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Blue mussels *Mytilus edulis* in the Baltic: good news for foraging eiders *Somateria mollissima*

Markus Öst & Mikael Kilpi

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We analysed the food of eiders *Somateria mollissima* at Hanko, Finland, in the northern Baltic, by examining the contents of mussels in the faeces and digestive system of eiders. The aim of our study was to determine whether size selection of the main food, blue mussels *Mytilus edulis*, occurs and if so why. Generally, diving ducks seem to choose mussels smaller than the average found on mussel beds. One hypothesis states that size selection of mussels occurs because eiders choose to minimise the daily intake of shell material. We did not find unambiguous evidence of size selective feeding on blue mussels in our study area. Although eiders selected mussels somewhat smaller than the average found on mussel beds when the entire data set was analysed, this minor discrepancy can probably be attributed to the fact that benthic sampling was conducted in areas which were partly different from the areas in which eider specimens and faeces were collected. Individual differences among eiders were significant. The meat content of northern Baltic mussels was generally higher than that of Atlantic blue mussels, with only a slightly decreasing trend with increasing mussel size. Shell weight increased more than meat weight with increasing mussel size. However, the shell weight that birds have to ingest to obtain their daily requirement of food is many times greater in the Atlantic than in our study area for all size categories of mussels. Thus, shell mass minimisation is probably not of crucial importance to eiders in the northern Baltic.

Key words: Baltic Sea, blue mussel, eider, shell mass, size selection, *Somateria mollissima*

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The eider *Somateria mollissima* feeds mainly on molluscs, especially blue mussels *Mytilus edulis* (e.g. Pethon 1967, Cramp & Simmons 1977, Bustnes & Erikstad 1988). In the Baltic, blue mussels, dominating the animal biomass on harder substrates (Kautsky 1981), is the staple food of eiders (e.g. Bagge, Lemmetyinen & Raitis 1973, Nilsson 1980, Öst 1995). Generally, eiders tend to select mussels smaller than the average found on mussel beds (Madsen 1954,

Player 1971, Swennen 1976, Thompson 1985, Bustnes & Erikstad 1990, Nehls 1991, Nyström, Pehrsson & Broman 1991). This trend has been found in other diving ducks as well (Draulans 1982, 1984, Nyström & Pehrsson 1988, de Leeuw & van Eerden 1992), but size selection of smaller mussels is not always the rule (see e.g. Nehls 1991, Hamilton, Ankney & Bailey 1994, Guillemette, Reed & Himmelman 1996).

The Baltic blue mussel differs in many physiological and morphological aspects from oceanic blue mussels (Kautsky 1982a, Tedengren & Kautsky 1986, Kautsky, Johannesson & Tedengren 1990, McDonald, Seed & Koehn 1991). Recent development in molecular techniques has challenged the traditional taxonomy of the mussel *Mytilus*. Many scientists now consider the Baltic blue mussel as a semi-species (Väinölä & Hvilsum 1991), or even as a distinct species *M. trossulus* (McDonald et al. 1991, Beynon & Skibinski 1996). However, the phylogenetic relationship within the genus *Mytilus* remains unresolved (Beynon & Skibinski 1996). No detailed study on size selection of Baltic blue mussels by eiders has been conducted before.

Several hypotheses have been put forward to explain why diving ducks prefer small mussels:

- 1) Energetic costs of salt excretion; by choosing small mussels the ducks may minimise salt intake, as mussels are swallowed whole and the proportion of locked-in sea water increases with increasing mussel size (Nyström & Pehrsson 1988, Nyström et al. 1991). The excretion of excess salt is an extra energetic cost that affects the growth rate and may disturb the energy balance of the birds (Schmidt-Nielsen & Kim 1964, Nyström & Pehrsson 1988);
- 2) Risk of choking; by choosing smaller mussels the ducks may minimise the risk of taking a mussel too large to be swallowed (Swennen 1976, Elner & Hughes 1978, Draulans 1982, 1984);
- 3) Maximisation of energy; There are several sub-hypotheses based on the energy maximisation principle, which postulates that the forager maximises profitability, defined as net energetic gains per handling time (see Stephens & Krebs 1986 and references therein). Selection of small mussels can result from the following proximate factors:
 - 3a) Constraint of diving; a bird may do better to swallow several small mussels in one dive, instead of a large one which contains more meat than a small one, and which has to be eaten at the surface (Draulans 1982, de Leeuw & van Eerden 1992);
 - 3b) The energy content of larger mussels is often more variable; therefore it may be profitable for the birds to select smaller mussels associated with less variance, thereby reducing the risk of taking mussels

of low profitability (Draulans 1982, Durell & Goss-Custard 1984, Bustnes & Erikstad 1990);

- 3c) Energy loss of detaching mussels: mussels are attached to the substratum with byssus-threads and larger mussels may be harder to detach from the bottom (Bustnes & Erikstad 1990);
- 3d) Shell weight minimisation; ducks choose small mussels in order to minimise the daily intake of shell material (Bustnes & Erikstad 1990). The ingestion of shell material requires both time and energy (Guillemette, Ydenberg & Himmelman 1992, de Leeuw & van Eerden 1992), which diminishes profitability, measured as net energetic gains per handling time (Stephens & Krebs 1986). Energy assimilation in the eider is constrained by the rate of digestion; the rate of ingestion of mussel shells is two times higher than the defecation rate and, as a consequence, shells accumulate in the gut as ingestion progresses (Guillemette 1994).

