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?

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A storm surge barrier and secondary dams were built in the Oosterschelde estuary (The Netherlands) resulting in a 30% decrease in intertidal area. If the birds that previously fed behind the secondary dams were able to establish themselves in the intertidal areas outside that remained, their densities should have increased in these areas. To test this, the densities of Oystercatchers, *Haematopus ostralegus*, were studied in relation to their main prey, Cockles *Cerastoderma edule*, and Mussels *Mytilus edulis*, before and after the reduction in tidal area. As the tide ebbed Oystercatchers moved quickly through the higher part of the intertidal area towards the preferred feeding areas below mid tidal level. The distribution of the birds then became related to their food supply. As the number of birds in the whole area increased, the birds gradually spread out from the preferred feeding plots towards the less preferred ones, leading to a sequential pattern of filling of the feeding area. This pattern did not change after the dams were built. After the main loss of intertidal habitat had occurred, densities of Oystercatchers feeding on Cockles were within the range predicted by prey biomass-bird density relationships that had been measured before the environmental changes. On mussel beds, however, densities of Oystercatchers became much higher after 1987/1988 at a given total prey biomass. This was caused by an increase in cockle biomass on the mussel beds due to an abundant spatfall in 1985. It is argued that because the harvestable fraction of Mussels represent only a small proportion of the total mussel population on the bed, whereas a large proportion of the cockle population is harvestable, a given combined biomass of Cockles and Mussels supports higher densities of Oystercatcher as the proportion that consists of Cockles increases.

Key words: Oystercatcher - *Haematopus ostralegus* - numerical response - carrying capacity - bird density - prey density - sequential filling

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INTRODUCTION

Understanding the effects of habitat loss has become a central 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, especially waders, offer very good subjects for the 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 (Smit & Piersma 1989). Furthermore, intertidal areas are threatened with destruction all over the world. Much attention is therefore being paid, mainly in the Netherlands and the United Kingdom, to studying the influence of loss of intertidal area on waders (Goss-Custard & Durell 1990, Evans 1991, Sutherland & Goss-Custard 1991, Meire 1993, Meininger *et al.* 1994).

When assessing the impact of the 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 plateau values in preferred feeding areas (Zwarts 1974, Goss-Custard 1977a & b, Zwarts & Drent 1981, Hicklin & Smith 1984, Meire & Kuijken 1984) and that interference causes the birds to disperse over the available feeding sites (Ens & Goss-Custard 1984, Goss-Custard & Durell 1987). Hence it would expected that given a constant amount of food, densities would not necessarily be able to increase after a loss of feeding areas. Few studies are available however, where both the occurrence of waders and their food supply has been studied before, during and after the removal of intertidal area (Evans *et al.* 1979).

The Delta area in the south-west of the Netherlands consists of the estuaries of the rivers Rijn, Maas and Schelde. The implementation of the 'Delta Plan' resulted in the closure of most estuaries but, in the Oosterschelde, a storm surge barrier was built as a compromise between safety and environmental considerations. Its construction nonetheless, resulted in a substantial reduction in intertidal area (Nienhuis & Smaal 1994). As this offered a good opportunity for studying the effects of habitat loss on non-breeding waders, a long-term study on the benthic food supply and the numbers, distribution and foraging behaviour of birds was started (Meire & Kuijken 1984, 1987, Schekkerman *et al.* 1994, Seys *et al.* 1994).

After a reduction in intertidal area, wader densities would be expected to increase if birds displaced from the reclaimed area were able to establish themselves in the remaining area. But if no increase in density were to occur we would need further evidence that this was due to competition. In this paper, I try to address these issues using 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 barrier and dams. 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 construction of barrier and dams strongly reduced the tidal amplitude in 1986 and 1987. On the completion of the secondary dams in April 1987, the total intertidal area was reduced by some 30%, from 17 000 to 11 365 ha, and the tidal amplitude increased again to 3.25 m compared to 3.7 m before the works started (Smaal & Boeije 1991, Smaal *et al.* 1991, Nienhuis & Smaal 1994). The reduction in intertidal area was caused mainly by the closure of the Krammer-Volkerak, the northern branch of the estuary although, even by 1983 some 1800 ha of intertidal area had been lost. In the tidal area that remained, 680 ha of tidal flats were lost due to the reduced tidal amplitude. The data in this paper are split into two: prior to April 1987 is the pre-barrier period and afterwards is the post-barrier period. Detailed observations on waders and their food supply were carried out on the Slikken van Vianen, a small intertidal flat in the middle of the estuary, described by Meire & Kuijken (1987).

