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Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands

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Abstract

The number of waders in the Oosterschelde, S.W. Netherlands, declined after a reduction in intertidal area due to the construction of a storm surge barrier and secondary dams, suggesting that the carrying capacity had been reached (Schekkerman *et al.*, 1993). In this paper we present data on consumption and predation pressure by birds to explore whether the reduction in their numbers is due to prey depletion or to other factors.

The total annual consumption of benthic invertebrates by birds in the Oosterschelde amounted to 1573×10^3 g ADW y^{-1} in the period before the coastal engineering works (pre-barrier) and 1500×10^3 kg ADW y^{-1} in the post-barrier period. More than half of the total amount of biomass is eaten by the Oystercatcher, and only seven (pre-barrier) or even six (post-barrier) bird species together take 90% of the total.

Although the consumption by individual species may vary considerably among years, the total consumption was remarkably stable, with a CV of only 3–4% of the mean, especially compared to the variability of the prey populations. In the pre-barrier period, consumption was lowest in mid summer, increased sharply from August onwards until a peak was reached in January. A sharp decrease took place in March. In the post-barrier period, consumption peaked in October.

The total consumption per unit area per year does not differ much between different sectors of the Oosterschelde, apart from a distinctly lower value in the eastern part. Of the total amount of food taken by birds, only 0.1–0.4% is taken in the subtidal compartment. In several study plots on an individual tidal flat, there was a clear relation between consumption and benthic biomass.

The predation pressure was 13 and 23% of the standing stock, in the post- and pre-barrier period respectively. When cockles, mussels and their main predator, the Oystercatcher, are excluded from the calculations, the predation pressure of the other species was 30 and 37% of the biomass, respectively.

Predation pressure of Oystercatchers in individual study plots varied from less than 10% to more than 70% of the standing stock. On cockle beds the predation pressure was positively related to the average length of the cockles present.

Based on these results and a comparison with the literature we conclude that, at least for several species that feed intertidally, carrying capacity could be limited by the stocks of food. This does not mean that birds face food shortage each season. As the variability of the benthos populations is much higher

than that of the bird densities it is likely that at some times food is not limiting, at other times it is. On the other hand, consumption is very low in the subtidal compartment and species feeding here could potentially increase substantially in numbers in the Oosterschelde.

Introduction

Within the Oosterschelde, a large estuary in the SW Netherlands, important coastal engineering works have taken place in the 1980s (Nienhuis & Smaal, 1994). As part of the ecological studies investigating the impact of these works, a simulation model of the Oosterschelde ecosystem (SMOES; Klepper *et al.*, 1994) has been made, which calculated the major carbon-flows between different components of the ecosystem. The higher trophic levels, especially fish and birds, however, were not included in this model, as their role in the overall C-balance of the estuary was considered to be negligible.

Despite the relatively unimportant trophic role of birds in the overall C-balance of the Oosterschelde ecosystem, the Oosterschelde is nevertheless of great significance for bird populations, especially waders, ducks and geese (Schekkerman *et al.*, 1994). This significance has played a prominent role in deciding whether the Oosterschelde should be closed or remain tidal (Nienhuis & Smaal, 1993). Eventually, a storm-surge barrier has been built, which has resulted in a considerable loss of the intertidal area. For more details of the coastal engineering works see Nienhuis & Smaal (1994).

Wader densities in the Oosterschelde used to be high compared to other Western European intertidal areas (Smaal & Boeije, 1991) and the major question has been posed as to whether a reduction in intertidal area would cause a drop in bird numbers or not. Habitat loss in estuarine areas is a widespread phenomenon all over the world, but its effects on waders have been studied in only a few occasions. The construction of the storm surge barrier in the Oosterschelde provided an opportunity to test whether or not the carrying capacity of the area had been reached. Carrying capacity is defined here as the density at which the addition of any further birds results in other birds dying or leaving the area because they fail to achieve adequate intake rates due to increased interference and/or depletion of prey stocks (Sutherland & Goss-Custard, 1991). Schekkerman *et al.* (1994) showed that the number of waders in the Oosterschelde declined after the construction of the coastal engineering works as predicted by Meire & Kuijken (1987), suggesting that the carrying capacity had been reached. In this paper we present data on consumption and predation pressure by birds on benthic invertebrates in the Oosterschelde. By comparing the biomass consumed by birds with the total benthic biomass present in late summer, we explore the question whether carrying capacity could be directly limited by the size of the potential food stocks. Alternatively, carrying capacity could be determined by the spatial needs of the birds, resulting from specific foraging techniques or social factors such as interference and territoriality.

Material and methods

Consumption by birds

Total Oosterschelde: overall estimate

Consumption by birds in the whole Oosterschelde was determined on the basis of monthly high-tide counts of birds in the whole estuary (Schekkerman *et al.*, 1993). Data from two periods, one pre-barrier (five seasons, 1978/79–1982/83), and the other post-barrier (three seasons, 1987/88–1989/90) are used in the analysis. Gulls were only counted during the pre-barrier period; it was assumed that total numbers and seasonal patterns were the same in the post-barrier period. All counts refer to the Oosterschelde, excluding the brackish Krammer-Volkerak. For the pre-barrier period, the counts include the birds counted in the now fresh and stagnant Zoommeer and Markiezaat, which were dammed in 1983–1986. The total intertidal area was 13669 ha in the pre-barrier, and 11365 ha in the post-barrier period, so that 17% of the intertidal area was lost due to the engineering works. For some of the analyses the intertidal area of the Oosterschelde was divided into four different sectors (west, centre, east and north) (Fig. 1).

The total monthly consumption per species was calculated (Table 1) using the equation:

$$C = (30 \times N \times 3 \times \text{BMR} \times (1/Q)/F) * 1000$$

in which C = total monthly consumption by species (kg Ash-free Dry Weight ADW); N = the number of birds present; BMR = Basal Metabolic Rate (kJ day^{-1}); Q = the assimilation efficiency of the food, and F its energy content in kJ g^{-1}.

BMR, the energy consumption of a resting bird at thermoneutrality, was estimated using the equations:

BMR = $5.06 \times LW^{0.729}$ for waders (Kersten & Piersma, 1987);
BMR = $3.56 \times LW^{0.734}$ for other species (Aschoff & Pohl, 1970),

in which LW = the lean (fat-free) weight of the species in g. Lean weights were used because fat stores are largely energetically inactive. Lean weights of waders were estimated from wing length, using the formulae given by Davidson (1983). For gulls, the lean weight was obtained by subtracting 10% from their weight in the breeding period, on the basis of the body composition of Herring Gulls (see Table 1 for scientific bird names) reported by Norstrom *et al.* (1986). The lean weights of grebes were based on Piersma