In this study we analysed the food of eiders at Hanko, Finland, in the northern Baltic. We measured blue mussels in both freshly collected faeces and in the digestive system of eiders, and the data was compared with mussels sampled from the bottom in the same region. The aim was to determine whether size selection occurs and to evaluate our results in the light of the hypotheses which have been put forward. We particularly focused on the 'shell weight minimisation-hypothesis' (3d) put forward by Bustnes & Erikstad (1990). In order to do this, we measured the flesh content and shell weight of mussels of different sizes.

Methods

Study area

The study was carried out in the tideless Baltic Sea in 1992, off the Hanko peninsula (60°N, 23°E), in the northern Baltic. The benthic samples of mussels and the eider faeces were both collected in the same area west of the Hanko peninsula (see map in Öst 1995). Our sampling sites, all of which represent typical hard bottom mussel beds frequented by foraging eiders, ranged in mean depth within 4-10 m according to the depth measurements we conducted in

1992. The salinity in the area is 6-7‰ (Sunila 1981). Eider specimens used for analyses of mussels from the digestive system were collected east of the Hanko peninsula, close to the Tvärminne Zoological Station (see map in Kilpi, Lindström, Candolin & Roslin 1990). Generally, the Hanko archipelago can be described as a fine-scaled mosaic of islands, islets and small skerries with suitable foraging patches for both eider adults and ducklings (Öst & Kilpi 1997). Adult mussels suitable as food for eiders are found in mussel beds and small, less than 3 mm long individuals settle in filamentous algae outside the mussel bed (primary and secondary settlement system) (Sunila 1981, Kautsky 1982b, Sunila 1987). The mussel beds in our study area range in depth within ca 4-12 m with the highest biomass observed at depths of 8-10 m (Olli Mustonen, pers. comm.). The filamentous algal zone dominated by *Cladophora* spp. ranges in depth within 0.2-2 m (Kiirikki 1996).

Sampling design

The mussel size distribution in areas where eiders normally feed was determined by sampling in March-July 1992 from two adjacent areas west of the Hanko peninsula, Möön and Rödkär-Flintskär-Garpen, respectively. We used a triangular bottom scraper with a gap width of 0.4 m which was dragged along, and thus continuously scraped, underwater slopes in the mussel beds starting from a depth of approximately 10 m and ending when the upper boundary of the mussel bed habitat had been encountered at a depth of about 4 m. One such drag constituted a sample and the mussels thus collected were put in plastic jars. The sample was then sieved through a 1-mm mesh screen and 30 mussels were randomly chosen and measured by a vernier calliper to the nearest 0.1 mm (except for one sample containing only 20 mussels). The mean mussel length of the sample was used in further analyses to avoid problems with multiple testing. In total, 19 samples consisting of 560 mussels were collected: nine samples from Möön (3 samples on 23 March, N = 90 mussels; 3 samples on 28 May, N = 80; 3 samples on 24 July, N = 90) and 10 samples from Rödkär-Flintskär-Garpen (3 samples on 24 March, N = 90; 3 samples on 7 June, N = 90; 4 samples on 23 July, N = 120).

To determine the flesh weight and shell mass of different size classes of mussels, the flesh of 275 mussels covering all size classes was carefully removed, and both the flesh and the shells were dried

(48 hours at 60°C). The dry weight of shell and flesh was then measured to the nearest 10 µg using a Cahn 28 balance.

Mussels <5 mm were excluded from the analyses. Firstly, the fraction of mussels <5 mm in the mussel beds is insignificant, as mussel smaller than about 3 mm are absent from the mussel beds, settling in filamentous algae (Sunila 1981, Kautsky 1982b, Sunila 1987). Secondly, the smallest mussels are probably secondary food for eiders, swallowed accidentally along with the primary prey (Madsen 1954). Finally, it is technically difficult to remove the flesh of the smallest mussels (cf. Bustnes & Erikstad 1990).

