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Stable mussel *Mytilus edulis* beds in the Wadden Sea – They're just for the birds

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ABSTRACT: Predation by eiders, oystercatchers and herring gulls on natural mussel beds *Mytilus edulis* was studied in the Königshafen, a sheltered bay in the Wadden Sea. About 15 ha (2.5 %) of the Königshafen were covered with mussel patches of a biomass of about 1300 g AFDW m^{-2}. The biomass on the mussel beds was dominated by old mussels and found to be constant over several years. Birds annually removed 30 % of the standing stock. Eiders were by far the most important predators and consumed 346 g AFDW m^{-2}, followed by oystercatchers with 28 g AFDW m^{-2} and herring gulls with 3.6 g AFDW m^{-2}. Birds consumed a substantial part of the annual production of the mussel beds which was estimated from literature data to be approx. 500 to 600 g AFDW m^{-2}. As other predators were absent, the production of the mussels was sufficient to sustain the high predation rate by birds. Stable mussel beds form a short and efficient link between primary production and bird predation which is unusual for the Wadden Sea, where the main part of primary food supply is thought to be unavailable for higher trophic levels.

INTRODUCTION

Mussels hold key positions in coastal ecosystems in terms of production, consumption of primary production and as a food source for invertebrates, fish and birds (Gosling, 1992; Dame, 1993). Mussel *Mytilus edulis* beds are the most productive benthic communities of the Wadden Sea ecosystem. Their biomass reaches values 25 times higher than those of the surrounding flats (Asmus, 1987) and although only a low percent of the tidal flats of the Wadden Sea is covered by mussel beds they hold a substantial proportion of the total benthic biomass (Beukema, 1983). The population dynamics of mussels in the Wadden Sea are characterized by erratic spatfalls and destructive events like ice cover and storms which may clear large areas of mussels (Dankers & Koelemaij, 1989; Beukema et al., 1993; Nehls & Thiel, 1993). However, despite the high variability in time, the spatial distribution of mussel beds in the Wadden Sea was shown to be constant over decades as mussel beds tend to reestablish in the same locations (Dankers & Koelemaij,

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1989; Obert & Michaelis, 1991; Nehls & Thiel, 1993). Two types of mussel beds in the intertidal zone of the Wadden Sea can be distinguished: Dynamic beds in exposed locations which are prone to ice and storms are only present in some years, and stable beds in sheltered locations where the impact of storms and ice is less severe. Stable mussel beds may persist over long periods and are dominated by large and relatively old mussels and characterized by a high biomass and a rich epi- and endofauna. Predation is assumed to have stabilizing effects on these beds because thinning of adult mussels enhances settlement of new spat (Dankers, 1993). Asmus (1987) studied the production of such a mature mussel bed and found that a relatively low productivity (P/B ratio of 0.36) was sufficient to sustain a constantly high biomass.

We studied the predation by eiders, *Somateria mollissima*, oystercatchers, *Haematopus ostralegus*, and herring gulls, *Larus argentatus*, on mussel beds in the area investigated by Asmus (1987), the Königshafen on the Wadden Sea island of Sylt. The species are abundant in the Wadden Sea and known to include substantial parts of mussels in their diet (Smit & Wolff, 1983). Their populations and feeding ecology were subject of several investigations carried out within the project Ecosystem Research Wadden Sea (Dernedde, 1993; Hertzler, 1995; Nehls, 1995; Nehls & Ketzenberg, in press; Scheiffarth & Nehls, 1997, this volume). In this study we summarize our results on mussel beds in order to quantify the predation by birds and to address the question whether bird predation can be balanced by production on stable mussel beds.

MATERIAL AND METHODS

Mussel beds

Data on the distribution of mussel beds in the Königshafen were derived from vertical aerial photographs taken in August 1993. The extension of mussel beds was measured on enlargements at a scale of 1:25000. The coverage with mussels was measured on transects on the photographs.

