SIZE SELECTION AND COMPETITION FOR MUSSELS, *MYTILUS EDULIS*, BY OYSTERCATCHERS, *HAEMATOPUS OSTRALEGUS*, HERRING GULLS, *LARUS ARGENTATUS*, AND COMMON EIDERS, *SOMATERIA MOLLISSIMA*

Gudrun Hilgerloh[1] and *Dietmar Pfeifer*[2]

[1]Forschungszentrum Terramare, Schleusenstr. 1, D-26382 Wilhelmshaven, Germany.
Present address: Institut für Zoologie, Abt. V, Johannes Gutenberg-Universität Mainz, Becherweg 13, D-55099 Mainz

[2]Fachbereich Mathematik, Universität Oldenburg, Postfach 2503, D-26111 Oldenburg

ABSTRACT

Investigations on size selection of blue mussels, *Mytilus edulis*, and exploitation competition by ventral hammering oystercatchers, *Haematopus ostralegus*, herring gulls, *Larus argentatus*, and common eiders, *Somateria mollissima*, were carried out on various blue mussel beds on the tidal flats of Spiekeroog (Niedersachsen/Germany). The size-class was considered to be the ideal one, which would be selected if all size-classes were available. On one mussel bed the mussel sizes selected by oystercatchers were the most abundant mussel sizes, the median being 51 mm. It was concluded that the most abundant size-class corresponded to the ideal size-class which was much bigger than predicted for ventral hammering oystercatchers. If all mussels available were smaller than the ideal size, they selected the largest ones. Unlike oystercatchers, eiders did not select the largest mussels present when they were all smaller than the ideal size. Instead, they selected mussels that were only slightly longer than the median of the available mussels. As eiders dive for several mussels when they are feeding on small mussels, they are time-restricted and less selective than if diving for single large mussels. For herring gulls, the ideal mussel size seemed to be 20 mm. Mussel sizes selected by different bird species on the same mussel bed differed significantly. Each species chose other size-classes if the ideal size was not available. The species never competed for the same size-class on a mussel bed.

Keywords: size selection, competition, blue mussel (*Mytilus edulis*), eider (*Somateria mollissima*), oystercatcher (*Haematopus ostralegus*), herring gull (*Larus argentatus*).

INTRODUCTION

On the tidal flats of the Wadden Sea (southern North Sea), the most significant avian predators on blue mussels are oystercatchers (*Haematopus ostralegus*), herring gulls (*Larus argentatus*) and common eiders (*Somateria mollissima*) (Hilgerloh 1997). Responding to different constraints, each species differ in the most taken size-class. Herring gulls, which are studied here, and eiders swallow the whole mussel while oystercatchers open the mussel and eat only the flesh. Thus, the gape of the bill and the diameter of the oesophagus could limit the size of mussels that could be swallowed by herring gulls and eiders. The thickness of the shell and the energetic value can be critical for all three species.

Mussel populations may show a large variation of size structure and abundance within and between years, which has consequences for their exploitation by different predators. Birds are known to feed on prey yielding the highest benefit for them which thus is the optimal prey (Krebs & Kacelnik 1991). The optimal size can vary very much between sites depending on the available mussels. There is, however, an ideal size that would be taken, if all mussel sizes were available at a site. Since mussel sizes and characteristics correlate with the size variation between the sites, the ideal size is not always available. At any given situation the birds feed on the optimal size.

The ideal size is expected to differ between the species according to the species specific constraints. If the ideal size is not available or too scarce, the bird predator can cope with smaller sizes. There is, however, a minimum size for each predator species. They would hardly derive any benefit from the prey below the minimum size, which accordingly they would not take (Krebs & Kacelnik 1991).

Oystercatchers use one of three different methods to open the mussels (Sutherland & Ens 1987, Hulscher 1996). Mussels are opened (i) by hammering dorsally, (ii) by hammering ventrally and (iii) by `stabbing` whilst the mussel is filtering. All mussels encountered in this study were opened ventrally. Ventrally hammering birds are known to select intermediate sizes, with a median of ideal sizes between 35 and 45 mm (Drinnan 1958, Norton-Griffith 1967, Zwarts & Drent 1981, Ens 1982, Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996). If the ideal size is not available, they try to feed on mussel sizes that are as close as possible to the ideal size (as long as costs or time restrictions are not too high) (Drinnan 1958, Northon-Griffith 1967, Zwarts et al. 1996a, Leopold et al. 1996). In general, they do not take mussels with barnacles attached (e.g. Meire & Ervynck 1986, Ens & Alting 1996). Even though mussels with a barnacle cover do not have thicker shells or less flesh content than other mussels of the same size (Ens & Alting 1996). It will be tested whether the selectivity of oystercatchers can be confirmed for the study sites.

According to the differences on the mussel beds between the sites a prediction will be made for ventral hammerers at each site. It will be based on the following model (Fig. 1).

In eiders, optimal mussel sizes ranged between 10 and 53 mm (Madsen 1954, Player 1971, Dunthorn 1971, Milne & Dunnet 1972, Swennen 1976, Kirchhoff 1979, Bustnes 1998, Raffaelli et al. 1990, Meissner & Bräger 1990, Nehls 1991, 1995, Guillemette et al. 1992, Meire 1993, Kallenborn et al. 1994, Hamilton et al. 1999, Hilgerloh 2000, Leopold et al. 2001). Sizes selected by eiders change in the course of a year, being larger in winter than in summer (Ketzenberg 1991, Nehls 1995, Hamilton et al. 1999, Hilgerloh 2000). From cases in which the frequency distribution of the mussels present on the mussel bed was known one could conclude that the ideal size they dive for in winter occurred in the range of 35 to 55 mm length (Nehls 1995). These also have the best energy output (Nehls 1995). For eiders, the hypothesis needs to be tested that they take mussels that are as close as possible to the ideal size. The model on which the prediction will be based is as follows (Fig. 2).

Herring gulls that swallow mussels are known to take small ones. The ideal size-class is not yet known (Spaans 1971, Milne & Dunnet 1972, Meire 1993). In the following, selectivity is studied of predators faced with a variety of prey-size distributions.

