit to the data but we believe we selected the most important ones.

These results also have some ecological implications. Since the prey population measurable in the field and the one experienced by Oystercatchers are very different (which is likely to be true in many other predator-prey systems), one should be extremely cautious when calculating functional and numerical responses based on measured prey densities.

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REFERENCES

Charnov, E. L., 1976. Optimal foraging: attack strategy of a mantid. Am. Nat. 110: 141-151.

Dare, P. J. & D. B. Edwards, 1975. Seasonal changes in flesh weight and biochemical composition of mussels (*Mytilus edulis* L.) in the Conway Estuary, North Wales. J. exp. mar. Biol. Ecol. 18: 89-97.

Drinnan, R. E., 1958. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. Fish. Incest., London: Ser. II 22: 1-15.

Durell le V. dit, S. E. A. & J. D. Goss-Custard, 1984. Prey selection within a size-class of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*, Anim. Behav. 32: 1197-1203.

Ens, B., 1982. Size selection in mussel-feeding Oystercatchers. Wader Study Group Bull. 34: 16-20.

Goss-Custard, J. D., 1977. Optimal foraging and the size selection of worms by Redshank, *Tringa totanus*, in the field. Anim. Behav. 25: 10-29.

Krebs, J. R., 1978. Optimal foraging: decision rules for predators. In J.R. Krebs & N.B. Davies (eds), Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications, Oxford: 23-63.

Krebs, J. R. & R. McCleery, 1984. Optimization in behavioural ecology. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology: An Evolutionary Approach, 2nd edn. Blackwell Scientific Publications, Oxford: 91-121.

Krebs, J. R., D. W. Stephens & W. J. Sutherland, 1983. Perspectives in optimal foraging. In G. A. Clark & A. H. Brush (eds), Perspectives in Ornithology. Cambridge University Press, New York: 165-216.

Meire, P. M. & E. Kuijken, 1984. Relation between the distribution of waders and the intertidal benthic fauna of the Oosterschelde. Netherlands. In P. R. Evans, J. D. Goss-Custard & W. Hale (eds), Coastal Waders and Waterfowl in Winter. Cambridge University Press, Cambridge: 57-68.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner & K. Brent, 1975. Statistical Package for the Social Sciences. McGraw-Hill, New York.

Norton Griffiths, M., 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*). Ibis 109: 412-424.

Pyke, G. H., H. R. Pulliam & E. L. Charnov, 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137-154.

Sutherland, W. J., 1982. Do Oystercatchers select the most profitable prey? Anim. Behav. 30: 857-861.

Taylor, L. R., 1969. Aggregation, variance and the mean. Nature, Lond. 189: 732-735.

Thompson, D. B. A., 1983. Prey assessment in plovers (*Charadreiidae*): net rate of energy intake and vulnerability to kleptoparasites. Anim. Behav. 31: 1226-1236.

Thompson, D. B. A. & C. J. Barnard, 1984. Prey selection by plovers: optimal foraging in mixed-species groups. Anim. Behav. 32: 554-563.

Zach, R. & J. N. Smith, 1981. Optimal foraging in wild birds? In A. L. Kamil & T. D. Sargent (eds), Foraging Behaviour, Ecological, Ethological and Psychological Approaches. Garland STPM press, New York: 95-109.

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 (eds), Feeding and Survival Strategies of Estuarine Organisms. Plenum Press, New York: 193-216.

Chapter 8

INTERACTIONS BETWEEN OYSTERCATCHERS(*Haematopus ostralegus*) AND MUSSELS (*Mytilus edulis*): IMPLICATIONS FROM OPTIMAL FORAGING THEORY.

PATRICK M. MEIRE

Submitted to Ardea

ABSTRACT

In a previous paper (Meire & Ervynck, 1986) it was shown that Oystercatchers, opening mussels by the hammering method, selected the most profitable length classes of mussels. However the birds also selected, within a length class, the thin shelled mussels. In this paper I analyse whether this selection can be understood as a foraging strategy that maximizes energy gain.

The number of blows of an artificial Oystercatcher bill, necessary to open a mussel, was measured experimentally and was found to increase supraproportionally with shell thickness.

Based on this experiment and measurements in the field the profitability of mussels as a function of shell thickness was calculated for different length classes. Profitability decreased sharply with shell thickness and differed, for each shell thickness class, between length classes. Based on this result it was predicted that 1) per length class of mussels, the thick shelled mussels should be dropped from the diet and 2) that the shell thickness of mussels accepted should increase with mussel length. Both predictions were supported by the data.

As birds selected the thin shelled mussels it was expected that the average shell thickness of the mussels on the bed should increase in the course of the winter. This was not found. However the fraction of the mussel population that is harvestable for hammering Oystercatchers was very small and the consumption of the birds over the winter amounts to 70% of the production of the harvestable fraction.

It is concluded that a clear description and understanding of the foraging behaviour is crucial to understand the relation between the distribution of a predator and its prey.

INTRODUCTION

Optimal Foraging Theory (OFT) is based on the observation that all animals must make decisions while foraging. Without implying any conscious choice, birds must decide on when and where to feed and what to forage on. These decisions can be analysed in terms of cost and benefits of alternative courses of action (Krebs & Kacelnik, 1991). The rationale behind the first generation of OFT models is that animals are designed to take these decisions that maximize the net rate of energy intake, which is assumed to correlate with fitness. For the different decisions to make by the animals, formal mathematical models were constructed making both the assumptions underlying the hypothesis and the predictions clear and unambiguous (Krebs & Kacelnik, 1991). In many laboratory or field experiments and observations the predictions of the OFT models were tested on a large variety of species (see reviews in Krebs *et al.*, 1983; Krebs & McCleery, 1984; Pyke, 1984; Stephens & Krebs, 1986; Krebs & Kacelnik, 1991). The relatively simple foraging models have generally proved to be successful up to a certain level but, to improve the fit with the data, they had to be modified by incorporating constraints. Factors such as nutrient content of the prey, predation risk, kleptoparasitism, imperfect knowledge, sampling and recognition errors were studied (for review see Stephens & Krebs, 1986).

Although by several people (e.g., Gould & Lewontin, 1979; Gray, 1987; Pierce & Ollason, 1987) there can be little doubt that research on Optimal Foraging Theory has greatly increased our understanding of the factors underlying foraging behaviour of animals. Although interesting in itself, this knowledge is also very important for a better insight in both the impact of the predators on their prey populations and in the distribution of animals over their feeding areas (Werner *et al.*, 1983; Meire, 1987). For instance, a deeper understanding of prey selection has resulted in better estimates of the fraction of the prey population which is actually harvestable by birds (Zwarts & Wanink, 1984; 1989; Zwarts & Blomert, 1992; Zwarts *et al.*, 1992). This is crucial for understanding the relationship between the distribution of predators and their prey populations and for solving the question whether or not the carrying capacity of an area is reached. In times where habitat loss or degradation occur at an ever increasing speed this is a very important applied question. Werner *et al.* (1983) utilized optimal foraging theory and laboratory estimates of foraging costs to predict the choice of food and use of habitats by fish in the field with great success (see Werner & Mittlebach, 1981 and Werner, 1984 for reviews). Thus optimal foraging models are a potentially useful tool in environmental management.

Wading birds, *Charadrii*, have proved to be very useful for studying several aspects of OFT, especially in the field. Among waders, Oystercatchers (*Haematopus ostralegus* L.) have received special attention and their selection between prey species and between different size-classes of several prey species has been studied in detail (see Zwarts *et al.*, in press for a review).

The results in these studies on waders have matched those in the subject as a whole. The size selection of Oystercatchers feeding on mussels by ventral hammering was predicted quite accurately by an optimal diet model when recognition errors where incalculated (Meire & Ervynck, 1986). But, as found by Durell & Goss-Custard (1984), Meire & Ervynck (1986), Sutherland & Ens (1987) and Cayford & Goss-Custard (1990) within a size class the birds select for the mussels with the thinnest shell. In the paper of Meire & Ervynck (1986) this selection was taken as a constraint but here I analyse whether this selection can be understood as an energy maximizing foraging strategy. I use the model to estimate the harvestable part of the mussel population and the impact of Oystercatchers on their prey. Finally I explore the possible influences of these prey characteristics on interference and the distribution of birds.

METHODS

Mussels on the bed and opened by Oystercatchers.

The mussel population was sampled in study plot PQ 6 on a musselbed on the Slikken van Vianen (Oosterschelde, the Netherlands; for a description of the study area see Meire & Kuijken, 1987). Fifteen core samples were taken on 21 October and 5 December 1981, 2 March and 9 September 1982 with a core of 176 cm^2. All mussels were counted and measured. Mussel length, height, breadth and the thickness of the shell on the ventral side were measured to the nearest 0.05 mm with a vernier callipers. The shell thickness on the ventral side was measured about 2 mm from the edge near the posterior adductor muscle. A flatness index was calculated as the ratio of height to breadth. A sample of mussels (30) was used to determine ash-free dry weight by cutting the flesh from the shell, drying for 12 h at 110°C, weighing and subsequently incinerating at 550°c for 2h. Mussels taken by hammering Oystercatchers are almost free of barnacles, yet many mussels on the bed are extensively covered by barnacles. The mussels from the samples were therefore designated as edible (with no or only a few barnacles) and inedible (for the greater part overgrown by barnacles): the difference was usually very obvious as few mussels with intermediate coverage were present.

Mussels opened by hammering Oystercatchers were collected in September 1981 and 1982 in the same study plot and measured as mentioned above. For more details on the methods see Meire & Ervynck (1986) and Craeymeersch *et al.* (1986).

For the analysis, the data on shell length and thickness were grouped in classes (length 20-24.99; 25-29.99 etc.; thickness 50-59.99; 60-69.99 etc.). In the text and figures these classes are indicated by the class mean.

Artificial Oystercatcher bill.

To estimate the force necessary to open a mussel, an artificial Oystercatcher bill, made of copper and weighing 105 g, was dropped vertically from a standard height (35 cm) onto the mussel (Fig. 1). The bill tip was made in accordance with the measures given by Swennen *et al.* (1983) for hammering Oystercatchers (with 1.6 mm and depth 4.5 mm). The bill was held in an electromagnetic field so that when the current was interrupted the bill fell vertically onto a mussel clamped with the ventral side upwards. The mussel was oriented so that the bill always hit one valve, near to the edge. The number of blows needed to break the mussel was recorded. The damage done by the artificial bill to the ventral shell margins of the shell was almost indistinguishable from that done by real birds. A random sample of mussels from the study plot

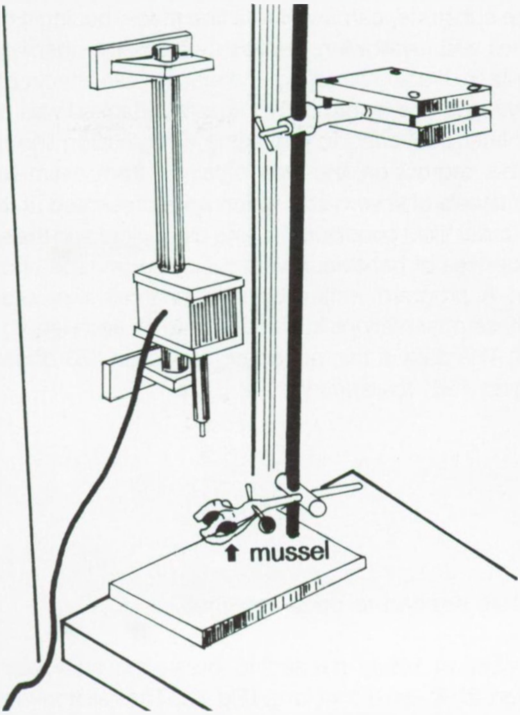

Figure 1. The artificial Oystercatcher bill as used in the experiment.

was used in this experiment.

Feeding observations

The numbers and activity of birds in study plot PQ 6 were noted every 30 min the greater part of the tidal cycle. In the first and last hour in which the plot was exposed, counts were made at least every 15 min, as bird numbers could change quickly at that time. On average twelve to fifteen counts were made per tidal cycle. In the period July 1981 - April 1982 data were collected during 32 tidal cycles. Based on these counts, the average density and the number of feeding minutes per plot per tide were calculated. In between the counts individually birds were observed for at least 5 min. A focal animal was selected at random and its foraging behaviour was recorded in detail. The following events were noted: *Social interactions*: all interactions with other Oystercatchers or other species. *Non foraging*: preening, sleeping etc. *Handling a prey*:-hammerers: pulling a mussel from the substrate, carrying it to a firm place, putting it down, hammering through the shell and swallowing the flesh; -stabbers: opening the mussel and swallowing the flesh. *Wasted handling*: the mussel was attacked but the bird gave up without opening it. The length of the mussels attacked was measured against bill length, and later converted to mm using a regression line relating estimates to real size. This regression line was obtained from estimates, made by the observers, of mussels of known size which were presented at the bill of a stuffed Oystercatcher under 'field conditions' (using binoculars and the same observation distance). Sequences of behaviour were recorded on tape and later transferred to a computer. A program written by L. Vanhercke was available to time all events. From these observations the feeding rate on each length class of mussels was calculated. The data in this paper are based on 233 observations made in the period August 1981 to January 1982.

RESULTS

Number of blows needed to open the shell.

The number of blows needed to break the shell was determined for mussels between 31.9 - 58.6 mm long (Fig. 2). The relation with shell thickness was supraproportional. A stepwise multiple regression analysis, in which the dependent variable was log number of blows and the independent variables were shell-length, -height, -breadth, -thickness and flatness index showed that the number of blows was largely determined by shell thickness in every size-class (Table 1). Only for mussels between 45-50 mm was an additional variable, shell breadth, incorporated in the regression model along with shell thickness. Using the data of all length classes, shell thickness was also the only variable that entered in the equation.

Selection for shell thickness.

In Fig. 3 the frequency distributions of shell thickness of mussels present on the bed and those taken by Oystercatchers are plotted for the four most predated length classes, together with the number of blows necessary to break into the shell. Clearly, the birds selected the thin-shelled mussels (see also Durell & Goss-Custard, 1984; Meire & Ervynck, 1986).

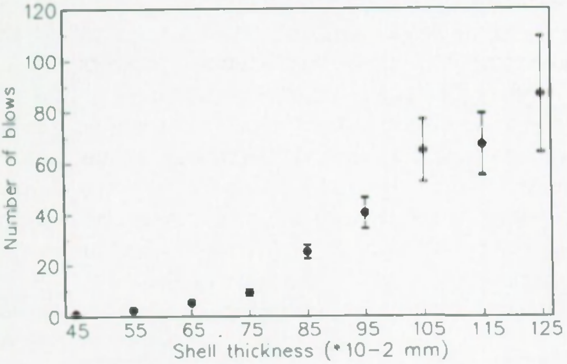

Figure 2. The average number of blows (± SE) necessary to break a mussel shell in function of shell thickness. Data of all length clases were pooled per thickness class. (N = 203).

Table 1. Results of a stepwise multiple regression of log number of blows necessary to break the shell (dependent variable) and shell-breadth, -height, -thickness, -length and the flatness index for several size classes. In all but one size class shell thickness was the only variable that entered in the regression equation.

	Size	<35mm	37.5mm	42.5mm	47.5mm	52.5mm	all
Shell thickness	B	0.083	0.079	0.077	0.055	0.037	0.062
	se B	0.015	0.010	0.006	0.006	0.017	0.003
Shell breadth	B				-0.135		
	se B				0.052		
Constant	A	-4.065	-3.622	-3.754	0.712	-0.621	-2.564
	se A	1.044	0.697	0.498	0.917	1.606	0.246
	R	0.783	0.719	0.853	0.791	0.519	0.817
	F	26.96	57.99	149.47	40.96	4.8	405.23
	df	1,17	1,54	1,56	2,49	1,13	1,201
	P	<0.001	<0.001	<0.001	<0.001	<0.05	<0.001

Is selecting thin shelled mussel optimal?

To test whether this selection pattern can be predicted by foraging theory we must know the profitability of thin- and thick-shelled mussels. The profitability of the mussels taken in the field is known from field measurements (Meire & Ervynck, 1986). In order to estimate, for each length class of mussels, the profitability as a function of shell thickness, the following assumptions were made: 1) the energy content (ADW) of mussels of one length class is independent of shell thickness and 2) there is a linear relationship between the time (and energy)

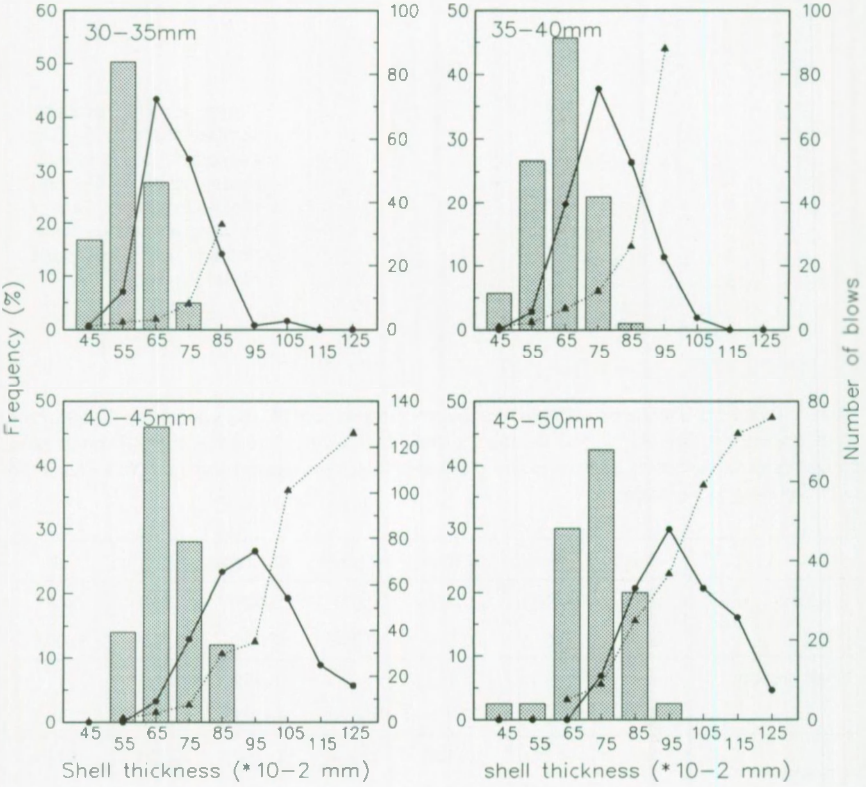

Figure 3. Frequency distribution of the shell thickness of mussels present on the musselbed (line), taken by Oystercatchers (histogram) and the mean numbers of blows necessary to open the shell (broken line) for four different size classes.

needed by the birds to open a mussel and the number of blows needed to open the mussel as measured in our experiment. Based on these assumptions the profitability was calculated as follows: For each length class of mussels the average shell thickness of mussels opened in the field was calculated. The measured profitability in the field was attributed to this thickness class (class i). To obtain the profitability of the other thickness classes per length class of mussels, this value was multiplied by the ratio (number of blows needed to open class i/number of blows to open class i± 1,2 etc.). The results are summarized in Fig. 4. For each length class of mussels the profitability clearly decreases

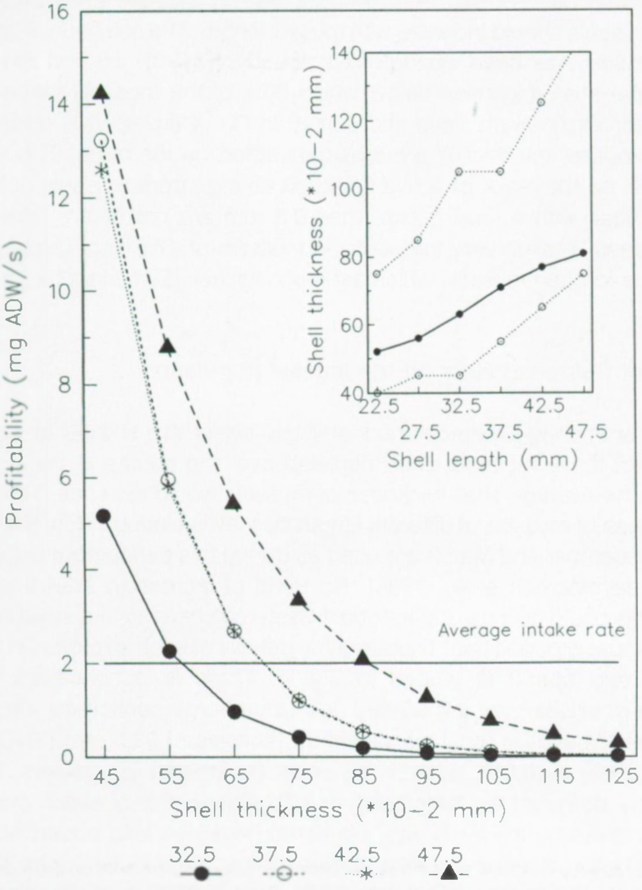

Figure 4. Profitabilty of mussels of four different length classes in function of shell thickness. In the inset, for each length class, the shell thickness below which 90% of the mussels taken fell (solid line) and the range of shell thickness present (dotted line), are plotted. For the calculation of profitability see text.

with increasing shell thickness. The values are however different for the different length classes (with the exception of length classes 37.5 and 42.5 mm). The average intake rate of Oystercatchers in the field is also plotted in the figure. According to the optimal diet model mussels with a profitability lower than the average intake should be dropped from the diet . Based on the results presented in figure 4 one can predict that 1) per length class of mussels, the thick shelled mussels should be dropped from the diet and 2) that the shell thickness of accepted mussels should increase with mussel length. The selection against thick shelled mussels has been documented already (Fig. 3). To test the second prediction the shell thickness below which 90% of the mussels taken fell was calculated for each length class and plotted in Fig. 4 (inset). It is clear that the longer the mussel the thicker are those accepted by the birds. This selection pattern must be the result of active selection as e.g., from mussels of 32.5 mm in length, those with a shell thicker than 0.8 mm are not taken, whereas this thickness class is taken very frequently in mussels of 47.5 mm. Oystercatchers are also able to open mussels which are much thicker (Sutherland & Ens, 1987).

Influence of Oystercatchers on the mussel population.

As hammering Oystercatchers strongly select thin-shelled mussels, one would expect these mussels to be depleted over the course of the winter and hence that the average shell thickness of mussels would increase. The average shell thickness of mussels of different length classes is plotted in Fig. 5. Data from October, December and March are used as during this period no mussel growth occurs (Craeymeersch *et al.*, 1986). No trend of increasing shell thickness is obvious. This could only be understood if Oystercatchers have a small impact on the overall mussel population. Therefore the density of each size class in October, December and March is plotted in Fig. 6. There is a consistent trend of decreasing densities over the winter. Due to the large confidence intervals the decrease was, however, only significant for mussels of 32.5 mm (ANOVA, $F = 3.2$; $df = 2,42$; $p<0.05$), one of the most preferred size classes. Can this decrease be attributed to Oystercatchers? To answer this question the number of mussels taken by the birds was estimated based on field observations. The density of Oystercatchers and their number of feeding minutes in the study plot was measured during the period July 1981 - April 1982 (Fig. 7). Density was low in summer and gradually increased as birds arrived in the area during August and September. From January onwards numbers started to decline again. Assuming the birds feed as much during the night as during the day the number of feeding minutes between October and March was estimated at 296 m^{-2}. However, not all Oystercatchers in the study plot took mussels by hammering. Based on the feeding observations of birds chosen at random, it was estimated that approximately half of the birds were hammerers, the other stabbers. Therefore the number of feeding minutes must be divided by two to obtain the number of feeding minutes spent in the plot by hammerers. Based on observations in the field the feeding rate of hammering Oystercatchers on mussels of different size classes is known. Multiplied with the number of feeding minutes this gives us an estimate of the number of mussels removed by the birds. This is summarized in Table 2. During the six months considered, 73 mussels m^{-2} were removed by hammering Oystercatchers, about 27% of the total number of mussels which

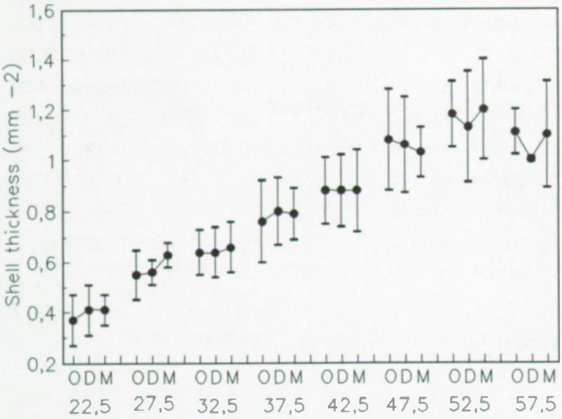

Figure 5. Average shell thickness (± SE) of mussels of different length-classes in October and December 1981 and March 1982 on a musselbed of the Slikken van Vianen.

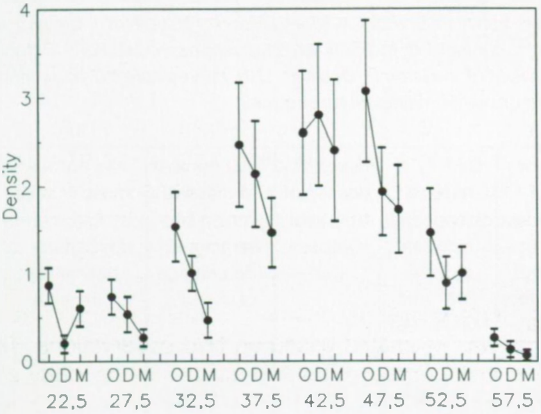

Figure 6. Average number of mussels (± SE) of different size classes per sample in October and December 1981 and March 1982 on a musselbed of the Slikken van Vianen.

disappeared in this period. Compared with the number per length class, hammerers took between 2.4 and 35 % of the mussels present, or overall 9%. However not all the mussels on the bed were harvestable. Indeed due to the selection for thin shelled mussels, and the avoidance of mussels overgrown by barnacles, only a fraction of the population present was harvestable. This fraction was calculated for each length class by multiplying the density with the fraction within the shell thickness classes taken by hammerers and then with the fraction of mussels overgrown by barnacles (Table 2). If we compare now the number of mussels taken with the harvestable density we see that, especially for the larger, more profitable mussels, a large part is removed over winter. However, as this still is a small fraction of the total population, this could explain why we did not find a significant increase in shell thickness over the winter.

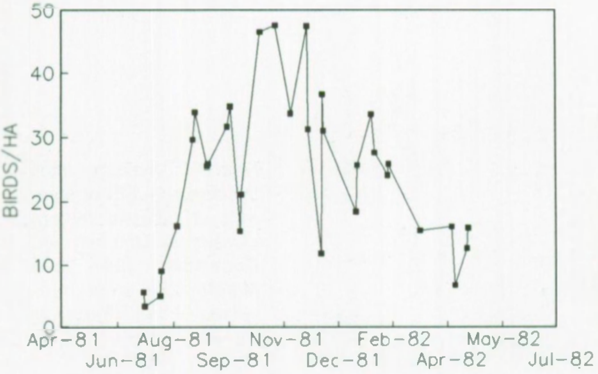

Figure 7. Density of feeding Oystercatchers (average for one tidal cycle) in the study plot during the season 1981-82.

Table 2. Impact of Oystercatchers on the mussel population. For each length class of mussels, the feeding rate (number of mussels taken/300 sec of foraging), the total number of mussels taken by hammering Oystercatchers between October 1981 and March 1982 (N/m^2), the density of mussels in October 1981 (N/m^2), numbers of mussels which disappeared between October 1981 and March 1982 (N/m^2), density of mussels in October 1981 harvestable for hammering Oystercatchers (N/m^2). For details about the calculations see text.

Length class (mm)	Feeding rate	Total number of mussels taken by hammerers	Density of mussels on the bed October 1981	Density of mussels disappeared between October 1981 and March 1982	Harvestable density of mussels October 1981	Total number of mussels taken by hammerers (Percentage of density)	Total number of mussels taken by hammerers (Percentage of harvestable density)
17.5	0.057	2	49	-7.54	49	4	4
22.5	1.171	5	49	15.09	49	10	10
27.5	0.171	5	41	26.40	38	12	13
32.5	0.486	15	87	60.36	78	17	19
37.5	0.429	13	140	56.58	74	9	18
42.5	0.714	21	147	7.54	26	14	81
47.5	0.343	10	174	75.45	13	6	77
52.5	0.057	2	83	22.63	1	2	200
57.5	0	0	15	7.54	0		
sum	2.428	73	792	271.62	328	9	22

DISCUSSION

Mussel selection

The influence of the shell thickness of mussels on the feeding behaviour and prey selection of Oystercatchers was first discussed by Norton Griffiths (1967). In an experiment, very similar to the one described here, he found differences in the force needed to open mussels from different beds. Although not measured, he attributed this result to differences in shell thickness between mussels from the two beds. This difference was reflected in the size selection of hammering Oystercatchers. On the lower part of the Ravenglass musselbeds, where the shells were thicker, no mussels longer than 40 mm were hammered, whereas on the Pensar beds, where shells were thin, all sizes were hammered (Norton Griffiths, 1967). Shell thickness does, however, not only influence size selection. More recently, it has been shown that, even within one length class of mussels, there is a strong selection for the thin-shelled mussels (Durell & Goss-Custard, 1984; Meire & Ervynck, 1986; Sutherland & Ens, 1987; Cayford & Goss-Custard, 1990).

The results of our experiment show a supraproportional relation between the number of blows needed to open a mussel and its shell thickness. As Norton Griffiths (1967) also showed, no relation with mussel length or indeed any of the other measures such as the height or breath of the shell and the force necessary to open the shell is found. Consistent with this is that Durell & Goss-Custard (1984) did not find any difference in shell width, depth and volume between shells taken by ventral hammerers and shells taken at random from the musselbed.

The effect of shell thickness on the profitability of mussels is considerable. I do not have data to test whether handling time increases with increasing shell thickness for mussels of a given size, as assumed in calculating profitability, but Sutherland & Ens (1987) did find a relation between shell thickness and handling time for mussels of 35-40 mm. The estimate of profitability remains qualitative, as it was not the real force to open a mussel that was measured. However, the results convincingly show a decreasing profitability with increasing shell thickness, a profitability which differs between length classes. The now well documented selection for thin shelled mussels and the acceptance of thicker mussels within the larger length classes (Fig. 3) are clear evidence that the prey selection of Oystercatchers is in accordance with an energy maximization foraging strategy.

From these results we can easily predict that, if the intake rate declines, for whatever reason, hammerers should accept thicker mussels in their diet. No field data are available at present to test this possibility convincingly, but Sutherland & Ens (1987) found in an experiment with captive birds that, once the preferred prey had been depleted, birds took the thicker-shelled mussels.

From the results presented in this paper and from previous studies we can conclude that the selection of mussels by ventral hammerers depends on several factors: the coverage by barnacles (Ens, 1982; Durell & Goss-Custard, 1984; Meire & Ervynck, 1986), shell thickness (Norton Griffiths, 1967; Durell & Goss-Custard, 1984; Meire & Ervynck, 1986; Sutherland & Ens, 1987), how firmly the mussels are attached to the substrate (Norton Griffiths, 1967) and, of course their density (Meire & Ervynck, 1986). The flesh-content of the mussel is also important. This is not only highly variable on one musselbed (Durell & Goss-Custard, 1984) but also shows distinct seasonal variations with the lowest flesh-content occurring in spring (Craeymeersch *et al.*, 1986; Cayford & Goss-Custard, 1990).

Ecological consequences of prey characteristics

As so many different characteristics of the mussels present on a bed influence prey selection and hence intake rate we would expect differences in these parameters to influence the distribution of Oystercatchers between beds. Indeed Goss-Custard *et al.* (1981) found a significant partial correlation between shell thickness of the mussels on a bed and the density of Oystercatchers. The ecological consequences of the prey characteristics may, however, go still further.

Interference is thought to be important in determining the distribution of the birds over their feeding areas (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987a, b, c; Meire, 1987), though the cause of interference is not yet completely understood. Ens & Goss-Custard (1984) propose that it is possible to attribute interference to a basic cause, i.e., the increased opportunities for stealing at high bird densities among birds in a well established dominance hierarchy. Prey robbing among Oystercatchers (Ens & Goss-Custard, 1984) or kleptoparasitism by Herring Gulls (Koene, 1978), can be very important and significantly reduce intake rate. Prey robbing can be viewed simply as a problem of prey choice (Dunbrack, 1979; Barnard & Stephens, 1981; Thompson & Barnard, 1984; Thompson, 1986; Ens *et al.*, 1990) with attacks being initiated so as to maximize the net rate of energy gain. Whether or not a robbing attempt will be profitable depends on the energy content of the prey, the handling time and the probability of a successful attack. When we compare our study area with the Exe estuary, robbing seldom occurs in the Oosterschelde (Table 3). This difference could be attributed to the difference in shell thickness and handling time or preferred mussel-size between both study areas (Table 3). Because the densities of birds and mussels are both comparable, it seems that the differences in robbing, result from the differences in the prey characteristics indicating that, in Vianen, it is not profitable to steal mussels. Generally, since the larger the prey, the longer the handling time and the higher the profitability, kleptoparasitism is directed mostly towards prey with a long handling time. For hammering Oystercathers, the handling time of mussels is dependent on shell thickness and is at least 75% longer in the Exe than in Vianen.

Table 3. Comparison between some characteristics of both the Oystercatcher and mussel populations in the Exe estuary and on the Slikken van Vianen. For the data of the Exe estuary the source is given.

	OYSTERCATCHERS		
	Vianen	Exe	Source
Densities (N/ha)	up to 50	up to 40	1
Number of interactions (N/5 min)	0.48	1.13	2
Contribution of stolen mussels to total number consumed (%)	0.01	6	3
Handling time (45mm) (s)	90	173	4
	MUSSELS		
	Vianen	Exe	Source
Population density	up to 600	up to 550	1
Shell thickness (45mm) (mm)	0.9	1.1	5
Biomass (45mm) (mg AFDW)	380	350-650	5

1 Goss-Custard *et al.* 1982 (*); 2 Goss-Custard *et al.* 1984; 3 Goss-Custard & Durell, 1987; 4 Ens, 1982; 5 Durell & Goss-Custard, 1984;

(*) In many papers on the Oystercatchers of the Exe estuary much higher densities are mentioned. Density can, however, be measured in different ways. The data given here can be compared.

Notwithstanding the low level of aggression and food robbing, interference, the depression of intake rate in function of bird density, occurs at the Slikken van Vianen (unpublished data). Furthermore the Oystercatchers disperse themselves over the musselbeds in a fashion similar to that found in the Exe (Meire & Kuijken, 1984; Meire, 1991; this thesis). Therefore frequent aggression is not required for interference to occur, as has been assumed by Ens & Goss-Custard (1984). Rather bird density per se, avoidance, or some other factor must cause interference. Nor does interspecific kleptoparasitism provide an explanation of the difference as it was also unimportant at the Slikken van Vianen.

Food supply and Oystercatcher densities

Predation by shorebirds can substantially reduce prey populations over the winter (Goss-Custard, 1980; Baird *et al.*, 1985; Meire *et al.*, 1993). As only a small proportion of the prey is actually available and harvestable to the predators (see e.g., Zwarts & Blomert, 1992; Zwarts *et al.*, 1992), the depletion of their food resource is much more important than suggested by the depletion of the population as a whole. For the musselbed studied in this paper this is clearly shown by the data in Table 3. The estimate of the harvestable fraction is without doubt subject to much error. The shell thickness classes taken by the birds were determined by shell collections in September. It is well possible that in the course of the winter thicker shells are taken. No data are available to test this. The division of mussels as edible or not based on the barnacle cover is subjective, especially in mussels not extensively covered. On the other hand Meire (1991) showed that of the total population only a small proportion of mussels is visible at the surface and thus available to Oystercatchers. This was not accounted for in this study. Therefore, although the estimate of the harvestable fraction is subject to error, it is certain that the fraction is small. It is probably even much smaller for the smaller mussels than estimated here, as especially these are covered by others (Meire, 1991). Hammering Oystercatchers remove a substantial part of the harvestable fraction. For the stabbing birds no estimates of the harvestable fraction can be made yet as no information on the gaping behaviour of the mussels is available.