Bird counts

Counts on the Slikken van Vianen were carried out at low and high water (Meire & Kuijken 1987, Meire & Meininger 1993). At low water, Oystercatcher numbers in six permanent plots (0.5-1 ha), marked out with stakes, 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 the exposure period. Counts were made at least every 15 min during the first and last hour in which a plot was exposed, as bird numbers could change quickly at that time. The average densities of feeding birds and of all birds, along with the number of feeding minutes ha^{-1} were calculated for each plot on each observation day. As the feeding density (average number of feeding birds ha^{-1} over the whole low tide period) and the number of feeding minutes were closely correlated, only feeding density was used in the analysis.

Six plots, located on mussel bed or mudflat and covering the entire gradient from the high to the low water line were followed through the entire study period. For this paper, additional data from eleven plots, scattered over the study area and studied in 1984, are also used. The plots PQ 6, PQ 10 and PQ 22 were situated on a mussel bed, the other three being on a mudflat. Days with very short exposure time are omitted from the analysis, as also are data from the season 1986/1987 when the storm surge barrier was used to manipulate the tide. For relating bird densities to prey biomass, only data from December counts when bird numbers are at their maximum, were used.

Benthic invertebrates

The benthic invertebrates in all study plots on the Slikken van Vianen 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 mussel beds, the biomass of Cockles and Mussels was summed.

To measure the visibility of Mussels, 40 cores (15 cm diameter) were taken on two mussel beds. 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. The maximum length of each Mussel was measured.

RESULTS

Distribution of the birds at low water: pre barrier

The areas with the highest biomass of Cockles and Mussels occurred low in the intertidal zone, although large differences occurred between sites at similar levels (Fig. 1). This affected the movement of birds as the tide ebbed and their distribution at low tide. In general, all birds roosted on the salt marsh or on adjacent arable land over high tide (Fig. 2). When the tide ebbed, some birds immediately started to feed on the exposed flats which had low biomasses. These birds followed the tide edge, presumably to reach the low-level richer feeding areas as soon as possible. This behaviour resulted in a clear peak of birds moving through the high-level plots (PQ 32) as the tide

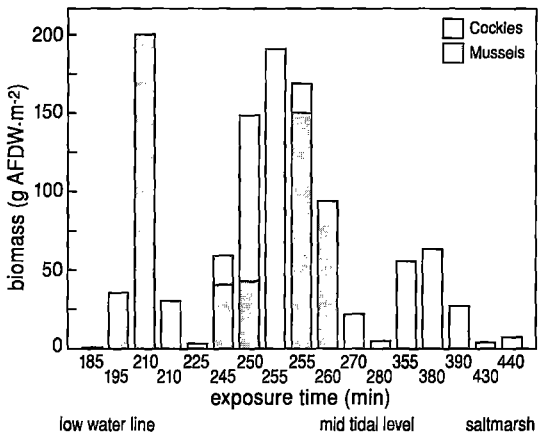

Fig. 1. Biomass of Cockles and Mussels in autumn 1984 in the different study plots. The plots were ranked according to exposure time, which is indicated on the *x*-axis.

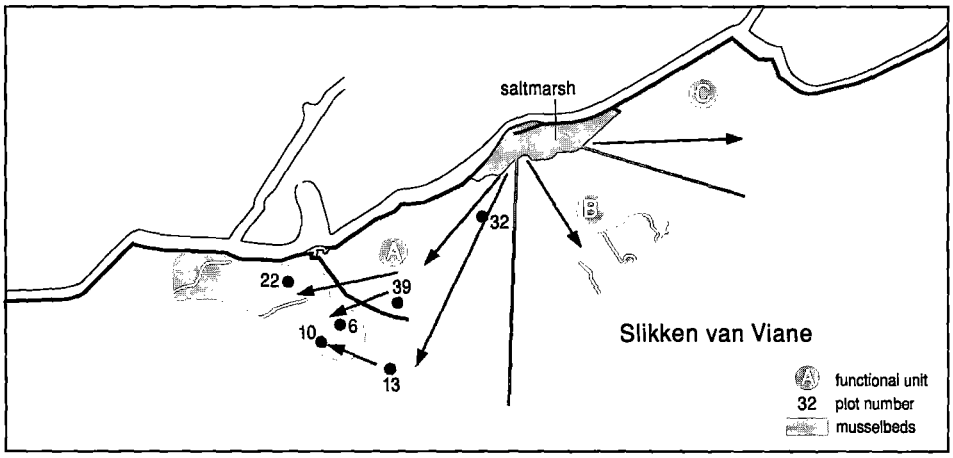

Fig. 2. Map of the Slikken van Vianen showing the tidal movement pattern of Oystercatchers and the three functional units.