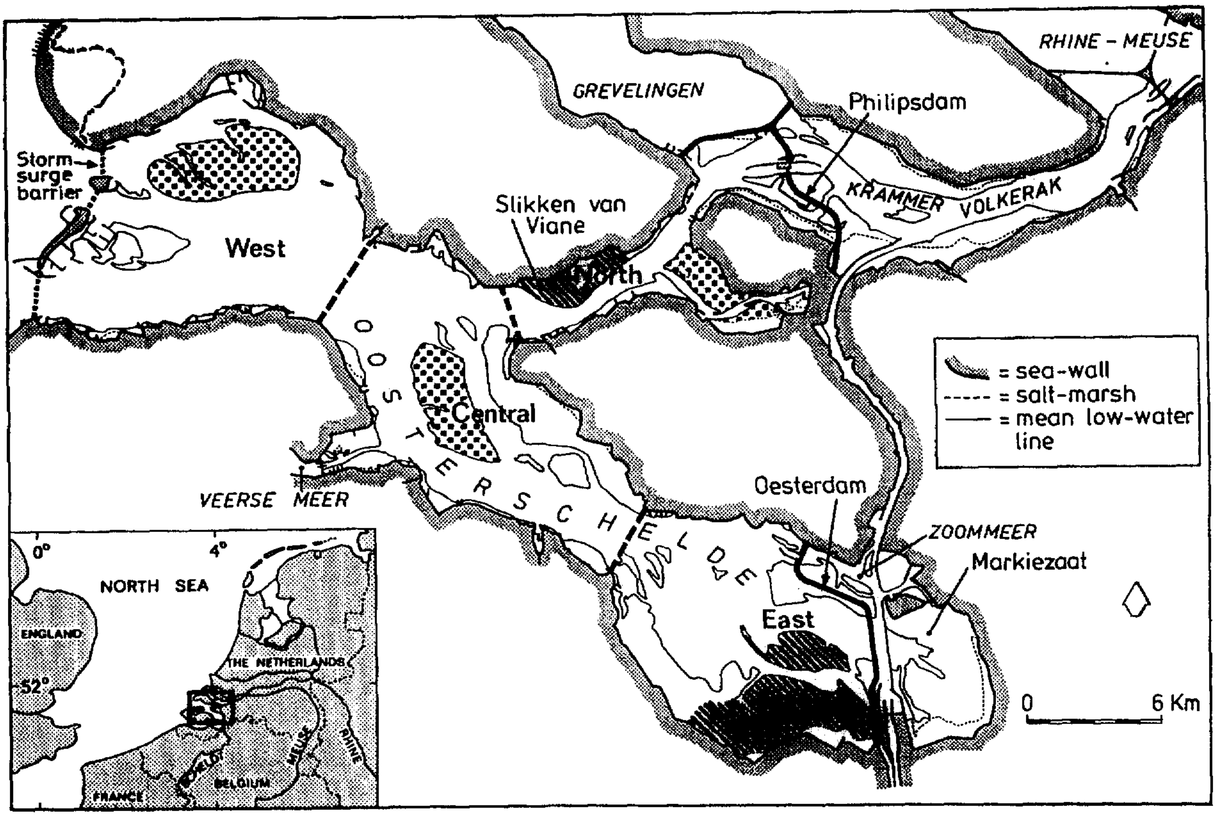


Fig. 1. Map of the Oosterschelde estuary with the location of the four compartments, Vianen mudflats, and the sampled areas in both 1985 and 1989 (stippled) and in 1985 (hatched) only.

Table 1. Basic assumptions and total consumption by benthivorous birds in the Oosterschelde.

Species	Lean weight (kg)	BMR ($kJ\ d^{-1}$)	Daily intake ($gAWD\ d^{-1}$)	Bird-days/year ($n \times 1000$) 78-82	Bird-days/year ($n \times 1000$) 87-89	Consumption $gADW\ m^2\ y^{-1}$ 78-82	Consumption $gADW\ m^2\ y^{-1}$ 87-89	% of total benthic cons. 78-82	% of total benthic cons. 87-89
Subtidal areas									
Eider (*Somateria mollissima*)	1.90	505	81	8	42	0.005	0.029	0.0	0.2
Goldeneye (*Bucephala clangula*)	0.75	255	41	28	52	0.008	0.018	0.1	0.1
Tidal flats									
Oystercatcher (*Haematopus ostralegus*)	0.53	275	44	20085	19901	6.381	7.605	55.4	57.6
Herring Gull (*Larus argentatus*)	0.95	303	49	4824	4824	1.690	2.032	14.7	15.4
Curlew(*Numenius arquata*)	0.70	337	54	2212	2277	0.861	1.066	7.5	8.1
Dunlin (*Calidris alpina*)	0.05	49	8	9556	6602	0.543	0.451	4.7	3.4
Bar-tailed Godwit (*Limosa lapponica*)	0.27	168	27	1909	1811	0.371	0.423	3.2	3.2
Shelduck (*Tadorna tadorna*)	1.08	333	54	1045	721	0.402	0.333	3.5	2.5
Black-headed Gull (*Larus ridibundus*)	0.23	107	17	1888	1888	0.233	0.281	2.0	2.1
Knot (*Calidris canutus*)	0.14	104	17	2367	1824	0.285	0.264	2.5	2.0
Grey Plover (*Pluvialis squatarola*)	0.19	130	21	1711	1439	0.257	0.260	2.2	2.0
Pintail (*Anas acuta*)	0.85	280	45	463	328	0.150	0.127	1.3	1.0
Redshank (*Tringa totanus*)	0.14	104	16	747	556	0.090	0.080	0.8	0.6
Common Gull (*Larus canus*)	0.35	146	23	381	382	0.064	0.077	0.6	0.6
Shoveler (*Anas clypeata*)	0.55	203	33	225	103	0.053	0.029	0.5	0.2
Turnstone (*Arenaria interpres*)	0.08	69	11	357	289	0.029	0.028	0.2	0.2
Great Black-backed Gull (*Larus marinus*)	1.44	412	66	46	46	0.022	0.026	0.2	0.2
Avocet (*Recurvirostra avosetta*)	0.24	154	25	161	94	0.029	0.020	0.2	0.2
Spotted Redshank (*Tringa erythropus*)	0.14	104	17	119	123	0.014	0.018	0.1	0.1
Ringed Plover (*Charadrius hiaticula*)	0.05	49	8	116	135	0.007	0.009	0.1	0.1
Greenshank (*Tringa nebularia*)	0.18	125	21	52	50	0.007	0.009	0.1	0.1
Lesser Black-backed Gull (*Larus fuscus*)	0.73	250	40	14	14	0.004	0.005	<0.1	<0.1
Sanderling (*Calidris alba*)	0.05	49	8	31	49	0.002	0.003	<0.1	<0.1
Kentish Plover (*Charadrius alexandrinus*)	0.05	49	8	64	37	0.004	0.003	<0.1	<0.1
Whimbril (*Numenius phaeopus*)	0.41	228	37	5	3	0.001	0.001	<0.1	<0.1

Totals

Species	Total consumption $*10^3 kg\ ADW$ 78-82	Total consumption $*10^3 kg\ ADW$ 87-89	Total consumption $gADW\ m^{-2}\ y^{-1}$ 78-82	Total consumption $gADW\ m^{-2}\ y^{-1}$ 87-89	% of total benthic cons. 78-82	% of total benthic cons. 87-89
Subtidal areas total	1.6	5.4	0.006	0.020	0.1	0.4
Tidal flats total	1571.7	1494.6	11.49	13.15	99.9	99.6
Ducks	82.8	55.7	0.60	0.49	5.3	3.7
Oystercatcher	872.2	846.3	6.38	7.61	55.5	56.4
Other waders	341.7	299.5	2.50	2.64	21.7	20.0
Gulls	275.2	275.2	2.01	2.42	17.4	18.3

(1984). For the remaining species, the lower values from the range of weights given by Cramp & Simmons (1977, 1983) were used to estimate lean weight. The obtained BMR value was converted in $KJ \cdot d^{-1}$. Total daily energy expenditure (DEE) was assumed to amount to three times BMR (Drent *et al.*, 1978; Kersten & Piersma, 1987; Smith, 1975; Castro *et al.*, 1992). For fish and benthic invertebrates, a digestibility of $Q = 0.85$ was used (Kersten & Piersma, 1987; Zwarts & Blomert, 1990) and an energetic value of F = 22kJ g^{-1} ADW (Zwarts & Blomert, 1990). To obtain yearly consumption monthly consumption was summed. For comparisons with other areas, consumption was expressed in gADW m^{-2} y^{-1}.

The method gives a rather crude estimation of total consumption for several reasons. Firstly, it was assumed that all birds were feeding exclusively in the benthic compartment of the Oosterschelde. Gulls however, may have taken part of their food from the pelagic compartment, or even outside the boundaries of the Oosterschelde (e.g., at rubbish tips). Secondly, species classified as benthivores were assumed to forage exclusively on this type of food. Pintail and Shoveler may, however, have included a significant proportion of vegetable matter in their diet. Furthermore, no adjustments were made for variations in energy expenditure within the annual cycle due to physiological processes like thermoregulation, deposition of energy reserves for wintering and migration, moult, gonad development or egg-formation. Finally, the amount of food taken from the estuary to feed chicks has not been taken into account. It is expected, however, that the latter assumption will have relatively little effect on the estimated total consumption, as the number of birds feeding young is small in comparison with the numbers present in the non-breeding season.

The consumption was calculated separately for the subtidal (below mean low water) and intertidal areas. It was assumed that Eider & Goldeneye were feeding in the subtidal part of the Oosterschelde.

Slikken van Vianen: detailed estimate

The foraging behaviour of waders was studied in detail on the Slikken van Vianen, a small intertidal area in the middle part of the Oosterschelde (Fig. 1) (Meire & Kuijken, 1984; Meire, 1987). Birds were counted at both low and high tide. At low tide, numbers were counted in permanent plots (0.5–1 ha) during an entire tidal cycle on 220 days between 1979 and 1990. For each day the average density of foraging birds and bird feeding minutes were calculated. Until 1985 14 plots were studied, six of these also in the remaining years. Days with very short exposure time, caused by manipulation of the storm surge barrier or storms, were omitted from the analyses.