Populations are limited by their food supply only if their consumption equals the production of the harvestable fraction (Piersma, 1987). No studies are available yet where this was measured although the work of Zwarts and coworkers give very detailed estimates of the harvestable fraction of different prey for several wader species (Zwarts & Wanink, 1984; 1989; Zwarts & Blomert, 1992; Zwarts *et al.*, 1992). Craeymeersch *et al.* (1986) estimated for the same study plot on the Slikken van Vianen in the same period the annual production of the entire mussel population to be about 156 g AFDW m^{-2} y^{-1}. By multiplying, for each size class, the production with the percentage mussels harvestable, the total production of the harvestable mussels in the preferred size classes (25 - 60mm) can be estimated at 46 g AFDW m^{-2} y^{-1}. The total consumption by Oystercatchers on a yearly basis cannot be estimated based on the feeding rates measured in autumn (see Table 3) since it is known that in spring the birds tend to feed on much smaller mussels (Cayford & Goss-Custard, 1990). The yearly consumption of hammerers, estimated by multiplying the total number of feeding minutes m^{-2} y^{-1} with an average intake of 150 mg AFDW min^{-1}, is 32 g AFDW m^{-2} y^{-1}, or about 70% of the production. Taking in account the fact that not all smaller mussels are visible and hence not harvestable for the birds, the consumption by hammerers is near to the production. This could indicate they are limited by their food supply. There is also other circumstantial evidence for this conclusion. Indeed, in 1987 a huge biomass of second year cockles occurred in the same study plot and the numbers of Oystercatchers did increase quite substantially (Meire, 1991).

Conclusions

The results presented in this paper, along with those from other papers, clearly show that the mussel selection by hammering Oystercatchers can be well understood and modelled within the framework of the Optimal Foraging Theory. Without a detailed knowledge of the foraging behaviour of the predator it is not possible to give an adequate estimate of the harvestable prey density. This is essential in order to solve the problem of carrying capacity, a question often asked by conservationists. Ultimately one should succeed in modelling habitat distribution of birds on the basis of foraging models as done for example by Werner *et al.* (1983) for fish.

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REFERENCES

Baird, D. , P. R. Evans, H. Milne & N. W. Pienkowski, 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanogr. Mar. Biol. annu. Rev. 23: 573-597.

Barnard, C. J. & H. Stephens, 1981. Prey size selection by Lapwings in Lapwing/Gull associations. Behaviour 77: 1-22.

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.

Craeymeersch, J. A., P. M. J. Herman & P. M. Meire, 1986. Secondary production of an intertidal mussel (*Mytilus edulis*) population in the Eastern Scheldt (S.W. Netherland). Hydrobiologia 133: 107-115.

Dunbrack, R. L,. 1979. A re-examination of robbing behavior in foraging egrets. Ecology 60: 644-645.

Durell, Le V. Dit, S. E. A. & J. D. Goss-Custard, 1984. Prey selection within a size-class of mussels, *Mytilus edulis,* by Oystercatchers, *Haematopus ostralegus*. Anim. Behav. 32: 1197-1203.

Ens, B., 1982. Size selection in mussel-feeding Oystercatchers. Wader Study Group Bull. 34: 16-20.

Ens, B. & J. D. Goss-Custard, 1984. Interference among Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. J. anim. Ecol. 53: 217-231.

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.

Goss-Custard, J. D., 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J. D. & S. E. A. Durell Le V. Dit, 1987a. 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. & S. E. A. Durell Le V. Dit, 1987b. Age-related effects in Oystercatchers *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*. II. Aggression. J. anim. Ecol. 56: 537-548.

Goss-Custard, J. D. & S. E. A. Durell Le V. Dit, 1987c. Age-related effects in Oystercatchers *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*. III. The effect of interference on overall intake rate. J. anim. Ecol. 56: 549-558.

Goss-Custard, J. D., R. T. Clarke & S. E. A. le V. Dit Durell, 1984. Rates of food intake and aggression of Oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. J. anim. Ecol. 53: 233-245.

Goss-Custard, J. D., S. E. A. le V. dit Durell & B. J. Ens, 1982. Individual differences in aggressiveness and food stealing among wintering Oystercatchers, *Haematopus ostralegus* L. Anim. Behav. 30: 917-928.

Goss-Custard, J. D., S. E. A. Le V. Dit Durell, S. McGrorty, C. J. Reading & R. T. Clarke, 1981. Factors affecting the occupation of mussel (*Mytilus edulis*) beds by Oystercatchers (*Haematopus ostralegus*) on the Exe estuary, Devon. In N. V. Jones & W. J. W. Wolff (eds), Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 217-230.

Gould, S. J. & R. C. Lewontin, 1979. The spandrels of San Marco and the Panglossian paradigm. Proc. R. Soc. Lond. B 205: 581-598.

Gray, R. D., 1987. Faith and foraging: a critique of the 'paradigm argument from design'. In A. C. Kamil, J. R. Krebs & H. R. Pulliam (eds), Foraging Behavior. Plenum Press, New York: 69-140

Koene, P., 1978. De Scholekster: aantalseffecten op de voedselopname. Msc. Thesis, Zoölogisch Laboratorium, University of Groningen, Groningen.

Krebs, J. R. & A. Kacelnik, 1991. Decision-making. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology: an evolutionary approach. Sinauer Associates, Sunderland, MA: 105-136.

Krebs, J. R. & R. H. McCleery, 1984. Optimization in behavioural ecology. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology: an evolutionary approach. Sinauer Associates, Sunderland, MA: 91-121.

Krebs, J. R., D. W. Stephens & W. J. Sutherland, 1983. Perspectives in Optimal Foraging. In G. A. Clark & A. H. Brush (eds), Perspectives in Ornithology. Cambridge University Press, New York: 165-216.

Meire, P. M., 1987. Foraging behaviour of some wintering waders: prey-selection and habitat distribution. In A. C. Kamil, J. R. Krebs & H. R. Pulliam (eds), Foraging behavior. Plenum Press, New york: 215-237.

Meire, P. M., 1991. Effects of a substantial reduction in intertidal area on numbers and densities of waders. Acta XX Congr. Int. Ornithol.: 2219-2227.

Meire, P. M. & A. Ervynck, 1986. Are Oystercatchers, (*Haematopus ostralegus*), selecting the most profitable mussels (*Mytilus edulis*)? Anim. Behav. 34: 1427-1435.

Meire, P. M. & E. Kuijken, 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal Waders and wildfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. M. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, the Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77: 283-311.

Meire, P. M., H. Schekkerman & P. L. Meininger, 1993. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands. Hydrobiologia: in press.

Norton Griffiths, M., 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher, *Haematopus ostralegus*, on the edible mussel, *Mytilus edulis*. Ibis 109: 412-424.

Pierce, G. J. & J. G. Ollason, 1987. Eight reasons why optimal foraging theory is a complete waste of time. Oikos 49: 111-117.

Piersma, T., 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Mar. Ecol. Progr. Ser. 38: 187-196.

Pyke, G. H., 1984. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. 15: 523-575.

Stephens, D. W. & J. R. Krebs, 1986. Foraging Theory. Princeton University Press, Princeton.

Sutherland, W. J., 1982. Do Oystercatchers select the most profitable Cockles? Anim. Behav. 30: 857-861.

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., 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.

Thompson, D. B. A., 1986. The economics of kleptoparasitism: optimal foraging, host and prey selection by gulls. Anim. Behav. 34: 1189-1205.

Thompson, D. B. A. & C. J. Barnard, 1984. Prey selection by plovers: optimal foraging in mixed species groups. Anim. Behav. 32: 554-563.

Werner, E. E., 1984. The mechanisms of species interactions and community organization in fish. In D. R. Jr. Strong, D. Simberloff, L. G. Abele & A. B. Thistle (eds), Ecological Communities: Conceptual Issues and Evidence. Princeton University Press, Princeton, New Jersey, U.S.A.

Werner, E. E. & G. G. Mittelbach, 1981. Optimal foraging: field tests of diet choice and habitat switching. Am. Zool. 21: 813-829.

Werner, E. E., G. G. Mittelbach, D. J. Hall & J. F. Gilliam, 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64: 1525-1539

Zwarts, L., 1986. Burying depth of the benthic bivalve *Scrobicularia plana* (Da Costa) in relation to siphon-cropping. J. exp. mar. Biol. Ecol. 101: 25-39.

Zwarts, L. & A-M. Blommert, 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. & J. Wanink, 1984. How Oystercatchers and Curlews successively deplete clams. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal Waders and wildfowl in winter. Cambridge University Press, Cambridge: 69-83.

Zwarts, L. & J. H. Wanink, 1989. Siphon size and burying depth in deposit- and suspension feeding benthic bivalves. Mar. Biol. 100: 227-240.

Zwarts, L., A-M. Blommert & J. H. Wannink, 1992. Annual and seasonal variation in the food supply harvestable for Knot *Calidris canutus* staging in the Wadden Sea in late summer. Mar. Ecol. Prog. Ser. 83: 128-139.

Zwarts, L., J. T. Cayford, J. B. Hulscher, P. M. Meire & P. Triplet, in press. Size Selection and intake rate in Oystercatcher. In J.D. Goss-Custard (Ed), Behavioral Ecology of the Oystercatcher. Oxford University press, Oxford: in press.

Chapter 9

DISTRIBUTION OF OYSTERCATCHERS (*Haematopus ostralegus*) OVER A TIDAL FLAT IN RELATION TO THEIR MAIN PREY SPECIES, COCKLES (*Cerastoderma edule*) AND MUSSELS (*Mytilus edulis*): DID IT CHANGE AFTER A SUBSTANTIAL HABITAT LOSS?

Patrick M. Meire

An extension of the paper:

Meire, P., 1991 : Effects of a substantial reduction in intertidal area on numbers and densities of waders. Acta XX Congr. Int. Ornithol.: 2219-2227.

ABSTRACT

A storm surge barrier and secondary dams were built in the Oosterschelde estuary (The Netherlands) resulting in a 30% decrease of intertidal area. If the birds, previously feeding behind the secondary dams, could establish themselves in the remaining intertidal areas, their densities should increase.

To test this, the distribution of Oystercatchers, *Haematopus ostralegus*, in relation to their main prey, cockles, *Cerastoderma edule*, and mussels *Mytilus edulis*, was studied before and after the reduction in tidal area.

During one tidal cycle, the birds are moving quickly through the highest part of the intertidal area towards the preferred feeding areas below mid tidal level. The distribution of the birds was related to their food supply. As the number of birds in the whole area increased, the birds gradually spread from the preferred feeding plots towards the less preferred ones, a pattern of sequential filling of the feeding area. This pattern did not change after the environmental changes.

After the major loss of intertidal habitat occurred, densities of Oystercatchers feeding on cockles were within the range predicted by prey biomass - bird density relationships as measured before the environmental changes. On musselbeds, however, densities of Oystercatchers are much higher since 1987/88. It is shown that this is caused by an increase in the cockle biomass due to an abundant spatfall in 1985, after a severe winter. It is argued that there is a different availability of mussels and cockles. It is concluded that the number of Oystercatchers in the Oosterschelde is linked very closely to their food supply.

INTRODUCTION

Understanding the effects of habitat loss has become an essential theme in applied ecology. Ultimately one should be able to forecast the effects of the removal of part of the habitat on the total population size of the species that use it.

Birds, and especially waders, offer very good subjects for study of this problem. Several species are restricted to intertidal areas during the non-breeding season and, unlike many other organisms, it is possible to get estimates, through internationally organized counts, of their total population size (e.g., Smit & Piersma, 1989). Intertidal areas are very threatened with destruction all over the world. Hence much attention is being paid, mainly in the Netherlands and the United Kingdom, to studying the influence of loss of intertidal area on waders (e.g., Evans, 1991; Goss-Custard & Durell, 1990; Sutherland & Goss-Custard, 1991).

When assessing the impact of loss of intertidal areas on wader populations, three main issues must be resolved. First, can birds, displaced from one area, establish themselves somewhere else? Second, does an increase in density of birds affect their rates of survival and reproduction because of changes in the intensity of predation, disease or competition for food? Finally what effect do these changed rates have on population size, from the local to the species level (Goss-Custard & Durell, 1990)? The first two questions have received by far the most attention. The evidence at present indicates that bird densities reach plateaux values in preferred feeding areas (e.g., Hicklin & Smith, 1984; Goss-Custard, 1977a,b; Meire & Kuijken, 1984; Zwarts, 1974; Zwarts & Drent, 1981) and that interference causes the birds to disperse over the available feeding sites (e.g., Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987); hence it is expected that given a constant amount of food, densities will not increase after a loss of feeding areas. Few studies are available however, where both the occurrence of waders and their food supply was studied before, during and after the removal of intertidal area (e.g., Evans *et al.*, 1979).

The Delta area in the southwestern part of the Netherlands consists of the estuaries of the rivers Rijn, Maas and Schelde. The execution of the "Delta Plan" resulted in the closure of most estuaries. In the Oosterschelde a storm surge barrier was built as a compromise between safety and environmental considerations. Its construction resulted, however, still in a substantial reduction in intertidal area (e.g., Nienhuis & Smaal, 1993). As these works offered a good possibility for studying the effects of habitat loss on non-breeding waders a long term study on both the benthic food supply, bird numbers and the distribution and foraging behaviour of birds was started (Meire & Kuijken, 1984; 1987; Schekkerman *et al.*, 1993; Seys *et al.*, 1993).

After the reduction of the intertidal area, wader densities should increase, at least if birds, displaced from the reclaimed area, can establish themselves in the remaining area. In this paper I try to answer this question based on detailed observations of the distribution of the birds over their low water feeding areas from well before to three years after the completion of the coastal engineering works. Only data on the Oystercatcher (*Haematopus ostralegus*) in relation to its major prey, the edible mussel (*Mytilus edulis*) and Cockles (*Cerastoderma edule*) are presented here.

MATERIAL AND METHODS

Study area

The Oosterschelde is a major estuary in the southwestern part of the Netherlands. A storm surge barrier was built in the mouth of the estuary and two secondary dams inland. These works resulted in a strongly reduced tidal amplitude in 1986 and 1987. On completion of the secondary dams in April 1987 the total intertidal area was reduced by some 30% from 17000 to 11365 ha and the tidal amplitude increased again to 3.25 m compared to 3.7 m before works started (Smaal *et al.*, 1991; Smaal & Boeije, 1991; Nienhuis & Smaal, 1993). The reduction in tidal area is caused mainly by the closure of the Krammer-Volkerak, the northern branch of the estuary, although in the eastern part of the estuary, already in 1983 some 1800 ha intertidal area was lost. In the remaining tidal part, 680 ha of tidal flats were lost due to the reduced tidal amplitude. In this paper the data are divided into two groups: until April 1987 is the pre-barrier situation, after April 1987 is the post-barrier situation. Detailed observations on the occurrence of waders in relation to their food supply were carried out at the Slikken van Vianen, a small intertidal flat in the middle of the estuary. A description of this site is given by Meire & Kuijken (1987).

Bird counts

At the Slikken van Vianen counts were carried out both at low and high water (see Meire & Kuijken, 1987; Meire & Meininger, 1993). At low water, numbers in permanent plots (0.5 - 1 ha), marked out with stakes on the flats, were counted during an entire tidal cycle on 220 days between 1979 and 1990. The numbers and activity of birds in the plots were noted every 30 min during most of a whole tidal cycle. In the first and last hour in which a plot was exposed, counts were made at least every 15 min, as bird numbers could change quickly at that time. Based on these counts, both the average feeding and total density and the number of feeding minutes per plot (expressed per ha) per tide were calculated. The feeding density and the number of feeding minutes were very well correlated (e.g., PQ6, autumn 1984 data: $r^2=0.92$, $N=22$, $P<0.001$; PQ32, autumn 1984 data: $r^2=0.88$, $N=18$, $P<0.001$). Therefore in further analysis only feeding density was used.

Six plots were followed through the entire study period and for this paper additional data from 11 plots studied in 1984 are also used. The plots PQ6, 10 and 22 were situated on a musselbed, the other three plots on a mudflat. Days with very short exposure time are omitted from the analysis, as also are data from the season 1986/87 when the storm surge barrier was used to manipulate the tide. For relating bird densities with prey biomass only data from December counts were used. At this time, bird numbers are at their maximum.

Benthic invertebrates

At the Slikken van Vianen the benthic invertebrates in all study plots were sampled annually in September or October (see Meire & Dereu, 1990 for details). In this paper the total biomass (expressed in g ash free dry weight, AFDW) of cockles and mussels is used, including all size-classes. For the musselbeds the biomass of cockles and mussels was summed.

To measure the visibility of mussels, 40 cores (15 cm diameter) were taken on two musselbeds. The cores were brought to the laboratory where all mussels visible at the surface were painted with typex. After sieving they could easily be separated from the ones not visible. All mussels were measured (maximum length).

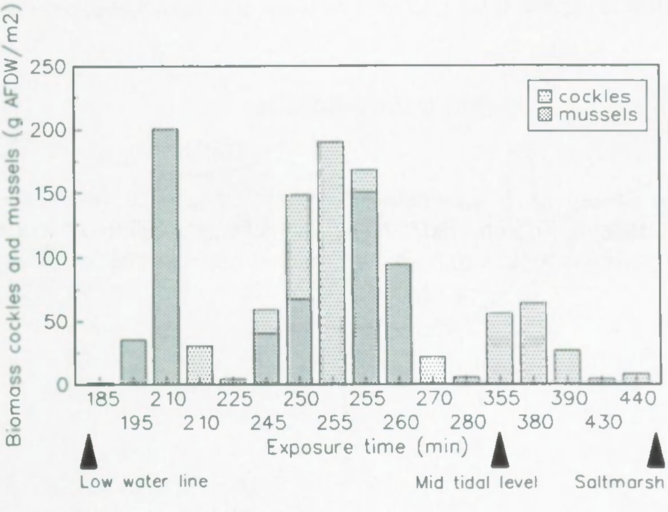

Figure 1. Biomass of cockles and mussels in autumn 1984 in the different study plots. The plots were ranked according to their exposure time, which is indicated on the X axis.

RESULTS

Distribution of the birds at low water: pre-barrier

Cockles and mussels, the major prey species of Oystercatchers were not spread uniformly over the tidal flats. As shown in Fig. 1, the areas with the highest biomass occurred lower in the intertidal zone (low exposure time), although also here large differences exist between sites. The upper parts of tidal flats had in general lower benthic biomasses.

This has a pronounced effect on the tidal migration and the distribution of the birds at low tide. In general all birds roost on the salt marsh or on adjacent arable land during high tide (Fig. 2). When the tide ebbs some birds immediately start to feed. The exposed flats have, however, low biomasses. Hence the birds tend to follow the waterline, to reach as soon as possible the lower, richer feeding areas. In the study plots situated high in the intertidal zone (e.g., PQ 32), this behaviour results in a clear peak of birds moving through the plots as the waterline passes through it. A few birds remain for some time in this area (Fig. 3a) but at low water the area is virtually abandoned. About 2.5 hours after high tide, most birds left the high tide roosts and follow the waterline. Near mid tidal level we see still a clear peak of birds

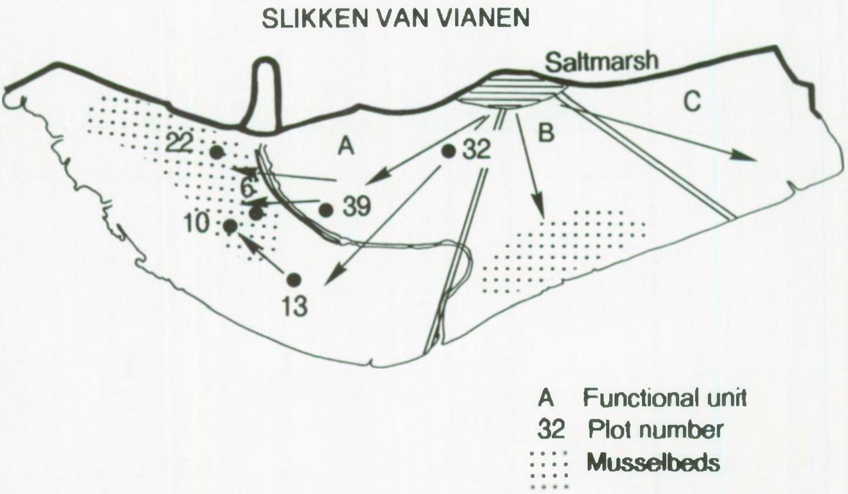

Figure 2. Map of the Slikken van Vianen showing the tidal migration pattern of Oystercatchers and the three functional units.

as a plot becomes exposed (Fig. 3b). From here the birds move to their preferred feeding areas below mid tidal level where the pattern of occurrence is quite different. Mostly the birds remain in a particular feeding area until it is flooded again (Fig. 3,d,e,f). In these sites the density remains fairly constant during the whole exposure of the site. The distribution of the birds is most pronounced at low tide when some areas may accommodate more than hundred birds per hectare and other areas, previously having high

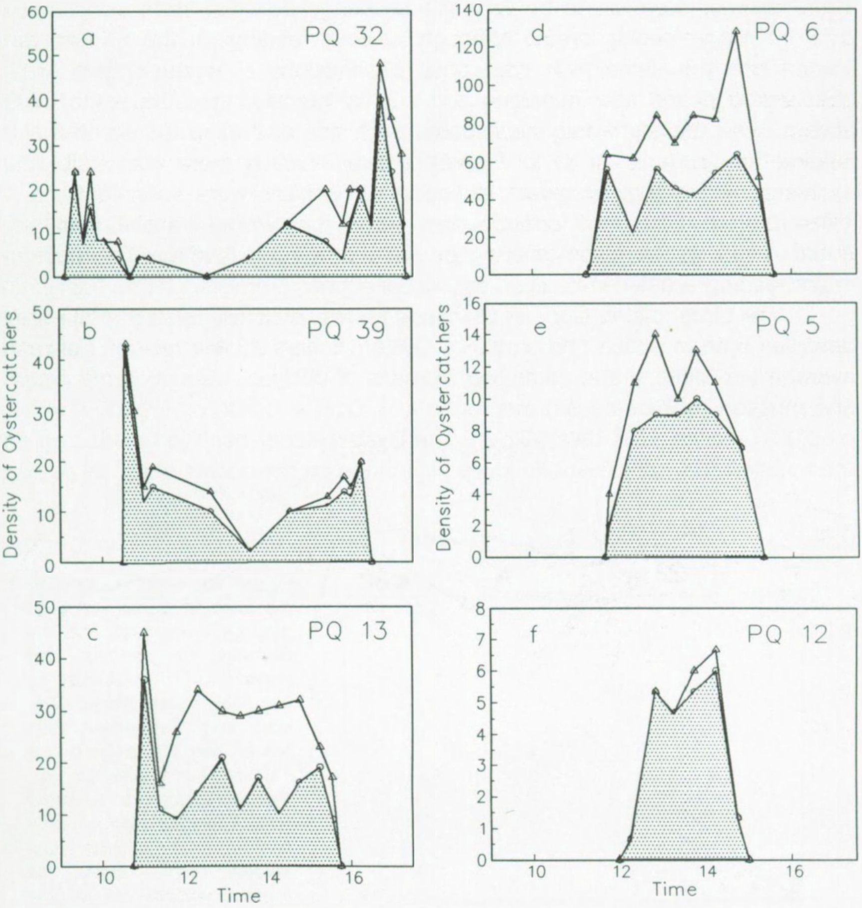

Figure 3. Density of Oystercatchers (birds/ha) as a function of time in 6 different plots situated along the tidal gradient. Both total density (upper line) and feeding density (shaded part), as measured on 17 October 1984, are given for the whole exposure time of each plot. PQ 32 has the longest exposure time, PQ 12 the shortest.

densities, are almost completely abandoned. When the tide floods, the opposite migration takes place. This pattern is however subject to many variations. Disturbance, which occurs very regularly, can profoundly change the distribution patterns. Especially the peak of birds moving through the higher plots is subject to much variation. This peak is usually much more pronounced in winter than in summer, and after severe disturbance at low tide. The pattern described here is based on observations from a small but representative part of the study area (Fig. 2). The migration pattern of birds to the other preferred feeding areas at low water (sites B and C, Fig. 2) is similar. There seems, however, to be very little exchange between birds using these different major feeding areas. Although all birds feeding on the Slikken van Vianen use the same high tide roost, observations of colour-ringed birds, observation of the tidal migration and counts indicated that the same birds always used the same migration routes each tide and used the same major feeding areas (A, B or C in Fig. 2), between which there was very little exchange. After, e.g., a severe disturbance, no birds were seen to fly to a different area, rather they formed a flock where they waited inactive, until they could return to the place where they were previously feeding. These three major feeding areas can be seen as functional units (Tamisier, 1974; 1981).

The birds' distribution, as described above, is closely related to the prey densities both in space and time. For Oystercatchers a clear relation between average bird density and combined biomass of cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*) was found ($y = 0.56 + 0.22x$; $r^2 = 0.81$, $N = 17$, $p<0.001$) for the 1984 data (Fig. 4). The Oystercatcher densities measured on the musselbeds were relatively lower than those on the cockle plots, as can be

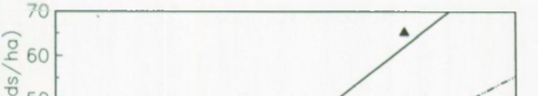

Figure 4. Relation between the average density of foraging Oystercatchers and the biomass of cockles and mussel in 17 studyplots of the Slikken van Vianen. The data from December 1984 are plotted. Musselplots are indicated with solid circles, the regression as a dotted line. Triangles and a solid line are plots outside musselbeds (cockle plots). The regression line for all the data is given as a dashed line.

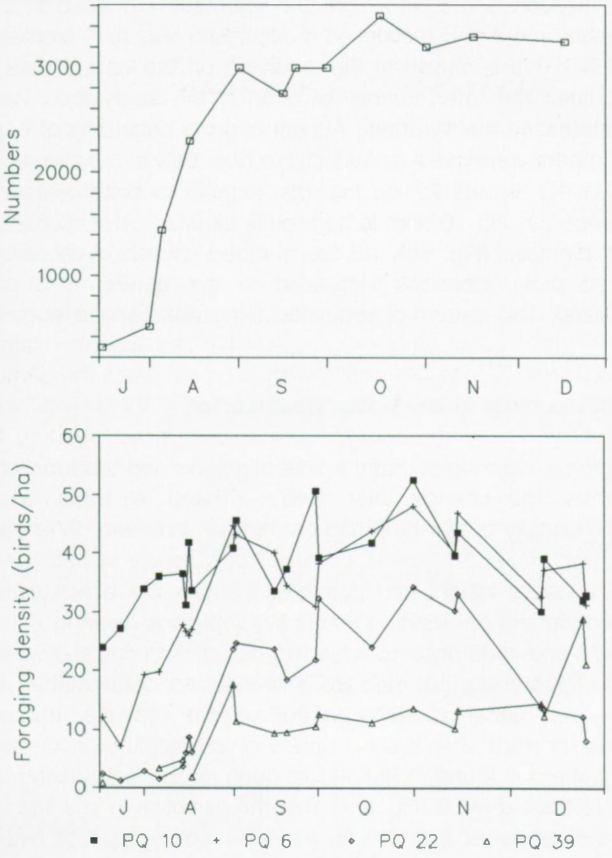

Figure 5. Total number of Oystercatchers on the Slikken van Vianen (upper panel) and feeding densities in 4 plots between July and December 1984. The biomass of the plots were respectively 167, 148, 94 and 55 g AFDW m^{-2} for PQ 10, 6, 22 and 39. All but one plot (39) were situated on a musselbed.

seen from the regression line based on only the musselbed plots ($y = -0.55 + 0.18x$; $r^2 = 0.74$, $N = 6$, $p<0.05$) or only the cockle plots ($y=-0.63 + 0.32x$; $r^2 = 0.92$, $N = 11$, $p<0.001$). The slope of both regressions differs significantly (ANCOVA, $F=16.32$, df (1,13), $p<0.05$).

Prey density not only influences the spatial distribution and density of birds, it also determines the sequence in which different areas are used in the course of the season. Plots with high prey biomass are used first; as bird numbers increase, more and more feed in plots with less prey biomass (Meire & Kuijken, 1984). This is shown in Fig. 5 based on the data of late summer and autumn 1984. The total number of birds in the study area was low in summer and increased mainly during August and the beginning of September, after which numbers were more or less stable (Fig. 5a). In July nearly no birds were present in PQ 39 and 22; as the total number of birds was increasing, densities increased in PQ 10 and 6, both plots situated on a musselbed, and having a high biomass (Fig. 5b). As the numbers stabilized more or less in these preferred plots, densities increased in the others, until also here densities stabilized. This pattern of sequential filling was seen in each season.

Distribution of the birds at low water: post-barrier

There are no indications that the tidal migration and the functional units, described above, did change after 1987. Therefore, what could have changed, is the density of the birds and the relation between density and prey biomass.

To get a better insight into possible changes the average density of foraging Oystercatchers per month in three study plots is given in Fig. 6. In PQ 6, between 1979 and 1986 maximum feeding densities during the winter varied around 50 Oystercatchers per hectare and seemed quite stable. Densities increased however, rather suddenly in the season 1987/88, and stabilized around 80 birds/hectare after a short period of extremely high densities (Fig. 6a). A similar pattern is found in PQ 10, although, in the last season, densities decreased more than in PQ 6 (Fig. 6b). That the densities in late summer 1979 in PQ 10 were much lower than in later years is because at that time the plot was not yet a musselbed and had only a low biomass of cockles. In PQ 13 (Fig. 6c) the pattern is different and densities increased gradually in the course of the whole study period. The increased densities in PQ 6 and 10 coincided with the closure of the Krammer-Volkerak, but the question arises whether this loss of intertidal areas or another change, e.g., prey biomass, was the cause. In Fig. 7 and 9 the relation between foraging density and prey biomass density is given for plots on musselbeds and other plots separately, based on all available data from the six plots followed during the whole study period and from all the plots studied in 1984. In the pre-barrier period a clear relation between cockle biomass and Oystercatcher densities was found ($y = 0.46 + .32x$; $r^2 = 0.95$, $N = 18$, $p < 0.001$)(Fig. 7). After completion of the works, with one exception (PQ39 in 1988), the densities of Oystercathers are comparable to those before closure at similar prey biomass, at least when the biomass values were low. At higher biomass values there is more scatter. In the post-barrier period there is also a significant relationship between Oystercatcher density and cockle biomass($y = 5.7 + .17x$; $r_2=0.67$, $N=8$, $p<0.05$; without PQ39, 1988). The slope of both regressions does however differ significantly (ANCOVA, $F=13.13$, df (1,22), $p<0.05$), the slope being smaller after 1987. The increase in density in PQ 13 is also related to an increase in the cockle biomass. Indeed there is a good correlation between the density

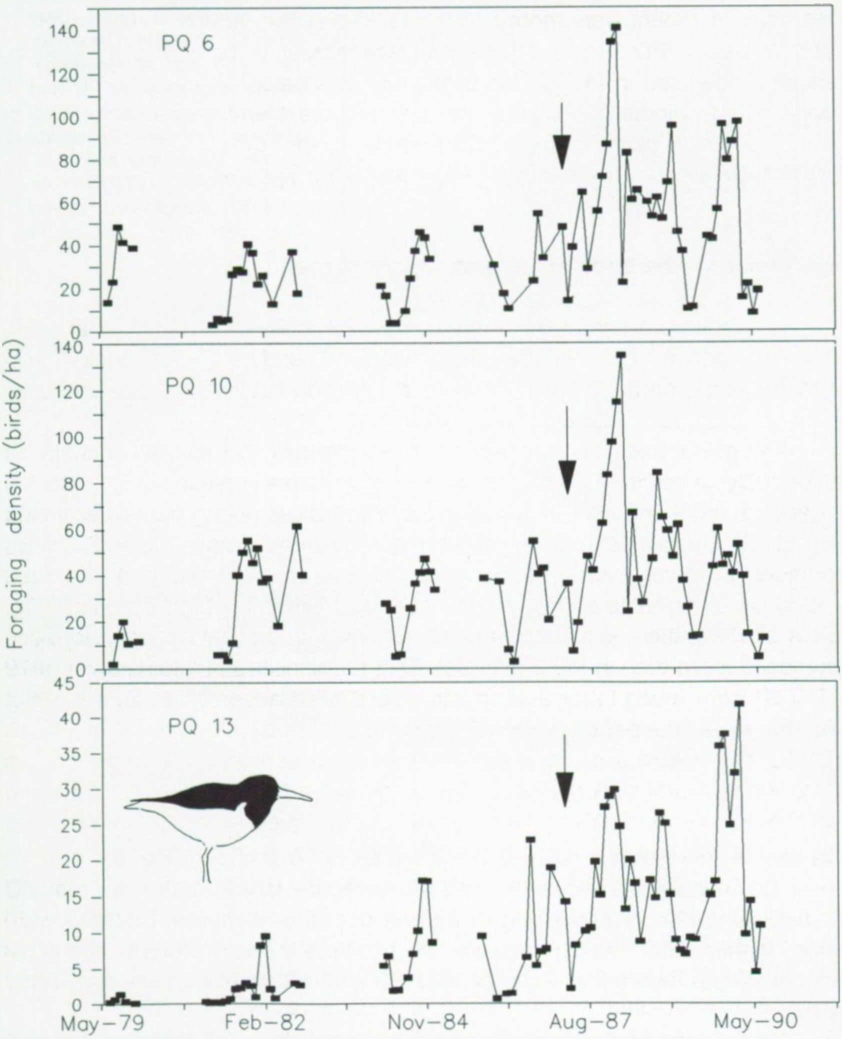

Figure 6. Density of foraging Oystercatchers (average per month) in three study plots between July 1979 and June 1990. The arrow indicates the closure of the Philipsdam, causing the major loss of intertidal area.

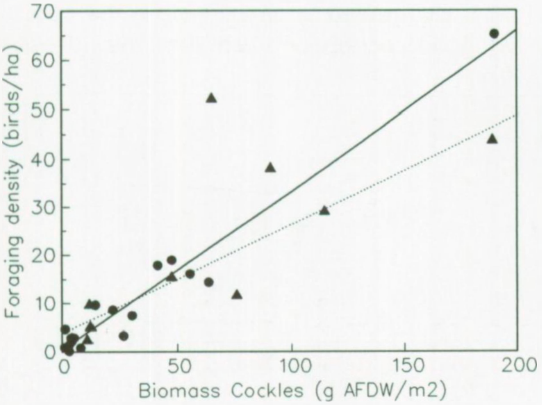

Figure 7. Relation between prey biomass and density of foraging Oystercatchers in non musselbed plots. Data from all plots in December 1984 (17) and all December values from plots 13, 32 and 39 were used. Values are the averages of all December counts. (circle and solid line: data from 1979/80 to 1986/87; triangle and dotted line: data from 1987/88 to 1989/90)

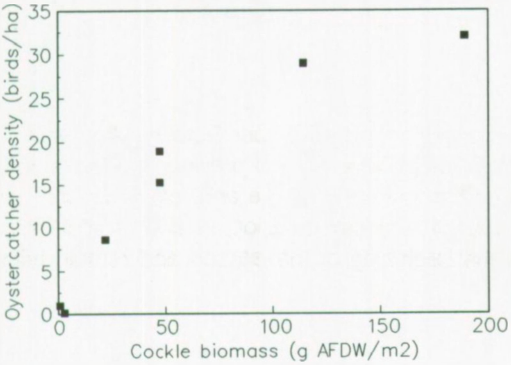

Figure 8. Relationship between the feeding density of Oystercatchers and cockles in PQ 13. All available December data between 1979 and 1989 are plotted.

and cockle biomass ($y= 4.5 + 0.17x$; $r^2=0.86$, $N=7$, $p<0.05$) (Fig. 8).

On musselbeds, however, with the exception of the data from plot PQ 22, bird densities corresponding to a given cockle plus mussel biomass were much higher after barrier closure than before. Two different numerical responses one before the winter of 1987/88 and one thereafter are suggested by Fig. 9.