Fresh eider faeces were collected at Möön on 3 April and 23 April 1992. The sampling of faeces was done on exactly the same spot where we conducted part of the benthic sampling of mussels. We observed foraging eiders using of a 30X spotting scope and whenever an eider stopped foraging and went ashore on a rock or reef leaving a dropping this was collected immediately. The droppings were sieved through a 1-mm mesh screen and the thickness of umbos in 20 individual droppings was measured (30 umbos/dropping). In accordance with Swennen (1976) we made the following assumptions: (i) one dropping, whatever the volume might be, was considered to represent one 'meal'; this meal obviously consisted of mussels consumed in the particular site under study, (ii) all droppings belonged to different birds. The mean mussel length from a single dropping (30 umbos) was used in the analyses as one sample to avoid problems with multiple testing. Our sample thus consisted of 20 eider specimens (N = 600 mussels).

Six eiders (three females and three males) were shot for scientific purposes on 15 April 1992 outside Tvärminne. We measured mussels found in the digestive system (gullet, oesophagus, gizzard and intestines) after sieving the visceral contents through a 1-mm mesh screen. Because of the grinding action of the gizzard, most of this material consisted of small shell fragments. We therefore reconstructed mussel length based on measurements of the thickness of the umbo, which remains more or less intact through digestion. This method of reconstructing mussel size has successfully been used by Nehls (1991) and Nyström et al. (1991). We tried to attain an equal sample size of umbos measured for each eider specimen, but this proved to be difficult. Our total sample from eider intestines consisted of 429 mussels (49, 50, 79, 80, 80, 91 in the six eiders, respectively). The

number of whole, intact shells was negligible, and only the smallest mussels remained intact through digestion. Consequently these mussels were excluded from further analyses.

Reconstructing mussel size

In order to establish the relationship between mussel length and thickness of the umbo, 70 mussel shells of all size classes were broken into pieces. The thickness of the umbo was then measured, using a microscope, with an accuracy of 20 μm. There was a strong linear regression between mussel length, L (mm) and the thickness of the umbo, T (mm):

$$L = 3.538 + 30.182 \times T \text{ (} R^2 = 0.80, N = 70, P < 0.001 \text{)}$$

The relationship between mussel length and thickness of the umbo was used in further analyses of mussels from the eider intestines and faeces.

Statistical analysis

We carefully checked if the data conformed to a normal distribution (Wilk Shapiro’s test), and if variances were homogeneous (Bartlett’s test). If these assumptions were not met, non-parametric tests were used. In order to establish the allometric relationship between mussel size (linear function) and flesh weight and shell mass (exponential functions) we used non-linear regression models. Non-linear regression equations fitted our data equally well as log-transformation of the variables, but the advantage of non-linear regression models is that absolute values can be extracted directly. Numerical values are expressed as means ± SD.

Results

Size selection of mussels by eiders

The size-frequency distribution of mussels from benthic samples, eider faeces and eider intestines is shown in Figure 1. The mean size of mussels sampled from the mussel beds was 21.0 ± 3.6 mm (N = 19 samples/560 mussels). There were no differences

Table 1. Length of blue mussels (mean ± SD) sampled from the bottom, and from the digestive system and droppings of eiders.

	Mean (mm)	SD	Samples	No of mussels
Bottom	21.0	3.6	19	560
Intestines	17.4	1.1	6	429
Faeces	18.2	1.8	20	600

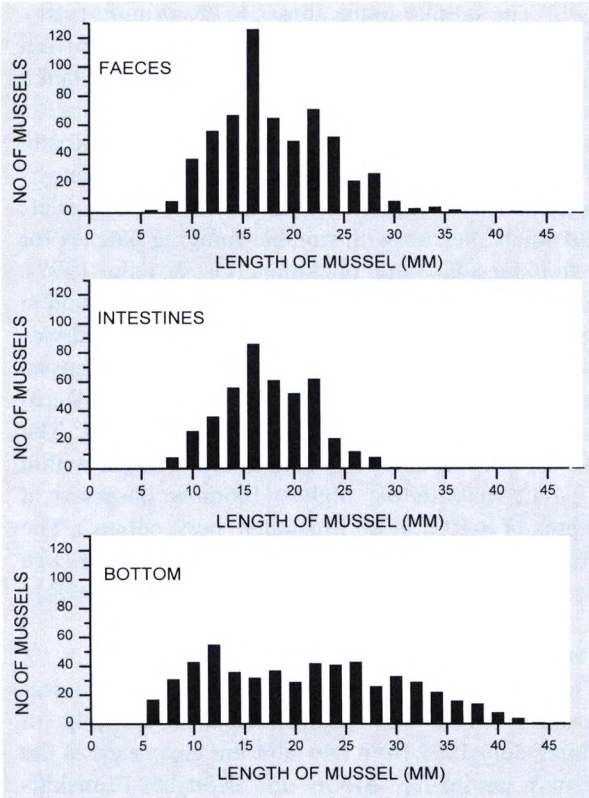


Figure 1. Size-frequency distribution of mussels from eider faeces (N = 20 eiders/600 mussels), intestines (N = 6 eiders/429 mussels) and from the bottom (N = 19 samples/560 mussels). The data is grouped in 2 mm size classes.

