

The influence of predation by herring gulls *Larus argentatus* and oystercatchers *Haematopus ostralegus* on a newly established mussel *Mytilus edulis* bed in autumn and winter

G. Hilgerloh¹, M. Herlyn² & H. Michaelis²

¹Forschungszentrum Terramare; Schleusenstr. 1, D-26382 Wilhelmshaven

²NLÖ-Forschungsstelle Küste; An der Mühle 5, D-26548 Norderney

ABSTRACT: Predation by herring gulls *Larus argentatus* and oystercatchers *Haematopus ostralegus* was evaluated on a newly established mussel *Mytilus edulis* bed on tidal flats of the German Wadden Sea. The mussel bed covered an area of 2 ha and showed a decrease in biomass of 40 % in the most densely covered parts from August to January. Synchronously, the extent of the mussel bed was reduced, resulting in a decrease of average biomass of 98 % over the whole mussel bed. From the beginning of August 1994 to mid January 1995, the average size of mussels increased from 10.7 to 20.3 mm. The P/B-ratio was 0.68 in August and 0.18 between September and November. Herring gulls and oystercatchers were the most important mussel predators. On average, 266 herring gulls and 63 oystercatchers were present on the mussel bed during one low tide; 34 % of the herring gulls and 78 % of the oystercatchers were observed to be feeding. Herring gulls fed at a rate of 4.2 mussels per minute and oystercatchers at a rate of 1.3 mussels per minute. While herring gulls took the most common mussel sizes (mean: 20 mm), oystercatchers searched for the largest mussels available (mean: 25 mm). Herring gulls consumed 13 mussels/m² (0.3g AFDW) during one day and oystercatchers 1.7 mussels/m² (0.1 g AFDW). Predation by birds was compensated by 33 % of the production. The proportion removed by bird predation amounted to 10 % of abundance and to 16 % of biomass (including production). Oystercatchers were responsible for 1 % of the reduction in abundance and for 3 % of biomass. Removal was highest in the most common size classes of mussels, mainly caused by herring gulls. However, the highest proportion of mussels was eaten in the largest size classes, mainly by oystercatchers.

INTRODUCTION

The epibenthic blue mussels *Mytilus edulis* are consumed by several bird species, the main mussel eaters being eiders *Somateria mollissima*, oystercatchers *Haematopus ostralegus* and herring gulls *Larus argentatus*. Predation effects on mussel beds by these species have been studied on the tidal flats of the North Sea and on hard bottoms of the Baltic Sea (Milne & Dunnet, 1972; Baird & Milne, 1981; Kautsky, 1981; Zwarts & Drent, 1981; Worrall and Widdows, 1984; Craeymeersch et al., 1986; Raffaelli et al., 1990; Egerup & Hoegh Laursen, 1992; Faldborg et al., 1994; Nehls et al., 1995; Hilgerloh, 1997). The strongest effect, with regard to the higher food consumption per day, was observed in eiders (Milne & Dunnet, 1972; Craeymeersch et al., 1986; Nehls et al., 1995). Till now, no

evidence could be found that the annual predation by birds ever exceeded annual production (Baird & Milne, 1981; Egerrup & Hoegh Laursen, 1992; Faldborg et al., 1994; Nehls et al., 1995; Hilgerloh, 1997). Thus, if predation by birds were the only mussel-reducing factor, the mussel populations would be expected to increase or to remain at the same level. However, other factors, such as predation by crabs *Carcinus maenas* and by fishes, parasites and physical factors, also contribute to the loss of biomass. In order to know the significance of predation for the development of a mussel population, predation by birds has to be considered in relation to those other factors. Two very different methods of approach have been applied: one study was based on exclosures (Worral & Widdows, 1984) and the other assessed predation effects by birds on tidal flats including several mussel beds (Faldborg et al., 1994; Hilgerloh, 1997). According to the results, predation by birds could be unimportant or account for more than half of the loss.

Especially the period of the establishment of a new mussel bed seems to be a crucial phase because many of the new beds disappeared after the first winter. Considering the strong loss of abundance caused by birds which may occur on a mussel bed over winter (Zwarts & Drent, 1981; Raffaelli et al., 1990), it is not certain whether predation by birds plays an important role during the development of newly established mussel beds over the first winter.

This study estimates the influence of predation by herring gulls and oystercatchers on a newly established mussel bed. It investigates whether predation by these bird species has an important influence on the development of the mussel bed in autumn and winter and whether it can provoke a severe decrease therein.

MATERIAL AND METHODS

Investigations on the mussel bed

The study was performed on an intertidal mussel bed on the Neuharlingersieler Nacken (53° 43.25 N, 7° 44.00 E), which is situated in the German Wadden Sea (North Sea) close to the village Neuharlingersiel in Lower Saxony. A heavy fall of spat had resulted in large parts of the bed being covered by newly-established seed mussels. Mussel coverage on a young bed is more homogenous than on a mature bed. Samples with a surface area of 38.5 cm² and a depth of 10 cm were taken in those parts of the seedling beds which were most densely covered by mussels (Hilgerloh & Herlyn, 1996).

The biomass/m² was estimated with the equation:

$$B = (P \cdot S \cdot S')/10\,000$$

where P is the biomass/m² in dense mussel parts of the seedling beds, S the percent of the whole mussel bed covered by seed mussels and S' the coverage (%) of seed areas by mussels. S was measured along one transect which crossed the whole mussel bed. S' was estimated from a 1 × 2 m area divided into five parallel sections of 20 cm width. Gaps in the mussel cover smaller than the diameter of the samples were ignored. Six samples were taken at regular intervals along the transect used to determine S. Samples were taken 4 times over the period August–January.

Biomass determination

An equation relating mussel length and individual biomass was obtained using mussels from an adjacent bed, where young mussels had settled at the same time as on the study site. Dry and ash weight and length of individual mussels were determined. Mussel length was measured by callipers with a precision of 1/100 mm. The flesh of single mussels was dried at 80 °C for 3 days to constant weight. Ash content was determined after combustion in a furnace at 500 °C for 24 hours and measured to an accuracy of ±1 mg. The relation between mussel length and biomass was:

$$\text{g AFDW} = 0.0008 \cdot e^{(0.1787 \cdot M)}$$

($r^2 = 0.96$; $p < 0.0001$), where M is the mussel shell length. The equation is valid for mussels from 5 to 40 mm length. All weight and individual biomass data are given as ashfree dry weight (AFDW).