The sequential filling of different study plots was also found after 1987. One important difference could be noted however. During the season 1987/88, the first season after the closure of the Krammer- Volkerak and also the first season with a high cockle biomass we see that in July the densities of Oystercatchers were indeed higher in PQ 6 and 10 compared to

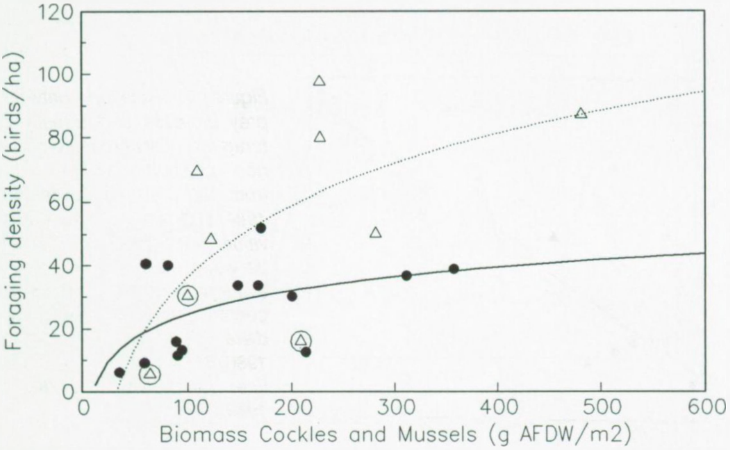

Figure 9. Relation between prey biomass and density of foraging Oystercatchers in mussel plots. Data from all plots in December 1984 (17) and all December values from plots 6, 10, 22, were used. Values are the averages of all December counts. (filled circle and solid line: data from 1979/80 to 1986/87; open triangle and dotted line: data from 1987/88 to 1988/89; the data from plot 22 are encircled). Lines fitted by eye.

PQ 22. In the last plot, densities increased in September-October after which they remained rather constant and at a level similar to previous years. In both PQ 6 and 10, however, densities continued to increase and reached only their peak values in February (Fig. 10a). In the next season, in both these plots, densities are already high from the beginning of the season and remain fairly constant (Fig. 10b).

Prey availability

The difference in the relationships between Oystercatcher densities and prey densities on the mussel beds between the two study periods might be due to a difference in prey availability. On musselbeds Oystercatchers feed both on cockles and mussels. The average biomass of cockles and mussels in each plot until 1986 and from 1987 onwards is plotted in Fig. 11. On musselbed PQ 22 cockles occur in very low densities throughout the study period. Before 1987, cockles contributed, on average, 25 and 39 % of the total biomass in two study plots (PQ 6, 10) on musselbeds, but 66 and 78% respectively between 1987/88 and 1989/90. This change was due to an enormous spatfall in spring 1985, after the severe winter of 1984/85. This increase in the cockle population is also reflected in a substantial increase in

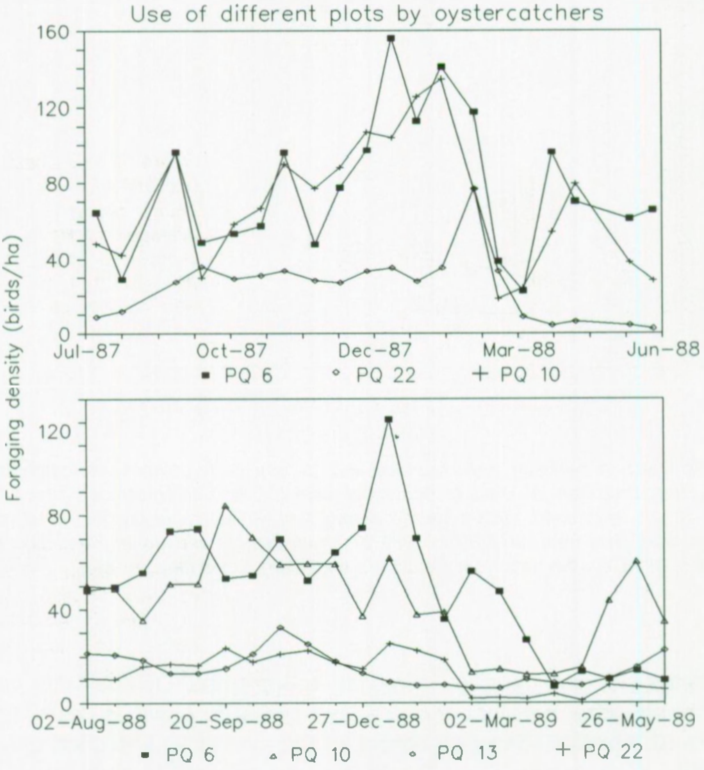

Figure 10. Feeding densities of Oystercatcher in several study plots in the season 1987/88 and 1988/89.

cockle biomass in the non musselbed plots, especially in PQ 13 and 39 (Fig. 11). In Fig. 12 the average Oystercatcher densities before 1987 and after 1987 are plotted for each PQ (averages of all December observations in both periods are used). On the musselbeds we see a clear increase in PQ 6 and 10 where the cockle biomass increased and not in PQ 22, where cockles are nearly absent. The increase is also clear in both PQ 13 and 39 where cockle biomass also increased substantially.

These data show that the increase of Oystercatcher densities is related to the increase in cockle biomass. Why are the Oystercatcher densities then lower at a similar biomass of mussels as suggested by the two numerical

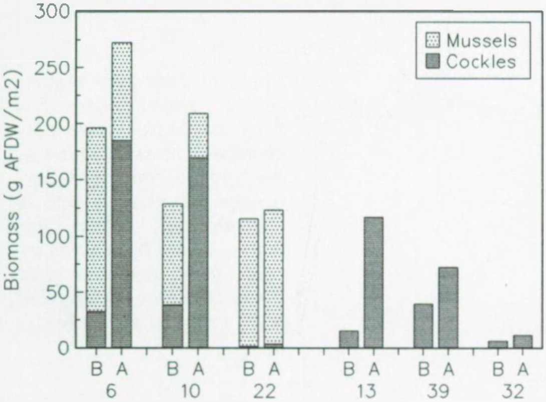

Figure 11. Biomass of cockles and mussels in each studyplot. The average values of all samplings before 1987 (B) and from 1987 onwards (A) are given.

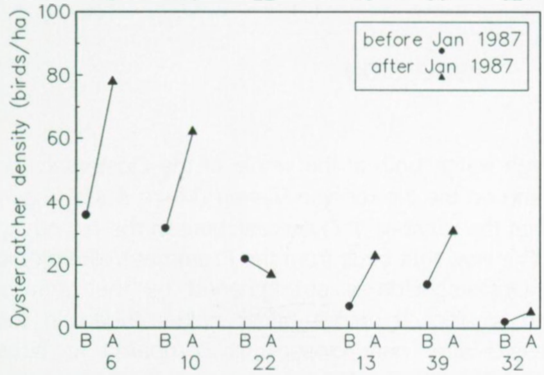

Figure 12. Average density of feeding Oystercatchers in each study plot (december values) before 1987 and from 1987 onwards.

responses in Fig. 9. In Fig. 13 the proportion of mussels visible at the surface and with a shell thickness within the range normally taken by Oystercatchers (see Meire & Ervynck, 1986), is plotted by length class. Larger mussels, visible at the surface, are mostly too thick for Oystercatchers. The total amount of biomass, as measured in the normal sampling procedure, is therefore not a good indicator of mussel availability for Oystercatchers, whereas it probably is for cockles. They all occur in the top few centimeters of the sediment, never one on top of the other, and thus are all available. Birds do not seem to select them by shell thickness. The very low bird densities in PQ22 compared to a rather high biomass density can also been explained by low prey availability. All mussels in this plot were larger than 40 mm, hence only a small fraction could have been taken by Oystercatcher.

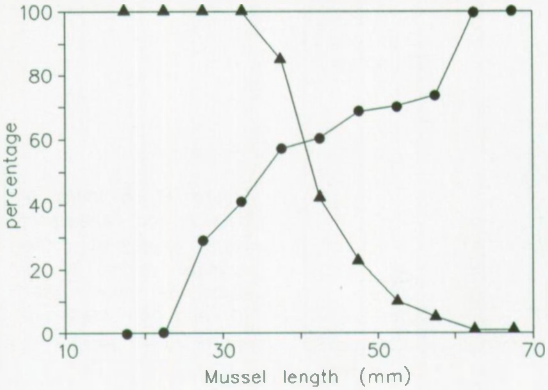

Figure 13. Availability of mussels to Oystercatchers. For each length-class the percentage of mussels visible at the surface (dot) and percentage of mussels with a shellthickness within the range taken by Oystercatchers (calculated from data given by Meire & Ervynck, 1986) (triangle) are shown.

DISCUSSION

From the counts at high water, both in the whole of the Oosterschelde (Schekkerman *et al.*, 1993) and on the Slikken van Vianen (Meire & Meininger, 1993) it can be concluded that the number of Oystercatchers in the remaining tidal parts did not increase. The view that birds from the Krammer-Volkerak did not fit into the remaining Oosterschelde is strengthened by the data of Lambeck (1991) who found significantly more birds, colour-ringed in the Krammer-Volkerak, disappeared after dam closure as compared to birds ringed in the remaining part of the estuary. Although total numbers using the remaining intertidal areas stayed quite constant, minor changes in distribution within the estuary occurred. At the Slikken van Vianen numbers increased somewhat from the season 1987/88 onwards (Meire & Meininger, 1993), coincident with and possibly related to the loss of intertidal area in the nearby Krammer-Volkerak? This question can only be answered based on detailed knowledge of the distribution of the birds over their feeding areas and the underlying causes.

On tidal flats, birds distribute themselves, as the tide ebbs. Several distribution patterns could be detected. First of all, three functional units occur on the Slikken van Vianen. A functional unit was defined by Tamisier (1974; 1981) as a geographical sector of a wintering area, where all individuals belonging to a group can fulfill the whole of their requirements. Between units there is nearly no exchange. The distribution pattern of Oystercatchers on the Slikken van Vianen can also be seen as a system of functional units with the exception that all birds use the same roost. They obtain however, all of their food from within the unit. This does not mean that each bird is always feeding in the same spot. Indeed Goss-Custard *et al.* (1982) found that several birds were seen virtually all tides on the spot on a musselbed, but others were not. They can be feeding in other sites within the functional unit. This is confirmed by observations of colour-ringed birds (Meire, in prep.). Swennen (1984) showed that there was little exchange between roosts and that individual birds were also faithful to one roost from year to year.

During one tidal cycle the birds move with the tide edge from the upper part of the tidal zone to the lower feeding areas and back. This caused a distinct pattern of occurrence of birds in the different parts of the intertidal area. In plots high in the tidal zone, clear peaks in bird density occurred just after the plot became exposed and/or just before it was covered again. In the preferred feeding areas a much more stable pattern of occurrence was found. Densities did not only differ within one tide and between plots, but changed within one plot during the course of the season. The birds spread out from the initially occupied areas in a highly ordered fashion, both on one tidal flat (Goss-Custard, 1977a,b; Zwarts & Drent, 1981; Meire & Kuijken, 1984), between tidal flats within an estuary (Goss-Custard *et al.*, 1981; 1982) or between entire estuaries (Moser, 1988). This pattern of sequential filling of feeding areas has also been described for Teal (Zwarts, 1974) and geese (Meire & Kuijken, 1991). This spreading out over the food gradient occurs probably because interference competition for the preferred feeding areas intensifies (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987) and is expected based on the Ideal Free distribution with unequal competitors (Sutherland & Parker, 1985). It is similar to the buffer hypothesis formulated by Kluyver & Tinbergen (1953) to describe how birds occupy territories in heterogeneous habitats. No difference in these patterns in the course of the study period were either expected nor observed.

The difference in densities between the different sites are likely to be caused by a difference in the prey populations. Indeed in many different studies it has been shown that the density of feeding waders is related to their food supply (e.g., Goss-Custard, 1970; Goss-Custard, Kay & Blindell, 1977; O'Connor & Brown, 1977; Bryant, 1979; Sutherland, 1982; Goss-Custard *et al.*, 1991a). This relation seems to hold both within an estuary (e.g., Bryant, 1979) and between estuaries (e.g., Goss-Custard *et al.*, 1977; 1991a). The relation can be obscured because birds are feeding on different species or size-classes within one species. To overcome this problem Sutherland (1982) related Oystercatcher densities to the measured intake rate of cockles and found a clear positive relation that was not found when relating bird densities to prey density. Intake rate can however be affected by many additional factors and the food gradient may have to be defined in terms of several factors. Goss-Custard *et al.* (1991b) measured the part played by several factors (densities of several length classes, shell thickness, beds-area, flatness, exposure time, algae coverage, softness of sediment and distance to roost) in determining the between-bed variation. Density of large mussels, shell thickness, substrate softness and distance to roost had a significant effect on bird densities but the effect depended on the population size of the Oystercatchers in the estuary. Even this detailed analysis remains quite weak. Indeed Oystercatchers are using essentially two methods to open mussels (Norton-Griffiths, 1967) and different characteristics of the prey are relevant to both groups. Different proportions of birds using each feeding method on the different beds could influence the analysis. Even more the real availability of mussels to the birds might differ substantially from the measured prey density (Meire & Ervynck, 1986; Cayford & Goss-Custard, 1990) and there is not essentially a relation between the total density and the available density. The visibility of the mussels at the surface, as shown in this paper, can substantially reduce the available density. Relating bird densities to prey densities therefore is subject to many possible errors. Furthermore, Evans & Dugan (1984) argued that, although in some localized areas a relationship between bird densities and absolute densities of prey can be demonstrated, the precise form of the relationship must vary with latitude because of differences in average temperature and other weather factors. Our study period includes three severe winters 1984/85 -1986/87. The relationships between prey and predator given in this paper are therefore rather crude.

Without studying this relation it is however not possible to understand why bird densities did increase in some of our study plots. The data show however that on non-musselbed plots the relation between bird and prey density was similar before and after the closure of the Krammer-Volkerak. The opposite was true for the musselbeds. From the present and earlier data (Meire & Kuijken, 1984) we believe that densities had reached a plateau value on the musselbeds. The data from 1987/88 onwards, however, show that bird densities can reach much higher values. As the measured and available biomass differs in mussels, the plateau value could well be an artefact of the measure of prey biomass used. Above a certain density only a certain amount of mussels will be visible at the surface, hence available biomass does not increase further with total mussel biomass and could explain the plateau found in the data. As the biomass became dominated by cockles in 1987/88 the total available biomass increased substantially, as did the bird densities. The data suggest a new plateau but at much higher bird densities; another artefact? At present we do not know what regulates the density of birds. Contrary to expectations (e.g., Goss-Custard 1980) their aggressiveness did not increase with bird density (unpublished data).

From this information we can conclude that the increase in bird numbers and densities on the Slikken van Vianen after the closure of the Krammer-Volkerak was entirely caused by an increased food supply. Why then did total numbers in the whole estuary not increase, as the important spatfall of cockles in spring 1985 was not restricted to the Slikken van Vianen? This was probably due to the cockle fisheries. Normally around one million kg fish-meat of cockles are taken annually from the Oosterschelde. Because of small stocks in the Wadden Sea and the high biomass in the Oosterschelde all cockle fishermen came in September 1987 to the Oosterschelde and removed nearly seven million kg fish-meat of cockles from the estuary (Coosen *et al.*, 1993; Meire *et al.*, 1993). On the Slikken van Vianen no cockles were fished. This probably explains why Oystercatcher numbers increased there (especially in some plots), contrary to the rest of the Oosterschelde. Had cockles not been fished, it is most probable that birds displaced from the Krammer-Volkerak after the dam closure, could have established themselves in the Oosterschelde, indicating that Oystercatchers numbers are now tightly linked to the available prey biomass or the estuary is at carrying capacity (Meire *et al.*, 1993).

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REFERENCES

Bryant, D. M., 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). Estuar. coast. mar. Sci. 9: 369-384.

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.

Coosen, J., F. Twisk, M. W. M. Van Der Tol, R. H. D. Lambeck, M. R. Van Stralen & P. M. Meire, 1993. Variability in stock assessment of cockles (*Cerastoderma edule* L.) in the Oosterschelde (in 1980-1990), in relation to environmental factors. Hydrobiologia: in press.

Ens, B. J. & J. D. Goss-Custard, 1984. Interference among Oystercatchers *Haematopus ostralegus* L. feeding on mussels, *Mytilus edulis* L., on the Exe estuary. J. anim. Ecol. 53: 217-232.

Evans, P. R., 1991. Introductionary remarks: habitat loss-effects on shorebird populations. Acta XX Congr. Int. Ornithol.: 2197-2198.

Evans, P. R. & P. J. Dugan, 1984. Coastal birds: numbers in relation to food resources. In P. R. Evans, J. D. Goss-Custard, W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 8-28.

Evans, P. R., D. M. Henderson, P. J. Knights & M. W. Pienkowski, 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. Oecologia 41: 183-206.

Goss-Custard, J. D., 1970. The responses of Redshank *Tringa totanus* to spatial variations in the density of their prey. J. anim. Ecol. 39: 91-114.

Goss-Custard, J. D., 1977a. 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., 1977b. Predator responses and prey mortality in Redshank, *Tringa totanus* (L.) and a preferred prey, *Corophium volutator* (Pallas). J. anim. Ecol. 46: 21-35.

Goss-Custard, J. D., 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1987. Age-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. III. The effect of interference on overall intake rate. J. anim. Ecol. 53: 233-245.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Goss-Custard, J. D., R. W. G. Caldow & R. T. Clarke, 1991b. Correlates of the density of foraging Oystercatchers *Haematopus ostralegus* at different population sizes. J. anim. Ecol. 60.

Goss-Custard, J. D., D. J. Kay & R. M. Blindell, 1977. The density of migratory and overwintering Redshank *Tringa totanus* and Curlew *Numenius arquata* in relation to the density of their prey in south-east England. Estuar. coast. mar. Sci. 5: 497-510.

Goss-Custard, J. D., S. E. A. Le V. Dit Durell, S. McGrorty, C. J. Reading, 1982. Use of mussel *Mytilus edulis* beds by Oystercatchers *Haematopus ostralegus* according to age and population size. J. anim. Ecol. 51: 543-554.

Goss-Custard, J. D., S. E. A. Le V. Dit Durell, S. McGrorty, C. J. Reading & R. T. Clarke, 1981. Factors affecting the occupation of mussel (*Mytilus edulis*) beds by Oystercatchers (*Haematopus ostralegus*) on the Exe estuary, Devon. In N. V. Jones & W. J. Wolff (Eds), Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 217-229.

Goss Custard, J. D., R. M. Warwick, R. Kirby, S. McGrorty, R. T. Clarke, B. Pearson, W. E. Rispin, S. E. A. Le V. Dit Durell & R. J. Rose, 1991a. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn estuary. J. appl. Ecol. 28: 1004-1026.

Hicklin, P. W., P. C. Smith, 1984. Selection of foraging sites and invertebrate prey by migrant Semipalmated Sandpipers, *Calidris pusilla* (Pallas), in Minas Basin, Bay of Fundy. Can. J. Zool. 62: 2201-2211.

Kluijver, H. N. & L. Tinbergen, 1953. Territory and the regulation of density in titmice. Arch. Néerl. Zool. 10: 265-289.

Lambeck, R. H. D., 1991. Changes in abundance, distribution and mortality of wintering Oystercatchers after habitat loss in the Delta area, SW Netherlands. Acta XX Congr. Int. Ornithol.: 2208-2218 .

Meire, P. M. & J. Dereu, 1990. Use of the abundance/biomass comparison method for detecting environmental stress: some considerations based on intertidal macrozoobenthos and bird communities. J. appl. Ecol. 27: 210-223.

Meire, P. M. & A. Ervynck, 1986. Are Oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? Anim. Behav. 34: 1427-1435.

Meire, P. M. & E. Kuijken, 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. M. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, The Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77: 283-311.

Meire, P. M. & E. Kuyken, 1991. Factors affecting the number and distribution of wintering geese and some implications for their conservation in Flanders, Belgium. Ardea 79:

143-158.

Meire, P. M. & P. L. Meininger, 1993. Changes in wader populations at the slikken van Vianen (Oosterschelde NL) after major environmental changes (1979-1990). This thesis.

Meire, P. M., H. Schekkerman & P. L. Meininger, 1993. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands. Hydrobiologia: in press.

Moser, M. E., 1988. Limits to the numbers of Grey Plovers *Pluvialis squatarola* wintering on British estuaries: an analysis of long-term population trends. J. appl. Ecol. 25: 473-486.

Nienhuis, P. N. & A. C. Smaal, 1993. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction. Hydrobiologia: in press.

Norton-Griffiths, M., 1967. Some ecological aspects of the feeding bahaviour of the Oystercatcher, *Haematopus ostralegus*, on the edible mussel, *Mytilus edulis*. Ibis, 109: 412-424.

O'Connor, R. J. & R. A. Brown, 1977. Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. Oecologia 27: 75-92.

Schekkerman, H., P. L. Meininger & P. M. Meire, 1993. Changes in the waterbird populations of the Oosterschelde, SW. Netherlands, as a result of large scale coastal engineering works. Hydrobiologia: In press.

Seys, J. J., P. M. Meire, J. Coosen & J. Craeymeersch, 1993. Long-term changes (1979-89) in the intertidal macrozoobenthos of the Oosterschelde estuary: are patterns in total density, biomass and diversity induced by the construction of the storm surge barrier? Hydrobiologia: In press.

Smaal, A. C. & R. C. Boeije, 1991. Veilig getij, de effecten van de waterbouwkundige werken op het getijdenmilieu van de Oosterschelde. Nota GWWS 91.088 Rijkswaterstaat, Middelburg.

Smaal, A. C., M. Knoester, P. H. Nienhuis, P. M. Meire, 1991. Changes in the Oosterschelde ecosystem induced by the Delta works. In M. Elliot & J. P. Ducrotoy (Eds), Estuaries and Coasts: Spatial and Temporal intercomparisons. ECSA 19 Symposium. Olson & Olson, Fredensborg: 375-384.

Smit, C. J. & T. Piersma, 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In H. Boyd & J-Y. Pirot (Eds), Flyways and reserve networks for water birds. IWRB Special publication No.9, Slimbridge: 24-63.

Sutherland, W. J., 1982. Spatial variations in the predation of cockles by Oystercatchers at Traeth Melynog, Anglesey. II. The pattern of predation. J. anim. Ecol. 51: 491-500.

Sutherland, W. J. & J. D. Goss-Custard, 1991. Predicting the consequences of habitat loss on shorebird populations. Acta XX Congr. Int. Ornithol.: 2199-2207.

Sutherland, W. J. & G. A. Parker, 1985. Distribution of unequal competitors. In R. M. Sibly & R. H. Smith (Eds), Behavioural ecology, ecological consequences of adaptive behaviour, Blackwell Scientific Publishers, Oxford: 255-276.

Swennen, C., 1984. Differences in quality of roosting flocks of Oystercatchers. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 177-189.

Tamisier, A., 1974. Etho-ecologiacl studies of Teal wintering in the Camargue (Rhône Delta, France). Wildfowl 25: 107-117.

Tamisier, A., 1981. The functional units of wintering ducks: a spatial integration of their comfort and feeding requirements. Verh. Orn. Ges. Bayern 23: 229-238.

Zwarts, L., 1974. Vogels van het brakke getijgebied. Bondsuitgeverij, Amsterdam.

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 (Eds), Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 193-216

Chapter 10

FEEDING BEHAVIOUR OF OYSTERCATCHERS (*Haematopus ostralegus)* DURING A PERIOD OF TIDAL MANIPULATIONS.

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Submitted to Ardea

ABSTRACT

Due to the construction of a storm surge barrier in the mouth of the Oosterschelde (SW Netherlands), the tidal amplitude in the estuary can be manipulated. For engineering purposes the barrier was closed for some time during the autumn of 1986. In this paper we describe the effects of this closure on the numbers, distribution and foraging behaviour of Oystercatchers on the Slikken van Vianen, a tidal flat in the Oosterschelde.

During a closure, which lasted once for six consecutive tides, the water level remained high and only the upper part of the intertidal area was exposed. Oystercatchers spent most of their time feeding in this zone, where they normally spent only a very short time during their migration towards the preferred feeding areas below mid tidal level. When, during a severe gale, feeding conditions further deteriorated, birds stopped feeding altogether. When the tidal regime was restored, birds distributed themselves over the feeding areas as before.

Based on measurements of food intake it could be calculated that, during the closure of the barrier, a bird, on average, obtained only two thirds of the food that it would have taken under normal conditions. Therefore we expected that, if Oystercatchers are able to increase their intake rate, they would do so the first time they could feed again on their preferred feeding areas. However, no changes in intake rates were found, indicating that birds were feeding at their maximum rates. This contrasts with some experimental results in the literature. The possible causes are discussed.

No effects on total numbers of birds present in the study area during this period of closure could be detected, although the consumption deficit could have influenced the condition of the birds.

INTRODUCTION

Kersten & Piersma (1987) showed waders to have a basal metabolic rate which is on average 42% above the level predicted for non-passerine birds by the formula of Aschoff & Pohl (1970). This leads to a high daily energy expenditure. During pre-migratory fattening or in mid-winter energy demands of these birds will further increase.

During periods of increased energy demands the birds could feed for longer (Zwarts *et al.*, 1990). This is however rarely possibly for birds feeding in the intertidal zone, as the exposure time of their feeding areas is determined by the state of the tide. Even more, during severe weather conditions, the available feeding time might be further reduced. The only possibility for the birds to obtain the necessary energy is to increase their intake rate while foraging.

However, optimal foraging theory is based on the assumption that birds are maximizing their intake rate (e.g., Stephens & Krebs, 1986). Indeed, in many studies it was shown that waders do select the energetically more profitable kind of prey species, size classes of one prey species, or places in which to feed. Evidence that waders usually select the more profitable option does not necessarily imply that they are also foraging at the maximum possible rate. Indeed, many variables of the foraging behaviour may be under the birds' control. The obvious example is walking speed: by increasing the walking speed the bird may increase the encounter rate with prey and hence the intake rate. Birds might be expected to do this, for instance when the time available for feeding is limited or when energy demands are particularly high (Goss-Custard, 1985). However very few studies until now could test whether birds are really feeding at a maximum rate or not. The clearest evidence that Oystercatchers can increase their intake rate while foraging comes from an experimental study (Swennen *et al.*, 1989). From field studies there are only some indications, that birds increased their intake rates (e.g., Hulscher, 1982).

The closure of the storm surge barrier in the Oosterschelde during October 1986, when the preferred feeding areas of waders were not exposed for six consecutive tides, provided an opportunity to study the effects of reduced feeding time on the foraging behaviour of waders and to test whether these birds were feeding at their maximum rate.

In this paper we describe the environmental conditions during the period of closure of the storm surge barrier and its effects on numbers, distribution over the feeding areas, prey selection and foraging behaviour of Oystercatchers (*Haematopus ostralegus*). The total consumption of the population during the period of tidal manipulation was estimated and the different ways in which the birds could compensate for their consumption deficit are analysed.

MATERIAL AND METHODS

1. Study area

1.1 The Oosterschelde

The Oosterschelde is a major estuary in the so called "Delta area" of SW-Netherland. A storm surge barrier (completed in 1986) was built in the mouth of the estuary together with two secondary dams more inland (Oesterdam and Philipsdam) (Fig. 1). In the final phase of the closure of the

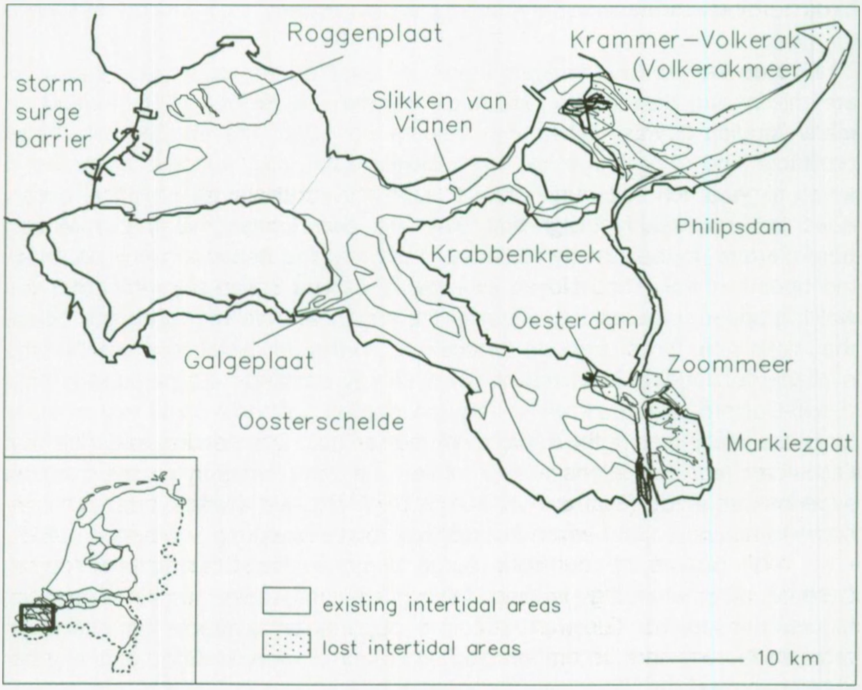

Figure 1. Map of the Oosterschelde estuary with the location of the study area, the storm surge barrier and the secondary dams.

two secondary dams, the storm surge barrier was closed in October 1986 and April 1987 to reduce the impact of tidal currents on the constructions. This paper deals only with the period of closure in October 1986 (for details on the coastal engineering works see Smaal *et al.*, 1991; Nienhuis & Smaal, 1993).

1.2 The Slikken van Vianen

The "Slikken van Vianen" is a tidal flat of ca 510 ha, bordering the south-east coast of Schouwen-Duiveland (fig. 1) (see Meire & Kuijken (1987) for a detailed description of the study area). On the flat, 6 permanent plots (PQ's), measuring between 0.5 and 1 ha, were marked out with stakes. The location of the plots covered both a gradient in prey density and tidal elevation. Each plot was situated in an area that was, at least visually, very homogeneous. PQ 6, 10 and 22 were situated on a musselbed, the other three (13, 32 and 39) on the mudflat.

2. Bird observations

2.1 Bird counts

2.1.1 High tide counts.

Birds which fed during low tide on the mudflats of the Slikken van Vianen, concentrated at high tide on "high tide roosts", mainly on the salt marsh and on adjacent fields. Here birds were counted on 7 occasions between July 1986 and November 1986 (see Meire & Meininger, 1993 for details about the counts).

2.1.2 Low tide counts.

Bird numbers in the PQ's were counted during an entire tidal cycle, at least when light conditions allowed. The number and activity of birds in the plots were noted at least every 30 min during most of a whole tidal cycle. In the first and last hour in which the plot was exposed, counts were made much more frequently, as bird numbers could change quickly at that time. Based on these counts, the average feeding and total density and the number of feeding minutes per plot per tide were calculated. Counts are available from 14 days between August and December 1986. Between 16 and 24 October the plots were counted daily.

2.2 Feeding behaviour

In the different study plots, except PQ 13 that was too far away from the observation points, individual birds were observed for at least 5 min. A focal animal was selected at random and its foraging behaviour was recorded in detail. When the bird stopped foraging for a longer time (e.g., started sleeping) the observation was stopped. The following events were noted: *Social interactions*: all interactions with other Oystercatchers or other species. *Non foraging*: preening, sleeping etc. *Handling a prey* depending on the foraging technique: -hammerers: pulling a mussel or cockle from the substrate, carrying it to a firm place, putting it down, hammering through the shell and swallowing the flesh; -stabbers: stabbing the bill between the open valves, prizing them apart and swallowing the flesh. *Wasted handling*: the prey was attacked but the bird gave up without opening it. Sequences of behaviour were recorded on tape and later transferred to a computer. From these observations the percentage time spent in different activities was calculated. In total 663 observations from 5 PQ's were available for analysis. The average values per plot were calculated. For some analyses the data were grouped into three periods: before, during (19-23 October 1986) and after manipulation.

The length of the mussels and cockles attacked was measured against bill length, and later converted to mm using a regression line relating estimates to real size. This regression line was obtained from estimates, made by the observers, of mussels of known size that were presented at the bill of a stuffed Oystercatcher under 'field conditions' (using binoculars and the same observation distance). In some plots the birds fed on very small cockles. The length of these cockles was determined by collecting some sediment from the plot and sorting out the shells opened by the birds. These estimates of prey length, combined with the biomass of each size-class, which is known for each PQ (see below), allowed us to calculate the intake rate. Both intake and feeding rate were calculated per 5 min feeding.

2.3 Calculation of the consumption by the Oystercatcher population

Since birds were not individually marked, no estimate of the consumption by single birds during one tide could be made. To overcome this, we estimated the consumption of the entire population. The birds feeding in the sector of the Slikken van Vianen where our study plots are situated can be regarded as a functional unit (Meire, 1993). Each tide the same group of birds was using that area to feed. The functional unit was divided into three different sectors that are more or less homogeneous and in which the benthic biomass is rather similar. Sector 1 (90ha) consists of the upper part of the intertidal zone and is characterized by a low biomass of cockles. Sector 2 is the area situated around mid tidal level and measures about 40ha. Sector 3 (40 ha) enclose the low lying areas with a high biomass and comprising the musselbeds. PQ 32 is situated in sector 1, PQ 39 and 13 in sector 2 and the three musselplots in sector 3. Based on the feeding observations in each plot the average intake rate per sector was estimated. This was multiplied by the number of feeding minutes that were measured in the plots and by the area of the sector to obtain the consumption of the birds per sector. Combining the data from the three sectors gives an estimate of the total consumption of the population using the functional unit.

To calculate the cumulative intake during the period of tidal manipulations (15-24 October 1986) the values for each tide were summed. For the low water periods at night the same value for the preceding tide during day-time was used.

3. Benthos

The benthic invertebrates in all study plots were sampled in September 1986. On the musselbeds 15, in the other plots 10 core samples (15 cm diameter) were taken to a depth of 30 cm and preserved in 7% neutral formaline. In the laboratory all animals were picked out after sieving the samples on a 1 mm mesh sieve, identified, counted, measured and weighed (see Meire & Dereu, 1990 for details). In this paper the biomass (expressed in g ash free dry weight, AFDW) of cockles and mussels is used. For mussels this includes all size-classes >10mm.

4. Environmental variables

Data on the water-level, the percentage closure of the barrier and the exposure time of the study plots (calculated from the measured tidal height in front of the study area and the known height of the plots) were kindly supplied by Ir. Tom Pieters, Rijkswaterstaat-Tidal Waters Division.

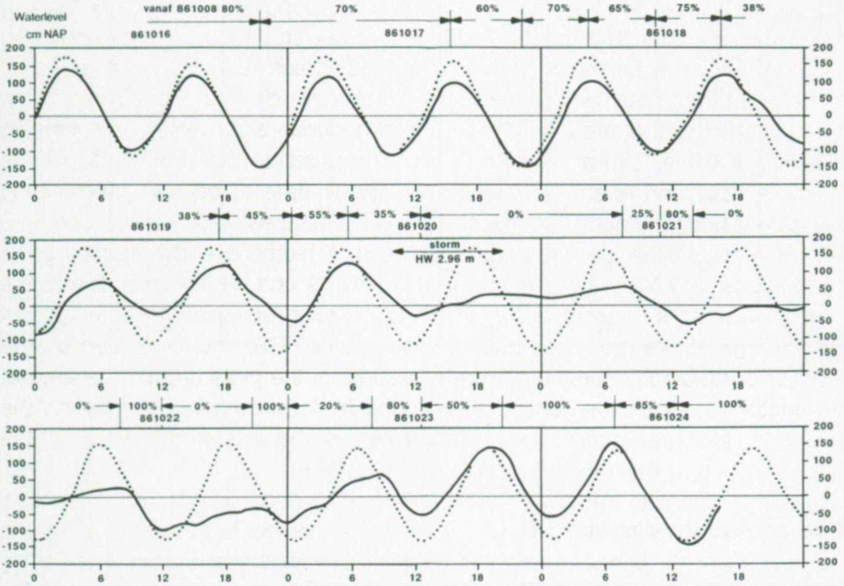

Figure. 2. Waterlevels near Yerseke between 16-10-86 and 24-10-86. The predicted waterlevel (dotted line) and the observed waterlevel (full line) are plotted, together with the percentage opening of the storm surge barrier.

Table 1. Exposure time of the six study plots at each low tide during the period of tidal manipulations. For each plot also the tidal height (in cm NAP) is given.

