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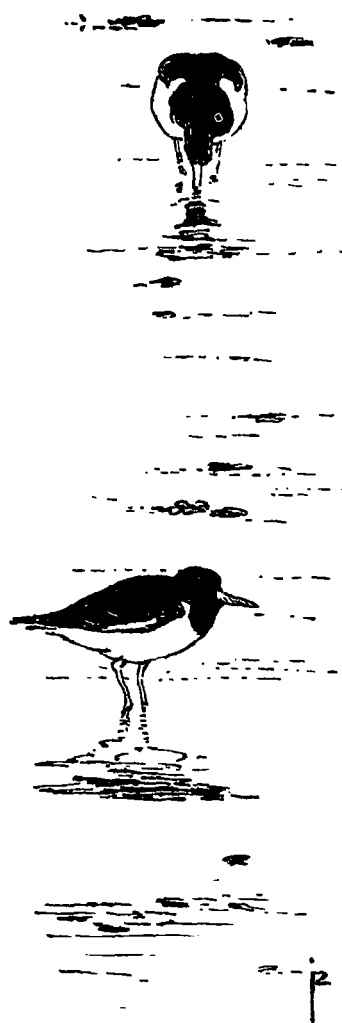
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**PREDICTING SEASONAL AND ANNUAL FLUCTUATIONS IN THE
LOCAL EXPLOITATION OF DIFFERENT PREY BY
OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS*:
A TEN-YEAR STUDY IN THE WADDEN SEA**

LEO ZWARTS¹, JAN H. WANINK² & BRUNO J. ENS³

Zwarts L., J.H. Wanink & B.J. Ens 1996. Predicting seasonal and annual fluctuations in the local exploitation of different prey by Oystercatchers *Haematopus ostralegus*: a ten-year study in the Wadden Sea. *Ardea* 84A: 401-440.



We predict the intake rate and prey choice of Oystercatchers feeding along the Frisian coast, Dutch Wadden Sea, combining the optimal prey choice model (Charnov 1976) with detailed measurements of the widely fluctuating food supply. Assuming that the birds maximize their intake rate, the birds should never eat Mussels *Mytilus edulis* during 10 years of observations, *Mya arenaria* during two short periods, *Macoma balthica* and *Scrobicularia plana* during most summers and Cockles *Cerastoderma edule* in most winters. Observations on feeding Oystercatchers confirmed the predictions. Due to the seasonal variation in burying depth of *Scrobicularia* and *Macoma*, these prey were in winter, if not inaccessible, hardly worthwhile exploiting because of the increase of handling time and searching time with burying depth. Hence, the seasonal variation in intake rate was very large in these deep-living prey compared to surface prey, such as Cockles and Mussels. Consequently, Oystercatchers usually switch from surface to deep-living prey in spring and back to surface prey in autumn in order to maximize their intake rate. Oystercatchers will never achieve a high intake rate when they feed on small prey, even when these prey would occur in extremely high densities. The reason for this is that the yield of small prey during handling is even less than the intake rate during feeding of 1 mg ash-free dry weight (AFDW) s⁻¹, which Oystercatchers need to meet their energy demands during the limited feeding periods in the tidal habitat. Since Oystercatchers eat only large bivalves, they might be vulnerable because cohorts of prey may disappear completely before they can be harvested. Despite the very large annual variation in the biomass of the different prey species in the Wadden Sea, the total food supply harvestable by Oystercatchers is large enough for them to stay in the area, unless ice covers the tidal flats. However, Oystercatchers cannot survive in the Wadden Sea when their diet is restricted to one or two prey species. They need to switch between at least 3 or 4 prey species. For the same reason, the birds have to roam over feeding areas measuring at least some ten's of km². The winter remains a difficult period, however. The mortality is higher in winter than in summer and increases with the severity of the winter. Besides, the winter mortality increases when the food consumption is reduced, due to either a low intake rate and/or a short feeding time. Therefore, the wintering numbers of Oystercatchers in the Wadden Sea are limited during circumstances which occur in only some of the winters, viz. when ice covers the feeding areas and the harvestable food supplies are low.

The total biomass of the five bivalve species in the study area amounted to 81 g ash-free dry flesh (AFDW) m⁻², on average. The annual production was 56 g m⁻², but only 32 g m⁻² can be considered as exploitable by Oyster-

catchers. Oystercatchers did not harvest the $9 \text{ g m}^{-2} \text{ year}^{-1}$ produced by large *Mya* living out of reach of the bill, nor the 5 g m^{-2} produced by bivalves too small to be eaten by Oystercatchers. Moreover 9 g m^{-2} disappeared during disasters (e.g. frost) and could not be eaten by birds. Oystercatchers consumed $12 \text{ g m}^{-2} \text{ year}^{-1}$, on average, thus more than the 10 g m^{-2} taken by all other shorebird species together. Half of the prey biomass disappearing due to mortality between August and March could be attributed to Oystercatcher predation. The predation pressure by Oystercatchers was much lower in *Scrobicularia* and *Macoma*. In contrast, 80% of the second year *Mya* was eaten by Oystercatchers in some months. The numbers of Oystercatchers feeding in the study area were weakly related to the annual variations in the total food supply, but strongly related to those of the harvestable food supply. This high correlation must be due to two causal relationships: the bird density increases with the intake rate, and intake rate increases with the harvestable food supply.

Key words: Oystercatcher - *Haematopus ostralegus* - Wadden Sea - optimal diet model - food exploitation - food intake rate - prey switching

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INTRODUCTION

Many workers have attempted to answer the question whether the numbers of shorebirds feeding on the intertidal flats are limited by their food supply. It is commonly assumed that such a limitation can occur either through actual depletion of the food supply or interference, where high densities of feeding birds impair the ability of the individual to collect food (Goss-Custard 1980). There is abundant evidence that Oystercatchers interfere with each other at high feeding densities (Zwarts & Drent 1981, Ens & Goss-Custard 1984, Goss-Custard & Durell 1987, 1988) and this may explain why many birds are often found feeding in poor areas, instead of all concentrating in the best feeding areas (Goss-Custard *et al.* 1982, 1984).

In this paper we explore the hypothesis that low intake rates limited the number of birds that used our study area. We refine our measurements of what part of the food supply can be considered harvestable for the birds (*sensu* Zwarts & Wanink 1993) and the extent to which the harvestable fraction is actually harvested in any given year.

To this end we apply the optimal prey choice model developed by Charnov (1976). It is necessary to consider several potential prey species, because the Oystercatchers have to take more prey species due to the wide year-to-year fluctuations in the prey densities (Beukema *et al.* 1993).

After parameterizing our application of the prey choice model, the paper will give a description of the seasonal and annual variation in the food supply of Oystercatchers. These data will then be used to make quantitative predictions on the intake rate. Assuming that the birds maximize their intake rate, the predicted diet can be ascertained. The next step is to compare the predicted intake rates and diet to the quantitative data on intake rate and diet. The data on predicted intake rate will then be combined with the bird count data to investigate whether the study area attracts more birds at high intake rates and/or a certain food supply. Finally, the calculated total predation pressure exerted by the Oystercatchers on the different prey species will be compared to the observed mortality of the different potential prey species. This will give a further check on the predicted diet. More important, it will allow us to de-

termine the predation pressure of Oystercatchers on their tidal-flat invertebrates and the extent to which the harvestable prey are actually harvested. The data will be used to analyse whether the winter mortality in the oystercatcher population in our study area is related to the food supply and the intake rate.

Predicting prey choice, intake rate, biomass consumption and exploitable biomass

Our aim is to predict the optimal prey choice and the associated intake rate of the Oystercatchers, as well as the exploitable part of the biomass, for each sampling of the food supply in our study area. Optimal foraging theory (see e.g. Krebs & Kacelnik 1991) has proven a useful tool for achieving the first two goals and, as we will show, it can also help to achieve the third goal. There are three simplifications in our study. We ignore (1) spatial variation in prey density through averaging over larger areas, (2) feeding specializations among the birds, and (3) interference.

A common and convenient assumption of optimal foraging models is that animals attempt to maximize their intake rate of energy while feeding. A realistic model of intake rate should therefore take into account (1) the weight and associated energy gain E_i (J) from an item of prey type i , (2) the handling time h_i (s) of each prey of type i and (3) search times of different prey types, which can also be characterized by λ_i , the encounter rate (s^{-1}) with prey type i . The multi-species functional response equation, also known as the simple or 'classic' optimal prey choice model (Charnov 1976), is based upon these three variables. In the model, prey of different species and sizes are ranked by their profitability, i.e. the rate of energy gain during handling. The ranking may include prey characteristics like prey size, but also shell thickness and burying depth. From the rate at which prey of a given class are encountered during searching, which classes should or should not be taken to achieve the maximum rate of energy gain during feeding can then be calculated. For i prey types:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i P_i}{1 + \sum \lambda_i h_i P_i}$$

where E is total energy intake (J) during observation time T (s) and P_i is the decision variable. P_i represents the probability that the predator takes a prey item of type i after it is encountered. When prey with a profitability below the critical threshold are encountered, it is more efficient to continue searching than to handle and eat those prey, i.e. $P_i = 1$ if $E/T < E_i/h_i$ and $P_i = 0$ if $E/T > E_i/h_i$ (Charnov 1976). The optimal P_i , i.e. the prey choice that maximizes intake rate of energy, can be found if the encounter rates λ_i are treated as fixed constants.

How then should we deal with spatial heterogeneity in the food supply and temporal variability in the searching behaviour of the bird? First, the prey species of the Oystercatcher usually occur in different patches within the tidal zone. For instance, the birds have to decide whether to go to a mussel bed to feed on Edible Mussels *Mytilus edulis* or to a mudflat to feed on the clam *Scrobicularia plana*. Second, even if Oystercatchers feed on a mudflat where two prey species, for instance Edible Cockles *Cerastoderma edule* and *Scrobicularia*, occur together, they may be forced to adapt their searching behaviour depending on which species they exploit. For instance, it is sufficient to bring the bill tip into contact with the mud surface to encounter *Cerastoderma* but the birds have to probe their full bill into the mud to find *Scrobicularia*, so searching for surface prey and deep-living prey is not easily compatible. For the same reason, Oystercatchers have to compromise if they search simultaneously for conspicuous and cryptic prey. They search slowly if they feed on prey hidden in the substrate, but speed up their walking rate if they feed on easy prey, such as Ragworms *Nereis diversicolor* that graze at the surface around their burrow (Ens *et al.* 1996).

In the following we therefore assume as a first approximation that, with one exception, searching for prey species i implies a zero encounter rate with all other prey species. To find under these

conditions the prey choice that maximizes intake rate, we first have to calculate the optimal prey selection within a prey species. This will yield a profitability threshold for each prey species and an associated intake rate. We then choose the highest one among these intake rates and identify this prey and the associated selection criteria as the optimal choice for that sampling date. As we will discuss when deriving parameter estimates, the one exception that we currently allow is where the bird can choose between *Scrobicularia* and the Baltic Tellin *Macoma balthica*, both of which live buried in the mud.

We find the harvestable biomass at any one time by extracting the biomass of all prey that cannot be harvested from the total biomass. First of all, prey are excluded that are unavailable, i.e. buried beyond reach of the Oystercatcher's bill. Second, for each prey species, we exclude all prey with a profitability below the minimal intake rate required for the birds to maintain energy balance.

The fraction of prey actually being exploited may be smaller than the harvestable fraction. Moribund Cockles found at the surface with gaping valves are highly profitable and extremely accessible and thus harvestable prey, but only a fraction of these prey can be consumed if they are all dying at the same moment. Moreover, for the sufficiently profitable prey, we can imagine that they are exploited until the density is so low that the minimal intake rate is reached. With a further decrease in density, the prey remain profitable and accessible, but the search time will become so long that the intake rate will drop below the acceptance level.

What should we take as the minimal intake rate for a given date? The available feeding time determines the minimum intake rate required for the birds to achieve the daily consumption. Oystercatchers need at thermoneutrality 36 g ash-free dry flesh weight (AFDW) per day (Zwarts *et al.* 1996c). If they could feed 24 h a day, their intake rate during feeding must be at least 0.42 mg s^{-1} . It must always be higher than this, because the birds need some time for other activities. Furthermore,

their feeding areas in the tidal zone are exposed for only 4 to 6 h per low water period. This amounts to about 10 h a day, assuming that the birds also feed at night (Table 2.1 in Hulscher 1996). Therefore, an intake rate of at least $3.6 \text{ g AFDW h}^{-1}$ or 1 mg AFDW s^{-1} is obligatory. The minimal intake rate may be a bit lower when the birds are able to extend the feeding period, or to catabolize their own energy stores. The latter gives only temporary relief, while extension of the feeding period is only locally possible, i.e. where birds can feed in grasslands at high tide. Furthermore, the energy requirements increase by 50% if the temperature drops from thermoneutrality (10°C) to freezing point (Kersten & Piersma 1987). Therefore, the minimal intake rate will increase by 5% for every degree that the average daily temperature falls below the lower critical temperature of 10°C .

METHODS

Study area

The study was performed between 1977 and 1986 on intertidal flats along the Frisian coast in the Dutch Wadden Sea (Fig. 1). The study area was intersected by long rows of poles, these being the remnants of brushwood groynes made in the sixties to enhance sedimentation. The former groynes delimited the study area, in total 396 ha, and divided it into 53 subareas. The eastern subareas were situated around mean sea level and the clay fraction ($< 2 \mu\text{m}$) in the substrate was 2-5%. The more western subareas were at about 25 cm above mean sea level and the substrate was soft with a clay content of 10-20%. For a more extensive description of the study area, see Zwarts *et al.* (1992).

The Oystercatchers feeding in this area used several roosts in the immediate surroundings, but at high tide the majority were found in the Paesenserpolder or on the island Engelsmanplaat. In total, about 20 000 Oystercatchers foraged on the tidal flats between the Frisian coast and the island Engelsmanplaat. We individually marked more

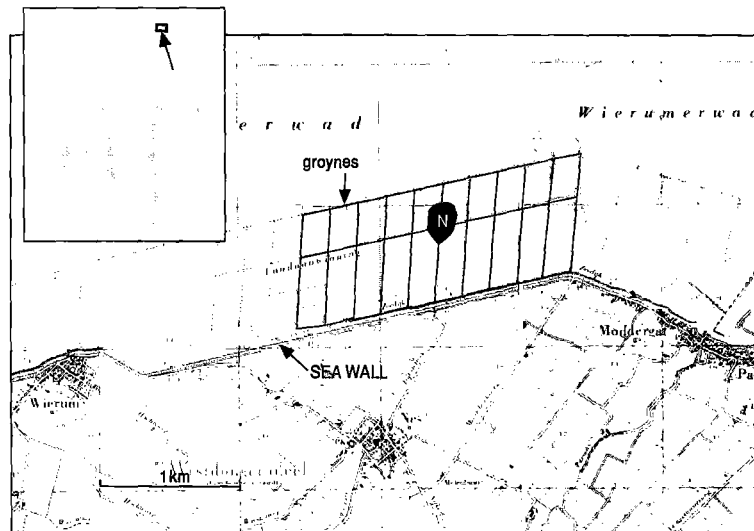


Fig. 1. Map of the study area along the Frisian coast. The food supply was measured in the Nes area (7.3 ha; site N). The birds were counted in the Nes area and in 20 counting areas around the Nes area, in total 100 ha of tidal flats. See also the map of Fig. 19.

than 3000 birds with the aid of 3 colour rings per bird, of which one with bar-codes. Most were captured with mist and cannon nets on the tidal roost in the Paesenserpolder.

Measuring the food supply

Sampling Samples of the macrozoobenthos inhabiting the mudflats were taken along 27 transects in August during four years (1977-1980). More detailed data were collected in the eastern part of the study area, where 146 plots of 0.1 ha were pegged out around two observation towers. One to four samples of the benthic fauna (179 cm²) were taken nearly every month during seven years (1980-1986, and less frequently in 1978 and 1979) in the 73 sites around one of these towers, the Nes area, in earlier papers also indicated as site N. This series of measurements is used here. A comparison between the Nes data and the samples taken along the transects covering the entire area showed that the Nes samples were representative for the area as a whole, especially for the most eastern part of the area (Zwarts 1988). The measurements in the Nes area started in December

1977 but, to extend the series of measurements, we will use for August 1977 the samples of two of the 27 transects that crossed the Nes area.

Condition, growth and mortality The laboratory procedures used to determine the biomass of the benthic animals have been described in Zwarts (1991). The growth of the bivalves could sometimes be calculated directly from the length frequency distribution in the monthly samples, but this was usually impossible because two or even more year classes occurred together. The year classes were identified using the Bhattacharya method for separating cohorts (MPA module of the Compleat ELEFAN software package, version 1.0; Gayanilo *et al.* 1988). This technique made it possible to estimate the monthly mortality and growth in length for the separate cohorts.