Macrozoobenthos was sampled from different structures on the central mussel bed A in the Königshafen in June and August 1993 (Fig. 1). Six samples were taken at four stations with a corer of 500 cm^2, and samples were washed in a 0.5-mm sieve. All animals retained in the sieve were sorted and determined to species level; mussel length measured to the nearest millimeter. To determine the biomass, mussels and animals from other taxonomic groups were dried at 80 °C for three days to constant weight and incinerated in a furnace at 510 °C for 24 hours. Dry weight and ash-free-dry-weight (AFDW) were determined with an accuracy of 0.001 g. In mussels, biomass was determined in a subsample. The length-weight relation:

$$\text{Weight (AFDW)} = 2.761\ (\text{length}) - 4.8741,\ r^2 = 0.86,\ p = 0.001,\ n = 112,$$

was used to calculate biomass from the length-frequency distribution of the mussel bed.

Bird numbers and utilization of mussel beds

Birds were counted at high tide every 15 days from dikes and dunes surrounding the bay using binoculars and telescopes (see Scheiffarth & Nehls 1997, this volume).

Low-tide bird densities on mussel beds were assessed on mussel beds A and B (Fig. 1) at the opening of the Königshafen by counting birds on 10 plots of 50 m × 50 m in

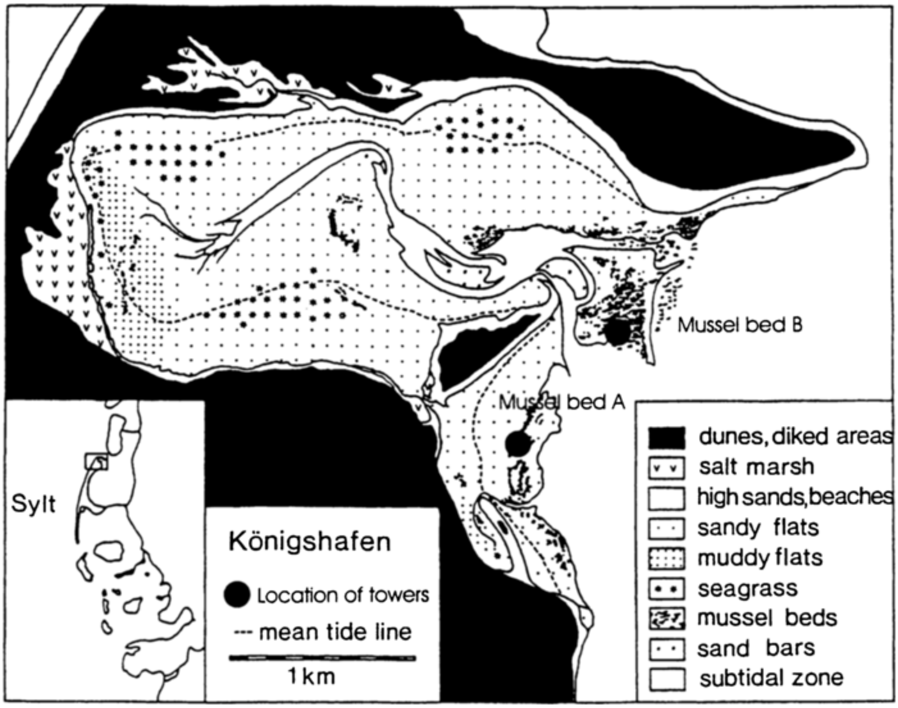

Fig. 1. Distribution of the benthic communities in the Königshafen (from Reise et al. 1994) and location of study sites

10-minute intervals for whole emersion periods. Food choice was observed with telescopes from observation towers situated on the mussel beds (see Nehls & Tiedemann, 1993; Hertzler, 1995 for details).

The daily food demand of oystercatchers and herring gulls was estimated from allometric equations (see Scheiffarth & Nehls, 1997, this volume) to be 48 and 53 g AFDW, respectively.

Food choice, foraging activity and daily food demand of eiders were subjects of a detailed investigation in this area from 1990 to 1994 (Nehls & Ketzenberg, in press; Nehls, 1995), and data have been taken from these studies.

