

# DO COMMON EIDERS *SOMATERIA MOLLISSIMA* EXHAUST THEIR FOOD RESOURCES? A STUDY ON NATURAL MUSSEL *MYTILUS EDULIS* BEDS IN THE WADDEN SEA

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The feeding ecology of common eiders *Somateria mollissima* was studied on natural mussel *Mytilus edulis* beds in Königshafen on the island of Sylt, which forms a sheltered bay in the Wadden Sea of Schleswig-Holstein. The depletion of the mussel stocks was examined by comparing the size selection of eiders and the development of the structure of the mussel population. Eider numbers in Königshafen varied from 400 to 4,500 with the highest numbers recorded during autumn migration and winter. The eiders predominantly fed on mussels forming dense beds close to the low water line. In most months mussels formed the main part (>80%) of the eiders' diet. The importance of cockles *Cerastoderma edule* increased with increasing numbers of eiders in Königshafen. When eider numbers were at their maximum, up to 50% of the birds present were feeding aside the mussel beds. A significant negative correlation was found between the proportion of eiders feeding on the largest central mussel bed first occupied by eiders and the total numbers of eiders present in the area. This characterises this mussel bed as the preferred feeding ground and shows that a density regulation of eider numbers occurred. The size of the mussels selected by eiders showed a marked seasonal change with the largest mussels (median about 50 mm) being taken in midwinter and the smallest mussels (median about 35 mm) being taken after spawning in April. The biomass on the preferred mussel bed increased from 1,390 g AFDW (ash free dry weight) m<sup>-2</sup> in June 1990 to 1,960 g AFDW m<sup>-2</sup> in February 1991 and has remained at this level since then. In the meantime the density fell from 2,900 individuals m<sup>-2</sup> to 1,700 individuals m<sup>-2</sup>. The contrasting trends of density and biomass were explained by growth, as the median size of the mussels increased from 38 mm to 53 mm. Spatfall was estimated to contribute about 10% to mussel density annually and annual losses were calculated to amount to 20% of the mussels. A comparison of the changes in the structure of the mussel bed and the mussel sizes taken by eiders indicated that eider predation contributed significantly to mussel mortality. The constant biomass of the mussel bed, despite decreasing abundance, lead to the assumption that predation was compensated for by production. It is concluded that social interactions limit the density of feeding eiders below a level which would lead to prey exhaustion.

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A general consensus exists on the significance of limited food resources in determining the size of consumer populations. However, controversy exists on the problem of the frequency at which a given population will face situations of food shortage and at which level this mechanism acts (e.g. Newton 1980). Social interactions may determine which part of a population will have access to a given resource and which part will not. Resource depletion may thus be inhibited by behavioural mechanisms at a level below the actual capacity of a resource. This might be beneficial in the case of resources which are not renewed regularly and predictably, so that behavioural mechanisms allow utilisation for a longer period, though by a limited number of individuals only.

Extensive work on oystercatchers *Haematopus ostralegus* feeding in intertidal mussel beds, showed that interference limits the density of feeding birds, keeping the annual depletion even of the best feeding grounds and preferred size classes to 25-40% (e.g. Goss-Custard & Durell 1984, Zwarts & Drent 1981). Therefore, in the feeding territory of an oystercatcher, mussel abundance exceeds what the bird is able to consume during the time of its presence. It is thus generally accepted that territorial behaviour may limit population density independently of resource levels (Patterson 1980). Gregarious waterfowl, often feeding in large and dense flocks, represent another way of avian exploitation behaviour. There seems to be no upper limit for flock sizes, and feeding densities appear to be defined by the minimal individual distance between specimen. Depletion to an extent where a resource is no longer exploitable is a common feature and has been noted for herbivorous waterfowl (van Eerden 1984, Madsen 1988), diving ducks (Suter 1982) and eiders (Raffaelli, Falcy & Galbraith 1990), which may remove more than 80% of their food stocks in areas where densities are high. However, interference which results in a reduction in feeding rate as densities increase (Goss-Custard 1980) may cause a dispersal of birds and thus reduce local food depletion. The strength of interference depends on the

aggression of the birds and their densities. The response to interference will depend on the available food resources. Considerable differences in dispersal and local predation pressure thus occur between species and between different areas, and prey depletion may be either positively or negatively density dependent (Bernstein, Krebs & Kacelnik 1991).

We investigated the predation of eiders on natural mussel beds in Königshafen in the northern part of the Wadden Sea. The common eider is one of the most numerous waterfowl species in the Wadden Sea and in terms of consumption the most important avian predator of the area (Smit & Wolff 1983). However, the consumption by eiders only reaches 12% of the average production of their prey species, i.e. mussels and cockles (Nehls 1991), and is considerably lower than reported from other areas. On the other hand, seasonal changes in the distribution of eiders within the Wadden Sea (Swennen, Nehls & Laursen 1989, Nehls 1989, 1991) may reflect local prey depletion.

In this paper we describe the seasonal pattern of the utilisation of mussel beds and compare the impact of eiders on different mussel beds. The aim of the study was to analyse the significance of eider predation on the density and structure of mussel beds and to assess whether behavioural responses to eider density or numerical responses to changing mussel populations affect predation pressure.