in the mean size of mussels between the two areas sampled (Möön: 21.2 ± 4.7 mm, N = 9; Rödsjär-Flintskär-Garpen 20.8 ± 2.6 mm, N = 10; t = 0.22, df = 12.1, P = 0.83). In the digestive system of the six eiders collected, the mean size of mussels was 17.4 ± 1.1 mm (N = 6 samples/429 mussels). There was no difference in the sizes of mussels eaten by males (17.1 ± 1.3 mm, N = 3) and females (17.6 ± 1.0 mm, N = 3) (Mann-Whitney U-test, P = 0.35), and therefore data from the two sexes were pooled in further analyses. The mean size of mussels in the eider droppings was 18.2 ± 1.8 mm (N = 20 samples/600 mussels) (Table 1).

The size of mussels at the bottom and in the intestines and droppings differed significantly (Kruskal-Wallis test, H = 12.0, df = 2, P < 0.01). *Post hoc* comparisons revealed that mussels from both the intestines and droppings were significantly smaller than mussels from the bottom (P < 0.05). However, the mean size of mussels in eider faeces was not significantly different from mussels collected from the

bottom in exactly the same area, Möön, and at approximately the same time as the faeces (i.e. the benthic samples from July were excluded) (bottom: mean 19.1 ± 4.3 mm, $N = 6$; faeces: mean 18.2 ± 1.8 mm, $N = 20$; $t = 0.5$, $df = 5.5$, $P = 0.64$).

There were significant individual differences among eider specimens in the size of the mussels eaten. This was true for both mussels in eider intestines (Kruskal-Wallis test, $H = 18.69$, $df = 5$, $P = 0.002$) and in the droppings (Kruskal-Wallis test, $H = 60.43$, $df = 19$, $P < 0.001$).

Flesh weight and shell mass of Baltic blue mussels

The average proportion of dry flesh weight to total dry mussel weight was $14.6 \pm 5.0\%$ ($N = 275$) (Fig. 2). There was a significant negative correlation between mussel size and the proportion of dry flesh weight to dry mussel weight ($r = -0.18$, $N = 275$, $P = 0.002$). A regression analysis also showed a weak but significant negative relationship between the proportion of meat and mussel length (see Fig. 2).

Shell weight increased more than flesh weight with increasing mussel size (Fig. 3). For example, with an increase in mussel length from 14 to 40 mm, the flesh weight increased 9.4-fold (from 17.9 to 168 mg) and

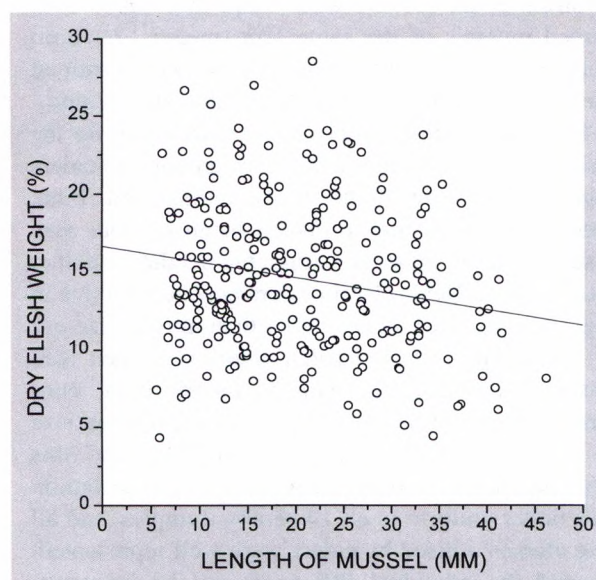


Figure 2. Meat content of Baltic blue mussels given as percentages of total mussel mass (dry flesh weight) for mussels of 5–46 mm. A regression analysis showed a weak but significant negative relationship between the meat content of mussels, M (%) and mussel length, L (mm): $M = 15.955 - 0.075 \times L$ ($R^2 = 0.022$, $N = 275$, $P = 0.01$).