Determination of production

The production per m^2 was calculated from changes in mean individual weight and mean abundance using the following equation (after Winberg, 1971):

$$P = (w_2 - w_1) \cdot 1/2 (n_1 + n_2)$$

where P is the production for a time interval; w_1 and w_2 are the mean individual weights at sampling dates 1 and 2; and n_1 and n_2 are mean numerical densities at sampling dates 1 and 2. Winberg (1971) made these calculations for single size classes but, in our study, all mussels settled in one single spatfall and so belonged to one size class.

Determination of mussel loss

Mussel loss per m^2 was calculated from changes in abundance and mean individual weight using the following equation (after Winberg, 1971):

$$E = (n_1 - n_2) \cdot 1/2 (w_1 + w_2)$$

where E is the elimination over a time interval, n_1 and n_2 are mean numerical densities at sampling dates 1 and 2; and w_1 and w_2 are mean individual weights at sampling dates 1 and 2.

Because of the homogeneous age structure of mussels, separation into size classes was again not necessary.

Observations of predators on the mussel bed

Counts were made 2–5 days per month from September to November, on a total of 10 days. Feeding and non-feeding birds were counted every 20 minutes from the time the mussel bed first emerged until it was covered. Feeding rate and the contribution of mussels to the food intake of individual birds were observed on 2 to 3 days per month from October to December (Martin & Bateson, 1986); only observations longer than one minute were used. For herring gulls, observations before and after 15th October, called

"autumn" and "winter" respectively, were analysed separately because the number of gulls present and the proportion feeding differed so much. Differences were tested by the Mann-Whitney U Wilcoxon test of the SPSS-program (Brosius & Brosius, 1995).

Determination of size preferences of predators

Faecal pellets of herring gulls and mussels opened by hammering oystercatchers were collected on 23rd November 1994. Hinges of mussels were extracted from 20 pellets and their widths were measured. The relationship between mussel length and width of hinge is given in the following equation, based on data from Janssand in 1992:

$$\text{mussel length} = 3.885 \cdot 19.593 \cdot \text{width of hinge}$$

($r^2 = 0.874$, $p = 0.0001$). The equation is valid for widths of hinge 0.45–2 mm.

Determination of daily food consumption

Daily food consumption was calculated in different ways (Hüppop, 1987; Goede, 1993; Hulscher, 1974; Lasiewski & Dawson, 1967). For a rough estimation of the daily food consumption, we used methods similar to those used by Meire et al. (1994) and Scheifarth & Nehls (1997), where costs for thermoregulation in winter were not considered. In this study, the basal metabolic rate of oystercatchers is taken from Kersten & Piersma (1987):

$$\text{BMR (watt)} = 5.06 \cdot \text{weight (kg)}^{0.729}$$

that of gulls from Aschoff & Pohl (1970):

$$\text{BMR (watt)} = 3.56 \cdot \text{weight (kg)}^{0.734}$$

Total daily energy expenditure (DEE) was assumed to amount to three times BMR (Drent et al., 1978; Kersten & Piersma, 1987; Castro et al., 1992). For benthic invertebrates a digestibility of $Q = 0.85$ was used (Kersten & Piersma, 1987; Zwarts & Blomert, 1992). Accordingly, the daily consumption is:

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

Weights of herring gulls are known from the breeding period on Mellum (Goethe, 1961); for oystercatchers monthly mean weights were available from the Netherlands (Swennen, in Cramp & Simmons, 1977), so that average daily consumption could be calculated for each month. 1 g AFDW of *Mytilus edulis* flesh corresponds to 20.77 kJ (Jansson & Wulff, 1977 and Asmus, pers. comm.). Average daily consumption of mussels amounted to 51 g AFDW for a herring gull, and varied, according to the month, between 43 and 52 g AFDW and 92 and 183 g AFDW for oystercatchers and eiders, respectively.

Predation model

Simple models were used to: (a) determine the daily food consumption by herring gulls and oystercatchers on the mussel bed; (b) determine the area-related consumption of the predators on the mussel bed; (c) determine the influence of predation on the mus-

sels. The calculation assumptions were as follows: the mean time of emergence of the mussel bed was taken to be the maximal time available for feeding; the time for which an individual fed on mussels was based on the proportion feeding and on the length of time the mussel bed was exposed. Consumption per low water period was calculated from feeding rate in three ways according to these assumptions: (i) each bird ate only mussels; (ii) all unidentified food items were assumed to be mussels; (iii) consumption was calculated by reducing the total consumption by the percentage of food items which were not mussels. The biomass of the mean mussel size taken by a species was taken as biomass for each mussel. Consumption per 24 h was calculated by extrapolating the daytime results during low tide to the following nocturnal low-tide period, with 1.97 low-tide periods/24 h, as investigations showed the same feeding activity at night as during daytime (Hulscher, 1976; Exo & Scheiffarth, 1994). Average area-related consumption was based on the mean number of feeding birds during one low-tide period, related to one m² of mussel bed. The influence of predation on the mussel bed was based on the four sampling dates and the mean of three consumption rates calculated under the three different assumptions.

The present evaluation of predation demonstrates how predation effects can be evaluated with a minimum of biological data. Predation effects were considered in autumn and winter only, because the newly established mussel bed was not discovered until the end of July and because mussel abundance within the seed areas and the coverage of the whole mussel bed diminished dramatically over half a year.

This evaluation is preliminary, as several assumptions may lead to an over- or underestimation of consumption. The latter is valid in the case of the calculation of the mean biomass of mussels eaten by each of the two species. Predation may be overestimated over the first months, as the preferred mussel size was determined in November. Predation might be underestimated because the average length of consumed mussels was taken as basis for the estimation of the mean biomass of a mussel and because the relation between mussel size and biomass was not linear. Predation may be overestimated, as the larger mussels are more likely to be seen if shells opened by oystercatchers are collected (Speakman, 1990).

RESULTS

Development of the mussel bed

The mussel bed was established on Neuharlingersieler Nacken in summer 1994 and covered an area of 18 979 m². By the end of November, it had reached a height of 45 cm. In the most densely covered parts, abundance as well as biomass decreased by 75 % and 40 %, respectively, between the beginning of August and mid January. But over the whole mussel bed, abundance decreased by 99 % and biomass by 97.6 % over the study period.