Estimating prey production Using the relationships between size and flesh weight, determined for all sampling data, we also calculated for each cohort the fluctuation in the biomass of the average individual and for the cohort population as a

whole. This allowed us to calculate the production per species, separately for the age classes. The production can be estimated by adding either the growth increments or the weight losses caused by size-dependent mortality (Crisp 1984). We estimated the production by calculation of the monthly weight loss since this made it possible to indicate to what degree the elimination of biomass due to prey mortality had been determined by the predation pressure of the Oystercatchers.

The elimination of the prey biomass is determined by the product of two terms: the mean weight of the prey averaged over two consecutive sampling dates and the decrease in the prey density between both sample dates. Both, prey weight and the numbers that disappeared, were calculated separately per cohort and recalculated per month if the intervening period was longer than a month. The eliminated biomass per cohort was summed to arrive at the total monthly elimination of biomass per prey species. Since Oystercatchers do not take Cockles < 10 mm, *Macoma* < 11 mm and the Soft-shell Clam *Mya arenaria* < 17 mm (Zwarts *et al.* 1996a), the elimination of biomass belonging to the size classes ignored by Oystercatchers will be given separately, as well as for prey living out of reach of the bill, i.e. *Mya* living more than 6 cm below the surface (Zwarts & Wanink 1984).

Burying depth The burying depth of the bivalves was measured once or twice a month during seven years (1980-1986). The methods have been described by Zwarts & Wanink (1989). The combination of biomass samples and the depth measurements was used to describe the annual fluctuation in the biomass actually accessible to Oystercatchers; see Zwarts & Wanink (1993) for a detailed description of the seasonal and annual variation in biomass and prey accessibility.

Human impact There was no human impact on the food supply in the study area. There was no dredging for Cockles within the study period and the few people digging for Lugworms *Arenicola marina* did not do so within the Nes area.

Counting and observing the birds

The Oystercatchers, and other bird species, were counted twice a month at low tide from the top of the sea wall which offered a splendid view over the whole area; in total 166 fortnightly counts were made between summer 1977 and autumn 1985. The birds were dispersed over the feeding area and were counted one by one. Counts of the birds feeding in the 73 0.1 ha plots in the Nes area were also often made from the observation tower, but since only a few of these counts were available for the winter months, the series of counts made from the sea wall will be used instead. For two reasons we took the bird counts from the eastern 100 ha (Fig. 1), and not from the entire area, as measure of the bird density. First, as already indicated, our measure of the food supply in the Nes area was more representative for the eastern part than for the entire area. Second, prey and size selection and intake rate were studied in Oystercatchers feeding around the towers in the eastern part of the study area. These data were collected during the first five years of observations (1977-1981) by Hulscher (1982 & unpubl.), Blomert *et al.* (1983), Zwarts & Wanink (1984), Hulsman (unpubl.) and Zwarts (unpubl.); see Zwarts *et al.* (1996b) for a summary. Only qualitative data on the prey selection are available during the latter five years (1982-1986).

Comparison of the low water counts in the 100 ha and the 7.3 ha around the Nes hide in the centre of this area showed that the Oystercatcher density in the Nes area as a whole was highly correlated ($r = 0.93$, $n = 35$) with the density measured on the same day in the 100 ha being, on average, 1.3 times higher. This difference was to be expected since the upper 1/4 of the 100 ha, situated along the dike, was hardly used when the tide was out. All bird numbers were therefore expressed as bird densities for the lower 3/4 of the study area, i.e. situated between 10 cm above and 20 cm below mean sea level. Despite the high correlation between bird densities on 100 and 7.3 ha, there was one period where the counts of 100 ha would highly overestimate the density on the 7.3 ha. In November 1979, most birds left the Nes

area for some months but remained to feed on the lower shore within the 100 ha. Therefore, we used the bird densities measured in the Nes area for these months.

Estimating parameters of the prey choice model

For each prey species, we need to know the profitability of the various prey classes and their respective encounter rates. For profitability we can draw on a recent review (Zwarts *et al.* 1996b). The profitability is defined as mg ash-free dry

weight (AFDW) s^{-1} handling and varies between 1 and 16 mg AFDW s^{-1} for the hard-shelled prey usually taken by Oystercatchers. In all prey species, the profitability increases with size (Fig. 2A, based on Table 2 in Zwarts *et al.* 1996b).

Oystercatchers feed only on middle-sized and large bivalves. Small size classes are ignored as being extremely unprofitable. The intake rate, defined as mg AFDW s^{-1} foraging varies between 0.5 and 3 mg AFDW s^{-1} and also increases with prey size (Fig. 2B, based on Figs. 12-14 in Zwarts *et al.* 1996b). This increase is a logical consequence of the positive relationship between profitability and prey weight (Zwarts *et al.* 1996b). Nonetheless, this cannot be the whole story, as the density of the prey also influences intake rate, through its effect on encounter rate. Thus, prey density must be included in the prediction of intake rate.

We describe below for each species, or combination of species, how we estimated encounter rates and intake rates, or, if we failed to estimate these, what alternative procedure we used to predict intake rate from prey characteristics.

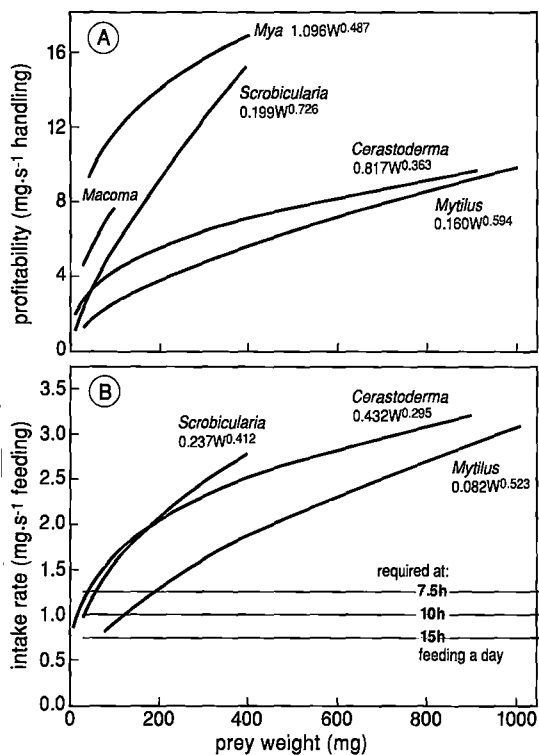


Fig. 2. (A) Average profitability ($mg s^{-1}$ handling) and (B) average intake rate ($mg s^{-1}$ feeding) as a function of average weight of the prey taken by Oystercatchers feeding on five different prey species. The profitabilities and intake rates are taken from Zwarts *et al.* (1996b). The minimal intake rate required to meet the energy requirements at thermoneutral conditions is indicated for the usual daily range in the available feeding time.

Scrobicularia Assuming that Oystercatchers probe their bill at random in the mud when they search for buried bivalves, it is possible to predict the searching time from the prey density (Hulscher 1976, 1982). To make precise predictions on intake rate, it is necessary to divide the prey into different depth categories and to measure the effect of burying depth on handling as well as on searching time (Wanink & Zwarts 1985). One also needs to know the relationship between burying depth and prey weight since the accessible shallow-living bivalves may represent marginal prey compared to the prey of similar size living at larger depths (Zwarts & Wanink 1991). The encounter rate $\lambda = aD$, where a is the instantaneous rate of discovery ($m^2 s^{-1}$) and D ($n m^{-2}$) the density of the prey. The searching time is the inverse of the encounter rate λ , which is the product of three variables: (1) the time needed to thrust the bill a certain distance into the mud, (2) the number of probes that has to be made to encounter a prey

and (3) the proportion of the searching time spent in probing. All three relationships were measured: (1) the relation between probing time (T , s) and probing depth (P , cm) was quantified using a high-speed film:

$$T = \exp(0.39P - 2.49) \text{ (Wanink \& Zwarts 1985);}$$

(2) the encounter rate was derived from the prey density and the 'effective touch area', i.e. the surface area of the prey (S , cm²) as a function of prey length (L , mm):

$$S = 0.154 L^{2.09} \text{ (Zwarts \& Blomert 1992),}$$

enlarged with the surface area of the bill tip (Hulscher 1982, Zwarts *et al.* 1996a: Table 2.1); (3) the probing time appeared to be a fixed proportion of the total searching time, 30% independent of the prey density of *Scrobicularia* (Wanink & Zwarts 1985).

Wanink & Zwarts (1985) offered a captive bird *Scrobicularia* 35-36 mm long, buried at different depths and predicted the intake rate, using the multi-species functional response equation (Charnov 1976). Extrapolation of this model to free-living birds was possible because the relationship between effective touch area and prey size has been quantified for different bivalve species (Zwarts & Blomert 1992), as well as the relationship between handling time and prey weight for the same prey species (Zwarts *et al.* 1996b). Based on this information, Wanink & Zwarts (1996) have estimated the encounter rate of free-living Oystercatchers feeding on *Scrobicularia* using the six-year data base of the bimonthly depth measurements (Zwarts & Wanink 1989, 1993). The handling time (H , s) of *Scrobicularia* as a function of burying depth (B , cm) and prey length (L , mm) was based on the empirical relationship:

$$H = (0.093 L^{1.549}/23.4) - (3.7B + 24.9)$$

The flesh weight of all mm classes was known per cm depth class, so it was possible to calculate the intake rate under the assumption that Oyster-

catchers probe their bill at random into the mud. The calculation was repeated for birds probing 2, 3, ... 8 cm deep. If all prey were deeply buried, the birds would achieve the highest intake by probing as deeply as possible, but if many live close to the surface, the optimal depth selection could be attained by ignoring all deep-living *Scrobicularia*.

Macoma The intake rate of Oystercatchers feeding on *Macoma* could be predicted in the same way as in *Scrobicularia*. However, whereas the relationships between handling time and burying depth and shell length were available for *Scrobicularia*, this must be estimated for *Macoma*. Our only clue was the relationship between handling time and prey weight for two periods where prey depth could be estimated, i.e. spring and late summer, when the animals lived 2 and 4 cm, on average, beneath the surface of the mud, respectively (Fig. 5 in Zwarts *et al.* 1996b). From that figure it could be concluded that prey weight correlated better with handling time than prey length, so that for practical reasons we used prey weight, instead of prey length to predict the handling time. To obtain the handling time of *Macoma* as function of prey weight (W , mg) for other burying depths, we performed linear interpolation, resulting in the following equation:

$$H = 0.231B \times 0.602W^{0.571} = 0.139B \times W^{0.571}$$

Since we know that Oystercatchers never take *Macoma* < 11 mm long (Hulscher 1982, Zwarts *et al.* 1996a), the calculations were based on the assumption that the birds took all *Macoma* \geq 11 mm that they encountered.

Scrobicularia + Macoma *Scrobicularia* and *Macoma* occurred in the same habitat, reaching the highest density on the mid-shore and living buried in the substrate. Hence, Oystercatchers encountered both prey if they probed the mud with their bill. Assuming that Oystercatchers took all *Scrobicularia* and *Macoma* \geq 11 mm, it was possible to calculate the intake rate for both species combined. As an example, Fig. 3 shows for three

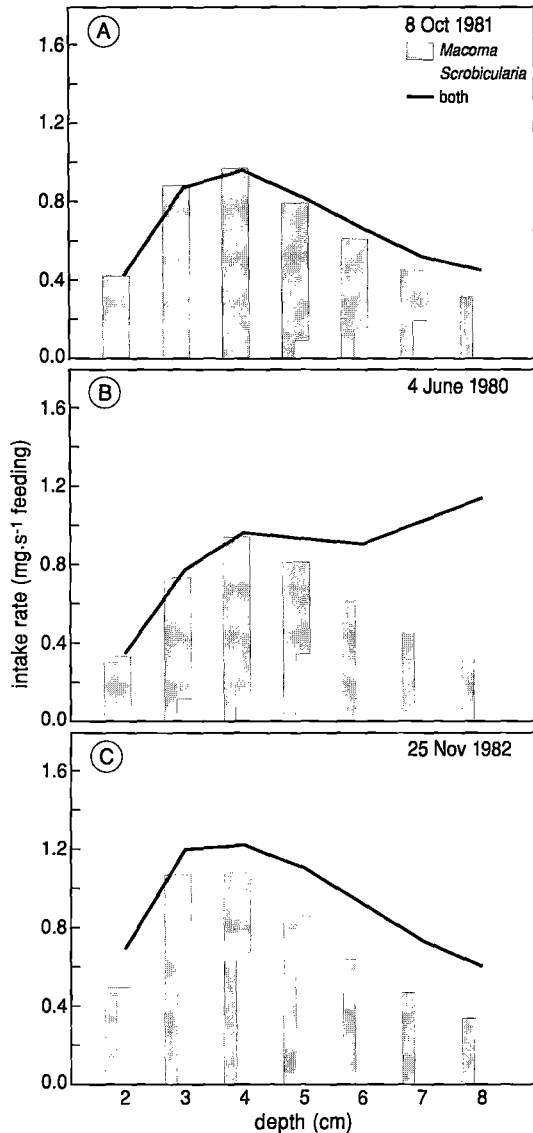


Fig. 3. Predicted intake rate (mg s^{-1} feeding) in free-living Oystercatchers on three different days when they had selected only *Scrobicularia* or *Macoma*, or taken both species, as a function of depth selection. The intake rate would have been maximized if the birds had selected only *Scrobicularia* on 4 June, only *Macoma* on 8 October and taken both species on 25 November. The optimal depth selection was also different.

different days the predicted intake rate of Oystercatchers feeding either solely on *Scrobicularia* and *Macoma*, or on both species together.

On 8 October 1981, the birds should select *Macoma* from the upper 4 cm in order to maximize their intake rate (Fig. 3A). The birds would have to probe as deeply as possible were they to feed solely on *Scrobicularia*, but their intake rate would remain very low because only a small fraction of these prey would be accessible and none would be found in the upper 5 cm. If the birds were to feed on both species, they would be able to increase their intake rate if they probed deeply, but since a higher intake rate still could be reached by selecting only prey from the upper 4 cm, the prediction remained that only *Macoma* would be taken.

The second example shows that, on 4 June 1980, Oystercatchers feeding on *Macoma* would reach the highest intake rate if they took all prey from the upper 4 cm of the substrate and ignored all prey living more deeply (Fig. 3B). In contrast, if Oystercatchers restricted their diet to *Scrobicularia*, they would have to probe as deep as possible and take all prey within reach of the bill. In the latter case, the intake rate would be higher than if only *Macoma* were taken. Hence, the prediction was that the birds would take *Scrobicularia*. The intake rate would decrease if the birds added *Macoma* to a diet of *Scrobicularia*, so for this day the prediction remained that only *Scrobicularia* would be selected.

On 25 November 1982, the highest intake rate could be achieved by selecting *Macoma* living in the upper 3 cm or *Scrobicularia* from the upper 5 cm (Fig. 3C). However, the birds would maximize their intake rate if they selected prey of both species from the upper 4 cm, in which case 85% of the biomass would consist of *Macoma*.

Calculations such as depicted for these three days (Fig. 3) were repeated for all 88 days of sampling. There were 53 sampling days out of a total of 88 during which both prey species were common. In this period, Oystercatchers rarely raised their intake rate by taking both species (Fig. 4). They even lowered their intake rate on seven days

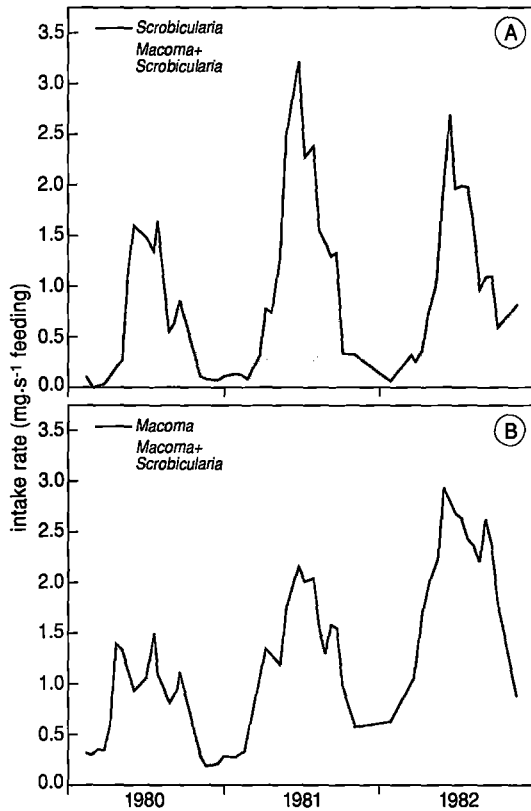


Fig. 4. Predicted intake rate in Oystercatchers feeding on (A) *Scrobicularia*, (B) *Macoma* compared to when an optimal mixture of both prey species is taken. The intake rates are calculated on the assumption that the birds performed optimal depth selection, as shown for three days in Fig. 3.

by adding *Macoma* to a diet of *Scrobicularia* (Fig. 4A); in contrast, it hardly affected their intake rate when they added *Scrobicularia* to a diet of *Macoma* (Fig. 4B). Since the intake rates predicted for birds feeding on *Macoma* or on both species did not differ much, we decided to treat these two prey species as a single species for calculations on intake rate and prey choice.