The intake rate (mg ADW ingested/minute of feeding) of Oystercatchers was estimated from visual observations in all study plots (see Meire & Ervynck, (1986) for details). For the other bird species an average intake rate was estimated from the known daily consumption of each species (see Table 1) and an estimate of the total feeding time per tide (Meire, unpublished data). This estimate is probably an overestimation of the real intake rate in plots with a low biomass and an underestimation in plots with a large biomass. In order to correct the intake rate in plots with a biomass less than 10 g ADW m^{-2} (excluding cockles and mussels) the intake rate was multiplied by 0.5, in plots with a biomass higher than 30 g ADW m^{-2} it was multiplied by 1.5. For Bar-tailed Godwits, the values obtained in this way did not differ significantly from the field data (Meire, unpublished data). Consumption per plot was then calculated by multiplying the number of feeding minutes and the intake rate. It was thereby assumed that both the number of feeding minutes and the intake rate were similar at night and during the day. The annual consumption and predation pressure of Oystercatchers was calculated for two seasons: 1984/85 and 1986/87. For all species the consumption was calculated for the months September/October 1984 and expressed as gADW m^{-2} d^{-1}.

Benthic biomass

The estimate of macrozoobenthic biomass in the entire Oosterschelde is derived from two large scale surveys carried out in August 1985 and 1989 (Meire *et al.*, 1994; Seys *et al.*, 1994). At this time of the year benthic biomass reaches its maximum values (Beukema, 1974). In winter growth and reproduction are small, so these values can be considered as the maximum potential food source available to the birds during the next winter season. The survey of 1985 covered most of the intertidal areas of the Oosterschelde: the Roggenplaat, Galgenplaat, Verdronken Land van Zuid-Beveland, Slikken van Vianen and Krabbekreek (Fig. 1). In 1989 only the Roggeplaat, Galgeplaat and Krabbekreek were sampled. These biomass data are used to compare with the consumption of birds as no information on benthic production is available.

In all permanent plots on the Slikken van Vianen, macrozoobenthos was sampled each year in September. Density and biomass of all species in the samples were determined and all molluscs were measured to the nearest mm (Meire & Dereu, 1990).

Results

Consumption by benthivorous birds in the Oosterschelde

Total consumption

The total annual consumption of benthic invertebrates by birds in the Oosterschelde amounted to 1573×10^3 kg ADW y^{-1} in the pre-barrier period (Table 1). Similar results were obtained by Meire *et al.* (1989) who estimated the consumption of benthivorous bird species in the Oosterschelde to be 1448×10^3 kg ADW y^{-1} for the period 1976–1984. Although methods of calculation and division of bird species into functional groups differed slightly from those used in this paper (Meire *et al.*, 1989), the results are very similar and can be used to compare consumption by benthivores to that of herbivorous and piscivorous birds. Total consumption by piscivores was estimated at 8.7×10^3 kg ADW y^{-1} and of herbivores at 520×10^3 kg ADW y^{-1} (Meire *et al.*, 1989). Compared to these figures, consumption by benthivores in the Oosterschelde ecosystem is very high.

In the post-barrier period, total benthic consumption was estimated at 1500×10^3 kg ADW y^{-1}, a reduction of about 4% compared to the pre-barrier period. The decrease is not evenly spread over the different species. For Oystercatchers the decrease is 3%, for 'other waders' it is 12.3%. Consumption by ducks decreased by 32.8%.

Share of individual species

A striking feature in the breakdown of consumption of benthic invertebrates over the species is the dominance of only a few bird species (Table 1). More than half of the total amount of biomass is eaten by the Oystercatcher, and only seven (pre-barrier) or even six (post-barrier) species together take 90% of the total. The most important species are Oystercatcher, Herring Gull, Curlew, Dunlin, Bar-tailed Godwit, Shelduck and Black-headed Gull. There was very little difference between the two study periods in the order and relative contribution of individual species.

Temporal patterns of bird predation

Interannual variations in consumption and benthic biomass

Waterbird populations are known to show considerable year to year variation in numbers, due to factors such as variation in local food supply and breeding success. In order to establish the among-year variations in total consumption by waders and dabbling ducks in the Oosterschelde, consumption was calculated separately for each year and the coefficient of variation (CV) for both study periods determined. It should be noted that due to the method of calculation, between-year variation in the estimated consumption is due only to variations in bird numbers, not to other factors such as varying winter temperatures. Table 2 shows that, although consumption by particular species may vary considerably among years, the total consumption was remarkably stable, with a CV of only 3–4% of the mean. This stability was mainly caused by the Oystercatcher, which takes more than half of the total consumption. The stability of Oystercatcher consumption is remarkable in view of the highly variable biomass of mussels and cockles (Coosen *et al.*, 1994a; Van Stralen & Dijkema, 1994). Although the pattern of consumption of benthic invertebrates for all

Table 2. Yearly variations in benthic concumption by waders and dabbling ducks in the Oosterschelde in 1978/79–1982/83 and in 1987/88–1989/90. Given are minimum, maximum (in gADW $m^{-2}y^{-1}$) and coefficient of variation (cv = 100·sd/mean) for each period.

Species	1978/79-1982/83 (n = 5)			1987/88-1989/90 (n = 3)		
	Min	Max	cv (%)	Min	Max	cv (%)
Oystercatcher	6.110	6.720	3.3	5.992	6.274	2.1
Curlew	0.764	0.892	6.0	0.806	1.013	10.2
Dunlin	0.497	0.661	12.8	0.285	0.442	17.6
Bar-tailed Godwit	0.298	0.425	15.9	0.309	0.388	9.4
Shelduck	0.296	0.490	16.0	0.216	0.334	17.4
Knot	0.198	0.319	14.9	0.189	0.254	13.0
Grey Plover	0.244	0.276	5.0	0.188	0.245	10.8
Pintail	0.075	0.207	31.8	0.079	0.125	18.6
Redshank	0.075	0.106	12.7	0.056	0.073	10.8
Shoveler	0.032	0.068	24.4	0.012	0.031	34.7
Turnstone	0.025	0.027	2.9	0.021	0.027	12.2
Spotted Redshank	0.010	0.017	20.8	0.012	0.018	17.4
Greenshank	0.004	0.010	36.1	0.006	0.008	12.7
Avocet	0.003	0.003	5.4	0.001	0.002	17.5
Ringed Plover	0.001	0.001	16.2	0.001	0.01	24.1
Total	8.884	9.644	3.5	8.446	9.146	3.3
Excl. Oystercatcher	2.164	3.251	13.3	2.187	2.871	11.2

other bird species varied more, the overall variability is still rather small (Table 2; CV 11 to 13%) especially compared to the variability in the prey populations. This is exemplified in Table 3 which shows the CV of total density and biomass of different trophic groups, based on eight or nine late autumn samplings in the period 1979–1989 on six permanent plots on the Slikken van Vianen. It is clear that the variability of the benthos is much larger than that of the predation by birds, with the combined CV ranging between 20 and 76% for different trophic groups.

Seasonal pattern of predation

Within-year variation of consumption is shown in Fig. 2. Again, consumption as calculated reflects only variations in bird numbers, not effects of wheather conditions, moult and deposition of fat

Table 3. Yearly variations in benthic invertebrates in 6 study plots on the Slikken van Vianen. The coefficients of variation (%) for 8 or 9 autumn biomass values (years) are given for total density and biomass, and the biomass of deposit feeders, filter feeders, grazers and omnivores.

Plot	Total Density	Total Biomass	Biomass Deposit feeders	Biomass Filter feeders	Biomass Grazers	Biomass Omnivores
10 (n = 9)	41.8	42.6	47.1	45.7	109.5	62.7
13 (n = 9)	68.6	110.6	66.9	121.1	183.7	74.7
22 (n = 8)	36.8	34.7	64.7	40.3	69.2	106.4
32 (n = 8)	43.2	30.0	39.5	52.2	148.6	99.1
39 (n = 8)	51.9	36.2	44.9	50.7	130.1	75.6
60 (n = 9)	39.0	59.6	50.2	62.2	133.1	80.2
Total (n = 8)	28.9	36.1	20.2	42.3	75.5	42.7