		Exposure time (min)					
Date	LW	32	39	13	22	6	10
16/10	9.00	430	310	60	224	222	182
	21.00	495	380	250	317	300	295
17/10	10.00	470	338	145	266	229	234
	22.00	530	370	250	319	300	298
18/10	11.00	390	355	120	242	185	207
	24.00	510	360	0	161	130	120
19/10	11.00	405	235	0	0	0	0
	23.00	360	0	0	0	0	0
20/10	12.00		0	0	0	0	0
21/10	0.00		0	0	0	0	0
	12.00	2905	420	0	0	0	0
22/10	1.00		0	0	0	0	0
	12.30		493	165	413	220	300
23/10	1.00		300	0	115	30	0
	13.00	385	210	0	0	0	0
24/10	1.30	350	230	0	0	0	0
	14.00	460	380	200	273	234	251
height		43	-18	-80	-50	-56	-60

RESULTS

Tide and weather conditions

In 1985 the tidal amplitude (3.7 m) started to decline, especially in the eastern part of the estuary, in 1986 in the whole estuary (Vroon, 1993). Tidal amplitude was reduced to about 2.6 m in October 1986 when the manipulation of the barrier started in order to close the Oesterdam. The percentage opening of the barrier and both predicted and observed water levels (expressed in cm NAP, the Dutch ordnance level) between 15 and 24 October 1986 are given in Fig. 2. The exposure time of the study plots is summarized in Table 1. In the lower ones, exposure time decreased significantly on 18 October 1986 and they were not exposed for six consecutive low water periods. On 22 October 1986 one more or less normal low water occurred, followed again by three tides in which the plots were not exposed. From 24 October 1986 onwards the normal tidal regime was restored. PQ 39, situated near mid tidal level was not exposed for 3 consecutive tides, PQ 32 on the other hand was not covered by water during four days! (table 1).

During the period of tidal manipulations the average air temperature varied between 10 and 13°C, which is normal for this time of the year. On 19 and 20 October there was, however, a severe gale with maximum wind speeds of 122 km/h on 20 October. From 19 to 24 October there was heavy rainfall (up to 18mm/day).

Numbers of Oystercatchers present

During the manipulation of the barrier, high water counts of Oystercatchers on the Slikken van Vianen showed a rather large variation between 1500 and 2500 birds. Low numbers were probably caused by missing some groups of birds, roosting at unusual places, especially during the storm. As several counts in the period of tidal manipulations were around 2500 birds we believe that the population in the study area remained rather stable during that period.

In the whole of the Oosterschelde, 83200 Oystercatchers were counted half October, 79600 birds one month later, indicating also almost no birds left the Oosterschelde during that time.

During the period of tidal manipulations about 1300 birds were using the functional unit where our study plots were located.

Table 2. Density (N/m^2) and biomass (g $AFDW/m^2$) of cockles and mussels (> 10mm) in the six study plots on the Slikken van Vianen in September 1986. For the three musselbeds, the musselcover (% of the plot covered by mussels) is also indicated.

PQ	6	10	22	13	39	32
Mussel biomass	36.8	20.7	58.1			
density	286.2	166.5	281.5			
cover	40.9	28.7	41.8			
cockle biomass	45.4	68.4	2.1	47.4	24.2	1.8
cockle density	3535	2295	92	1194	5432	543.2
Total	82.2	89.1	60.2	47.4	24.2	1.8

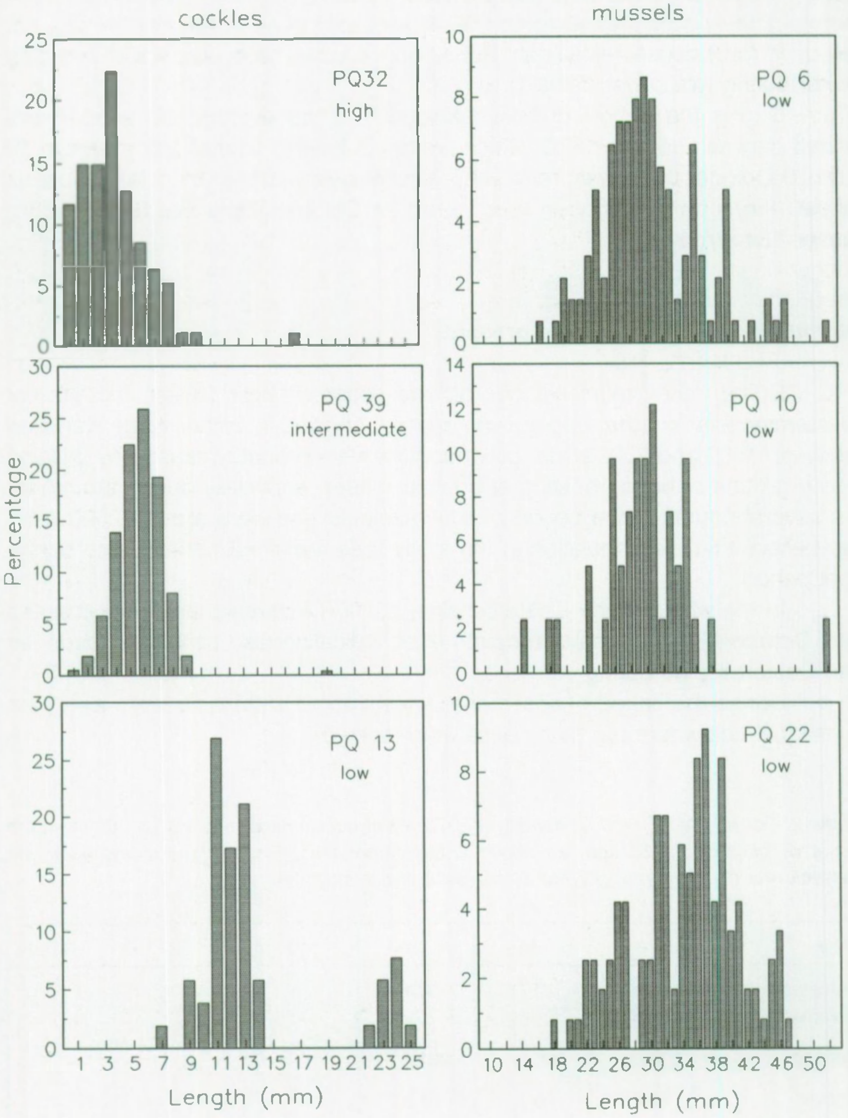

Figure 3. Length frequency distribution of cockles (PQ 32, 39 and 13) and mussels (PQ 6, 10 and 22) present in the different study plots in October 1986. For each plot the tidal elevation is indicated.

Prey populations

Cockles and mussels are the major prey species of Oystercatchers on the Slikken van Vianen. Estimates of the biomass of both bivalves are given in Table 2. The mussel population consisted mainly of mussels between 30 and 40mm in PQ 6 and 10 (Fig. 3). In PQ 22 larger mussels were also present. The cockle population was characterized by a dominance of small individuals (<15 mm), in PQ 32 and 39 the average length was only 4.5 mm and 6mm respectively (Fig. 3). Second year cockles were very rare in PQ 32 and 39 and occurred in low densities in PQ 13 and on the musselsbeds (PQ 6, 10). Length frequency distributions of cockles in PQ 6 and 10 are not plotted since they are very similar to that of PQ 13.

The highest biomass values were found on the musselbeds, followed by PQ 13. The values in PQ 39 were intermediate and PQ 32 was characterized by a very low biomass figure.

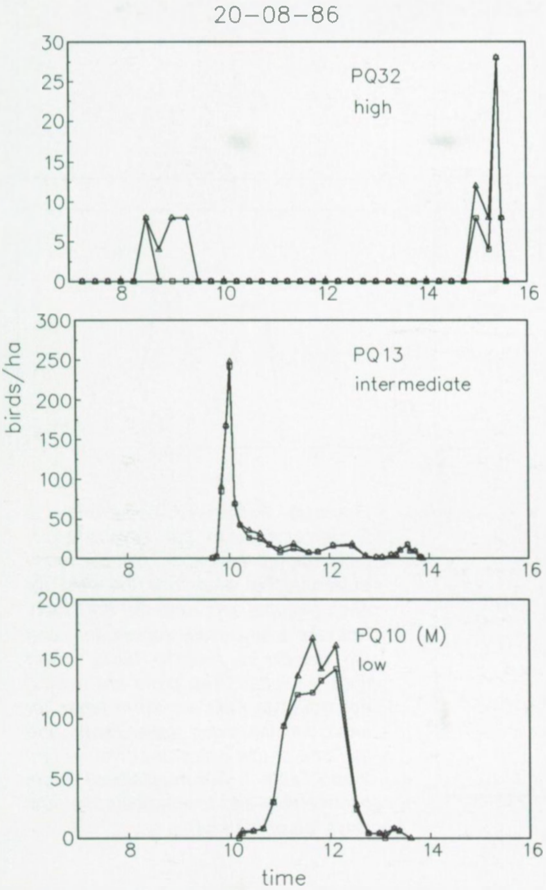

Figure 4. Pattern of occurrence of Oystercatchers during one tidal cycle in three different study plots located along a tidal gradient during normal tidal conditions (20 August 1986). Both the total density (upper line) and the density of feeding birds (lower line) is plotted. (M=musselbed)(high, intermediate and low indicate the tidal elevation of the plot)

Effect of manipulation on distribution

At high water, Oystercatchers are resting on the saltmarsh. As the water ebbs, during normal tidal conditions, the birds leave the high tide roost and follow the waterline on their way to the lower plots where the benthos biomass is highest. This results in a clear peak of birds in the higher plots as they become exposed (Fig. 4, PQ 32 and 39). At low water these plots are nearly abandoned by birds whereas high numbers are present during most of the exposure time in the lower preferred plots (Fig. 4, PQ 10). During flood, the opposite migration takes place, although some birds may fly immediately to the roost (see Meire, 1993). During the period of tidal manipulations about 1300 birds were using this unit.

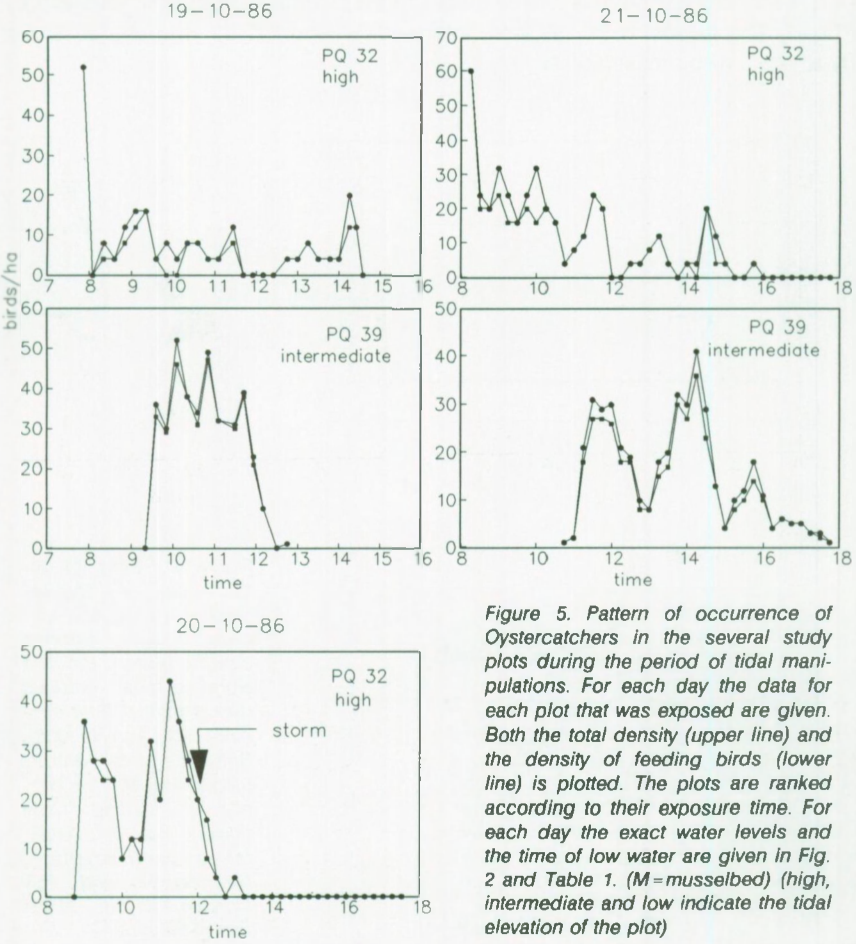

Figure 5. Pattern of occurrence of Oystercatchers in the several study plots during the period of tidal manipulations. For each day the data for each plot that was exposed are given. Both the total density (upper line) and the density of feeding birds (lower line) is plotted. The plots are ranked according to their exposure time. For each day the exact water levels and the time of low water are given in Fig. 2 and Table 1. (M=musselbed) (high, intermediate and low indicate the tidal elevation of the plot)

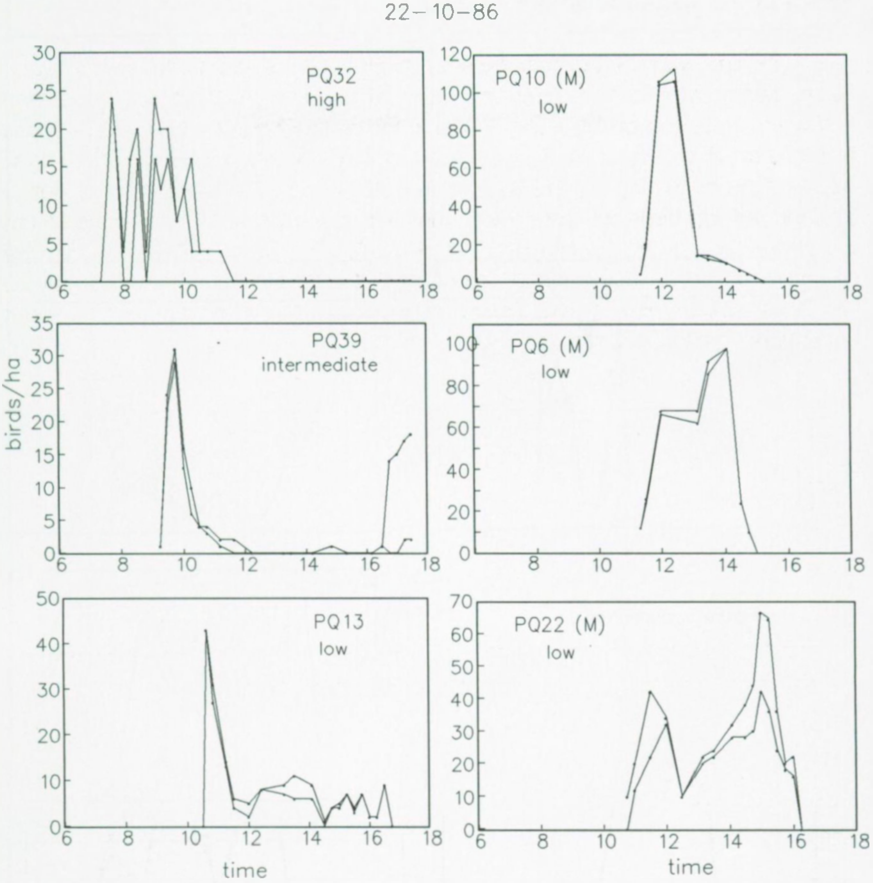

Figure 5, continued

During the tidal manipulations the distribution of the birds differed markedly from the normal pattern described above. The data for each PQ, during all the days of tidal manipulation, are given in Fig. 5. During high water in the night of 19 October 86, PQ 32 was not inundated and at dawn only few birds were on the exposed flats. As the water receded very slowly, most birds left the high water roosts and were feeding as deep as possible in the water line. High densities were present all the time in PQ 39, but also in PQ 32 birds fed permanently. When the water started to rise again, most birds went immediately to their roost near the saltmarsh, not feeding extensively on the

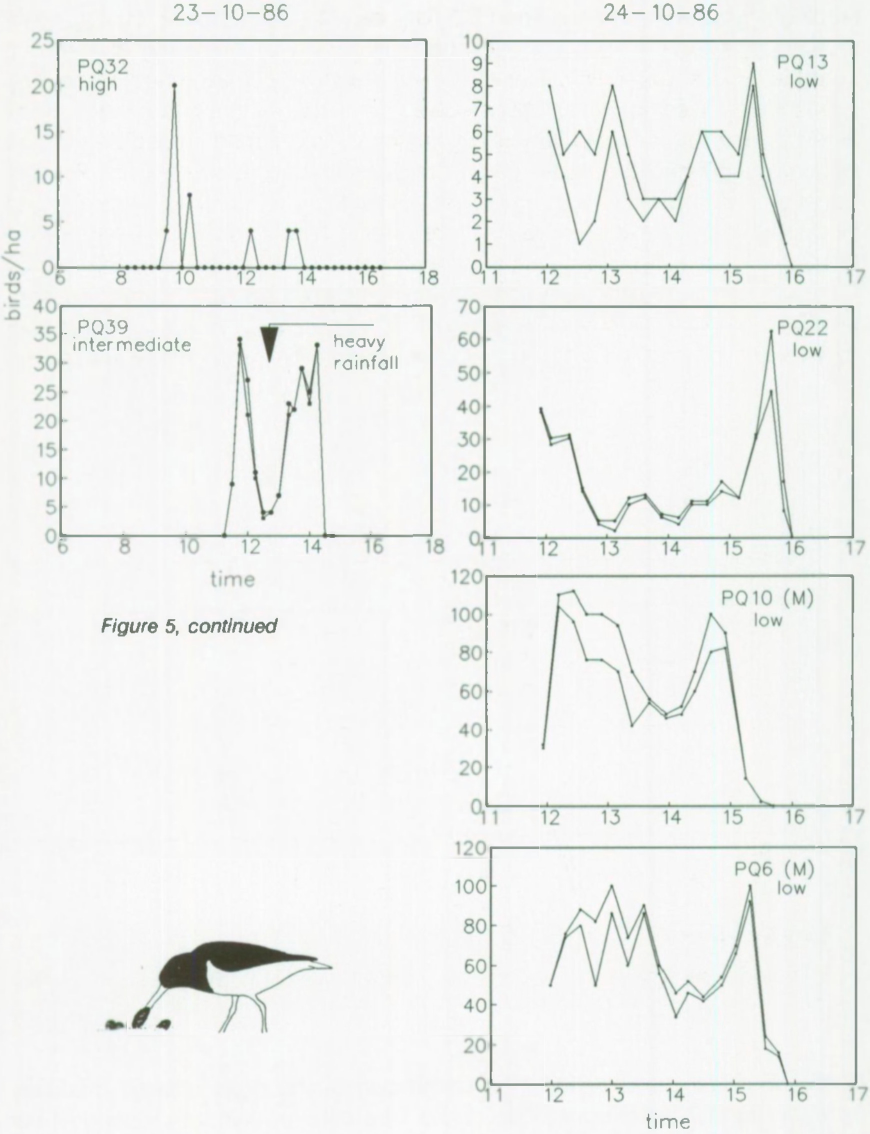

Figure 5, continued

upper part of the flats. On 20 October many Oystercatchers were feeding on the upper part of the flats and high densities of feeding birds remained present for several hours in PQ 32 since the lower areas did not become exposed. As the weather conditions deteriorated (severe gale) in the middle of the day, all birds left the tidal flat and although the flats remained exposed no birds were feeding anymore. In the morning of 21 October many birds were feeding again on the upper part of the tidal flats and others were seen wading as deep as possible in the water line. Densities were high in PQ 39 when it became exposed but also in PQ 32 birds were nearly permanently present. As the water started to rise again very slowly, many birds returned immediately to the saltmarsh, ignoring the upper part of the intertidal zone (see Fig. 5, PQ 32). Because the barrier was re-opened in the morning of 22 October a more or less normal low water occurred. In preceeding hours, densities were high in PQ 32, but as ebbing really started, birds passed quickly through PQ 39 and 13 to the lowest feeding grounds. On the musselbeds a rather normal pattern of occurrence was seen. On 23 October densities in PQ 32 were rather variable, mainly due to disturbance. Birds again moved with the water line to

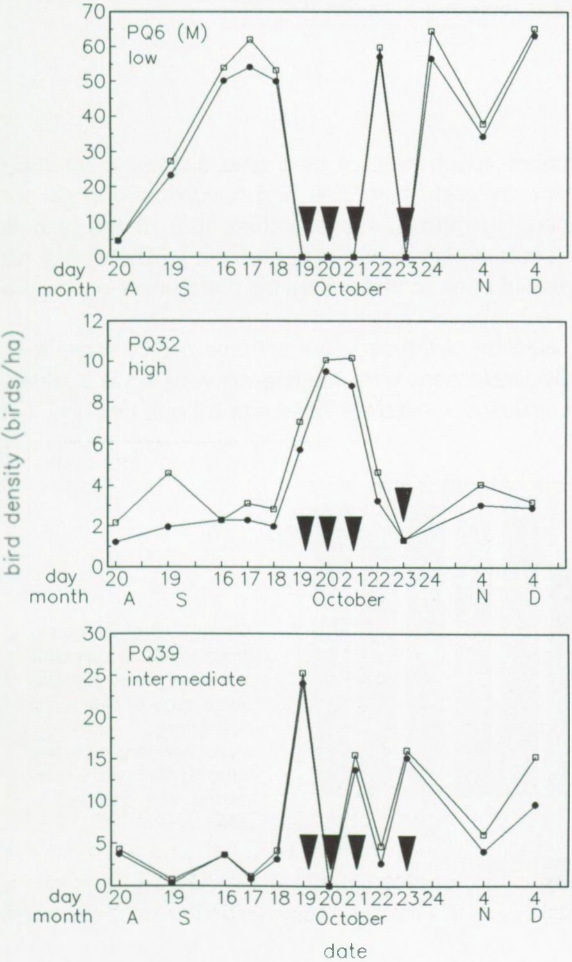

Figure 6. Average density (birds/ha) of Oystercatchers per day between August and December 1986 in three permanent plots. The arrows indicate the days when the musselbeds were not exposed due to the tidal manipulations. (A August; S September; N November; D December; M Musselbed).

the lower areas and high densities were recorded in PQ 39, which was the lowest plot exposed by the tide. In the middle of the day birds left the plot during extreme rainfall, after which they gradually returned to feed. At the end of the day, when PQ 39 was flooded, most birds returned immediately to the roost. On 24 October, when the barrier war re-opened definitely, more or less normal tidal conditions were restored; the distribution patterns of birds normalized.

The counts in the individual PQ's are summarized in Fig. 6 for three PQ's. The average density per tide was rather stable in PQ 6 after an increase from August to the beginning of October. There was no indication that the densities varied during the period of tidal manipulation. The same pattern was found in PQ 10 and 22, although in both these plots the densities are more variable. In PQ 32 and 39 on the other hand we see a clear increase of the densities when the lower plots were not exposed (Fig. 6).

Feeding behaviour

Foraging Oystercatchers spent most of their time searching for food (Fig. 7). Both the time spent on waste handlings and handlings is larger for hammerers than for stabbers. In most cases less than 10% of the time is spent in other activities (social interactions, vigilance etc.). There are no indications that the time spent in each of these activities did change during the observations.

Details of the prey selection of the birds are summarized in Table 3. In PQ 32 and 39, stabbing Oystercatchers were feeding on very small cockles. The birds stabbed into the molluscs, moved the head and bill one or twice

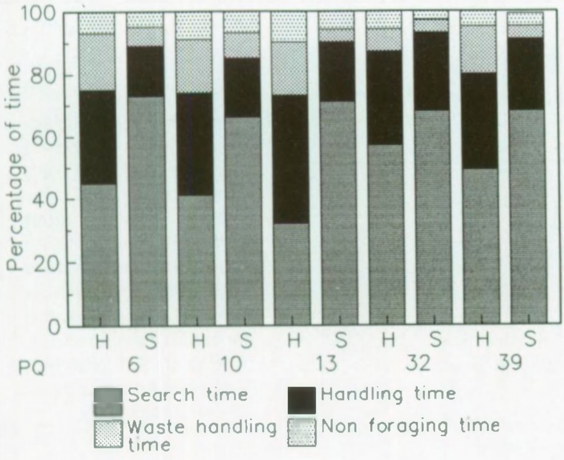

Figure 7. Time budget of foraging Oystercatchers. For each study plot the percentage of time spent searching, handling, waste handling and non foraging for both hammerers and stabbers is given.

Table 3. Some characteristics of the foraging behaviour of Oystercatchers in 5 study plots between September and November 1986. Average values (± SE) and the number of observations (between bracets) is given.

	PQ 32	PQ 39	PQ 6	PQ 10	PQ 22
Stabbers					
Average length taken		8±0.6 (33)	38.7±1.2 (45)	35.0±1.5 (27)	41.1±0.9 (42)
Handling time	8.4	2.7	31	33.4	34.6
Feeding rate	13.6±2.9 (25)	37.6±2.7 (95)	5.0±0.8 (63)	6.5±0.8 (56)	4.2±0.7 (34)
Hammerers					
Average length taken	21.0	22.0	39.6±0.6 (110)	41.9±0.9 (65)	41.3±0.9 (42)
Handling time			62.9	73.1	103.5
Feeding rate	7.8±0.7 (47)	6.9±1.2 (24)	5.6±0.5 (89)	5.9±0.8 (52)	5.9±0.9 (43)

very slightly from left to right, prized the valves apart and removed the flesh, without lifting the shells. The handling time for these small cockles was very short and the birds achieved high feeding rates (Table 3). Hammering Oystercatchers only took the larger cockles. On the musselbeds, nearly all birds fed exclusively on mussels. Although very abundant, no small cockles were taken. The average mussel length taken by both hammerers and stabbers varied between 25 and 60mm with the average length between 35 and 41mm. The handling times measured in PQ 22 were relatively long compared to both other mussel plots.

The intake rate differed markedly both between feeding methods and between plots and is clearly related to the prey density (Fig. 8). In all but one plot (PQ 22) the intake rate of stabbers is lower than that of hammerers. The intake rate is much higher on the musselbeds, where intake rate of hammerers was rather similar.

The intake rate on the musselbed plots could be compared between the period before, during and after the manipulation of the barrier. The results for PQ 6 are given in Fig. 9. Based on a Kruskall-Wallis test no significant difference between periods could be found in any of the three plots, where the comparison could be made.

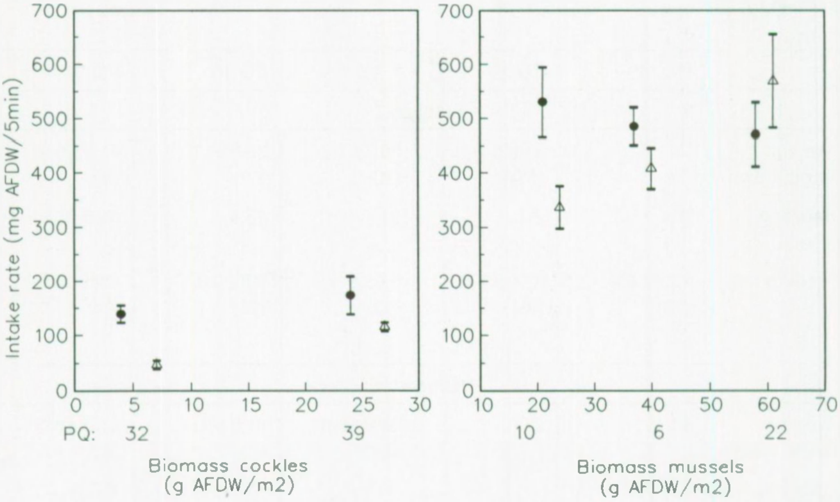

Figure 8. Average intake rate (± SE) of hammerers (solid circle) and stabbers (triangle) in 5 different study plots as a function of benthic biomass (cockles or mussels).

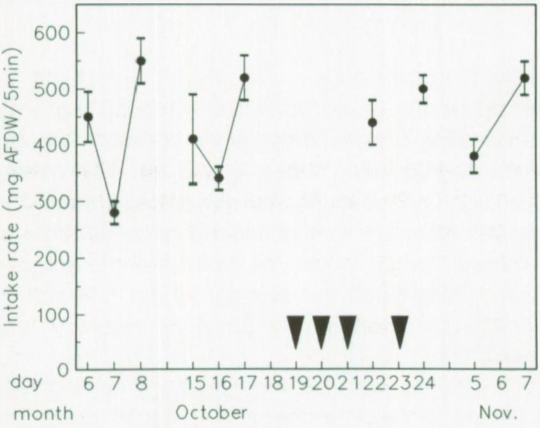

Figure 9. Average intake rate (± SE) in PQ 6 during different days before, during and after the tidal manipulation.

Feeding time

On the feeding areas birds are not spending all their time in feeding activities but also to resting, preening, walking and interactions with other animals. In the preferred feeding areas (PQ 6, 10 and 13) birds spent most of their time feeding and no clear difference between the three periods is

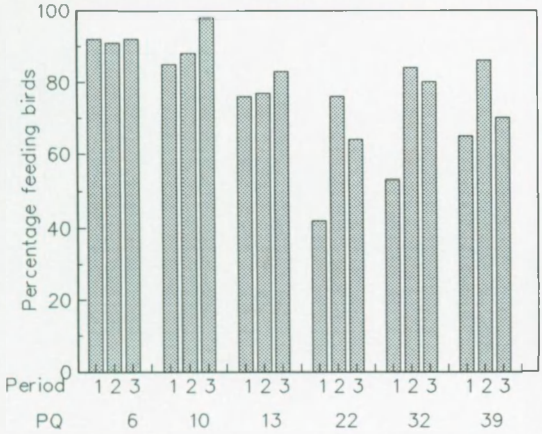

Figure 10. Percentage of the time spent feeding by birds in each plot during three different periods (1 before, 2 during, 3 after the period of tidal manipulations).

obvious. In the other plots a clear increase in the time spent foraging is seen between the period before and during manipulation (Fig. 10).

Cumulative food intake

Based on the detailed feeding observations in the plots, the food intake of the population in each sector of the functional unit was calculated by multiplying the intake rate by the number of feeding minutes and the surface of the sector. As the birds are moving from one site to the other, the consumption can be summed and gives an idea of what the whole population of birds consumed during that one tide. It was assumed that the number of feeding minutes and the intake rate were similar at night than by day. The food intake was cumulated for several tides. This was done both for the real intake and for the intake assuming normal conditions as measured on 16 October 1986 (Fig. 11). During the time of tidal manipulation the number of birds using the functional unit was constant so the intake of an average bird was one third lower of what it should have been under normal conditions. These data also show the importance of the lower feeding areas in the total energy budget of the birds.

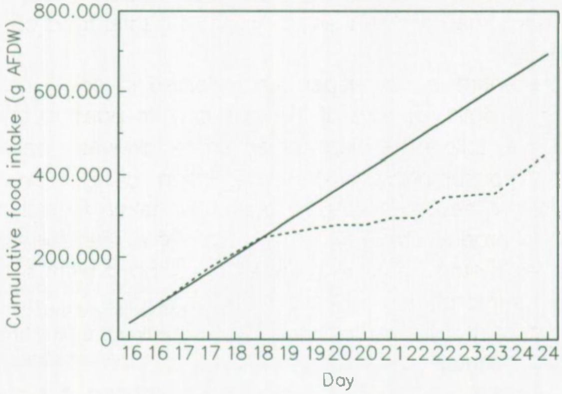

Figure 11. Cumulative food intake of the Oystercatcher population feeding in one functional unit on the Slikken van Vianen during the period of tidal manipulations (16 - 24 October 1986). Each low water is indicated on the X axis. The full line gives the consumption if the birds had fed each day the amount they took on 16 October under normal tidal conditions. The dotted line is the real consumption.

DISCUSSION

In autumn 1986 when the Oystercatchers returned to their wintering areas in the Oosterschelde and in particular to the Slikken van Vianen, they were confronted with a rather low food supply. The density of mussels on the beds was low compared to previous years and the populations consisted of rather small individuals (Craeymeersch *et al.*, 1986; Meire & Ervynck, 1986; Meire & Meininger, 1993). Although the densities of cockles were high in several of the study plots, the population was dominated by spat. Densities of second year and older cockles were low (see also Coosen *et al.*, 1993). The birds were also confronted with reduced feeding times at the richest feeding areas below mid tidal level, due to a much reduced tidal amplitude. The musselbeds were exposed between 30 and 50 minutes less per tide than in the pre-barrier situation. Both factors probably caused for the rather small numbers of Oystercatchers present in the study area during the winter 1986/87 (Meire & Meininger, 1993). After a peak count in September the winter population was about 2000 birds less than under normal conditions. Also the numbers in the whole Oosterschelde were rather low (Meininger & Van Haperen, 1988).

Besides this situation, the manipulation of the barrier in October 1986 had a pronounced effect on the water level within the Oosterschelde estuary.

The fact that the lower preferred feeding areas were not exposed, in total for 8-10 low water periods, had a significant effect on the total food consumption of the Oystercatchers.

The data presented in this paper are collected in one functional unit (Meire, 1993). Due to both the size of this unit and its position towards the dike it was possible to follow the birds for an entire low-water period and to calculate the food consumption of the population using this unit. This calculation is subject to several errors but care was taken to reduce this as much as possible to produce reliable figures. First of all the surface of each sector had to be estimated. This was done based on previous samplings, topographical and geomorphological maps and knowledge of the distribution of the birds in the area, but it remains a crude estimate. The estimates of the number of feeding minutes of Oystercatchers and their intake rate were measured only in small spot-checks. They were chosen however to be representative for the whole area and counted very frequently. The consumption of birds at night has been the subject of some debate. In an experimental setup, the Oystercatchers studied by Hulscher (1974, 1976) had intake rates at night varying from 0.86 to 1.45 that during daytime. Swennen *et al.* (1989), found that the ratio of day-time and night-time consumption in four birds tested was 0.95. Given the rather large difference in consumption between test-days the day and night values were considered similar. These experimental results contrast with the field observations on Oystercatchers. Drinnan (1958) and Heppleston (1971) both found Oystercatchers to be eating less during darkness. Sutherland (1982a, b) estimated the intake at night at three-eights of that during the day and Goss-Custard & Durell (1987), found the night feeding rate to be half that of the day time feeding rate, irrespective of light intensity. Swennen (1990), however, found no difference in Oystercatchers feeding on the Banc d'Arguin. Therefore, we assumed the intake at night was similar to that during the day. This assumption does not influence the conclusions. We also assumed that the distribution of birds at night was the same during the night than during the day. This is an acceptable assumption as similar numbers on the feeding areas at day and by night were counted by Sutherland (1982a) and Goss-Custard & Durell (1987).

From the calculations it is clear that during the period of tidal manipulations the consumption of the birds was less than normal. The birds could compensate for it in essentially two different ways: 1) feeding more elsewhere either at the intertidal flats or inland; 2) feeding for longer and faster. These possibilities are discussed here. First of all, they could make more use of the upper part of the intertidal zone that was exposed for longer. The results showed that when the lower, more profitable, feeding areas were unavailable, birds made much more use of the exposed upper parts of the intertidal area. Birds were, however, not permanently feeding there. When the weather conditions deteriorated Oystercatchers stopped foraging on two occasions. This is to be inspected when feeding provides insufficient energy to cover the costs of foraging, and the rate of net energy gain would become negative (Evans, 1976). Data do not allow to test whether the intake rate declined in response to the bad weather but it is very likely. As the intake rate in the upper part of the tidal flats (PQ 32) was already low because it is plausible that any further reduction results in a negative energy balance. That birds stayed on their roost throughout potential feeding periods during gales has been recorded already by Evans & Smith (1975) for Bar-tailed Godwits at Lindisfarne and Townshend *et al.* (1984) for Grey Plover at Teesmouth. Hulscher and Lambeck (pers. comm.) recorded Oystercatchers remaining on the roosts during extreme cold weather in spite of an ebbtide.

Once exposed, under normal weather conditions, PQ 39 was always used, PQ 32 not. On several days, birds went to their high tide roost at the time under normal tidal conditions the flats would have been covered and no feeding took place anymore although rather large areas of the upper part of the tidal flats were still exposed. We can conclude therefore that birds compensated the loss of feeding time on the preferred feeding areas by feeding more in the upper part of the tidal flats but that they did not use all the available time here. Rather they kept more or less to the normal tidal regime.

The birds also could compensate for the consumption deficit by increasing the time spent feeding at the expense of other activities. This is possible in two ways. Birds are not always foraging but feeding bouts alternate with periods of sleeping, preening or other comfort handlings. The birds could increase their feeding time by reducing the time spent in these other activities. On the musselbeds (PQ 6 and 10) and in PQ 13 the time spent feeding was already high so a further increase was not possible. In PQ 22 however there was a clear increase. This was also seen in the two other plots. However, also during foraging a bird could increase its foraging time. Indeed, a foraging bird always spends some time in other activities, such as vigilance, and social interactions. It is known that to increase the intake rate during the pre-migratory fattening, adult Turnstones (*Arenaria interpres*) significantly reduced the time of anti-predatory behaviour (vigilance), increasing the risk of predation (Metcalfe & Furness, 1984). Foraging Oystercatchers spend a very small amount of time to non foraging activities (Fig. 8) and the data do not indicate a further reduction of this time during the period of tidal manipulations.

