

USING OPTIMAL FORAGING THEORY TO DETERMINE THE DENSITY OF MUSSELS *MYTILUS EDULIS* THAT CAN BE HARVESTED BY HAMMERING OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS*

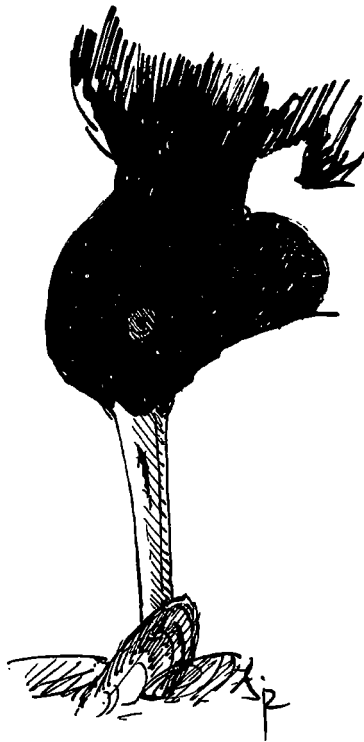
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In a previous paper (Meire & Ervynck 1986) it was shown that Oystercatchers, opening Mussels by the hammering method, selected the most profitable length classes of Mussels in terms of energy gain. It was assumed in the model that thick-shelled Mussels could not be opened. In this paper the possibility is explored that opening is not impossible, but would take a disproportionate amount of time. To this end, the numbers of blows of an artificial Oystercatcher bill, necessary to open a Mussel, was measured experimentally and was found to increase supraproportionally with shell thickness. Based on this experiment and measurements in the field the profitability of Mussels as a function of shell thickness was calculated for different length classes. Profitability decreased sharply with shell thickness and differed, for each shell thickness class, between length classes. Based on this result it was predicted that (1) per length class of Mussels, the thick-shelled Mussels should be dropped from the diet and (2) that the shell thickness of Mussels accepted should increase with mussel length. Both predictions were supported by the data. As birds selected the thin-shelled Mussels it was expected that the average shell thickness of the Mussels on the bed should increase in the course of the winter. This was not found, probably because the fraction of the mussel population that is harvestable for hammering Oystercatchers was very small. However, the consumption of the birds over the winter amounts to 70% of the production of this harvestable fraction. It is concluded that a clear description and understanding of the foraging behaviour is crucial to understand the relation between the distribution of a predator and its prey.

Key words: Oystercatcher - *Haematopus ostralegus* - *Mytilus edulis* - prey choice - energy intake - shell thickness - prey availability - carrying capacity

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INTRODUCTION

Optimal Foraging Theory (OFT) is based on the observation that all animals must make decisions while foraging. Without implying any conscious choice, birds must decide on when and where to

feed and what to forage on. These decisions can be analysed in terms of cost and benefits of alternative courses of action (Krebs & Kacelnik 1991). The rationale behind the first generation of OFT models is that animals are designed to take these decisions that maximize the net rate of energy in-

take, which is assumed to correlate with fitness. For the different decisions to make by the animals, formal mathematical models were constructed making both the assumptions underlying the hypothesis and the predictions clear and unambiguous (Krebs & Kacelnik 1991). In many laboratory or field experiments and observations the predictions of the OFT models were tested on a large variety of species (see reviews in Krebs *et al.* 1983, Krebs & McCleery 1984, Pyke 1984, Stephens & Krebs 1986, Krebs & Kacelnik 1991). The relatively simple foraging models have generally proved to be successful up to a certain level but, to improve the fit with the data, they had to be modified by incorporating additional constraints. Factors such as nutrient content of the prey, predation risk, kleptoparasitism, imperfect knowledge and sampling and recognition errors were studied (for review see Stephens & Krebs 1986).