## Study area and methods

### *Study area*

Our investigations were carried out in Königshafen on the island of Sylt in the northern part of the Wadden Sea (Fig. 1). Königshafen is a shallow bay formed by a bending chain of dunes. The area encloses about 4.5 km<sup>2</sup> of tidal flats which are characterised by coarse sand. Tidal range averages 1.8 m and is smaller than in the more central parts of the Wadden Sea where tides may exceed 3

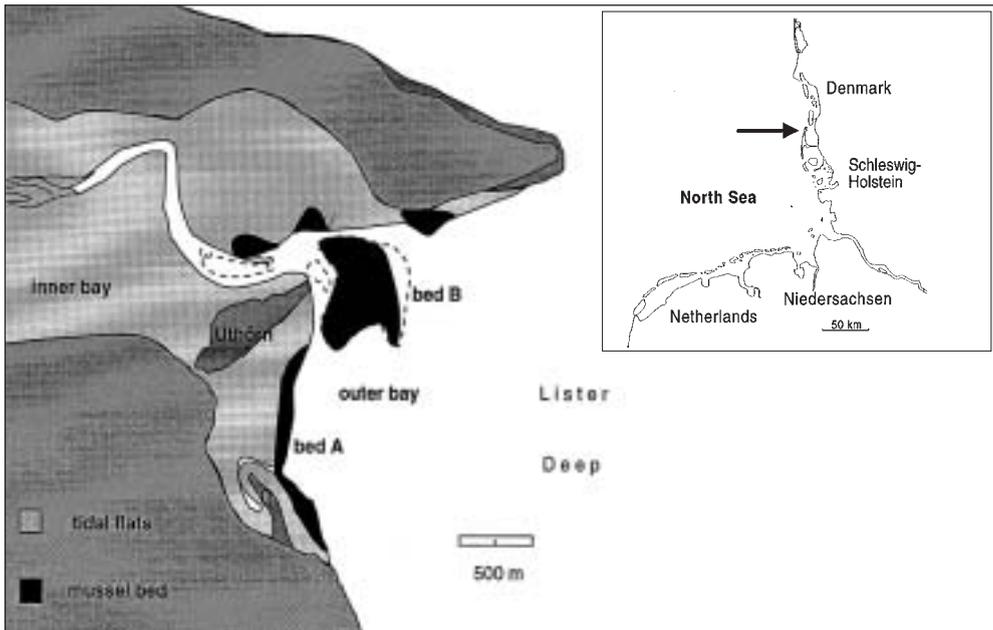


Figure 1. The Königshafen study area with distribution of mussel beds and tidal flats.

m. Since the 1930s mussel beds have increased in the area and they cover about 5% of the mudflats during the time of the study. The productivity of the area is of the same magnitude as in other parts of the Wadden Sea (Asmus & Asmus 1990). Mussel beds form the most productive community and reach biomass values over 1.5 kg AFDW (ash free dry weight)  $m^{-2}$ , which exceeds the average biomass of the surrounding tidal flats (16-30 g AFDW  $m^{-2}$ ) by far (Asmus 1987).

### *Eider numbers*

From March 1990 to June 1992, eider numbers were surveyed every fortnight by ground based investigations. Their distribution on the feeding grounds was mapped every 15 or 30 minutes over whole tidal cycles for 49 days from an observation tower placed on the tip of the island of Uthörn (see Fig. 1). For this purpose the study area was subdivided into eight units where eider num-

bers and activity were monitored, thus allowing separate analysis of the different feeding grounds.

### *Eider food*

Eider faeces were collected on a high tide roost on the island of Uthörn, adjacent to the mussel beds. Eider faeces contain a large proportion of indigestible fragments (e.g. mollusc shells and crab claws) which are easy to determine. As eiders tend to feed on one prey species at a time (Ketzenberg 1991, Nehls 1991), the majority of faeces contain fragments of only one prey species. To assess the proportion of the different species in the eiders' diet, we simply counted the number of faeces containing the different prey types on the roost. For detailed analysis a subsample of faeces was collected and washed through a sieve in the laboratory. The umbos of mussels were separated from the remains and were used to calculate the size of mussels taken by eiders. For calculation of mussel length (L)

the following regression relating umbo width (U) and length of intact mussels was used:

$$L = 40.927 * U - 5.502 * U^2 - 9.638,$$

$$r^2 = 0.908, P = 0.0001, N = 101$$

As the umbo\*length relation may differ regionally, depending on age structure and growth condition of the mussels, this regression was based on biometric data of mussels from Königshafen. A non-linear regression in our study results from a high portion of older mussels because growth rate decreases with age whereas shell thickness continues to increase (e.g. Nehls 1991).

### Mussel population

Most mussel beds of the Königshafen area are found close to the low water line where the bay opens to the deeper parts of the Wadden Sea. The intertidal mussel population of Königshafen concentrated in five beds of which two were regarded in this study, i.e. bed A, which stretches along the low-water line from Uthörn to the main island, and bed B, which is the largest mussel bed of the area, an island-like mussel bed between two gullies leading to the inner Königshafen (see Fig. 1).

Samples of mussels were taken using a 500 cm<sup>2</sup> corer. Numbers of samples per sta-

tion varied from 4 to 6, depending on the purpose of sampling. In February 1991 only three samples per station were taken. Samples were sieved (mesh width 1.5 mm) and all mussels measured to the nearest millimetre. All samples were taken within patches of mussels. For establishment of length/frequency distributions, data from all stations were pooled. Biomass data were not measured directly but calculated using the following length/weight equation, which was derived from pooled data of all samples:

$$\ln \text{AFDW (g)} = \ln \text{lenght (mm)} * 2.962 - 11.643,$$

$$r^2 = 0.943, P = 0.0001, N = 282$$

Due to the seasonal changes in the condition of the mussels the values presented here will differ somewhat from the real situation. However, for our purpose, which is to detect increases or decreases over a longer period, it seems justifiable to ignore the annual pattern of spawning and condition regaining.