The birds also could compensate by increasing their intake rate. Indeed, Hulscher (1982) showed that an adult male Oystercatcher increased its feeding rate from about 2.5 *Macoma balthica* eaten/min feeding to over 6/min and that in a period of two weeks time in which its breeding commitment increased and subsequently the bird spent less time foraging. He did not analyse how the bird did increase its intake rate.

In general, an increase in intake rate could be achieved by selecting more profitable prey, by increasing the walking speed to increase the encounter rate with prey or by reducing the handling time.

The prey selection of Oystercatchers has been analysed in detail and it was found that birds either feeding on cockles or mussels select the most profitable mussels (Zwarts *et al.*, in press). Moreover, Meire & Ervynck (1986) showed that the cost of including less profitable mussels, in terms of intake rate, was very small indeed. Therefore birds probably could not increase their intake rate by changing their diet. It is remarkable that stabbers took the very small cockles in PQ 32 and 39, a size class that is normally not eaten by Oystercatchers. They were probably taken because the density of the large cockles was too low.

Swennen *et al.* (1989) showed in a very elegant series of experiments that Oystercatchers faced with reduced feeding times could compensate this by spending more time in feeding and reducing both the duration of prey handling and search time. Therefore they concluded that Oystercatchers adapt their foraging strategy to the available prey and time, and are not constantly trying to maximize their intake rate, but that birds can work harder when necessary. This was true, however, only when the birds were faced with regular predictable tides. When faced with irregular unpredictable tides, their mean consumption over a longer period was the same as during a period of regular predictable tides but the tidal consumption greatly varied. Tidal consumption correlated better with the cumulative consumption deficit than with the consumption of the previous tide (Swennen *et al.*, 1989).

Although the birds had not fed on the musselbeds for 6 consecutive tides and they had an important consumption deficit we expected the birds to increase their intake rate, if possible, when they first returned to the musselbeds. The data indicate, however, that the birds did not increase the intake rate. The possibility to increase the intake rate also might depend on the prey population. Therefore it is interesting to compare the situation in which the birds of Swennen *et al.* (1989) were foraging with ours. Although the prey densities used in the experiments occur in the field, both the density and the average size of the cockles was large (150-1020 m^{-2} for cockles of 29-39 mm or 1750-2450 m^{-2} for cockles of 20mm), whereas in this study the birds were confronted with the lowest prey densities measured between 1979 and 1989. The intake rate measured on the musselbeds in this study was not so much lower than the highest intake rates measured by Swennen *et al.* (1989) (500 versus 660 mg AFDW/5 min). This is strong evidence that the birds in our study area were indeed feeding at a maximum rate. If they could feed even harder it is likely that a digestive bottleneck could limit the intake (Zwarts & Dirksen, 1990; Weiner, 1992; Zwarts *et al.*, in press).

When the birds could not increase their food intake on the tidal flats, they could move inland to feed on arable land. The importance of inland feeding for waders has been shown already by several authors (e.g., Evans, 1981; Townshend, 1981; Velasquez & Hockey, 1992). Although sometimes Oystercatchers did feed inland in our study area, no birds did so during the period of tidal manipulations. Probably no good feeding opportunities were available at that time.

Although the intake on the upper parts of the tidal area was rather small, it was probably important in providing some food to the birds when the musselbeds were not exposed. A clear difference in mortality of Oystercatchers at several roosts sites in the Dutch Wadden Sea was attributed to the fact that at the "good" roosts (lower mortality), the tidal flats descended gradually from high to low tide level whereas at the other roosts the flats extended only from about mid-tide to low tide level (Swennen, 1984). When the lower level feeding areas were not available due to high water levels (e.g., during gales) birds from the "good" roosts fed on the higher tidal flats, whereas the other birds remained the whole day on the roosts probably causing the difference in mortality (Swennen, 1984). We do not know however what the effect of the observed consumption deficit was on the conditions of the birds. It probably had an effect as indirectly suggested by the results of Lambeck (pers. comm.) who found an unusual high percentage of Oystercatchers with arrested moult in the winter of 1986/87. However there are no indications that some birds left the Oosterschelde during the period of tidal manipulations.

The results presented in this paper show that the Oystercatchers had to work hard to achieve their daily intake rate and that they had no real possibilities to compensate for lost feeding time. It is therefore not surprising that during a cold spell in early 1987 large numbers of birds died (Meininger *et al.*, 1991; Schekkerman *et al.*, 1993).

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REFERENCES

Aschoff, J. & H. Pohl, 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. J. Orn. 111: 38-47.

Coosen, J., F. Twisk, M. W. M. Van Der Tol, R. H. D. Lambeck, M. R. Van Stralen & P. M. Meire, 1993. Variability in stock assessment of cockles (*Cerastoderma edule* L.) in the Oosterschelde (in 1980-1990), in relation to environmental factors. Hydrobiologia: in press.

Craeymeersch, J., P. Herman & P. Meire, 1986. Secondary production of an intertidal mussel (Mytilus edulis L.) population in the Eastern Scheldt (S.W. Netherlands). Hydrobiologia 133: 107-115.

Drinnan, R. E., 1958. Observations on the feeding of the Oystercatcher in captivity. Br. Birds 51: 139-149.

Evans, P. R., 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distribution and movements in the non-breeding season. Ardea 64: 117-139.

Evans, P. R., 1981. Reclamation of intertidal land: some effects on Shelduck and wader populations in the Tees estuary. Verh. Orn. Ges. Bayern 23: 147-168.

Evans, P. R. & P. C. Smith, 1975. Studies of shorebirds at Lindisfarne, Northumberland. II Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. Wildfowl 26: 64-76.

Goss-Custard, J. D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (Eds), Behavioural ecology, ecological consequences of adaptive behaviour. Blackwell Scientific Publishers, Oxford: 169-205.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1987. Age-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. III. The effect of interference on overall intake rate. J. anim. Ecol. 56: 549-558.

Heppleston, P. B., 1971. The feeding ecology of Oystercatchers (*Haematopus ostralegus*) in winter in Northern Scotland. J. anim. Ecol. 40 : 651-672.

Hulscher, J. B., 1974. An experimental study of the food intake of the Oystercatchers, *Haematopus ostralegus* L. in captivity during the summer. Ardea 62: 155-171.

Hulscher, J. B., 1976. Localisation of cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. Ardea 64: 292-310.

Hulscher, J. B., 1982. The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. Ardea 70: 89-152.

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.

Meininger, P. L. & A. M. M. Van Haperen, 1988. Vogeltellingen in het zuidelijk Deltagebied in 1984/85 - 1986/87. Nota GWAO-88.1010. Rijkswaterstaat, Middelburg.

Meininger, P. L., A-M. Blomert & E. C. 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., 1993. Distribution of Oystercatchers (*Haematopus ostralegus*) over a tidal flat in relation to their main prey species, cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*): did it change after a substantial habitat loss? This thesis.

Meire, P. M. & J. Dereu, 1990. Use of the abundance/biomass comparison method for detecting environmental stress: some considerations based on intertidal macrozoobenthos and bird communities. J. applied Ecol. 27: 210-223.

Meire, P. M. & A. Ervynck, 1986. Are Oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? Anim. Behav. 34: 1427-1435.

Meire, P. M. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, The Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77: 283-311.

Meire, P. M. & P. L. Meininger, 1993. Changes in wader populations at the slikken van Vianen (Oosterschelde NL.) after major environmental changes (1979-1990). This thesis.

Metcalfe, N. B. & R. W. Furness, 1984. Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. Behav. Ecol. Sociobiol. 15: 203-206.

Nienhuis, P. N. & A. C. Smaal, 1993. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction. Hydrobiologia: in press.

Schekkerman, H., P. L. Meininger & P. M. Meire, 1993. Changes in the waterbird populations of the Oosterschelde, SW. Netherlands, as a result of large scale coastal engineering works. Hydrobiologia: in press.

Smaal, A. C., M. Knoester, P. H. Nienhuis & P. M. Meire, 1991. Changes in the Oosterschelde ecosystem induced by the Delta works. In M. Elliot & J. P. Ducrotoy (Eds), Estuaries and Coasts: Spatial and Temporal intercomparisons. ECSA 19 Symposium. Olson & Olson, Fredensborg: 375-384.

Stephens, D. W. & J. R. Krebs, 1986. Foraging Theory. Princeton University Press, Princeton.

Sutherland, W. J., 1982a. Do Oystercatchers select the most profitable cockles? Anim. Behav. 30: 857-861.

Sutherland, W. J., 1982b. Spatial variation in the predation of cockles by Oystercathers at Traeth Melynog, Anglesey. II. The pattern of mortality. J. anim. Ecol. 51: 491-500.

Swennen, C., 1984. Differences in quality of roosting flocks of Oystercatchers. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 177-189.

Swennen, C., 1990. Oystercatchers feeding on giant bloody cockles on the Banc d'Arquin, Mauritania. Ardea 78: 53-62.

Swennen, C., M. F. Leopold & L. L. M. De Bruijn, 1989. Time-stressed Oystercatchers, *Haematopus ostralegus*, can increase their intake rate. Anim. Behav. 38: 8-22.

Townshend, 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 (Eds), Feeding and survival strategies of estuarine organisms. Plenum Press, New-York: 261-274.

Townshend, D. J., P. J. Dugan & M. W. Pienkowski, 1984. The unsociable plover-use of intertidal areas by Grey Plover. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 140-159.

Velasquez, C. R. & P. A. R. Hockey, 1992. The importance of supratidal foraging habitats for waders at a south temperature estuary. Ardea 80: 243-253.

Vroon, J., 1993. Hydrodynamical characteristics of the Oosterschelde over the last decades. Hydrobiologia: in press.

Weiner, J., 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends in Ecol. Evol. 7: 384-388.

Zwarts, L. & S. Dirksen, 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing their departure from the Banc d'Arguin, Mauritania, in spring. Ardea 78: 257-278.

Zwarts, L., A-M., Blomert & R. Hupkes, 1990. Increase of feeding time in waders preparing their spring migration from the Banc d'Arguin, Mauritania. Ardea 78: 257-278.

Zwarts, L., J. T. Cayford, J. B. Hulscher, P. M. Meire & P. Triplet in press. Size selection and intake rate in Oystercatchers. In J. D. Goss-Custard (Ed.), Behavioural ecology of the Oystercatcher. Oxford University Press, Oxford, in press.

Chapter 11

CONSUMPTION OF BENTHIC INVERTEBRATES BY WATERBIRDS IN THE OOSTERSCHELDE ESTUARY, SW NETHERLANDS.

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ABSTRACT

The number of waders in the Oosterschelde, S.W. Netherlands, declined after a reduction in intertidal area due to the construction of a storm surge barrier and secondary dams, suggesting that the carrying capacity had been reached (Schekkerman *et al.*, 1993). In this paper we present data on consumption and predation pressure by birds to explore whether the reduction in their numbers is due to prey depletion or to other factors.

The total annual consumption of benthic invertebrates by birds in the Oosterschelde amounted to $1573*10^3$g ADW y^{-1} in the period before the coastal engineering works (pre-barrier) and $1500*10^3$ kg ADW y^{-1} in the post-barrier period. More than half of the total amount of biomass is eaten by the Oystercatcher, and only seven (pre-barrier) or even six (post-barrier) bird species together take 90% of the total.

Although the consumption by individual species may vary considerably among years, the total consumption was remarkably stable, with a CV of only 3-4% of the mean, especially compared to the variability of the prey populations. In the pre-barrier period, consumption was lowest in mid summer, increased sharply from August onwards until a peak was reached in January. A sharp decrease took place in March. In the post-barrier period, consumption peaked in October.

The total consumption per unit area per year does not differ much between different sectors of the Oosterschelde, apart from a distinctly lower value in the eastern part. Of the total amount of food taken by birds, only 0.1-0.4% is taken in the subtidal compartment. In several study plots on an individual tidal flat, there was a clear relation between consumption and benthic biomass.

The predation pressure was 13 and 23 % of the standing stock, in the post- and pre-barrier period respectively. When cockles, mussels and their main predator, the Oystercatcher, are excluded from the calculations, the predation pressure of the other species was 30 and 37% of the biomass, respectively.

Predation pressure of Oystercatchers in individual study plots varied from less than 10% to more than 70% of the standing stock. On cockle beds the predation pressure was positively related to the average length of the cockles present.

Based on these results and a comparison with the literature we conclude that, at least for several species that feed intertidally, carrying capacity could be limited by the stocks of food. This does not mean that birds face food shortage each season. As the variability of the benthos populations is much higher than that of the bird densities it is likely that at some times, food is not limiting, at other times it is. On the other hand, consumption is very low in the subtidal compartment and species feeding here could potentially

increase substantially in numbers in the Oosterschelde.

INTRODUCTION.

Within the Oosterschelde, a large estuary in the SW Netherlands, important coastal engineering works have taken place in the 1980s (Nienhuis & Smaal, 1993). As part of the ecological studies investigating the impact of these works, a simulation model of the Oosterschelde ecosystem (SMOES; Klepper *et al.*, 1993) has been made, which calculated the major carbon-flows between different components of the ecosystem. The higher trophic levels, especially fish and birds, however, were not included in this model, as their role in the overall C-balance of the estuary was considered to be negligible.

Despite the relatively unimportant trophic role of birds in the overall C-balance of the Oosterschelde ecosystem, the Oosterschelde is nevertheless of great significance for bird populations, especially waders, ducks and geese (Schekkerman *et al.*, 1993). This significance has played a prominent role in deciding whether the Oosterschelde should be closed or remain tidal (Nienhuis & Smaal, 1993). Eventually, a storm surge barrier has been built, which has resulted in a considerable loss of the intertidal area. For more details of the coastal engineering works see Nienhuis & Smaal (1993).

Wader densities in the Oosterschelde used to be high compared to other Western European intertidal areas (Smaal & Boeije, 1991) and the major question has been posed as to whether a reduction in intertidal area would cause a drop in bird numbers or not. Habitat loss in estuarine areas is a widespread phenomenon all over the world, but its effects on waders have been studied in only a few occasions. The construction of the storm surge barrier in the Oosterschelde provided an opportunity to test whether or not the carrying capacity of the area had been reached. Carrying capacity is defined here as the density at which the addition of any further birds results in other birds dying or leaving the area because they fail to achieve adequate intake rates due to increased interference and/or depletion of prey stocks (Sutherland & Goss-Custard, 1991). Schekkerman *et al.* (1993) showed that the number of waders in the Oosterschelde declined after the construction of the coastal engineering works as predicted by Meire & Kuijken (1987), suggesting that the carrying capacity had been reached. In this paper we present data on consumption and predation pressure by birds on benthic invertebrates in the Oosterschelde. By comparing the biomass consumed by birds with the total benthic biomass present in late summer, we explore the question whether carrying capacity could be directly limited by the size of the potential food stocks. Alternatively, carrying capacity could be determined by the spatial needs of the birds, resulting from specific foraging techniques or social factors such as interference and territoriality.

MATERIAL AND METHODS

1. Consumption by birds

1.1 Total Oosterschelde: overall estimate

Consumption by birds in the whole Oosterschelde was determined on the basis of monthly high-tide counts of birds in the whole estuary (Schekkerman *et al.*, 1993). Data from two periods, one pre-barrier (five seasons, 1978/79-1982/83), and the other post-barrier (three seasons, 1987/88-1989/90) are used in the analysis. Gulls were only counted during the pre-barrier period; it was assumed that total numbers and seasonal patterns

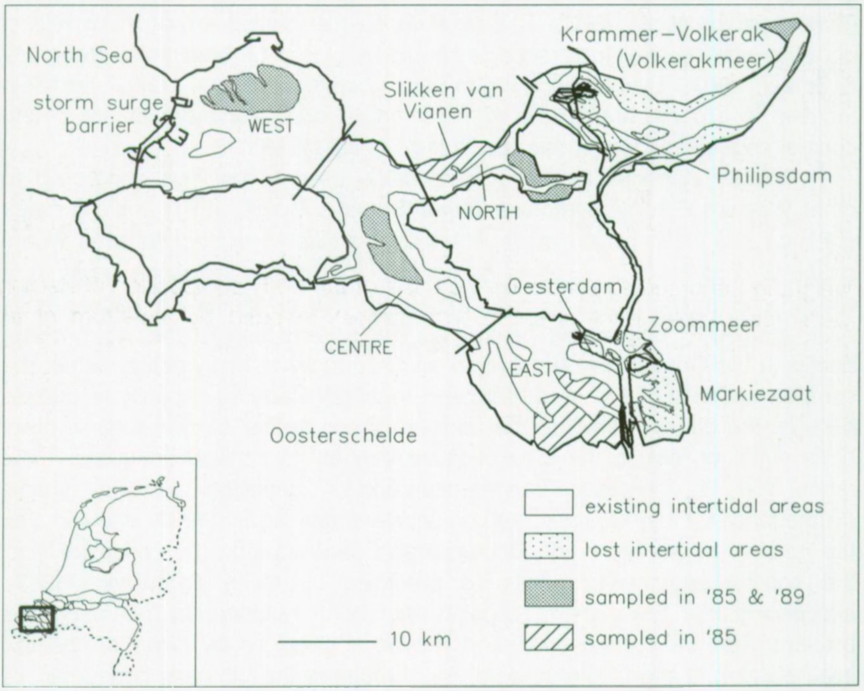

Figure 1. Map of the Oosterschelde estuary with the location of the four compartments, Vianen mudflats, and the sampled areas in both 1985 and 1989 (stippled) and in 1985 (hatched) only.

were the same in the post-barrier period. All counts refer to the Oosterschelde, excluding the brackish Krammer-Volkerak. For the pre-barrier period, the counts include the birds counted in the now fresh and stagnant Zoommeer and Markiezaat, which were dammed in 1983-1986. The total intertidal area was 13669 ha in the pre-barrier, and 11365 ha in the post-barrier period, so that 17% of the intertidal area was lost due to the engineering works. For some of the analyses the intertidal area of the Oosterschelde was divided into four different sectors (west, centre, east and north) (Fig. 1).

The total monthly consumption per species was calculated (Table 1) using the equation:

$$C = (30 \times N \times 3 \times BMR \times (1/Q) \;/\; F)*1000$$

in which C = total monthly consumption by species (kg Ash-free Dry Weight ADW); N = the number of birds present; BMR= Basal Metabolic Rate (kJ day^{-1}); Q = the assimilation efficiency of the food, and F its energy content in kJ g^{-1}.

BMR, the energy consumption of a resting bird at thermoneutrality, was estimated using the equations:

$BMR = 5.06 \times LW^{0.729}$ for waders (Kersten & Piersma, 1987);
$BMR = 3.56 \times LW^{0.734}$ for other species (Aschoff & Pohl, 1970),

in which LW = the lean (fat-free) weight of the species in g. Lean weights were used because fat stores are largely energetically inactive. Lean weights of waders were estimated from wing length, using the formulae given by Davidson (1983). For gulls, the lean weight was obtained by subtracting 10% from their weight in the breeding period, on the basis of the body composition of Herring Gulls (see Table 1 for scientific bird names) reported by Norstrom *et al.* (1986). The lean weights of grebes were based on Piersma (1984). For the remaining species, the lower values from the range of weights given by Cramp & Simmons (1977, 1983) were used to estimate lean weight. The obtained BMR value was converted in KJ. day^{-1}. Total daily energy expenditure (DEE) was assumed to amount to three times BMR (Drent *et al.*, 1978; Kersten & Piersma, 1987; Smith, 1975; Castro *et al.*, 1992). For fish and benthic invertebrates, a digestibility of $Q=0.85$ was used (Kersten & Piersma, 1987; Zwarts & Blomert, 1990) and an energetic value of $F = 22$kJ g^{-1}ADW (Zwarts & Blomert, 1990). To obtain yearly consumption monthly consumption was summed. For comparisons with other areas, consumption was expressed in g ADW m^{-2} y^{-1}.

The method gives a rather crude estimation of total consumption for several reasons. Firstly, it was assumed that all birds were feeding exclusively in benthic compartment of the Oosterschelde. Gulls however, may have taken part of their food from the pelagic compartment, or even outside the

Table 1. Basic assumptions and total consumption by benthivorous birds in the Oosterschelde

species	lean weight (kg)	BMR (kJ d^{-1})	daily intake (gADW d^{-1})	bird-days/year (n x 1000) 78-82	87-89	Consumption gADW m^{-2} y^{-1} 78-82	87-89	% of total benthic cons. 78-82	87-89
subtidal areas									
Eider (*Somateria mollissima*)	1.90	505	81	8	42	0.005	0.029	0.0	0.2
Goldeneye (*Bucephala clangula*)	0.75	255	41	28	52	0.008	0.018	0.1	0.1
tidal flats									
Oystercatcher (*Haematopus ostralegus*)	0.53	275	44	20085	19901	6.381	7.605	55.4	57.6
Herring Gull (*Larus argentatus*)	0.95	303	49	4824	4824	1.690	2.032	14.7	15.4
Curlew (*Numenius arquata*)	0.70	337	54	2212	2277	0.861	1.066	7.5	8.1
Dunlin (*Calidris alpina*)	0.05	49	8	9556	6602	0.543	0.451	4.7	3.4
Bar-tailed Godwit (*Limosa lapponica*)	0.27	168	27	1909	1811	0.371	0.423	3.2	3.2
Shelduck (*Tadorna tadorna*)	1.08	333	54	1045	721	0.402	0.333	3.5	2.5
Black-headed Gull (*Larus ridibundus*)	0.23	107	17	1888	1888	0.233	0.281	2.0	2.1
Knot (*Calidris canutus*)	0.14	104	17	2367	1824	0.285	0.264	2.5	2.0
Grey Plover (*Pluvialis squatarola*)	0.19	130	21	1711	1439	0.257	0.260	2.2	2.0
Pintail (*Anas acuta*)	0.85	280	45	463	328	0.150	0.127	1.3	1.0
Redshank (*Tringa totanus*)	0.14	104	16	747	556	0.090	0.080	0.8	0.6
Common Gull (*Larus canus*)	0.35	146	23	381	382	0.064	0.077	0.6	0.6
Shoveler (*Anas clypeata*)	0.55	203	33	225	103	0.053	0.029	0.5	0.2
Turnstone (*Arenaria interpres*)	0.08	69	11	357	289	0.029	0.028	0.2	0.2
Great Black-backed Gull (*Larus marinus*)	1.44	412	66	46	46	0.022	0.026	0.2	0.2
Avocet (*Recurvirostra avosetta*)	0.24	154	25	161	94	0.029	0.020	0.2	0.2
Spotted Redshank (*Tringa erythropus*)	0.14	104	17	119	123	0.014	0.018	0.1	0.1
Ringed Plover (*Charadrius hiaticula*)	0.05	49	8	116	135	0.007	0.009	0.1	0.1
Greenshank (*Tringa nebularia*)	0.18	125	21	52	50	0.007	0.009	0.1	0.1
Lesser Black-backed Gull (*Larus fuscus*)	0.73	250	40	14	14	0.004	0.005	<0.1	<0.1
Sanderling (*Calidris alba*)	0.05	49	8	31	49	0.002	0.003	<0.1	<0.1
Kentish Plover (*Charadrius alexandrinus*)	0.05	49	8	64	37	0.004	0.003	<0.1	<0.1
Whimbrel (*Numenius phaeopus*)	0.41	228	37	5	3	0.001	0.001	<0.1	<0.1

totals

species	Total consumption *10^3kg ADW 78-82	87-89	Total consumption gADW m^{-2} y^{-1} 78-82	87-89	% of total benthic cons. 78-82	87-89
subtidal areas total	1.6	5.4	0.006	0.020	0.1	0.4
tidal flats total	1571.7	1494.6	11.49	13.15	99.9	99.6
Ducks	82.8	55.7	0.60	0.49	5.3	3.7
Oystercatcher	872.2	846.3	6.38	7.61	55.5	56.4
Other waders	341.7	299.5	2.50	2.64	21.7	20.0
Gulls	275.2	275.2	2.01	2.42	17.4	18.3

boundaries of the Oosterschelde (e.g., at rubbish tips). Secondly, species classified as benthivores were assumed to forage exclusively on this type of food. Pintail and Shoveler may, however, have included a significant proportion of vegetable matter in their diet. Furthermore, no adjustments were made for variations in energy expenditure within the annual cycle due to physiological processes like thermoregulation, deposition of energy reserves for wintering and migration, moult, gonad development or egg-formation. Finally, the amount of food taken from the estuary to feed chicks has not been taken into account. It is expected, however, that the latter assumption will have relatively little effect on the estimated total consumption, as the number of birds feeding young is small in comparison with the numbers present in the non-breeding season.

The consumption was calculated separately for the subtidal (below mean low water) and intertidal areas. It was assumed that Eider and Goldeneye were feeding in the subtidal part of the Oosterschelde.

1.2 Slikken van Vianen: detailed estimate

The foraging behaviour of waders was studied in detail on the Slikken van Vianen, a small intertidal area in the middle part of the Oosterschelde (Fig. 1) (Meire & Kuijken, 1984; Meire, 1987). Birds were counted at both low and high tide. At low tide, numbers were counted in permanent plots (0.5 - 1 ha) during an entire tidal cycle on 220 days between 1979 and 1990. For each day the average density of foraging birds and bird feeding minutes were calculated. Until 1985 14 plots were studied, six of these also in the remaining years. Days with very short exposure time, caused by manipulation of the storm surge barrier or storms, were omitted from the analyses.

The intake rate (mg ADW ingested/minute of feeding) of Oystercatchers was estimated from visual observations in all study plots (see Meire & Ervynck (1986) for details). For the other bird species an average intake rate was estimated from the known daily consumption of each species (see Table 1) and an estimate of the total feeding time per tide (Meire, unpublished data). This estimate is probably an overestimation of the real intake rate in plots with a low biomass and an underestimation in plots with a large biomass. In order to correct the intake rate in plots with a biomass less than 10 g ADW m^{-2} (excluding cockles and mussels) the intake rate was multiplied by 0.5, in plots with a biomass higher than 30 g ADW m^{-2} it was multiplied by 1.5. For Bar-tailed Godwits, the values obtained in this way did not differ significantly from the field data (Meire unpublished data). Consumption per plot was then calculated by multiplying the number of feeding minutes and the intake rate. It was thereby assumed that both the number of feeding minutes and the intake rate were similar at night and during the day. The annual consumption and predation pressure of Oystercatchers was calculated for two seasons: 1984/85 and 1986/87. For all species the consumption was calculated for the months

September/October 1984 and expressed as g ADW m^{-2} day^{-1}.

2. Benthic biomass

The estimate of macrozoobenthic biomass in the entire Oosterschelde is derived from two large scale surveys carried out in August 1985 and 1989 (Meire *et al.*, 1991; Meire *et al.*, 1993; Seys *et al.*, 1993). At this time of the year benthic biomass reaches its maximum values (Beukema, 1974). In winter growth and reproduction are small, so these values can be considered as the maximum potential food source available to the birds during the next winter season. The survey of 1985 covered most of the intertidal areas of the Oosterschelde: the Roggenplaat, Galgeplaat, Verdronken Land van Zuid-Beveland, Slikken van Vianen and Krabbenkreek (Fig.1). In 1989 only the Roggenplaat, Galgeplaat and Krabbenkreek were sampled. These biomass data are used to compare with the consumption of birds as no information on benthic production is available.

In all permanent plots on the Slikken van Vianen, macrozoobenthos was sampled each year in September. Density and biomass of all species in the samples were determined and all molluscs were measured to the nearest mm (Meire & Dereu, 1990).

RESULTS

1. Consumption by benthivorous birds in the Oosterschelde

1.1 Total consumption

The total annual consumption of benthic invertebrates by birds in the Oosterschelde amounted to $1573*10^3$ kg ADW y^{-1} in the pre-barrier period (Table 1). Similar results were obtained by Meire *et al.* (1989) who estimated the consumption of benthivorous bird species in the Oosterschelde to be $1448*10^3$ kg ADW y^{-1} for the period 1976 - 1984. Although methods of calculation and division of bird species into functional groups differed slightly from those used in this paper (Meire *et al.*, 1989), the results are very similar and can be used to compare consumption by benthivores to that of herbivorous and piscivorous birds. Total consumption by piscivores was estimated at $8.7*10^3$ kg ADW y^{-1}, and of herbivores at $520*10^3$ kg ADW y^{-1} (Meire *et al.*, 1989). Compared to these figures, consumption by benthivores in the Oosterschelde ecosystem is very high.

In the post-barrier period, total benthic consumption was estimated at $1500*10^3$ kg ADW y^{-1}, a reduction of about 4% compared to the pre-barrier period. The decrease is not evenly spread over the different species. For Oystercatchers the decrease is 3%, for "other waders" it is 12.3%. Consumption by ducks decreased by 32.8%.

1.2 Share of individual species

A striking feature in the breakdown of consumption of benthic invertebrates over the species is the dominance of only a few bird species (Table 1). More than half of the total amount of biomass is eaten by the Oystercatcher, and only seven (pre-barrier) or even six (post-barrier) species together take 90% of the total. The most important species are Oystercatcher, Herring Gull, Curlew, Dunlin, Bar-tailed Godwit, Shelduck and Black-headed

*Table 2. Yearly variations in benthic consumption by waders and dabbling ducks in the Oosterschelde in 1978/79 - 1982/83 and in 1987/88 - 1989/90. Given are minimum, maximum (in g ADW m^{-2} y^{-1}) and coefficient of variation (CV= 100*sd/mean) for each period.*

species	1978/79 - 1982/83 (n=5) 1987/88 - 1989/90 (n=3)					
	min	max	CV (%)	min	max	CV (%)
Oystercatcher	6.110	6.720	3.3	5.992	6.274	2.1
Curlew	0.764	0.892	6.0	0.806	1.013	10.2
Dunlin	0.497	0.661	12.8	0.285	0.442	17.6
Bar-tailed Godwit	0.298	0.425	15.9	0.309	0.388	9.4
Shelduck	0.296	0.490	16.0	0.216	0.334	17.4
Knot	0.198	0.319	14.9	0.189	0.254	13.0
Grey Plover	0.244	0.276	5.0	0.188	0.245	10.8
Pintail	0.075	0.207	31.8	0.079	0.125	18.6
Redshank	0.075	0.106	12.7	0.056	0.073	10.8
Shoveler	0.032	0.068	24.4	0.012	0.031	34.7
Turnstone	0.025	0.027	2.9	0.021	0.027	12.2
Spotted Redshank	0.010	0.017	20.8	0.012	0.018	17.4
Greenshank	0.004	0.010	36.1	0.006	0.008	12.7
Avocet	0.003	0.003	5.4	0.001	0.002	17.5
Ringed Plover	0.001	0.001	16.2	0.001	0.001	24.1
total	8.884	9.644	3.5	8.446	9.146	3.3
excl. Oystercatcher	2.164	3.251	13.3	2.187	2.871	11.2

Gull. There was very little difference between the two study periods in the order and relative contribution of individual species.

2. Temporal patterns of bird predation

2.1 Interannual variations in consumption and benthic biomass

Waterbird populations are known to show considerable year to year variation in numbers, due to factors such as variation in local food supply and breeding success. In order to establish the among-year variations in total consumption by waders and dabbling ducks in the Oosterschelde, consumption was calculated separately for each year and the coefficient of variation (CV) for both study periods determined. It should be noted that due to the method of calculation, between-year variation in the estimated consumption is due only to variations in bird numbers, not to other factors such as varying winter temperatures. Table 2 shows that, although consumption by particular species may vary considerably among years, the total consumption was remarkably stable, with a CV of only 3-4% of the mean. This stability was mainly caused by the Oystercatcher, which takes more than half of the total consumption. The stability of Oystercatcher consumption is remarkable in view of the highly variable biomass of mussels and cockles (Coosen *et al.*, 1993a; Van Stralen *et al.*, 1993). Although the pattern of consumption of benthic invertebrates for all other bird species varied more, the overall variability is still rather small (Table 2; CV 11 to 13%) especially compared to the variability in the prey populations. This is exemplified in Table 3 which shows the CV of total density and biomass of different trophic groups,

Table 3. Yearly variations in benthic invertebrates in 6 study plots on the Slikken van Vianen. The coefficients of variation (%) for 8 or 9 autumn biomass values (years) are given for total density and biomass, and the biomass of deposit feeders (Biodep), filter feeders (Biofil), grazers (Biogra) and omnivores (Bioomn).

Plot	Total Density	Total Biomass	Biomass Deposit feeders	Biomass Filter feeders	Biomass Grazers	Biomass Omnivores
10 (N=9)	41.8	42.6	47.1	45.7	109.5	62.7
13 (N=9)	68.6	110.6	66.9	121.1	183.7	74.7
22 (N=8)	36.8	34.7	64.7	40.3	69.2	106.4
32 (N=8)	43.2	30.0	39.5	52.2	148.6	99.1
39 (N=8)	51.9	36.2	44.9	50.7	130.1	75.6
60 (N=9)	39.0	59.6	50.2	62.2	133.1	80.2
Total (N=8)	28.9	36.1	20.2	42.3	75.5	42.7

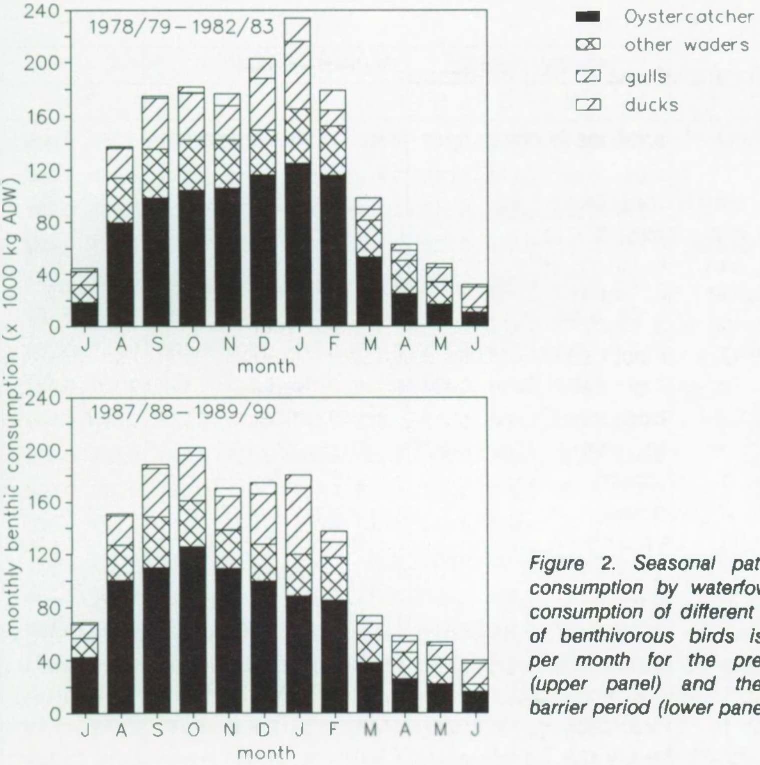

Figure 2. Seasonal pattern of consumption by waterfowl. The consumption of different groups of benthivorous birds is given per month for the pre-barrier (upper panel) and the post-barrier period (lower panel).

based on eight or nine late autumn samplings in the period 1979 - 1989 on six permanent plots on the Slikken van Vianen. It is clear that the variability of the benthos is much larger than that of the predation by birds, with the combined CV ranging between 20 and 76% for different trophic groups.

2.2 Seasonal pattern of predation

Within-year variation of consumption is shown in Fig. 2. Again, consumption as calculated reflects only variations in bird numbers, not effects of weather conditions, moult and deposition of fat stores. In general, energy requirements will be above the 3 BMR used in this paper during the winter months, while they will fall below this during summer. In the pre-barrier period, consumption was lowest in mid summer, but in August a sharp increase occurred with the arrival of large numbers of waders, especially Oystercatchers.