Although criticized by several people (e.g. Gould & Lewontin 1979, Gray 1987, Pierce & Olason 1987) there can be little doubt that research on optimal foraging theory has greatly increased our understanding of the factors underlying foraging behaviour of animals. Although interesting in itself, this knowledge is also very important for a better insight in both the impact of the predators on their prey populations and in the distribution of animals over their feeding areas (Werner *et al.* 1983, Meire 1987). For instance, a deeper understanding of prey selection has resulted in better estimates of the fraction of the prey population which is actually harvestable by birds (Zwarts & Wanink 1984, 1989, Zwarts & Blomert 1992, Zwarts *et al.* 1992). This is crucial for understanding the relationship between the distribution of predators and their prey populations and for solving the question whether or not the carrying capacity of an area is reached. In times where habitat loss or degradation occur at an ever increasing speed this is a very important applied question. Werner *et al.* (1983) utilized optimal foraging theory and laboratory estimates of foraging costs to predict the choice of food and use of habitats by fish in the field with great success (see Werner & Mittelbach 1981 and Werner 1984 for reviews).

Thus optimal foraging models are a potentially useful tool in environmental management.

Habitat loss is considered a major threat to many wading bird species (Charadrii). They have also proved to be very useful for studying several aspects of OFT, especially in the field. Among waders, Oystercatchers *Haematopus ostralegus* L. have received special attention and their selection between prey species and between different size-classes of several prey species has been studied in detail (see Zwarts *et al.* 1996 for a review).

The results in these studies on waders have matched those in the subject as a whole. After an initial failure to account for the selection against the large and highly profitable Mussels (Ens 1982), the size selection of Oystercatchers feeding on Mussels by ventral hammering was predicted quite accurately by an Optimal Prey Choice Model when recognition errors were incorporated (Meire & Ervynck 1986). It was assumed that only Mussels with a thin shell could be opened, as found by Durell & Goss-Custard (1984), Meire & Ervynck (1986), Sutherland & Ens (1987), Cayford & Goss-Custard (1990) and Ens & Alting (1996). Whereas in the paper of Meire & Ervynck (1986) this selection was taken as a constraint, the present paper investigates whether thick shells can be opened, but take a disproportionate handling time.

I then use the model to estimate the harvestable part of the mussel population and the impact of Oystercatchers on their prey. Finally I explore the possible influences of these prey characteristics on interference and the distribution of birds.

METHODS

Mussels on the bed and opened by Oystercatchers.

The mussel population was sampled in study plot PQ 6 on a mussel bed on the Slikken van Vianen (Oosterschelde, the Netherlands; for a description of the study area see Meire & Kuijken 1987). Fifteen core samples were taken on 21 October and 5 December 1981, 2 March and 9 September 1982

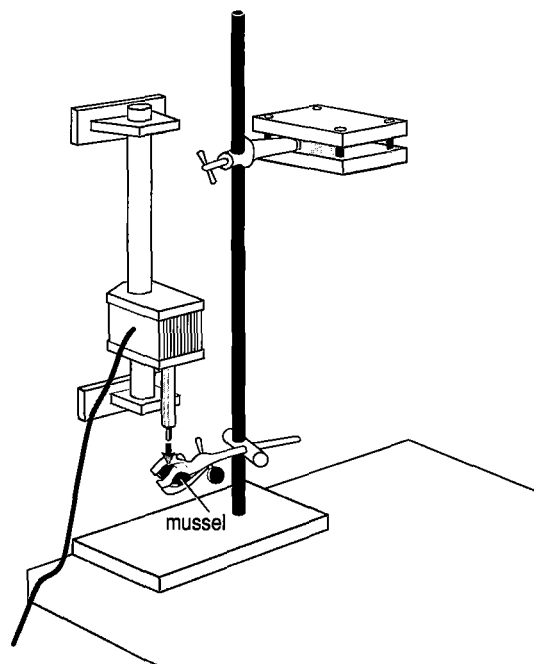


Fig. 1. The artificial Oystercatcher bill as used in the experiment.

with a core of 176 cm². All Mussels were counted and measured. Mussel length, height, breadth and the thickness of the shell on the ventral side were measured to the nearest 0.05 mm with a vernier callipers. The shell thickness on the ventral side was measured about 2 mm from the edge near the posterior adductor muscle. A flatness index was calculated as the ratio of height to breadth. A sample of Mussels (30) was used to determine ash-free dry weight by cutting the flesh from the shell, drying for twelve hours at 110°C, weighing and subsequently incinerating at 550°C for two hours. Mussels taken by hammering Oystercatchers are almost free of barnacles, yet many Mussels on the bed are extensively covered by barnacles. The Mussels from the samples were therefore designated as edible (with no or only a few barnacles) and inedible (for the greater part overgrown by barnacles); the difference was usually very obvi-

ous as few Mussels with intermediate coverage were present.