If several bird species feed on one mussel bed, they might select the same mussel size-class; and so their cumulative effect could decrease the abundance of this size-class. Competition through the exploitation of a common resource is indirect competition.

Competition for size-classes of a single species of prey was studied by descriptive methods. However, the problem of quantitative comparisons between prey-size distributions selected by different predator species has not been addressed. In view of the different constraints mentioned above we anticipate that different predator species on the same mussel bed will not compete for the same mussel size but select differently. This hypothesis will be tested by quantitative comparisons.

RESULTS

Size selection and competition by oystercatchers and herring gulls on a newly settled mussel bed on the Neuharlingersieler Nacken in 1994. – Young mussels settled in 1994 on the Neuharlingersieler Nacken (Hilgerloh & Herlyn 1996). It was predicted that oystercatchers select the largest mussels. The mussels selected differed from the mussels available (Tables 1-2, Fig. 3). Since oystercatchers selected the largest mussels the prediction was confirmed.

Selection by herring gulls was only proven through differences in the frequency distribution of mussel size (Tables 1-2, Fig. 3). The median of available mussels seemed to represent the ideal mussel size for herring gulls.
It was predicted that different predator species take different sizes on one mussel bed. As selection by both oystercatchers and by herring gulls differed from each other (Tables 1-3) the prediction was confirmed.

Size selection by oystercatchers on a mature mussel bed with newly settled young mussels on the Janssand in 1993. – The frequency distribution of mussels on the mussel bed located on the Janssand was characterised by mature mussels of sizes between 47 and 70 mm, which were encrusted by barnacles and by young mussels to a size of 37 mm with a gap between both cohorts (Fig. 4, Table 1).

It was predicted that oystercatchers would choose the largest of the young mussels. Since oystercatchers took the less abundant mussel sizes, located between two peaks of the fre-

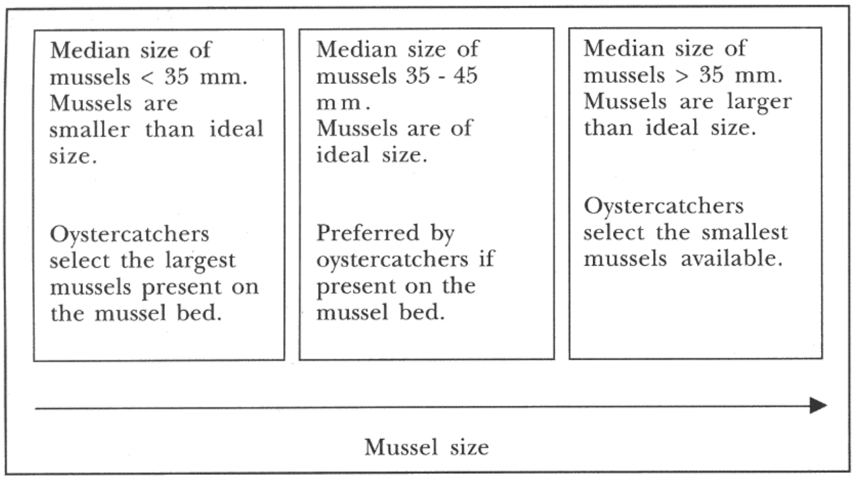

Fig. 1. Oystercatcher model. The model predicts what sizes oystercatchers select on mussel beds with different mussel size distributions.

quency distribution of size (Tables 1-3, Fig. 4) the hypothesis was confirmed.

Size selection and competition by oystercatchers, herring gulls and eiders on a mature mussel bed with newly settled young mussels on the Janssand in 1994. – Young mussels settled in spring 1994. In November 1994, there were hardly any of the mature mussels left which had been present in September 1993 (Figs 4-5). It is predicted that oystercatchers select the largest of the available mussels. Selected mussels differed from those available (Tables 1-2, Fig. 5). These results and the sizes selected confirmed the prediction.

Herring gulls selected mussels that differed from the available and were on median 3 mm longer than the mussels available (Tables 1-2). It was predicted that eiders select the biggest mussels. The median size of the available mussels was 5 mm less than the size preferred by eiders (Tables 1-2). While the median size on the mussel bed amounted to 17 mm, eiders fed on mussels with a median size of 22 mm and oystercatchers of 31 mm. Although eiders selected larger mussels than the most frequent ones, the prediction was not confirmed.

The hypothesis was tested that all three species select on average different sizes. The mussel selections of oystercatchers, herring gulls and eiders differed statistically from each other (Kruskal-Wallis test $p < 0.00001$) (Fig. 5). Since the pair-wise comparisons showed that mussel selections of all species differed from each other (Tables 1-3) the prediction was confirmed.

Comparison of size selection by herring gulls on mussels on Neuharlingersieler Nacken and on Janssand in 1994. – Selectivity of herring gulls with respect to the median size could be proven on the mussel bed of the Janssand, but not on that of the Neuharlingersieler Nacken where the

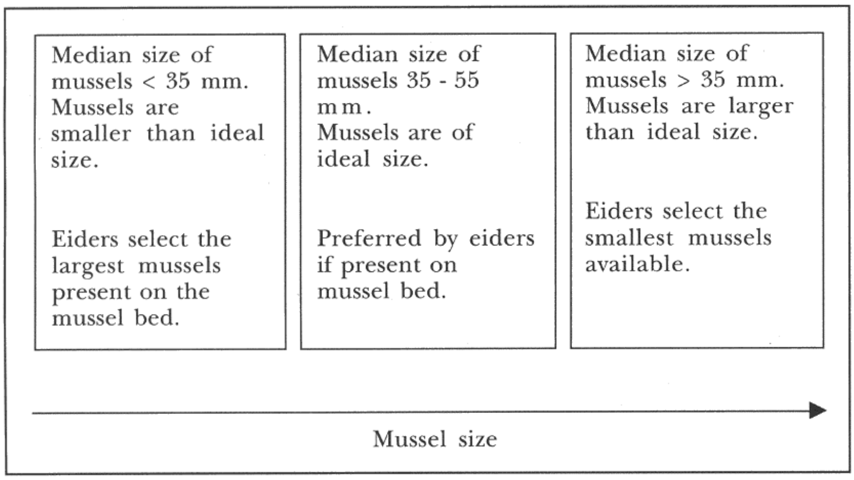

Fig. 2. Eider model. The model predicts what sizes eiders select on mussel beds with different mussel size distributions.