Biomass increased in August but decreased over the following months (Fig. 1) as a result of two processes: the growth of individual mussels (Fig. 2) and a decrease of abundance (Fig. 3). Over the whole study period the length of mussels increased from 10.7 ± 2.7 mm ($n = 945$) to 20.3 ± 3.6 mm ($n = 235$) (Hilgerloh & Herlyn, 1996). In August, biomass increased because the decrease in abundance was compensated by growth of individual mussels. From September to November, biomass decreased, because mussels

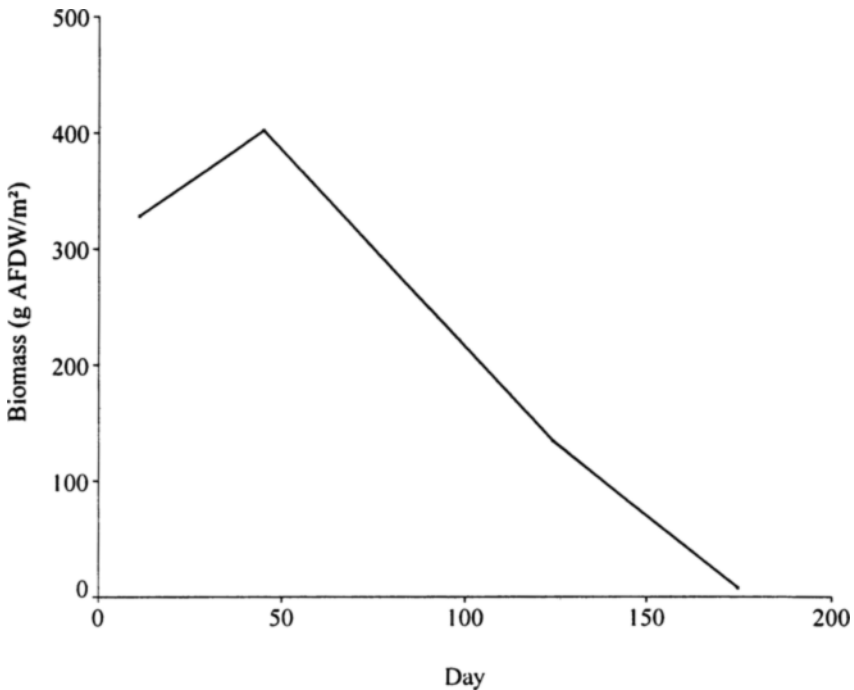


Fig. 1. Average biomass at the sampling dates (linear interpolation between dates). Day 11 = 5th Aug. 1994, day 45 = 2nd Sept. 1994, day 124 = 23rd Nov. 1994, day 175 = 13th Jan. 1995

grew less per day compared to August (Fig. 2), and at an insufficient rate to compensate for the decreasing abundance (Fig. 3). In December and January, mussels did not grow, so that a decrease in abundance, and also in biomass, continued (Fig. 1).

Production was highest in August (Fig. 4) because of the high abundance (Fig. 3) and strongest growth of individual mussels (Fig. 2). The production/biomass ratio (P/B) was 0.76 in the seed beds. For the period of September to November, the P/B ratio was only 0.19. Over the whole mussel bed the P/B ratios, as a whole, were 0.68 and 0.18 respectively.

On average, mussel loss amounted to 201.51 mussels/m²/day, or 4.28 g AFDW/m²/day. Abundance was reduced in August by 32 %, by 74 % from September to November and by 94 % by January. Biomass and production decreased by 35 % in August, by 80 % from September to November and by 94 % from November to January. During the study period as a whole, total production amounted to 296 g AFDW/m² and total loss to 33047 mussels or 617 g AFDW/m². Over the study period, there was clearly a large net loss of mussel biomass.

Number and feeding rate of birds

The two most significant mussel eaters on this mussel bed at low tide were herring gulls and oystercatchers. On average, 266 herring gulls and 63 oystercatchers were

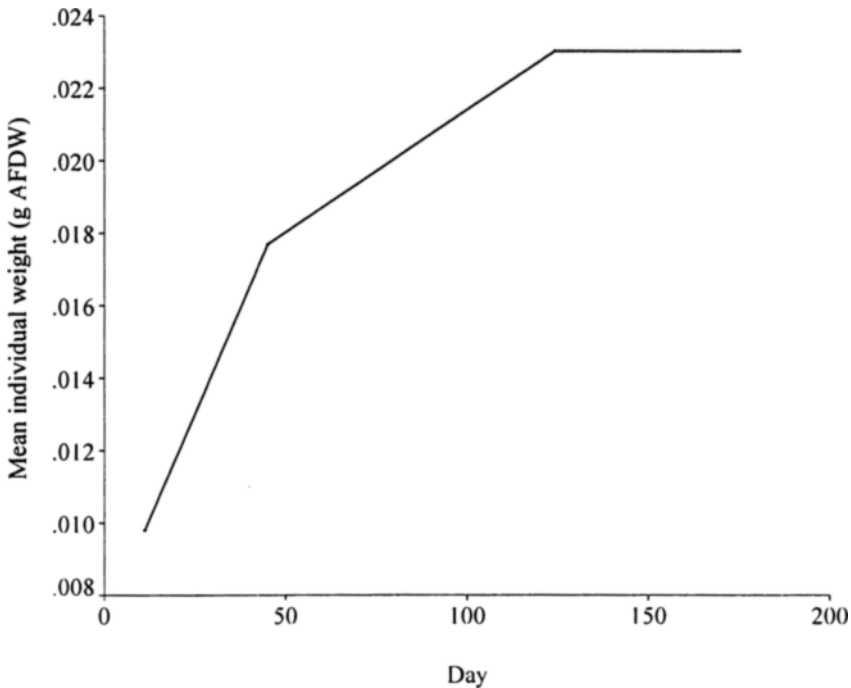


Fig. 2. Average weight of an individual mussel at the sampling dates (linear interpolation between dates) (For explanations regarding the days, see legend of Fig. 1)

present. Herring gull numbers were more variable compared to those of oystercatchers (Table 1). On average, 34 % of herring gulls and 78 % of oystercatchers were observed feeding (Table 1).

Extremely high numbers of herring gulls were present from the second half of October onwards, and the proportion feeding was higher than previously recorded (Table 2) ($P < 0.0001$).

The proportion of mussels in the diet was 74 % in herring gulls and 69 % in oystercatchers (Table 3). Oystercatchers fed at a rate of 1.3 to 1.4 food items per minute while herring gulls fed at a rate of 4.1 to 5 items. On average, mussels were taken by oystercatchers and by herring gulls at the rates of 1.3 and 4.2 per minute, respectively (Table 4).

Mussel sizes preferred by predators

The mean sizes of mussels eaten by herring gulls and oystercatchers were 19.76 ± 6.82 mm ($n = 1398$) and 25.48 ± 2.66 mm ($n = 308$), respectively. Herring gulls fed on the most common size classes of mussels on the bed whereas oystercatchers preferred the largest sizes; the corresponding biomass for the mean mussel length amounted to 0.027 g AFDW for herring gulls and to 0.076 g AFDW for oystercatchers.