Mussels opened by hammering Oystercatchers were collected in September 1981 and 1982 in the same study plot and measured as mentioned above. For more details on the methods see Meire & Ervynck (1986) and Craeymeersch *et al.* (1986).

For the analysis the data on shell length and thickness were grouped in classes (length 20-24.99; 25-29.99 etc.; thickness 50-59.99; 60-69.99 etc.). In the text and figures these classes are indicated by the class mean.

Artificial Oystercatcher bill

To estimate the force necessary to open a Mussel, an artificial Oystercatcher bill, made of copper and weighing 105 g, was dropped vertically from a standard height (35 cm) onto the Mussel (Fig. 1). The bill tip was made in accordance with the measures given by Swennen *et al.* (1983) for hammering Oystercatchers (width 1.6 mm and depth 4.5 mm). The bill was held in an electromagnetic field so that when the current was interrupted the 'bill' fell vertically onto a Mussel clamped with the ventral side upwards. The Mussel was oriented so that the bill always hit one valve, near to the edge. The number of blows needed to break the Mussel was recorded. The damage done by the artificial bill to the ventral shell margins of the shell was almost indistinguishable from that done by real birds. A random sample of Mussels from the study plot was used in this experiment.

Feeding observations

The numbers and activity of birds in study plot PQ6 were noted every 30 min the greater part of the tidal cycle. In the first and last hour in which the plot was exposed, counts were made at least every 15 min, as bird numbers could change quickly at that time. On average twelve to fifteen counts were made per tidal cycle. In the period July 1981-April 1982 data were collected during 32 tidal cycles. Based on these counts, the average density and the number of feeding minutes per plot per tide were calculated. In between the

counts individual birds were observed for at least 5 min. A focal animal was selected at random and its foraging behaviour was recorded in detail. The following events were noted: (1) social interactions: all interactions with other Oystercatchers or other species. (2) Non foraging: preening, sleeping etc. (3) Handling a prey: hammerers: pulling a Mussel from the substrate, carrying it to a firm place, putting it down, hammering through the shell and swallowing the flesh; stabbers: opening the Mussel and swallowing the flesh. (4) Wasted handling: the Mussel was attacked but the bird gave up without opening it. The length of the Mussels attacked was measured against bill length, and later converted to mm using a regression line relating estimates to real size. This regression line was obtained from estimates, made by the observers, of Mussels of known size which were presented at the bill of a stuffed Oystercatcher under 'field conditions' (using binoculars and the same observation distance). Sequences of behaviour were recorded on tape and later transferred to a computer. A program written by L. Vanhercke was available to time all events. From these observations the feeding rate on each length class of Mussels was calculated. The data in this paper are based on 233 5 min observations made in the period August 1981 to January 1982.

RESULTS

Number of blows needed to open the shell.

The number of blows needed to break the shell was determined for Mussels between 31.9-58.6 mm long (Fig. 2). The relation with shell thickness was supraproportional. A stepwise multiple regression analysis, in which the dependent variable was $\log(\text{number of blows})$ and the independent variables were shell-length, -height, -breadth, -thickness and flatness index showed that the number of blows was largely determined by shell thickness in every size-class (Table 1). Only for Mussels between 45-50 mm was an additional variable, shell width, incorporated in the regression model along with shell thickness. Us-