## Results

### Eider numbers

Eiders visited Königshafen throughout the year with the lowest numbers below 500 non-breeders during the breeding season (May-June) and the highest numbers with up

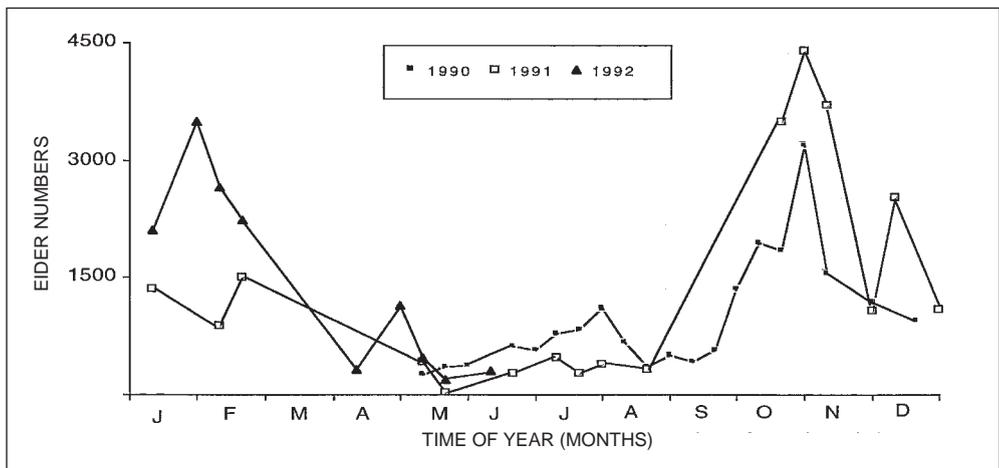


Figure 2. Phenology of eider numbers in Königshafen, based on fortnightly counts during 1990 - 1992

to 4,500 during autumn migration (Fig. 2) Immigration of birds originating from Baltic breeding grounds started in June. During the moulting period (July-August) the eider population mainly consisted of immature birds (> 80%); this is in contrast to the large concentrations of moulting eiders in the Wadden Sea where > 80% of the population consists of adult males (Nehls 1991). Numbers of moulting eiders rarely exceeded 1,000 birds, because frequent disturbances caused by recreational activities drove the eiders away (Ketzenberg 1993). During autumn migration the composition of the eider population in Königshafen equalled that in the rest of the Wadden Sea, holding a slight majority of adult males. No obvious changes in numbers or phenology were detected during the study period.

### *Distribution on feeding grounds*

Eiders foraged in mussel beds, gullies or tidal flats by diving or head-dipping. Trampling, which is mainly used to wash cockles out of the sediments, was rarely seen during the study period. The feeding activity was related to the tidal cycle with the activity being highest in periods of low water levels. On

most mussel beds in Königshafen foraging activities and eider numbers were highest in the four hours of low tide level. However, the birds left the mussel beds when these became completely immersed. In the summer months, when eiders spent only little time feeding, the presence of the birds on the mussel beds was almost restricted to this period whereas in the winter months, when much more time was spent feeding, eiders were present on the mussel beds during the whole day except when the beds became dry. Many birds that foraged at mussel beds in the eastern part of Königshafen rested on the island of Uthörn during high tide and left by ebbing tide for the mussel bed and returned by rising tide to the roost, thus getting two times free transport to and from the roost.

Eiders predominantly used the mussel beds in the eastern part of Königshafen, where the bay opens to the Lister Deep. Daily variations in the spatial distribution within Königshafen were mainly attributed to human disturbances (see Ketzenberg 1993) or variations in the tidal amplitude. There was a significant negative correlation between eider numbers present in Königshafen and the proportion of eiders feeding at the mussel bed (Fig. 3). At times when eider numbers were low, the majority of birds were feeding at bed

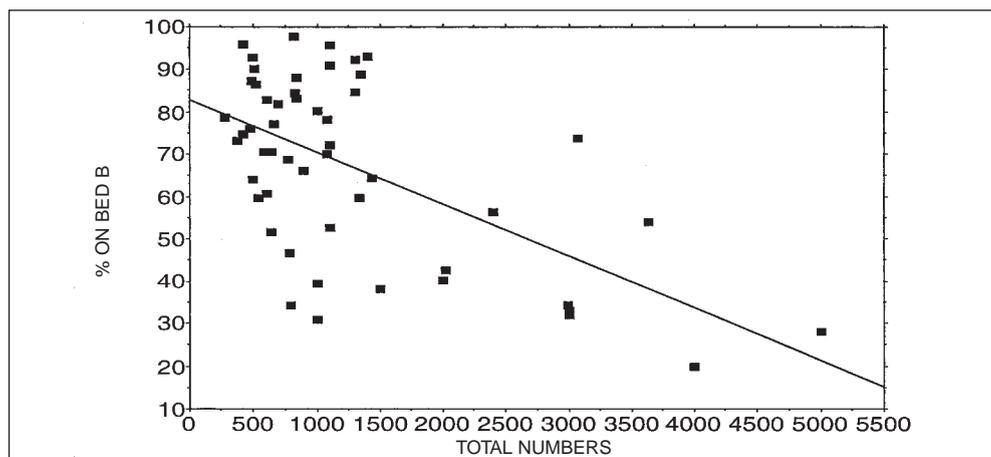


Figure 3. Correlation of eider numbers on mussel bed B and total numbers in Königshafen ( $r^2 = 0.348$ ,  $P = 0.0001$ ). Data of counts from 1990 to 1992 are pooled. Numbers on bed B are maximum numbers during low water level, when feeding activities are highest, selected from continuous scan observations of the time from two hours before to two hours after low tide.