RESULTS

Mussel beds

In 1993, six mussel beds were located in the Königshafen (Fig. 1), but their borders were not clearly defined as dispersed mussel clumps were abundant among the more dense beds. Most beds were situated close to the low-tide line. Total area of mussel beds was 75 ha, of which 15 ha (20 %) was actually covered with mussels. Our estimates of mussel bed sizes are considerably higher than those previously published by Reise et al.

(1994) of 4 ha; however, our findings were confirmed by D. Murphy (pers. comm.) from more detailed analyses of several series of aerial photographs taken in 1993.

The length-frequency-distribution of mussel abundance (Fig. 2) was characterized by the dominance of larger mussels up to 70 mm. There were no peaks which would allow to separate cohorts among the larger sized mussels. The age of the mussel beds in 1993 was six years, as the last destructive impact occurred in the cold winter of 1986/87. The length-frequency-distribution of the biomass reveals a clear dominance of the older mussels (Fig. 2).

Biomass and mussel density on bed A were highest in mussel patches without *Fucus vesiculosus* cover (Table 1). Within the patches more than 95 % of the biomass was made up of mussels. Biomass values closely correspond to earlier investigations on this and adjacent beds (Asmus, 1987; Reise et al., 1994; Lackschewitz, 1995; Nehls & Ketzenberg, in press). Total biomass of mussels in the Königshafen is calculated at 195 t AFDW, using a mean biomass of 1300 g AFDW m^{-2}, which takes a wide cover by *Fucus* and lower densities in the subtidal areas into account. This biomass value was also found as the mean biomass for mussel beds in the adjacent Sylt-Rømø Wadden Sea (Lackschewitz, 1995).

Table 1. Biomass of mussels and other taxa on mussel bed B in the Königshafen 1993 in g AFDW m^{-2} (mean ± SD)

	Mussels	Shore crabs	Polychaetes	Others	Total
June					
Patch without *Fucus*	1349 ± 319	3 ± 1	3 ± 2	54 ± 27	1406 ± 532
Patch with *Fucus*	900 ± 521	27 ± 19	2 ± 1	51 ± 18	980 ± 285
Edge	195 ± 190	6 ± 7	4 ± 3	43 ± 30	249 ± 174
Puddle	20 ± 34	0	17 ± 10	14 ± 7	50 ± 29
Mudflat	0	0	7 ± 5	1 ± 1	8 ± 5
August					
Patch without *Fucus*	1827 ± 739	4 ± 1	7 ± 5	6 ± 2	1844 ± 530
Patch with *Fucus*	691 ± 110	5 ± 1	8 ± 5	39 ± 7	743 ± 167
Edge	237 ± 193	15 ± 8	3 ± 1	47 ± 17	302 ± 117
Puddle	1 ± 1	0	2 ± 2	6 ± 7	8 ± 8

Bird numbers and predation on mussel beds

Eiders, oystercatchers and herring gulls were present all the year round in the Königshafen. Eiders and oystercatchers reached highest numbers in autumn and lowest numbers in May and June which is the breeding season (Fig. 3). Herring gulls were most abundant in spring and late summer; however, their numbers were quite low as no larger breeding colony is found in the vicinity of Sylt.

More than 80 % of the diet of the eiders consists at most times of mussels (Nehls & Ketzenberg, in press). The eiders feed on the mussel beds at all stages of the tide, except when the musssel beds are completely emersed. Highest feeding activities are generally reached when water levels are suitable for head-dipping. In October and November, when eider numbers may reach 4500 individuals in the Königshafen, a high proportion