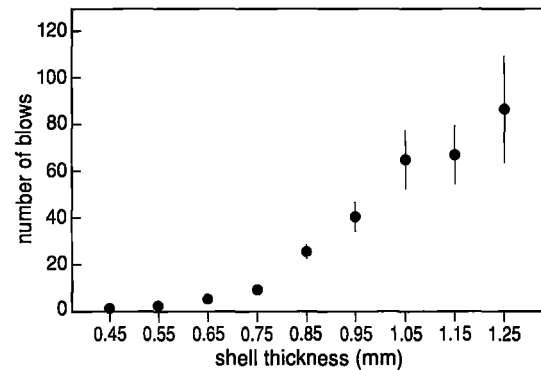


Fig. 2. The average number of blows (\pm SE) necessary to break a mussel shell in function of shell thickness. Data of all length classes were pooled per thickness class. ($n = 203$).

ing the data of all length classes, shell thickness was also the only variable that entered in the equation.

Is selecting thin-shelled Mussel optimal?

In Fig. 3 the frequency distributions of shell thickness of Mussels present on the bed and those taken by Oystercatchers is plotted for the four most predated length classes, together with the number of blows necessary to break into the shell. Clearly, the birds selected the thin-shelled Mussels.

To test whether this selection pattern can be predicted by foraging theory, we must know the profitability of thin- and thick-shelled Mussels. The profitability of the Mussels taken in the field is known from field measurements (Meire & Eryvynck 1986). In order to estimate, for each length class of Mussels, the profitability as a function of shell thickness, the following assumptions were made: (1) the energy content (AFDW) of Mussels of one length class is independent of shell thickness and (2) there is a linear relationship between the time (and energy) needed by the birds to open a Mussel and the number of blows needed to open the Mussel as measured in our experiment. Based on these assumptions the profitability was calculated as follows: For each length class of Mussels

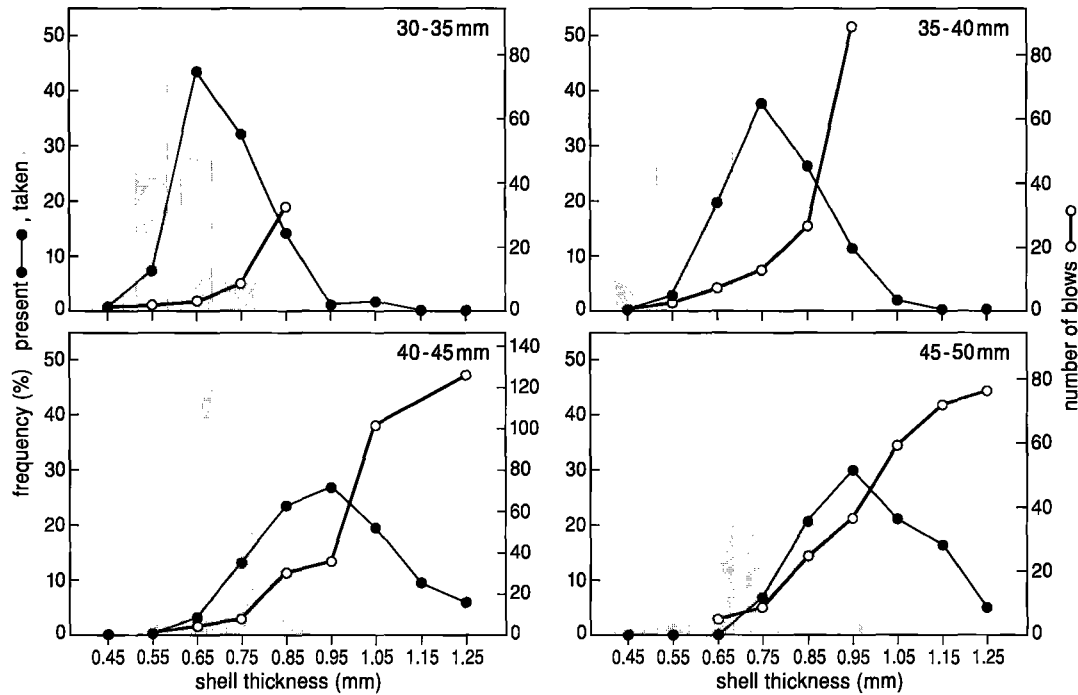


Fig. 3. Frequency distribution of the shell thickness of Mussels present on the mussel bed, taken by Oystercatchers (histogram) and the mean numbers of blows necessary to open the shell for four different size classes.