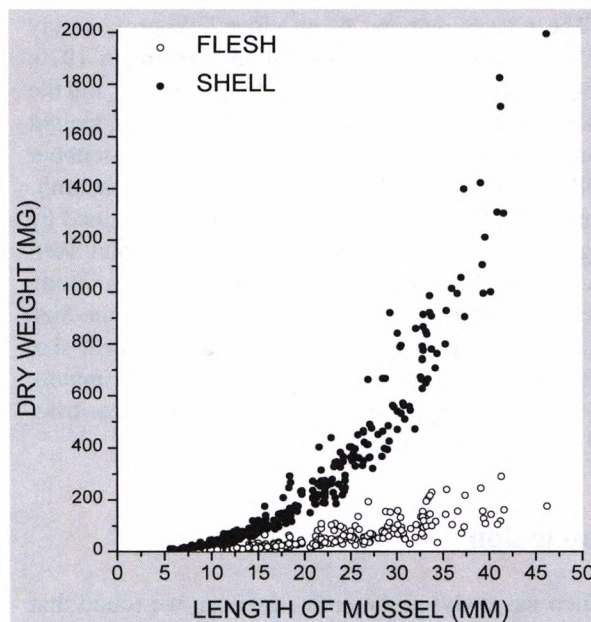


Figure 3. Relationship between mussel length (mm) and dry flesh weight (\circ) and dry shell mass (\bullet) of mussels (mg). The relationships are best described by non-linear regression equations: flesh = $0.0645 \times \text{length}^{2.132}$ ($R^2 = 0.72$, $N = 275$, $P < 0.05$); shell = $0.0475 \times \text{length}^{2.770}$ ($R^2 = 0.95$, $N = 275$, $P < 0.05$).

shell weight 18-fold (from 71.1 to 1,300 mg) (calculated from the equations given in Fig. 3).

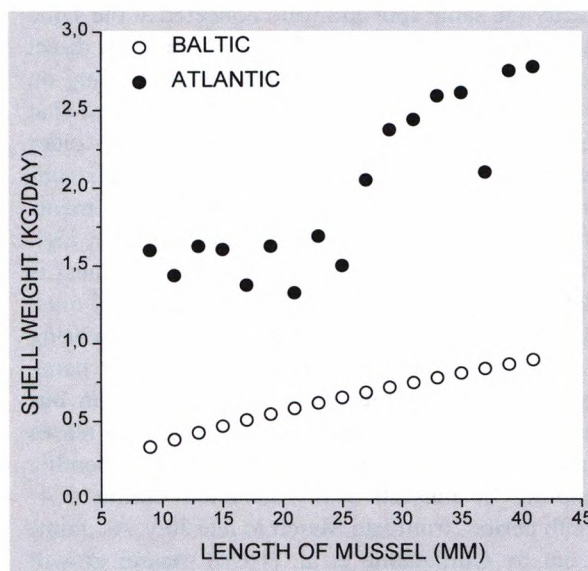


Figure 4. Total shell weight (kg) which eiders have to ingest per day in order to meet their energy demand if feeding exclusively on mussels of 9–41 mm in the Baltic (\circ) and in the Atlantic (\bullet). (Atlantic data modified from Bustnes & Erikstad 1990).

The energy demand of an eider is approximately 555 kcal/day (1 kcal = 4.1868 kJ) (Swennen 1976, Thompson 1985, Nyström & Pehrsson 1988), and the energy content of mussels is 4.9 kcal/g dry weight varying little throughout the year (Loo & Rosenberg 1983, Thompson 1985). Accordingly, the consumption of 555 kcal per eider per day can be obtained by ingesting 113 g of dry mussel flesh. The total shell weight that birds have to ingest per day in our study area, if feeding exclusively on mussels of one size class, varies from about 230 g for the smallest size class of mussels (measuring 5 mm) to approximately 900 g for the largest size class of mussels (measuring 40–45 mm) found in our study area (Fig. 4).

Discussion

When we analysed the entire data set, we found that eiders feed on mussels somewhat smaller than the average found in mussel beds. However, this result may reflect the fact that benthic sampling was conducted in areas which in part were different from the areas in which eider specimens and faeces were collected. The eider specimens originated from an area where the mean mussel size at the bottom is markedly smaller (Öst & Kilpi 1997). The mean mussel size at the bottom did not differ from the mussel size in eider faeces, when both samples originated from exactly the same spot and were collected at the same time. Thus, our conclusion is that there is no direct proof that eiders are size selective when feeding on mussels in our study area. Our results showed that there are individual differences among the eider specimens in regard to the size of the mussels consumed. The results of the dry weight measurements showed that the meat content of mussels is fairly high in our study area, and that the proportion of meat is relatively constant in different size classes of mussels; only a slightly decreasing trend with increasing mussel size could be discerned. On the other hand, the shell mass of mussels is relatively low in our study area, and the proportion of shell mass increases slightly with increasing mussel size. The benthic sampling of mussels was conducted during a 4-month period, from late March to late July. As pointed out by Guillemette et al. (1996) mussel growth occurs in summer and might therefore influence our estimate of the size of mussels available at the bottom. The growth rate of Baltic blue mussels is very low compared to the growth rate of oceanic mussels

(e.g. Kautsky 1982a, Tedengren & Kautsky 1986, Kautsky et al. 1990). In an experimental study conducted in the Stockholm archipelago, Sweden, which closely resembles our study area, growth in middle-sized mussels measuring 3–20 mm from mussel populations found at depths of 3–6 m and 10–15 m was only 3.1 and 2.2 mm year⁻¹, respectively (Kautsky 1982a). Hence, the growth taking place during March–July would be only about 1 mm. Furthermore, subtracting 1 mm from the length of mussels sampled from the bottom in order to compensate for the mussels sampled in July would reduce the discrepancy between the mussel size at the bottom and that observed in the diet of eiders. Consequently, this tends to support our conclusion that eiders are not overly size selective when feeding on mussels in our study area.