Table 1. Sizes (median, lower and upper quartile) of mussels present on the mussel beds and of mussels eaten by eiders, herring gulls and oystercatchers on the different mussel beds

Site	Mussels	Median (mm)	Lower quartile (mm)	Upper quartile (mm)	n
Neuharlingersi-eler Nacken 1994	On the mussel bed	20	18	22	263
	Eaten by oystercatchers	25.8	23.6	27.5	308
	Eaten by herring gulls	19.6	17.6	21.5	1398
Janssand 1993	On the mussel bed	20	8	52	232
	Eaten by oystercatchers	33	29.8	36.3	78
Janssand 1994	On the mussel bed	17	12	22	934
	Eaten by oystercatchers	30.8	28.4	33.3	425
	Eaten by herring gulls	19.6	18.5	21.5	218
	Eaten by eiders	21.5	18.6	24.5	553
Swinnplate 1993	On the mussel bed	50.7	47.3	53.9	113
	Eaten by oystercatchers	51.3	48.5	53.6	224

mussels had settled a bit earlier than on the Janssand. (Tables 1-2). No difference in size choice was observed between the two sites (Tables 1- 2). It would appear that the selected size-class corresponded to the ideal size-class for herring gulls at both sites.

Size selection by oystercatchers on a mature mussel bed on the Swinnplate. – It was predicted that oystercatchers select the smallest of the most abundant sizes. As mussels selected by oystercatchers did not differ from the available mussels, selectivity could not be proven (Tables 1-2, Fig. 6) and the prediction had to be rejected.

DISCUSSION

Size selection by oystercatchers. – Only on the Swinnplate the did mussels selected by oystercatchers not differ from those available on the mussel bed. This suggests that the selected size-class of 51 mm was the ideal size-class on this mussel bed. On the basis of published data only size-classes up to 45 mm would be predicted to belong to the ideal size-class of ventral hammering oystercatchers (Drinnan 1958, Norton-Griffith 1967, Ens 1982, Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996). The variation of ideal mussel size is thought to be due to differences in parameters

Table 2. Selectivity: statistical values from comparisons between mussels available on the mussel beds and those eaten by the bird species.

Site	Compared samples: Mussels (sample 1)	Mussels (sample 2)	Mann-Whitney U test: U	One-, two-sided	P	Kolmogorov Smirnov test: Z	P
Neuharlin-gersieler Nacken 1994	On the mussel bed	Eaten by oystercatchers	4838	One	<0.0001	9.44	<0.0001
	On the mussel bed	Eaten by herring gulls	180138	Two	0.60	1.35	0.05
Janssand 1993	On the mussel bed	Eaten by oystercatchers	5638	Two	<0.0001	4.41	<0.0001
Janssand 1994	On the mussel bed	Eaten by oystercatchers	15176	One	<0.0001	14.24	<0.0001
	On the mussel bed	Eaten by herring gulls	71504	One	<0.0001	5.37	<0.0001
	On the mussel bed	Eaten by eiders	147225	One	<0.0001	8.03	<0.0001
Janssand 1994/ Neuharlingersieler Nacken 1994	On the mussel bed	On the mussel bed	91692	One	<0.0001	4.76	<0.0001
	Eaten by herring gulls	Eaten by herring gulls	144400	One	0.21	0.60	0.87
Swinnplate	On the mussel bed	Eaten by oystercatchers	17194	One	0.36	0.93	0.35

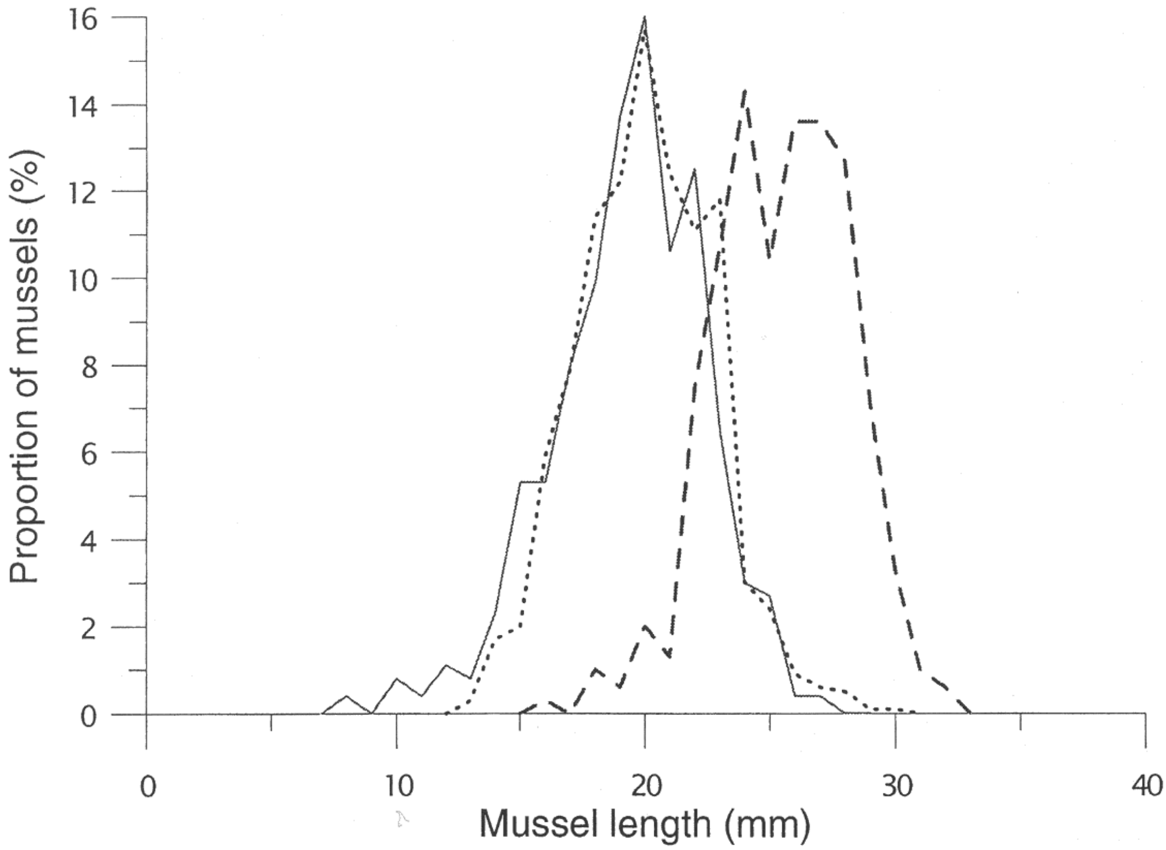

Fig. 3. Neuharlingersieler Nacken, winter 1994: lengths of available blue mussels (n = 263) (solid line) and of mussels eaten by oystercatchers (n = 308) (dashed line) and by herring gulls (n = 1398) (dotted line).