edge passed through it. Few birds stayed for some time in this area (Fig. 3A) which is virtually abandoned at low water. Almost all birds left the roosts 2.5 hours after high tide and followed the tide edge. Near mid tidal level bird densities peaked as a plot became exposed (Fig. 3B). From here the birds moved to the preferred low-level feeding areas. Here birds remained in a particular feeding area until it was flooded again (Figs. 3C-G), so the density remained fairly constant throughout. The uneven distribution of the birds over the tidal flats is most pronounced at low tide when some areas may accommodate more than hundred birds h^{-1} and other areas, previously having high densities, are almost completely abandoned. As the tide flooded, the reverse movement took place, although it was subject to many variations, especially as birds moved through the higher plots. Here, the peak during flood was usually much more pronounced in winter than in summer, and after severe disturbance at low tide. Disturbance, which occurred regularly, could profoundly change the overall distribution patterns.

The pattern described here is based on observations from a small but representative part of the study area (site A, Fig. 2). The tidal movement of birds to the other preferred feeding areas at low water (sites B and C, Fig. 2) was similar. There seemed, however, to be very little exchange between birds using the different major feeding areas. Although all birds feeding on the Slikken van Vianen used the same high tide roost, observations of colour-ringed birds, observation of the tidal movement routes and counts indicated that the same birds always used the same 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 a severe disturbance for example, no birds flew to a different area; rather they formed a flock where they waited inactive until they could return to the place where they had previously been feeding. These three major feeding areas can be seen as functional units (Tamisier 1974, 1981).

The birds' distribution over the low water period was closely related to prey density in both space and time. A clear relation between average bird density and the combined biomass density of Cockles and Mussels was found ($y = 0.56 + 0.22x$; $R^2 = 0.81$, $n = 17$, $p < 0.001$) for the 1984 data (Fig. 4). Oystercatcher densities on the mussel beds were lower than on the Cockle plots, as can be seen from the regression line based on only the mussel bed 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