Mya In principle, a similar depth-related model might be developed to predict the intake rate for Oystercatchers feeding on *Mya*. However, in this prey, the siphon holes are sometimes visible at the

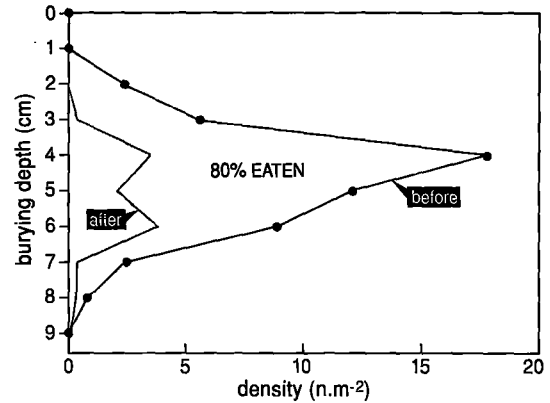


Fig. 5. Depth distribution of second year *Mya* in winter 1980/1981, before and after Oystercatchers had removed 80% of the prey, between September ($n = 82$) and February ($n = 40$), to show that Oystercatchers took the most shallow prey.

surface, by which they may be located by sight. This made a model based on randomly probing the mud less appropriate. *Mya* are only harvestable by Oystercatcher during a short period of their lives, being too small to be profitable before the second growing season and buried too deeply to be accessible after the third (Zwarts & Wanink 1984). Hence, the prey was harvestable by Oystercatchers during only two of the ten years of observation. The intake rate was actually measured in one of these two winter half years.

The birds achieved an intake rate of 1.86 mg s⁻¹ in October 1980 (correcting for the 30% overestimation of prey weight by Zwarts & Wanink 1984; see Zwarts *et al.* 1996c). We know that the birds continued to feed on *Mya* in the following months but did not measure the intake rate. The body condition of the prey decreased gradually by 20% from November to February, but the decline in intake rate would have been larger because the Oystercatchers depleted their food. The birds eliminated 80% of all the *Mya*, and 90% of the shallow, most profitable prey (Fig. 5). Consequently, the search time must have increased during these months of heavy exploitation. The decrease in intake rate could be estimated, because the *Mya*-

eating Oystercatchers in autumn foraged in 73 plots where the prey density was known. The feeding rate was significantly correlated with prey density ($r = 0.27$, $n = 80$ observation periods of 10 min, $p = 0.01$) and decreased from 4 clams min^{-1} at 100-250 clams m^{-2} to 2.2 clams min^{-1} at 50 clams m^{-2} . When the linear regression was extrapolated downwards to below 50 clams m^{-2} , the feeding rates must be too high. Therefore, we used a third-degree polynomial to describe the sigmoidal function of feeding rate (F , Mya min^{-1}) against prey density (D , Mya m^{-2}):

$$F = -0.21 + 0.66D - 0.00033D^2 + 0.00000056D^3$$

The density of the harvestable clams was reduced to only 15 clams m^{-2} at the end of the winter. Hence, by extrapolation downwards the intake rate must have dropped from 1.86 mg s^{-1} in October to the extremely low level of about 0.30 mg s^{-1} some months later.

The intake rate was unknown for the *Mya*-eating Oystercatcher in winter 1977/1978. Although the prey density was higher than in early autumn 1980, we estimated that the intake rate was 1.86 mg s^{-1} as in October 1980.

Cockle Cockles live close to the surface. Therefore it was sufficient to know the density and frequency distribution of the size classes to calculate the encounter rate with the prey, using the random touch model of Hulscher (1976). However, as Hulscher (1976) also showed, in daylight Oystercatchers hunt visually for Cockles. Moreover, he could show that the birds became more selective at high prey densities by ignoring the closed bivalves that could not be opened in a single stabbing movement. That is why random touch models could not be used to predict the intake rate of cockle-feeding Oystercatchers. Instead, the intake rate was predicted from the empirical relationship between intake rate (I , mg s^{-1}), prey density (D , $n \text{ m}^{-2}$) and prey weight (W , mg AFDW). The function was based on a multiple regression as a function of both, performed on the 38 available studies (Fig. 16 in Zwarts *et al.* 1996b):

$$I = \exp(0.476W + 0.238D - 0.0124D^2 - 2.727)$$

Sometimes the Oystercatchers could feed on Cockles that had recently died, e.g. due to frost bite after a cold spell. In these circumstances the birds simply extracted the flesh from the gaping valves and achieved intake rates well exceeding 3 mg s^{-1} (Hulscher & Zwarts unpubl.). For sampling dates where this happened, we used 3 mg s^{-1} as an estimate for intake rate on adult Cockles, irrespective of density and size.

Mussel The Oystercatchers in our study area used the stabbing technique to open Mussels. The slightly open Mussels were located by eye as well as by touch. In both cases, we needed to know the fraction of open Mussels before the encounter rate with accessible prey could be estimated. These data were lacking, but we knew that the intake rate strongly depended on the weight of the Mussels taken (Fig. 2B). Hence, we used the curve from Fig. 2B to estimate the intake rate from the flesh weight of Mussels.

Ragworm, Lugworm and Shore Crab There were potentially three alternative non-bivalve prey species in the study area: the Ragworm, the Lugworm and the Shore Crab *Carcinus maenas*. Of these three species, only Ragworms were common in the study area, but rarely taken by Oystercatchers. Their biomass varied between 2 and 14 g m^{-2} (Zwarts & Wanink 1993: Fig. 4F). The worms were large, 10 cm and longer (Zwarts & Esselink 1989: Fig. 9), and thus large enough to be highly profitable (Zwarts *et al.* 1996b: Fig. 8). This was surely the case in spring and early summer when worms fed at the surface (Esselink & Zwarts 1989). Indeed, Bunschoeke *et al.* (1996) found that the majority of the Oystercatchers took Ragworms at this time of the year on the mudflats near Schiermonnikoog, only 10 km from the study area, and this was also the case on the mudflats 2 km eastern of the Nes area (Hulscher & Zwarts unpubl.). Because Ragworms were obviously a summer prey taken by a few specialists among the small number of Oystercatcher that

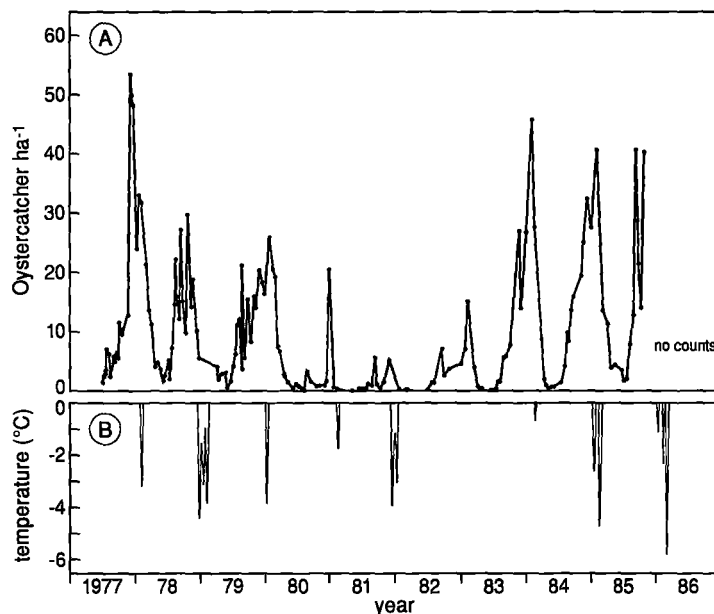


Fig. 6. (A) Annual and seasonal variation in Oystercatcher density (birds ha^{-1} at low water); (B) average air temperature per ten days, if below 0°C .

were present, we excluded them from the analysis.

Lugworms were rare in our study area, because the substrate was too soft. Their contribution to the prey biomass was only 1 to 2 g m^{-2} in most years, although they occurred with 4 to 11 g m^{-2} in 1977-1979 (Zwarts & Wanink 1993: Fig. 4G). Since we never saw an Oystercatcher take this prey species in the study area, there is no reason to take it into account.

First year Shore Crabs were very common on the tidal flats, but Oystercatchers ignored them. Older crabs were rare in our study area. Since only a few specimens were observed to be taken in early summer, also this species could safely be ignored in the calculation of the total food supply.

Estimating biomass consumption

We assumed that the Oystercatchers counted during low tide in the study area obtained all their food there, i.e. they did not consume appreciable amounts of food elsewhere either earlier or later in the tidal cycle, and that if night feeding occurred, the distribution over the area did not differ

from that by day. The daily consumption varies between 36 g in summer and 40-50 g in winter and amounts, on an annual basis, to 39.4 g. The predation pressure by the other shorebirds was estimated from the relationship between body weight and basal metabolic rate (*BMR*), according to Kersten & Piersma (1987), and further based on the general assumptions (e.g. Smit 1984, Zwarts *et al.* 1990) that the daily energy expenditure is equivalent to $2.2 \times \text{BMR}$, the energy content of flesh is 22 kJ g^{-1} and 85% of the ingested energy is digested.

To calculate for each period how much biomass of a particular prey was removed by the Oystercatchers, it was assumed that all Oystercatchers fed on the prey predicted to yield the highest intake rate. Except for *Macoma* and *Scrobicularia*, we assumed that the birds could prey on only one prey species at a time. As shown before, the actual choice between these two species did not matter much for the predicted intake rate, so that it was hard to reliably predict the optimal mix. Fortunately, *Scrobicularia* was absent dur-

ing the last four years. For the first four years, it was assumed that both prey were taken in an equal amount of biomass.

RESULTS

Bird density

The Oystercatcher was the most common shorebird in the study area with 8.4 birds ha^{-1} , averaged over the entire year, but there was a large variation in the density during 8.5 years of counting (Fig. 6A). Hardly any Oystercatcher fed in the area in 1981 and 1982. Nonetheless, the peak numbers were present each year in mid-winter and the lowest numbers occurred between mid-March and mid-August. No counts were made when ice covered the mudflats (Fig. 6B), but usually no Oystercatchers fed in the study area during such periods, since most birds left the area altogether and those remaining stayed on the roosts. If birds fed on the mudflats during frost periods, they did so outside the study area on the water's edge near the low water mark, the only place where the substrate was not frozen.

Oystercatchers and Cockles

The intake rate of Oystercatchers depended closely on the weight of the prey taken and, to a lesser degree, on the density in which these prey occurred. Figure 7 depicts how the intake rate was determined by both variables, according to the multiple regression equation given in 'Methods'. It also shows for five important cohorts the rela-

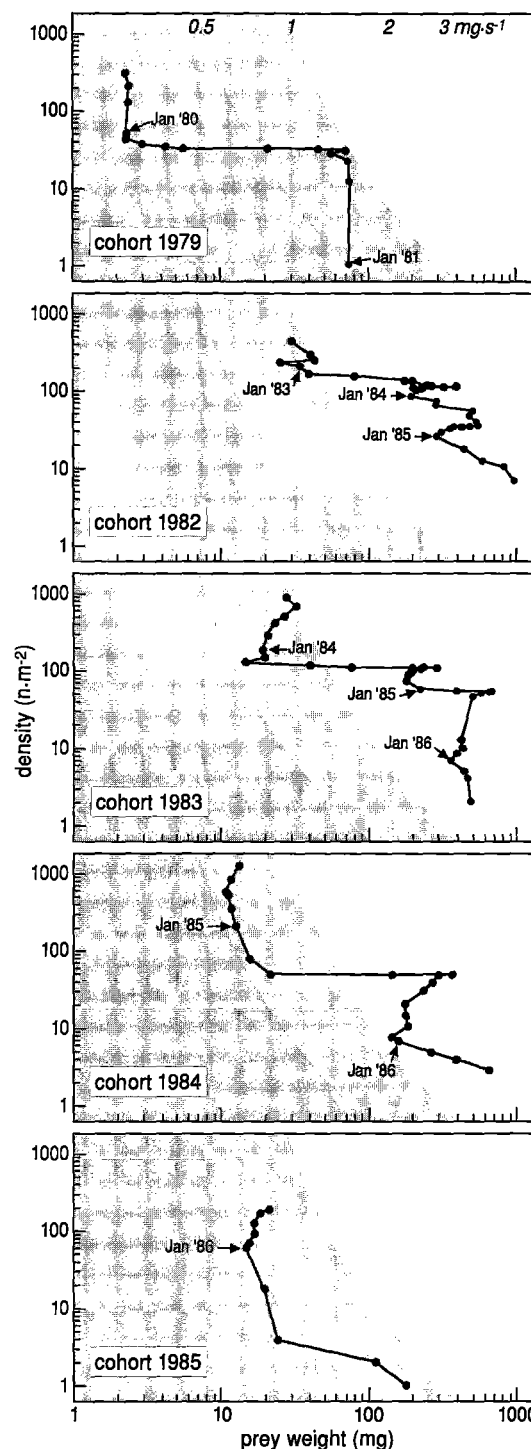


Fig. 7. *Cerastoderma*. Plot of density ($n \text{ m}^{-2}$) against average flesh weight (mg AFDW) for five different cohorts during one to three years. The lines connect the course of the change in density and average prey weight for as long as the cohort existed; based on monthly samples in the Nes area, from August in the year of settlement onwards. In each winter there was a decrease of the prey weight. Grey fields indicate the predicted intake rate of Oystercatchers as the combined function of prey weight and prey density (based on Fig. 16 in Zwarts *et al.* 1996b)

tionship between the increase of the flesh weight of the average Cockle and the concurrent decline in the density. After their settlement in summer, Cockles occurred at densities of many thousands per m^2 . There was a high mortality among these spat during their first summer, as a result of which the density was usually reduced to some hundreds per m^2 by September.

The change in the density and the average body weight in the five cohorts was based on monthly samples, and shown from August in the first year onwards (Fig. 7). The decrease of weight in winter was caused by the declining body condition. Obviously first year Cockles could never provide Oystercatchers with an intake rate exceeding the acceptance level of 1 mg

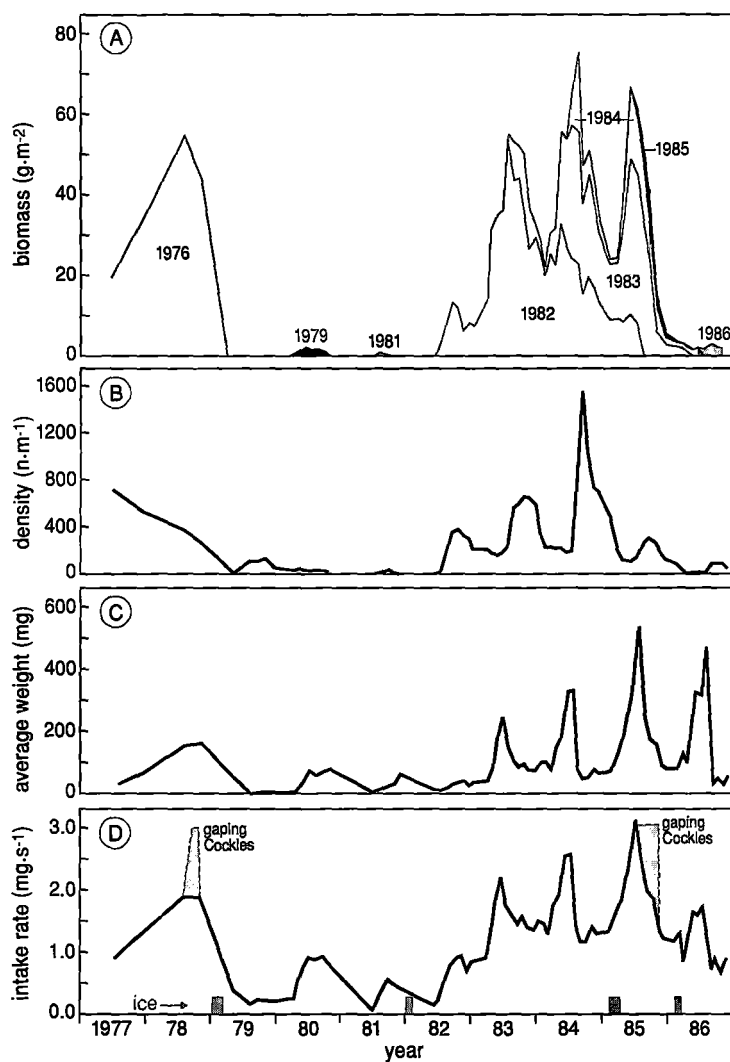


Fig. 8. *Cerastoderma*. (A) Biomass ($g \cdot m^{-2}$), (B) density ($n \cdot m^{-2}$), (C) average weight (mg AFDW) and (D) predicted highest intake rate ($mg \cdot s^{-1}$ feeding) of Oystercatchers feeding on Cockles during 10 years. The intake rate increased to 3 mg s^{-1} when the birds could feed on dying Cockles with gaping valves.

s⁻¹. Although the prey numbers steadily decreased later, the intake rate usually increased to 2 mg s⁻¹ in the second year and, if the cohort still existed, to about 3 mg s⁻¹ in the third.