Table 4. Total benthic consumption (g ADW $m^{-2}y^{-1}$) by birds in four sectors of the intertidal area of the Oosterschelde. W=west, C=centre, E=east, N=north, Pre, Post= pre and post-barrier.

species	1978/79 - 1982/83				1987/88 - 1989/90				Pre	Post
	W	C	E	N	W	C	E	N	Total	
Oystercatcher	8.900	7.513	3.820	8.722	8.693	10.37	4.750	7.895	6.381	7.605
Curlew	0.960	0.642	0.872	1.046	0.914	1.090	1.210	0.885	0.861	1.066
Dunlin	0.364	0.554	0.588	0.619	0.365	0.508	0.474	0.406	0.543	0.451
Bar-tailed Godwit	0.745	0.408	0.094	0.704	0.766	0.404	0.096	0.762	0.371	0.423
Shelduck	0.224	0.205	0.482	0.764	0.270	0.125	0.568	0.323	0.402	0.333
Knot	0.509	0.268	0.171	0.390	0.314	0.414	0.157	0.183	0.285	0.264
Grey Plover	0.258	0.283	0.219	0.313	0.285	0.311	0.236	0.198	0.257	0.260
Pintail	0.017	0.012	0.279	0.170	0.024	0.013	0.285	0.123	0.150	0.127
Redshank	0.070	0.078	0.095	0.116	0.073	0.107	0.073	0.072	0.090	0.080
Shoveler	0.038	0.010	0.082	0.056	0.060	0.009	0.028	0.028	0.053	0.029
Turnstone	0.035	0.040	0.013	0.048	0.033	0.032	0.011	0.054	0.029	0.028
Avocet	0.059	0.009	0.014	0.074	0.068	0.005	0.005	0.017	0.029	0.020
Spotted Redshank	0.018	0.019	0.005	0.033	0.024	0.025	0.012	0.010	0.014	0.018
Ringed Plover	0.003	0.007	0.004	0.018	0.011	0.013	0.008	0.016	0.007	0.009
Greenshank	0.003	0.007	0.008	0.014	0.006	0.012	0.009	0.005	0.007	0.009
Kentish Plover	0.004	0.006	0.001	0.009	0.003	0.003	0.001	0.004	0.004	0.003
TOTAL	14.23	12.08	8.76	15.11	14.34	15.86	10.35	13.40	11.49	13.15
Ducks	0.28	0.23	0.85	0.99	0.36	0.15	0.88	0.48	0.60	0.49
Oystercatcher	8.90	7.51	3.82	8.72	8.69	10.37	4.75	7.90	6.38	7.61
Other Waders	3.04	2.32	2.08	3.38	2.88	2.92	2.29	2.61	2.50	2.64
Gulls	2.01	2.01	2.01	2.01	2.41	2.41	2.41	2.41	2.01	2.42
Total excl gulls	12.22	10.08	6.75	13.10	13.93	13.45	7.94	10.99	9.48	10.74

A further increase occurred until a peak was reached in January. A sharp decrease took place in March when most Oystercatchers left the area for the breeding grounds. In the post-barrier period, the consumption pattern was somewhat different, mainly caused by different seasonal occurrence of the Oystercatcher (Lambeck, 1991). Numbers, and consequently consumption, in late summer were higher as compared to the pre-barrier period. Instead of an increase until January, numbers and consumption decreased after a peak in October.

3. Spatial pattern of consumption by birds in the Oosterschelde and relation with macrozoobenthos

3.1 Consumption by birds in different sectors of the Oosterschelde

Total consumption was calculated for each of the four sectors of the intertidal area of the Oosterschelde estuary, using the total number of bird days per year per sector as a basis. These figures were not available for gulls; therefore gulls were assumed to be distributed homogeneously over the intertidal area. The results for the 12 most important bird species are presented in Table 4. Total consumption is given including and excluding gulls. The total consumption per unit area per year does not differ much among sectors, apart from a distinctly lower value in the eastern part. This lower value is almost totally caused by the lower densities of Oystercatchers in this area, which in turn can probably be explained by the small surface area of intertidal mussel beds and lower biomass of cockles, as illustrated by data from 1985 in Fig. 3a. The biomass value for the northern sector is probably an underestimate as some musselbeds were not covered in the survey. The lower consumption by other wader species in the central and eastern sector coincides with lower biomass (total biomass - biomass cockles and mussels) values here in 1985 (Fig. 3b).

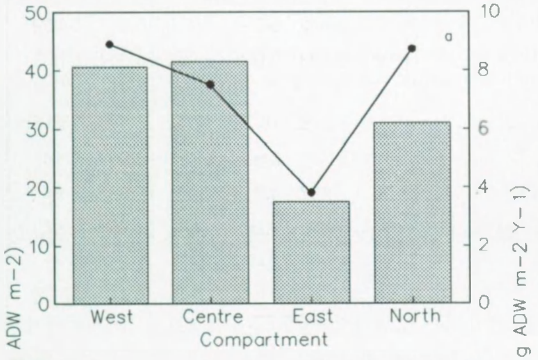

Figure 3a. Consumption of Oystercatchers (dots) in the pre-barrier period and benthic biomass of suspension feeders (bars) in August 1985 in each com-partment of the Oosterschelde.

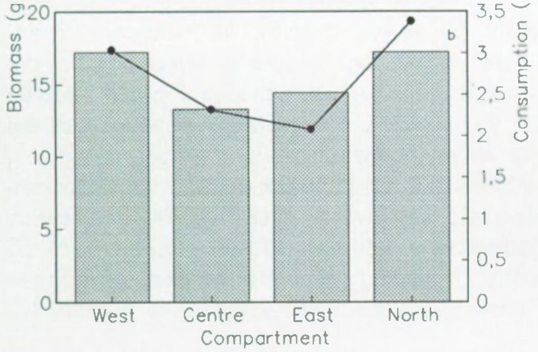

Figure 3b. Consumption of waders (minus Oystercatchers) (dots) in the pre-barier period and benthic biomass (minus suspension feeders) (bars) in August 1985 in each compartment of the Oosterschelde.

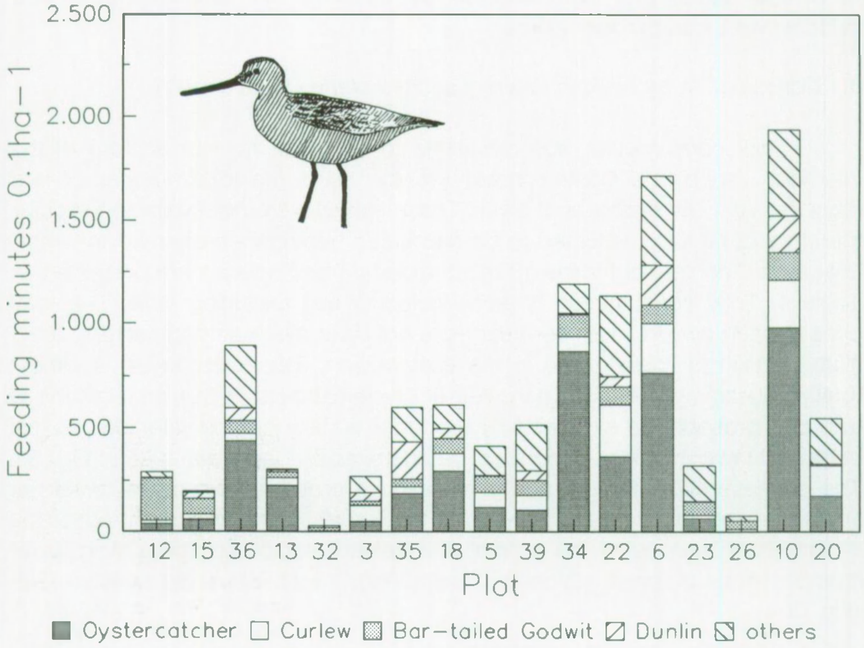

Figure 4. Feeding minutes of waders per plot (average for the period August-September 1984) on the Vianen mudflat. Plots are ranked according to benthic biomass, being lowest in 12 and highest in 20.

3.2 Consumption in relation to the tidal and subtidal zone, and benthic biomass.

Of the total amount of food taken by birds, only 0.1-0.4% is taken in the subtidal compartment (Table 1). In fact, it is even less than that since Goldeneye and Eider, the only diving benthivores that regularly occurred in the estuary, take part of their food from intertidal areas during high tide. Compared with the Wadden Sea where diving ducks, mainly Eider, take ca 30% of the total consumption (Smit, 1981), the absence of avian subtidal benthivores in the Oosterschelde is very noteworthy.

On the tidal flats, the birds are not distributed at random but aggregate on certain parts of the tidal flats. Consumption therefore varies considerably among sites. This is exemplified with the data from Vianen from the 1984/85 season. In Fig. 4 the total number of feeding minutes of all wader species in different study plots is given, showing variation between plots by a factor 20.

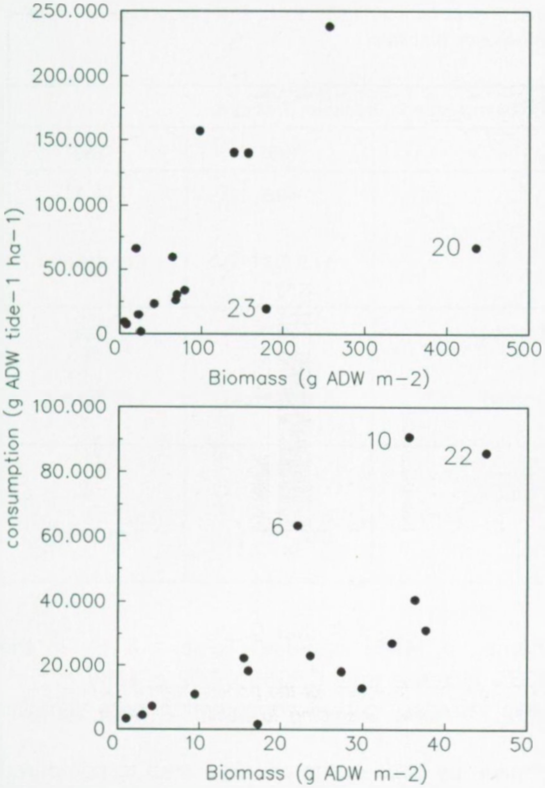

Figure 5. Consumption of waders in relation to benthic biomass on different study plots of the Vianen mudflat. (a) for all species and (b) excluding Oystercatchers, cockles and mussels. The consumption was calculated based on observations from September/October 1984, benthic biomass was sampled in September 1984.

There is a clear relation between consumption and benthic biomass when all species are considered (Fig. 5a)($r^2=0.8$; $N=15$; $p<0.01$ after removing plots 23 and 20). The two aberrant points, plots 20 and 23, are both situated on a very muddy mussel bed, low in the intertidal area and characterized by large pools at low tide. This relation also holds when leaving out consumption by Oystercatchers and the biomass of cockle and mussel, although a remarkably high consumption was seen in plots 6,10 and 22, three plots situated on mussel beds (Fig. 5b)($r^2=0.74$, $N=14$, $p<0.01$ after removing plots 6,10 and 22).

3.3 Predation pressure

3.3.1 General

Assuming that all predation by gulls is confined to the intertidal areas, the yearly consumption of benthic invertebrates in the intertidal part of the Oosterschelde was estimated at 11.5 g ADW m^{-2} y^{-1} pre-barrier and

Table 5. Total macrobenthic biomass in the Oosterschelde and estimated predation pressure by birds in a pre-barrier (1985) and a post-barrier (1989) year. The percentage of benthic biomass removed by birds is given between brackets.

Biomass, Consumption and Predation Pressure		
Year	1985	1989
Total biomass (g ADW m^{-2})	49.3	99.3
Total consumption (g ADW m^{-2} y^{-1})	11.5 (23.3%)	13.2 (13.3%)
Biomass (excluding Cockles & Mussels) (g ADW m^{-2})	17	14.9
Consumption (excluding Oystercatcher) (g ADW m^{-2} y^{-1})	5.11 (30.1%)	5.54 (37.2%)
Biomass (cockles and mussels) (g ADW/m^{2})	32.3	84.4
Consumption by Oystercatchers (g ADW m^{-2} y^{-1})	6.38 (19.7%)	7.61 (9.0%)

13.2 g ADW m^{-2} y^{-1} post-barrier, a 14.4% increase (Table 1 & 5). In the subtidal zone there was a 233% increase from 0.006 to 0.02 g ADW m^{-2} y^{-1} (Table 1). Notwithstanding this increase, overall consumption here remains very low.

In Table 5 the consumption by birds in the intertidal area is compared to the benthic biomass to estimate the predation pressure, which was found to be 23 and 13 % of the standing stock, in the pre- and post-barrier period respectively. Total biomass showed large yearly variations. This is mainly due to the biomass of the filter-feeding cockles and mussels. When excluding cockles and mussels and Oystercatchers, their main predator, from the calculations, the predation pressure of the other species was 30 and 37% of the biomass (Table 5).

3.3.2 Predation pressure by Oystercatchers

The predation pressure by Oystercatchers in relation to the biomass of cockles and mussels is given in Table 5 and amounted to 20% in 1985 and 9% in 1989.

Based on observations of Oystercatchers at low tide in permanent plots at the Slikken van Vianen during the seasons 1984/85 and 1986/1987, predation pressure per plot was estimated and plotted in Fig. 6.

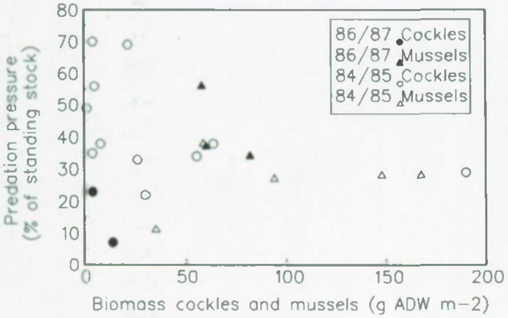

Figure 6. Predation pressure (percentage of standing stock of cockles and mussels measured in August removed during one year) by Oystercatcher in relation to the biomass of cockles and mussels. Plotted are the data from several study plots on the Slikken van Vianen for both the season 1984/85 and 1986/87.

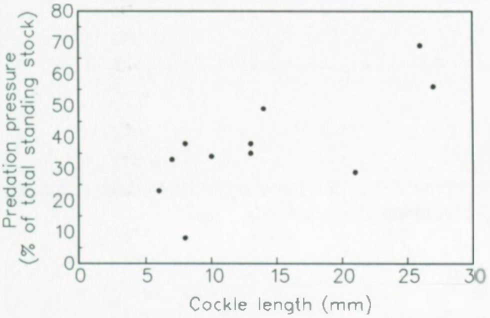

Figure 7. Relation between predation pressure of Oystercatchers on cockles and the average length of cockles. Data from the season 1984/85 and 1986/87 from several study plots on the Slikken van Vianen are given.

Predation pressure varied from less than 10% to more than 70% of the standing stock. The data suggest a large scatter at low biomass values and an average predation pressure of about 30% at higher biomass values (musselbeds), without a correlation between biomass and the percentage taken. The large scatter in the data from plots outside musselbeds is to a large extent dependent on the average length of the cockles present as shown in Fig. 7. In plots with larger cockles the predation pressure was significantly higher ($r=0.74$, $n=11$, $p<0.01$).

The seasonal pattern of Oystercatcher numbers changed in the Oosterschelde in the post-barrier period (Lambeck, 1991; Schekkerman *et al.*, 1993). Numbers present in July-September increased, but from October onwards they decreased. Midwinter numbers were 23% lower in the post-barrier period. One possible explanation could be that in autumn, the food supply was depleted so rapidly by the higher numbers of birds, that birds were forced to leave. This seems unlikely. The difference in numbers is not large enough to explain a sudden depletion. Another explanation could be a change in the food supply. In Fig. 8 the estimated total stock of cockles in August

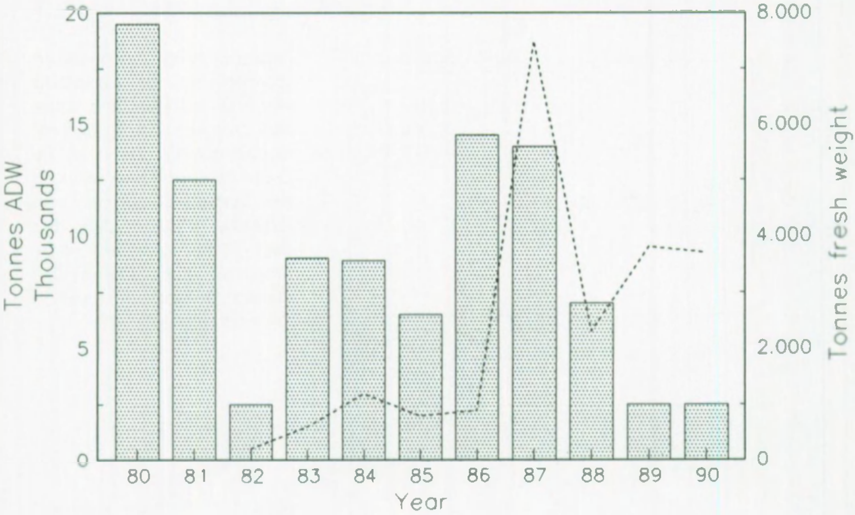

Figure 8. Cockle standing stock in tonnes ADW (bars) and amount of cockles in tonnes fresh weight removed by fisheries (line) in the Oosterschelde.

based on Coosen *et al.*, 1993b) and the amount of cockles removed by cockle-fishers is plotted. Cockle fisheries (M. Van Stralen, pers. comm.) increased dramatically in the post-barrier period and coincided with low cockle stocks in recent years. As cockle fisheries removed most animals between October and December, the drop in Oystercatcher winter numbers could well be related to this.

4. Prey availability

One of the effects of the construction of the storm surge barrier in the Oosterschelde is the erosion of the intertidal flats (Mulder & Louters, 1993). This is shown in Fig. 9 for one of the major intertidal flats. The total food availability for birds can be expressed as the product of surface, benthos biomass and exposure time. Although benthos biomass did not change in relation to tidal elevation the overall food availability index (product of surface, benthos biomass and exposure time) decreased by 17% between 1984 and 1989, mainly due to the decreased tidal elevation of the flat. If this trend continues, as expected, this will further reduce food availability.

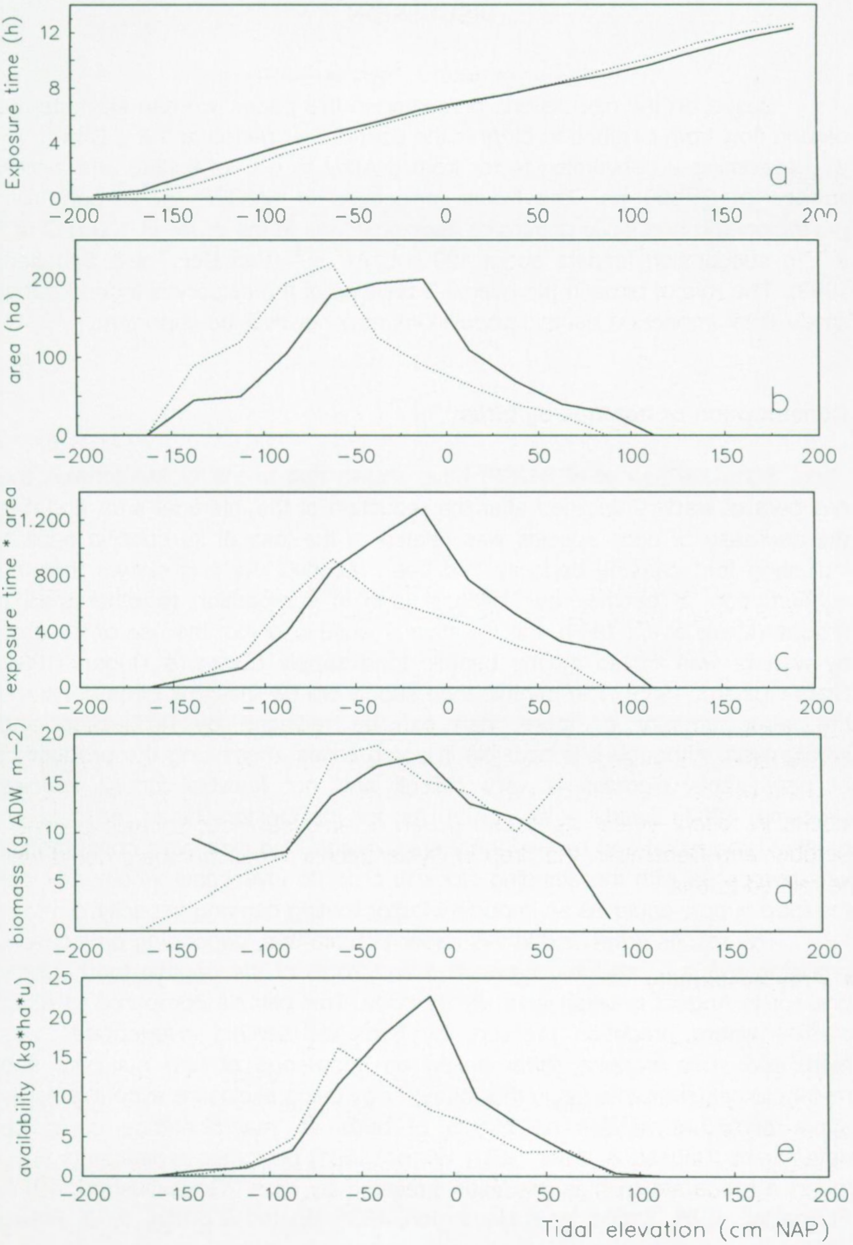

Figure 9. Exposure time, surface, benthic biomass and food availability, expressed as the product of exposure time, surface and benthic biomass at different tidal elevations of the Roggenplaat in 1985 (solid line) and 1989 (dotted line).

DISCUSSION

Based on the calculations presented in this paper, we can estimate the carbon flow from benthos to birds in the post-barrier period at 1.8 g C m^{-2} y^{-1}., assuming a conversion factor from g ADW to g C of 0.4348 and a total surface of 35,100 ha. The fluxes, calculated in SMOES, of carbon from phytoplankton and labile detritus to zooplankton is in the order of 100 g C m^{-2} y^{-1}, to suspension feeders about 120 g C m^{-2} y^{-1} (Van Der Tol & Scholten, 1993). The role of birds in the overall C-balance of the estuary is indeed rather small. Their impact on benthic populations may however be important.

Consumption of benthos by birds

Schekkerman *et al.* (1993) have shown that in the Oosterschelde the numbers of waders declined after the reduction of the intertidal area and that the decrease of each species was related to the loss of its specific habitat, indicating that carrying capacity had been reached. As it is shown that the consumption of benthivorous birds is high in comparison to other trophic groups (Meire *et al.*, 1989), the question is whether or not the use of the area by waders was limited by the benthic food supply (Evans & Dugan, 1984; Goss-Custard, 1985). The benthic food supply will be limiting if birds consume the same amount or more than can be replaced by production and immigration. Although it is possible in some cases, measuring the production of harvestable biomass is very difficult and not feasible for all species (Piersma, 1987; Zwarts *et al.*, 1992). As, for the Oosterschelde, no data on benthic production and harvestability are available, the estimated consumption was compared with the standing stock in order to investigate whether or not the food supply could be an important factor limiting carrying capacity or not.

The results presented in this paper indicate that, depending on location, predator and prey species, between 5 and 70 % of the benthic food supply present in August is taken annually by birds. This can be compared to other studies where predation pressure by birds on benthic invertebrates was measured. This is done either based on knowledge of bird numbers and metabolic requirements (as in this study) or by using exclosure experiments. In some exclosure studies no effects of birds on macrobenthos could be determined (Raffaelli & Milne, 1987; Wilson, 1991) but other experiments have found a moderate to high predation pressure by birds (Goss-Custard, 1977; Schneider, 1978; Schneider & Harrington, 1981; Boates & Smith, 1979; Reise, 1985).

The methods used in this paper to estimate the amount of food removed by waterbirds are similar to those used in other studies (Table 6). Although studies differed in assumptions or methods of calculations, with

Table 6: Consumption, estimated from bird numbers and metabolic requirements, of waders and ducks in different estuaries. The consumption in g ADW m^{-2} y^{-1}, the autumn or mean annual biomass in g ADW m^{-2} and annual production in g ADW m^{-2} y^{-1} and the predation pressure (between brackets) are given.

Site	Consumption	Autumn biomass (% consumed)	Mean biomass	Production	Reference
Oosterschelde	11.5 - 13.15 (*)	49.3 (23.3%) - 99.3 (13.3%) (*)			this paper
Westerschelde	4.1	15.1 (27.2%)			Meire *et al.* 1989; Stuart *et al.*, 1989
Grevelingen	8.2		72 (11.4%)		Wolff *et al.* 1976; Wolff & De Wolf, 1977
Waddenzee	4.7		26.6 (17.6%)	28 (17%)	Smit, 1981; Beukema, 1976, 1981; De Wilde & Beukema, 1984
Ythan estuary	22		59.8 (36.7%)	111.4 (19.7%)	Baird & Milne, 1981
Tees estuary	17.2	44.41 (38.3%)		38.6 (44%)	Evans *et al.* (1979)
Ventjager	5.5	11.63 (47.3%) - 16.18 (34%)			Zwarts 1974
Langebaan	6.4			32 (20%)	Summers, 1977; Baird et al.,1985
Berg River estuary	26.7			109.4 (26%)	Kaletja (1992)
Banc d'Arguin	11.5		14.5 (82.7%)	27 (42.6%)	Wolff & Smit, 1990

(*) Pre- and post-barrier data (see Table 1)

some caution the results can nevertheless be compared. For instance, Smit (1981) used Lasiewski & Dawson's (1967) or Aschoff & Pohl's (1970) formula for estimating BMR of waders, which results in a lower figure than the equation given by Kersten & Piersma (1987). On the other hand, he used mean annual body mass including fat stores to estimate BMR instead of lean weights, and a factor 5 instead of (1/0.85 x3)=3.5 to convert BMR into DEE; both factors resulting in a higher consumption. Calculating the consumption in the Wadden Sea using the number of birds given by Smit and the body masses and formulae applied for the Oosterschelde, the yearly consumption does not differ much from Smit's original figure: 4.3 g ADW m^{-2} y^{-1} versus 4.7 g ADW m^{-2} y^{-1}. We used 0.85 as a value of assimilation efficiency Q, while 0.80 (Wolff & Smit, 1990) or 0.75 (Castro *et al.*, 1989) might be a more realistic value. Use of Q=0.85 causes an underestimation of the consumption by 11% compared to Q=0.75.

Another ground for differences in results lies in the conversion of predicted BMR to an estimate of DEE in the field. We used a conversion factor of 3, following Drent *et al.* (1978), Smith (1975), Kersten & Piersma (1987) and Castro *et al.* (1992). Recently, Wiersma & Piersma (1993), using climatic data, estimated the energy expenditure under field conditions for Knots in the Dutch Wadden Sea, taking into account effects of temperature, solar radiation and wind. Compared to a constant rate of 3 times BMR, the total annual energy expenditure per bird was estimated by Wiersma & Piersma (1993) was 19% higher. Because Knots, like most species, are most numerous in the Oosterschelde in winter when thermostatic costs are high, the resulting estimate of consumption would be as much as 28% higher than ours. The true difference is probably somewhat smaller as the winter climate of the Oosterschelde is more benign than that of the Wadden Sea. The difference as found in Knots cannot be assumed to apply to all species occurring in the Oosterschelde, since the thermostatic cost relative to BMR decreases with increasing body size (Wiersma *et al.*, 1993). Thus the true energy expenditure of birds larger than Knots, which are most important in determining the total amount of food removed by birds in the Oosterschelde, is expected to be closer to the level estimated by our assumptions of 3*BMR than that of Knots.

The data from Table 6 show that waders are able to remove a substantial part of benthic biomass or production, as already found by Baird *et al.* (1985). The values for the Oosterschelde, including cockles, mussels and Oystercatchers are on the low side, but excluding them they are comparable to, or higher than those for other areas.

Within an estuary the consumption is not evenly spread over the flats. Data from the permanent plots at Vianen indicate a clear positive relationship between consumption and benthic biomass. Zwarts (1988), working in the Wadden Sea and Sidi Moussa (Morocco) found a similar relationship between consumption and benthic biomass, although the observed relationship differed significantly between study areas. In the Oosterschelde, predation pressure by Oystercatchers did not show any relation with the overall biomass. It is likely, however, that predation pressure is related to the amount of prey that can be economically harvested as suggested by the relationship between predation pressure and average cockle length. In plots with large cockles, which are both available and profitable for Oystercatchers, predation pressure is very high (up to 70%).

Besides consumption by birds, other epibenthic predators take their share of the macrobenthic food supply. Smit (1981) and Beukema (1981) estimated the consumption by crabs, shrimps and fish for the Wadden Sea at

10 g ADW m^{-2} y^{-1}, twice as large as the total consumption by birds. Sanchez-Salazar *et al.* (1987) found the consumption of adult crabs *Carcinus maenas* on cockles to be 25 times more important in numbers or twice as much in biomass than that of Oystercatchers. In addition to epibenthic predators, also several infaunal predators are present in the sediment. Although their role is less well understood they can have an important impact on the other benthic species (Ambrose, 1991).

Based on the evidence presented above it is clear that epibenthic predators and birds together must consume a substantial part of the benthic biomass. Furthermore, the percentage of the prey populations which are predated by birds were calculated based on the total amount of biomass present on the flats and not on the biomass harvestable by the birds. It is known that due to prey escape behaviour, burying depth, prey-size, coverage by barnacles etc. the biomass harvestable to birds at any one moment is much lower than the total biomass present (Durell & Goss-Custard, 1984; Esselink & Zwarts, 1989; Evans, 1976; Evans 1987; Meire, 1991; Meire & Ervynck, 1986; Zwarts & Wanink, 1984, 1989). Zwarts *et al.* (1992) found on average over 10 years only 13.5% of the total biomass of bivalves to be harvestable by Knots. Meire & Ervynck (1986) estimated that, depending on the mussel bed, on average 30% of the mussels of the size classes taken by hammering Oystercatchers were available to the birds. Predation pressure on harvestable biomass must therefore be higher than the figures given above. To prove carrying capacity is reached due to shortage of food, it is crucial to know the amount of harvestable prey which is removed in relation to production of harvestable biomass (Piersma, 1987). These data are not available. The date discussed above do suggest that birds consume a substantial part of the total food supply, which moreover they have to share with other epibenthic and endobenthic predators consuming at least the same quantity of food.

Carrying capacity

Recent studies showed that bird numbers reach plateau values in some estuaries or feeding areas (Meire & Kuijken, 1984; Moser, 1988; Zwarts, 1974) and Schekkerman *et al.* (1993) showed that wader numbers decreased in the Oosterschelde in response to the reduction of intertidal area. We believe this provides circumstantial evidence that, at least for several species, the decline in numbers in the Oosterschelde (Schekkerman *et al.*, 1993) could be due to food shortage. This does not mean that birds face food shortage each season. As the variability of the benthos is much higher than that of the birds it is likely that food will not be limiting at some times, while at other times it does. During severe winters, food shortage in combination with cold stress can cause the death of many birds (Lambeck, 1991; Meininger *et al.*, 1991). As the variability of cockle and mussel biomass is very high it is likely that at some times, when biomass is very high, much more is harvestable by Oystercatchers than is actually taken. At other times when biomass is low (caused by natural variation or by fisheries) it might limit Oystercatcher numbers. If this is true, any further loss of intertidal area, food supply, or availability will result in a further reduction of bird numbers. In recent years populations of both mussels and cockles have been very small in the Wadden Sea causing high mortality in Eider and decreasing numbers of Oystercatchers (Beukema & Swennen, pers. comm.). Whether or not this will have an effect on population level is another question (Goss-Custard & Durell, 1990).

The results from the intertidal area are in contrast with those from the subtidal compartment. Here consumption is very low compared to other areas as the Wadden Sea (Smit, 1981) or the saline lakes of the Delta area (Meire *et al.*, 1989). Although no data on benthic invertebrates of the subtidal compartment are available for the years analysed in this paper, present investigations by Craeymeersch (pers. com.) indicate that benthic biomass is comparable to that of the Wadden Sea (Dekker, 1989), resulting in a very low predation pressure in the Oosterschelde. If not limited by other factors, bird species like Eiders, feeding in the subtidal compartment, probably could increase substantially in numbers in the Oosterschelde, a trend that seems to have started already.

Historical perspective

The present results contrast with previous findings in the Delta area. There is no evidence that wader numbers in the whole Delta area of South-West Netherlands decreased after the closure of the estuaries Veerse Gat, Haringvliet and Grevelingen (Saeijs & Baptist, 1977; Leewis *et al.*, 1984; Meininger *et al.*, 1984). After the closure of the Grevelingen, an estuary adjacent to the Oosterschelde, wader numbers increased substantially in the Krammer-Volkerak, the northern branch of the Oosterschelde (Leewis *et al.*, 1984; Meininger *et al.*, 1984) and numbers of Oystercatchers and Bar-tailed Godwits increased abruptly on a large tidal flat in the mouth of the Oosterschelde (Lambeck *et al.*, 1989). In the Krammer-Volkerak, however, important changes occurred due to the coastal engineering works. Tidal amplitude and current velocity increased, chlorinity rose from 0.5-5 to 9-13%. In response to these abiotic changes, especially the chlorinity, the diversity of macrozoobenthos increased substantially (Wolff, 1971) and mussel cultures became established in the area. Although no data are available we can reasonably assume that in the Krammer-Volkerak the food availability increased substantially, increasing the carrying capacity for waders. If in the Oosterschelde (excluding Krammer-Volkerak) and Westerschelde, the two remaining estuaries, the benthic biomass did not change (increase) it seems that carrying capacity had not yet been reached in the 1960s. This also might hold in other Western European estuaries where numbers of some wader species increased in the last decades (Smit & Piersma, 1989) notwithstanding a reduction in intertidal area. In the past decades the benthic production might have increased due to eutrophication as is shown for the Wadden Sea (Beukema & Cadée, 1986) and hence carrying capacity as suggested by Van Impe (1985) to explain an increase in bird numbers in a part of the Westerschelde estuary. Tubbs *et al.* (1992) suggested that the increase in Dunlin numbers in the Solent since the 1950s reflects release from hunting pressure. A combination of both factors might indeed explain the increasing population sizes of most species in a period of decreasing feeding areas. For several species the balance now seems to have been reached and any further loss in intertidal habitat or deterioration in food supplies will ultimately result in a decrease of wader numbers.

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REFERENCES

Ambrose, W. G., 1991. Are infaunal predators important in structuring marine soft-bottom communities? Am. Zool. 31: 849-860.

Aschoff, J. & H. Pohl, 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. J. Orn. 111: 38-47.

Baird, D. & H. Milne, 1981. Energy flow in the Ythan estuary, Aberdeenshire, Scotland. Estuar. Coast. Shelf Sci. 13: 455-472.

Baird, D., P. R. Evans, H. Milne & N. W. Pienkowski, 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanogr. Mar. Biol. annu. Rev. 23: 573-597.

Beukema, J. J., 1974. Seasonal changes in the biomass of the macrobenthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 94-107.

Beukema, J. J., 1976. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 10: 236-261.

Beukema, J. J., 1981. The role of the larger invertebrates in the Wadden Sea ecosystem. In W. J. Wolff (ed.), Ecology of the Wadden Sea. Balkema, Rotterdam: Vol 3: 211-221.

Beukema, J. J. & C. Cadée, 1986. Zoobenthos responses to eutrophication of the Dutsch Wadden Sea. Ophelia 26: 55-64.

Boates, J. S. & P. C. Smith, 1979. Length-weight relationships, energy content and the effects of predation on *Corophium volutator* (Pallas) (Crustacea: Amphipoda). Proc. N. S. Inst. Sci. 29: 489-499.

Castro, G., J. P. Myers & R. E. Ricklefs, 1992. Ecology and energetics of Sanderlings migrating to four latitudes. Ecology 73: 833-844.

Castro, G., N. Stoyan & J.P. Myers, 1989. Assimilation efficiency in birds: a function of taxon or food type? Comp. Biochem. Physiol. 92A: 271-278.

Coosen, J., J. Seys & P. M. Meire, 1993a. Effect of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde on distribution, density and biomass of some common macrobenthic species: *Spio martinensis* (Mesnil), *Hydrobia ulvae* (Pennant), *Arenicola marina* (L.), *Scoloplos armiger* (Muller) and *Bathyporeia sp.*. Hydrobiologia: in press.

Coosen, J., F. Twisk, M. Van Der Tol, R. H. D. Lambeck, M. Van Stralen & P. M. Meire, 1993b. Spatfall, growth and biomass of the cockle (*Cerastoderma edule*) in the Oosterschelde (1980-1990). Hydrobiologia: in press.

Cramp, S. & K. E. L. Simmons, 1977. Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the Western Palearctic. Vol 1: Ostrich-Ducks. Oxford University Press, Oxford.