B, which thus could be characterised as the preferred, and first occupied, feeding ground of Königshafen. In July, up to 90% of all eiders in Königshafen were feeding there. It further indicated that a density regulation occurs as eider numbers on bed B level off at about 1,000-1,500 individuals. When eider numbers increased during autumn migration, the birds dispersed over the total area of Königshafen and the proportion on bed B fell to 35%. During the time when maximum numbers were present (October-November) a large proportion fed aside the mussel beds at the tidal flats where mainly cockles were taken (compare Fig. 4), but as numbers went down in late winter, the birds once again concentrated on bed B, where up to 80% were found in spring. During the time of the study no marked annual differences in the spatial distribution and habitat utilisation of eiders in Königshafen were observed.

*mus maenas* contributed significantly to the eiders' diet. Other species, including razor clams *Ensis directus*, hermit crabs *Eupagurus bernhardii*, seastars *Asterias rubens*, urchins *Echinoidea* sp. and snails *Littorna littorea* and *Crepidula fornicata* were taken regularly, but by very few birds only. Other species, such as ragworms *Nereis virens* were taken only occasionally. Mussels formed the main part of the eiders' diet in Königshafen for most of the year. In the period from May 1990 to February 1991, when faeces were investigated each fortnight, other species were only important as food items in May and October- November, and only in this period was the share of mussels in the eiders' diet below 80% (Fig. 4). Additional sampling in 1991 and 1992 revealed the same trend, with a relatively high portion of shorecrabs being taken in May and June and a share of about 50% of cockles in October and November.

*Eider food*

The remains of 11 macrobenthic invertebrate species were identified in the faeces of eiders. Mussels, cockles and shorecrabs *Carci-*

*Size selection*

Eiders consumed almost all sizes of mussels available ranging from 5 to 63 mm, with median sizes varying within 32-52 mm. De-

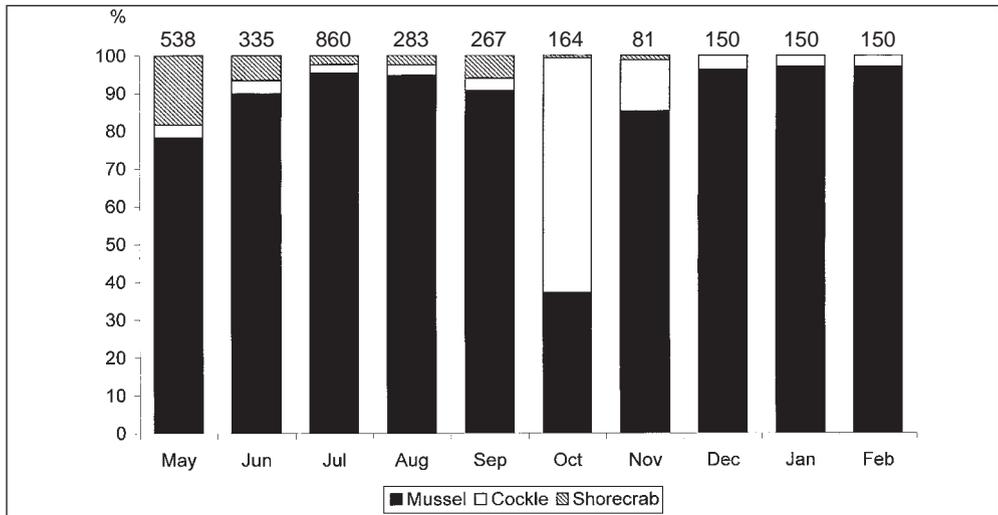


Figure 4. Seasonal changes in the composition of eider food in Königshafen as derived from indigestible fragments in faeces during 1990 - 1991. The bars give the percentages of faeces containing the most important food items. Numbers on top of the bars indicate sample sizes.

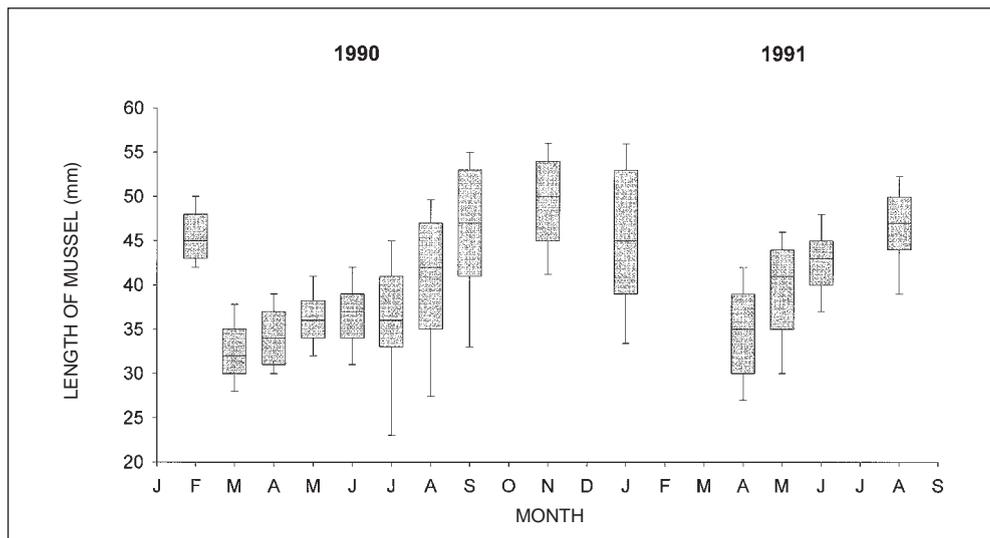


Figure 5. Seasonal changes in the sizes of mussels consumed by eiders during 1990 - 1992. Box plots indicate median, 50% (box) and 80% (bars) of the data.

spite the wide range of mussels that were consumed by eiders, strong selection of certain sizes was found as shown by the seasonal variation of in the sizes of mussels taken by eiders based on data from 1990 to 1992 (Fig. 5). The sizes of mussels consumed showed a marked seasonal trend, with the largest mussels being taken during winter and the smallest being taken in late spring, which probably represents a response to changes in the condition of mussels due to spawning in spring (see Cayford & Goss-Custard 1990). Of all mussels consumed by eiders, 80% ranged in size within 30-55 mm. Eider predation thus concentrated on about one third of the sizes found in the mussel population on the beds studied (see below).

