

Consumption of benthic fauna by carnivorous birds in the Wadden Sea

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ABSTRACT: Consumption by carnivorous birds was estimated for the Sylt-Rømø tidal inlet in the northern part of the Wadden Sea, as well as the subarea Königshafen, a small, tidal bay. The bird community of the Sylt-Rømø Wadden Sea was dominated by Dunlin (35 % of all birds counted), Eider (9 %), Oystercatcher (8 %), Knot (8 %), and Shelduck (7 %). The community in the Königshafen was dominated by Eider (20 %), Knot (17 %), Bar-tailed Godwit (17 %), Dunlin (13 %), and Oystercatcher (8 %). Annual consumption was estimated at 3.4 g AFDW · m⁻² · year⁻¹ for the entire Sylt-Rømø Wadden Sea and 19.2 g AFDW · m⁻² · year⁻¹ for the Königshafen. Restricting the calculations to the intertidal area resulted in a consumption of 8.7 g AFDW · m⁻² · year⁻¹ for the Sylt-Rømø Wadden Sea and 17.6 g AFDW · m⁻² · year⁻¹ for the Königshafen. In the two areas, consumption was dominated by the Eider with 37 % and 60 % of the total consumption, respectively. In comparison to the western parts of the Wadden Sea the seasonal pattern of consumption as well as species composition differed, most probably as an effect of different climatic conditions, whereas annual consumption on intertidal flats seems to be in the same order of magnitude. On average, 15–25 % of the mean annual macrozoobenthic biomass seems to be taken by carnivorous birds in the Wadden Sea, which is in the same order of magnitude as in other northern temperate estuarine areas.

INTRODUCTION

The Wadden Sea, a large intertidal area (8000 km²) stretching along the south-eastern shore of the North Sea, is of particular importance for migratory birds, which use this area as a stop-over site on their annual migrations between southern wintering and northern breeding areas. About 10–12 million birds spend at least a part of their annual life cycle in this area (Meltofte et al., 1994). Birds are the most prominent members of intertidal ecosystems, often roaming around in spectacular flocks of many thousands. Although the efficiency of energy transfer to birds in intertidal systems is high in comparison to terrestrial ecosystems (Baird & Milne, 1981; Baird et al., 1985; Krebs, 1985), their role in intertidal ecosystems, if measured as their contribution to energy or carbon flow, is generally considered to be of minor importance, since their consumption only affects a small fraction of primary production and detritus import (Kuipers et al., 1981; Baird et al.,

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1991; Baird & Ulanowicz, 1993; Meire et al., 1994). This reflects partly the high trophic level of birds and the low production efficiency of animals (Humphreys, 1979; Banse, 1995). However, large differences between areas in the densities of birds and the utilization of benthic communities (Zwarts, 1988; Wolff, 1991; Hockey et al., 1992) indicate that structural differences in these areas affect avian predation pressure. Several mechanisms mitigating avian predation pressure have been proposed: (a) the degree of seasonal synchronisation between production and predation by birds: birds wintering in northern temperate areas use these places at times when annual production is lowest, whereas birds wintering south of the equator meet the annual production peak (Evans, 1979; Hockey et al., 1992); (b) high interannual fluctuations of the benthic macrofauna biomass in northern areas lead to low average consumption (Nehls, 1989; Wolff, 1991); (c) the harvestable fraction of benthic communities, as determined by the quality and the availability of benthic invertebrates to birds, differs seasonally and regionally with low availability and quality in temperate regions in winter (Beukema et al., 1993; Zwarts & Wanink, 1993); (d) the size of tidal areas, with higher densities of birds in smaller areas (Prater, 1981; Hockey et al., 1992). The first three of the four mechanisms mentioned are caused by the climatic conditions as determined by the geographical positions of the intertidal areas. The geographical position further influences the suitability for birds, as the climatic conditions influence their daily food requirements (Castro et al., 1992; Wiersma & Piersma, 1994). The consequences of these climatic influences are that the densities of most migratory shorebirds and the total consumption by birds are much higher in southern areas (Zwarts, 1988; Hockey et al., 1992).