Our results differ somewhat from the results of studies made in truly marine habitats, where eiders remarkably often select small mussels (e.g. Player 1971, Swennen 1976, Bustnes & Erikstad 1990, Nyström et al. 1991). In northern Norway, for example, the mean length of mussels consumed by eiders was smaller than in our study area (only 13.9 mm, Bustnes & Erikstad 1990), though Atlantic blue mussels are much larger on average than Baltic blue mussels. Our results are in accordance with the results of Nyström et al. (1991), who found that eiders consumed mussels of the same size (mean: 17.2 mm) both on the west and east coast of Sweden, in spite of the mussels being much smaller in the latter region.

There are at least two possible explanations for the existence of individual differences among the eiders regarding the size of the mussels consumed. First, these differences may reflect a heterogeneous size distribution of mussels within the feeding habitat. According to Nehls (1991) eiders may be selective in regard to feeding patches rather than mussel size *per se*. Within the selected patch eiders may then feed unselectively, and they might therefore be constrained by the scarcity of mussels of the optimal size in some feeding patches. However, we find this explanation less probable since the size distribution was rather uniform in all 19 benthic samples, and all size classes utilised by eiders were well represented. Second, the individual differences may be the consequence of individual birds differing in their ability to forage optimally. This has been demonstrated by Ball (1994) working with canvasback ducks *Aythya valisineria* under seminatural conditions. Optimal foraging studies often tend to ignore variation in individ-

ual optima and model the responses of the animal representing the 'golden mean' (Ball 1994).

The distinctive morphological features of Baltic blue mussels influence the relevancy of the 'shell minimisation hypothesis' (3d). The average meat content of mussels in our study area, 14.6%, is higher than in Atlantic blue mussels (*cf.* e.g. Thompson 1985, Bustnes & Erikstad 1990, Kautsky et al. 1990). In Scotland, the meat content varies within 5.9–12.9% (Thompson 1985) and in northern Norway within 4.2–8.6% in different size categories being greatest in the mussels most frequently fed upon (Bustnes & Erikstad 1990). According to results from reciprocal transplantations of Baltic and North Sea mussels, more biomass is allocated to meat in Baltic mussels (14.7% vs 11.2%) owing to genetic differentiation (Kautsky et al. 1990). In northern Norway, the total shell weight ingested by eiders in order to obtain their daily energy requirement was 1.5 kg for small mussels (measuring 9–15 mm), increasing steeply to more than 2.5 kg for the largest mussels (measuring 41–43 mm) (Bustnes & Erikstad 1990, see Fig. 4). In Scotland, the amount of shell ingested per eider per day varied from 0.74 to 1.82 kg depending on the time of year for 23-mm long blue mussels, the average size of mussels consumed by eiders in the area (Thompson 1985). Since the amount of shell ingested by eiders outside the Baltic is many times greater than in our study area (see Fig. 4), it is probable that size selective feeding with the aim of minimising daily shell intake is of minor importance in the northern Baltic.

The eider digestive mechanism requires the bird to break up the mussel shells within the gizzard. Therefore, thickness of the shell rather than total shell weight may be a more useful measurement to investigate (Galbraith 1987). Even in this respect, Baltic blue mussels seem to be favourable food for eiders despite their minor size, since they are thin-shelled and have a weak shell structure due to a low calcium content (Kautsky et al. 1990). In a study from Scotland, Galbraith (1987) found that eiders preferred cultivated mussels to their thicker-shelled counterparts of similar size from intertidal areas. So, eiders are obviously able to discriminate between the shell characteristics and possibly also the meat content of their prey.

It is unlikely that dietary salt content of mussels (hypothesis 1) is an important criterion for size selection, especially since the salinity in our study area is only 6–7‰. The energetic costs of salt turnover are

low in eiders (Nehls 1996). It is also controversial whether the minimisation of salt intake by eiders should lead to selection for small mussels (Nyström & Pehrsson 1988, Nyström et al. 1991) or large mussels, as the study by Nehls (1996) suggests.

Unfortunately, nothing is known about the exact relationship between the strength of mussel attachment to the bottom and mussel size in the Baltic (hypothesis 3c). However, according to Kautsky (1981) Baltic blue mussels are only loosely attached to the substratum by byssus-threads. Therefore, the attachment to the bottom is unlikely to affect the foraging decisions of birds to any greater extent. Experimental evidence on tufted ducks *Aythya fuligula* feeding on zebra mussels *Dreissena polymorpha* also showed that the profitability of mussels of different sizes was more or less unaffected by attachment to the bottom (Draulans 1982). In the Wadden Sea, however, blue mussels are often tightly clumped by byssus-threads, which certainly affects the handling time of mussels (Nehls 1991).