other than size that influence the profitability (e.g. shell thicknesss, flesh content), and on seasonal differences of the ideal size (e.g. Durell & Goss-Custard 1984, Krebs & Kacelnik 1991, Zwarts & Wanink 1993, Goss-Custard et al. 1993, Goss-Custard et al. 1996c). If oystercatchers had the choice between mussels larger than the ideal size with barnacle cover and smaller mussels (see Fig. 4), they selected the largest of the smaller mussels. Factors such as shell thickness and barnacle cover are thought to influence the profitability of the mussels and the selectivity of the oystercatchers (Durell and Goss-Custard 1984, Meire & Ervynck 1986, Zwarts & Wanink 1993, Ens & Alting 1996). If most mussels were smaller than the ideal size-

Table 3. Competition: statistical values from comparisons between mussels eaten by different bird species.

Site	Compared samples: Mussels (sample 1)	Mussels (sample 2)	Mann-Whitney U test: U	One-, two-sided	P	Kolmogorov Smirnov test: Z	P
Neuharlingersieler Nacken 1994	Eaten by oystercatchers	Eaten by herring gulls	33407	One	<0.00001	11.96	<0.0001
Janssand 1994	Eaten by oystercatchers	Eaten by eiders	14689	One	<0.0001	12.22	<0.0001
	Eaten by oystercatchers	Eaten by herring gulls	1633	One	<0.00001	10.81	<0.00001
	Eaten by eiders	Eaten by herring gulls	45672	One	<0.00001	2.66	<0.00001

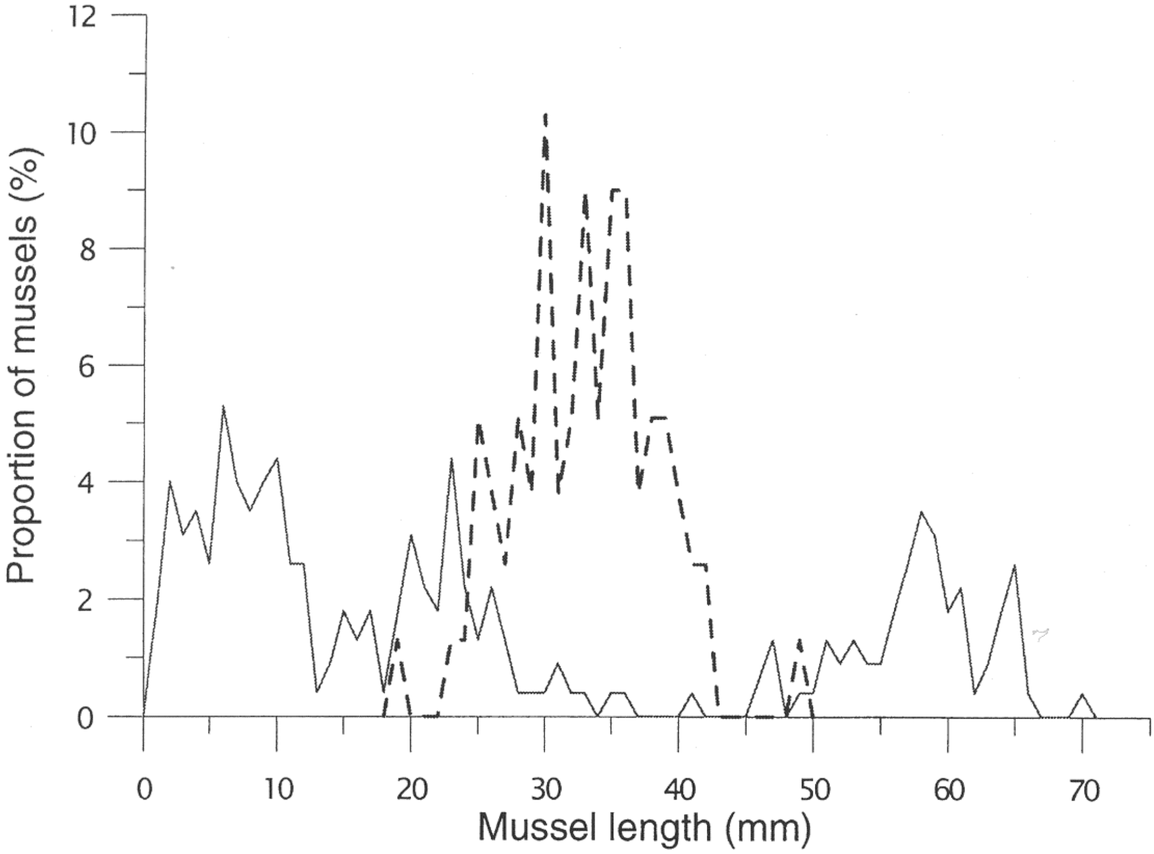

Fig. 4. Janssand, autumn 1993: lengths of available blue mussels (n = 227) (solid line) and of mussels eaten by oystercatchers (n = 78) (dashed line).

class, oystercatchers selected mussels from the upper end of the available mussel sizes (Figs. 3, 5). They preferred the largest mussels, although they were rarely encountered. Similar observations have been made by other authors (Cayford & Goss-Custard 1990, Norton-Griffiths 1967).