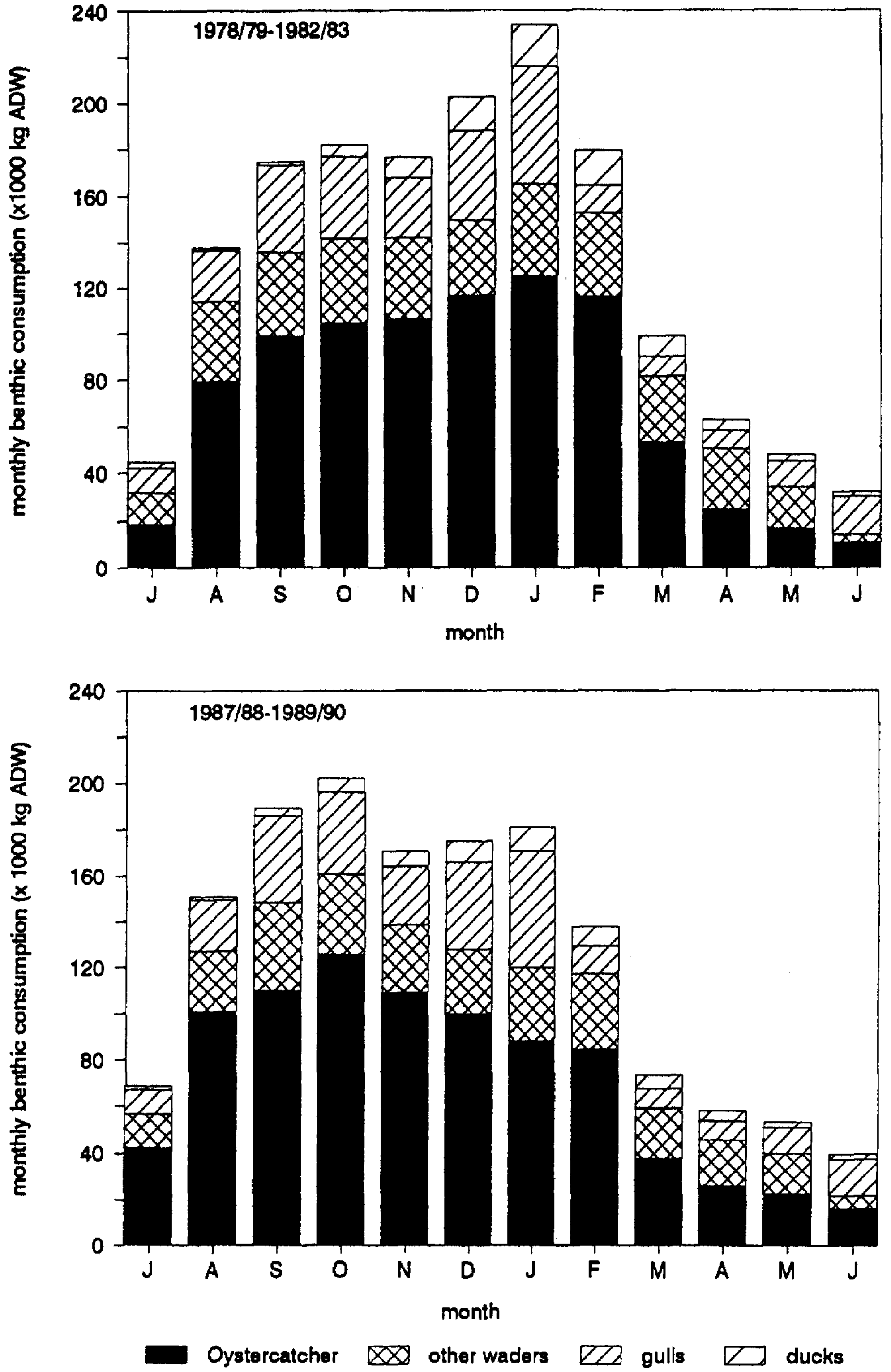


Fig. 2. Seasonal pattern of consumption by waterfowl. The consumption of different groups of benthivorous birds is given per month for the pre-barrier (upper panel) and the post-barrier period (lower panel).

stores. In general, energy requirements will be above the 3 BMR used in this paper during the winter months, while they will fall below this during summer. In the pre-barrier period, consumption was lowest in mid summer, but in August a sharp increase occurred with the arrival of large numbers of waders, especially Oystercatchers. A further increase occurred until a peak was reached in January. A sharp decrease took place in March, when most Oystercatchers left the area for the breeding grounds. In the post-barrier period, the consumption pattern was somewhat different, mainly caused by different seasonal occurrence of the Oystercatcher (Lambeck, 1991). Numbers, and consequently consumption, in late summer were higher as compared to the pre-barrier period. Instead of an increase until January, numbers and consumption decreased after a peak in October.

Spatial pattern of consumption by birds in the Oosterschelde and relation with macrozoobenthos

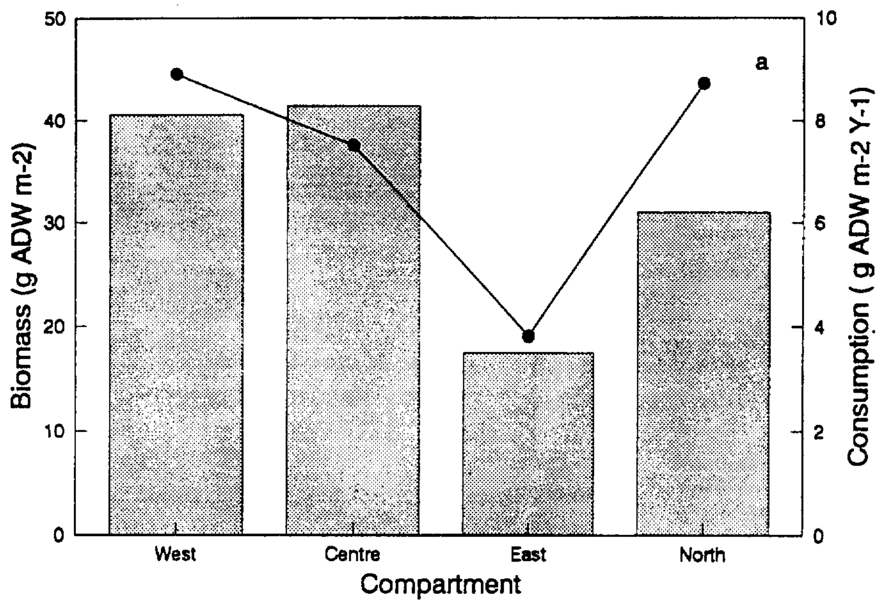
Consumption by birds in different sectors of the Oosterschelde

Total consumption was calculated for each of the four sectors of the intertidal area of the Oosterschelde estuary, using the total number of bird days per year per sector as a basis. These figures were not available for gulls; therefore gulls were assumed to be distributed homogeneously over the intertidal area. The results for the 12 most important bird species are presented in Table 4. Total consumption is given including and excluding gulls. The total consumption per unit area per year does not differ much among sectors, apart from a distinctly lower value in the eastern part. This lower value is almost totally caused by the lower densities of Oystercatchers in this area,

Table 4. Total benthic consumption (gADW $m^{-2} y^{-1}$) by birds in four sectors of the intertidal area of the Oosterschelde. W = west, C = centre, E = east, N = north, Pre, Post = pre and post-barrier.

Species	1978/79–1982/83				1987/88–1989/90				Total	
	W	C	E	N	W	C	E	N	Pre	Post
Oystercatcher	8.900	7.513	3.820	8.722	8.693	10.37	4.750	7.895	6.381	7.605
Curlew	0.960	0.642	0.872	1.046	0.914	1.090	1.210	0.885	0.861	1.066
Dunlin	0.364	0.554	0.588	0.619	0.365	0.508	0.474	0.406	0.543	0.451
Bar-tailed Godwit	0.745	0.408	0.094	0.704	0.766	0.404	0.096	0.762	0.371	0.423
Shelduck	0.224	0.205	0.482	0.764	0.270	0.125	0.568	0.323	0.402	0.333
Knot	0.509	0.268	0.171	0.390	0.314	0.414	0.157	0.183	0.285	0.264
Grey Plover	0.258	0.283	0.219	0.313	0.285	0.311	0.236	0.198	0.257	0.260
Pintail	0.017	0.012	0.279	0.170	0.024	0.013	0.285	0.123	0.150	0.127
Redshank	0.070	0.078	0.095	0.116	0.073	0.107	0.073	0.072	0.090	0.080
Shoveler	0.038	0.010	0.082	0.056	0.060	0.009	0.028	0.028	0.053	0.029
Turnstone	0.035	0.040	0.013	0.048	0.033	0.032	0.011	0.054	0.029	0.028
Avocet	0.059	0.009	0.014	0.074	0.068	0.005	0.005	0.017	0.029	0.020
Spotted Redshank	0.018	0.019	0.005	0.033	0.024	0.025	0.012	0.010	0.014	0.018
Ringed Plover	0.003	0.007	0.004	0.018	0.011	0.013	0.008	0.016	0.007	0.009
Greenshank	0.003	0.007	0.008	0.014	0.006	0.012	0.009	0.005	0.007	0.009
Kentish Plover	0.004	0.006	0.001	0.009	0.003	0.003	0.001	0.004	0.004	0.003
TOTAL	14.23	12.08	8.76	15.11	14.34	15.86	10.35	13.40	11.49	13.15
Ducks	0.28	0.23	0.85	0.99	0.36	0.15	0.88	0.48	0.60	0.49
Oystercatcher	8.90	7.51	3.82	8.72	8.69	10.37	4.75	7.90	6.38	7.61
Other waders	3.04	2.32	2.08	3.38	2.88	2.92	2.29	2.61	2.50	2.64
Gulls	2.01	2.01	2.01	2.01	2.41	2.41	2.41	2.41	2.01	2.42
Total excl gulls	12.22	10.08	6.75	13.10	13.93	13.45	7.94	10.99	9.48	10.74

which in turn can probably be explained by the small surface area of intertidal mussel beds and lower biomass of cockles, as illustrated by data from 1985 in Fig. 3a. The biomass value for the northern sector is probably an underestimate as some musselbeds were not covered in the survey. The lower consumption by other wader species in the central and eastern sector coincides with lower biomass (total biomass – biomass cockles and mussels) values here in 1985 (Fig. 3b).