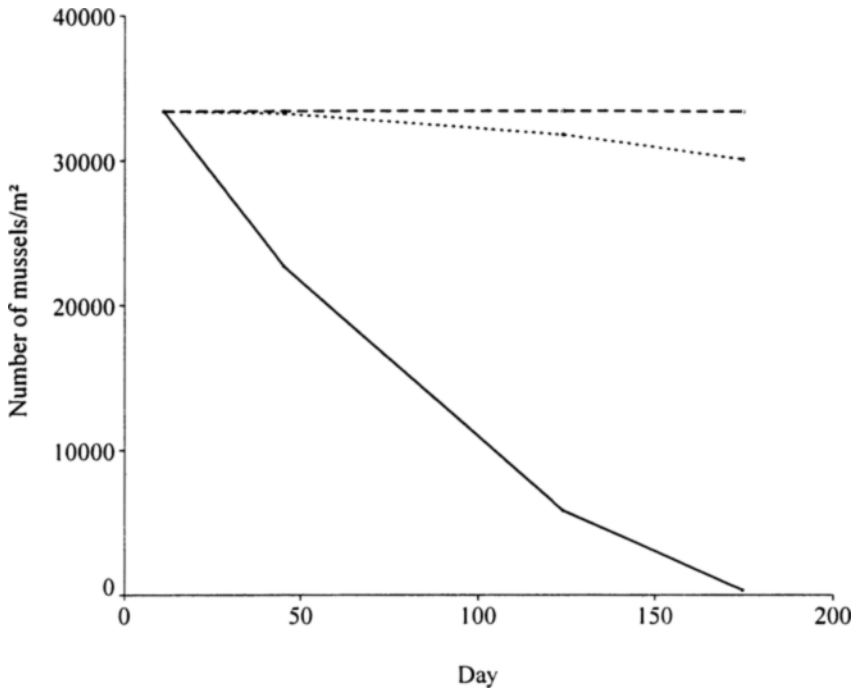


Fig. 3. Effect of predation on abundance (linear interpolation between dates). Dashed line = abundance at the beginning, and assuming no subsequent change; dotted line = loss of abundance caused by predation by birds; continuous line = total loss of abundance

Daily consumption of blue mussels by an individual bird

Daily consumption by a single herring gull was 742 mussels or 20 g AFDW on average, ranging between 15 to 23 g AFDW. Thus, on average 39 % of the daily food requirement was met by consuming mussels. In autumn, a herring gull ate 500 mussels per day, corresponding to 13.5 g AFDW and 26 % of the daily food demand. In winter, 1125 mussels or 30.4 g AFDW were eaten by herring gulls per day, equivalent to 60 % of the daily food demand. Over the study period, an oystercatcher consumed 523 mussels per day, corresponding to 39.7 g AFDW. Thus 83 % of daily food demand was met by consuming mussels.

Area-related consumption of mussels

Over one low tide period, 5–8 mussels/m², corresponding to 0.2–0.4 g AFDW, were eaten by herring gulls over the study period as a whole. In autumn, three mussels (0.088 g AFDW) and in winter, 31 mussels (0.761 g AFDW) were eaten per m² and day. Oystercatchers consumed 1.7 mussels per m² daily, corresponding to 0.129 g AFDW.

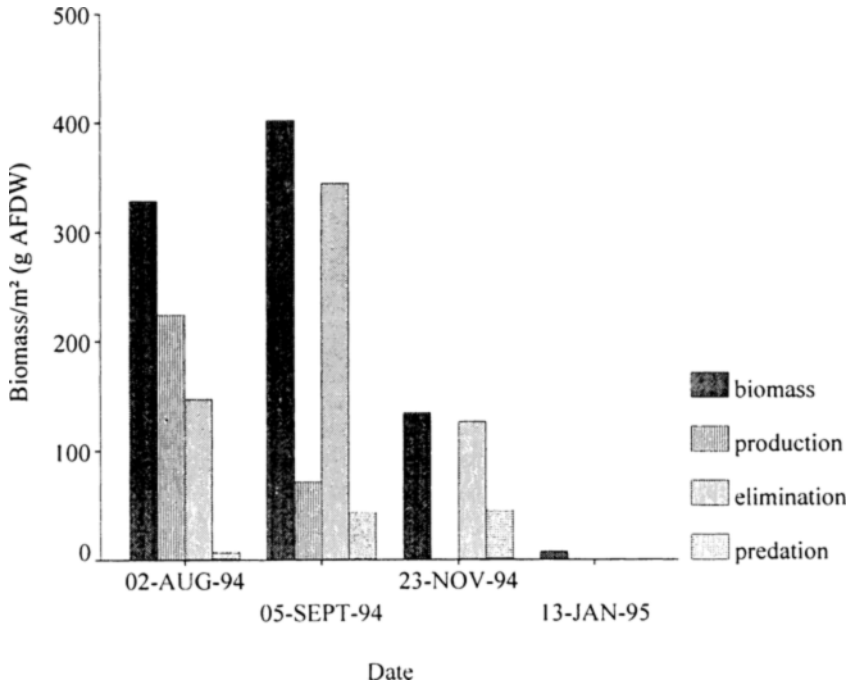


Fig. 4. Average biomass at sampling dates, production, total elimination and elimination by predation between sampling dates

Table 1. Average number of feeding and non-feeding herring gulls and oystercatchers on the mussel bed during one low tide (average of 10 low tides)

	Minimum	25 %	Median	Arithm. mean	75 %	Maximum	Counts (n)
Herring gull							
Total	1	66	212	266 ± 242	384	1043	160
Feeding	0	16	40	112 ± 145	183	601	160
Not feeding	1	40	122	154 ± 133	238	608	160
% feeding	0	15.26	28.73	33.84 ± 23	52.95	90	160
Oystercatcher							
Total	1	24	63	63 ± 43	92	180	153
Feeding	0	19	43	48 ± 34	77	147	153
Not feeding	0	4	8	15 ± 18	22	102	153
% feeding	0	71.66	82.46	77.98 ± 21	91.95	100	153

Table 2. Average number of feeding and non-feeding herring gulls, subdivided in autumn and winter

	Mini- mum	25 %	Median	Arithm. mean	75 %	Maxi- mum	Counts (n)
Autumn							
Total	1	38	98	139 ± 125	237	460	98
Feeding	0	7	21	28 ± 30	39	180	98
Not feeding	1	23	75	110 ± 112	185	420	98
% feeding	0	9.92	19.65	22.79 ± 19.14	30.56	90	98
Winter							
Total	31	313	411	467 ± 246	618	1043	62
Feeding	10	117	217	244 ± 157	330	601	62
Not feeding	20	139	198	223 ± 135	273	608	62
% feeding	9.37	37.38	53.73	51.30 ± 17.15	64.25	83.74	62