The consumption by birds in the Wadden Sea has been mainly investigated in the westernmost parts of the area, where birds consume $5 \text{ g AFDW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, which are 10–20 % of the annual macrozoobenthic production (Smit, 1980; Wolff, 1991). Since the entire Wadden Sea spans a region of 2.5° latitude and 4° longitude, the climatic conditions at the western end are milder than at its northern end (Eisma, 1980) and bird densities apparently respond to these differences. The densities of wintering waders and hence their consumption was estimated to be eight to ten times higher in the western Dutch Wadden Sea than in the northern Danish Wadden Sea (Zwarts, 1988). We investigated bird populations in a tidal inlet in the northern part of the Wadden Sea and calculated their annual consumption. The aim of the study was to analyse whether consumption by birds is actually lower in this part of the Wadden Sea, or whether differences in species composition and seasonal pattern of consumption result in an equal amount of annual consumption. By comparing a relatively large intertidal area with a small bay we further investigated the impact of area size on bird densities and consumption.

MATERIAL AND METHODS

Study area

This study was carried out in the Sylt-Rømø Wadden Sea, a tidal basin in the northern part of the Wadden Sea in the German-Danish borderland (Fig. 1). The islands of Sylt and Rømø, which protect the area from the North Sea, are connected with the main land by causeways. These borders enclose a clearly defined area, which comprises 137.7 km^2 of intertidal flats and 299.9 km^2 of subtidal area (Table 1). Sandflats are the most common