Spatfall of Cockles did not occur each year. In our study area, there was settlement of Cockles in seven of the eleven summers, of which only three were substantial. Figure 8A shows the course of the biomass, given separately per year class. Each cohort reached its maximal biomass in the second summer. This implied that the decrease in the population after that (Fig. 8B) was larger than the increase of the average body weight (Fig. 8C). The intake rate was the combined function of both variables and therefore could be predicted for the entire observation period (Fig. 8D). The Oystercatchers encountered many dying Cockles after frost periods in January-February 1979, 1985 and 1986, and there was also a mass mortality in October 1978 and October/November 1985. As explained in the methods, Oystercatchers achieved very high intake rates under these circumstances.

Oystercatchers and *Scrobicularia*

There was no spatfall of *Scrobicularia* during the years of observation, but the course of the year class born in 1976, the year before the observations started, could be followed completely (Fig. 9). The average prey size gradually increased from 22 mm after their second growing season in 1977 to 35 mm in 1979. From then on the length increment was 1 mm per year. Over the same period, the body weight increased from 50 mg in 1977 to about 300 mg from 1981 onwards (Fig. 9C). The seasonal variation in the body weight was large, however, being in March 40% below the level reached nine months before in June (Fig. 9C; see also Fig. 8 in Zwarts 1991). There was a rather low mortality between 1977 and 1982, but the population collapsed in 1983 when the animals were seven years old (Fig. 9B). In the three years before, the biomass varied seasonally between 40 and 60 g m⁻² (Fig. 9A). However, the seasonal variation in biomass accessible to Oystercatchers was much larger, between 0 and

60 g m⁻², because *Scrobicularia* lived in winter out of reach of the bill, except during the winter of 1982/1983 (Fig. 9A).

The predicted intake rate of Oystercatchers feeding on *Scrobicularia* depended mainly on the burying depth of their prey (Fig. 9D), being high in June when the burying depth was minimal and close to zero in winter when the majority of the prey lived out of reach of the bill. Again, the exception was the winter 1982/1983 when the intake rate was predicted to have been 0.8 mg s⁻¹. The intake rate before 1980 was estimated by assuming that the seasonal variation in burying depth did not deviate from the average depth in 1980-1982. The high intake rate in 1979 was due to the very good prey condition of the individual *Scrobicularia* (Fig. 9C). *Scrobicularia* were still small before the growing season of 1979 (Fig. 9C), which explains the low intake rate in 1978. Although they were still smaller, and thus less profitable, in 1977 and 1978, this was compensated by a higher fraction of the prey being accessible. Whereas *Scrobicularia* > 25 mm buried in winter out of reach of the Oystercatcher's bill, specimens < 25 mm remained accessible (Zwarts & Wanink 1989), and were indeed taken by Oystercatchers in winter (Habekotté 1987).

Oystercatchers and *Macoma*

There was spatfall of *Macoma* during six of the eleven years, but only the 1979 recruitment was extremely large (Fig. 10B). Oystercatchers always ignore *Macoma* < 11 mm (Hulscher 1982) and take above this lower size limit relatively much more of the largest size classes (Zwarts *et al.* 1996a). *Macoma* > 15 mm were rare between 1977 and 1982, but 2-3 times more common in 1983-1985 (Fig. 10B). *Macoma* grew slowly. The year class 1979 measured 6 mm after one growing season, reached the length of 12 mm in 1980, after which the growth in length was 1 mm per year (Zwarts *et al.* 1992). The first heavy spatfall after 1979 took place in 1985. In the years between, the population density remained remarkably stable, which would suggest there was no mortality. However, a closer look on Fig. 10B

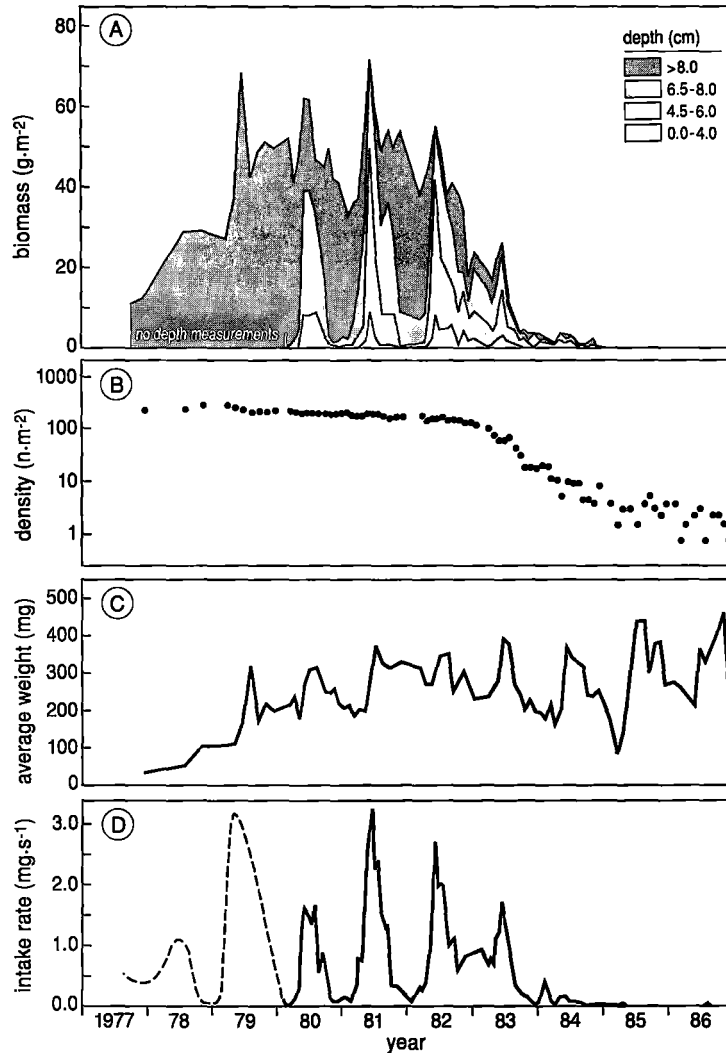


Fig. 9. *Scrobicularia*. (A) Biomass (g m^{-2}), (B) density ($n \text{ m}^{-2}$), (C) average weight (mg AFDW) and (D) predicted highest intake rate (mg s^{-1} feeding) of Oystercatchers solely feeding on this prey during 10 years. The biomass from 1980 onwards is given separately per depth class. The predicted intake rate before 1980 is based on the assumption that the burying depth of the prey did not deviate from the average seasonal depth variation recorded in 1980-1982.

shows there was a seasonal variation in the numbers. The population increased each year in March-May and decreased over the rest of the year. The increase in the Nes area in early spring must have been due to a change in distribution pattern of *Macoma* by which animals living fur-

ther upshore resettled in the Nes area, such as has been documented by Beukema (1993b) elsewhere in the Wadden Sea. Careful inspection of the monthly size-frequency distribution revealed that the immigrating animals were small compared to those from the Nes area. This difference was to be

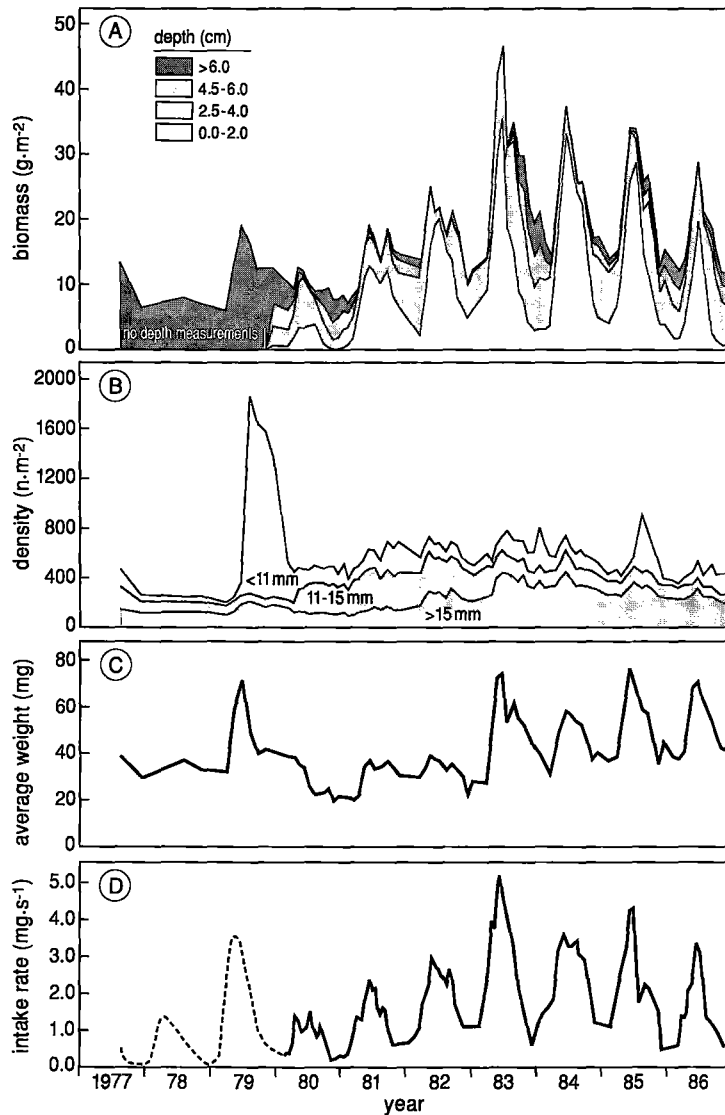


Fig. 10. *Macoma*. (A) Biomass (g m^{-2}), (B) density ($n \text{ m}^{-2}$), (C) average weight (mg AFDW of specimens > 15 mm) and (D) predicted highest intake rate (mg s^{-1} feeding) of Oystercatchers solely feeding on this prey during 10 years. The biomass from 1980 onwards is given separately per depth class. The predicted intake rate before 1980 is based on the assumption that the burying depth of the prey did not deviate from the average seasonal depth variation recorded in 1980-1986.

expected since growth is retarded on high-level mudflats (Wanink & Zwarts 1993). The immigrating specimens were each year larger than in the preceding year, which suggests that the immi-

gration was of clams of the strong year class 1979 and thus the migration from high to low flats continued over several years.

The biomass varied seasonally (Fig. 10A).

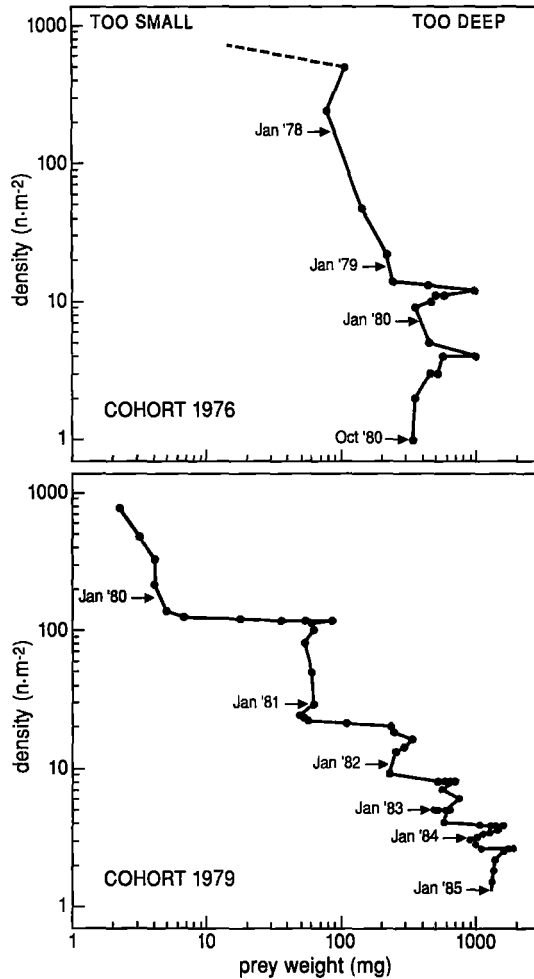


Fig. 11. Density of *Mya* belonging to two different cohorts as a function of flesh weight during four years. The lines connect the course of the change in the density and average prey weight as long as the cohort existed; based on monthly samples in the Nes area. In each winter there was a decrease of the prey weight due to a decline in the body condition. Prey < 10 mg are too small to be harvested by Oystercatchers, whereas prey > 200 mg live too deeply buried to be accessible.

This was mainly due to the variation in the average weight of the larger prey (Fig. 10C; see also Fig. 8 in Zwarts 1991). Clearly, the winter would be a very difficult period for Oystercatchers if

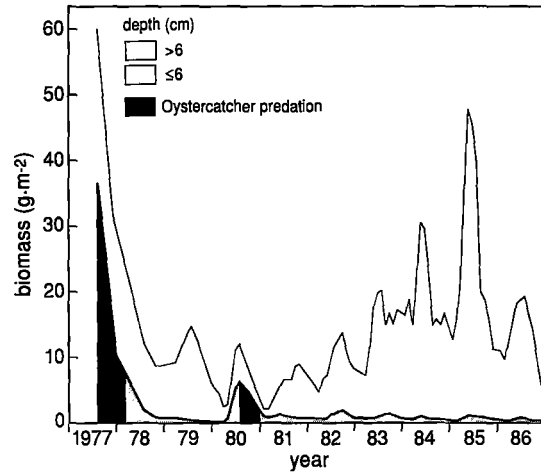


Fig. 12. *Mya*. Total biomass and biomass of the specimens living in the upper 6 cm of the substrate (g m^{-2}) during 10 years. Periods during which Oystercatchers heavily exploit this food resource are indicated.

they were to depend solely on *Macoma*. Not only was the body condition of the prey 40% below the summer level, but the prey also had to be located at a larger depth (Fig. 10A). Consequently, the predicted intake rate was much lower in winter than in summer (Fig. 10D). Since no depth measurements were made before 1980, the predicted intake rate could not be calculated, but on the assumption that the seasonal variation in burying depth did not deviate from average, the intake could be estimated. The intake rate was expected to have been low in the first years of observation due to the low density of large *Macoma* (Fig. 10B); the exception was in the summer of 1979 when the bivalves had an exceptionally good body condition (Fig. 10C; Zwarts 1991: Fig. 8).

Oystercatchers and *Mya*

There was recruitment of *Mya* in 1976 and in 1979 but not in the other nine years. The relationship between density and prey weight is shown for both cohorts in Fig. 11. Oystercatchers did not feed on *Mya* < 17 mm, and thus ignored prey containing less than 10-15 mg. Hence, the decline in the population during the first year of life was not

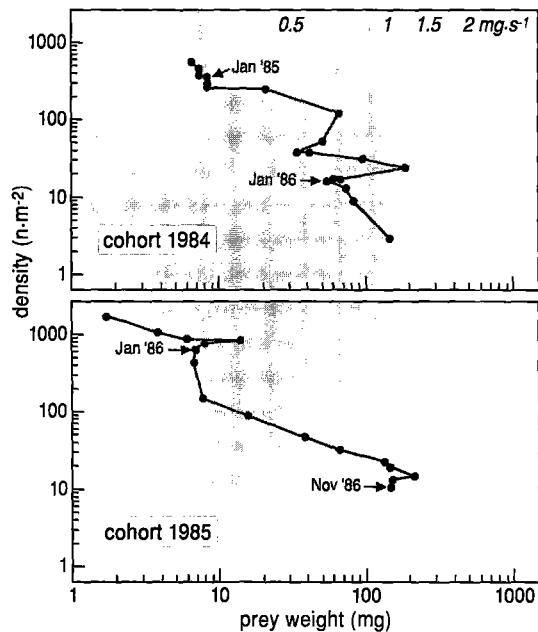


Fig. 13. *Mytilus*. Density of Mussels belonging to two different cohorts as a function of flesh weight during two years. The lines connect the course of the change in density and average prey weight as long as the cohort existed; based on monthly samples in the Nes area, from October or August in the year of settlement, 1984 and 1985 respectively, onwards. In each winter there was a decrease of the prey weight due to a decline in the body condition.

due to Oystercatcher predation. During the second year, however, Oystercatchers exerted a heavy predation pressure on the remainder. After the next growing season, *Mya* measured 45 mm and weighed 700 to 1000 mg. At this size, they all lived out of reach of the Oystercatcher's bill (Zwarts & Wanink 1984, 1993).