Table 3. Food items of feeding oystercatchers and herring gulls

Species	<i>Mytilus edulis</i> (%)	<i>Carcinus maenas</i> (%)	Worms (%)	Other mussels (%)	Not identi- fied (%)	Number of food items (n)	Minutes ob- served
Oystercatcher	69.02	1.96	0.39	7.06	21.57	255	177.9
Herring gull	73.8	0.3	11.4	0	14.6	403	97

Table 4. Feeding rate per minute of herring gulls and oystercatchers

	25 %	Median	Arithm. mean	75 %	Minutes observed	Number of birds
Herring gull						
(1) Only blue mussels	2.41	3.33	4.24 ± 3.15	5	35	15
(2) Blue mussels/ not identified	3.92	5.14	5.02 ± 1.80	5.74	34.7	13
(1) and (2)	2.90	4.48	4.60 ± 2.60	5.65	69.7	28
Total	2.61	4.18	4.07 ± 2.62	5.15	97	37
Oystercatcher						
(1) Only blue mussels	0.885	1.43	1.28 ± 0.38	1.59	25.5	5
(2) Blue mussels/ not identified	0.836	1.36	1.42 ± 0.67	1.82	65.8	14
(1) and (2)	0.93	1.43	1.38 ± 0.60	1.64	91.3	19
Total	0.93	1.32	1.39 ± 0.74	1.70	177.9	40

Effect of predation on mussel biomass and abundance

The percentage of observed loss in mussel abundance attributable to herring gulls and oystercatchers was 2 % in August, 9 % from September till November and 30 % in December and January. Over the whole study period, the loss of abundance due to predation was 10 % (Fig. 3). The percentage of the observed loss in mussel biomass attributable to birds was 5 % in August (Fig. 5), 13 % from September till November and 36 % in December and January. Over the whole study period, 16 % of the biomass loss could be explained by predation of herring gull and oystercatcher, and predation was compensated by 33 % of the production.

Loss of abundance in size classes of mussels by predation

Predation affected the frequency distribution of mussel size classes. Greatest losses occurred in the medium size classes due to intensive predation by birds from October to December, caused mainly by herring gulls (Fig. 5). Considering individual size classes, the greatest effect is found in the larger size classes (Fig. 6) because of predating oystercatchers.

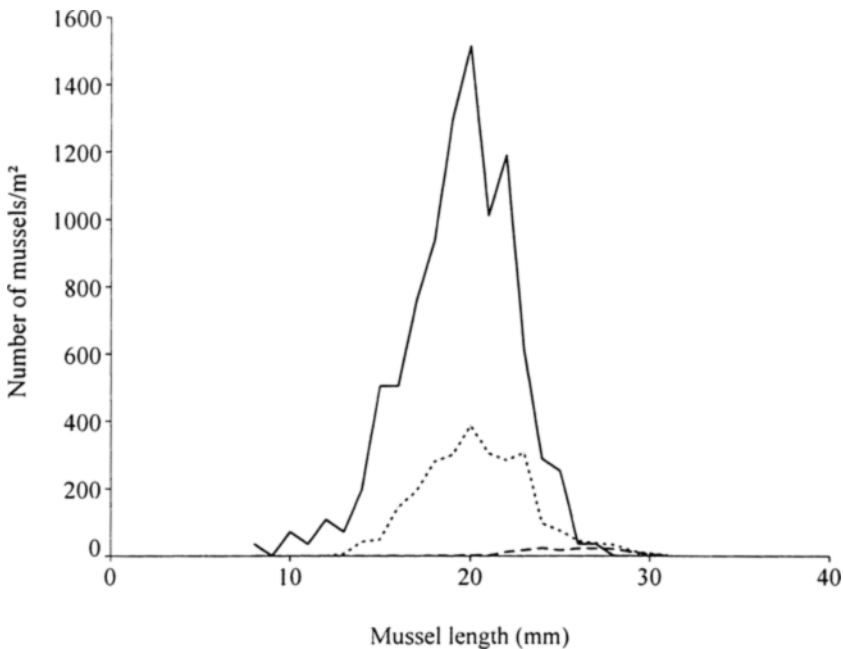


Fig. 5. Number of mussels of each size class eaten by oystercatchers (dashed line) and by herring gulls (dotted) during three months. Total number eaten by the two bird species = firm line

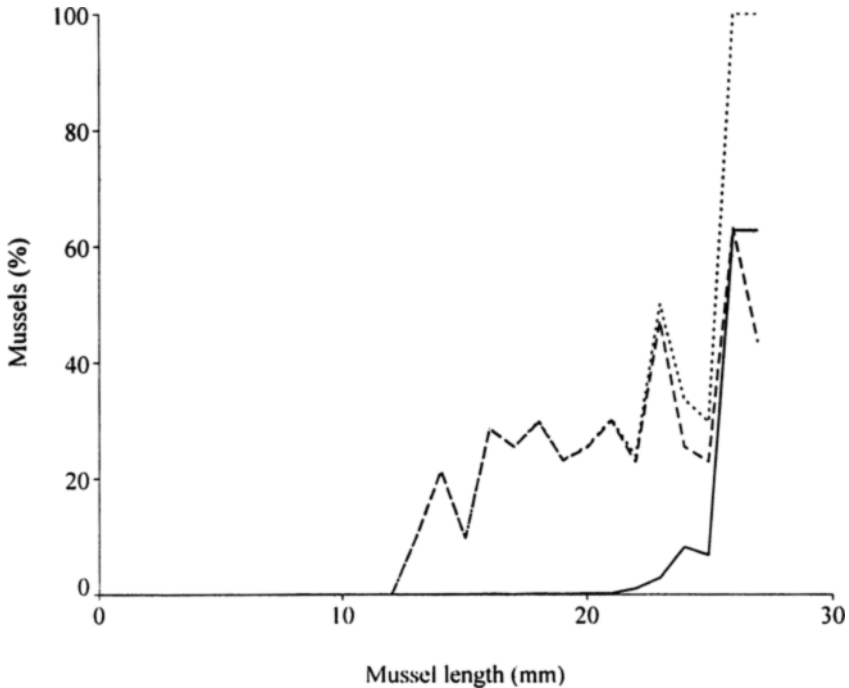


Fig. 6. Percentage of mussels in each size class eaten by oystercatchers (firm line) and herring gulls (dashed line) during three months. Total number eaten by the two bird species = dotted line

DISCUSSION

Daily food consumption

Oystercatchers spent most time on the mussel bed feeding and probably obtained all their daily food requirement from there. In contrast, the percentage of herring gulls feeding on the mussel bed was low and their daily food demand was not met by mussels alone. Oystercatchers specialize in feeding on intertidal organisms, while herring gulls are omnivorous and can use other food sources and places. In addition to mussels, they probably consumed energetically rich food over a short period at high tide outside the mussel beds.