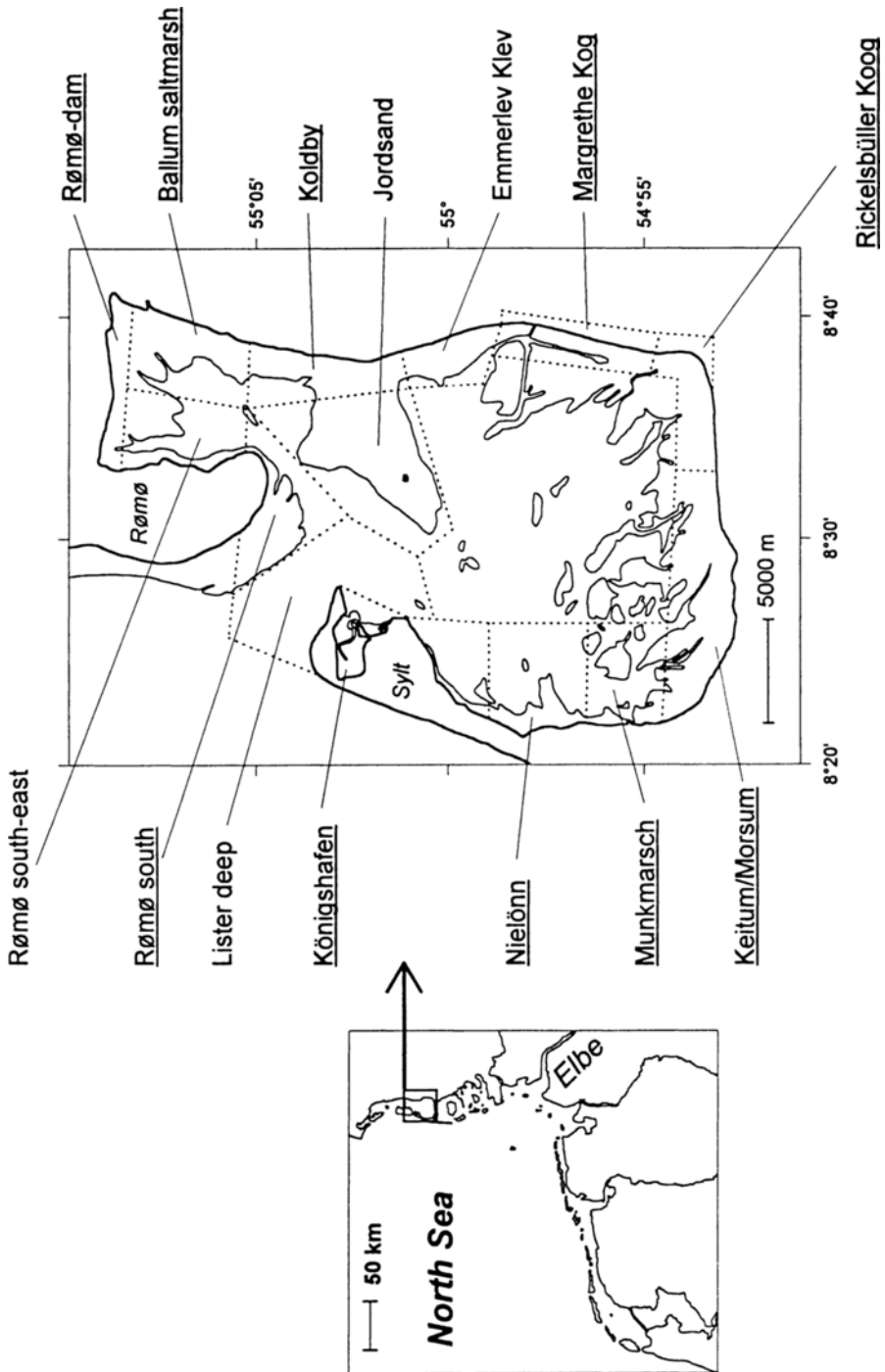


Fig. 1. Sylt-Rømø Wadden Sea with subareas used for counting birds. In sectors with underlined names, regular land-based spring-tide counts were conducted. Thin line delimits intertidal flats

Table 1. Biomass and area composition of the Sylt-Rømø Wadden Sea and the Königshafen

	Sylt-Rømø Wadden Sea	Königs- hafen	Source
Mean intertidal biomass [g AFDW · m ⁻²]	50	65	Reise et al. (1994); Lackschewitz (1995)
Mean intertidal biomass, without mollusc shells [g AFDW · m ⁻²]	40	56	Lackschewitz (1995)
Total area (sub- + intertidal) [10 ⁶ m ²]	437.6	5.75	Backhaus et al. (1995)
Intertidal area [10 ⁶ m ²]	137.7	4.32	Backhaus et al. (1995)
% mudflat	2.96	0.4	Bayerl (pers. comm.); Austen (1994)
% sandy mudflat	21.79	10.8	
% sandflat	75.25	88.8	
% intertidal covered by mussels	0.28	1	Reise et al. (1994); Lackschewitz (1995)

type of tidal flats, whereas only a small proportion of the area is covered by mudflats, mainly near the two dams.

The results of the investigation on the whole Sylt-Rømø Wadden Sea are compared with those covering the subarea Königshafen. The latter is a shallow tidal bay at the northern end of Sylt with 4.32 km² of intertidal and 1.43 km² of subtidal area. Intertidal sediments consist predominantly of coarse sand, blown in by the wind from nearby dunes, which makes this bay different from other sheltered bays in the Wadden Sea (Austen, 1994). Additionally, a relatively high proportion of the area is covered by mussel-beds (*Mytilus edulis*) (Reise et al., 1994), concentrated at the mouth of the bay near the low-water line (for a further description, see Reise, 1985). The Königshafen is relatively isolated within the Sylt-Rømø Wadden Sea with the next high-tide roosts for birds 8–9 km away and the next feeding areas at a distance of 6–7 km.

Bird counts

Birds were counted in 10 subareas (Fig. 1, underlined areas) during high-tide at each spring-tide (approx. every 15 days) between 1989 and 1995 from dikes, dams or dunes, with the help of telescopes (for a description of the spring-tide counts, see Rösner & Prokosch, 1992). Breeding and non-breeding birds were not differentiated. On average, in 3.4 years (SD: 1.3, range: 0–6) 5.2 counts (SD: 2.7, range: 0–14) per month and subarea were conducted. Additionally, aerial surveys were conducted by the Danish National Environmental Research Institute with 37 counts in the northern and eastern parts of the investigation area (Lister Deep – Rickelsbüller Koog) and 8 counts in the western part of the area (Königshafen – Keitum/Morsum; for method, see Pihl & Frikke, 1992). In the analysis of the aerial counts the results from the subareas Margrethe Kog and Rickelsbüller Koog were excluded, since there were major differences between the latter and simulta-

neous ground surveys. Usually, the aerial estimates in these areas, which were difficult to scan, were below the estimates of the ground surveys. Redshank, Curlew, Ringed Plover, and Turnstone were excluded from the analysis of all aerial surveys because of major disagreements with ground surveys, which were thought to be more accurate in these species.

For Eiders, special aerial surveys were conducted. Since 1988, 65 surveys were analysed (for a description of the methods, see Nehls, 1991). Ground surveys were only used for the Königshafen, which is the only subarea where Eider numbers can be realistically obtained by land-based counts.

As birds are highly mobile animals, the two dams north and south of the investigation area are no real borders restricting the movements of the birds. This can be a problem when relating bird numbers to a distinct area. Certainly, there is an exchange in birds with adjacent areas, but it was neglected here, as immigration and emigration were supposed to cancel each other out. The problem may become more difficult when relating high-tide counts from the Königshafen to its intertidal area. At least for gulls (Dernedde, 1993), Bar-tailed Godwit and Eider, low-tide counts gave equal numbers for most of the counts. Nevertheless, there may be a slight overestimation of the density estimates for some species based on high-tide counts.