There was a large annual and seasonal variation in the total biomass of *Mya* (Fig. 12). The year-to-year variation was still larger for the biomass accessible to Oystercatchers (Fig. 12). In fact, only in two years were Oystercatchers able to feed on this prey. From the observations in October 1980, we estimated the intake rate that the birds achieved (see 'Methods'). The Oystercatchers also foraged on *Mya* in the winter of

1977/1978, when they took prey of about the same size as in autumn 1980 but the prey density was higher. Since the intake rate was not measured, we assumed that it did not differ from that three years later.

Oystercatchers and Mussels

Mussels might have been an alternative prey for Oystercatchers in 1985 and 1986, when the biomass of this prey reached a level of 10 g m^{-2} (Zwarts & Wanink 1993: Fig. 4E). In both years, the population consisted of spat. There was a huge mortality: 99% of the population disappeared in the first year of life (Fig. 13) by which time the survivors had attained 30 to 60 mg AFDW. It is unlikely that Oystercatchers will take first year Mussels. Even second year Mussels provide a rather low intake rate. Hence, in our study period, the Mussels did not reach a weight sufficient to make them a harvestable prey for Oystercatchers (Goss-Custard *et al.* 1996c).

Did prey selection conform to prediction?

The previous sections predicted the highest possible intake for birds feeding on Cockles (Fig. 8D), *Scrobicularia* (Fig. 9D), *Macoma* (Fig. 10D), *Scrobicularia* + *Macoma* (Fig. 4), *Mya* (see text) and Mussels (Fig. 13). If birds maximized their intake rate, we would expect that they selected the prey species that delivered the highest intake rate. The predicted highest intake rate varied between 0.2 and 5 mg s^{-1} (Fig. 14). To achieve this intake rate, the birds had to change their prey choice as indicated in Fig. 14. Mussels should never be taken in the study area. *Scrobicularia* and *Macoma* were predicted to be the dominant food resources in summer, whereas Oystercatchers were expected to take *Mya* and Cockles predominantly in winter. Did the birds behave as predicted in Fig. 14? There were four periods for which this could be checked.

(1) It was predicted that the birds should take *Mya* in the winter of 1977/1978, which the Oystercatchers were indeed observed to do (Zwarts & Wanink 1984). The low mortality rates of Cockles (Fig. 8B), *Scrobicularia* (Fig. 9B) and *Macoma*

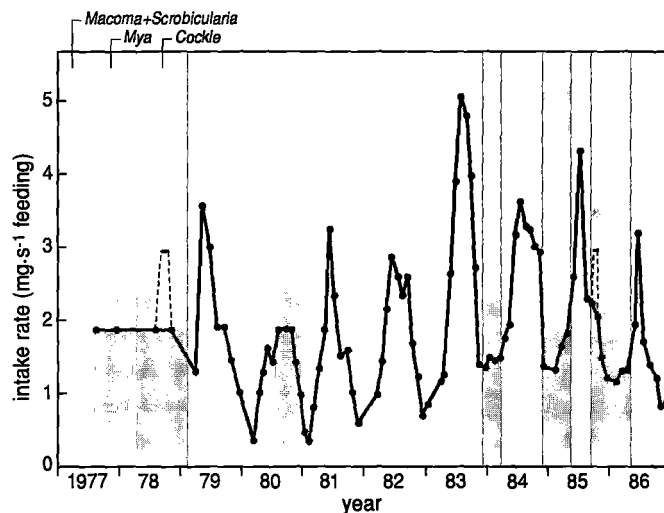


Fig. 14. Predicted intake rate when the food supply consists of Cockles, *Scrobicularia*, *Macoma*, *Mya* and Mussels, assuming that the birds take the prey providing the highest intake rate; based on Figs. 8D, 9D, 10D and 13; for *Mya* see text. The predicted prey selection is indicated. Mussels should never be selected.

(Fig. 10B) also suggested that these alternative prey were either not, or hardly ever, taken.

(2) After the growing season of 1978, *Mya* lived beyond the reach of Oystercatchers and the birds were expected to feed on Cockles. Extensive observations of Hulsman (unpubl.) between March and November 1978 showed that the Oystercatchers did indeed take Cockles. The birds achieved an intake rate of 1.49 mg s^{-1} (Zwarts *et al.* 1996b), which was close to prediction.

(3) There was a mass mortality of the Cockles in late autumn 1978 and none was still alive after the severe winter of 1978/1979. Therefore, only *Scrobicularia* and *Macoma* were left as prey. Since the depth distribution was not measured, the estimations of the predicted intake rate are rough. Oystercatchers observed in March 1979 fed on *Scrobicularia*, even though *Macoma* was calculated to yield a higher intake rate. They took small specimens (29 mm long weighing only 94 mg) which they took from great depths at a low intake rate of 1.29 mg s^{-1} (Zwarts *et al.* 1996b). The birds took in May mainly *Macoma*, achieving a rather high intake rate of 2.09 mg s^{-1} (Huls-

cher 1982; Zwarts *et al.* 1996b). The prey selection and intake rate was studied in detail between July and October 1979 by Blomert *et al.* (1983). In July, the birds took *Scrobicularia* and *Macoma*, but later in the season the proportion of *Scrobicularia* increased; again this was against prediction that they should have switched increasingly to *Macoma*. The intake rate of birds feeding on both prey combined, was 1.84 and 1.92 mg s^{-1} in July and August, respectively and decreased to 1.54 in September and 1.02 mg s^{-1} in October. The last data were collected on the few birds that remained to feed around the tower, since the majority of the birds moved 0.5 km to the NE., just outside the study area, where they started to feed on small Cockles some months old. There had also been some cockle spatfall in the Nes area (Fig. 8A), but the Cockles had grown larger at the lower-level and less muddy tidal flats which the birds started to exploit: the Cockles there were 10 mm, instead of 5 mm such as in the Nes area (Wanink & Zwarts 1993). However, even *Cerastoderma* of 10 mm delivered an extremely low intake rate (Fig. 7), so it is certain that 1979/1980

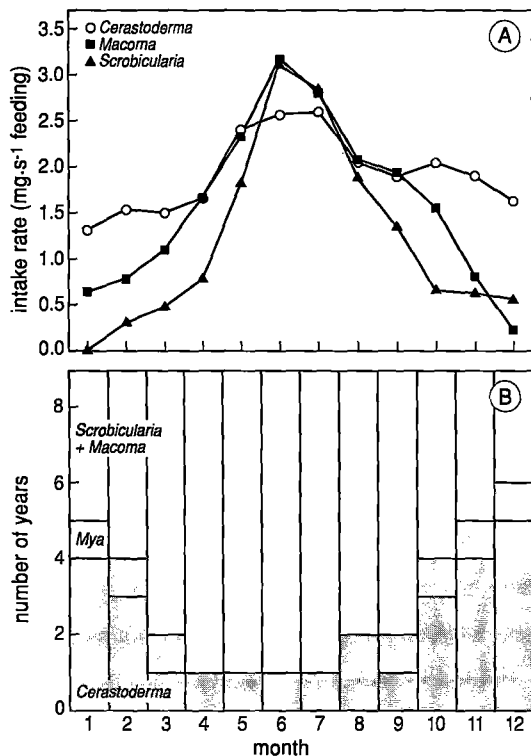


Fig. 15. Seasonal variation in (A) the predicted intake rate of Oystercatchers feeding on Cockles, *Scrobicularia* or *Macoma* averaged over the years when the prey were present and (B) the predicted diet during nine years (from data shown in Fig. 14).

was a very meagre period for the Oystercatchers remaining in the study area. Summarizing, the 1979 measurements of the intake rate agreed with the predictions: the intake rate was low in late winter, high in summer and decreasing in autumn. In contrast, predicting whether the birds should select either *Macoma* or *Scrobicularia* proved impossible, providing further arguments in favour of lumping these two prey species.

(4) A year later, in the autumn of 1980, the Oystercatchers preyed upon *Mya* (Zwarts & Wanink 1984) as predicted.

In conclusion, when we lump *Scrobicularia* and *Macoma*, all measurements on intake rate and prey selection were in agreement with the predictions (Fig. 14).

Seasonal variation in intake rate and prey selection

In all prey species there was a seasonal variation in the predicted intake rate, particularly in birds feeding on *Scrobicularia* (Fig. 9D) or *Macoma* (Fig. 10D). The intake rate of cockle-eating Oystercatchers was also predicted to be higher in summer than in winter (Fig. 8D), but the seasonal variation was not as large as in the two deep-living bivalve species (Fig. 15A). The explanation for this difference was that the seasonal variation in burying depth of the deep-living bivalves made them very unattractive to feed on in winter, because the majority of prey were inaccessible to the probing bird, and if the prey were accessible, they were hardly profitable (Zwarts *et al.* 1996b). In contrast, Cockles remained living at, or just beneath, the surface for the entire year, so that the accessible fraction did not vary seasonally.

Since the seasonal amplitude in intake rate differed so much between the prey species, Oystercatchers achieved the highest intake rate when they took the buried prey, *Scrobicularia* and *Macoma*, in summer and Cockles in winter (Fig. 15B). In this figure we lumped *Scrobicularia* and *Macoma* because, as explained before, we could not predict accurately enough which of the two species should be taken.

Annual variation in bird density, intake rate, prey selection and food supply

Although the number of Oystercatchers present in the study area varied seasonally, a close look at Fig. 6 reveals that, in some years, the monthly numbers were systematically lower than in other years. To analyse whether these year-to-year variations were due to variation in the food supply, we examined the data from December. There was a gradual decrease in the total winter biomass of the prey species combined over the years, but the annual fluctuations were large, varying between 40 and 100 g m⁻² during ten years (Fig. 16A). After subtraction of the biomass of prey either too small or too deep to be taken, the biomass harvestable for Oystercatchers appeared to differ even more, being extremely low in 1979-

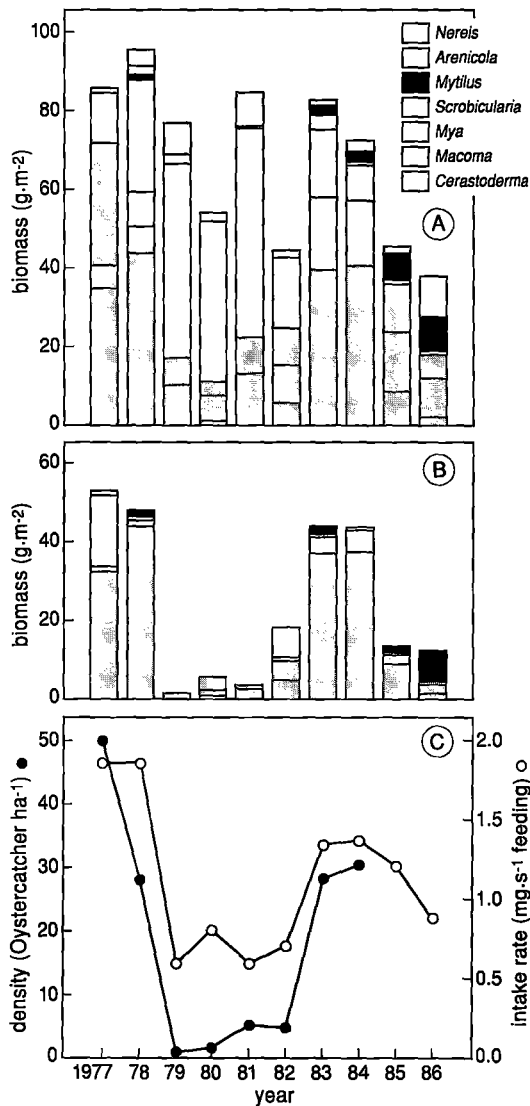


Fig. 16. Variation in (A) total biomass, (B) harvestable biomass, (C) the average bird density and predicted intake rate in December. Harvestable biomass is defined as the summed biomass, excluding Cockles < 10 mm long, *Scrobicularia* < 13 mm long or living > 6 cm deep, *Macoma* < 11 mm long or living > 4 cm deep, *Mya* < 17 mm or living > 6 cm deep, and Mussels < 25 mm. Original data are given in Figs. 8A, 9A, 10A and 12 for biomass values, Fig. 14 for predicted intake rates and Fig. 6A for bird densities; no bird counts are available for December 1985 and 1986.

1982 (Fig. 16B). In the first three of these years, *Scrobicularia* contributed about 3/4 to the total biomass, but this part of the food supply was largely not accessible to Oystercatchers. The variation in wader density was even larger, being less than 3 Oystercatchers ha⁻¹ in the three years when *Scrobicularia* was the dominant food supply and more than 25 birds ha⁻¹ in four years when the prey biomass of the Cockles reached high values. The predicted intake rate was clearly below the critical lower acceptance level of 1 mg s⁻¹ in the four poor winters in succession, 1979-1982.

Comparing elimination of biomass and predation pressure

The average total predation pressure by Oystercatchers was estimated at 12 g m⁻² year⁻¹, but due to the very large variation in density (Fig. 6A), the predation pressure varied considerably between and within years. Assuming that the birds only took the prey which would have given the highest intake rate (Fig. 14), the predation pressure on the different prey species could be compared to the total biomass that was actually eliminated (Fig. 17). Note that the production by elimination of the small prey was usually very low, except for first year Cockles in 1985 and 1986, and *Macoma* and *Mya* in the first year after the spatfall 1979.

Cockles The prediction was that Oystercatchers would have fed on Cockles in 1978 and in the winters of 1984, 1985 and 1986 (Fig. 17E). Indeed, these were periods of high losses of cockle biomass (Fig. 17A). Oystercatchers were not responsible for the sometimes considerable summer mortality. Taking all data together, Oystercatchers would have consumed 6.3 g Cockles m⁻² year⁻¹, whereas the total annual elimination of cockle biomass was estimated at 27.1 g m⁻², of which 24.5 g m⁻² was contributed by specimens ≥ 10 mm.

There are two main reasons why the mortality of Cockles was so erratic. First, many Cockles died in the frost periods of February 1979, 1985 and 1986: 26% of the average annual loss of biomass through mortality took place in these peri-

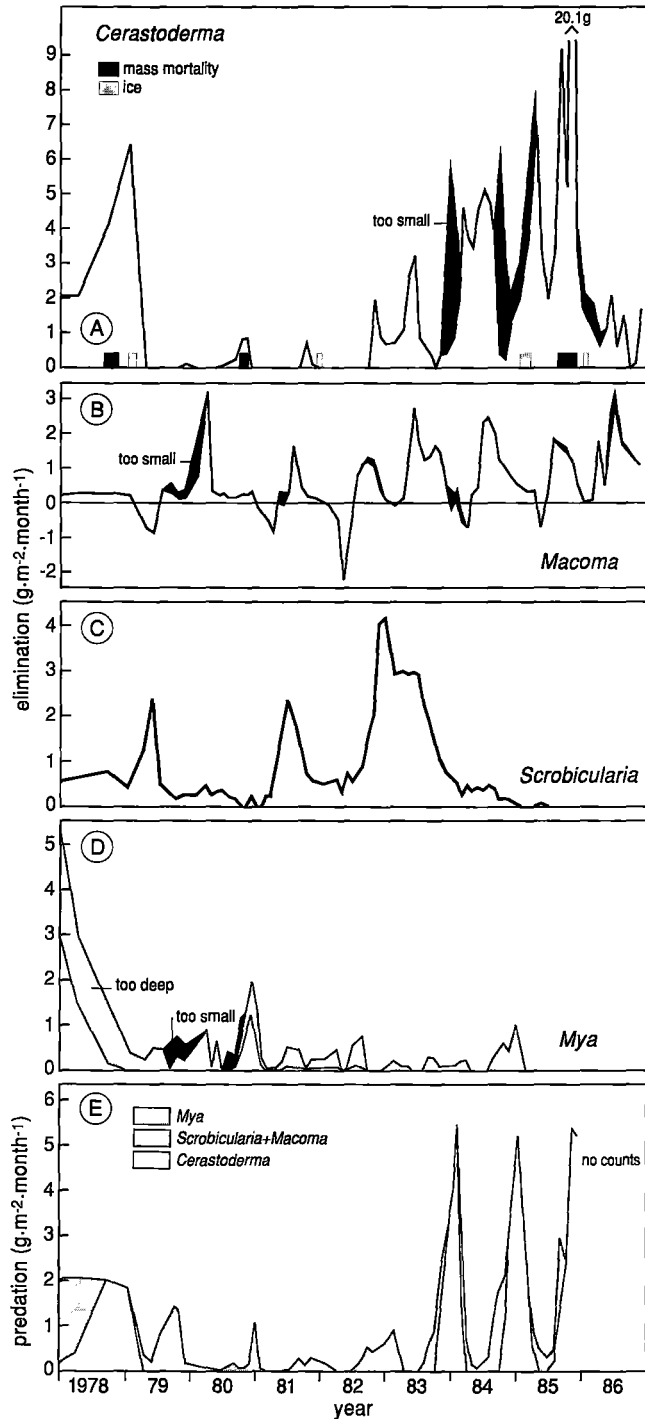


Fig. 17. Elimination of biomass for (A)-(D) four different bivalve species ($\text{g m}^{-2} \text{ month}^{-1}$) and (E) calculated consumption ($\text{g m}^{-2} \text{ month}^{-1}$) by Oystercatchers assuming that all birds foraged each month only on the prey species that delivered the highest intake rate (Fig. 14). The elimination, summed for different cohorts, has been defined as the product of average prey weight and the numbers that disappeared ($\text{m}^{-2} \text{ month}^{-1}$). The apparent negative elimination in *Macoma* is due to resettlement by which the density rose from March to May. The elimination of the small size classes, which would have been ignored by Oystercatchers, and the large *Mya*, that would have been out of reach of the Oystercatcher's bill, are marked separately. The total bird consumption is the product of Oystercatcher density (Fig. 6A) and consumption per bird (varying between 36 g day^{-1} in summer, and depending on ambient temperature, increasing to 50 g on cold winter days).

ods. Second, for unknown reasons, there was mass mortality in October 1978, 1980 and 1985, when there were so many dying and gaping Cockles on the surface that the mudflats, over many km², gave off a nasty smell of decay. In October 1978 and 1985 about 15 and 20 g m⁻² respectively disappeared within a couple of weeks. Oystercatchers and other waders were observed to eat from the gaping Cockles, but the majority of the flesh disappeared without being eaten by birds.