#### *Mussel population and impact of eider predation*

The mussel beds were not evenly covered with mussels. Mussel patches alternated with pools or bare sandflats. The coverage of bed B was estimated by aerial photographs taken in August 1992. The total area of mussel bed B was 0.14 km<sup>2</sup>, of which 25-30% was covered

with mussels. Bed A was estimated to contain a similar area covered with mussels, but as its borders were less clear and mussels were more spread out, it could not be accurately determined from the aerial photographs.

The structure of the mussel beds showed the characteristics of an older population formed by more than one year-class (Fig. 6). In June 1990 the length/frequency distribution of the mussels showed a maximum of around 40 mm. Mussels of this size probably represented the spatfall of 1987, which built up most of the mussel population in the Wadden Sea of Schleswig-Holstein at that time. Only very few mussels had reached their maximum length of about 70 mm, indicating that a high mortality of older mussels occurred in the time before the study, probably during the cold winters before 1987.

Changes in the structure of the mussel populations during the study period were caused by three different factors: 1) New spat recruited to the population, 2) growth of the mussels lead to an increase in average mussel size, and 3) predation, especially by eiders, caused size-specific mortality.

The changes in population structure from June 1990 to February 1991 differed be-

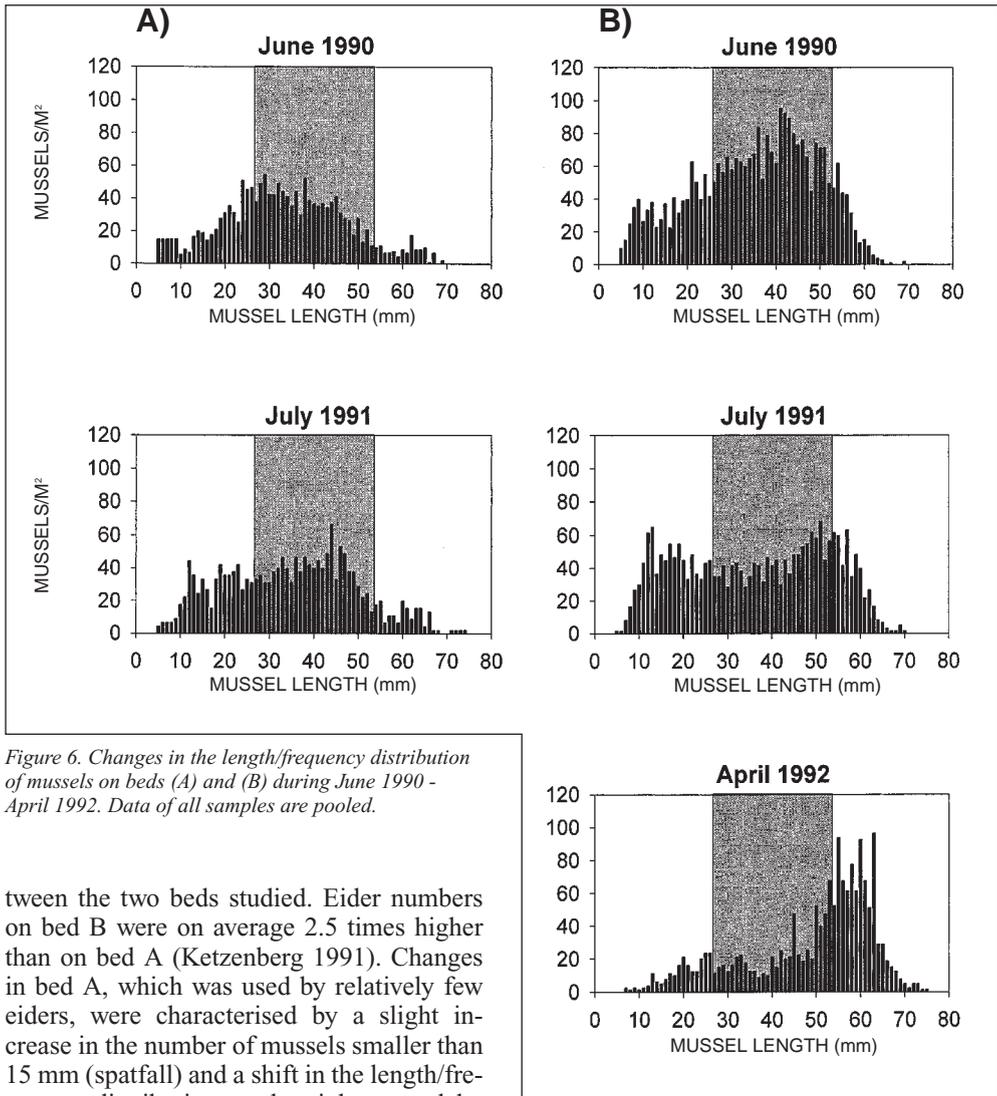


Figure 6. Changes in the length/frequency distribution of mussels on beds (A) and (B) during June 1990 - April 1992. Data of all samples are pooled.