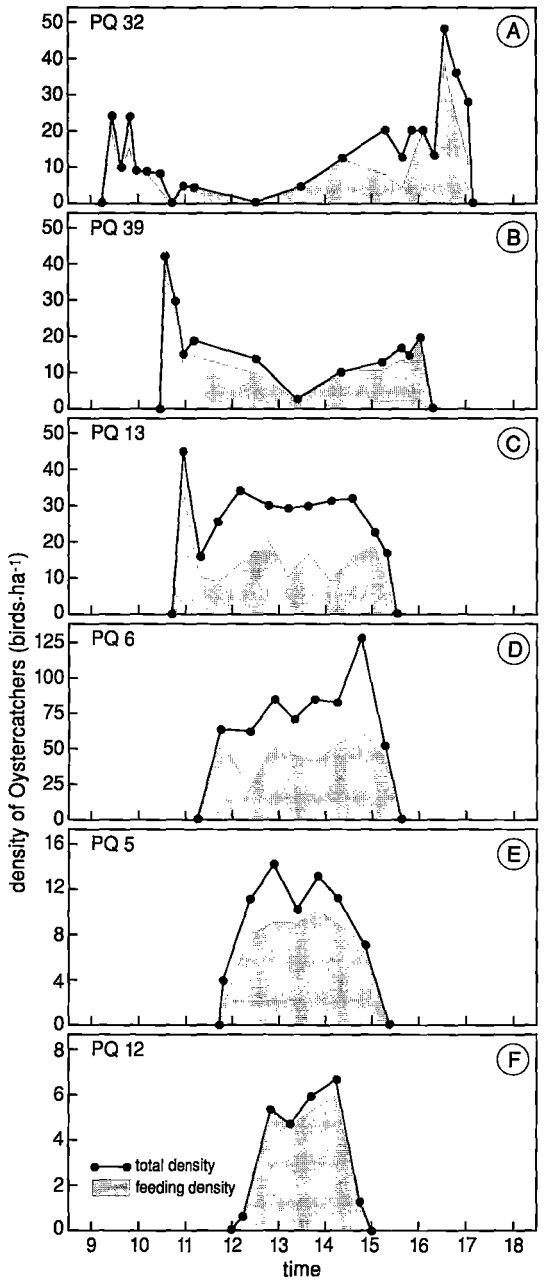

Fig. 3. Density of Oystercatchers (birds ha^{-1}) as a function of time in six different plots situated along the tidal gradient. Both total density (upper line) and feeding density (shaded part), as measured on 17 October 1984, are given for the whole exposure time of each plot. PQ 32 has the longest exposure time, PQ 12 the shortest.

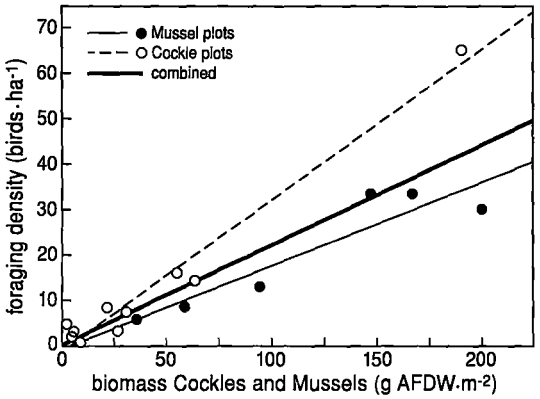

Fig. 4. Relationship between the average density of foraging Oystercatchers and the biomass of Cockles and Mussels in 17 study plots of the Slikken van Vianen. The data from December 1984 are plotted.

slope of both regressions differs significantly (ANCOVA, $F = 16.32$, $df_{1,13}$, $p < 0.05$).

Prey density not only influenced the density of birds at any one time, it also determined the sequence in which different areas were used during the season. Plots with high prey biomass were used first but, as bird numbers increased, more and more fed in plots with low prey biomass (Meire & Kuijken 1984). Such sequential filling was seen in each season, but is illustrated in Fig. 5, using data from 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, virtually no birds were present in PQ 39 and PQ 22. As the total number increased, densities increased in PQ 10 and PQ 6, both of which were situated on a mussel bed and had a high prey biomass (Fig. 5B). About one month later densities started to increase in PQ 39 and PQ 22, both of which had a low biomass.

Distribution of the birds at low water: post barrier

The tidal movements and functional units did not change after the dams were built in 1987. To

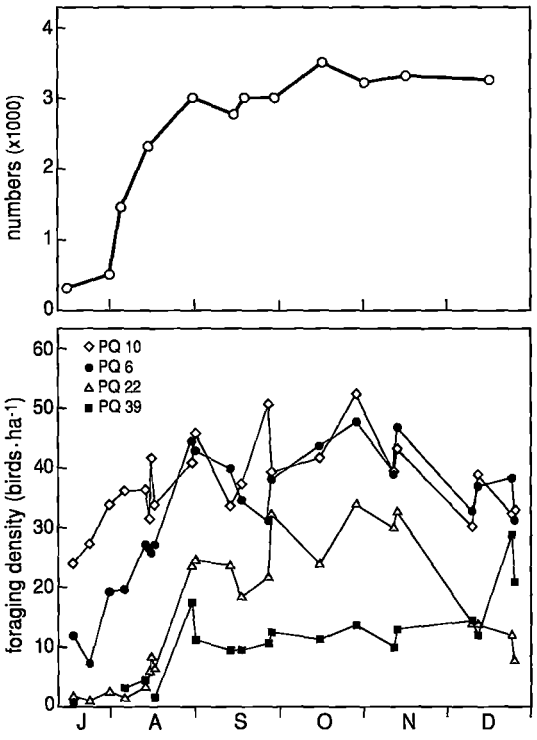

Fig. 5. (A) Total number of Oystercatchers on the Slikken van Vianen and (B) feeding densities in four plots between July and December 1984. The biomass of the plots were respectively 167, 148, 94 and 55 g AFDW m^{-2} for PQ 10, 6, 22 and 39. All but one plot (39) were situated on a mussel bed.