On Spiekeroog (Hilgerloh, unpubl.) mussels provided 42 % of the food of herring gulls in summer. This is in accordance with other studies performed over longer periods in other parts of the Wadden Sea (Dernedde, 1993; Ehlert, 1961; Hartwig & Söhl, 1979; Meijering, 1954; Spaans, 1971) in which mussels on average contributed to 30 % of the food of these gulls.

The increased number of herring gulls on mussel beds in winter compared to other seasons, along with their higher food demand there, may be related to the loss of other food sources, such as, for example, the discharge from crab fishery, and the growth of mussels to a more profitable size for herring gulls.

Feeding rate

Feeding rates vary according to the size of prey and to other characteristics such as shell thickness (Goss-Custard et al., 1993). Oystercatchers took mussels at a rate of 1.3 to 1.4 mussels per minute. This rate was much higher than that observed in the study of Zwarts & Drent (1981), where mussels of comparable size were eaten at a rate of 0.45 mussels per minute. The difference may be explained by higher interference due to higher density of oystercatchers on the sample plots in their study (Zwarts & Drent, 1981). Feeding rates of herring gulls lay between 4.1 and 5 mussels per minute. There are no comparable data from other areas on the feeding rates of mussels.

Biomass, production and elimination

Some authors compare the biomass/m² present at the start of a period with the biomass/m² subsequently eaten by birds (Kautsky, 1981; Swennen et al., 1989; Nehls, 1989; Egerrup & Hoegh Laursen, 1992; Meire et al., 1994). However, as mussels may go on growing, production also has to be taken into account. Within our study period of five and a half months, 296 g AFDW/m² were produced on the mussel bed. The highest production occurred in August (147 g AFDW/m²; Fig. 5). On a mature mussel bed of the German Wadden Sea, the P/B ratio amounted to 0.36 (Asmus, 1987). On a newly established mussel bed production generally is much higher. However, on the studied mussel bed the P/B ratio amounted to 0.68 and was unusually low for a newly established mussel bed. In this case it can be explained by the extreme loss of abundance and the fact that only autumn and winter were considered. In our study the P/B ratio decreased during the first autumn whereas in Morecambe Bay for example, the production remained at a high level over the first 16 months (Dare, 1976) resulting in a P/B ratio of 1.1 to 3.4 (Asmus, 1987).

When the production of all mussels over half a year is compared with the biomass eaten by birds, just one third of the production is enough to compensate for the losses caused by the birds. On other mussel beds, the proportion of annual production predated varied between 39 and 83 % for eiders (Milne & Dunnet, 1972; Nehls et al., 1995), amounted to 40 % for oystercatchers (Craeymeersch et al., 1986) and varied between 45 % and 90 % when eiders, oystercatchers and herring gulls were predated (Baird & Milne, 1981; Egerrup & Hoegh Laursen, 1992; Faldborg et al., 1994; Nehls et al., 1995). On the mussel bed of the Neuharlingersielser Nacken, the total loss due to all factors amounted to 617 g AFDW/m², of which only 16 % was taken by birds.

The parameter „elimination“ helps to evaluate the relevance of predation in relation to other elimination factors but it is also – together with the parameters of biomass and production – a measure for characterizing the development of the mussel bed. According to the biomass at the beginning of the study, the production and the elimination later on, it is apparent that elimination exceeded production and that consequently biomass of the mussel bed had to decrease strongly.

The influence of predation on the abundance and biomass of mussels

During the study period, 10 % of the loss in abundance was caused by predation, of which 1 % was due to oystercatchers and 9 % to herring gulls. A re-evaluation of the results of Zwarts & Drent (1981) shows that the proportion of predation that was due to

oystercatchers amounted to 50 % of the total losses over half a year (May to November), if 30 to 50 % were covered by mussels. Winter losses amounted to 40 % of the initial abundance. That study, however, was conducted on a mature mussel bed and only mussels larger than 40 mm were considered. Although the absolute number of mussels removed by birds was higher in our study – though the mussels were smaller – the effect was less because of the very high density of mussels present at the beginning and the strong decrease afterwards. Different feeding bird species were observed in these studies. While many herring gulls and few oystercatchers fed on the newly established mussel bed of the Neuharlingersieler Nacken, no herring gulls feed where mussels are larger, whereas oystercatchers do feed on larger mussels, as revealed by the Dutch study. Comparing the results of both studies, the preliminary conclusion is that, on young and unstable mussel beds predation by birds is not as important as on mature mussel beds.

In contrast to these results, Worrall & Widdows (1984) found out that only 16 % of the total annual mussel mortality at Linher river/Plymouth was caused by predating oystercatchers. The highest mortality was due to death at spawning in the bigger mussels. According to a regional study on the tidal flats of Lower Saxony, predation by birds amounted in one year to 9 % and in another year to 15 % of the annual loss of the mussel biomass (Hilgerloh, 1997). The mussel population was characterized by a high proportion of young mussels, of which most were eliminated in winter by physical factors. In contrast, a regional study in the Danish Wadden Sea showed that potential predation by birds caused 64 % of the annual loss (Faldborg et al., 1994). But as it was assumed that 100 % of the daily food demand of oystercatchers, herring gulls and eiders is met by mussels, the predation estimates were far too high. In one other study carried out on a young mussel bed (Raffaelli et al., 1990), it was assumed that eiders accounted for nearly 100 % of the total loss of abundance. The ducks removed 80 % of the abundance during winter. These results contrast with ours at Neuharlingersieler Nacken, where only 16 % of the loss of biomass could be explained by predation by birds, with 3 % of the loss due to oystercatchers. The differences can be explained by differences in the predating species. Eider ducks eat far more than do oystercatchers or herring gulls. Although eiders were important predators of mussels in the tidal flats of Spiekeroog (Hilgerloh, 1996, 1997), they were not observed in our study area. We concluded that the influence of predation by herring gulls and oystercatchers on the newly established mussel bed was very small. A much higher loss was probably caused by other factors, such as gales, crabs, heat exhaustion, undernourishment, diseases, freezing and parasites. Crabs *Carcinus maenas* are important predators on young mussel beds until October. So, as large areas were depleted of mussels at the end of November, we presume that physical factors were the most important cause of mussel loss (Hilgerloh & Herlyn, 1996), as recorded two years earlier at an adjacent young mussel bed on the Neuharlingersieler Nacken (Flemming & Delafontaine, 1994).