Scrobicularia* and *Macoma A comparison between the elimination of biomass and predation pressure was more complicated in *Scrobicularia* and *Macoma* than in Cockles. First, the predictions for the intake rate of birds feeding on one of these prey species, or on both combined, usually did not differ much from each other (Fig. 4). Hence, it made little sense to distinguish when the birds should take one of both, or both, species. The second problem was that the elimination of *Macoma* was negative in March-May (Fig. 17B), which was due to the increase, instead of the decrease, of the densities of the cohorts in spring. Since we had no independent estimate of the immigrated biomass, we could give no estimate of

the eliminated biomass for the period March-May. It is clear from Fig. 17B, however, that more biomass was eliminated in summer than in winter. Oystercatchers were predicted to take *Macoma* in summer (Fig. 17E), but the predation pressure was usually only a fraction of the total amount actually eliminated (Fig. 17B).

The elimination of biomass in *Scrobicularia* was also higher in summer than in winter, except for the winter of 1982/1983 (Fig. 17C), when the population started to decline at a fast rate (Fig. 9B). Oystercatchers were predicted to take *Scrobicularia* in summer, and also in the winter of 1982/1983, when *Scrobicularia* did not return to the safe, deep winter depth which makes them for Oystercatchers hardly worthwhile exploiting. The calculated predation pressure by Oystercatchers in this winter was, however, not high enough to explain the huge loss of biomass.

Mya The predation pressure of Oystercatchers on *Mya* was restricted to second year clams, because after the first growing season, the prey were still too small to be exploited, while after the third growing season, they were buried too deeply. Oystercatchers exerted a heavy predation pres-

Table 1. Average annual consumption by Oystercatcher in the Nes area (g m⁻²), compared to the average annual production, due to the annual elimination of biomass (g m⁻²) for all cohorts combined ('total'), for the size classes large enough to be profitable for Oystercatchers (excluding Cockles < 10 mm long, *Scrobicularia* < 13 mm long, *Macoma* < 11 mm long, *Mya* < 17 mm and Mussels < 25 mm), and for prey being exploitable i.e. beside profitable and accessible (*Mya* < 45 mm; *Scrobicularia* in winters when all specimens live > 6 cm deep), also not dying in mass starvation during extremely short periods, as occurred in Cockles. The calculations refer to the period August 1977 to December 1985.

	elimination			consumption
	total	profitable	exploitable	
<i>Cerastoderma</i>	25.3	23.1	16.6	6.3
<i>Scrobicularia</i>	8.8	8.8	8.2	1.9
<i>Macoma</i>	6.8	6.4	6.4	1.6
<i>Mya</i>	12.9	12.3	3.0	2.2
<i>Mytilus</i>	2.4	0.4	0.4	0.0
Total	56.2	51.0	34.6	12.0

Table 2. As Table 1, but calculated for 15 August-15 March.

	elimination			consumption
	total	profitable	exploitable	
<i>Cerastoderma</i>	17.0	15.4	8.9	5.7
<i>Scrobicularia</i>	4.7	4.7	4.1	1.6
<i>Macoma</i>	5.1	3.4	3.4	1.2
<i>Mya</i>	9.3	9.0	2.8	2.0
<i>Mytilus</i>	1.2	0.3	0.3	0.0
Total	37.3	32.8	19.5	10.5

sure on *Mya* in the intervening period. The estimated predation was close to the total of eliminated biomass (Fig. 17D).

Species combined The Cockle was the major prey for the Oystercatchers in our area. More than half of their average annual consumption consisted of cockle flesh. Cockles also attributed about half of the total elimination summed over the five bivalve species (Table 1). Oystercatchers took 25% of the total elimination by Cockles and *Macoma*, 22% of *Mya*, 17% of *Scrobicularia* and 0% in Mussels. These percentages refer to the entire year, but Oystercatchers were hardly present in summer. To investigate to what degree the elimination of winter biomass was due to oystercatcher predation, the data were divided into two periods: 15 August-15 March ('winter') and the remaining five months ('summer'). Oystercatchers took during the seven winter months seven times as much food as during the five summer months, respectively 1.5 and 10.5 g year⁻¹. The total elimination was in the winter twice as high as during the summer, 19 and 37.3 g year⁻¹ respectively (Table 2). Hence, Oystercatchers took only 8% of the elimination in summer, against 28% of the winter elimination.

These calculations show that the predation pressure by Oystercatcher was not a very important cause of mortality for these bivalve prey, but the risk of a bivalve being taken by Oystercatchers varied enormously between different categories.

First, Oystercatchers ignore the small, unprofitable prey. The elimination of these prey was relatively small, except in Mussels (Tables 1 & 2). It was more important to take into account the elimination by prey living out of reach of the bill. All *Mya* > 45 mm were inaccessible for Oystercatchers, as a result of which only 1/4 of the elimination of *Mya* could be harvested by Oystercatchers. All *Scrobicularia* were also out of reach of the bill during most of the winters. This reduced the annual harvestable elimination from 8.8 g to 8.2 g. Gaping Cockles during short periods of mass mortality are an example of a food resource that, although harvestable, could not be fully utilized. On an annual base, 4.7 and 4.6 g Cockle biomass disappeared during mass starvation in October and during ice periods in winter, respectively. Assuming that Oystercatchers took in these periods not more than what they needed to meet their daily energy demand, they consumed 1.3 and 1.5 g of these amounts, respectively. Hence, 3.4 g during the October starvation periods and 3.1 g during the cold spells were, for the Oystercatchers, wasted. This reduced the annual elimination of profitable Cockles from 23.1 to 16.6 g. The elimination of prey after the above-mentioned restrictions was called the elimination of prey *exploitable* by Oystercatchers. The percentage of the exploitable elimination actually taken by Oystercatchers varied between the prey species, being extremely high in *Mya* and Cockles and low in the other species (Table 1). In the win-

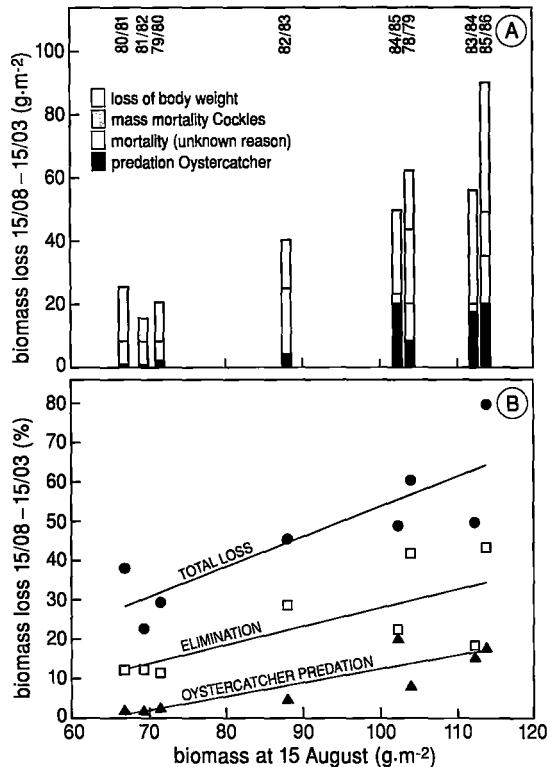


Fig. 18. Loss of biomass by Cockles, *Scrobicularia*, *Macoma*, *Mya* and Mussels between 15 August and 15 March of the next year in relation to the total biomass present at 15 August. The loss of biomass is due to a decrease in the body condition and to mortality, the latter given separately for Oystercatcher predation, mass mortality in Cockles (see text) and other causes. Panel (A) gives the absolute loss of biomass (g m^{-2}), and (B) the loss as percentage of the initial biomass.

ter period, 3/4 of the eliminated *Mya* biomass and 2/3 of the cockle biomass could be attributed to oystercatcher predation (Table 2).

Year-to-year variation The average winter predation by Oystercatchers amounted to 10.5 g m^{-2} (Table 2), but it was only 1.3 g m^{-2} in 1981/1982 and 23.2 g m^{-2} in 1985/1986, respectively 0.12 and $2.2 \times$ the long-term average. The variation in the total elimination during the seven winter months was less extreme, being between 7.3 g m^{-2} in 1979/1980 and 66.9 in 1985/1986. The total loss

of biomass from August to March was larger than the elimination, due to the loss of condition in the individual bivalves, which varied between 15.9 and 89.9 g m^{-2} . Figure 18 plots the total loss of biomass during the seven winter months in relation to the biomass on 15 August. Four types of biomass loss were distinguished. First, loss of body weight in the macrozoobenthos still alive on 15 March, and three types of elimination of biomass due to mortality: oystercatcher predation, mass starvation of Cockles not consumed by Oystercatchers, and other sources. The higher the biomass, the higher the loss (Fig. 18A). The macrozoobenthos lost about 20% of their body weight between 15 August and 15 March, and this fraction was independent of the initial density. In contrast, the total elimination was highly positively density dependent (Fig. 18B). This was completely due to the response of the Oystercatchers, because the elimination of prey which was not due to oystercatcher predation only weakly increased with density from 10 to 15%. In contrast, Oystercatchers consumed only some per cent when the food supply was poor and this increased to 17% in winters with a rich food supply.

DISCUSSION

Model assumptions

In this paper we predicted the feeding behaviour of the Oystercatcher on the basis of measurements on the prey. This required several simplifying assumptions. Before we discuss our results in some detail, it seems prudent to investigate some limitations in our approach.

Spatial variation In our model calculations we ignored the spatial variation in prey density. The samples of the macrozoobenthos in the Nes area were taken at 73 sites and we know from this that *Macoma* and *Scrobicularia* on the rich sites were twice as common as on the poor sites and that the ratio was even three in Cockles and *Mya* (Zwarts 1988). In principle, it would have been possible to repeat all calculations done for the Nes area as a

whole for the 73 sites individually. This would not have changed the average trends shown for prey choice and intake rate. However, whereas we predicted that all birds would everywhere have switched at the same moment from one prey to the other, the timing would have been different between sites, so that more gradual changes would be expected for the Nes area as a whole.

Feeding specializations First, we assumed that all birds selected one prey species, with the exception that they could take a mixture of *Scrobicularia* and *Macoma*. This was certainly not the only exception, because birds also took Cockles and *Macoma*. This was only observed, however, in summer when *Macoma* lived close to the surface at the same depth as Cockles (Hulscher 1976, Hulsman unpubl.). Consequently, we were probably wrong in predicting that birds would have taken only *Macoma* in summer 1984 and 1985 and ignored Cockles.

Another simplification was that all birds should perform the same prey selection, whereas direct observations also showed that this was not true. For instance, one female took only Ragworms among the 29 other colour-banded birds feeding in the Nes area on *Scrobicularia* and *Macoma* (Blomert *et al.* 1983). Bill length has a large effect on the prey selection. The last birds feeding on *Scrobicularia* in October 1979 and the first ones in early spring 1980 were all females with long bills, because the prey then lived out of reach of the shorter bill of the males. Also the depletion of the second year *Mya* in autumn 1980 was due to predation by females. The bill length of the birds feeding on *Mya* was, on average 1 cm longer than for the birds feeding at the same time on a cockle bed, just north of the study area. Hence, it is to be expected that the seasonal variation in intake rate and harvestable food supply, of which the averages have been given in this paper, were larger for males and smaller for females.

Interference Our predictions of the intake rate of the birds only depended on the characteristics of the food supply, and not on the feeding density of

the birds. Thus, we ignored the possibility that high feeding densities may have depressed the intake rates of some or all of the birds. Yet, there is a considerable amount of field evidence for such interference in Oystercatchers (Koene 1978, Zwarts & Drent 1981, Ens & Goss-Custard 1984, Goss-Custard *et al.* 1984, Goss-Custard & Durell 1987, Boates 1988, Cayford 1988). However, as the review by Ens & Cayford (1996) shows, strong evidence comes exclusively from Oystercatchers feeding on Mussels. Ens & Cayford (1996) also conclude that interference may ultimately be due to food stealing, which triggers adaptive responses in the individuals that are most susceptible to such kleptoparasitism, at the cost of a reduced capture rate. Food stealing occurs primarily for prey that are profitable to steal, i.e. prey that are large and require a long time to open. None of the prey in our study area reached the sizes nor needed the handling times that would bring them on a par with the Mussels that are so regularly kleptoparasitized. It follows that, in most years, interference may have been minimal and was therefore safely ignored.

Estimating parameters The estimates of the intake rate of birds feeding on *Scrobicularia* and *Macoma* were based on three variables: density, weight and burying depth of the prey. The estimates for birds eating Cockles were based on two variables, density and weight of the prey, whereas the predictions for birds consuming second year *Mya* were based on prey density and for Mussel-eaters on prey weight. The predictions for the five prey species were all based on prey variables, but there is one important difference. The predictions for birds eating *Scrobicularia* and *Macoma* were based on the principles of the random touch model and the optimal prey choice model, whereas the other three extrapolated intake rates from prey density and/or prey weight. Although refinements of the predictions are still desirable, the models do seem to give realistic estimates.

Other predators The Oystercatcher was by far the most important bird predator on the benthic

food supply in our study area. The oystercatcher density was 8.4 birds ha⁻¹, averaged over the entire year. All other bird species together foraged at an average annual density of 9.3. birds ha⁻¹, of which only four species reached a density above 1 bird ha⁻¹: Curlew *Numenius arquata* 2.6, Redshank *Tringa totanus* 1.7, Black-headed Gull *Larus ridibundus* 1.3 and Dunlin *Calidris alpina* 1.1 birds ha⁻¹ year⁻¹. Oystercatchers took 12 g m⁻² year⁻¹, but all the other bird species together only 10.3 g m⁻² year⁻¹, with three species taking more than 1 g m⁻² year⁻¹: Curlew 4.8, Herring Gull *Larus argentatus* 1.4 and Black-headed Gull 1.1 g m⁻² year⁻¹.

There was hardly any overlap in the choice of the prey species by Oystercatchers and the other species. In the few cases that the Oystercatcher and other bird species fed on the same prey species, different size classes were selected: (1) Herring Gulls took Mussels in 1985 that were still too small to be taken by Oystercatchers (Zwarts unpubl.); (2) Knot *Calidris canutus* selected medium-sized *Macoma* hardly taken by Oystercatchers (Zwarts & Blomert 1992); (3) Oystercatchers took second year *Mya* still ignored by Curlews (Zwarts & Wanink 1984). Hence, although different bird predators successively contribute to the decline of the prey cohorts, there was no reason to take into account the predation pressure of the other bird species when we compared oystercatcher predation to the elimination of the prey biomass harvestable by Oystercatchers.

Seasonal variation in intake rate and prey selection

The intake rate of Oystercatchers varied seasonally, being high in summer and low in winter. This trend was more pronounced in the burying prey species, *Scrobicularia* and *Macoma*, than in the surface prey, the Cockle (Fig. 15A). The seasonal variation in intake rate was even smaller in Mussel-eating Oystercatchers (Goss-Custard & Durell 1987; Fig. 17 in Zwarts *et al.* 1996b). The explanation is that, due to the variation in burying depth, the encounter rate with burying prey was reduced in winter. There was no such a difference

in surface prey, although birds stabbing the bill between the valves may more often encounter closed bivalves in winter than in the summer, when Cockles and Mussels feed more often themselves. This may explain why the seasonal variation in intake rate in Mussel-eating Oystercatchers was larger in stabbers than in hammerers (Goss-Custard & Durell 1987).