Analysis of the counts

Despite the integration of the bird counts in an international monitoring project (see Rösner et al., 1994), there were only very few simultaneous counts covering all subareas. To calculate the mean bird numbers for the whole Sylt-Rømø Wadden Sea, each subarea and species had to be treated separately. For each month in each year an average was calculated. Thereafter, the mean for each month across all years was calculated. This method of calculation stresses more the variation between years as if only the mean of all counts per month had been calculated. For June, the missing values for five subareas were interpolated. To obtain the bird numbers for the whole Sylt-Rømø Wadden Sea, the monthly means of each subarea were added up.

Calculation of consumption

To convert bird numbers into consumption, several assumptions have to be made. We followed the approach of Meire et al. (1994), with few alterations.

The basic formula for conversion is as follows:

$$C = D \cdot 3 \cdot \text{BMR} \cdot (1/Q)/E$$

where: C = monthly consumption for each species [g AFDW] (ash free dry weight per month)

D = number of bird-days per month

BMR = basal metabolic rate, estimated by using weight dependent equations:

BMR [W] = $5.06 \cdot W^{0.729}$ for waders (Kersten & Piersma, 1987)

BMR [W] = $4.8 \cdot W^{0.672}$ for Anseriformes (Brunckhorst & Hüppop, pers. comm.)

BMR [W] = $3.56 \cdot W^{0.734}$ for all other species (Aschoff & Pohl, 1970)

W [kg] = weight of the target species; for each month the actual weight was used.

Weights were obtained from literature with data which were recorded as close to the investigation area as possible. This resulted in the following ranking of sources: 1. Prokosch (1988), 2. Smit & Wolff (1980), 3. Cramp & Simmons (1983).

BMR values were transformed into KJ/day

Q = assimilation efficiency (80 %; mean value of different sources; Kersten & Piersma, 1987; Castro et al., 1989; Zwarts & Blomert, 1990)

E = 22 KJ/g AFDW; mean energy content of marine benthic animals in the Wadden Sea (Zwarts & Wanink, 1993)

Daily energy expenditure (DEE) was assumed to be $3 \cdot \text{BMR}$ (Kersten & Piersma, 1987). For Eiders, monthly consumption estimates from a feeding study in the Königshafen were used (Nehls, 1995).

Further assumptions were:

- divers, terns, Cormorant, and Greater Black-backed Gull feed exclusively in the pelagic zone
- Teal, Mallard, Pintail and Golden Plover fulfil 50 % of their energy demands on the zoobenthos of intertidal flats
- diving ducks feed 50 % in the subtidal zone and 50 % in the intertidal zone
- gulls, other than Greater Black-backed Gull, were supposed to rely on food resources from the Wadden Sea. Although these species may also feed on anthropogenic food sources (e.g.: discards, waste), these play only a minor role in the diet in this area (Derenedde, 1993)

Reliability of consumption estimates

Calculation of consumption is based on allometric equations as well as on many assumptions. However, biomass intake of the main predator, the Eider, is based on observations in the Königshafen. A principal assumption for all other birds was a constant DEE of $3 \cdot \text{BMR}$ throughout the year. Observations of feeding Bar-tailed Godwits in the Königshafen during the migration periods confirmed this value (Scheiffarth, in prep.). The smaller the birds are, the more pronounced a seasonal pattern of DEE becomes (Wiersma et al., 1993), which was not considered in the calculations. We do not think that this has a large effect on the results, since most of the smaller birds leave the area in winter, when DEE is highest. At this time of year, the dominance of the Eider is even more pronounced, so that consumption values appear to be reliable (for further discussion of calculation of consumption, see Meire et al., 1994).

RESULTS

Species composition

Regarding carnivorous species only, Dunlin is the most abundant species (35 %) in the Sylt-Rømø Wadden Sea followed by Eider (9 %), Oystercatcher (8 %), Knot (8 %), and Shelduck (7 %). These five species comprise 67 % of all carnivorous birds (Fig. 2). Similarly, again five species make up 75 % of all individuals in the Königshafen subarea.