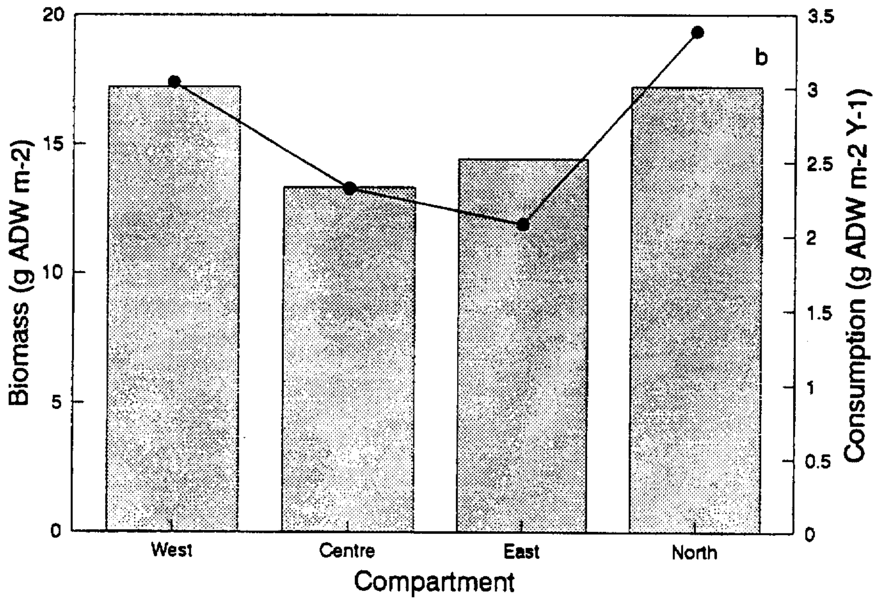


Fig. 3a. Consumption by Oystercatchers (dots) in the pre-barrier period and benthic biomass of suspension feeders (bars) in August 1985 in each compartment of the Oosterschelde.

Fig. 3b. Consumption by waders (minus Oystercatchers) (dots) in the pre-barrier period and benthic biomass (minus suspension feeders) (bars) in August 1985 in each compartment of the Oosterschelde.

Consumption in relation to the tidal and subtidal zone, and benthic biomass
Of the total amount of food taken by birds, only 0.1–0.4% is taken in the subtidal compartment (Table 1). In fact, it is even less than that since Goldeneye and Eider, the only diving benthivores that regularly occurred in the estuary, take part of their food from intertidal areas during high tide. Compared with the Wadden Sea where diving ducks, mainly Eider, take *ca* 30% of the total consumption (Smit, 1981), the absence of avian subtidal benthivores in the Oosterschelde is very noteworthy.

On the tidal flats, the birds are not distributed at random but aggregate on certain parts of the tidal flats. Consumption therefore varies considerably among sites. This is exemplified with the data from Vianen from the 1984/85 season. In Fig. 4 the total number of feeding minutes of all wader species in different study plots is given, showing variation between plots by a factor 20. There is a clear relation between consumption and benthic biomass when all species are considered (Fig. 5a) ($r^2 = 0.8$; $N = 15$; $p < 0.01$ after removing plots 23 and 20). The two aberrant points, plots 20 and 23, are both situated on a very muddy mussel bed, low in the intertidal area and characterised by large pools at low tide. This relation also holds when leaving out consumption by Oystercatchers and the biomass of cockle and mussel, although a remarkably high consumption was seen in plots 6, 10 and 22, three plots situated on mussel beds (Fig. 5b) ($r^2 = 0.74$, $N = 14$, $p < 0.01$ after removing plots 6, 10 and 22).

Predation pressure
General. Assuming that all predation by gulls is confined to the intertidal areas, the yearly consumption of benthic invertebrates in the intertidal part of the Oosterschelde was estimated at 11.5 g ADW m^{-2} y^{-1} pre-barrier and 13.2 g ADW m^{-2} y^{-1} post-barrier, a 14.4% increase (Tables 1 & 5). In the subtidal zone there was a 233% increase from 0.006 to 0.02 g ADW m^{-2} y^{-1} (Table 1). Notwith-standing this increase, overall consumption here remains very low.

In Table 5 the consumption by birds in the intertidal area is compared to the benthic biomass

Fig. 4. Feeding minutes of waders per plot (average for the period August–September 1984) on the Vianen mudflat. Plots are ranked according to benthic biomass, being lowest in 12 and highest in 20.

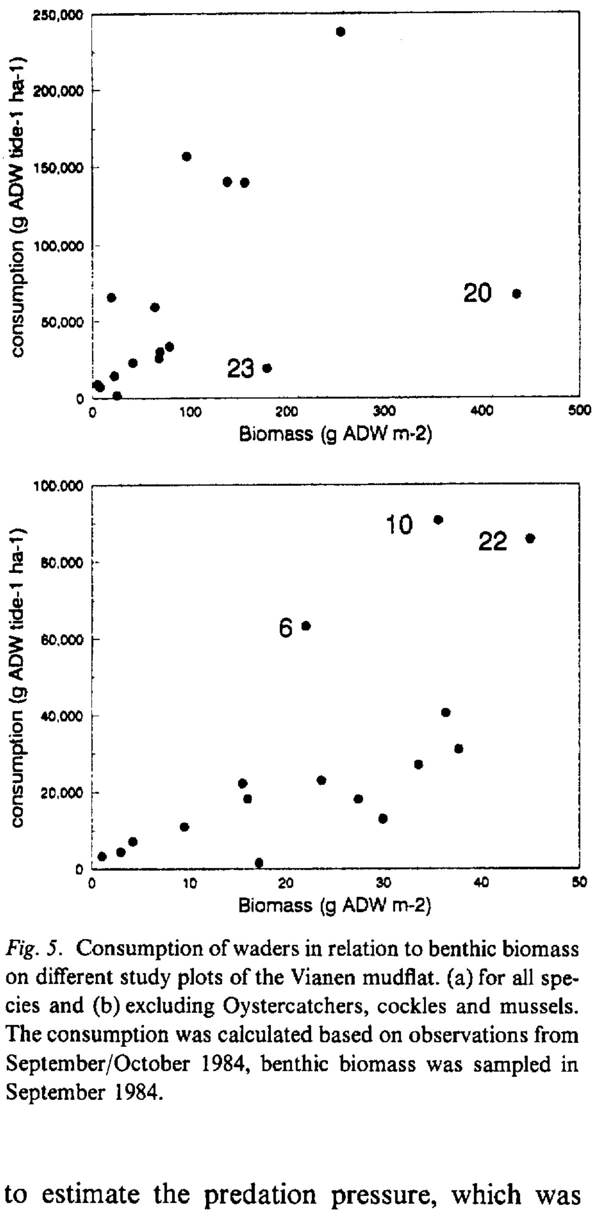


Fig. 5. Consumption of waders in relation to benthic biomass on different study plots of the Vianen mudflat. (a) for all species and (b) excluding Oystercatchers, cockles and mussels. The consumption was calculated based on observations from September/October 1984, benthic biomass was sampled in September 1984.

to estimate the predation pressure, which was found to be 23 and 13% of the standing stock, in the pre- and post-barrier period respectively. Total biomass showed large yearly variations. This is mainly due to the biomass of the filter-feeding cockles and mussels. When excluding cockles and mussels and Oystercatchers, their main predator, from the calculations, the predation pressure of the other species was 30 and 37% of the biomass (Table 5).

Predation pressure by Oystercatchers. The predation pressure by Oystercathers in relation to the biomass of cockles and mussels is given in Table 5 and amounted to 20% in 1985 and 9% in 1989.

Based on observations of Oystercatchers at low tide in permanent plots at the Slikken van Vianen during the seasons 1984/85 and 1986/1987, predation pressure per plot was estimated and plotted in Fig. 6. Predation pressure varied from less than 10% to more than 70% of the standing stock. The data suggest a large scatter at low biomass values and an average predation pressure of about 30% at higher biomass values (musselbeds), without a correlation between biomass and the percentage taken. The large scatter in the data from plots outside musselbeds is to a large extent dependent on the average length of the cockles present as shown in Fig. 7. In plots with larger cockles the predation pressure was significantly higher ($r = 0.74$, $n = 11$, $p < 0.01$).