Cramp, S. & K. E. L. Simmons, 1983. Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the Western Palearctic. Vol 3: Waders to gulls. Oxford University Press, Oxford.

Davidson, N. C., 1983. Formulae for estimating the lean weight and fat reserves of live shorebirds. Ring. & Migr. 4: 159-166.

Dekker, R., 1989. The macrozoobenthos of the subtidal western Dutch Wadden Sea. I. Biomass and species richness. Neth. J. Sea Res. 23: 57-68.

De Wilde, P. & J. J. Beukema, 1984. The role of zoobenthos in the consumption of organic matter in the Dutch Wadden Sea. In R. W. P. J. Laane & W. J. Wolff (eds), The role of organic matter in the Wadden Sea. Nioz Publ. Ser. 10: 145-158.

Drent, R., B. Ebbinge & B. Weijand, 1978. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. Orn. Ges. Bayern 23: 239-263.

Durell le V. dit, S. E. A. & J. D. Goss-Custard, 1984. Prey selection within a size-class of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*. Anim. Behav. 32: 1197-1203.

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.

Evans, A., 1987. Relative availability of the prey of wading birds by day and by night. Mar. Ecol. Prog. Ser. 37: 103-107.

Evans, P. R., 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distribution and movements in the non-breeding season. Ardea 64: 117-139.

Evans, P. R. & P. J. Dugan, 1984. Coastal birds: numbers in relation to food resources. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 8-28.

Evans, P. R., D. M. Herdson, P. J. Knights & M. W. Pienkowski, 1979. Short-term effects on reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. Oecologia 41: 183-206.

Goss-Custard, J. D., 1977. 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., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford: 169-188.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Kalejta, B., 1992. Time budgets and predatory impact of waders at the Berg River Estuary, South Africa. Ardea, 80: 327-342.

Kersten, M. & T. Piersma, 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an expensive way of life. Ardea 75: 175-187.

Klepper, O., H. Scholten & M. Van Der Tol, 1993. Description of SMOES - simulation model for the Oosterschelde ecosystem. Hydrobiologia: in press.

Lambeck, R. H. D., 1991. Changes in abundance, distribution and mortality of wintering Oystercatchers after habitat loss in the Delta area, SW Netherlands. Acta XX Congr. Int. ornithol.: 2208-2218.

Lambeck, R. H. D., A. J. J. Sandee & L. De Wolf, 1989. Long-term patterns in the wader usage of an intertidal flat in the Oosterschelde (SW Netherlands) and the impact of the closure of an adjacent estuary. J. appl. Ecol. 26: 419-431.

Lasiewski, R. C. & W. R. Dawson, 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69: 13-23.

Leeuwis, R. J., H. J. M. Baptist & P. L. Meininger, 1984. The Dutch delta area. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 253-260.

Meininger, P. L., H. J. M. Baptist & G. J. Slob, 1984. Vogeltellingen in het Deltagebied in 1975/1976 - 1979/1980. Nota DDMI-84.23, Rijkswaterstaat Deltadienst, Middelburg & Staatsbosbeheer Zeeland, Goes.

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., 1987. Foraging behaviour of some wintering waders: prey selection and habitat distribution. In A. C. Kamil, J. R. Krebs & H. R. Pulliam (eds), Foraging behavior. Plenum Press, New York.

Meire, P. M., 1991. Effects of a substantial reduction in intertidal area on numbers and densities of waders. Acta XX Congr. int. Ornithol. : 2219-2227.

Meire, P. M. & J. Dereu, 1990. Use of the abundance/biomass comparison method for detecting environmental stress: some considerations based on intertidal macrozoobenthos and bird communities. J. appl. Ecol. 27: 210-223.

Meire, P. M. & A. Ervynck, 1986. Are Oystercatchers (*Haematopus ostralegus)* selecting the most profitable mussels (*Mytilus edulis)*? Anim. Behav. 34: 1427-1435.

Meire, P. M. & E. Kuijken, 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 57-68.

Meire, P. M. & E. Kuijken, 1987. A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, The Netherlands) before major environmental changes and some predictions on expected changes. De Giervalk 77: 283-311.

Meire, P. M., J. Seys, J. Buijs & J. Coosen, 1993. Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm surge barrier? Hydrohiologia: in press.

Meire, P. M., J. Seys, T. Ysebaert, P. I. Meininger & H. J. M. Baptist, 1989. A changing Delta: effects of large coastal engineering works on feeding ecological relationships as illustrated by waterbirds. In J. C. Hooghart & C. W. S. Posthumus (eds), Hydro-ecological relations in the Delta waters of the South-West Netherlands. Lakerveld B.V., the Hague: 109-143.

Meire, P. M., J. Buys, J. Van Der Meer, A. Van Den Dool, A. Engelberts, F. Twisk, E. Stikvoort, D. De Jong, R. H. D. Lambeck & J. Polderman, 1991a. Macrozoobenthos in de Oosterschelde in het najaar 1985. Een situering van de gegevens. Rapport RUG-WWE nr. 27, Gent; Rijkswaterstaat, Middelburg; DIHO, Yerseke.

Moser, M. E., 1988. Limits to the numbers of Grey Plovers *Pluvialis squatarola* wintering on British estuaries: an analysis of long term population trends. J. appl. Ecol. 25: 473-485.

Mulder, J. P. M. & T. Louters, 1993. Changes in basin geomorphology after the implementation of the Oosterschelde project. Hydrobiologia: in press.

Nienhuis, P. H. & A. C. Smaal, 1993. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction. Hydrobiologia: in press.

Norstrom, R. J., T. P. Clark, J. P. Kearney & A. P. Gilman, 1986. Herring Gull energy requi rements and body constituents in the Great Lakes. Ardea 74: 1-23.

Piersma, T., 1984. Estimating energy reserves of Great Crested Grebes *Podiceps cristatus* on the basis of body dimensions. Ardea 72: 119-126.

Piersma, T., 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Mar. Ecol. Prog. Ser. 38: 187-196.

Raffaelli, D. & H. Milne, 1987. An experimental investigation of the effects of shorebird and flatfish predation on estuarine invertebrates. Estuar. coast. shelf Sci. 24: 1-13.

Reise, K., 1985. Tidal flat ecology - An experimental approach to species interactions. Springer-Verlag, Berlin Heidelberg.

Saeijs, H. L. F. & H. J. M. Baptist, 1977. Wetland criteria and birds in a changing Delta. Biol. Cons. 11: 251-266.

Sanchez-Salazar, M. E., C. L. Griffiths & R. Seed, 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. Estuar. coast. Shelf Sci. 25: 245-260.

Schekkerman, H., P. L. Meininger & P. M. Meire, 1993. Changes in the waterbird populations of the Oosterschelde, SW. Netherlands, as a result of large scale coastal engineering works. Hydrobiologia: in press.

Schneider, D., 1978. Equalisation of prey numbers by migratory shorebirds. Nature 271: 353-354.

Schneider, D. C. & B. A. Harrington, 1981. Timing of shorebird migration in relation to prey depletion. The Auk 98: 801-811.

Seys J. J., P. M. Meire & J. Coosen, 1993. Long-term changes (1979-89) in the intertidal macrozoobenthos of the Oosterschelde: are patterns in total density, biomass and diversity induced by the construction of the storm-surge barrier? Hydrobiologia: in press.

Smaal, A. & R. Boeije, 1991. Veilig getij, de effecten van de waterbouwkundige werken op het getijdenmilieu van de Oosterschelde. Nota GWWS 91.088 DGW/directie Zeeland, Middelburg.

Smit, C. J., 1981. Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea area. In W.J. Wolff (ed.), Ecology of the Wadden Sea. Balkema, Rotterdam: Vol. 3: 290-301.

Smit, C. J. & T. Piersma, 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In H. Boyd & J.-Y. Pirot (eds), Flyways and reserve networks for water birds. IWRB special Publication No. 9, Slimbridge: 24-63.

Smith, P. C., 1975. A study of the winter feeding ecology of the Bar-tailed Godwit *Limosa lapponica*. Ph. D. Thesis, University of Durham.

Stuart, J. J., P. L. Meininger & P. M. Meire, 1989. Watervogels van de Westerschelde. Rapport WWE nr. 14; RWS nota AO 89.1010. University of Gent, Gent.

Summers, R.W., 1977. Distribution, abundance and energy relationships of waders (Aves: Charadrii) at Langebaan Lagoon. Trans. Roy. Soc. S. Afr. 42: 483-494.

Sutherland, W. J. & J. D. Goss-Custard, 1991. Predicting the consequence of habitat loss on shorebird populations. Acta XX congr. Int. Ornithol.: 2199-2207.

Tubbs, C. R., J. M. Tubbs & J. S. Kirby, 1992. Dunlin *Calidris alpina alpina* in the Solent, southern England. Biol. Cons. 60: 15-24.

Van Der Tol, M .W. M. & H. Scholten, 1993. Response of the Eastern Scheldt ecosystem to a changing environment: functional or adaptive? Neth. J. Sea Res. 30: 175-190.

Van Impe, J. 1985. Estuarine pollution as a probable cause of increase of estuarine birds. Mar. Poll. Bull. 16: 271-276.

Van Stralen, M. R. & R. D. Dijkema, 1993. Mussel culture in a changing environment: the effects of a coastal engineering project on mussel culture in the Oosterschelde. Hydrobiologia: in press.

Wiersma, P. & T. Piersma, 1993. Living exposed and in the cold: seasonal changes in the thermostatic costs of temperate-wintering Red knots. Condor: in press.

Wiersma, P., L. Bruynzeel & T. Piersma, 1993. Energie besparing bij wadvogels: over de kieren van de Kanoet. Limosa: in press.

Wilson, W. H. Jr., 1991. The foraging ecology of migratory shorebirds in marine soft-sediment communities: the effects of episodic predation on prey populations. Am. Zool. 31: 840-848.

Wolff, W. J., 1971. Changes in intertidal benthos communities after an increase in salinity. Thalassia Jugoslavica 7: 429-434.

Wolff, W.J. & L. De Wolf, 1977. Biomass and production of Zoobenthos in the Grevelingen estuary, The Netherlands. Estuar. coast. mar. Sci. 5: 1-24.

Wolff, W. J. & C. J. Smit, 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. Ardea 78: 17-38.

Wolff, W. J., A. M. M. Van Haperen, A. J. J. Sandee, H. J. M. Baptist & H. L. F. Saeijs, 1976. The trophic role of birds in the Grevelingen estuary, The Netherlands, as compared to their role in the saline Lake Grevelingen. In G. Persoone & E. Jaspers (Eds), Proceedings of the 10th European Symposium on Marine Biology. Universa Press, Wetteren: Vol. 2: 673-689.

Zwarts, L., 1974. Vogels van het brakke getij-gebied. Bondsuitgeverij van de jeugdbonden voor natuurstudie, Amsterdam.

Zwarts, L., 1988. Numbers and distribution of coastal waders in Guinea-Bissau. Ardea 76: 42-55.

Zwarts, L. & A.-M. Blomert, 1990. Selectivity of Whimbrels feeding on fiddler crabs explained by component specific digestibilities. Ardea 78: 193-208.

Zwarts, L. & J. Wanink, 1984. How Oystercatchers and Curlew successively deplete clams. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 69-83.

Zwarts, L. & J. Wanink, 1989. Siphon size and burying depth in deposit- and suspension feeding benthic bivalves. Mar. Biol. 100: 227-240.

Zwarts, L., A.-M. Blomert & J. H. Wanink, 1992. Annual and seasonal variation in the food supply harvestable for Knot *Calidris canutus* staging in the Wadden Sea in late summer. Mar. Ecol. Prog. Ser. 83: 128-139.

Chapter 12

EPILOGUE

As indicated in the introduction, habitat loss is a very widespread problem. The physical loss of a site is the clearest form of habitat loss. However degradation of the habitat by many different factors is at least as important. In the case of the Oosterschelde it is likely that the physical loss of habitat will continue due to morphological processes (see Mulder & Louters, 1993). Also increasing disturbance due to recreation, bait digging and a further increase in e.g., the cockle fisheries, could cause a clear degradation of the remaining habitat. The same threats hold for the Wadden Sea and Davidson *et al.* (1991) showed that in more than 50% of the British estuaries there were plans for new barrage shemes, marina's etc.

Therefore it is clear that answering the question: "what is the effect of habitat loss and/or degradation on waterbird populations" is a priority in conservation and also should be asked in environmental impact studies when proposals are presented for changing the land-use of an area. The coastal engineering works in the Oosterschelde, resulting in a loss of more than 30% of the intertidal area, provided a good opportunity to study the effects on waterbirds in general and waders in particular. Several studies were undertaken, some of them being included in this thesis. Both macrobenthic and waterbird populations were measured before, during and after the environmental changes. Additionally, the foraging behaviour of waders, especially the Oystercatcher (*Haematopus ostralegus*), was studied, including distribution over a tidal flat, relationship with the prey populations and prey selection. Most data were collected at the Slikken van Vianen, others in the Oosterschelde as a whole.

The results presented in this thesis indicate that the macrozoobenthic populations show a large annual variability. This is to some extent influenced by severe winters. There is no evidence that species composition, density and biomass of the macrozoobenthos changed yet, in respons to the environmental changes. Although sediment characteristics (especially the mud content) and the tidal elevation are important parameters influencing benthic invertebrates they explain only a part of the observed variability. Based on several considerations it is argued that the benthic populations are situated more towards the nonequilibrium end of the continuum between nonequilibrium and equilibrium communities as defined by Wiens (1984), implicating a rather loose community structuring. If the morphological changes (especially the erosion of the tidal flats) continue as predicted (Mulder & Louters, 1993) changes in the overall food supply of waders are to be expected.

The total bird numbers for the Oosterschelde as a whole declined in 8 species, increased in 2 species; the changes were not significant in 13 species, although several showed a clear decrease. The underlying causes for these changes were further analysed mainly for the Oystercatcher by detailed studies of feeding behaviour at the Slikken van Vianen.

Feeding Oystercatchers, opening their prey by the hammering method, select thin shelled mussels between 30 and 45 mm long, not overgrown by barnacles, in accordance with an extended optimal diet model. The analysis of prey selection was a necessary step to divide the total mussel population present on the bed into different fractions in order to calculate the harvestable fraction for the birds, a crucial step to understand the relation between bird and prey density, a relation which seemed not to have changed after the environmental changes.

As the total number of Oystercatchers in the study area increased, the less profitable feeding areas were gradually occupied while densities at the best sites remained stable. Due to the manipulation of the barrier, the feeding time of birds was severally reduced in October 1986 resulting in a serious consumption deficit (intake rate was one third less than normal over a period of five days) leading to a reduced condition of the birds. It was also found that at that time, birds were feeding at a maximum rate. The total consumption of benthic invertebrates by waterbirds, calculated for the Oosterschelde as a whole and for several study plots on the Slikken van Vianen, was high compared to the standing stock of macrobenthos. In some occasions the consumption by Oystercatchers was in the order of magnitude of the production of harvestable prey, leading to the conclusion that the use of the area was limited by food supply and that carrying capacity was, at least temporarily, reached. Thus the birds excluded from the lost intertidal areas could not be accommodated in the remaining part. It is assumed that a similar reasoning held for the other species which declined.

In each chapter of this thesis, dealing with a specific problem, the results were discussed in detail. Therefore, in this epilogue I will not once more discuss the results but rather try to evaluate the overall approach of the study and the study itself and put forward some implications for further research and conservation of waterbirds and waders in estuaries.

1. Evaluation of the approach followed during this study

1.1 complications inherent to field work

The coastal engineering works in the Oosterschelde can be seen as a unique experiment to study large scale effects of environmental changes but there are some serious restrictions: 1) there are no replica's (N=1) and 2) there is no control within the area. This inevitably reduces the reliability of the interpretation of the results and their causation. The interpretation remains tentative and is not unequivocal.

Furthermore field studies often suffer from unforeseen and/or uncontrollable confounding variables. Within the present study two problems arose in this context. First of all the Markiezaat was closed already in 1983. About 1800 ha of intertidal area disappeared, but at that time the tidal conditions did not yet change in the remaining part of the Oosterschelde. In most studies, therefore, the pre-barrier period runs until 1985 when the tidal range started to decline. This was so in the papers dealing with benthos (chapter 2 and 3) and the low water distribution of birds at the Slikken van Vianen (chapter 9). It is however unlikely that this would influence the results: the hydrodynamic changes, possibly affecting the benthos did nearly change after the closure of the Markiezaat and there are no indications that birds from there moved to other parts of the estuary. In the papers dealing with the total populations of waders and waterbirds (chapter 5 and 6) the pre-barrier period included only seasons before the closure of the Markiezaat.

The second problem was the occurrence of three severe winters (1984/85 - 1986/87) in a row just during the period of maximal tidal reduction. Especially for the study of the benthic populations this is an important confounding variable because it can cause extra variability hiding some overall trends or effects of the hydrodynamic changes that occurred in the same period. For the wader studies it gave some additional information on mortalities but could have of course an influence on their populations. These problems are, however, inherent to this type of studies.

1.2 the approach

In the introduction a simple conceptual model was presented as a guideline for studying the effects of habitat loss on waders. The proposed factors and links of that model can be grouped into three main questions: 1) can the birds which are excluded from the reclaimed areas settle elsewhere, in other words can bird densities increase or is the carrying capacity reached?; 2) are the mortality rates of birds affected in the new situation?; 3) have changed mortality rates an effect on total population size? (see also Goss-Custard & Durell, 1990; Sutherland & Goss-Custard, 1991). These different questions and the answers found in this thesis will be discussed to evaluate the approach followed in this study.

1.2.1 Can bird densities increase or is carrying capacity reached?

In this thesis, and in many other studies, the assumption is made that birds confronted with habitat loss have the behavioural plasticity to move to other sites. Sutherland (1982) showed that a considerable cockle spatfall was quickly discovered by Oystercatchers, indicating the importance of dispersal. However most birds arriving were young ones. Whether adults, of which it is known that they may be very site faithful (e.g., Swennen, 1984), can easily move elsewhere is unclear and can only be answered by analysing the ringing recoveries. This is likely to differ between species.

- Total population of birds

At least for several species the total number of birds present in the Oosterschelde after the loss of intertidal habitat was less than before (chapter 5 & 6). This is, on its own, no indication that carrying capacity was reached. Indeed, total bird numbers are influenced by a great many different factors, acting both within and outside the area. Due to bad reproduction, very good food conditions in other estuaries or still other factors, there might have been no more birds "available" to settle in the Oosterschelde after the habitat loss occurred. If this is true, carrying capacity was not reached. Therefore based on bird counts alone no conclusions could be drawn. The data had to be compared with the overall populations of each species. In this respect, waders and waterbirds form a rather unique situation as estimates of the overall population size are available due to an international network of observers coordinated by the International Waterfowl and Wetland Research Bureau (see, e.g., Smit, 1984). These estimates are published only after several years. In Chapter 5 and 6 the data were therefore compared with the British data, but it will be necessary to check the trends with the total population sizes as they come available. The trends in the Oosterschelde did differ for most species from the British trends, strengthening the opinion that the observed changes in the Oosterschelde were a local phenomenon and hence possible related to the environmental changes.

- benthos populations

However, as the total bird population in the estuary is also dependent on the food supply and the distribution of the birds at low water, the data could still not be interpreted without information about the macrobenthic populations and its relationships with the birds. These data were not often collected in similar studies (see introduction). Lack of data on benthos also was the reason why the effects of previous habitat loss in the Delta area could not be interpreted. It was likely that the food supply changed but this is not documented (see discussion chapter 6 and 11). The benthic populations are however characterized by large fluctuations, both in biomass and species composition. Although the Oosterschelde can be seen as a rather homogeneous area, compared to other estuaries like the Westerschelde (Meire *et al.*, 1991) or Eems-Dollard (Ysebaert & Meire, 1993) and thus the range of some environmental parameters (mud content; salinity) being very small indeed, clear gradients in prey densities were found. Although the data on benthos indicate no clear patterns in density or biomass no overall estimate of the total standing stock of macrobenthos in the whole area was made.

- Feeding ecology of birds

The distribution of birds at low water in relation to these food gradients was studied in detail only for the Oystercatcher and its main food, mussels (*Mytilus edulis*) and cockles (*Cerastoderma edule*). Annual variations in the density of feeding birds within a plot were related to the changes in food supply. Within a year the richest feeding areas were occupied first and as total numbers increased all feeding areas were gradually filled. Such distribution patterns are predicted by the Ideal Free or the Ideal Despotic distribution (Fretwell & Lucas, 1970; Fretwell, 1972). Recently there have been several theoretical developments with these models (Bernstein *et al.*, 1991; Sutherland & Parker, 1985; Milinski & Parker, 1991) pointing to the importance of a different competitive ability between the birds. Indeed, interference, the reversible depression of intake rate due to increasing bird densities (Goss-Custard, 1980), does not affect all individuals equally (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987). Therefore individuals are not distributed at random over the feeding areas. Juvenile, subadult and adult Oystercatchers are feeding in different parts of the estuary (e.g., Goss-Custard & Durell, 1984, Swennen, 1984). During this study we could not rely on colour ringed birds (except for a short period in 1984). Therefore the distribution of individuals over a tidal flat was not studied.

Also in other species clear differences in distribution (both within or between estuaries) between sexes or age classes were found. (e.g., Van Der Have *et al.* 1984). If so, habitat loss can have a disproportionate impact on some parts of the population. Indeed if e.g., the habitat loss occurs in an area were mainly juveniles occur, they will be more affected compared than other segments of the population.

Measuring bird densities is also subject to difficulties. Indeed Oystercatchers have essentially two different ways to open their prey: either by hammering or stabbing (Norton-Griffiths, 1967). However both groups are depending on different prey populations: the hammerers on the thin-shelled mussels not overgrown by barnacles, the stabbers on mussels which are slightly gaping. When, in relating bird densities to e.g., the harvestable prey densities of hammerers, the proportion of stabbers and hammers differs, this can strongly influence the results.

When plotting bird density against prey density, both in this study and in others (see chapter 9) plateaux values were found and interpreted as a limit to the densities or maximum densities. This is based on the assumption that habitat suitability increases indefinitely with prey density. In chapter 9 it was shown that the plateaux values were artefacts and it is clear that habitat suitability did not increase with prey density, certainly not in mussels. This points to the importance of measuring harvestable prey densities (see introduction for definitions). Problem is, however, to determine what is harvestable. It was shown that optimal diet models can be extremely useful in providing insight into the mechanisms of prey selection and hence in the harvestable fraction of the prey population (see also Zwarts *et al.*, 1992; Meire 1993). It was not possible yet to determine both the harvestable density and production for several benthic species per study plot per year. Most species also depend on several prey species whose availability is determined largely by their behaviour. Here the estimate of harvestable prey densities is extremely difficult, although possible (e.g., Esselink & Zwarts, 1989).

The different types of interactions between standing stock, prey selection, harvestable density and bird density have, however, an important consequence: it is logically impossible to discover the limits set by food supply to shorebird density simply by plotting shorebird densities as a dependent variable of benthic standing crop or production (called the trophic explanatory pathway by Piersma, 1987). Indeed, instantaneous bird predation or density will be directly limited by the density of harvestable prey. In the long term cumulative shorebird predation will also be limited by the production (including immigration) of harvestable prey (Piersma, 1987).

This all points to the fact that one should be very careful to relate bird densities uncritically to prey densities, and especially to extrapolate the results from one site to another (Evans & Dugan, 1984). Therefore we may have some doubts about the results of Goss-Custard *et al.*, (1991) relating bird and prey densities from 40 sites in 6 estuaries to predict post-barrier densities in the Severn estuary. However, until now it might be the only way to make some predictions at all.

- Other factors influencing carrying capacity

Next to the main factors mentioned, still others could influence the carrying capacity. Disturbance is known to be very important for birds (e.g., Pfister *et al.*, 1992). Both in the whole of the Oosterschelde and on the Slikken van Vianen there has been a gradual increase of recreation, and hence of disturbance (Smaal & Boeije, 1991). This is caused on the one hand by bait-digging and on the other hand by people walking on the tidal flats. There is also an increase in the number of low flying sports-planes, which can cause very severe disturbance. No quantitative data on disturbance levels are available however, and it probably differs much between sites, days, state of the tide and season. On the Slikken van Vianen, most plots are situated in an area of musselbeds, without free access. Therefore we believe that the distribution patterns described in this thesis are not influenced by disturbance. For the whole of the Oosterschelde, however, this might not be true (see Dunlins, chapter 6).

- Other species

The discussion until now was focussed mainly on the situation for

Oystercatchers at Vianen. It is likely, however, that for other species, e.g., Bar-tailed Godwits, which increased at the Slikken van Vianen, other patterns will be found. Even more, interactions between species were not studied, although known to occur (e.g., Zwarts, 1980). Evans (1981) found that after reclamation of a major part of Seal Sands (Tees estuary), the numbers of some species were negatively correlated with those of others possibly indicating competition. Loss of part of a feeding area is thus likely to heighten interspecific competition and so affect different bird species to different extents (Evans & Pienkowski, 1983)

Notwithstanding all the uncertainties explained above, we believe that for the case of the Oosterschelde, there is evidence that at least for some species the carrying capacity was reached. Although carrying capacity is a rather vague term which one should not use (Evans, 1984; Dhondt, 1988), once clearly defined, it can be a useful concept. In this study the carrying capacity was defined as the density of birds at which the addition of one further bird would result in another either starving or leaving that locality to seek a better feeding area (Goss-Custard, 1985; Sutherland & Goss-Custard, 1991). When this point is reached, no net increase in bird density can take place, and the carrying capacity would have been reached. From this definition it is clear that the carrying capacity of an area must vary from year to year and also can vary in the course of a season. Indeed as conditions deteriorate the needs of the birds increase and fewer birds could be supported (see e.g., Meire, 1987). Therefore it is unlikely that capacity was reached permanently for each species, but at some times it was.

1.2.2 Are the mortality rates of birds affected in the new situation?

The overall food intake of an individual will determine to a large extend its condition and this in turn whether or not it will stay in the area, migrate or die. It was not possible in this study to measure directly if the mortality of waders increased as a consequence of the changed environmental conditions. Hopefully these data will become available through the ringing program carried out (e.g., Lambeck, 1991; etc.)

However the occurrence of three severe winters (1985, 1986 and 1987), in which many birds died in the Oosterschelde (Meininger *et al.*, 1991; Lambeck, 1991) can give some circumstantial evidence that mortality rates of birds were affected in the Oosterschelde. In general the mortality of juveniles is much higher than that of adults, a normal pattern (see e.g., Evans & Pienkowski, 1984; Hulscher 1989; Swennen, 1984) which was also found in 1985. However in 1986 and 1987, first the proportion of Oystercatchers on the total number of dead birds increased significantly (Lambeck, 1991), and secondly the age composition of the starved birds and the live population was much closer in 1986 and 1987 (Lambeck, 1991), indicating a higher mortality of adults. This is probably caused by the environmental changes. Indeed the tidal amplitude in the Oosterschelde was reduced from 3.7 m to 3.2 m in 1986 and even to 2.4 m in 1987, resulting in both a loss of feeding area of 4 and 12% respectively and in reduced feeding times below mid tidal level. The results presented in chapter 10 show that a reduced feeding time on the lower feeding areas can lead to an important consumption deficit. This obviously can result in a reduced condition of the birds (smaller fat content) and hence increase the mortality rate during severe winter conditions (Lambeck, 1991). It was striking that the other species did not suffer a higher mortality in these two winters. Probably they could better compensate the consumption deficit on the higher part of the intertidal area. Indeed cockles and mussels, the main food of the Oystercatchers occurred mainly below mid tidal level (chapter 2) whereas other benthic species occur more evenly over the flats.

1.2.3 Have changed mortality rates an effect on total population size?

The question whether or not habitat loss was likely to affect the overall population size was often coupled on the question where the population is limited. If the threshold population size is higher on the breeding sites than on wintering grounds the population will be limited on the wintering grounds and vice versa. If the population is limited on the wintering grounds an increase in mortality can have an important effect on the total population size.

Sutherland & Goss-Custard (1991) and Goss-Custard (1993) argued, based on the concept of equilibrium population size, that the idea of a distinction between winter and summer limitation is not useful. Even if a powerful regulatory factor operates on the breeding population in summer, the population size is very much affected by juvenile mortality rates in the winter. The simulations suggest that increasing the winter mortality rate of just the juveniles through habitat loss can have a considerable effect on the size of the population as a whole. The equilibrium population size is affected by both the summer reproductive rate and the winter mortality rate. As long as at least one population variable is affected by factors on the wintering grounds, it is the interaction between summer and winter factors that will determine population size. This means that if mortality rates at the wintering areas are increasing it is very likely that the overall population will decline. (Goss-Custard, 1993).

An important question is, however, if the total population (either number of birds in autumn or in spring) is the most relevant parameter. This could well be the number of breeding pairs. Indeed if there are many birds in the population, which are physiological able to breed but do not breed, which is the case in the Oystercatcher (Ens, 1992), an increased mortality will not necessarily lead to fewer breeding pairs.

Information on population dynamics of waders is rather scarce (e.g., Goss-Custard, 1981; Evans & Pienkowski, 1984; Evans, 1991) and much work remains before the effects of increased winter mortality due to habitat loss on the population dynamics will be resolved.

1.3 Conclusion

Based on the above discussion, it can be concluded that
the reason why the answers on the main questions dealt with in this thesis, are only tentative and sometimes unequivocal is not due to the approach followed, but rather to the amount of data that could be collected. Indeed, the model, presented in the introduction, provided a useful guideline for studying the impact of habitat loss on waders and incorporated the most significant factors influencing bird numbers. Of course each point could be further elaborated as was done by Piersma (1987) who made a heuristic model incorporating all details of shorebird ecology, ecophysiology and marine biology. Many of the variables (e.g., ecophysiology of the bird), included in that model, are, however, not influenced by the changing environment in the Oosterschelde and are therefore less relevant to be studied in this context, although they can provide very important and necessary information for interpreting the results. The major gap of our model is probably that it does not put enough emphasis on the different functions, the area fulfills for different species: e.g., for moulting waders other factors are probably important than for species moving quickly through the area.

The main shortcoming of this study is beyond doubt that not every aspect of our model was studied, that the focus was mainly on one bird species, that no individually marked birds were followed and that the time series, especially after the finishing of the works was rather short. As most of the species (both benthos and birds) are longlived, effects could only become apparent after several years.

2. The future: long term research, preserving natural habitats and nature development.

Before the works in the Oosterschelde started ecologist warned that the expected environmental changes could have an important impact on the ecosystem, especially on birds, however, they had to base their statement on limited knowledge and some speculation. Their insight proved however right. However, neither the work presented in this thesis nor that of many other researchers could provide yet clear cut answers about the effect of habitat loss on waterbirds. Therefore, as many new proposals for reclaiming intertidal habitats are on the drawing tables of planners or on the desks of politicians, we need to continue the research on the effects of habitat loss and/or degradation but on the other hand we must take precautionary measures.

From the results obtained in this thesis it is clear that, in the future, studies dealing with the effects of habitat loss, should be a combination of monitoring (both birds and their prey) and behavioural ecology of the important species. The recent developments in behavioural ecology (e.g., Krebs & Davies, 1991) and some of its implications for conservation (e.g., Perrins *et al.*, 1991) provide a stimulating environment and framework for further study.

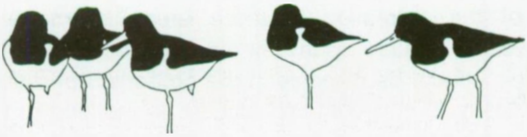
For waterbirds and waders there is the great advantage that overall population sizes are monitored due to a network of professionals and amateurs (e.g., Boyd & Pirot, 1989). Much less information is available on the breeding populations of waders and waterbirds. The first overview of the breeding populations of waders was only published in 1986 by Piersma, followed by a review of grassland breeding waders by Hötker in 1991. Therefore the ultimate question if habitat loss or degradation will have an impact on the population is not likely to be solved by field work alone. Goss-Custard (1993) argues that these studies should be complemented by mathematical modelling of the whole population. The results from monitoring and behavioural ecology are needed to test the biological assumptions underlying the model, estimating the parameter values and testing the predictions.

An experimental approach combined with long-term studies to detect time trends in ecosystems is believed to be essential to solve the major ecological questions of the next century (Krebs, 1991).

Based on all the available evidence, it is likely that any further loss of intertidal areas will affect waders and waterbirds. Therefore it is essential to protect as much as possible of the remaining tidal areas. This of course is important not only for birds but for all elements of the estuarine ecosytem. Next, one should be very cautious about each new development. Indeed, ecologist, confronted with other scientist, are sometimes ashamed by their lack of understanding of the system, or at least by the lack of formal models, but it appears that the predictions of engineers and other scientist are not always so precise as they are believed to be. Most interventions have often several unexpected effects, the erosion of the tidal flats in the Oosterschelde possibly leading to a further serious reduction in the surface of the tidal flats within the next decades (Mulder & Louters, 1993) being only one example. Furthermore each development attracts others, e.g., the construction of the secondary dams in the Oosterschelde has an important impact on the development of the recreation in these areas leading to much higher disturbance levels. Therefore each new development should be evaluated in much detail. This should be reflected in the proportion of money of the whole project that is spent on environmental studies. In the long run this could save much money. If the decision, to build a storm surge barrier or to reinforce all the existing dikes so that a similar safety level is reached, should be made again, I doubt whether the same decision would be taken.....

Although the first priority, safeguarding the remaining areas should be only one side of the strategy. Indeed, recently, there is a growing belief that habitat restoration and development is, next to traditional ways of nature management, essential to achieve a sustainable conservation of nature. Davidson & Evans (1986; 1987) and Evans (1991) have shown already the possibilities of creating new wetlands for the conservation of waders. The provision of supplementary feeding sites may be an important management tool to restore the potential of degraded estuaries to support shorebirds. Habitat restoration also can be seen as an interesting experiment and a technique for basic ecological research (Jordan *et al.*, 1987).

It must therefore be a challenge for ecologist to turn the knowledge compiled in studying the effects of habitat loss into plans for habitat restoration.



References

Bernstein, C., J. R. Krebs & A. Kacelnik, 1991. Distribution of birds amongst habitats: theory and relevance to conservation. In Perrins, C.M., J.-D. Lebreton & G.J.M. Hirons (Eds) Bird population studies. Relevance to conservation and management. Oxford University Press, Oxford: 317-345.

Boyd, H. & J.-Y. Pirot, 1989. Flyways and reserve networks for water birds. IWRB Special Publication No. 9, Slimbridge.

Dhondt, A. A., 1988. Carrying capacity: a confusing concept. Acta Oecologia 9: 337-346.

Davidson, N. C. & P. R. Evans, 1986. The role and potential of man-made and man-modified wetlands in the enhancement of the survival of overwintering shorebirds. Colonial Waterbirds, 9: 176-188.

Davidson, N.C. & P.R. Evans, 1987. Habitat restoration and creation: its role and potential in the conservation of waders. In N. C. Davidson & M. W. Pienkowski (Eds), The conservation of international flyway populations of waders. Wader Study Group Bull. 49, Suppl./IWRB Special Publ. 7.: 139-145.

Davidson, N. C., D. d'A. Laffoley, J. P. Doody, L. S. Way, J. Gordon, R. Key, C. M. Drake, M. W. Pienkoswki, R. Mitchell & K. L. Duff., 1991. Nature conservation and estuaries in Great Britain. Nature Conservancy Council, Peterborough.

Ens, B. J., 1992. The social prisoner. Causes of natural variation in reproductive success of the Oystercatcher. PhD Thesis, University of Groningen, Groningen.

Ens, B. & J. D. Goss-Custard, 1984. Interference among Oystercatchers *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. Journal of Animal Ecology 53: 217-231.

Esselink, P. & L. Zwarts, 1989. Seasonal trend in burrow depth and tidal variation in surface feeding of *Nereis diversicolor*. Mar. Ecol. Prog. Ser. 56: 243-254.

Evans, P. R., 1981. Reclamation of intertidal land: some effects on Shelduck and wader populations in the Tees estuary. Verh. Orn. Ges. Bayern 23: 147-168.

Evans, P. R., 1984. Introduction. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 3-7.

Evans, P. R., 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. In C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons (Eds), Bird population studies. Relevance to conservation and management. Oxford University Press, Oxford: 346-359.

Evans, P. R. & P. J. Dugan, 1984. Coastal birds: numbers in relation to food resources. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 8-28.

Evans, P. R. & M. W. Pienkowski, 1983. Implications for coastal engineering projects of studies at the Tees estuary on the effects of reclamation of intertidal land on shorebird populations. Wat. Sci. Tech. 16: 347-354.