test for possible changes in the relationship between predator and prey density, the average densities of foraging Oystercatchers per month in three study plots are given in Fig. 6; data from the other three plots not shown were similar. In PQ 6, maximum feeding densities during the winter between 1979 and 1986 varied around 50 Oystercatchers h^{-1} and seemed quite stable. Densities increased however, rather suddenly, in the season 1987/1988, and stabilized around 80 birds h^{-1} after a short period of extremely high densities (Fig. 6). A similar pattern occurred in PQ 10 although, in the last season studied, densities decreased more than in PQ 6 (Fig. 6). The densities in late summer 1979 in PQ 10 were much

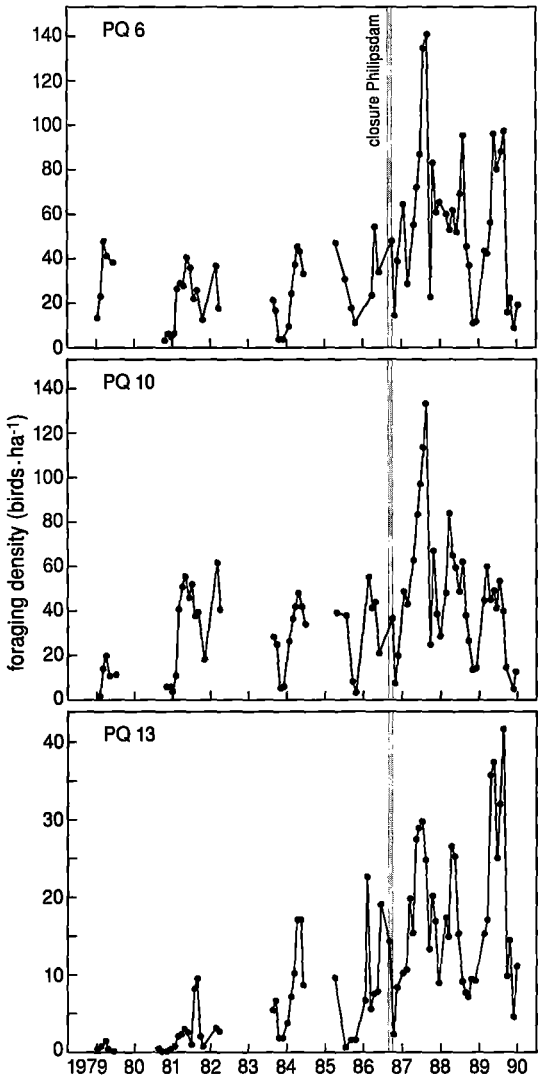

Fig. 6. Density of foraging Oystercatchers (average per month) in three study plots between July 1979 and June 1990. The grey line indicates the closure of the Philipsdam, which caused the major loss of intertidal area.

lower than in later years because, at that time, the plot had no mussel bed and contained only a low biomass of Cockles. In PQ 13 (Fig. 6), the pattern was different and densities increased gradually over the study period. This increase was related to an increase in the cockle biomass (y = 4.5 +

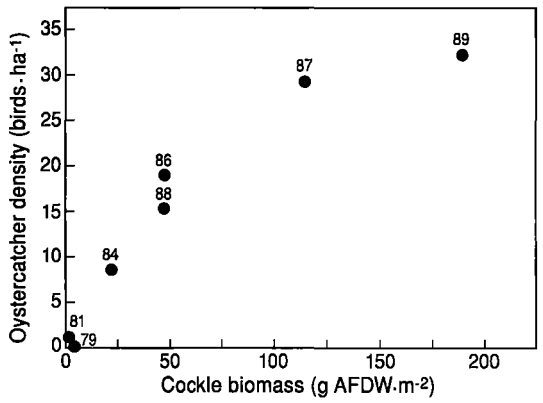

Fig. 7. Relationship between the feeding density of Oystercatchers and Cockles in PQ 13. All available December data between 1979 and 1989 were plotted.

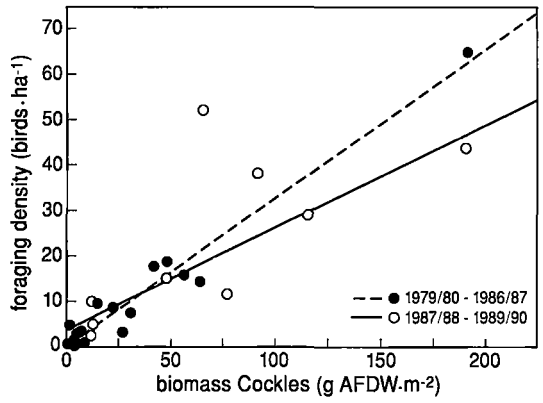

Fig. 8. Relationship between prey biomass and density of foraging Oystercatchers in non-mussel bed plots. Data from all plots in December 1984 (17) and all December values from plots 13, 32 and 39 were used. Values are the averages of all December counts.