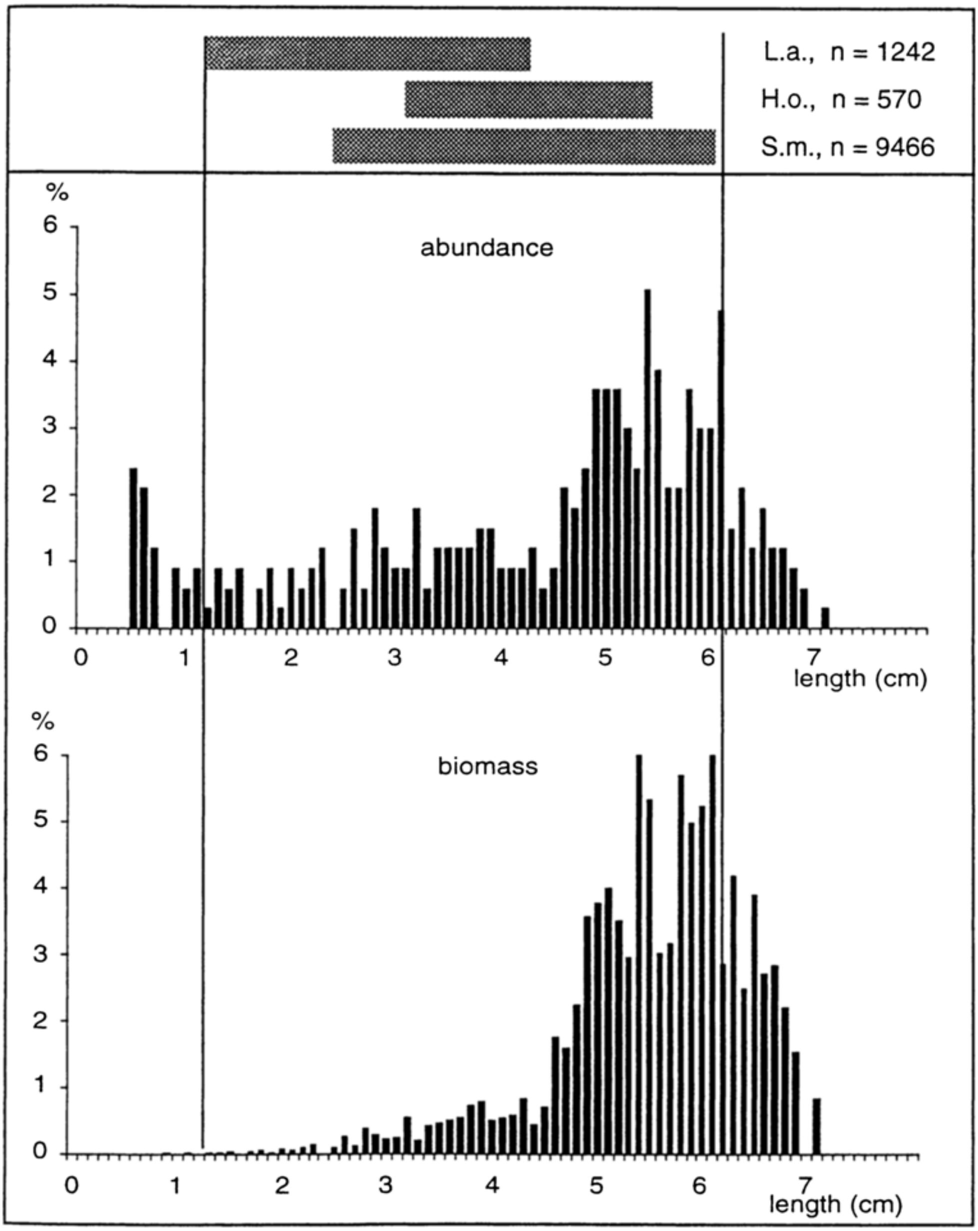

Fig. 2. Length-frequency distribution of mussel abundance and biomass on bed B in August 1993. Bars on top of the figure indicate mussel sizes consumed by eiders (S. m.), oystercatchers (H. o.) and herring gulls (L. a.). The extension of the bars mark lower and upper limits of monthly 80 % quantiles. Data for eiders were obtained 1990–93, oystercatchers 1993 and herring gulls 1991