According to the predictions (Fig. 15B) and direct observations (see text), burying prey were selected in summer and only taken in winter when there were no surface prey. Several other studies provide similar evidence for such a seasonal shift in the diet of the Oystercatcher. Bunschoke *et al.* (1996) and Hulscher *et al.* (1996) show that *Macoma* was the main prey on Schiermonnikoog in spring and completely disappeared from the Oystercatcher's diet in late summer. That *Macoma* is indeed a summer prey, hardly taken by Oystercatchers in winter, is also evident from the work of Beukema (1993a) on the Balgzand in the western part of the Wadden Sea. He found that the monthly mortality of *Macoma* between mid-March and mid-August (five months) was, on average, three times as large as in the remaining seven winter months (Beukema 1993a: Fig. 6). Bird counts indicated that the monthly predation pressure by Oystercatchers was only 1/4 the level in the five summer months compared to the seven winter months (Beukema 1993a: Fig. 4). Assuming that the mortality of adult *Macoma* was completely due to oystercatcher predation, it follows that an individual Oystercatcher took *Macoma* in spring and summer 12 times as often as in autumn and winter. The significance of *Macoma* as autumn + winter prey for Oystercatchers must be still lower, because large numbers of Knot winter on the Balgzand (Zegers & Kwint 1992), and this species must be responsible for a major part of the mortality in autumn and winter.

Another source of information on the seasonal variation in prey selection may be derived from the many field studies assembled from different areas in NW. Europe (Zwarts *et al.* 1996b & c). Not one of the 276 studies from September to March refer to *Macoma*-eating Oystercatchers, but

77 of 311 studies during the four summer months. This suggests again that *Macoma* disappears from the diet in late summer.

Winter predation by Oystercatchers of *Scrobicularia* must be impossible during the majority of the winters because the prey live too deep. There are, however, two winter studies of Oystercatchers feeding on *Scrobicularia*. In one case, this concerned birds on Schiermonnikoog feeding on relatively small prey 20 mm long, of which the majority lived just within reach of the bill (Habe-kotté 1987). The other study was done by Boates & Goss-Custard (1989) in the Exe estuary. Although the majority of the birds in the Exe are found on the mussel beds, some birds feed each winter on *Scrobicularia*. Perhaps this prey on the Exe in winter do not live as deeply buried as in the Wadden Sea. If so, the seasonal variation in intake rate would not be expected to be as large as in the more northern tidal flats where the accessible fraction of *Scrobicularia* is much lower in winter than in summer (Zwarts & Wanink 1993).

Seasonal variation in bird density

Despite the large variation in the number of Oystercatchers feeding in the area from year to year, the trends were similar each year (Fig. 6A). The seasonal course of the change in numbers in the study area (Fig. 19A) deviated from those elsewhere in the eastern part of the Wadden Sea, where the Oystercatchers decreased from October onwards. As an example, Fig. 19B shows the monthly averages for nearby Schiermonnikoog, given separately for the eastern and western part of the island.

How can we explain why our study area attracted so many Oystercatchers in mid-winter? The simplest explanation is that birds leave a feeding site if they can achieve a higher intake rate elsewhere. If so, birds feeding in summer on mudflats with buried bivalves and Ragworms as the only prey would leave these areas in late summer to move to mussel and cockle beds (Fig. 15A). Since cockle and mussel beds are usually found on the lower part of the shore, and *Macoma* and Ragworms occur on mudflats often situated

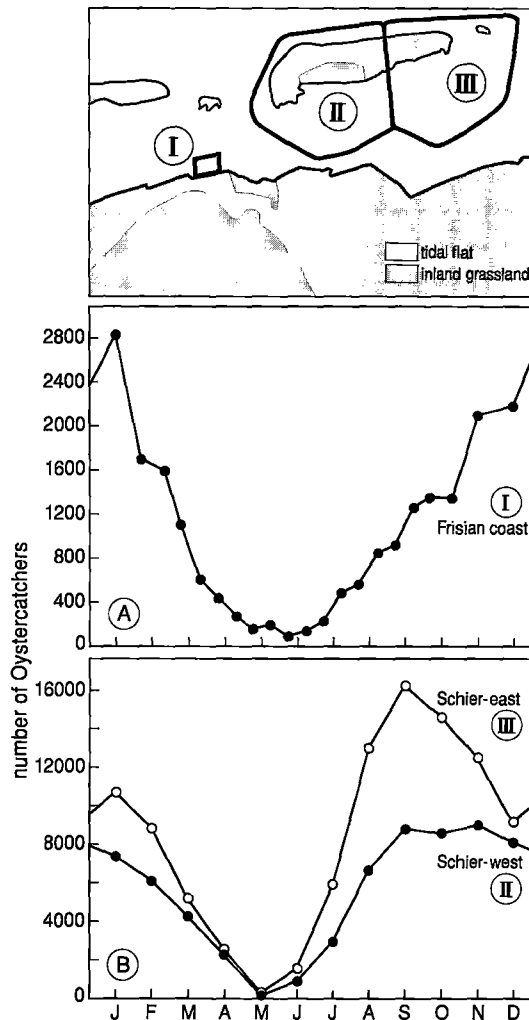


Fig. 19. Seasonal variation in the number of Oystercatcher feeding along (A) the Frisian coast, (B) the west and east side of Schiermonnikoog. The map indicates the three tidal feeding areas and adjacent grassland where the birds may feed at high tide. The birds on Schiermonnikoog were counted on roosts at high water, but the birds along the Frisian coast on 100 ha of tidal flats at low tide (see Fig. 1).

above mean sea level, the high shore is in summer a relatively more important feeding area than in winter. However, it is unlikely that this explains why our study area attracted so many Oystercatchers in winter. The tidal flats in our study area

consisted of mud and the greater part were situated above mean sea level, so fewer birds would be expected to remain to feed in winter. In fact, the reverse was found (Fig. 19). Possibly, the tendency of Oystercatchers to concentrate from October onwards on tidal flats adjacent to inland feeding areas (Fig. 19) explains this unexpected finding. This would explain the relatively low numbers remaining to winter on the eastern part of Schiermonnikoog, where there is no grassland, and the relatively high numbers wintering along the Frisian coast and on western Schiermonnikoog where grassland is available. The bird census data of the Dutch Wadden Sea (Zegers & Kwint 1992) also revealed that the number of Oystercatchers on Vlieland, an island without inland feeding areas, is in winter 47% lower than in late summer, whereas the winter numbers along the mainland coast of the provinces Noord-Holland, Friesland and Groningen, with extensive grasslands next to the sea wall, are 28% higher, on average, than in late summer; this calculation is based upon a comparison between the January counts from the four mild winters 1981, 1983, 1989 and 1991, and preceding counts from August or September. As shown elsewhere (Zwarts *et al.* 1996e), the daily variation in exposure time of the low water feeding areas in the Wadden Sea is much larger in winter than in summer. Consequently, the ability to compensate at high tide for short feeding periods is more important in the winter half of the year than in the summer half. This opportunity is apparently important enough for Oystercatchers to move to parts of the Wadden Sea where compensatory feeding on grassland is available.

Response of Oystercatchers to variation in harvestable prey biomass

The Nes area was certainly not a marginal feeding area. The biomass of the food supply and the feeding density of Oystercatchers were, on average, respectively, 4 and 10 times as high as the average for the tidal flats of the Dutch Wadden Sea as a whole (Beukema 1976, Zwarts & Wanink 1993). The bird density fluctuated in accordance

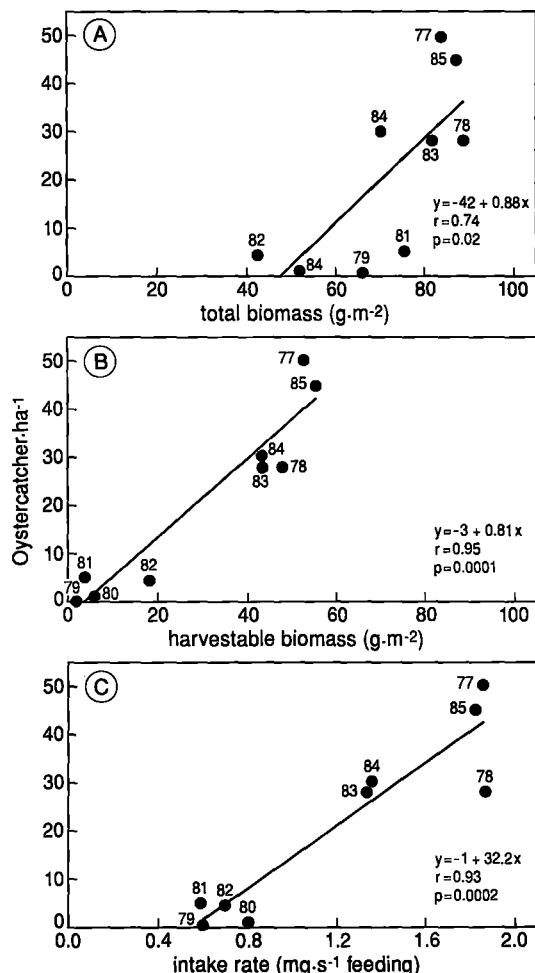


Fig. 20. Average feeding density in December (Oystercatcher ha⁻¹) as a function of (A) total biomass, (B) harvestable biomass and (C) predicted intake rate (mg s⁻¹ feeding); same data as Fig. 16. Since no bird counts were available for December 1985, we compared for that year food supply and bird density at the end of October. Bird density in December was, on average, 1.5 times as high as in October (Fig. 19); hence this multiplying factor was used to estimate the density in 1985.

with the food supply, as shown in Fig. 20A, using the December data from Fig. 16.

There is a good correlation between bird density and 'total biomass', $r = 0.74$, which is actually surprising, because total biomass is an inac-

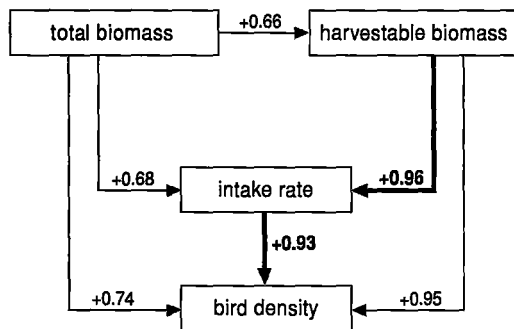


Fig. 21. Dependence of bird density on food supply and predicted intake rate. The correlations are shown along the arrows; same data as Fig. 20.

curate measure of the food supply, due to the highly variable fraction that is unharvestable. Because of this, we expect a better correlation between bird density and the biomass of the prey that is both profitable as well as available, and this indeed appeared to be the case, $r = 0.95$ (Fig. 20B). Very likely, this response is caused by the birds acting on the intake rates that they achieve (Fig. 20C). Figure 21 summarizes the causal relationships, as we see them. Two relationships are essential: bird density depends on intake rate, which in turn rate depends on the harvestable biomass. The high correlation between intake rate and harvestable biomass is not surprising, because the intake rate has been predicted from the density, size and burying depth of the prey, three variables which all contribute to harvestable biomass. It is already obvious, however, that many wintering Oystercatchers only occur in the study area when older Cockles or second year *Mya* are abundant and the intake rate is $> 1.2 \text{ mg s}^{-1}$. In contrast, when the wintering birds have to feed on *Scrobicularia* or *Macoma*, hardly any birds remain to feed in the area because of the extremely low intake rate.

The correlations shown alongside the arrows in Fig. 21, are based upon linear regressions. However, instead of a linear relationship between bird density and intake rate (Fig. 20C), we rather

expect a J- or S-curve. No birds should ever feed in the area when the intake is $< 1 \text{ mg s}^{-1}$, as we confirmed in this study (Fig. 20C). What will happen above this level will also depend on what the birds can obtain elsewhere. In other words, even at a rather high intake rate, few birds may be concentrated in the area if the situation elsewhere is even better. Once intake rates are so high that the area ranks among the best in the region, the bird density will increase until all 'available' birds have been attracted to the area, after which the density will level off at still higher intake rates because the supply of recruits dries up. How many birds are 'available' will depend on the total number of birds in the region and the size of the region, which will depend on the size of the home range of the birds. With extreme site fidelity, home ranges and therefore the region will be very small, so that the pool of 'available' birds is quickly depleted and very little relationship between bird density and food supply is to be expected when years are compared. If, on the other hand, home ranges are large and variation in food supply between years quite extreme, a high correlation between bird density and intake rate can occur, as was probably the case in our study. The sightings of the colour-banded birds certainly proved that movements of 1 to 3 km regularly occurred, although individuals could stay for months, and some even for years, on the same spot of less than 0.5 ha. The site fidelity of the Oystercatchers in our study area seems intermediate between that in the Exe estuary, where the mussel beds are extremely stable and home ranges often less than 1 ha (Goss-Custard *et al.* 1982), and the estuary of the Ribble, where an exceptionally large spatfall of Cockles caused a massive influx of Oystercatchers (Sutherland 1982).

Oystercatcher in the waiting room?

When different bird species feed on the same prey, the larger ones usually take the larger size classes. Pehrsson (1976) observed this trend in seven duck species feeding on Mussels and the same was found in waders feeding on the Shore

Crab (Zwarts 1981), the fiddler crab *Uca tangeri* (Zwarts 1985), or the amphipod *Corophium volutator* (Zwarts & Wanink 1993). However, when the size selection of the Oystercatcher is compared to that of other bird species, the species seems to be an exception to this general rule because it usually takes large bivalves that are even rejected by the Herring Gull (e.g. Harris 1965) and Eider *Somateria mollissima* (e.g. Nehls 1995), bird species that weigh 2 and 4 times as much, respectively, as the Oystercatcher.

The unique ability of Oystercatchers to open large hard-shelled prey facilitates exploitation of a rich food resource that cannot be harvested by bird species that eat bivalves and other armoured prey by swallowing them whole (Hulscher 1996). Bird species that swallow bivalves whole are limited by their gape width in the sizes they can take and are forced to maintain a large stomach to crush the shells. For instance, the stomach of an Oystercatcher is, relative to body weight, half as heavy as that of a Knot, a wader species that cracks small hard-shelled prey after swallowing them (Piersma *et al.* 1993). The quick reduction in stomach size of Knot during periods that they do not need it to crack shells (Piersma *et al.* 1993) suggests a high cost to maintaining it. Thus, Oystercatchers probably do not have the ability to crack shells in their stomach, because it did not pay to maintain a heavy stomach. Hence, Oystercatchers must also open small armoured prey which they could easily have ingested whole. It

always takes them some seconds to handle even the smallest bivalve (Zwarts *et al.* 1996a & b), whereas the same prey might be handled in less than 1 s if ingested whole (Zwarts & Wanink 1993: Fig. 12). Since Oystercatchers never swallow hard-shelled prey entirely, we do not know for sure how much faster they would be able to handle these small prey. Curlews, which usually extract the flesh from the shell when they feed on *Mya*, sometimes take these prey including the shell. The extraction of flesh from a 25 mm *Mya* takes them twice as much time as clams of similar size swallowed whole. Consequently, prey swallowed whole are twice as profitable as prey from which the flesh is eaten (Zwarts & Wanink 1984).

Since Oystercatchers depend on large prey, the predictability of their food supply might decrease due to the mortality of the prey before reaching the size taken by Oystercatchers. Oystercatchers would be able to overcome this possible problem by eating these small prey themselves, but when they do, they only lower their intake rate (Fig. 1B). To investigate whether the food supply harvestable by Oystercatchers is less predictable than the total biomass, we calculated for 2 months, August and December, the variation in the total and the harvestable biomass (Table 3). The total biomass varied between 53 and 111 g m⁻² in August, with a standard deviation (*SD*) of 19.5. The annual variation in the harvestable food supply was much larger with a range from 10 to 83 g m⁻² and a *SD* of 26.6. This result may be

Table 3. Variation in food supply in August and December in the Nes area between 1977 and 1986. The *RSD*, or relative standard deviation, is the *SD* as percentage of the mean. The total biomass is summed for five bivalves (g m⁻²; the August data are shown per bivalve species in Zwarts *et al.* 1992; Fig. 16A gives the December values per year). The harvestable biomass is defined as the summed biomass, excluding Cockles < 10 mm long, *Scrobicularia* < 13 mm long or living > 6 cm deep, *Macoma* < 11 mm long or living > 4 cm deep, *Mya* < 17 mm or living in > 6 cm deep, and Mussel < 25 mm (Fig. 16B gives the December values per year).

biomass	August		December	
	mean, g m ⁻²	<i>RSD</i> , %	mean, g m ⁻²	<i>RSD</i> , %
total	73.3	26.6	63.6	30.7
harvestable	40.3	65.9	24.1	79.5

compared directly to similar data for the Knot (Zwarts *et al.* 1992: Tables 1 & 2). The variation in the food supply harvestable by Knot in August was twice as large as the variation in the total biomass, but in Oystercatcher it was even 2.5 times as large. The biomass harvestable by Oystercatchers was even still less predictable in winter: it varied between 2 and 53 g m⁻² in December.