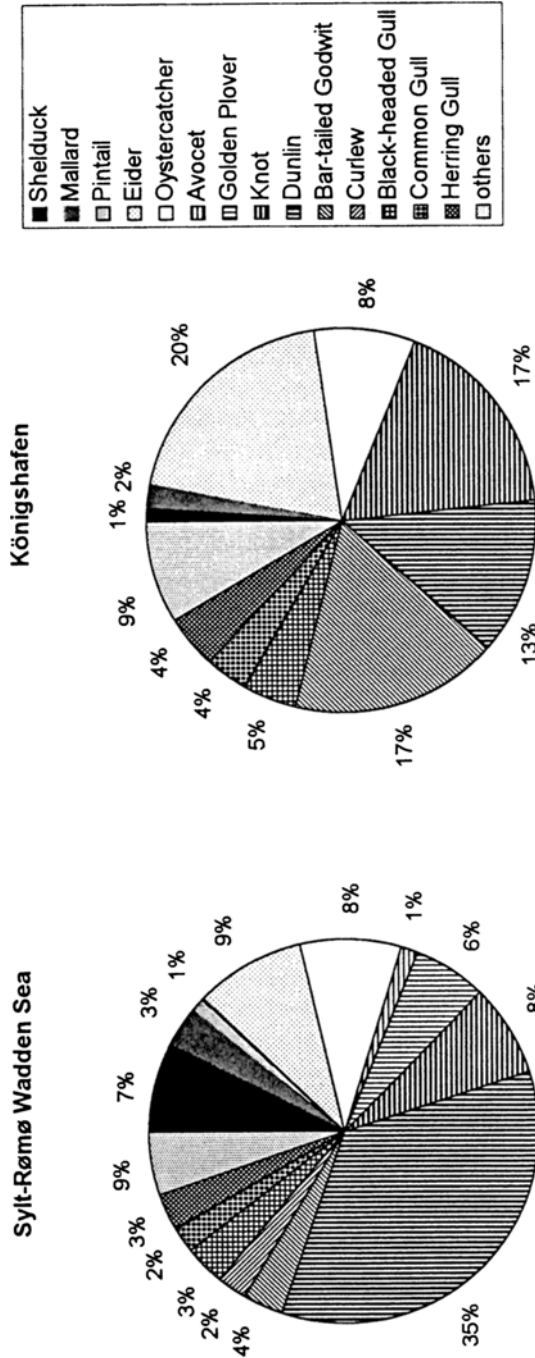


Fig. 2. Species composition of bird communities (carnivores) in the Sylt-Rømø Wadden Sea (left, 107 656 birds · month⁻¹) and the Königshafen (right, 5652 birds · month⁻¹)

However, in this subarea the Eider is the most abundant species (20 %) followed by Knot (17 %), Bar-tailed Godwit (17 %), Dunlin (13 %), and Oystercatcher (8 %). The major difference between both areas is the greater dominance of the Eider in the Königshafen, which is an effect of the higher coverage with mussel beds. Furthermore, in the Königshafen the bird community consists of a higher proportion of Bar-tailed Godwits, as well as a reduced proportion of Dunlin and Shelduck, both of which are supposed to be related to the difference in sediment composition between the two areas.

Consumption by birds

Converting bird numbers into biomass-consumption results in an annual consumption of 1490 t AFDW for the whole Sylt-Rømø Wadden Sea and 111 t AFDW for the Königshafen (Table 2). In the Sylt-Rømø Wadden Sea, the most important predator is the Eider, accounting for 37 % of biomass consumption. Together with Shelduck, Oystercatcher and Dunlin, these four species take 70 % of all biomass consumed by birds in this area. All other bird species play only a minor role (Fig. 3). Consumption is clearly dominated by large birds. Despite the fact that 4 times as many Dunlins as Eiders use the area, the former, small, species consumes only 22 % of the biomass consumed by the Eider. In the Königshafen, the dominance of the Eider in terms of consumption is even more pronounced: almost 2/3 of all biomass consumed by birds is taken by this species. Together with Bar-tailed Godwit, Oystercatcher and Knot, these four species account for 84 % of the consumption by birds.

In relation to the total area, consumption by birds amounts to $3.4 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ in the Sylt-Rømø Wadden Sea and $19.2 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ in the Königshafen (Table 3). Restricting these calculations to the intertidal area, where most of the species feed, consumption totals $8.7 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ for the Sylt-Rømø Wadden Sea and $17.6 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ for the Königshafen. Even when excluding from these calculations the most dominant predator, the Eider, 80 % of whose food consist of Mussels (Nehls, 1995), the difference between the two areas is still obvious. The subtidal compartment is heavily utilized in the Königshafen and remains almost unused in the Sylt-Rømø Wadden Sea. This difference is related to the much higher share of subtidal area in the Sylt-Rømø Wadden Sea than in the Königshafen, which results in a lower average density of predators in this compartment. Predation in the subtidal compartment is concentrated on Mussel or Cockle beds (*Cerastoderma edule*), whereas other food resources remain almost unexploited by birds. In both areas, biomass taken from the pelagial is negligible due to the low abundance of birds feeding on fish (ca 1 % of total consumption). Furthermore, consumption in this compartment is almost exclusively restricted to summer and early autumn.