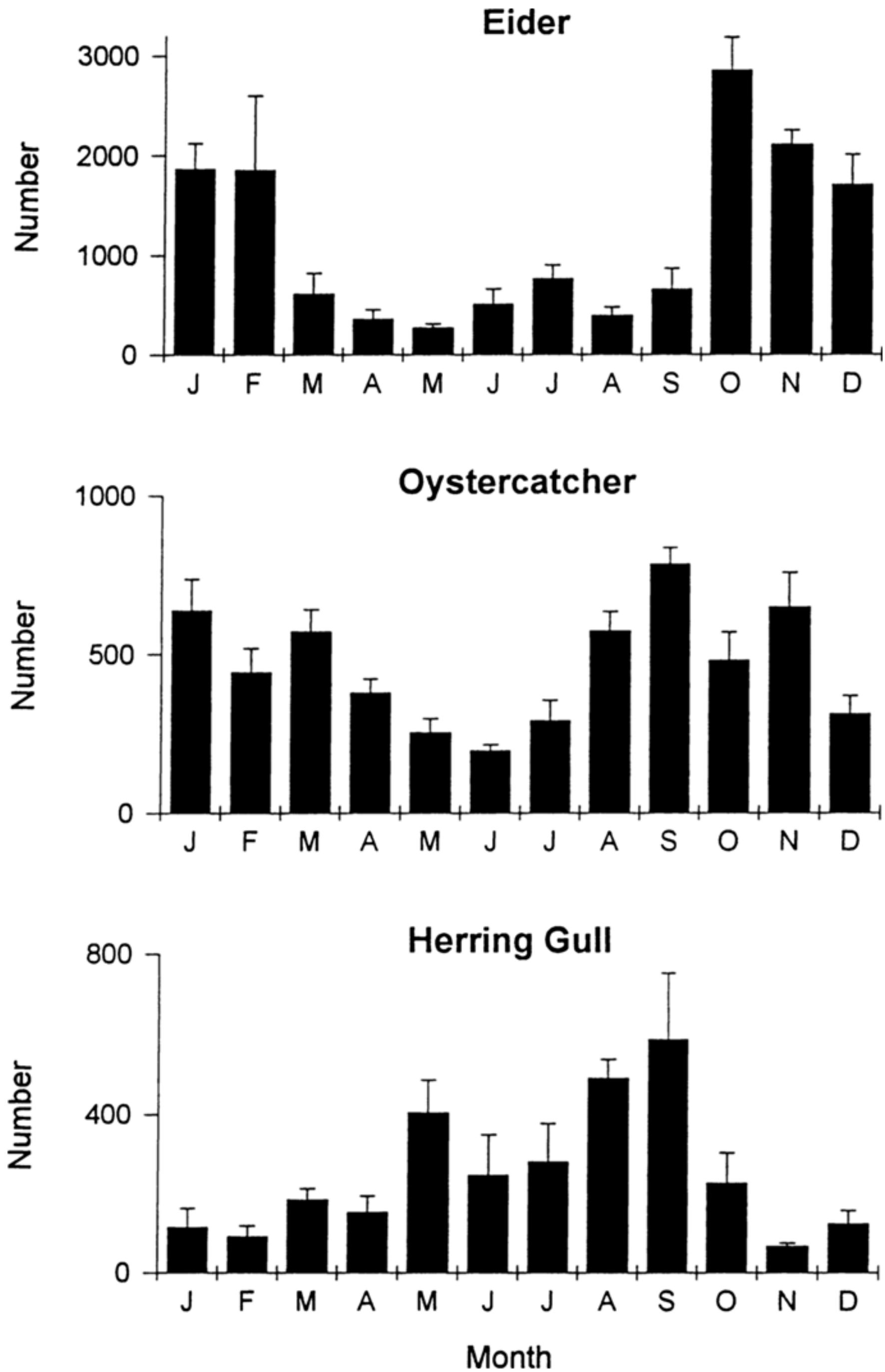

Fig. 3. Mean number per month of eiders, oystercatchers and herring gulls in the Königshafen as obtained from fortnightly counts 1990–94

feeds alongside the mussel beds. During this time, 50 % of their diet consists of cockles *Cerastoderma edule* (Nehls & Ketzenberg, in press). The food demand of eiders changes seasonally and increases from 130 g AFDW day^{-1} in summer to 180 g AFDW day^{-1} in winter (Nehls, 1995). Total mussel consumption by eiders was calculated considering that not more than 2000 eiders feed at the mussel beds at a time. Total annual consumption by eiders amounts to 65 t AFDW (Table 2). Assuming that 80 % of this value consists of mussels taken from mussel patches, 10 % of cockles and crabs, and 10 % of scattered mussel clumps, eider predation of the mussel beds reaches 52 t which is equal to 346 g AFDW m^{-2} year^{-1}.