It would be worthwhile to do the same calculations for the food supply of Oystercatchers elsewhere. It is striking, for instance, that the mussel beds in the Exe estuary (SW. England) provide Oystercatchers with a stable food supply (Goss-Custard *et al.* 1996b). In contrast to the Wadden Sea, mussel beds in the Exe do not disappear from gales and ice, such as occurs in the Wadden Sea (Dankers & Koelemaj 1989, Obert & Michaelis 1991). Moreover, since the annual recruitment of Mussels in the Exe is less erratic than in the Wadden Sea and the survival of spat strongly negatively density-dependent, the density of large Mussels does not vary much (McGrorty *et al.* 1990).

Were Oystercatchers dependent on one or two prey species in the Wadden Sea, they would not be able to survive a period longer than one to four years. The birds in our study area could only stay alive by switching regularly from one to another bivalve species and take, in total, four bivalve species during the ten years of observation (Fig. 14). Nevertheless, the intake rates would be insufficient during four years, and the birds had to move to alternative feeding areas. The high water counts showed that the total number of Oystercatchers did not decrease during these years along this part of the Frisian coast and the nearby island Engelsmanplaat (Zegers & Zwarts unpubl.). Therefore, the birds must have moved to feeding areas still within reach of the same high water roosts. Sightings of colour-banded birds showed that many of the Nes birds moved to mussel beds on the lower shore, at 1 to 4 km from the Nes area. In other words, the birds could not survive a ten year period if they restricted their feeding range to 1 km² of mudflats. However, by extending their individual feeding ranges to an area of 10-20 km², they could probably find enough food.

The large majority of Oystercatchers in the Wadden Sea depend in winter on Cockles and Mussels. The year-to-year variation in the occurrence of both prey is very large (Beukema *et al.* 1993). Unfortunately for their predators, recruitment and mortality of both species is related to the winter temperature, by which the fluctuations of the food stock of both species tend to be synchronized (Beukema *et al.* 1993). Hence, Oystercatchers wintering in the Wadden Sea must deal with a varying, and sometimes low, food supply.

Are Oystercatchers limited by their food supply?

Several prey species contribute to the benthic production, and since each bird species restricts its diet to a limited number of prey species and size classes, each bird species harvests only a part of the total production. Oystercatchers restrict their diet mainly to bivalves. They consumed in the Nes area yearly 12 g m⁻², on average, or 21% of the total yearly elimination of the five bivalve species combined (Table 1). The predation pressure by Oystercatchers on their prey has already often been measured, although usually not as fraction of the annual prey elimination, but as fraction of the total biomass being removed over the winter (see recent reviews by Meire 1993 and Goss-Custard *et al.* 1996b). Oystercatchers are able to remove between 10 and 80% of their prey in a winter, but in most studies it is 20 to 40%. Also this study reveals a large variation in the predation pressure between prey species (Tables 1 & 2), and between years (Fig. 18). In both cases, the variation in the predation pressure may be attributed to the intake rate. Oystercatchers exert a high predation pressure on prey such as Cockles and second year *Mya* which can be consumed with a high intake rate, whereas *Macoma* and *Scrobicularia* are hardly taken in winter due to their low intake rate. For the same reason, the predation pressure as fraction of the total biomass of the five prey species increases with the intake rate: $r = +0.87$ when the winter predation as per cent of the biomass (Fig. 18B) is plotted against intake rate in winter (Fig. 20C).

From the point of view of the predators, it is not in the first place the size of the harvestable food supply, or its production, that actually counts, but whether they can meet their daily energy requirements. Thus to answer the question: 'is there enough food for the predators, or could they have taken more?', it makes sense to reformulate this as: 'how often is the harvestable food supply too low to yield an intake rate sufficient to get the necessary amount of food within the restricted time the tidal feeding areas are exposed?'; see Goss-Custard *et al.* (1994, 1996e) for an extensive discussion why carrying capacity may be reached before the birds have depleted their food supply.

Oystercatchers deposit body reserves as an insurance against periods with too low a daily consumption. Their energy buffer is large enough to survive a starvation period of at least some days (Hulscher 1990, Zwarts *et al.* 1996d). Therefore, a possible short-term variation in the daily consumption due to adverse weather conditions does not affect the survival of Oystercatchers. However, if the daily consumption is systematically less than, for instance, half what the Oystercatchers need, they will die within two to three weeks. Hence, the birds will do all to attain the intake rate of at least 1 mg s^{-1} during feeding.

The optimal diet model assumes that, not only in critical, but in all, circumstances, the birds will attempt to maximize their intake rate and select the prey species, and the feeding area, that yield the highest intake rate. Hence, predators are creaming off the most profitable fraction of their food supply and, after depletion, switch to lower-ranking prey initially ignored. This may be prey that are less profitable since they are of smaller size (Meire *et al.* 1994, Zwarts *et al.* 1996b, and sources given there), but also specimens of similar size living more deeply buried below the mud surface (Fig. 5; Wanink & Zwarts 1985) or armoured prey with a thicker shell (Sutherland & Ens 1987, Meire 1996, Ens & Alting 1996). Thus, Oystercatchers by creaming off the most profitable prey, exert a high predation pressure on only a fraction of the prey and ignore not only the un-

profitable prey, but also the majority of prey which, by definition, still would be harvestable. Consequently, the predation pressure on the harvestable prey fraction as a whole is usually low.

The question remains then why are there not more Oystercatchers than there are now. The Oystercatcher is a long-living species with a low yearly recruitment and thus cannot increase its numbers immediately in a year with a high food supply. This implies that the predation pressure by Oystercatchers in the Wadden Sea might increase were the yearly variation in their harvestable food supply to decrease. It is thus of importance to study feeding Oystercatchers in the worst feeding conditions.

How often do poor years occur and do Oystercatchers die from starvation in these years? Winter mortality primarily depends on winter temperature (Hulscher 1990, Camphuysen *et al.* 1996, Goss-Custard *et al.* 1996a), so this has to be taken into account studying the possible effect of food supply on winter mortality. IJnsen (1991) has classified the severity of the winters. During the study period there were no 'normal' winters, because five winters were mild, three cold and two severe (IJnsen 1991). To analyse the winter mortality, we took 3424 adult Oystercatchers which were colour-banded along the Frisian coast between 1977 and 1984 (Zwarts *et al.* 1996d). Assuming that the annual mortality of adult Oystercatchers in the long-term, including severe winters, was 6.1% (J.B. Hulscher pers. comm.; Goss-Custard *et al.* 1996d) 1206 of these birds would still be alive on 1 October 1996. Until this datum, 426 birds, or 12.4%, were recovered, which would imply that 19.2% of our colour-banded birds were recovered after death. Using this as a correction factor, the variation in the absolute mortality can now be calculated. The risk to die in January or February was nearly 4 times as large as during the rest of the year (Zwarts *et al.* 1996d). To compare the winter mortality, we will also include March and April, because winter victims are still found in these months. The mortality between May and December was 2.7%, on average, and independent of the frost index of the foregoing winter period.

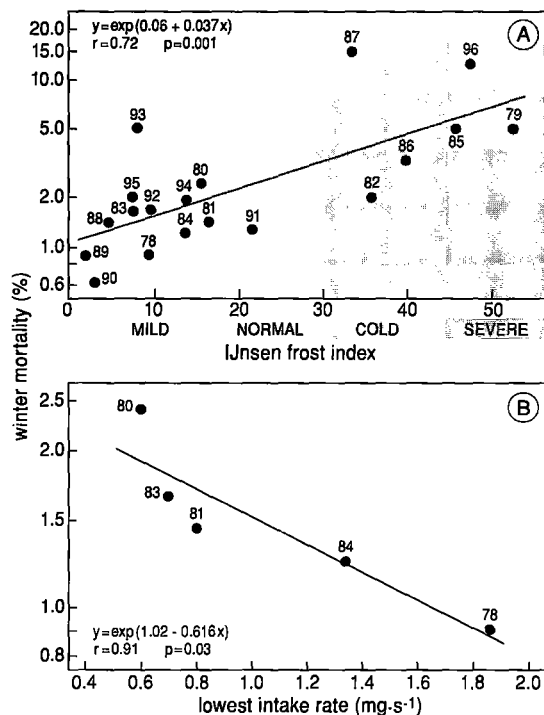


Fig. 22. Winter mortality of Oystercatchers captured along the Frisian coast as a function of (A) the IJnsen frost index and (B) the predicted lowest intake rate in mild winter in the Nes area; a selection is made for January–April. The analysis is based on 3424 colour-banded Oystercatchers and excluded the yearlings; from Zwarts *et al.* (1996d). The frost index of IJnsen (1991) is defined as $0.000275v^2 + 0.667y + 1.111z$, where v is the number of days with a minimum temperature $< 0^\circ\text{C}$, and y and z the number of days with a maximum temperature $< 0^\circ\text{C}$ and $< -10^\circ\text{C}$, respectively.

In agreement with other studies, the winter mortality was much higher during severe winters (Fig. 22A), which is equally due to hunting in France and to starvation in birds staying behind after the onset of the frost (Zwarts *et al.* 1996d). To exclude the effect of severity of the winter, we took the five mild winters to plot winter mortality against the lowest intake rate in the winter concerned (Fig. 22B). In these five winters, no birds were shot and nearly all were found dead in the study area. However, the winter mortality in the

three poor years appeared to be nearly twice as high as in the two years during which, due to the presence of large Cockles, the intake rate in winter could stay at a high level.

The biomass measurements in the Nes area ended in November 1986, some months too early, because the winter mortality of Oystercatchers was extremely high in winter 1987 when 17% of the population died, even though the winter was not extremely cold. The November samples showed that there were no *Scrobicularia* (Fig. 9) or second year *Mya* (Fig. 12) left and hardly any large Cockles (Fig. 8), whereas also large *Macoma* (Fig. 10) and second year Mussels (Fig. 13) had decreased. As a consequence, the intake rate was already extremely low in autumn 1986 (Fig. 14), and must have been so in the following months, and at least as low as in the poor winters 1980–1982. Hence, the remarkably high mortality in the winter of 1987 was probably due to the combination of a cold winter and a poor food supply. A remarkably high number of our birds were shot in France in 1987. This suggests that more Oystercatchers left the Frisian coast in a cold rush than usual in other cold winters. As Fig. 22A shows, there were three winters with an exceptional high mortality. The high mortality in 1987 was explained with a low food supply but, unfortunately, we do not know whether the food supply was also extremely low in the winters of 1993 and 1996.

When the Nes area could only offer a poor harvestable food supply, and consequently a low intake rate, most birds left to feed further down-shore. Apparently, the intake rate in these alternative areas was not high enough to prevent a higher mortality. We only know that these alternative feeding areas were exposed a shorter time, so possibly the reduced feeding time increased the risk of starvation.

Mortality due to starvation implies an exhaustion of the nutrient reserves. The feeding circumstances in our study area were poor between autumn 1979 and spring 1982, compared to the time before and after. However, the body weight of the Oystercatchers in these four years appeared not to

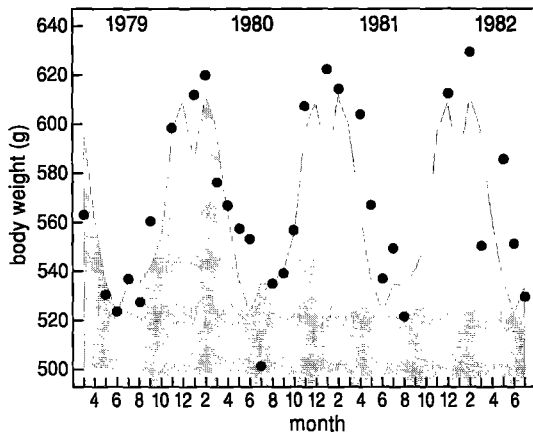


Fig. 23. The average body weight of Oystercatchers in 1979 ($n = 627$), 1980 ($n = 534$), 1981 ($n = 627$) and 1982 ($n = 255$) (•), compared to the average monthly mean in other years ($n = 4434$ for 1977, 1978 and 1983 to 1986; shaded field), to show that the poor food supply in the four intervening years did not negatively effect the average body condition of the Oystercatchers; from Zwarts *et al.* (1996d).

deviate from the long-term average monthly means (Fig. 23). Hence, the average Oystercatcher was, even in these winters, able to satisfy its energy requirements. This seems inconsistent with the higher mortality in the poor years (Fig. 22B). However, as shown elsewhere (Zwarts *et al.* 1996d), Oystercatchers attempt to increase their body weight as soon as their food supply is less predictable. Thus a higher body weight is to be expected if the average intake rate is low. On the other hand, some marginal birds will possibly not be able to attain the required higher consumption. If this is so, we would expect a larger variation in the body weights within the population in years with a poor food supply. The frequency distribution of the body weights in the three poor years, however, appeared not deviate from those of the other years. Possibly, the fraction of marginal birds which run a high risk of dying in periods of low temperatures and/or reduced daily consumption is too small to be detected in the bird catches we made.

Our general conclusion is that there are large local variations in the food supply harvestable to

Oystercatcher, but that the Wadden Sea, unless the mudflats are covered by ice, offers enough food for the birds, provided that they either switch between prey species and/or between areas. This is probably generally true for waders in Wadden Sea, since Zwarts & Drent (1981) and Zwarts *et al.* (1992) arrive at the same conclusion in their work on Oystercatchers on Schiermonnikoog and Knot along the Frisian coast, respectively. Nonetheless, the increase of winter mortality at a lower food supply, suggests that the winter remains a difficult period for the Oystercatcher, as also found by Camphuysen *et al.* (1996) who could show that, over a long series of 27 years, more Oystercatchers beached when the food supply for Oystercatchers in the western part of the Wadden Sea reached low levels (Beukema 1993a).

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SAMENVATTING

Het artikel is gebaseerd op precieze metingen van het voedselaanbod en tellingen van vogels langs de Friese waddenkust. De prooikeuze en de opnamesnelheid worden voorspeld op basis van de metingen aan de dichtheid en diepteverspreiding van de prooi en zijn mede gebaseerd op de aanname dat de vogels hun opnamesnelheid altijd zullen proberen te maximaliseren. We voorspellen dat de vogels nooit Mossels moeten eten, Kokkels in de meeste winters en Nonnetjes en Slijkschelpen in de meeste zomers. De waarnemingen komen goed overeen met de voorspellingen. 's Winters zitten de Nonnetjes en Slijkschelpen zo diep dat het nauwelijks de moeite waard is om naar ze te zoeken, maar 's zomers leveren ze meer op dan Kokkels omdat ze dan ondiep leven. Scholeksters hebben in de Waddenzee te maken met een grote variatie in voedselaanbod. De variatie is nog groter als we er rekening mee houden dat een deel van de prooien voor Scholeksters niet van belang is, omdat ze te weinig opleveren (b.v. alle kleine prooien) of omdat ze niet bereikbaar zijn. Als de produktie van alle bodemdieren wordt samengenomen, blijkt slechts 57% in principe exploiteerbaar te zijn voor Scholeksters, de rest betreft prooien die te klein zijn of te diep leven. Van die oogstbare prooien consumeren de vogels daadwerkelijk 38%. Dit is een gemiddelde, want in jaren met weinig voedsel is het veel lager omdat de vogels dan uitwijken naar een betere plek in de buurt, maar het is méér als er veel voedsel is. De verklaring is dat als er veel voedsel beschik-

baar is, de opnamesnelheid omhoog gaat en het gebied daardoor aantrekkelijker wordt voor de vogels. Het feit dat Scholeksters alleen grote prooien eten, maakt ze wél kwetsbaar omdat nieuwe generaties prooien al kunnen zijn verdwenen voordat ze groot genoeg zijn om door Scholeksters te kunnen worden gegeten. We concluderen dat de Scholeksters vrijwel altijd genoeg voedsel in de Waddenzee kunnen vinden. Dit lukt ech-

ter alleen als ze bereid zijn regelmatig over te stappen van de ene naar de andere prooi. Om dezelfde reden is het ook noodzakelijk dat ze nu en dan verhuizen binnen de Waddenzee. De winter is echter een moeilijke periode voor Scholeksters. Ten eerste gaan 10 tot 20% van de vogels dood in een strenge winter. Bovendien blijkt de sterfte veel groter te zijn in jaren met een relatief arm voedselaanbod.