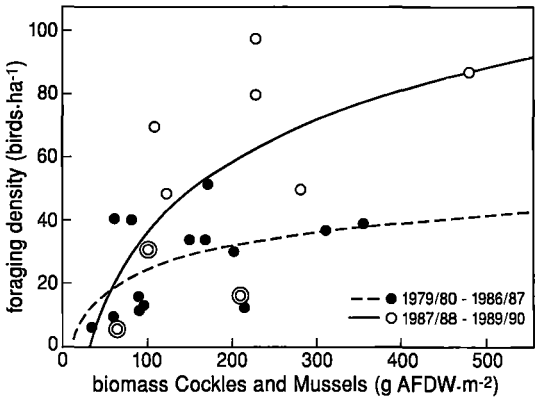

Fig. 9. Relationship between total prey biomass and density of foraging Oystercatchers in mussel plots. Data from all plots in December 1984 (17) and all December values from plots 6, 10 and 22 were used. Values are the averages of all December counts. The data from plot 22 are encircled. Lines fitted by eye.

$0.17x$; $R^2 = 0.86$, $n = 7$, $p < 0.05$, Fig. 7). The increased densities in PQ 6 and 10 coincided with the loss of intertidal areas following the closure of the Krammer-Volkerak. But was the loss of intertidal area or change in prey biomass the cause? In Figs. 8 & 9, the relationship between foraging density and prey biomass density is given for plots on mussel beds 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, there is a clear relationship between cockle biomass and Oystercatcher density ($y = 0.46 + 0.32x$; $R^2 = 0.95$, $n = 18$, $p < 0.001$, Fig. 8). Post-barrier, with one exception (plot 39 in 1988), the densities of Oystercatchers were comparable to those before closure at similar prey biomasses, at least when the biomass values were low. Post-barrier, there was also a significant relationship between Oystercatcher density and cockle biomass ($y = 5.7 + 0.17x$; $R^2 = 0.67$, $n = 8$, $p < 0.05$; without PQ 39, 1988). The slope of these regressions differ significantly however, (ANCOVA, $F = 13.13$, $df_{1,22}$, $p < 0.05$), the slope being smaller after 1987. On mussel beds, however, with the exception of plot PQ 22, bird densities at a given combined biomass of Cockles and Mussels were much higher after barrier closure than before. The numerical responses were thus different between the pre- and post-barrier periods (Fig. 9).

Although sequential filling of different study plots also occurred after 1987, there was one important difference. During the season 1987/1988, the first season after the closure of the Krammer-

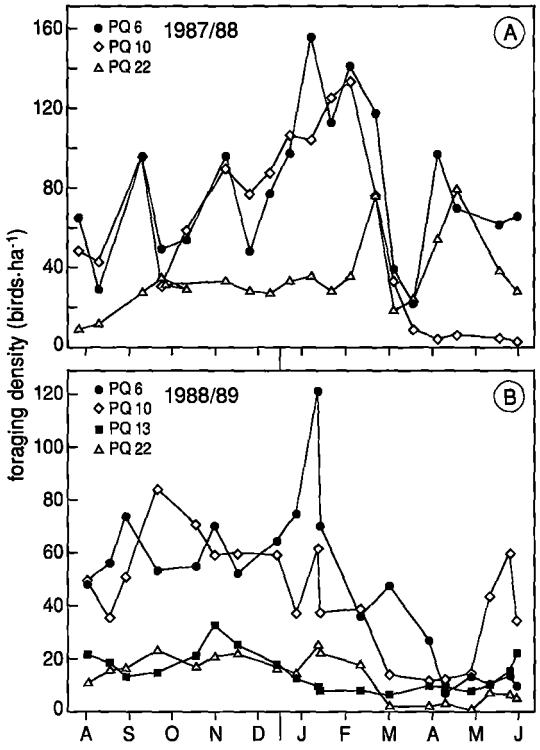

Fig. 10. Feeding densities of Oystercatcher in several study plots in the season 1987/1988 and 1988/1989.