Table 2. Mean numbers, daily food demand and consumption of eiders on mussel beds in the Königshafen. 80 % of the consumption is assumed to comprise mussels taken from mussel patches (see text)

Month	Total number of eiders	Number of eiders on mussel beds	Food demand (g AFDW/day)	Consumption (t AFDW/month)
January	2018	2000	180	11.2
February	1853	1853	180	9.3
March	491	491	180	2.7
April	398	398	170	2.0
May	294	294	170	1.5
June	562	562	150	2.5
July	772	772	130	3.1
August	464	464	130	1.9
September	668	668	130	2.6
October	2986	2000	150	9.3
November	2039	2000	170	10.2
December	1994	1994	180	11.1

Oystercatchers and herring gulls visited the mussel beds during emersion of the mussel beds which varied between three to six hours. Densities of both species reached highest values in the four hours around low tide (Fig. 4). These were always substantially higher than on the surrounding mudflats (Fig. 5). As only 60 % of the study plots were covered with mussel patches where oystercatchers and herring gulls preferably (80–85 %) foraged, the densities of these two species in relation to mussel patch area are about twice the presented values.

On the mussel beds, oystercatchers took almost exclusively mussels, selecting sizes of 30 to 60 mm. Mean sizes varied between 35 mm and 50 mm. Based on the mean densities measured at low tide (Fig. 4), it is estimated that about 16 oystercatchers per ha mussel patch take their daily food demand of 48 g AFDW from the mussel beds. Annual consumption is thus estimated at 28 g AFDW m^{-2}. This is a high estimate in relation to average numbers on the mussel beds. However, as there is some turnover during the low-tide period, total numbers of individual oystercatchers visiting the mussel bed and taking their daily food demand on it are higher than maximum numbers at low tide.

The diet of herring gulls consisted only partly of mussels. 30 to 60 % of the pellets collected 1991 on the main roost in the Königshafen contained mussel shells (Dernedde,

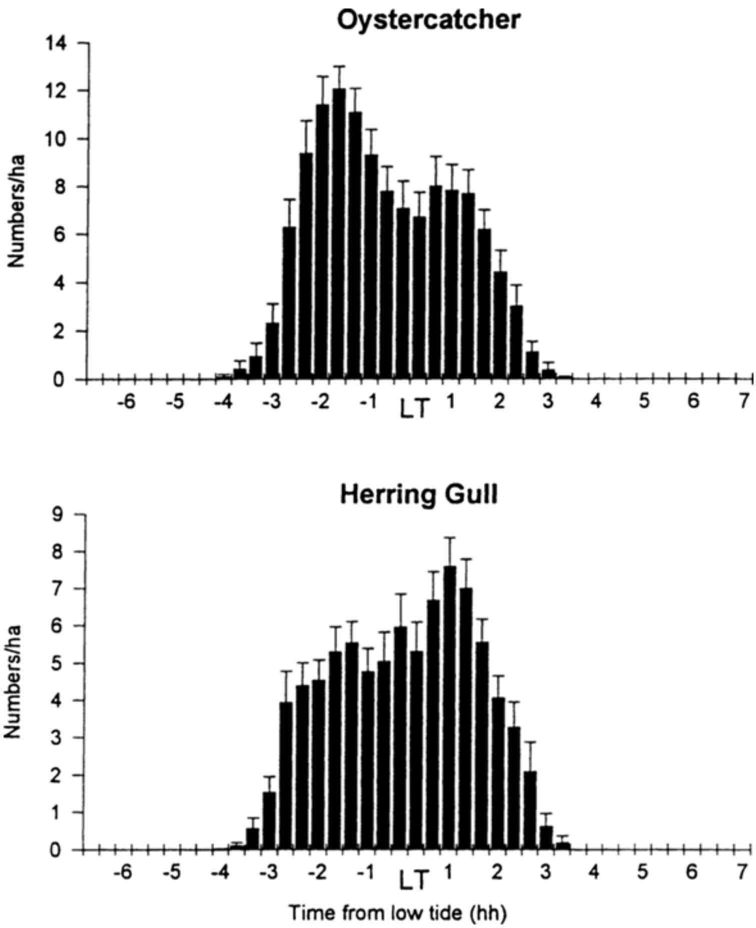

Fig. 4. Tidal pattern of the abundance of oystercatchers and herring gulls on mussel beds in the Königshafen. Mean values of 33 tides from July to November 1993