The seasonal pattern of Oystercatcher numbers changed in the Oosterschelde in the post-barrier period (Lambeck, 1991; Schekkerman *et al.*, 1994). Numbers present in July–September increased, but from October onwards they de-

Table 5. Total macrobenthic biomass in the Oosterschelde and estimated predation pressure by birds in a pre-barrier (1985) and a post-barrier (1989) year. The percentage of benthic biomass removed by birds is given between brackets.

Biomass, Consumption and Predation Pressure		
Year	1985	1989
Total biomass ($gADW\,m^{-2}$)	49.3	99.3
Total consumption ($gADW\,m^{-2}\,y^{-1}$)	11.5 (23.3%)	13.2 (13.3%)
Biomass (excluding cockles & mussels) ($gADW\,m^{-2}$)	17	14.9
Consumption (excluding Oystercatcher) ($gADW\,m^{-2}y^{-1}$)	5.11 (30.1%)	5.54 (37.2%)
Biomass (cockles and mussels) ($gADW\,m^{-2}$)	32.3	84.4
Consumption by Oystercatchers ($gADW\,m^{-2}\,y^{-1}$)	6.38 (19.7%)	7.61 (9.0%)

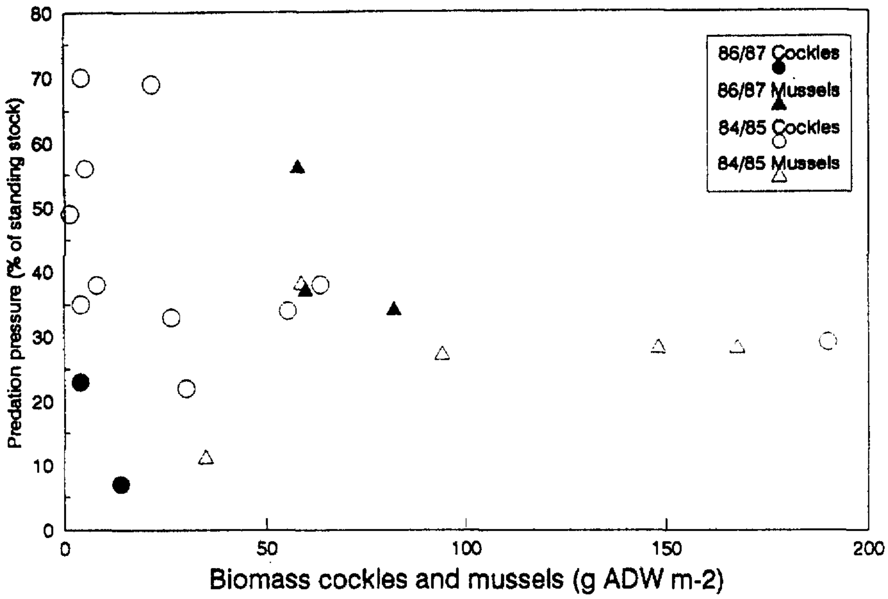


Fig. 6. Predation pressure (percentage of standing stock of cockles and mussels measured in August removed during one year) by Oystercatcher in relation to the biomass of cockles and mussels. Plotted are the data from several study plots on the Slikken van Vianen for both the season 1984/85 and 1986/87.

creased. Midwinter numbers were 23% lower in the post-barrier period. One possible explanation could be that in autumn, the food supply was depleted so rapidly by the higher numbers of birds, that birds were forced to leave. This seems unlikely. The difference in numbers is not large enough to explain a sudden depletion. Another explanation could be a change in the food supply.

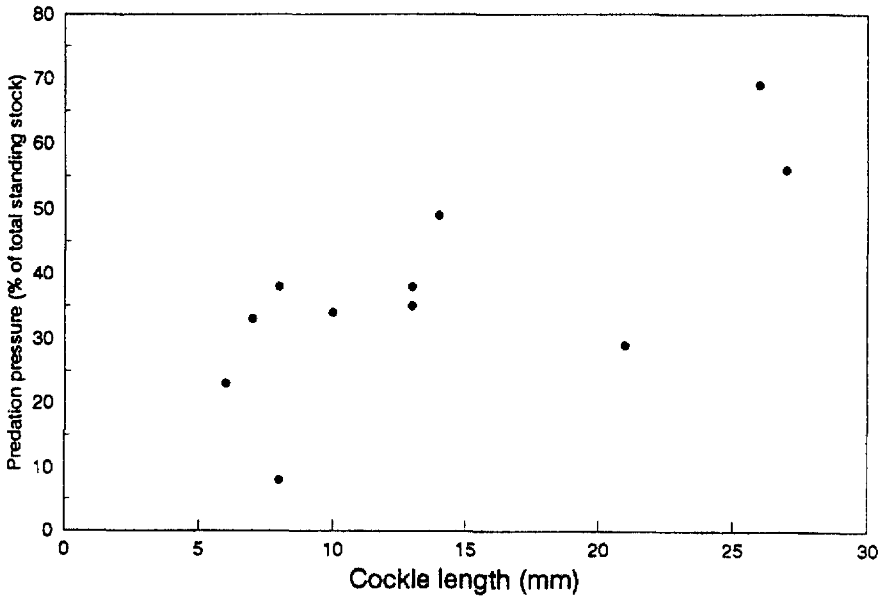


Fig. 7. Relation between predation pressure of Oystercatchers on cockles and the average length of cockles. Data from the season 1984/85 and 1986/87 from several study plots on the Slikken van Vianen are given.

In Fig. 8 the estimated total stock of cockles in August (based on Coosen *et al.*, 1994b) and the amount of cockles removed by cockle-fishers is plotted. Cockle fisheries (M. Van Stralen, pers. comm.) increased dramatically in the post-barrier period and coincided with low cockle stocks in recent years. As cockle fisheries removed most animals between October and December, the drop in Oystercatcher winter numbers could well be related to this.

Prey availability

One of the effects of the construction of the storm surge barrier in the Oosterschelde is the erosion of the intertidal flats (Mulder & Louters, 1994). This is shown in Fig. 9 for one of the major intertidal flats. The total food availability for birds can be expressed as the product of surface, benthos biomass and exposure time. Although benthos biomass did not change in relation to tidal elevation the overall food availability index (product of surface, benthos biomass and exposure time) decreased by 17% between 1984 and 1989, mainly due to the decreased tidal elevation of the flat. If this trend continues, as expected, this will further reduce food availability.

Discussion

Based on the calculations presented in this paper, we can estimate the carbon flow from benthos to birds in the post-barrier period at 1.8 g C m^{-2} y^{-1}, assuming a conversion factor from g ADW to g C of 0.4348 and a total surface of 35 100 ha. The fluxes, calculated in SMOES, of carbon from phytoplankton and labile detritus to zooplankton is in the order of 100 g C m^{-2} y^{-1}, to suspensionfeeders about 120 g C m^{-2} y^{-1} (Van der Tol & Scholten, 1993). The role of birds in the overall C-balance of the estuary is indeed rather small. Their impact on benthic populations may however be important.

Consumption of benthos by birds

Schekkerman *et al.* (1994) have shown that in the Oosterschelde the numbers of waders declined after the reduction of the intertidal area and that

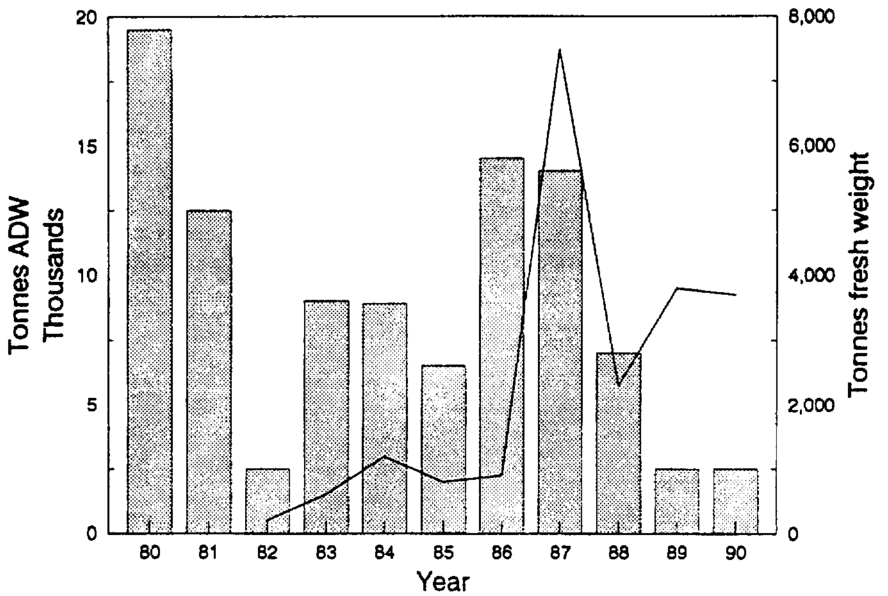


Fig. 8. Cockle standing stock in tonnes ADW (bars) and amount of cockles in tonnes fresh weight removed by fisheries (line) in the Oosterschelde