Due to migratory movements of birds, consumption is not equally distributed throughout the year. In the Sylt-Rømø Wadden Sea, consumption reaches a peak in autumn and remains on a high level until January (Fig. 4). This pattern is mostly influenced by the presence of Eiders and other ducks, especially Shelduck. In contrast, waders have the biggest share in consumption during spring.

The same seasonal pattern appears for the Königshafen. Again, this pattern is mostly influenced by the Eider, with an increasing importance of waders in spring. In all, high levels of consumption are reached, when benthic biomass is already decreasing or on a

Table 2. Mean numbers of birds and consumption in the Sylt-Rømø Wadden Sea and the Königshafen. For the calculation of consumption, monthly weight changes were considered; thus, annual consumption values cannot be calculated directly from mean daily biomass intake and mean number \cdot month $^{-1}$, for method of calculation, see text. For Eider, food intake was estimated on the results of a feeding study (Nehls, 1995), and not on the allometric relationship based on body weight

	Sylt-Rømø Wadden Sea		Königshafen		
	Mean weight [kg]	Mean number of birds \cdot month $^{-1}$	Consumption \cdot year $^{-1}$ [g AFDW \cdot 10 6]	Mean number of birds \cdot month $^{-1}$	Consumption \cdot year $^{-1}$ [g AFDW \cdot 10 6]
Shelduck <i>Tadorna tadorna</i>	1.038	8067	209.12	71	1.83
Mallard <i>Anas platyrhynchos</i>	1.080	3671	49.72	107	1.44
Pintail <i>Anas acuta</i>	0.810	1451	16.30		
Eider <i>Somateria mollissima</i>	(2.200)	9815	553.90	1112	66.35
Oystercatcher <i>Haematopus ostralegus</i>	0.546	8997	158.66	467	8.23
Avocet <i>Recurvirostra avosetta</i>	0.300	1414	16.17	4	
Golden Plover <i>Pluvialis apricaria</i>	0.216	6708	30.32	109	
Knot <i>Calidris canutus</i>	0.148	8226	57.67	980	6.61
Dunlin <i>Calidris alpina</i>	0.054	37940	123.01	742	2.42
Bar-tailed Godwit <i>Limosa lapponica</i>	0.324	3774	46.38	979	11.99
Curlew <i>Numenius arquata</i>	0.833	2623	63.49	12	
Black-headed Gull <i>Larus ridibundus</i>	0.271	3486	25.16	255	1.85
Common Gull <i>Larus canus</i>	0.394	2466	23.84	205	1.99
Herring Gull <i>Larus argentatus</i>	1.005	3458	66.58	242	4.67
Others		5557	49.71	365	3.47
Total			1490.03		110.85