tween the two beds studied. Eider numbers on bed B were on average 2.5 times higher than on bed A (Ketzenberg 1991). Changes in bed A, which was used by relatively few eiders, were characterised by a slight increase in the number of mussels smaller than 15 mm (spatfall) and a shift in the length/frequency distribution to the right caused by growth. However, the numbers of larger-sized mussels remained at a constant level (see Fig. 6). On bed B, which was intensively used by eiders, spatfall and growth was similar to those of bed A, but a decrease in the number of mussels ranging in size within 20-45 mm was observed. The abundance of mussels larger than 45 mm increased. However, the increase in the number of the larger mussels did not match the decrease in the number of smaller mussels and a reduction in the number of mussels larger than 20 mm

was thus evident. Although some spatfall occurred after June 1990 the abundance of mussels decreased slightly (Table 1, Fig. 7). Losses of mussels occurred in the sizes which were taken by eiders most frequently (compare Fig. 6). On bed B, where the changes could be monitored over a longer period (bed A was damaged by ice in February 1991), mussel densities decreased until spring 1992 despite some additional spatfall

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Table 1. Mean density, median size and biomass of mussels on bed B (see Fig. 1) during June 1990 - April 1992. N gives the number of samples taken, density is expressed as individuals/m<sup>2</sup> and biomass as g AFDW/m<sup>2</sup>.

Month	N	Mean density	Median size (mm)	Biomass/m <sup>2</sup>
June 1990	21	2899 ± 1306	38	1389
September 1990	24	2579 ± 1142	38	1400
February 1991	12	2465 ± 1029	37	1403
July 1991	16	2271 ± 691	37	1964
October 1991	16	1959 ± 693	47	1690
January 1992	16	2339 ± 1104	46	1805
April 1992	16	1695 ± 1887	53	1838

during summer 1991 (see Figs. 6 and 7). Assuming a successful mussel recruitment of 250 mussels m<sup>-2</sup> in both years, a decrease from 2,900 to 1,700 mussels m<sup>-2</sup> represents some 50% mortality from June 1990 to April 1992. Losses occurred mainly in mussel sizes below 55 mm and in April 1992 the

population was dominated by old, large-sized mussels (see Fig. 6 and Table 1). The biomass of the mussel bed followed a different trend and increased by 50% during the first year. Thereafter the biomass stayed more or less constant at about 1.8 kg AFDW m<sup>-2</sup>. A substantial part of the mussel population escaped eider predation by growing to a size unsuitable for eiders. In April 1992 about half the mussels present on bed B had surpassed the size classes suitable for eiders (< 55 mm). In June 1990, 93% of the individuals and 79% of the biomass on bed B were suitable for consumption by eiders, but only 50% of the sizes and 27% of the biomass remained so in April 1992 (see Figs. 6 and 7). Considering the decrease in mussel abundance in bed B and the shift in the size frequency distribution towards larger sizes it appears that the density of mussels suitable for consumption by eiders decreased by two-thirds. An additional sampling in February 1993 showed this situation to be stable, with some recruitment keeping the density high and about two-thirds of the biomass consisting of mussels larger than 55 mm, thereby being out of reach for the eiders (see Fig. 7).

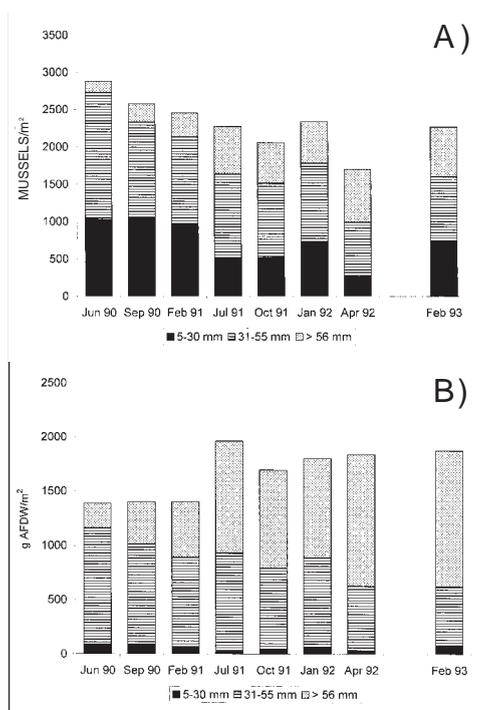


Figure 7. Density (A) and biomass (B) of mussel sizes on bed B during June 1990-April 1992. For comparison data for February 1993 are presented.

## Discussion

Following an eider population increase (Laursen 1989), parts of the Wadden Sea have only recently become inhabited by eiders, and areas where eiders were scarce in the 1960s now hold several ten thousand eiders. How-

ever, in the northern and western parts of the Wadden Sea where eiders were abundant before, numbers remained constant indicating that an upper limit of eider densities had been reached (Nehls, Bräger, Meißner & Thiel 1988, Swennen et al. 1989). Knowledge on the relation between eider predation and the dynamics of mussel beds in these areas may thus help us understand the underlying processes.

The population dynamics of mussels in the Wadden Sea are characterised by erratic spatfall and destructive events. Cold winters with extensive ice cover on the tidal flats and storms are the main factors influencing the abundance and distribution of mussel beds (Dankers, Koelemaij & Zegers 1989, Nehls & Thiel 1993). A common pattern is that a cold winter largely reduces the population and a strong spatfall restores it the next summer. However, in the time between two destructive events mussel beds are subject to predation by eiders and other predators, which have to adjust their behaviour and populations to highly variable food supplies.