1993). The content of the pellets is, however, biased towards hard shelled prey. On the mussel beds less than 10 % of the prey items taken by herring gulls could be identified as mussels (Dernedde, 1993; Hertzler, 1995). However, as the mussels taken by herring gulls were relatively large compared to other prey items, it is estimated that mussels made up 20 % of their food intake. From the densities at low tide (Figs 4 and 5) and the occurrence of herring gulls in the Königshafen (Fig. 3), it is estimated that on average 10 herring gulls ha^{-1} mussel patch take their daily food demand from mussel patches. Assuming a daily food demand of 53 g AFDW, annual mussel consumption is calculated at 3.6 g AFDW m^{-2}.

In total, the mussel consumption by these three bird species amounts to 378 g AFDW m^{-2} of which 92 % are taken by eiders. Birds, thus, consume annually 30 % of the average mussel biomass of the mussel beds in the Königshafen.

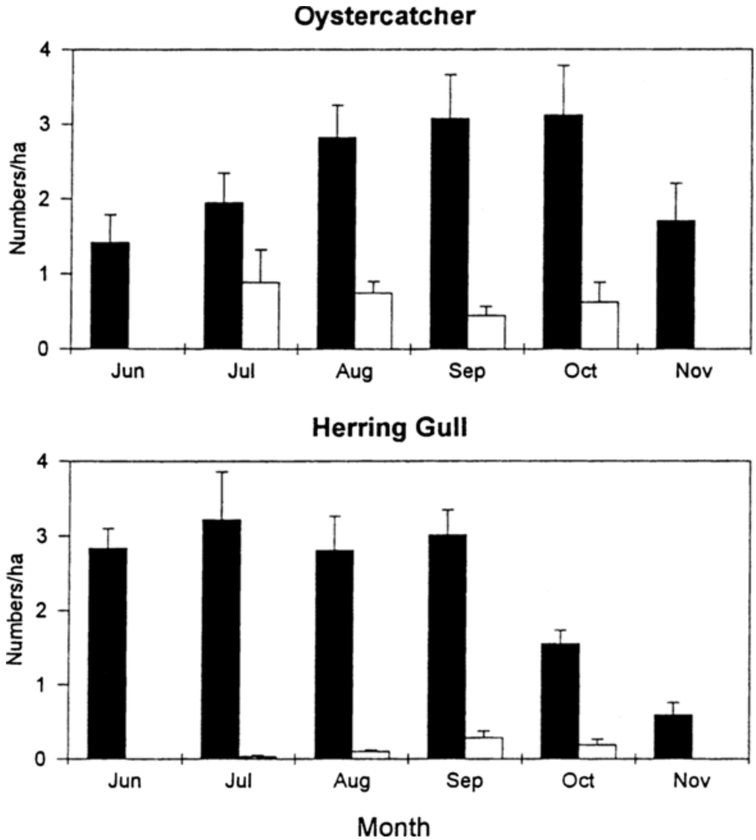

Fig. 5. Mean densities per tide (12.4 hours) of oystercatchers and herring gulls on mussel beds (black bars) and adjacent sandflats (white bars) in the Königshafen