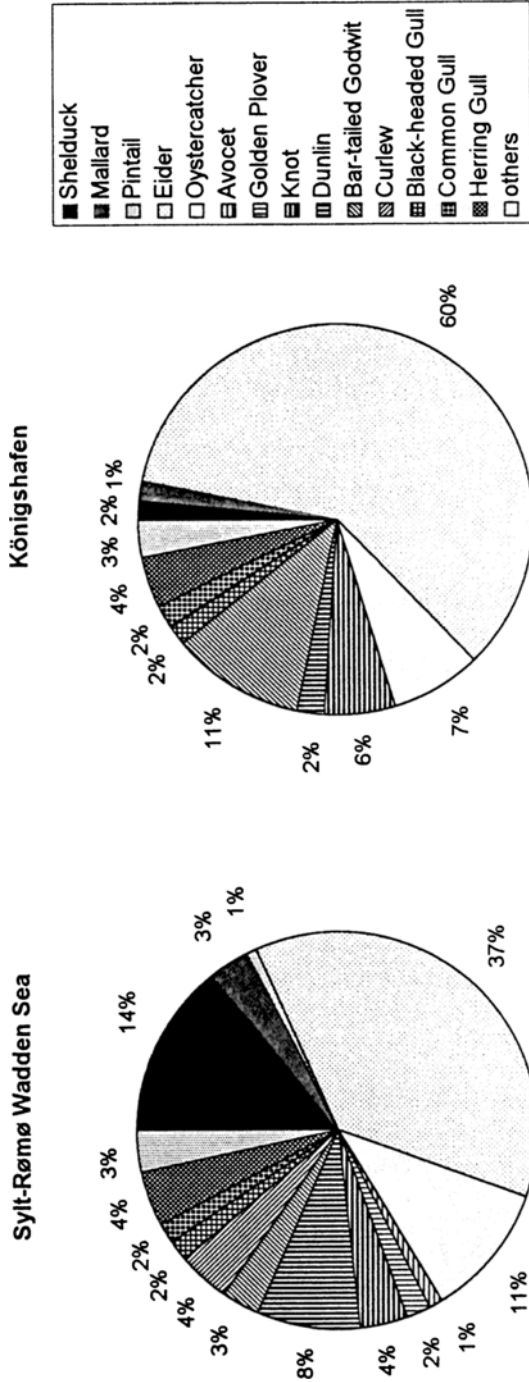
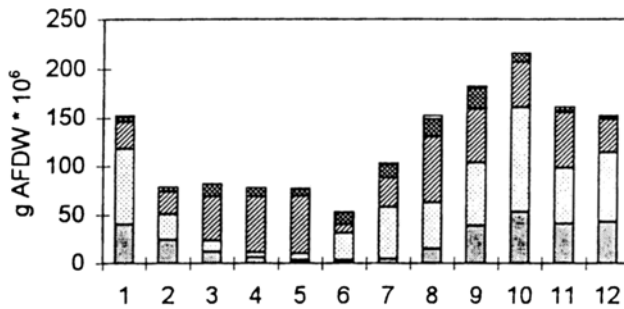


Fig. 3. Distribution of consumption by carnivorous birds over species in the Sylt-Rømø Wadden Sea (left, $1490 \cdot 10^6 \text{ g AFDW} \cdot \text{year}^{-1}$) and Königshafen (right, $111 \cdot 10^6 \text{ g AFDW} \cdot \text{year}^{-1}$)

Table 3. Consumption by carnivorous birds in the Sylt-Rømø Wadden Sea, in the Königshafen (both calculated from values given in Tables 1 and 2) and in the Dutch Wadden Sea (Smit, 1980; recalculated with assumptions used in this paper); values are in $\text{g AFDW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$

	Sylt-Rømø Wadden Sea	Königshafen	Dutch Wadden Sea
Sub- + intertidal area	3.4	19.2	3.9
Intertidal area	8.7	17.6	6.6
Subtidal area	0.93	23.3	1.4
Without Eider			
Sub- + intertidal area	2.1	7.7	2.5
Intertidal area	6.7	10.0	5

Sylt-Rømø Wadden Sea



Königshafen

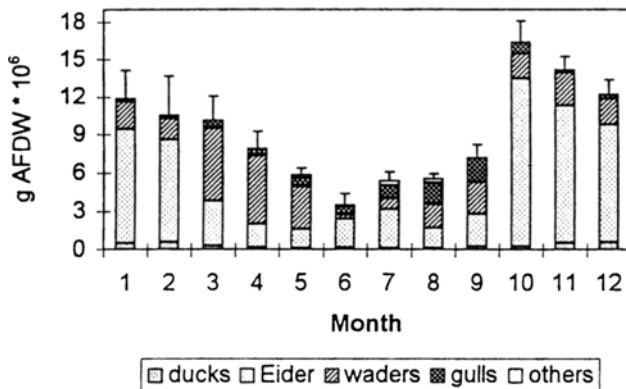


Fig. 4. Seasonal pattern of consumption by carnivorous birds in the Sylt-Rømø Wadden Sea (top) and the Königshafen (bottom, + 1 SE, 4–6 years per month)

low level (Beukema, 1981; Asmus, 1982, 1987). Only waders migrating through the area in May and August/September profit from the seasonal pattern of benthic production.