If oystercatchers feed mainly on mussels from the upper end of the range of mussel sizes, in years with a small spatfall, they may restrict the size-class composition of the mussel population to smaller sizes. The predator-prey-system would be top-down controlled. Only in years with heavy spatfalls would mussels get a chance to grow to sizes larger than those selected by oystercatchers. But, in general, the influence of predation by oystercatchers was not significant for the development of the mussel populations in Niedersachsen as revealed in the studies on the tidal flats of Spiekeroog (Hilgerloh 1997, Hilgerloh et al. 1997, Hilgerloh & Siemoneit 1999).

Size selection by herring gulls.- The studies on the mussel beds on the Neuharlingersieler Nacken and on the Janssand established that 20 mm is the ideal mussel length for herring gulls. Very few data are available from other areas: a range of mussel sizes between 2 and 10 mm eaten by herring gulls is known from a Scottish study (Milne & Dunnet 1972). According to a Dutch study (Spaans 1971) cockles of a median size of 21 mm were taken by herring gulls. One would have expected that they swallow larger mussels, as they are elongated compared with the sphaerical cockles.

Size selection by eiders. – Eiders did not select mussels that are as close as possible to the ideal size-class, if the latter was not available. While oystercatchers selected the biggest mussels, with a median 14 mm longer than the median of the available mussels, the median of mussels selected by eiders was only 5 mm longer. In the study by Raffaelli et al. (1990) where the length of

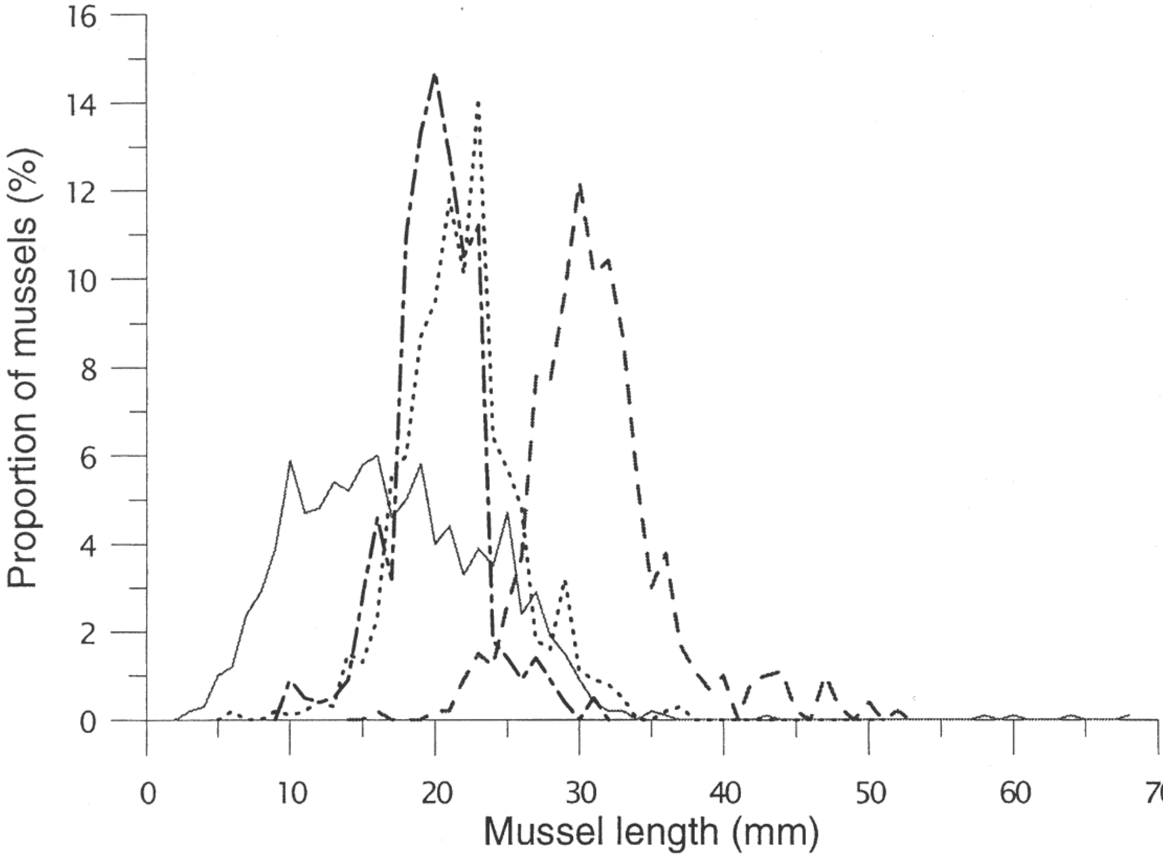

Fig. 5. Janssand, winter 1994: lengths of available blue mussels (n = 934) (solid line) and of mussels eaten by oystercatchers (n =425) (dashed line), by herring gulls (n = 218) (dotted line) and by eiders (n = 553) (dash-dot line).

the available mussels was smaller than on the Janssand, eider also selected mussels that were slightly longer than the median of the available mussels.

Normally, eiders select single mussels out of a mussel clump. When feeding on small mussels, they seem to adopt another feeding strategy: they eat several mussels on one dive, as concluded from diving time by Guillemette et al. (1992) and from observations from diving by Hoerschelmann (pers. comm.). Since time for searching is limited during a single dive, and the visibility is low in the tidal flats, median size of selected mussels is close to the median size of the available mussels. The advantage of selecting small mussels is the fact that the shell is very thin thus little effort is needed to crush the mussels (Bustnes 1998). Although the distribution of mussel beds influences the food composition of eiders (Hilgerloh 1999a), in years with heavy spatfall the proportion of blue mussels in the food of eiders is, in general, higher than in other years (Hilgerloh 1999b, 2000). This suggests that they take advantage of the spatfall of the year.