Two contrasting developments occurred on the mussel beds in Königshafen during the study period. The abundance decreased but the biomass initially increased and then remained constant at a level of 1.8 kg AFDW m<sup>2</sup>. Size selection by eiders directed the predation pressure to a third of the mussel sizes and a reduction in the abundance of mussels in the sizes preferred by eiders was observed on bed B. However, annual losses even of the preferred mussels were relatively low. A proportion of mussels, which was high enough to ensure a constant biomass, escaped eider predation by growing larger than 55 mm. Predation by eiders was thus compensated for by production although little recruitment renewed the mussel population. At the end of the study period the majority of the mussels were no longer affected by predation by eiders. Similar findings were reported on eiders utilising mussel cultures in the Wadden Sea (Nehls & Ruth 1994). Because eiders do not affect the main part of adult mussels, which are the crucial part of the population for reproduction, it is concluded that

eiders are not an important factor influencing the population dynamics of the mussels in Königshafen.

What are the reasons for the low predation pressure? The predation by eiders, like that of other waterfowl, may well lead to an exhaustion of their food resources. In the Ythan estuary in Scotland, eiders consume approximately 40% of the annual mussel production (Milne & Dunnet 1972) and may deplete preferred mussel beds by 80% over winter (Raffaelli et al. 1990). Predation rates by eiders on mussel beds of up to 55% have also been observed in Canadian waters (Guillemette, Himmelmann, Barette & Reed 1993). Eiders are numerous in the Lister Deep area which borders Königshafen and both moulting and wintering numbers often exceed 20,000 individuals (Nehls et al. 1988, Nehls 1991, G. Nehls, unpubl. data). The mussel beds in Königshafen formed an attractive food resource for eiders in the years of our study. Many mussel beds in the exposed parts of the Wadden Sea of Schleswig-Holstein were removed by severe storms in early spring 1990, but areas sheltered by islands, such as Königshafen, were not affected (Nehls & Thiel 1993). In the winters of 1990/91 and 1991/92 eiders concentrated in the areas east of the islands (G. Nehls, unpubl. data), so why did not more eiders occur in Königshafen? Foraging theory assumes that birds choose their feeding areas to maximise their intake, which is a function of patch quality, social interactions and individual performance (Kacelnik, Krebs & Bernstein 1992). Our data indicate that social interactions limit the number of eiders on the preferred feeding grounds in Königshafen. The development of eider numbers on bed B is characterised by the negative correlation of eider numbers present in Königshafen and the proportion feeding on this bed. This pattern has also been found in non-territorial waders (Goss-Custard 1980) and characterises such places as preferred feeding areas where densities are relatively high. The conclusion is based on the simple assumption that birds first occupy the best feeding areas and as densities increase, competition and

thus interference increase and birds disperse and start to occupy suboptimal areas. A typical observation is that dominant birds occupy the best sites (e.g. Monaghan 1980, Ens & Goss-Custard 1984, Goss-Custard & Durell 1984). A negative effect of density on the food intake has indeed been found in Scottish eiders (Ashcroft 1976). The observation of eiders feeding aside the mussel beds on cockles during the time when numbers are highest indicates that part of the population has no access to the preferred feeding areas. The alternative hypothesis that eiders dispersed because the quality of the preferred area decreased, either through depletion by eiders or other factors, can be excluded as the number on bed B did not decrease. Furthermore, the effects of decreasing quality of feeding grounds would have lasted for the whole study period, as only little spatfall recruited to the mussel population. In both years cockles were only important for a short time in autumn. In late winter when eider numbers decreased, most birds were found once again on bed B. In April 1992, 80% of the 1,000 eiders remaining in Königshafen were found at bed B. As mussels may live in dense layers of more than 10 cm a large reduction of their abundance is possible before a response to the birds feeding efficiency occurs. The quality of a mussel bed is therefore not linearly related to mussel density but reaches a ceiling at a certain density. This might explain why a decrease in the densities of the preferred mussels did not affect its quality from the eiders' point of view.

The second factor mitigating any predation impact is the high biomass and production of the mussel beds in Königshafen. Biomass values of 1.8 kg AFDW m<sup>-2</sup> represent the upper range of biomass values which intertidal or estuarine benthic communities can reach (see Asmus 1987) and are much higher than in other areas of the Wadden Sea of Schleswig-Holstein (M. Ruth, pers. comm.). Our finding, that the biomass did not increase beyond this level although annual mortality was low, indicates that individual growth of the mussels was density

dependent. Food (e.g. planctonic algae) for a mussel bed is supplied by horizontal transport of the tidal currents, and mussels filter the overlying water column through their gills. At high densities mussel beds may substantially reduce their food resource (e.g. Asmus & Asmus 1991). Production can be regarded as limited by mussel density if the filtration capacity of the mussel bed is higher than the food supply from the water column. Under favourable conditions Wadden Sea mussels may reach a length of 50 mm within one or two years (Dankers et al. 1989), but in our study growth was much slower and by the end of the study few mussels had reached their maximal length of about 70 mm.

A combination of density regulation in eiders and a very high biomass of mussels thus leads to the conclusion that eider predation reduces mussel density, but production compensates for biomass losses. It is likely that eider numbers could be even higher without reducing mussel production, but it is unclear to what extent a reduction in mussel density would enhance growth of the remaining mussels. It will depend on the age structure of the mussel bed as production decreases with increasing size (Asmus 1987). Predation can be compensated for as long as the filtration capacity of the mussel bed is high enough to utilise their food resource completely and density dependent growth occurs. Apparently, this was the situation found in Königshafen.