Eiders can ingest mussels ranging from 2–3 to 60 mm (Guillemette et al. 1996) with 80 mm documented as the maximum size (Madsen 1954). Since the largest mussel in our benthic sample was 46.2 mm long, it is obvious that all mussels present were potentially available for eiders. Thus, avoidance of mussels too large to be swallowed (hypothesis 2) is not a criterion for size selection. Nor did our data show any proof of larger mussels varying more in their flesh content (hypothesis 3b); the residuals of flesh content did not increase with mussel size. Finally, an eider might prefer to swallow several small mussels in one dive instead of taking a large one containing more meat, which has to be taken to the surface (hypothesis 3a). It is possible that most Baltic mussels are so small that several mussels can be picked up in one dive, which could explain the lack of apparent size selection in the area.

Eiders in our study area spend most of the year outside the Baltic, in highly saline habitats (Nehls 1991). Here, they are feeding on Atlantic blue mussels that on average are much larger, have much thicker shells, smaller proportions of meat, and more saline sea water locked inside the shell. In the Baltic, the properties of blue mussels are more favourable on the whole, and the fitness costs associated with consuming large vs small mussels are far less dramatic. We might therefore assume that size selection of mussels in the northern Baltic is not of such vital importance as in the Atlantic. In conclusion, despite their minor

size Baltic blue mussels are favourable food for eiders, and this may in part explain the abundance of eiders in the area.

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References

- Bagge, P., Lemmetyinen, R. & Raitis, T. 1973: Spring food of some diving waterfowl in the southwestern Finnish archipelago. - *Oikos Supplement* 15: 146-150.
- Ball, J.P. 1994: Prey choice of omnivorous canvasbacks: imperfectly optimal ducks? - *Oikos* 70: 233-244.
- Beynon, C.M. & Skibinski, D.O.F. 1996: The evolutionary relationships between three species of mussel (*Mytilus*) based on anonymous DNA polymorphisms. - *Journal of Experimental Marine Biology and Ecology* 203: 1-10.
- Bustnes, J.O. & Erikstad, K.E. 1988: The diets of sympatric wintering populations of common eider *Somateria mollissima* and king eider *S. spectabilis* in northern Norway. - *Ornis Fennica* 65: 163-168.
- Bustnes, J.O. & Erikstad, K.E. 1990: Size selection of blue mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization? - *Canadian Journal of Zoology* 68: 2280-2283.
- Cramp, S. & Simmons, K.E.L. (Eds.) 1977: *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 1. - Oxford University Press, Oxford, 722 pp.
- de Leeuw, J.J. & van Eerden, M.R. 1992: Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. - *Ardea* 80: 353-362.
- Draulans, D. 1982: Foraging and size selection of mussels by the Tufted Duck *Aythya fuligula*. - *Journal of Animal Ecology* 51: 943-956.
- Draulans, D. 1984: Sub-optimal mussel selection by Tufted Ducks *Aythya fuligula*: test of a hypothesis. - *Animal Behaviour* 32: 1192-1196.
- Durell, S.E.A. le V. dit & Goss-Custard, J.D. 1984: Prey selection within a size-class of mussels *Mytilus edulis* by Oystercatchers *Haematopus ostralegus*. - *Animal Behaviour* 32: 1197-1203.
- Elnor, R.W. & Hughes, R.N. 1978: Energy maximization in the diet of the shore crab, *Carcinus maenas*. - *Journal of Animal Ecology* 47: 103-116.
- Galbraith, C. 1987: Eider *Somateria mollissima* predation of cultivated mussels *Mytilus edulis*. - PhD Thesis, University of Aberdeen, Aberdeen, United Kingdom, 236 pp.
- Guillemette, M. 1994: Digestive rate constraint in wintering common eiders (*Somateria mollissima*): implications for flying capabilities. - *Auk* 111: 900-909.
- Guillemette, M., Ydenberg, R.C. & Himmelman, J.H. 1992: The role of energy intake rate in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. - *Journal of Animal Ecology* 61: 599-610.
- Guillemette, M., Reed, A. & Himmelman, J.H. 1996: Availability and consumption of food by common eiders wintering in the Gulf of St. Lawrence: evidence of prey depletion. - *Canadian Journal of Zoology* 74: 32-38.
- Hamilton, D.J., Ankney, C.D. & Bailey, R.C. 1994: Predation of zebra mussels by diving ducks: an enclosure study. - *Ecology* 75: 521-531.
- 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 Meeresforschungen, Sonderheft* 5: 454-461.
- Kautsky, N. 1982a: Growth and size structure in a Baltic *Mytilus edulis* population. - *Marine Biology* 68: 117-133.
- Kautsky, N. 1982b: Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. - *Marine Biology* 68: 143-160.
- Kautsky, N., Johannesson, K. & Tedengren, M. 1990: Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and morphology. - *Marine Ecology Progress Series* 59: 203-210.
- Kiirikki, M. 1996: Dynamics of macroalgal vegetation in the northern Baltic Sea - evaluating the effects of weather and eutrophication. - *Walter and Andrée de Nottbeck Foundation Scientific Reports No. 12*: 1-15.
- Kilpi, M., Lindström, K., Candolin, U. & Roslin, T. 1990: Distribution of eider (*Somateria mollissima*) broods off the Hanko peninsula during the breeding season. - *Memoranda Societatis Fauna Flora Fennica* 66: 91-96.
- Loo, L.O. & Rosenberg, R. 1983: *Mytilus edulis* culture: growth and reproduction in western Sweden. - *Aquaculture* 35: 137-150.
- Madsen, F.J. 1954: On the food habits of the diving ducks in Denmark. - *Danish Review of Game Biology* 2: 157-266.
- McDonald, J.H., Seed, R. & Koehn, R.K. 1991: Allozymes and morphometric characters of three species of *Mytilus* in the Northern and Southern Hemispheres. - *Marine Biology* 111: 323-333.
- Nehls, G. 1991: Bestand, Jahresrhythmus und Nahrungsökologie der Eiderente, *Somateria mollissima*, L. 1758, im Schleswig-Holsteinischen Wattenmeer (In German with English summary: Numbers, annual cycle and feeding ecology of the Common Eider, *Somateria mollissima*