Loss of abundance by predation within size classes of mussels

On this mussel bed herring gulls ate the most common mussel sizes, as their preferred size class corresponded to the available sizes (Hilgerloh, pers. observ.). Predation by herring gulls flatten the frequency distribution to make it comparable to those of mature mussel beds (Michaelis et al., 1995). Oystercatchers selected the biggest mussels avail-

able. In our study, predation by oystercatchers had no quantitative effect on the size distribution of mussels. However, further growth of the mussels would make them more attractive for oystercatchers, thus attracting more oystercatchers and in this way increasing the chances that they will make a quantitative effect. The search by oystercatchers for the biggest mussels is facilitated by the phenomenon that mussels growing at the border of seedling beds are bigger than the others (Svane & Ompi, 1991). In general, mussel-feeding birds take advantage of spatial variation of growth rates of invertebrates, in order to optimize efficiency of food intake (Wanink & Zwarts, 1993).

Mussel sizes taken by oystercatchers on the Neuharlingersieler Nacken were at the lower end of the range of their preferred mussel sizes (Drinnan, 1958; Ens, 1982; Durell & Goss-Custard, 1984; Sutherland & Ens, 1987; Cayford & Goss-Custard, 1990). Most profitable mussels should have at least a size of 40 mm (Zwarts & Drent, 1981; Ens, 1982; Meire & Ervynck, 1986). Oystercatchers change to smaller mussels, if the preferred sizes are not available (Hilgerloh, pers. observ.). Accordingly, they fed on the biggest mussels available on the Neuharlingersieler Nacken. One can expect that oystercatchers continue to choose the biggest mussels on this mussel bed.

The selection of the biggest mussels, as a consequence for the single mussel, means that the chance of a mussel to be eaten by an oystercatcher will be higher if it grows quicker than average. However, growing quickly has the advantage that the size classes preferred by oystercatchers are outgrown sooner (Gosling, 1992).

Acknowledgements. We express our thanks to D. Henning for ornithological observations and to M. Exo, C. Ketzenberg and G. Scheiffarth, with whom we had long discussions. Thanks are also due to R. Hasbargen and H. H. Kramer who did the laboratory work and to R. Pocklington for his help with the English language. M. Exo, H. Asmus and an anonymous referee made valuable contributions to the manuscript. This study is supported by the Federal Environmental Agency, Environmental Research Plan of the Minister for the Environment, Nature Conservation and Nuclear Safety of the Federal Republic of Germany (Grant 108 02 085/21), and by the state of Lower Saxony. This is publication no. 236 of the project Ecosystem Research Wadden Sea.

LITERATURE CITED

- Aschoff, J. & Pohl, H., 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. – *J. Orn.* 111, 38–47.
- Asmus, H., 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. – *Mar. Ecol. Prog. Ser.* 39, 251–266.
- Baird, D. & Milne, H., 1981. Energy flow in the Ythan estuary, Aberdeenshire, Scotland. – *Estuar. coast. Shelf Sci.* 13, 455–472.
- Brosius, G. & Brosius, F., 1995. SPSS. Base System and Professional Statistics. Thomson, Bonn, 1002 pp.
- Castro, G., Myers, J. P. & Ricklefs, R. E., 1992. Ecology and energetics of sanderlings migrating to four different latitudes. – *Ecology* 73, 833–844.
- Cayford, J. & Goss-Custard, J. D., 1990. Seasonal changes in the size selection of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*: an optimality approach. – *Anim. Behav.* 40, 609–624.
- Craeymeersch, J. A., Herman, P. M. J. & Meire, P. M., 1986. Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (SW-Netherlands). – *Hydrobiologia* 133, 107–115.
- Cramp, S. & Simmons, K. E. L., 1977. Handbook of the birds of Europe and the Middle East. Oxford Univ. Press, Oxford, 1, 17–35.

- Dare, P. J., 1976. Settlement, growth and production of the mussel, *Mytilus edulis* L. in Morecambe Bay, England. – Fishery Invest., Lond. (Ser. 2) 28 (1), 1–25.
- Dernedde, E. T., 1993. Vergleichende Untersuchungen zur Nahrungszusammensetzung von Silbermöwe (*Larus argentatus*), Sturmmöwe (*L. canus*) und Lachmöwe (*L. ridibundus*) im Königshafen/Sylt. – Corax 15, 222–240.
- Drent, R., Ebbinge, B. & Weijand, B., 1978. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. – Verh. orn. Ges. Bayern 23, 239–263.
- Drinnan, R. E., 1958. The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. – Fishery Invest., Lond. (Ser. 2) 22, 1–15.
- Durell, S. E. A. & Goss-Custard, J. D., 1984. Prey selection within a size-class of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*. – Anim. Behav. 32, 1197–1203.
- Egerrup, M. & Hoegh Laursen, M. L., 1992. Aspects of predation on intertidal blue mussels (*Mytilus edulis* L.) in the Danish Wadden Sea. – C. M./ICES K 25, 1–20.
- Ehlert, W., 1961. Weitere Untersuchungen über die Nahrungswelt der Silbermöwe (*Larus argentatus*) auf Mellum. – Vogelwarte 21, 48–50.
- Ens, B., 1982. Size selection in mussel-feeding oystercatchers. – Wader Study Group Bull. 34, 16–20.
- Exo, K.-M. & Scheiffarth, G., 1994. The day- and nighttime activity of oystercatchers breeding in the Wadden Sea. – J. Orn. 135, (Sonderh.), 146.
- Faldborg, K., Jensen, K. T. & Maargaard, L., 1994. Dynamics, growth, secondary production and elimination by waterfowl of an intertidal population of *Mytilus edulis* L. – Ophelia (Suppl.) 6, 187–200.
- Flemming, B. W. & Delafontaine, M. T., 1994. Biodeposition in a juvenile mussel bed of the East Frisian Wadden Sea (southern North Sea). – Neth. J. aquat. Ecol. 28, 289–297.
- Goede, A. A., 1993. Variation in the energy intake of captive oystercatchers *Haematopus ostralegus*. – Ardea 81, 89–97.
- Goethe, F., 1961. Zur Taxonomie der Silbermöwe im südlichen deutschen Nordseegebiet. – Vogelwarte 21, 1–24.
- Gosling, E. (Ed.), 1992. The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier, Amsterdam, 589 pp.
- Goss-Custard, J. D., Durell, S. E. A., McGroarty, S. & Reading, C. J., 1982. Use of mussel *Mytilus edulis* beds by oystercatchers *Haematopus ostralegus* according to age and population size. – J. Anim. Ecol. 51, 543–554.
- Goss-Custard, J. D., West, A. D. & Durell, S. E. A., 1993. The availability and quality of the mussel prey (*Mytilus edulis*) of oystercatchers (*Haematopus ostralegus*). – Neth. J. Sea Res. 31, 419–439.
- Hartwig, E. & Söhl, M., 1979. Zur Nahrung der Silbermöwe (*Larus argentatus*) auf der Nordseeinsel Sylt. II. Jahreszeitliche Änderungen in der Zusammensetzung der Nahrung. – Abh. Geb. Vogelkde 6, 67–86.
- Hilgerloh, G., 1996. Miesmuscheln (*Mytilus edulis*) in der Nahrung von Eiderenten (*Somateria mollissima*) auf den Nordseeinseln Langeoog und Spiekeroog. – Acta ornithoecol. 3 (3), 239–243.
- Hilgerloh, G., 1997. Predation by birds on blue mussel *Mytilus edulis* beds of the tidal flats of Spiekeroog (southern North Sea). – Mar. Ecol. Prog. Ser. 146, 61–72.
- Hilgerloh, G. & Herlyn, M., 1996. Auswirkungen der Prädation durch Vögel auf eine junge Miesmuschelbank (*Mytilus edulis*). – Verh. dt. zool. Ges. 84, 306.
- Hulscher, J. B., 1974. An experimental study of the food intake of the oystercatcher *Haematopus ostralegus* L. in captivity during the summer. – Ardea 62, 155–171.
- Hulscher, J. B., 1976. Localisation of cockles (*Cardium edule* L.) by the oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. – Ardea 64, 292–310.
- Hüppop, O., 1987. Der Einfluß von Wachstum, Thermoregulation und Verhalten auf den Energiehaushalt der Silbermöwe (*Larus argentatus* Pontoppidan, 1763). Diss. Univ. Hamburg, 207 pp.
- Jansson, B. O. & Wulff, F., 1977. Ecosystem analysis of a shallow sound in the northern Baltic – joint study by the Askö group. – Contr. Askö Lab. 18, 1–60.
- Kautsky, N., 1981. On the trophic role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. – Kieler Meeresforsch. (Sonderh.) 5, 454–461.