DISCUSSION

Comparing the results from the Sylt-Rømø Wadden Sea with the Königshafen, it appears that the size of an intertidal area has a strong impact on consumption by birds, as consumption is 50 % higher in the Königshafen than in the whole Sylt-Rømø Wadden Sea. Even in the light of a higher benthic biomass within the Königshafen, compared to that of the entire Sylt-Rømø Wadden Sea, a higher proportion of biomass is consumed by birds in the Königshafen. Probably, this is an effect of the sheltered bay with a large proportion of sandflats at mean tide level. Furthermore, short distances between high-tide roosts and low-tide foraging areas might be a criterion for habitat selection (cf. Swennen, 1984), since, even within the Königshafen, tidal flats near the high-tide roost were preferred for foraging (Scheiffarth & Nehls, 1995). In addition, the habit of many waders and gulls of foraging along the moving tideline for most of the year (Evans, 1979; Nehls & Tiedemann, 1993) enhances bird numbers in small bays with elongated tidelines as compared to a straight coastline (Evans & Dugan, 1984). In all, it seems almost independent of scale, whether comparing two adjacent areas (this study), a larger region like eastern England (Prater, 1981) or the entire East Atlantic Flyway (Hockey et al., 1992), that smaller intertidal areas face higher bird densities than larger areas.

For a large-scale comparison of consumption within the Wadden Sea, Smit's (1980) estimates for the Dutch Wadden Sea for the seventies were recalculated on the basis of our assumptions. This resulted in an annual consumption of $6.6 \text{ g AFDW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ for the tidal flats of the Dutch Wadden Sea (Table 3), which is 34 % below the value calculated for the tidal flats of the Sylt-Rømø Wadden Sea in the nineties. Whether this difference really exists remains open, since for most species an increase in numbers in all parts of the Wadden Sea has been observed (Meltofte et al., 1994; Rösner, 1994; Smit & Zegers, 1994). This is most probably due to both improved registration and a real increase in bird numbers. At least for the Dutch Wadden Sea, increasing bird numbers are paralleled by increasing benthic biomass due to eutrophication of the tidal flats (Beukema, 1989), so that the proportion of biomass taken by birds may not have changed. Whether or not there was an increase in benthic biomass in the northern part of the Wadden Sea during the last 20 years is not yet clear (Jensen, 1992; Reise et al., 1994).

At present the consumption by birds at the northern end of the Wadden Sea should not be lower than at the western end. As species richness and biomass of the macrobenthic communities in the Sylt-Rømø Wadden Sea are similar to those in the Dutch Wadden Sea (Reise et al., 1994; Lackschewitz, 1995), consumption by birds equals 15–25 % of the mean annual zoobenthic biomass in both areas. The equal amount of absolute consumption per m^2 as well as predation rate on tidal flats is in contrast to the much lower densities of wintering waders in the northern part of the Wadden Sea than in the Dutch part (Zwarts, 1988). Most of the smaller species leave the northern parts in winter. An equal level of consumption is not only achieved by higher numbers during spring or autumn, since the share of waders in total consumption reaches only 35 % in the Sylt-Rømø Wadden Sea as compared to 44 % in the Dutch Wadden Sea but also by the higher proportion of large and heavy birds, such as Shelduck, in the Sylt-Rømø Wadden

Sea. Especially in late autumn and winter, Eider and Shelduck dominate the bird community. This can be regarded as a reaction to the harsher conditions in the northern part of the Wadden Sea as compared to the western parts, because large birds have lower thermostatic costs than small birds (Wiersma et al., 1993). Additionally, the phenology of consumption reflects the unfavourable winter conditions for most of the bird species in the northern Wadden Sea. A sharp drop in bird numbers appears from January to February, when the risk of ice-cover is highest. In contrast, consumption in the western Wadden Sea is high throughout winter and reaches a peak in February (Smit, 1980). This may reflect immigration from the northern parts of the Wadden Sea. Although differences in the climatic conditions apparently affect species composition as well as the seasonal patterns of consumption in the two subareas of the Wadden Sea, this has no negative impact on total consumption by birds. Consumption within the Wadden Sea seems to differ only on a local scale related to structural elements in the landscape, e.g. sediment composition, bays, etc.

The proportion of 15–25 % of mean annual biomass taken by birds as calculated in this study falls well within the range of the results from other studies conducted in temperate estuaries on the European continent (for a recent review, see Meire et al., 1994). Only in Great Britain have slightly higher values apparently been achieved (Baird et al., 1985). In contrast, a much higher proportion of the mean biomass (82.7 %) as well as production (42.6 %) is consumed by birds on the Banc d'Arguin, Mauritania (Wolff & Smit, 1990). One major reason for this difference between temperate and tropical estuaries may be stability, with low annual variability and therefore long-term predictability of food resources on tropical mudflats (Wolff, 1991).

Until now the processes linking consumption by birds with production of their invertebrate prey are only marginally understood. Questions concerning whether or not bird numbers are limited by food resources in the Wadden Sea must be investigated on the species level, since different species have a different sensitivity to fluctuating food resources (Beukema et al., 1993).

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