DISCUSSION

This study shows that predation by birds annually removes a substantial proportion, i.e. 30 %, of the biomass of the intertidal mussel beds in the Königshafen. Bird predation on the mussel beds is more intense than on the surrounding flats where birds consume about 20 % of the mean biomass (see Scheiffarth & Nehls, 1997, this volume). The development of the mussel beds in the Königshafen since the cold winters of 1986/87 was characterized by an increase in biomass up to 1991 and constant biomass since then (Nehls & Ketzenberg, in press). As no substantial changes in bird numbers in this period were observed, our findings apparently reflect a stable situation which lasts for years. How is this stability achieved? In an earlier study Asmus (1987) estimated the annual production at mussel bed A (see Fig. 1) at 437 g AFDW m^{-2}, indicating a close match of production and consumption. However, production on the other mussel beds might well be somewhat higher, as these are placed closer to the tidal inlet and have shorter emersion periods. A natural mussel bed close to a tidal inlet in the Danish Wadden Sea reached an annual production of 675 g AFDW m^{-2} (Faldborg et al., 1994). The P/B (Production/Biomass) ratio of 0.36 found by Asmus (1987) was low compared to other studies. It thus appears to be realistic that the high predation rate is sustained by a production of 500 to 600 g AFDW m^{-2} and that birds remove a substantial proportion of the annual mussel production. This corresponds well with the constant biomass on the mussel beds observed over several years and the absence of other predators in this area. Starfish were absent on the mussel beds and crabs are assumed to be of minor importance because of the large sizes of mussels present. Size selection by the birds restricts the predation pressure to the smaller individuals of the mussel population so that a part apparently escapes predation by growth (Fig. 2). However, as the productivity of mussels decreases with their size (Asmus, 1987) this does not contradict our findings.

Similar conditions were found in the Ythan Estuary, Scotland, where again eiders, oystercatchers and herring gulls consume 73 % of the annual mussel production (Baird & Milne, 1981). Within the Wadden Sea the close fit between production and predation will probably be more the exception than the rule. Predation is likely to be limited by two factors: (1) The high mortality of mussels caused by storms or ice creates highly variable mussel stocks (Dankers & Koelemaij, 1989; Obert & Michaelis, 1991; Beukema et al., 1993; Nehls & Thiel, 1993). Because bird populations cannot adjust to these rapid changes, their predation rate usually reaches only 10 to 20 % of the annual production (Nehls 1989, Wolff 1991). (2) Some mussel beds will be unattractive for birds when flesh content is too low and mussel shells are too thick. Growth conditions of mussels are mainly influenced by tidal elevation (Goss-Custard et al., 1993; Faldborg et al., 1994; Pulfrich, 1995; Ruth, 1994) and by the position of a mussel bed within a tidal basin (Ruth, 1994). In general, growth conditions improve with increasing inundation time and with decreasing distance to the tidal inlet. As shell thickness and flesh content are negatively correlated (Goss-Custard et al. 1993), differences in the growth conditions may have significant effects on the mussel quality from a birds perspective. This is most likely to affect eiders, which swallow whole mussels and rely on high-quality mussels (Nehls, 1995). Mussel beds with long emersion periods are therefore unlikely to be attractive food sources for eiders. Although oystercatchers reach higher densities on mussel beds in other areas, their predation rate is always much lower than that of eiders in the Königshafen (Zwarts & Drent, 1980; Craymeersch et al., 1986; Meire, 1993; McGrorty et al., 1990). High predation rates, as observed in our study area, are thus most probably restricted to stable beds with favourable growth conditions for mussels.

Energy flow through mussel beds apparently forms a special case within the Wadden Sea ecosystem. There, most energy is thought to be unavailable for higher trophic levels due to a high energy turnover in the small food web (Kuipers et al., 1981). Mussel beds, in contrast, form a short link between primary production and avian predators. Mussel beds efficiently utilize their food resources in the overlaying water columns (Asmus & Asmus, 1993; Butman et al., 1994) and within the Wadden Sea their populations may reach sizes which are able to filtrate the whole water body of their tidal inlet in a short time (Danker & Koelemaij, 1989). The size of the mussel population has a considerable influence on total energy flow. In the Königshafen, although only 2.5 % of the area are actually covered with mussels, their share of the total biomass of the area reaches 50 %, because the biomass on the tidal flats only amounts to about 47 g AFDW m^{-2} (Asmus et al. 1996). Under stable conditions, mussels may thus take the dominance in the Wadden Sea ecosystem, and a much higher proportion of primary food supply than previously estimated may become available to higher trophic levels.

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