Competition for mussels between bird species. – On the two mussel beds on which several bird species were preying on blue mussels – on the Neuharlingersieler Nacken and on the Janssand – the sizes of the selected mussels differed significantly between the species. The question arose whether competition could occur in such a situation. According to Pianka (1974), potential competitors would tolerate a relatively high degree of overlap in resource use without experiencing critical levels of competition as long as the demand for resources is low relative to the supply. On both mussel beds studied here, abundant mussels were available in the size-classes chosen by herring gulls and eiders. Thus, no competition would occur between these species. However, sizes selected by oystercatchers were scarce. Competition did

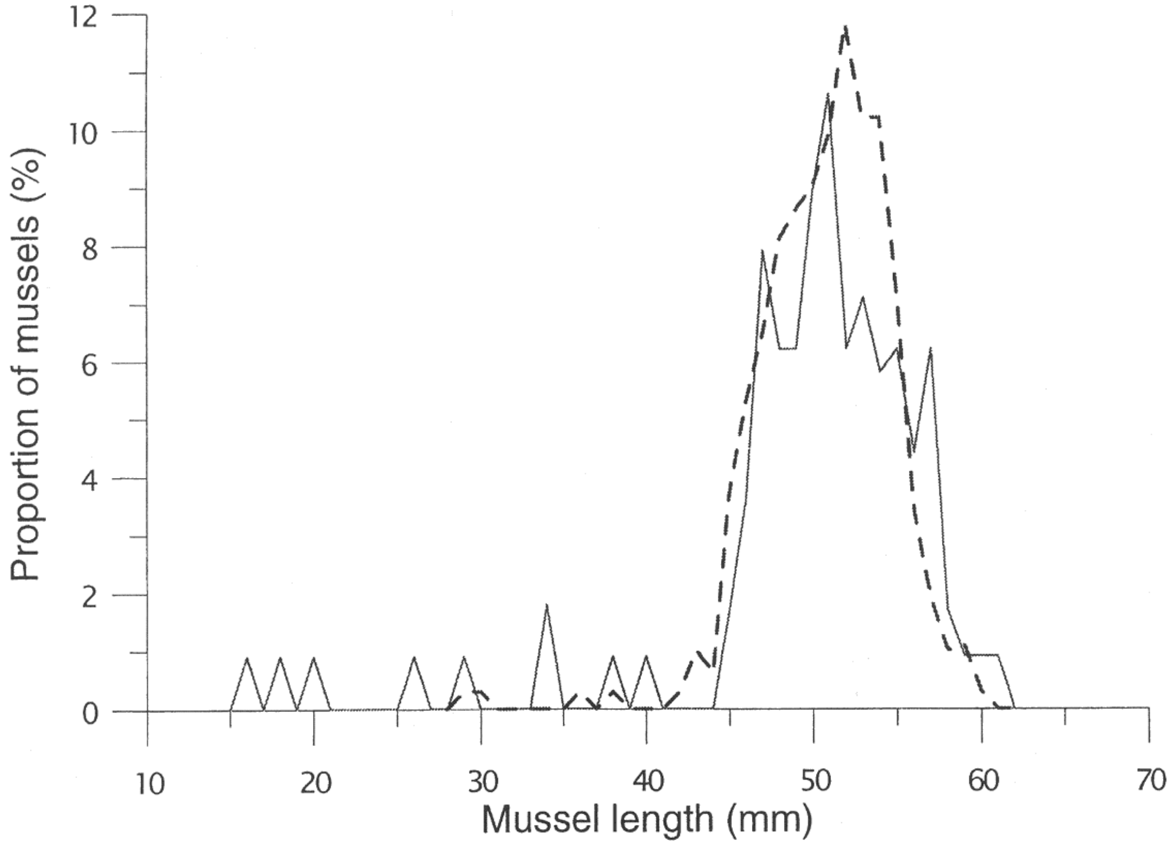

Fig. 6. Swinnplate, winter 1993: lengths of available blue mussels (n = 113) (solid line) and of mussels eaten by oystercatchers (n = 224) (dashed line).

not occur since the oystercatcher was the only species searching for these uncommon sizes. Before spring, the situation can change dramatically because mussels have a high winter mortality (Nehls & Thiel 1993, Michaelis et al. 1995, Hilgerloh 1997), which was observed in the tidal flats of Niedersachsen, thus competition is expected at the end of the winter.

The settlement of blue mussels is very unpredictable, and heavy spatfalls do not occur at regular time intervals. Most years, predators have to cope with the situation of light spatfalls and thus with limited resources. Therefore, competition for size-classes could occur in general.

The complexity of the phenomenon competition may be better appreciated if it is remembered that the mussels grow, thus changing size-class. Herring gulls, for example, could be important competitors for oystercatchers. If they deplete the stocks of small mussels to such an extent that hardly any mussels will grow to larger sizes, there will not be enough mussels left for oystercatchers (Zwarts & Drent 1981).

MATERIALS AND METHODS

Mussel beds.- The studied mussel beds were situated on the tidal flats between the East Frisian islands of Langeoog and Spiekeroog and the mainland of Niedersachsen. A mature mussel bed includes the seedling beds, which are characterized by distinct elevations formed from biodeposits of mussels and by mussel-free areas in between. On the newly settled mussel beds this distinction does not yet occur.

Estimates of the sizes of mussels on the mussel beds.- Six samples of mussels with a surface area of 38.5 cm^2 were taken at regular intervals along a transect running over the entire mussel beds on the Neuharlingersieler Nacken (53°43,25N, 7°44,00E) and on Janssand (53°44,00N, 7°42, 00E) in November 1994 (Herlyn & Michaelis 1996). In June 1993, twelve samples with a surface of 177 cm^2 were taken in twelve seedling beds located along transects running over the entire mussel bed of the Janssand and of the Swinnplate (53°44,75N, 7°44,00E) (Herlyn &

Michaelis 1996). In October and December, when the mussel bed on the Swinnplate had a dispersed settlement of mussels, randomly selected mussel clumps within the study area were taken as a basis for the frequency distribution of mussel sizes. Only on the Neuharlingersieler Nacken, numbers of birds are known: on an average 33 oystercatchers and 140 herring gulls per ha were observed during low tide (Hilgerloh et al. 1997).

Estimates of the sizes of mussels taken by avian predators. – Faecal pellets of herring gulls, faeces of eiders and mussels opened by ventral hammering oystercatchers were collected on the studied mussel beds. In order to make sure that pellets of herring gulls and faeces of eiders were not mixed, only pellets and faeces of birds were collected immediately after observed roosting. Eiders were seen feeding on the Janssand when the mussel bed was still covered by water. They roosted at the border when the mussel bed fell dry.