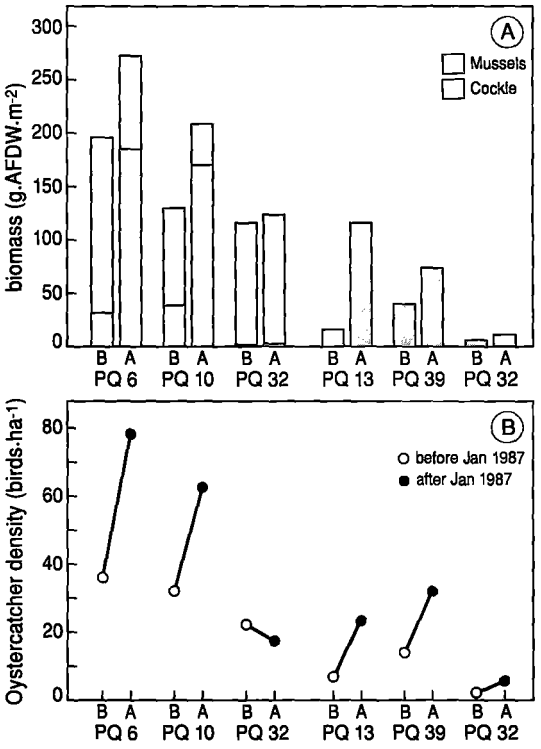

Fig. 11. Average biomass of Cockles and Mussels and average density of feeding Oystercatchers in December in each study plot, given separately (A) before 1987 and (B) from 1987 onwards.

Volkerak and also the first season with a high Cockle biomass, densities in July were indeed higher in PQ 6 and 10 compared to 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 their peak values only in February 1988 (Fig. 10A). In the next season, in both these plots, densities were high from the beginning of the season and remained fairly constant throughout (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 mussel beds, 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. 11A. On mussel bed PQ 22 Cockles occurred in very low densities throughout the study period. Before 1987, Cockles contributed, on average, 25 and 39% of the total biomass in two mussel beds study plots (PQ 6, PQ 10). However, they contributed 66 and 78% respectively between 1987/1988 and 1989/1990. This increased contribution from Cockles was due to an enormous spatfall in spring 1985, after the severe winter of 1984/1985. The increase in the cockle population was also reflected in a substantial increase in cockle biomass in non-mussel bed plots, especially in PQ 13 and PQ 39 (Fig.

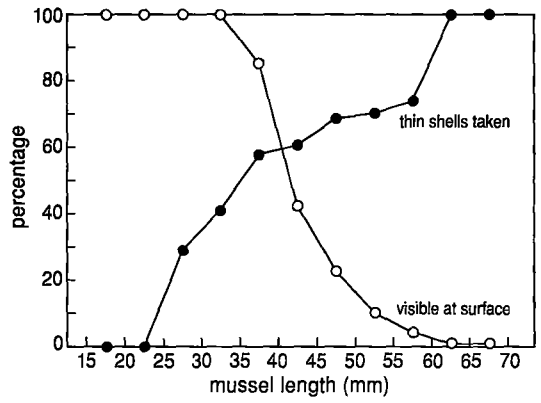

Fig. 12. Availability of Mussels to Oystercatchers. For each length-class the percentage of Mussels visible at the surface and percentage of Mussels with a shell thickness within the range taken by Oystercatchers (calculated from data given by Meire & Ervynck (1986)) are shown.

11A). The average Oystercatcher densities before 1987 and after 1987 are plotted for each PQ in Fig. 11B, the average of all December observations in both periods being used. There was a clear increase on the mussel beds in PQ 6 and PQ 10 where the cockle biomass increased but not in PQ 22, where Cockles were virtually absent. The increase was also clear in PQ 13 and PQ 39 where cockle biomass also increased substantially.