Evans, P. R. & M. W. Pienkowski, 1984. Population dynamics of shorebirds. In J. Burger & B. L. Olla (Eds), Shorebirds, breeding behaviour and populations. Plenum press, New York: 83-123.

Fretwell, S. D., 1972. Populations in a seasonal environment. Princeton University Press, Princeton.

Fretwell, S. D. & H. L. Jr. Lucas, 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta biotheoretica 19: 16-36.

Goss-Custard, J. D., 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J. D., 1981. Role of winter food supplies in the population ecology of common

British wading birds. Verh. Orn. Ges. Bayern 23: 125-146.

Goss-Custard, J. D., 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford: 169-188.

Goss-Custard, J. D., 1993. The effect of migration and scale on the study of bird populations: 1991 Witherby lecture. Bird Study 40: in press.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1984. Feeding ecology, winter mortality and the population dynamics of Oystercatchers on the Exe estuary. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 190-208.

Goss-Custard, J. D. & S. E. A. Durell Le V. Dit, 1987. Age-related effects in Oystercatchers *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*. III. The effect of interference on overall intake rate. J. anim. Ecol. 56: 549-558.

Goss-Custard, J. D. & S. E. A. Le V. Dit Durell, 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Goss-Custard, J. D., R. M. Warwick, R. Kirby, S. McGrorty, R. T. Clarke, B. Pearson, W. E. Rispin, S. E. A. Le V. Dit Durell & R. J. Rose, 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn estuary. J. appl. Ecol. 28: 1004-1026.

Hötker, H., 1991. Waders breeding on wet grasslands. Wader Study Group Bull. 61, Suppl.

Hulscher, J. B., 1989. Sterfte en overleving van Scholeksters *Haematopus ostralegus* bij strenge vorst. Limosa 62: 177-181.

Jordan, W. R., M. E. Gilpin & J. D. Aber, 1987. Restoration ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge.

Krebs, C. J., 1991. The experimental paradigm and long-term population studies. Ibis 133 suppl. 1: 3-8.

Krebs, J. R. & N. B. Davies, 1991. Behavioural Ecology: an evolutionary approach: 105-136. Sinauer Associates, Sunderland, MA.

Lambeck, R. H. D., 1991. Changes in abundance, distribution and mortality of wintering Oystercatchers after habitat loss in the Delta area, SW Netherlands. Acta XX Congr. Int. Ornithol.: 2208-2218.

Meininger, P. L. M., 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., 1987. Foraging behaviour of some wintering waders: prey selection and habitat distribution. In A. C. Kamil, J. R. Krebs & H. R. Pulliam (eds), Foraging behavior. Plenum Press, New York.

Meire, P., 1993. The impact of bird predation on marine and estuarine bivalve populations: a selective review of patterns and underlying causes. In R. Dame (Ed.), Bivalve filter feeders and marine ecosystem processes. Nato Advanced Research Workshop, Springer Verlag, New York: in press.

Meire, P., J. Seys, T. Ysebaert & J. Coosen, 1991. Comparing macrobenthic distribution and community structure between two estuaries in SW-Netherland. pp 221-230 In M. Elliot & J. P. Ducrotoy (Eds), Estuaries and Coasts: spatial and temporal intercomparisons. Olson & Olson, Fredensborg: 221-230.

Milinski, M. & G. A. Parker, 1991. Competition for resources. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology. Blackwells, Oxford: 137-168.

Mulder, J. P. M. & T. Louters, 1993. Changes in basin geomorphology after implementation of the Oosterschelde project. Hydrobiologia: in press.

Norton-Griffiths, M., 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher, *Haematopus ostralegus*, on the edible mussel, *Mytilus edulis*. Ibis, 109:

412-424.

Perrins, C. M., J.-D. Lebreton & G. J. M. Hirons, 1991. Bird population studies. Relevance to conservation and management. Oxford University Press, Oxford.

Pfister, C., B. A. Harrington & M. Lavine, 1992. The impact of human disturbance on shorebirds at a migration staging area. Biol. Cons. 60: 115-126.

Piersma, T., 1986. Breeding waders in Europe: a review of population estimates and a bibliography of information sources. Wader Study Group Bull. 48, Suppl.1.

Piersma, T., 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Mar. Ecol. Prog. Ser. 38: 187-196.

Smaal, A. C. & R. C. Boeije, 1991. Veilig getij, de effecten van de waterbouwkundige werken op het getijdemilieu van de Oosterschelde. Nota GWWS 91.088, Rijkswaterstaat, Middelburg.

Smit, C. J., 1984. Identification of important sites for waders by co-ordinated counts. In P. R. Evans, H. Hafner & P. L'Hermite (eds), Shorebirds and large Waterbirds Conservation. commission of the European Communities, Brussel: 43-51.

Sutherland, W. J., 1982. Food supply and dispersal in the determination of wintering population levels of Oystercatchers, *Haematopus ostralegus*. Est. coast. mar. Sci. 16: 223-229.

Sutherland, W. J. & J. D. Goss-Custard, 1991. Predicting the consequences of habitat loss on shorebird populations. Acta X Congr. Int. ornithol.: 2199-2207.

Sutherland, W. J. & G. A. Parker, 1985. The distribution of unequal competitors. In R. M. Sibly & R. H. Smith (eds), Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Blackwell, Oxford: 255-274.

Swennen, C., 1984. Differences in quality of roosting flocks of Oystercatchers. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 177-189.

Van Der Have, T. M., E. Nieboer & G. C. Boere, 1984. Age-related distribution of Dunlin in the Dutch Wadden Sea. In P. R. Evans, J. D. Goss-Custard & W. G. Hale (Eds), Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge: 160-177.

Wiens, J., 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In D. R. Strong, D. Simberloff, L. G. Abele & A.B. Thistle (Eds), Ecological communities. Conceptual issues and the evidence. Princeton University Press, Princeton: 439-457.

Ysebaert, T. & P. M. Meire, 1993. Het voorkomen van macrozoobenthos in het Schelde- en Eems estuarium. Rapport RUG-WWE nr. 29, Universiteit Gent, Gent.

Zwarts, L., 1980. Habitat selection and competition in wading birds. In C. J. Smit & W. J. Wolf (eds), Birds of the Wadden Sea. Balkema, Rotterdam: 271-279.

Zwarts, L., A.-M. Blomert & J. H. Wanink, 1992. Annual and seasonal variation in the food supply harvestable for Knot *Calidris canutus* staging in the Wadden Sea in late summer. Mar. Ecol. Prog. Ser. 83: 128-139

Samenvatting

Steltloper populaties en macrozoöbenthos in een veranderend estuarium: de Oosterschelde (Nl.).

Hoofdstuk 1: Inleiding

Habitat verlies en degradatie is één van de belangrijke ecologische problemen van deze eeuw. Hoewel alle ecosystemen hieronder te lijden hebben, blijken wetlands of waterrijke gebieden, op wereldschaal vrij zeldzame gebieden, onder zeer zware antropogene druk te staan. Het is daarom ook niet te verwonderen dat deze ecosystemen sinds meerdere jaren een belangrijke prioriteit vormen voor het natuurbehoud.

Binnen de wetlands vormen estuaria zeer produktieve systemen waarvan het rijke voedselaanbod wordt benut door grote aantallen steltlopers, die buiten het broedseizoen bijna volledig op dergelijke getijdengebieden zijn aangewezen. Het belang van het Deltagebied (Nl.) en met name de getijdengebieden van Ooster- en Westerschelde voor watervogels worden kort gesitueerd.

Het verlies van getijdengebieden binnen estuaria is een proces dat reeds honderden jaren geleden begon, maar de snelheid en vooral de manier waarop, zijn in de laatste jaren evenwel sterk veranderd. Waar vroeger slechts de "rijpe schorren" werden ingepolderd, worden nu gebieden die zich uitstrekken tussen de hoog- en laagwaterlijn of zelfs sublitorale gebieden ingenomen, wat door zijn effect op de hydrodynamiek van het estuarium vaak verstrekkende gevolgen heeft.

Het is dan ook verheugend dat het effect van verlies van getijdengebieden op het ecosysteem in het algemeen en op vogels in het bijzonder de aanleiding was voor diverse studies. Door de korte duur van de studies zijn de resultaten evenwel niet altijd eenduidig.

In het Nederlandse Deltagebied is met de uitvoering van het "Deltaplan" de oppervlakte slikken en schorren sterk afgenomen. De plannen om de Oosterschelde eveneens af te sluiten werden evenwel herzien. Als compromis tussen veiligheid, milieu en economie werd beslist om een stormvloedkering te bouwen in de monding van de Oosterschelde en twee secundaire dammen meer landinwaarts. Als gevolg van deze werken nam de getijdenamplitude af van 3.7 tot 3.25m, verminderden de stroomsnelheden en het areaal aan slikken van 17000 tot 11365 ha. De uitvoering van deze werken in de Oosterschelde was een geschikte gelegenheid om een lange termijn studie uit te voeren naar de mogelijke gevolgen van het verlies van getijdengebieden op watervogels. De doelstellingen van deze studie kunnen als volgt worden

weergegeven:
1) een beschrijving van de watervogelpopulaties en hun voedsel, het macrozoöbenthos, voor, tijdens en na de uitvoering van de werken (aantallen, densiteit, verspreiding)
2) een studie van het foerageergedrag van vogels en van de relatie tussen hun voorkomen en dat van hun voedsel
3) een beter inzicht te krijgen over de vraag of de draagkracht van het gebied voor watervogels al dan niet werd bereikt.

Deze studie maakte deel uit van een multidisciplinair onderzoek dat door Rijkswaterstaat (Nl.) werd gecoördineerd in samenwerking met verschillende universiteiten en instituten. Dit onderzoek naar bodemdieren en vogels liep in samenwerking met Rijkswaterstaat, Dienst Getijdenwateren en met het Nederlands Instituut voor Oecologisch Onderzoek, Centrum voor Estuarine en Mariene Oecologie (het vroegere Delta Instituut voor Hydrobiologisch Onderzoek).

Voor deze studie beschikten we over gegevens uit de periode 1976-1990. De meeste waarnemingen werden evenwel verzameld tussen 1981 en 1989.

Om de aanpak van het onderzoek te situeren werd in het inleidend hoofdstuk een eenvoudig conceptueel model besproken dat aangeeft welke de belangrijke factoren zijn die het voorkomen van vogels in een estuarium bepalen. Het onderzoek dat in dit proefschrift werd naar voor gebracht is gericht op een combinatie van monitoring van zowel de vogels als hun voedsel en op een detailstudie van het foerageergedrag. Voor dit laatste beperkten wij ons voornamelijk tot de Scholekster (*Haematopus ostralegus*) en zijn belangrijkste prooidieren de mossel (*mytilus edulis*) en de kokkel (*Cerastoderma edule*). De detailstudies gebeurden op de Slikken van Vianen.

In hoofdstuk 2 en 3 wordt ingegaan op het macrozoöbenthos van de Oosterschelde. In hoofdstuk 2 wordt de verspreiding van het macrozoöbenthos in de Oosterschelde en de relatie tussen benthos en enkele omgevingsfactoren besproken. Dit gebeurde aan de hand van twee grootschalige bemonsteringen, één in 1985 en één in 1989, respectievelijk voor en na de veranderingen en waarbij dezelfde 305 stations werden bemonsterd. De temporele patronen van het macrozoöbenthos werden in hoofdstuk 3 beschreven aan de hand van gegevens afkomstig van 14 permanente kwadraten verspreid over de gehele Oosterschelde.

Hoofdstuk 2: Ruimtelijke en temporele patronen van het macrozoöbenthos in de getijdengebieden van de Oosterschelde: werden die beïnvloed door de bouw van de stormvloedkering?

Galgeplaat en Krabbenkreek, drie grote slikgebieden in de Oosterschelde, kon gekarakteriseerd worden als fijn, goed gesorteerd zand met een gemiddeld slibgehalte (< 53µ) van ongeveer 2.5%. Tussen beide bemonsteringen (1985 en 1989) waren weinig verschillen, enkel het sediment van de Krabbenkreek bleek wat minder slibrijk te zijn in 1989. De monsterpunten waren gesitueerd tussen -1.5m en 1.25m NAP. De hoogteligging van de individuele punten bleek evenwel significant gedaald te zijn tussen beide jaren, wat wijst op een duidelijke erosie.

De dichtheid van het macrozoöbenthos was veel hoger in 1985 vergeleken met 1989. De biomassa daarentegen was veel hoger in 1989. De dichtheid werd gedomineerd door "deposit feeders", de biomassa door "filter feeders". Het verschil in biomassa tussen beide jaren was vooral te wijten aan een gevoelige toename van "filter feeders" (met name de kokkel) in 1989. Tussen de platen waren geen grote verschillen in dichtheid en biomassa maar wel tussen de verschillende stations.

Het aantal soorten per station was signifikant lager in 1989 dan in 1985. De frequentie van voorkomen daalde in 34 soorten en nam slechts toe in 13 soorten. De dichtheid nam toe in 13 soorten maar daalde in 34 soorten; de biomassa nam toe in 18 soorten en nam af in 29 soorten.

De bodemdiergemeenschappen werden gekarakteriseerd aan de hand van een TWINSPAN. De verschillende clusters werden beschreven maar zij vertoonden geen duidelijke geografische patronen waardoor geen zones van bepaalde gemeenschappen konden worden aangetoond binnen het gebied van de Oosterschelde.

Het verband tussen de dichtheid en de biomassa van verschillende trofische groepen enerzijds en het slibgehalte van de bodem en de hoogteligging anderzijds werd in detail onderzocht. In bepaalde gevallen was het verband duidelijk verschillend tussen beide jaren. Dit kwam eveneens tot uiting in de multiple regressies tussen dichtheid of biomassa van de individuele soorten en de omgevingsvariabelen. Hoewel in nagenoeg alle gevallen een significante relatie gevonden werd, was de multiple correlatie coëfficiënt meestal zeer laag, wat aangeeft dat slechts een klein deel van de variatie in dichtheid of biomassa van de soort werd verklaard. Het verband tussen de bodemdieren en de omgevingsvariabelen werd vervolgens verder onderzocht met behulp van canonische correlatie analyse en multivariate discriminant analyse. Beide analyses gaven een verschillend resultaat voor de gegevens van 1985 en 1989. Dit was mogelijk het gevolg van een brede tolerantie van de soorten ten opzichte van de waargenomen range van de omgevingsvariabelen in de Oosterschelde. Om dit verder na te gaan werd een TWINSPAN uitgevoerd op basis van alle dichtheidsgegevens van 1985 en 1989. Hieruit bleek dat in een cluster van stations, die een grote gelijkenis in bodemdierpopulaties vertoonde, en waarvan de abiotische karakteristieken niet veranderden van het ene jaar naar het andere, de bodemdierfauna zich in die verschillende stations toch verschillend ontwikkelde, waardoor die stations het verschillende stations toch verschillend ontwikkelde, waardoor die stations het volgende jaar niet terug samen één cluster vormden. Dit toonde aan dat de veranderingen in de fauna niet noodzakelijk gebonden zijn aan de gemeten omgevingsvariabelen.

In de discussie werd een vrij uitgebreid overzicht gegeven van de verschillende factoren die een invloed uitoefenen op het macrozoöbenthos. Dit leidde tot de hypothese dat de macrobenthische gemeenschappen zich in het "nonequilibrium - equilibrium" continuüm van Wiens (1984) vermoedelijk meer aan het nonequilibrium eind gelegen zijn.

Hoofdstuk 3: Lange termijn veranderingen (1979-1989) van het macrozoöbenthos van de getijdengebieden van het Oosterschelde estuarium: zijn patronen in dichtheid, biomassa en diversiteit beïnvloed door de bouw van de stormvloedkering?

Deze twee grootschalige bemonsteringen lieten ons niet toe om de evolutie in de tijd van het macrobenthos na te gaan. Dit werd in hoofdstuk 3 gedaan op basis van jaarlijks bemonsterde permanente kwadraten verspreid over de Oosterschelde.

Nazomer (augustus-september)-waarden van totale biomassa, totale dichtheid, aantal soorten, diversiteit evenals de ratio's dichtheid over aantal soorten en biomassa over dichtheid vertoonden geen significante trends in de loop van onze studieperiode. Er waren ook geen aanwijzingen dat de veranderingen in de hydrodynamiek en de morfologie van de Oosterschelde, na de voltooiing van de stormvloedkering de normale patronen van de benthische populaties hebben beïnvloed. De waargenomen patronen waren grotendeels bepaald door het voorkomen van strenge winters. Hoge dichtheden, lage biomassa's en hoge waarden van beide ratio's in 1985-1987 wezen op een verstoring door de strenge winters. Op één zeer hoog gelegen punt, COST-station 27, nam de biomassa zeer sterk af in 1985, als gevolg van de sterk toegenomen expositie duur van dit punt in die periode. Dit wijst erop dat effecten kunnen optreden in bepaalde gevallen.

Op basis van de gegevens konden we geen echte effecten van de veranderende omgevingsvariabelen aantonen. Gezien slechts drie jaar gegevens na de opgetreden veranderingen voorhanden waren, blijft het evenwel niet onmogelijk dat op langere termijn toch effecten te verwachten zijn.

Hoofdstuk 4: Een beschrijving van de habitats en de steltloper populaties op de Slikken van Vianen (Oosterschelde, Nl.) voor het optreden van belangrijke veranderingen in het abiotisch milieu en enkele voorspellingen.

Slikken van Vianen. Een gedetailleerde beschrijving van dit 510 ha groot slik voor de veranderingen wordt in dit hoofdstuk gegeven. Op het slik konden verschillende biocoenoses worden herkend die elk kort worden beschreven. Daarna volgt een uitgebreide bespreking van het voorkomen van de 11 belangrijkste soorten steltlopers in het studiegebied. Per soort wordt het aantalspatroon, gemiddeld over meerdere jaren, besproken en vergeleken met frequente tellingen uit 1981. Hieruit blijkt dat bepaalde soorten in het gebied overwinteren (bv. Scholekster), andere enkel op doortrek aanwezig zijn (bv. Bontbek- en Strandplevier) en weer andere zowel een doortrekpiek vertonen als ook in de winter aanwezig zijn. Het patroon van voorkomen wordt per soort vergeleken met dat voor de gehele Oosterschelde en gesitueerd in de globale verspreiding van de soort. Het blijkt dat het voorkomen van de soorten op de Slikken van Vianen zeer vergelijkbaar is met dat in de Oosterschelde zelf en veel minder met het patroon in de nabij gelegen Krammer/Volkerak.

In de discussie wordt nader ingegaan op de faktoren die het voorkomen van steltlopers bepalen en op de faktoren die de waargenomen variatie kunnen verklaren.

Op basis van de bestaande tellingen van steltlopers van de volledige Oosterschelde en Krammer/Volkerak werd vervolgens uitgerekend wat de stijging in dichtheid zou zijn indien alle vogels zouden blijven foerageren in het gebied na het verlies aan getijdengebied. Hieruit blijkt dat de dichtheden afhankelijk van soort en periode tot 50% zouden kunnen stijgen. Op basis van bestaande gegevens over verspreiding van vogels over hun foerageergebieden wordt voorspeld dat een dergelijke stijging niet kan en dat bijgevolg de aantallen zullen verminderen na het habitat verlies.

Hoofdstuk 5: Veranderingen in de steltloper populaties op de Slikken van Vianen (Oosterschelde, Nl.) na grote veranderingen in het abiotisch milieu (1976-1990).

In hoofdstuk 5 wordt voor hetzelfde studiegebied een vergelijking gemaakt tussen de gegevens van "voor" en "na" het uitvoeren van de werken in de Oosterschelde. Het habitat op de Slikken van Vianen is slechts in beperkte mate veranderd, hoewel de erosie van het slik en het uitspoelen van slib ook in onze permanente kwadraten duidelijk merkbaar zijn. Door de reductie van de getijamplitude is de totale oppervlakte van het slik met zo'n 20% afgenomen, wat minder is dan voor de Oosterschelde in zijn geheel.

Vervolgens worden de aantallen en de vogeldagen van 12 soorten steltlopers vergeleken tussen 5 seizoenen voor (1978/79 -1982/83) en drie (1987/88-1989/90) na de uitvoering van de werken. Hieruit blijkt dat voor 8 soorten het aantal vogeldagen afnam, voor 4 soorten nam het toe; maximale aantallen daarentegen namen toe voor 8 soorten en namen af voor 4. De waargenomen veranderingen zijn zeer vergelijkbaar met die voor de gehele

Oosterschelde. Op basis van deze gegevens kunnen we de hypothese vooropstellen dat de "carrying capacity" of draagkracht van het gebied, althans voor sommige soorten, bereikt was en dat enerzijds vogels verdwenen en anderzijds vogels uit de nabijgelegen Krammer/Volkerak niet werden opgevangen. Dit geldt evenwel niet voor de Rosse Grutto. Voor deze soort is het mogelijk dat een toename vanaf 1987/88 te wijten is aan het verplaatsen van vogels vanuit de Krammer/Volkerak.

Hoofdstuk 6: Veranderingen in de watervogel populaties van de Oosterschelde (Nl.) als gevolg van grootschalige werken.

Waar we in hoofdstuk 5 de effecten van de Oosterscheldewerken nagingen op één klein slikgebied worden in hoofdstuk 6 de resultaten van de hoogwater tellingen van watervogels in de gehele Oosterschelde geanalyseerd, eveneens op basis van (dezelfde) 5 pre- en 3 post kering seizoenen.

Voor het gehele Oosterschelde/Krammer-Volkerak gebied, nam het aantal overwinterende steltlopers sterk af maar het aantal eenden steeg. Maximale aantallen en het totaal aantal vogeldagen veranderde weinig maar het seizoenspatroon wijzigde enigszins; het maximaal aantal vogels komt nu eerder in de herfst dan in het midden van de winter voor.

Het effect van het habitat verlies op de aantallen wordt verder in detail bestudeerd op basis van de gegevens van de Oosterschelde zonder de Krammer-Volkerak, gezien in dit laatste gebied de tellingen minder volledig waren. In de Oosterschelde (excl. Krammer/Volkerak) verdween ongeveer 17% van het intergetijdengebied. De soorten die vooral op het open water foerageren namen toe in aantallen of bleven stabiel. Van de soorten die hun voedsel zoeken op de slikken (steltlopers en enkele eenden)(verder "slik-soorten" genoemd) gingen de aantallen en dichtheden over het algemeen achteruit. Voor deze "slik-soorten" werden de waargenomen trends vergeleken met gegevens van Britse estuaria waaruit bleek dat de populaties in de Oosterschelde ofwel sneller afnamen of minder toenamen, wat wijst op het feit dat lokale faktoren de populatie-grootte bepalen.

De veranderingen waren evenwel niet even groot voor alle soorten. Dit kon te wijten zijn aan het feit dat zowel de verspreiding van de soorten over het estuarium als het habitat verlies niet uniform was, waardoor bepaalde soorten meer habitat verloren dan anderen. Inderdaad, de aantallen van soorten die vooral in het oostelijk deel voorkwamen, het deel met het grootste habitat verlies, namen méér af dan van soorten waarvan het zwaartepunt van hun verspreiding meer in het westen lag.

De gegevens tonen eveneens aan dat de "slik-soorten" die foerageerden in de afgesloten gebieden zich niet konden vestigen in het overblijvende getijdengebied. Eendachtigen bleken vooral naar de nieuwe overblijvende getijdengebied. Eendachtigen bleken vooral naar de nieuwe zoetwatergebieden uit te wijken. Mortaliteit bij steltlopers tijdens de strenge winters (1984/85 -1986/87) kan bijgedragen hebben tot de afname van hun aantallen.

In de nazomer zijn de aantallen ruiende individuen van verschillende soorten sterker achteruit gegaan dan de aantallen buiten de ruitijd. Waarschijnlijk is dit te wijten aan een toegenomen recreatie tijdens deze periode van het jaar.

De bekomen resultaten maken het aannemelijk dat voor verschillende soorten de draagkracht van het gebied benaderd was en dat een verdere afname van het getijdengebied, zoals voorspeld door geomorfologische modellen, zal leiden tot een verdere afname van de populaties.

Hoofdstuk 7: Selekteren Scholeksters de meest voordelige mosselen?

Zoals aangegeven laten de waargenomen patronen in het aantalsverloop zowel in de gehele Oosterschelde als op de Slikken van Vianen vermoeden dat de draagkracht bereikt is. Het is evenwel van belang om niet alleen naar de totale aantallen te kijken maar ook naar de verspreiding van de diverse soorten bij laag water, hun voedselkeuze en de relatie tussen voedselaanbod en de dichtheid van vogels. Deze relaties werden in detail nagegaan op de Slikken van Vianen en in de volgende hoofdstukken behandeld. In hoofdstuk 7 en 8 wordt eerst nader ingegaan op de faktoren die de selektie van mosselen door de Scholekster bepalen.

Scholeksters, die hun prooi bemachtigen door het open "hameren" van de schelp, selecteren vooral mosselen tussen 30 en 45 mm lang, die niet begroeid zijn met zeepokken. Bovendien selekteren ze ook, vooral bij grotere mosselen, de dunne schelpen. Van dit selektie patroon worden verder de kosten en de baten geanalyseerd en samengebracht in een optimaal dieet model. Na aanpassing van het model voor het niet onmiddellijk herkennen van de prooien en het berekenen van de beschikbare prooipopulatie bleek er een goede overeenkomst te zijn tussen de voorspellingen en het dieet van de Scholeksters. Het opdelen van de prooipopulatie in een beschikbare en niet beschikbare fractie blijkt van zeer groot belang te zijn om verder de relatie tussen predator en prooi na te gaan.

Hoofdstuk 8: Interacties tussen Scholeksters en mosselen: implicaties van de "optimal foraging theory"

De selektie voor dunne mosselschelpen die werd geconstateerd in het vorige hoofdstuk is het uitgangspunt voor hoofdstuk 8. Inderdaad kunnen we deze selektie verklaren op basis van een foerageer-strategie die de opnamesnelheid van voedsel maximaliseert?

Om deze vraag te beantwoorden werd aan de hand van een artificiële Scholekster snavel nagegaan wat de kosten zijn voor het openen van dikkere schelpen. Hieruit bleek duidelijk dat het aantal slagen van deze snavel, nodig om de mossel te openen, supraproportioneel toenam met de schelpdikte.

De gegevens van het experiment werden gecombineerd met veldgegevens om de voordeligheid van mosselen met verschillende schelpdikte te berekenen. Hieruit bleek dat de voordeligheid sterk daalde met schelpdikte en dat de voordeligheid van een bepaalde schelpdikte verschilde afhankelijk van de schelplengte. Op basis hiervan konden we voorspellen dat 1) voor mosselen van een bepaalde lengte behoren de dikkere schelpen niet tot het optimale dieet en 2) de dikte van de genomen schelpen moet toenemen naarmate de mossel groter wordt. De resultaten waren in overeenstemming met de voorspellingen.

Deze gegevens over prooiselektie werden vervolgens verder gebruikt om de relatie tussen het aantal Scholeksters en hun voedselaanbod verder te analyseren. Hiervoor werd gestart vanuit de verwachting dat, gezien Scholeksters zeer selektief de dunnere schelpen selecteren, de gemiddelde schelpdikte van mosselen in de loop van de winter (wanneer de schelpen niet groeien) zou toenemen. Dit bleek evenwel niet zo te zijn. Dit kon verklaard worden door het feit dat de fractie van de totale mosselpopulatie op de mosselbank die geschikt is als prooi voor "hamerende" Scholeksters slechts zeer klein is. Wanneer we dan de consumptie door Scholeksters gedurende één seizoen vergelijken met de produktie van de fractie mosselen die geschikt is voor de Scholeksters dan blijken zij minimaal 70% van de produktie op te nemen. Op basis hiervan wordt geconcludeerd dat de dichtheid van de vogels vermoedelijk beperkt is door het voedselaanbod en dus niet kan stijgen.
Duidelijk is evenwel dat zonder een gedetailleerde studie van de prooiselektie en de prooibeschikbaarheid, het niet mogelijk is om een predator-prooi relatie te bestuderen.

Hoofdstuk 9: Verspreiding van Scholeksters over een slik in relatie tot zijn belangrijkste prooisoorten, de kokkel en de mossel: is dit veranderd na een belangrijk verlies van habitat?

Naast het beschrijven van de prooiselektie van de Scholekster wordt in hoofdstuk 9 de verspreiding van de vogels over het slik beschreven en dit zowel voor en na de uitvoering van de Oosterscheldewerken.

Vooreerst wordt de verspreiding van de vogels over het slik gedurende één tijcyclus beschreven. Met afgaand tij, volgen de vogels de waterlijn en passeren snel de hoger gelegen delen van het slik op weg naar de rijkere voedselgebieden. Met opkomend tij zien we een omgekeerde beweging. Dit patroon resulteert in een duidelijk verschillend gebruik van diverse gebieden van hoog naar laag.

De verspreiding van de vogels over hun voedselgebieden is duidelijk afhankelijk van de totale aantallen vogels aanwezig. In het vroege najaar, wanneer de totale aantallen laag zijn, blijken alleen de rijkste foerageergebieden bezet te zijn. Wanneer de aantallen stijgen nemen de dichtheden hier toe tot een bepaalde waarde en vanaf dit ogenblik zien we de dichtheden in andere gebieden stijgen. Een duidelijk patroon van het sequentieel opvullen van verschillende gebieden.

De verdeling van de vogels over het slik is duidelijk gerelateerd aan het voedselaanbod. Wel blijkt dat de dichtheden Scholeksters voor eenzelfde biomassa mosselen lager is dan bij kokkels.

De laagwatertrek van de vogels veranderde niet na voltooiing van de Oosterschelde werken. In de permanente kwadraten gekenmerkt door kokkels was het verband tussen kokkelbiomassa en Scholeksterdichtheid vergelijkbaar, hoewel iets lager na de werken. Op de mosselbanken daarentegen zien we dat in het najaar van 1987, na de afsluiting van de Krammer/Volkerak, de dichtheden Scholeksters sterk zijn toegenomen. Dit blijkt te verklaren door een sterke toename van de kokkels op de mosselbanken. Kokkels zijn makkelijker beschikbaar voor Scholeksters. De duidelijke respons van de vogels op de veranderingen in het voedselaanbod zijn een verdere aanwijzing dat er een nauw verband bestaat tussen de dichtheid aan vogels en dat van hun voedsel. Eens te meer werd het echter duidelijk dat dit verband niet kan ontdekt worden zonder gedetailleerde kennis van de voedselecologie van de predator en de karakteristieken van de prooipopulatie.

Hoofdstuk 10: Foerageergedrag van Scholeksters gedurende een periode van getijmanipulatie.

In hoofdstuk 10 worden de resultaten van het onderzoek naar voor gebracht dat werd verricht in oktober 1986 toen de stormvloedkering tijdelijk werd gesloten om sluiting van de Oesterdam mogelijk te maken. Tijdens de sluiting bleef het waterpeil in de Oosterschelde gedurende meerdere getijden vrij hoog waardoor de lager gelegen foerageergebieden niet vrij kwamen. De verspreiding van de Scholeksters over het slik tijdens deze periode is beschreven, waaruit bleek dat ze nu langdurig foerageerden in die gebieden waar ze anders slechts korte tijd doorbrengen. Er werd evenwel niet permanent gefoerageerd. De vogels keerden terug naar de hoogwater vluchtplaatsen ongeveer op het tijdstip dat ze dit onder normale omstandigheden zouden gedaan hebben, hoewel in de gegeven omstandigheden nog slik vrij was. Bovendien bleken alle vogels te stoppen met foerageren tijdens een zware storm. Wanneer het normale getijregime hersteld werd, was de verspreiding van de vogels onmiddellijk terug normaal.

Scholeksters in deze periode bepaald worden. Hieruit bleek dat na de periode van tijmanipulatie de vogels gemiddeld één derde minder voedsel hadden opgenomen, wat een behoorlijk consumptie deficit betekende. Daarom werd verwacht dat de dieren dit zouden kompenseren door sneller te gaan foerageren zodra ze terug op de rijkere voedselgronden konden komen. Dit bleek evenwel niet het geval te zijn, wat erop wijst dat de dieren in de gegeven omstandigheden aan een maximale snelheid foerageerden.

Gedurende de periode van getijmanipulatie, die in totaal 5 dagen duurde, zijn geen Scholeksters uit het gebied verdwenen. Wel blijkt dat het consumptiedeficit een effect had op de conditie van de vogels, zoals bleek uit abnormaal hoge percentages vogels met uitgestelde rui.

Hoofdstuk 11: Consumptie van benthische invertebraten door watervogels in de Oosterschelde (Nl.).

Een laatste stap in de analyse van de relatie tussen vogels en hun voedselaanbod wordt gezet in hoofdstuk 11. Hier wordt de consumptie van bodemdieren door vogels berekend, en dit zowel voor de gehele Oosterschelde als voor bepaalde permanente kwadraten op de Slikken van Vianen.

De totale jaarlijkse consumptie van macrozoöbenthos door vogels in de Oosterschelde werd geschat op $1573*10^3$g ADW y^{-1} in de periode voor de werken en op $1500*10^3$ kg ADW y^{-1} na voltooiing van de werken. De consumptie was niet evenredig verdeeld over de soorten. Meer dan de helft kwam voor rekening van de Scholekster. In de pre-kering periode waren 7, in de post-kering periode slechts 6 soorten verantwoordelijk voor 90% van de totale consumptie.

De consumptie van bepaalde soorten vertoonde sterke jaarlijkse schommelingen. De totale consumptie was daarentegen vrij stabiel, met een variatiecoëfficiënt van slechts 3-4%. De consumptie van benthische invertebraten door vogels vertoonde een duidelijk seizoensverloop, met lage waarden in de zomer, een duidelijke toename vanaf augustus, een piek in januari en een sterke terugval vanaf maart. In de post-kering periode daarentegen zagen we een piek in oktober.

De consumptie per oppervlakte-eenheid was, op het oostelijke deel van de Oosterschelde na, vrij gelijk over het gehele estuarium. De consumptie van vogels in het sublitoraal was evenwel zeer klein vergeleken met die in het litoraal. Er bleek een duidelijk verband te zijn tussen de consumptie en het voedselaanbod.

De predatiedruk (consumptie uitgedrukt als percentage van het aanwezige voedsel) variëerde tussen 13 en 23%. Zonder de Scholekster en kokkels en mosselen bedroeg de predatiedruk 30 à 37% van de aanwezige biomassa. De predatiedruk van Scholeksters op kokkels en mosselen kon in detail bepaald worden voor enkele permanente kwadraten op de Slikken van Vianen en die bleek te variëren tussen 10% en 70%. Op de kokkelbanken was er een duidelijk positief verband tussen predatiedruk en kokkellengte.

In de discussie worden de resultaten vergeleken met literatuurgegevens en op basis hiervan bleek het aannemelijk dat de aantallen van de vogels die in de getijdenzone hun voedsel zoeken, beperkt zijn door het voedselaanbod. Gezien de grote variabiliteit zal het voedsel evenwel niet altijd beperkend zijn, maar zeker in bepaalde perioden. In het sublitorale compartiment evenwel kunnen de aantallen van diverse soorten vermoedelijk nog sterk toenemen.

Hoofdstuk 12: Epiloog.

In de epiloog wordt de benadering, die tijdens deze studie werd gevolgd om het effect van habitat verlies op watervogels populaties na te gaan, geëvalueerd. Hieruit leiden wij af dat het uitblijven van eenduidige en definitieve antwoorden niet ligt aan de manier van aanpakken maar enerzijds aan de inherente beperkingen van veldwerk (geen replica's; onvoorziene omstandigheden) en aan het feit dat, niettegenstaande de inspanningen, slechts een beperkt aantal gegevens konden worden verzameld. Er wordt geargumenteerd dat het verder zetten van monitoring onderzoek in kombinatie met gedetailleerd gedragsecologisch onderzoek nodig is en dit in combinatie met het modelleren van de populatie-dynamiek van steltlopers.

Gezien we op basis van onze resultaten duidelijke indicaties hebben dat verder habitat verlies een negatief effect op steltloperpopulaties kan hebben moet verder habitat verlies voorkomen worden en moeten de mogelijkheden voor natuurontwikkeling onderzocht worden.

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Photos:

storm surge barrier: Rijkswaterstaat Middelburg
Oystercatchers: Marc Slootmaekers

Bird drawings:

Koen Devos

Lay-out and graphics:

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