From pellets and faeces, hinges of mussels were extracted and their widths (mm) were measured by calliper (e.g. Nehls 1995, Hilgerloh et al. 1997). The relation between mussel length and width of hinge is given in the following equation, based on mussels sampled on Janssand in September 1992 on transects: mussel length (mm) = 3.885 + 19.593 ¥ width of hinge (mm), ($r^2 = 0.874$, $p = 0.0001$, $n = 64$). The equation is valid for hinges of widths between 0.45 and 2 mm. All of the encountered hinges were within this size range. Only the mussels eaten by oystercatchers which open mussels by ventral hammering were investigated in this study.

Statistical evaluation. – In order to determine whether the birds consumed a certain selection of the available mussels or whether they ate all present sizes in proportion to their abundance, the non-parametric two-sample Mann-Whitney U test and Komogorov-Smirnow test were used to compare the sizes of available mussels and of mussels selected (for a survey and discussion of applications, see e.g. McBean & Rovers 1998). By available mussels we meant all mussels present on the mussel bed and not only those that are harvestable by the birds (Ens et al. 1994). The Mann-Whitney U test is a nonparametric test based on joined rank sums. It is therefore more sensitive with respect to differences of the median size, or more generally, to differences in the location of the distributions when their general shape is similar. In contrast, the Kolmogorov-Smirnow test measures the deviation between the cumulative distribution functions of size and is hence more sensitive with respect to general deviations of the frequency distribution of size (Sachs 1992). Likewise the two-sided Mann-Whitney U test is used to verify whether mussels of two samples are dissimilar in the sense of a deviation in the median, or more generally, the centre of the distribution in either direction. The one-sided test is used on the hypothesis of a cline in the data, that is, if mussel sizes are bigger in one sample than the other.

For each predator species, the assumption was made that an ideal mussel size-class exists, which would be selected if all size-classes were available. If the differences between the mussel sizes selected and those available were not significant, selectivity could not be proved statistically.

In order to determine whether the different species selected the same mussel size, the Kruskal-Wallis test (also called nonparametric ANOVA) was used to compare the size distributions selected by different predator species. For comparisons between two species only, the U test and the Kolmogorov-Smirnov test were applied. In conditions of limited food resources, according to the U test, if the differences between the mussels selected by the two species were not significant, it could be inferred that both species competed for the same sizes. If differences were not significant according to the U test, yet significant on the Kolmogorov-Smirnov test, it could be concluded that one species (B) experienced strong competition from the other species (A), while the species A also chose sizes not exploited by species B. Two-sided tests were performed with the SPSS-programme (Brosius & Brosius 1995) and the corresponding one-sided p-values were adjusted by hand.

ACKNOWLEDGEMENTS

We wish to express our sincere thanks to M. Herlyn for providing us with the data on mussel lengths of the mussel beds and to M.J. Feltham, G. Jorde and U. Schleier for their comments on an earlier draft of this paper. K. Wilson and S. Marousek checked the English. The 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 Niedersachsen. This is publication no. 239 of the project Ecosystem Research Wadden Sea.

REFERENCES

Brosius, G. & F. Brosius 1995. *SPSS. Base System and Professional Statistics.*–An internat. Thomson Publ. Comp.

Bustnes, J.O. 1998. Selection of blue mussels, Mytilus edulis, by common eiders, Somateria mollissima, by size in relation to shell content. – *Canadian Journal of Zoology* **76**: 1787-1790.

Cayford, J. & J.D. Goss-Custard 1990. Seasonal changes in the size selection of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*: an optimality approach. – *Animal Behaviour* **40**: 609-624.

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.

Dunthorn, A.A. 1971. The predation of cultivated mussels by eiders. – *Bird Study* **18**: 107-112.

Durell le V dit, S.E.A. & J.D. Goss-Custard 1984. Prey selection within a size-class of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*. – *Animal Behaviour* **32**: 1197-1203.

Ens, B. J. 1982. Size selection in mussel-feeding Oystercatchers. – *Wader Study Group Bulletin* **34**: 16-20.

Ens, B.J., Piersma, T & R.H. Drent 1994. The Dependence of Waders and Waterfowl Migrating along the East Atlantic Flyway on their Coastal Food Supplies: what is the most Profitable Research Programme? – *Ophelia*, Supplement **6**: 127-151.

Ens, B. J. & D. Alting 1996. Prey selection of a captive oystercatcher *Haematopus ostralegus* hammering mussels *Mytilus edulis* from the ventral side. *Ardea* **84A**: 215-219.

Goss-Custard, J.D., West, A.D. S.E.A. le V dit Durell 1993. The availability and quality of the mussel prey (*Mytilus edulis)* of oystercatchers (*Haematopus ostralegus*). – *Netherlands Journal of Sea Research* **31**: 419-139.

Guillemette, M., Ydenberg, R.C. & J.H. Himelman 1992. The role of energy intake in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. – *Journal of Animal Ecology* **61**: 599-610.

Hamilton, D.J., Nudds, T.D. & J. Neate 1999. Size-selective predation of Blue Mussels (*Mytilus edulis*) by Common Eiders (*Somateria mollissima*) unter controlled field conditions. *The Auk* **116**: 403-416.

Herlyn, M. and Michaelis, H. 1996. Abschlußbericht des ÖSF-Teilprojekts A 3.3: *Struktur und Funktion der Miesmuschelbestände.* – Nationalparkverwaltung Wilhelmshaven.

Hilgerloh, G. 1997. Predation by birds on blue mussel *Mytilus edulis* of the tidal flats of Spiekeroog (southern North Sea). – *Marine Ecology Progress Series* **146**: 61-72.

Hilgerloh, G. 1999a. *Die Nahrung der Eiderenten im Nationalpark Niedersächsisches Wattenmeer. – Umweltatlas Wattenmeer.* Band 2 Wattenmeer zwischen Elb- und Emsmündung: 90-91. Hrsg. Nationalparkverwaltung Niedersächsisches Wattenmeer & Umweltbundesamt, Ulmer Verlag.

Hilgerloh, G. 1999b. Year to year changes in the share of cockles (*Cerastoderma edule)* and blue mussels (*Mytilus edulis*) in the food of eiders (*Somateria mollissima*) on 6 East Frisian islands. – *Senckenbergiana maritima* **29** (Supplement), Frankfurt am Main: 71-73.