Whether or not this situation is typical of the Wadden Sea depends on the structure of the mussel beds as well as on the mechanisms of density regulation in the eider. As the biomass of the mussel beds in Königshafen is at the highest possible level and the density of eiders has levelled off as a result of interference, predation does not depress the mussel population below its production capacity. This might be different in areas where mussels are spread out and the density of eiders, if related to the density of mussels, may reach a higher level. Although a clumping of resources should generally favour its depletion by predators, because

intake rates will be less affected by decreasing prey abundance, a contrasting effect arises because the clumping of resources increases competition and thus interference (Milinski & Parker 1991). Consequently more birds may have access to a resource if it is spread out. This has been observed in oystercatchers feeding on mussel beds of the Wadden Sea, where the density of birds, as related to mussel bed surface, and hence predation impact was highest in areas with low mussel density (Zwarts & Drent 1981). This means, that the strongest predation pressure may not always occur in preferred areas. Mussel beds in other parts of the Wadden Sea generally show lower biomass values (500 g AFDW m<sup>-2</sup>, M. Ruth, pers. comm.) than those found in Königshafen. Therefore the density of eiders in relation to mussel density may favour a stronger depletion of mussel beds in other areas. In the Ythan estuary, Scotland, where predation by eiders causes a substantial reduction in mussel stocks, dense mussel beds only reach one third of the biomass value found in Königshafen (Milne & Dunnet 1972).

It is thus important to know how eiders distribute over food resources of different quality. The distribution of birds over feeding grounds of different quality depends on the mean level of interference leading to aggregation in species with low interference and to dispersed foraging in species with high interference (Sutherland & Parker 1985). If no interference occurs, all members of a population are expected to concentrate in the best food patch and disperse after depletion equalises patch quality. At higher levels of interference, densities should follow a gradient of the quality of different feeding sites. However, aggregation may alter this pattern considerably. Birds may aggregate in flocks because they are attracted by their companions or simply because they have to share a rare resource (Pulliam & Caraco 1984). Although eiders may gather in large and dense flocks, interference within these groups apparently is higher than in other waterfowl, e.g. geese. In the Wadden Sea, aggressive interactions between feeding or resting

eiders occur frequently (G. Nehls, pers. obs.). Flock formation in the Wadden Sea, where eiders rarely encounter predators, is at least partly, the result of clumped food resources: Observations of individually marked eiders only revealed a tide-induced synchronisation of the feeding behaviour of eiders and individual birds returning each tide to the same spots on the mussel beds (Ketzenberg 1991, Nehls 1995). When feeding on cockles, which are less aggregated than mussels, eider flocks disperse over large areas for foraging and may gather only on the roost (Nehls 1991). A dispersion of eiders in the Wadden Sea in relation to the quality of the feeding grounds is thus likely to occur. Feeding densities in other places will probably not be substantially higher than in Königshafen, though the feeding densities here may not represent the highest possible level.

This is in contrast to the findings of Guillemette et al. (1993) who observed high aggregation and synchronised foraging in the absence of aggressive interactions between eiders at mussel beds in Canadian reef habitats. Their results indicate aggregation as an important factor for habitat selection because of improved abilities to find suitable food patches: In large flocks the active part will always indicate the position of the food resource and serve as an orientation for birds resuming feeding after a rest. Although this behaviour has been observed in Königshafen (G. Nehls, unpubl. data) and in other tidal areas (Campbell 1978) during high tide, it is much less important in areas where most feeding activity occurs at low tide when mussels beds are exposed and visible. In contrast, tides restrict the availability of mussel beds to eiders and govern their activity pattern (Campbell 1978, Ketzenberg 1991, Nehls 1991, 1995), which can be regarded as a clumping of the resource in time and therefore should increase interference. As in our study, Campbell found that Scottish eiders used more feeding sites as numbers increased, but this was not the case in the Canadian study by Guillemette et al. (1993). Two different patterns of habitat exploitation

in eiders can be distinguished: 1) Aggregation and synchronised foraging in areas where eiders predominantly feed by diving (Campbell 1978, Mudge & Allen 1980, Goudie & Ankney 1988, Ydenberg & Guillemette 1991, Guillemette et al. 1993), leading to a concentration of the predation rate in preferred areas which will facilitate an uneven distribution of predation pressure and favour local prey depletion, and 2) dispersed foraging in tidal areas (Campbell 1978, G. Nehls, pers. obs.) as a result of interference when aggregation is not beneficial, which should facilitate an even distribution of predation pressure.

Regarding the generally low predation in relation to the average total production of mussels in the Wadden Sea (12%, Nehls 1991), it can be concluded that prey exhaustion probably will not occur regularly, and seasonal changes in the distribution of eiders are only partly caused by depletion of the feeding grounds. Other factors may be more important, such as seasonal changes in food demand (Ketzenberg 1991, Nehls 1991) and size-selection (this paper) or increased sensitivity to disturbances during moult (Thiel, Nehls, Bröger & Meißner 1992, Ketzenberg

1993). However, our study was carried out at a time of relatively high mussel populations and the situation may change in times of small mussel populations. The fact that the number of eiders in Königshafen was not affected by a two-third decrease in their food source indicates that eiders may continue foraging until severe depletion of their food occurs. A much stronger depletion of the food sources than observed in our study is likely to occur at times of general food shortage, which may occur after cold winters (see Beukema 1979) or by overfishing of the mussel stocks (Laurson & Frikke 1987, Swennen 1991), when eiders concentrate on the remaining mussel beds.

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