- L. 1758, in the Wadden Sea of Schleswig-Holstein). - Corax 14: 146-209.
- Nehls, G. 1996: Low costs of salt turnover in common eiders *Somateria mollissima*. - Ardea 84: 23-30.
- Nilsson, L. 1980: Wintering diving duck populations and available food resources in the Baltic. - Wildfowl 31: 131-143.
- Nyström, K.G.K. & Pehrsson, O. 1988: Salinity as a constraint affecting food and habitat choice of mussel-feeding diving ducks. - Ibis 130: 94-110.
- Nyström, K.G.K., Pehrsson, O. & Broman, D. 1991: Food of juvenile Common Eiders (*Somateria mollissima*) in areas of high and low salinity. - Auk 108: 250-256.
- Öst, M. 1995: Ejderns (*Somateria mollissima*) val av blåmusslor (*Mytilus edulis*) i Norra Östersjön - är små musslor bättre än stora? - MSc Thesis, University of Helsinki, Helsinki, Finland, 51 pp. (In Swedish).
- Öst, M. & Kilpi, M. 1997: A recent change in size distribution of blue mussels (*Mytilus edulis*) in the western part of the Gulf of Finland. - Annales Zoologici Fennici 34: 31-36.
- Pethon, P. 1967: Food and feeding habits of the Common Eider *Somateria mollissima*. - Nytt Magasin for Zoologi 15: 97-111.
- Player, P.V. 1971: Food and feeding habits of the common eider at Seafeld, Edinburgh, in winter. - Wildfowl 22: 100-106.
- Schmidt-Nielsen, K. & Kim, Y.T. 1964: The effect of salt intake on the size and function of the salt glands of ducks. - Auk 81: 160-172.
- Stephens, D.W. & Krebs, J.R. 1986: Foraging Theory. - Princeton University Press, Princeton, 247 pp.
- Sunila, I. 1981: Reproduction of *Mytilus edulis* L. (*Bivalvia*) in a brackish water area, the Gulf of Finland. - Annales Zoologici Fennici 18: 121-128.
- Sunila, I. 1987: Histopathological effects of environmental pollutants on the blue mussel, *Mytilus edulis* L. (Baltic Sea), and their application in marine monitoring. - PhD Thesis, University of Helsinki, Helsinki, Finland, 73 pp.
- Swennen, C. 1976: Populatie-structuur en voedsel van de Eidereend *Somateria m. mollissima* in de Nederlandse Waddenzee (In Dutch with English summary: Population structure and food of the eider *Somateria m. mollissima* in the Dutch Wadden Sea). - Ardea 64: 311-371.
- Tedengren, M. & Kautsky, N. 1986: Comparative study of the physiology and its probable effect on size in blue mussels (*Mytilus edulis* L.) from the North Sea and the northern Baltic proper. - Ophelia 25: 147-155.
- Thompson, A.B. 1985: Transmission dynamics of *Proficollis botulus* (*Acantocephala*) from crabs (*Carcinus maenas*) to Eider Ducks (*Somateria mollissima*) on the Ythan estuary, N. E. Scotland. - Journal of Animal Ecology 54: 605-616.
- Väinölä, R. & Hvilson, M.M. 1991: Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* populations (*Mytilidae*: *Mollusca*). - Biological Journal of the Linnean Society 43: 127-148.