These data show that the increase in Oystercatcher densities was related to the increase in cockle biomass. Why were the Oystercatcher densities then lower at a similar biomass of Mussels and Cockles, as suggested by the two numerical responses in Fig. 9. In Fig. 12, the proportion of Mussels visible at the surface and with a shell thickness within the range normally taken by Oystercatchers (Meire & Ervynck 1986) is plotted by length-class. Larger Mussels that are visible at the surface were mostly too thick for Oystercatchers to open. The total amount of biomass, as measured in the normal sampling procedure, is therefore not a good indicator of the food supply for Oystercatchers. In contrast gross biomass density probably is an appropriate measure for Cockles. Cockles all occur in the top few centimetres of the sediment and never with 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 Plot PQ 22 in comparison with a rather high biomass density can also been explained by low mussel availability. All Mussels in this plot were larger than 40 mm long, hence only a small fraction could have been taken by Oystercatcher.

DISCUSSION

The counts at high water over the whole Oosterschelde (Schekkerman *et al.* 1994) and on the Slikken van Vianen (Meire & Meininger 1993) suggested that the number of Oystercatchers in the intertidal areas that remained did not increase. The conclusion 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 that had been colour-ringed in the Krammer-Volkerak pre-barrier, disappeared after dam closure compared with birds ringed in the rest of the estuary. Although total numbers using the remaining intertidal areas stayed constant, minor changes in distribution within the estuary occurred. At the Slikken van Vianen, numbers increased somewhat after the season of 1987/1988 (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 fulfil 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 mussel bed, 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 unpubl.). 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 high-level plots 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 *Anas crecca* (Zwarts 1976) 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 (Ens & Goss-Custard 1984, Sutherland & Parker 1985). It is similar to the buffer hypothesis formulated by Kluijver & 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 bird density between sites was likely to be related to difference in the food supply. It has often been shown that the density of feeding waders is related to their food supply (Goss-Custard 1970, Goss-Custard *et al.* 1977, O'Connor & Brown 1977, Bryant 1979, Sutherland 1982, Goss-Custard *et al.* 1991). This relation seems to hold both within an estuary (Bryant 1979) and between estuaries (Goss-Custard *et al.* 1977, 1991). This relationship 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, hence the food gradient may have to be defined in terms of several factors. Goss-Custard *et al.* (1992) 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 methods 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 necessarily a relation between the total prey density and the available prey 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 1984/1985-1986/1987. 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-mussel bed plots the relationship between bird and prey densities was rather similar before and after the closure of the Krammer-Volkerak; the significant difference in slopes found between the two regressions was mainly due to a few data points at very high densities. The opposite was true for the mussel beds however. From the present and earlier data (Meire & Kuijken 1984), we had believed that densities had reached a plateau value on the mussel beds. The data from 1987/1988 onwards, however, showed that bird densities can reach even 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 1987/1988, 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 (Goss-Custard 1980), 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.* 1994, Meire *et al.* 1994). 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 Oystercatcher numbers are now tightly linked to the available prey biomass or the estuary is at carrying capacity (Meire *et al.* 1994).

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SAMENVATTING

Als gevolg van de aanleg vam de stormvloedkering en de secondaire dammen is het oppervlakte getijgebied in de Oosterschelde met 30% verminderd. Wanneer de vogels die vroeger achter de secondaire dammen voedsel zochten, zich gevoegd zouden hebben bij de vogels op het resterende wadgebied, moeten de dichtheden daar zijn toegenomen. Om dit te onderzoeken werd de

dichtheid van de Scholeksters gerelateerd aan die van hun belangrijkste prooien, de Mossel en de Kokkel, zowel voor als na de verkleining van de Oosterschelde. Bij afgaand water foerageren de vogels eerst hoog in de getijzone, volgen dan de waterlijn tot ze uitkomen op hun geprefereerde voedselgebieden die laag in de getijzone zijn gelegen. Zijn ze eenmaal daar dan is de vogelverspreiding gerelateerd aan de dichtheid van hun voedsel. Wanneer er meer vogels in het gebied zijn, gaan meer vogels op de minder geprefereerde voedselgebieden voedselzoeken. Dit patroon veranderde niet nadat de dammen waren aangelegd. Na het verlies van getijgebied was de dichtheid van de Scholekster in relatie tot de kokkeldichtheid zoals die eerder was gemeten. Op mosselbanken daarentegen was de dichtheid van de Scholekster veel groter geworden. Dit werd veroorzaakt door een toename van de kokkelbiomassa op de mosselbanken. Aangezien slechts een klein deel de mosselbiomassa oogstbaar is voor Scholeksters, tegen een groot deel van de kokkelbiomassa, nam met de aanwezigheid van grote kokkels de oogstbare biomassa op de mosselbanken aanzienlijk toe.