Hilgerloh, G. 2000. Interregional similarities in the food composition of eiders (*Somateria mollissima*). – *Die Seevögel* **21**: 108-111.

Hilgerloh, G. & M. Herlyn 1996. Auswirkungen der Prädation durch Vögel auf eine junge Miesmuschelbank. – *Verhandlungen der Deutschen Zoologischen Gesellschaft* **89**: 308.

Hilgerloh, G., Herlyn, M. & H. Michaelis 1997. 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. – *Helgoländer Meeresuntersuchungen* 51: 173-189.

Hilgerloh, G. & H. Siemoneit (1999): A simple mathematical model upon the effect of predation by birds on a blue mussel (*Mytilus edulis*) population. – *Ecological Modelling* **124**: 175-182.

Hulscher, J.B. 1996. Food and feeding behaviour. – In: Goss-Custard (ed.) *The Oystercatcher*, Oxford University Press, Oxford, pp 7-29.

Kallenborn, R., Hartwig, E. & H. Hühnerfuss 1994. Vergleich der Nahrung von Eiderenten (*Somateria mollissima* (L).) aus Oehe-Schleimünde mit Ergebnissen aus unterschiedlichen Nord- und Ostseegebieten. – *Die Seevögel* **15**: 31-37.

Ketzenberg, C. 1991. *Zur Nahrungsökologie der Eiderente im Königshafen von List/Sylt.* – Diplomarbeit, University of Kiel.

Kirchhof, K. 1979. *Nahrungsökologische Untersuchungen an benthosfressenden Enten in der Hohwachter Bucht.* – Diplomarbeit, University of Kiel.

Krebs, J.R. & A. Kacelnik 1991. Decision-making. – In: *Behavioural ecology. An Evolutionary Approach.* Edited by J.R. Krebs and N.B. Davies, pp 105-136. Blackwell, Oxford.

Leopold, M.F., von Elk, J.F., & Y.M. van Heezik 1996. Central place foraging in oystercatchers *Haematopus ostralegus*: can parents that transport mussels *Mytil-us edulis* to their young profit from size selection? – *Ardea* **84A**: 311-325.

Leopold, M. F., Kats, R. K. H. & B.J. Ens 2001. Diet (preferences) of Common Eiders Somateria mollissima. *Wadden Sea Newsletter* **1**: 25-31.

Madsen, F.J. 1954. On the food habits of the diving ducks in Denmark. – *Danish Review of Game Biology* **2, 3**: 157-226.

McBean, E.A. & F.A. Rovers 1998. *Statistical Procedures for Analysis of Environmental Monitoring Data and Risk Assessment.* Prentice Hall, New Jersey.

Meire, P. & A. Ervynck 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? – *Animal Behaviour* **34**: 1427-1435.

Meire, P. 1993. The impact of bird predation on marine and estuarine bivalve populations: a selective review of patterns and underlying causes. *In Bivalve Filter Feeders.* – Edited by R. Dame. Springer, Berlin, pp 197-243.

Meissner, J. & S. Bräger 1990. The feeding ecology of wintering eiders *Somateria mollissima* and common scoters *Melanitta nigra* on the Baltic Sea coast of Schleswig-Holstein, FRG. – *Wader Study Group Bull.* **58**: 10-12.

Michaelis, H., Obert, B. Schultenkötter, I. & L. Böcker 1995. Die Miesmuschelestände der niedersächsischen Watten, 1989-1991. – *Berichte der Forschungsstelle Küste, Norderney* **40**: 55-70.

Milne, H. & G.M. Dunnet 1972. Standing crop, productivity and trophic relations of the fauna of the Ythan

Estuary. – In: *The Estuarine Environment.* Edited by R.S.K. Barnes.and J. Green. Applied Science Publishers Ltd, London, pp 86-106.

Nehls, G. 1991. Eiderenten im schleswig-holsteinischen Wattenmeer. – *Corax* **14**: 3-66.

Nehls, G. 1995. *Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente* (Somateria mollissima) (L., 1758). – Dissertation, University of Kiel.

Nehls, G. & M. Thiel 1993. Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystem? – *Netherlands Journal of Sea Research.* **31**: 181-187.

Norton Griffiths, M. 1967. Some ecological aspects of the feeding behaviour of the oystercatcher, *Haematopus ostralegus*, on the edible mussel, *Mytilus edulis.* – *Ibis* **109**: 412-424.

Pianka, E.R. 1974. Niche overlap and diffuse competition. – *Proceedings of the National Academy of Science* **71**: 141-145.

Player, P.V. 1971. Food and feeding habits of the Common Eider at Seafield, Edinburgh, in winter. – *Wildfowl* **22**: 100-106.

Raffaelli, D., Falcy, C. and Galbraith, C. 1990. Eider predation and the dynamics of mussel bed communities. – In *Trophic Relations in the Marine Environment.* Edited by M. Varnes. and R.N. Gibson. Aberdeen Univ. Press, pp 157-169.

Sachs, L. 1992. *Angewandte Statistik: Anwendung statistischer Methoden.* – Springer-Verlag, Berlin.

Spaans, A.L. 1971. On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. – *Ardea* **59**: 73-185.

Sutherland, W. & B.Ens 1987. The criteria determining the selection of mussels *Mytilus edulis* by Oystercatchers *Haematopus ostralegus.* – *Behaviour* **103**: 187-202.

Swennen, C. 1976. Populatie-structuur en voedsel van de eidereend *Somateria mollissima* in de Nederlandse Waddenzee. – *Ardea* **64**: 171-311.

Zwarts, L. & R.H. Drent 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.* Edited by P. Jones and W. J. Wolff, Plenum Press, New York, pp. 193-216.

Zwarts, L. & J.H. Wanink 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. – *Netherlands Journal of Sea Research* 31: 441-476.

Zwarts, L., Cayford, J.T., Hulscher, J.B., Kersten, M., Meire, P. & P. Triplet 1996a. Prey size selection and intake rate. – In: Goss-Custard (ed): *The Oystercatcher.* Oxford University Press, Oxford, pp 30-55.