- Kersten, M. & Piersma, T., 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. – *Ardea* 75, 175–187.
- Lasiewski, R. C. & Dawson, W. R., 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. – *Condor* 69, 13–23.
- Martin, P. & Bateson, P., 1986. Measuring behaviour. – Cambridge Univ. Press, Cambridge, 1200 pp.
- Meijering, M. P. D., 1954. Zur Frage der Variation in der Ernährung der Silbermöwe, *Larus argentatus* Pont. – *Ardea* 42, 163–175.
- Meire, P. & Eryvynck, A., 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? – *Anim. Behav.* 34, 1427–1435.
- Meire, P. M., Schekkerman, H. & Meininger, P. L., 1994. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands. – *Hydrobiologia* 282/283, 525–546.
- Michaelis, H., Obert, B., Schultenkötter, I. & Böcker, L., 1995. Die Miesmuschelbestände der niedersächsischen Watten 1989–1991. – *Ber. NÖ-Forschungsst. Küste* 40, 1–71.
- Milne, H. & Dunnet, G. M., 1972. Standing crop, productivity and trophic relations of the fauna of the Ythan Estuary. In: The estuarine environment. Ed. by R. S. K. Barnes & J. Green. Applied Science Publ., London, 86–106.
- Nehls, G., 1989. Occurrence and food consumption of the common eider, *Somateria mollissima*, in the Wadden Sea of Schleswig-Holstein. – *Helgoländer Meeresunters.* 43, 385–393.
- Nehls, G., Hertzler, I. & Scheiffarth, G., 1995. Nutzung von Miesmuschelbänken durch Vögel. In: Trophischer und regulierender Stellenwert der Vögel im Ökosystem Wattenmeer. (Sylter Wattenmeer Austauschprozesse; Abschlußber.) Hrsg. von G. Nehls, G. Scheiffarth & R. Tiedemann. Forschungs- und Technologiezentrum Westküste, Buisum, 138–153.
- Raffaelli, D., Falcy, C. & Galbraith, C., 1990. Eider predation and the dynamics of mussel bed communities. In: Trophic relations in the marine environment. Ed. by S. M. Varne & R. N. Gibson. Aberdeen Univ. Press, Aberdeen, 157–169.
- Scheiffarth, G. & Nehls, G., 1997. Consumption of benthic fauna by carnivorous birds in the Wadden Sea. – *Helgoländer Meeresunters.* 51, (in press.).
- Spaans, A. L., 1971. On the feeding ecology of the herring gull *Larus argentatus* Pont. in the northern part of the Netherlands. – *Ardea* 5, 73–185.
- Speakman, J., 1990. Bias in the collection of mussel shells opened by oystercatchers. – *Wader Study Group Bull.* 58, 48–49.
- Sutherland, W. & Ens, B., 1987. The criteria determining the selection of mussels *Mytilus edulis* by oystercatchers *Haematopus ostralegus*. – *Behaviour* 103, 187–202.
- Svane, I. & Ompi, M., 1991. Patch dynamics in beds of the blue mussel *Mytilus edulis* L.: Effects of site, patch size, and position within a patch. – *Ophelia* 37, 187–202.
- Swennen, C. G., Nehls, G. & Laursen, K., 1989. Numbers and distribution of eiders *Somateria mollissima* in the Wadden Sea. – *Neth. J. Sea Res.* 24, 83–92.
- Wanink, J. H. & Zwarts, L., 1993. Environmental effects on the growth rate of intertidal invertebrates and some implications for foraging waders. – *Neth. J. Sea Res.* 3, 407–418.
- Winberg, G. G. (Ed.) 1971. Methods for estimation of production of aquatic animals. Acad. Press, London, 175 pp.
- Worral, C. M. & Widdows, J., 1984. Investigation of factors influencing mortality in *Mytilus edulis* L. – *Mar. Biol. Lett.* 5, 85–97.
- Zwarts, L. & Blomert, A. M., 1992. Why knot *Calidris canutus* take medium sized *Macoma balthica* when six prey species are available. – *Mar. Ecol. Prog. Ser.* 83, 113–128.
- Zwarts, L. & Drent, R. H., 1981. Prey depletion and the regulation of predator density: oystercatchers, *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*. In: Feeding and survival strategies of estuarine organisms. Ed. by P. Jones. & W. J. Wolff. Plenum Press, New York, 193–216.