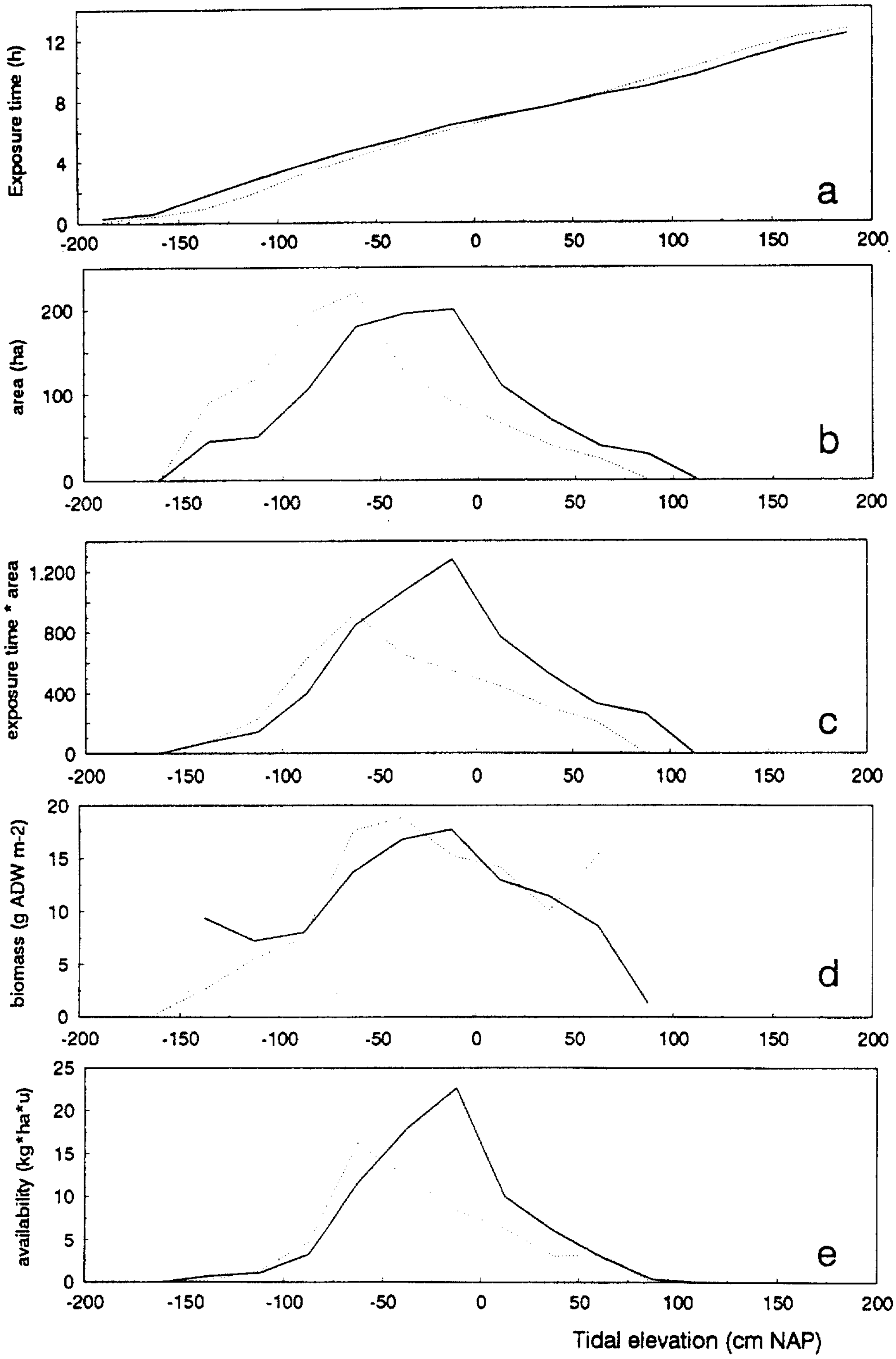


Fig. 9. Exposure time, surface, benthic biomass and food availability, expressed as the product of exposure time, surface and benthic biomass at different tidal elevations of the Roggenplaat in 1985 (solid line) and 1989 (dotted line).

the decrease of each species was related to the loss of its specific habitat, indicating that carrying capacity had been reached. As it is shown that the consumption of benthivorous birds is high in comparison to other trophic groups (Meire *et al.*, 1989), the question is whether or not the use of the area by waders was limited by the benthic food supply (Evans & Dugan, 1984; Goss-Custard, 1985). The benthic food supply will be limiting if birds consume the same amount or more than can be replaced by production and immigration. Although it is possible in some cases, measuring the production of harvestable biomass is very difficult and not feasible for all species (Piersma, 1987; Zwarts *et al.*, 1992). As, for the Oosterschelde, no data on benthic production and harvestability are available, the estimated consumption was compared with the standing stock in order to investigate whether or not the food supply could be an important factor limiting carrying capacity or not.

The results presented in this paper indicate that, depending on location, predator and prey species, between 5 and 70% of the benthic food supply present in August is taken annually by birds. This can be compared to other studies where predation pressure by birds on benthic invertebrates was measured. This is done either based on knowledge of bird numbers and metabolic requirements (as in this study) or by using exclosure experiments. In some exclosure studies no effects of birds on macrobenthos could be determined (Raffaelli & Milne, 1987; Wilson, 1991) but other experiments have found a moderate to high predation pressure by birds (Goss-Custard, 1977; Schneider, 1978; Schneider & Harrington, 1981; Boates & Smith, 1979; Reise, 1985).

The methods used in this paper to estimate the amount of food removed by waterbirds are similar to those used in other studies (Table 6). Although studies differed in assumptions or methods of calculations, with some caution the results can nevertheless be compared. For instance, Smit (1981) used Lasiewski & Dawson's (1967) or Aschoff & Pohl's (1970) formula for estimating BMR of waders, which results in a lower figure than the equation given by Kersten & Piersma (1987). On the other hand, he used mean

Table 6. Consumption, estimated from bird numbers and metabolic requirements, of waders and ducks in different estuaries. The consumption in gADW $m^{-2} y^{-1}$, the autumn or mean annual biomass in gADW m^{-2} and annual production in gADW $m^{-2} y^{-1}$ and the predation pressure (between brackets) are given.

Site	Consumption	Autumn biomass (% consumed)	Mean biomass	Production	Reference
Oosterschelde	11.5–13.15*	49.3(23.3%)–99.3(13.3%)*			this paper
Westerschelde	4.1	15.1(27.2%)			Meire *et al.* 1989; Stuart *et al.*., 1989
Gevelingen	8.2		72 (11.4%)		Wolff *et al.* 1976; Wolff & De Wolf, 1977
Waddenzee	4.7		26.6 (17.6%)	28 (17%)	Smit, 1981; Beukema, 1976, 1981; De Wilde & Beukema, 1984
Ythan estuary	22		59.8 (36.7%)	111.4 (19.7%)	Baird & Milne, 1981
Tees estuary	17.2	44.41(38.3%)		38.6 (44%)	Evans *et al.*, 1979
Ventjager	5.5	11.63(47.3%)–16.18(34%)			Zwarts 1974
Langebaan	6.4			32 (20%)	Summers, 1977; Baird *et al.*, 1985
Berg River estuary	26.7			109.4 (26%)	Kaletja, 1992
Banc d'Arguin	11.5		14.5 (82.7%)	27 (42.6%)	Wolff & Smit, 1990

* Pre- and post-barrier data (see Table 1)

annual body mass including fat stores to estimate BMR instead of lean weights, and a factor 5 instead of $(1/0.85 \times 3) = 3.5$ to convert BMR into DEE; both factors resulting in a higher consumption. Calculating the consumption in the Wadden Sea using the number of birds given by Smit and the body masses and formulae applied for the Oosterschelde, the yearly consumption does not differ much from Smit's original figure: 4.3 gADW m^{-2} y^{-1} versus 4.7 gADW m^{-2} y^{-1}. We used 0.85 as a value of assimilation efficiency Q, while 0.80 (Wolff & Smit, 1990) or 0.75 (Castro *et al.*, 1989) might be a more realistic value. Use of $Q = 0.85$ causes an underestimation of the consumption by 11% compared to $Q = 0.75$.

Another ground for differences in results lies in the conversion of predicted BMR to an estimate of DEE in the field. We used a conversion factor of 3, following Drent *et al.* (1978), Smith (1975), Kersten & Piersma (1987) and Castro *et al.* (1992). Recently, Wiersma & Piersma (1993), using climatic data, estimated the energy expenditure under field conditions for Knots in the Dutch Wadden Sea, taking into account effects of temperature, solar radiation and wind. Compared to a constant rate of 3 times BMR, the total annual energy expenditure per bird was estimated by Wiersma & Piersma was 19% higher. Because Knots, like most species, are most numerous in the Oosterschelde in winter when thermostatic costs are high, the resulting estimate of consumption would be as much as 28% higher than ours. The true difference is probably somewhat smaller as the winter climate of the Oosterschelde is more benign than that of the Wadden Sea. The difference as found in Knots cannot be assumed to apply to all species occurring in the Oosterschelde, since the thermostatic cost relative to BMR decreases with increasing body size (Wiersma *et al.*, 1993). Thus the true energy expenditure of birds larger than Knots, which are most important in determining the total amount of food removed by birds in the Oosterschelde, is expected to be closer to the level estimated by our assumptions of $3 \times$ BMR than that of Knots.

The data from Table 6 show that waders are able to remove a substantial part of benthic biomass or production, as already found by Baird *et al.* (1985). The values for the Oosterschelde, including cockles, mussels and Oystercatchers are on the low side, but excluding them they are comparable to, or higher than those for other areas.

Within an estuary the consumption is not evenly spread over the flats. Data from the permanent plots at Vianen indicate a clear positive relationship between consumption and benthic biomass. Zwarts (1988), working in the Wadden Sea and Sidi Moussa (Morocco) found a similar relationship between consumption and benthic biomass, although the observed relationship differed significantly between study areas. In the Oosterschelde, predation pressure by Oystercatchers did not show any relation with the overall biomass. It is likely, however, that predation pressure is related to the amount of prey that can be economically harvested as suggested by the relationship between predation pressure and average cockle length. In plots with large cockles, which are both available and profitable for Oystercatchers, predation pressure is very high (up to 70%).

Besides consumption by birds, other epibenthic predators take their share of the macrobenthic food supply. Smit (1981) and Beukema (1981) estimated the consumption by crabs, shrimps and fish for the Wadden Sea at 10 g ADW m^{-2} y^{-1}, twice as large as the total consumption by birds. Sanchez-Salazar *et al.* (1987) found the consumption of adult crabs *Carcinus maenas* on cockles to be 25 times more important in numbers or twice as much in biomass than that of Oystercatchers. In addition to epibenthic predators, also several infaunal predators are present in the sediment. Although their role is less well understood they can have an important impact on the other benthic species (Ambrose, 1991).

Based on the evidence presented above it is clear that epibenthic predators and birds together must consume a substantial part of the benthic biomass. Furthermore, the percentage of the prey populations which are predated by birds were calculated based on the total amount of biomass present on the flats and not on the biomass harvestable by the birds. It is known that due to prey escape behaviour, burying depth, prey-size, coverage by barnacles etc. the biomass harvestable to birds at any one moment is much lower than the total biomass present (Durell & Goss-Custard, 1984; Esselink & Zwarts, 1989; Evans, 1976; Evans, 1987; Meire, 1991; Meire & Ervynck, 1986; Zwarts & Wanink, 1984, 1989). Zwarts *et al.* (1992) found on average over 10 years only 13.5% of the total biomass of bivalves to be harvestable by Knots. Meire & Ervynck (1986) estimated that, depending on the mussel bed, on average 30% of the mussels of the size classes taken by hammering Oystercatchers were available to the birds. Predation pressure on harvestable biomass must therefore be higher than the figures given above. To prove carrying capacity is reached due to shortage of food, it is crucial to know the amount of harvestable prey which is removed in relation to production of harvestable biomass (Piersma, 1987). These data are not available. The date discussed above do suggest that birds consume a substantial part of the total food supply, which moreover they have to share with other epibenthic and endobenthic predators consuming at least the same quantity of food.

Carrying capacity

Recent studies showed that bird numbers reach plateau values in some estuaries or feeding areas (Meire & Kuijken, 1984; Moser, 1988; Zwarts, 1974) and Schekkerman *et al.* (1993) showed that wader numbers decreased in the Oosterschelde in response to the reduction of intertidal area. We believe this provides circumstantial evidence that, at least for several species, the decline in numbers in the Oosterschelde (Schekkerman *et al.*, 1994) could be due to food shortage. This does not mean that birds face food shortage each season. As the variability of the benthos is much higher than that of the birds it is likely that food will not be limiting at some times, while at other times it does. During severe winters, food shortage in combination with cold stress can cause the death of many birds (Lambeck, 1991; Meininger *et al.*, 1991). As the variability of cockle and mussel biomass is very high it is likely that at some times, when biomass is very high, much more is harvestable by Oystercatchers than is actually taken. At other times when biomass is low (caused by natural variation or by fisheries) it might limit Oystercatchernumbers. If this is true, any further loss of intertidal area, food supply, or availability will result in a further reduction of bird numbers. In recent years populations of both mussels and cockles have been very small in the Wadden Sea causing high mortality in Eider and decreasing numbers of Oystercatchers (Beukema & Swennen, pers. comm.). Whether or not this will have an effect on population level is another question (Goss-Custard & Durell, 1990).

The results from the intertidal area are in contrast with those from the subtidal compartment. Here consumption is very low compared to other areas as the Wadden Sea (Smit, 1981) or the saline lakes of the Delta area (Meire *et al.*, 1989). Although no data on benthic invertebrates of the subtidal compartment are available for the years analysed in this paper, present investigations by Craeymeersch (pers. com.) indicate that benthic biomass is comparable to that of the Wadden Sea (Dekker, 1989), resulting in a very low predation pressure in the Oosterschelde. If not limited by other factors, bird species like Eiders, feeding in the subtidal compartment, could probably increase substantially in numbers in the Oosterschelde, a trend which seems to have started already.

Historical perspective

The present results contrast with previous findings in the Delta area. There is no evidence that wader numbers in the whole Delta area of South-West Netherlands decreased after the closure of the estuaries Veerse Gat, Haringvliet and Grevelingen (Saeijs & Baptist, 1977; Leewis *et al.*, 1984; Meininger *et al.*, 1984). After the closure of the Grevelingen, an estuary adjacent to the Oosterschelde, wader numbers increased substantially in the Krammer-Volkerak, the northern branch of the Oosterschelde (Leewis *et al.*, 1984;

Meininger *et al.*, 1984) and numbers of Oystercatchers and Bar-tailed Godwits increased abruptly on a large tidal flat in the mouth of the Oosterschelde (Lambeck *et al.*, 1989). In the Krammer-Volkerak, however, important changes occurred due to the coastal engineering works. Tidal amplitude and current velocity increased, chlorinity rose from 0.5–5 to 9–13‰. In response to these abiotic changes, especially the chlorinity, the diversity of macrozoobenthos increased substantially (Wolff, 1971) and mussel cultures became established in the area. Although no data are available we can reasonably assume that in the Krammer-Volkerak the food availability increased substantially, increasing the carrying capacity for waders. If in the Oosterschelde (excluding Krammer-Volkerak) and Westerschelde, the two remaining estuaries, the benthic biomass did not change (increase) it seems that carrying capacity had not yet been reached in the 1960s. This might also hold in other Western European estuaries where numbers of some wader species increased in the last decades (Smit & Piersma, 1989) notwithstanding a reduction in intertidal area. In the past decades the benthic production might have increased due to eutrophication as is shown for the Wadden Sea (Beukema & Cadée, 1986) and hence carrying capacity as suggested by Van Impe (1985) to explain an increase in bird numbers in a part of the Westerschelde estuary. Tubbs *et al.* (1992) suggested that the increase in Dunlin numbers in the Solent since the 1950s reflects release from hunting pressure. A combination of both factors might indeed explain the increasing population sizes of most species in a period of decreasing feeding areas. For several species the balance now seems to have been reached and any further loss in intertidal habitat or deterioration in food supplies will ultimately result in a decrease of wader numbers.

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The results presented in this paper are based to a large extend on bird counts collected by many professional and amateur ornithologists. H. J. M. Baptist and G. J. Slob initiated and coordinated the counts for many years. R. H. D. Lambeck, E. Kuijken, T. Ysebaert, G. Degelder, J. J. Beukema and D. McLusky suggested many important improvements to the manuscript.

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