Table 1. Results of a stepwise multiple regression of \log_{10} number of blows necessary to break the shell (dependent variable) and shell breadth (mm), height, thickness (mm), length and the flatness index for several size classes (length, mm). In all but one shell thickness was the only variable that entered in the regression equation.

| Size | Shell thickness | | Shell breadth | | Constant | | R^2 | F | df | p |
|------|-----------------|-------|---------------|-------|----------|-------|-------|--------|-------|---------|
| | B | SE | B | SE | A | SE | | | | |
| < 35 | 0.083 | 0.015 | | | -4.065 | 1.044 | 0.783 | 26.96 | 1,17 | < 0.001 |
| 37.5 | 0.079 | 0.010 | | | -3.622 | 0.697 | 0.719 | 57.99 | 1,54 | < 0.001 |
| 42.5 | 0.077 | 0.006 | | | -3.754 | 0.498 | 0.853 | 149.47 | 1,56 | < 0.001 |
| 47.5 | 0.055 | 0.006 | -0.135 | 0.052 | 0.712 | 0.917 | 0.791 | 40.96 | 2,49 | < 0.001 |
| 52.5 | 0.037 | 0.017 | | | -0.621 | 1.606 | 0.519 | 4.8 | 1,13 | < 0.05 |
| all | 0.062 | 0.003 | | | -2.564 | 0.246 | 0.817 | 405.23 | 1,201 | < 0.001 |

the average shell thickness of Mussels opened in the field was calculated. The measured profitability in the field was attributed to this thickness class (class *i*). To obtain the profitability of the other thickness classes per length class of Mus-

sels this value was multiplied by the ratio (number of blows needed to open class *i*/number of blows to open class *i* ± 1, 2 etc.). The results are summarized in Fig. 4. For each length class of Mussels the profitability clearly decreases with

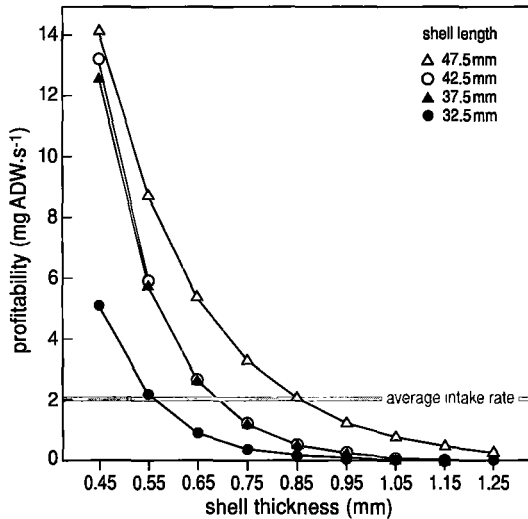


Fig. 4. Profitability of Mussels of four different length classes in function of shell thickness.

increasing shell thickness. The values are however different for the different length classes (with the exception of length classes 37.5 and 42.5 mm). The average intake rate of Oystercatchers in the field is also plotted in the figure. In the absence of detailed measurements on encounter rates, average intake rate was used to predict prey choice. According to the optimal prey choice model Mussels with a profitability lower than the average intake should be dropped from the diet. Based on the results presented in Fig. 4 one can predict that (1) per length class of Mussels, the thick-shelled Mussels should be dropped from the diet and (2) that the shell thickness of accepted Mussels should increase with mussel length. The selection against thick-shelled Mussels has been documented already (Fig. 3). To test the second prediction the shell thickness below which 90% of the Mussels taken fell was calculated for each length class and plotted in Fig. 5. It is clear that the longer the Mussel the thicker are those accepted by the birds and the values are close to the predicted threshold. This selection pattern must be the result of active selection as e.g. from Mussels of 32.5 mm in length, those with a shell thick-

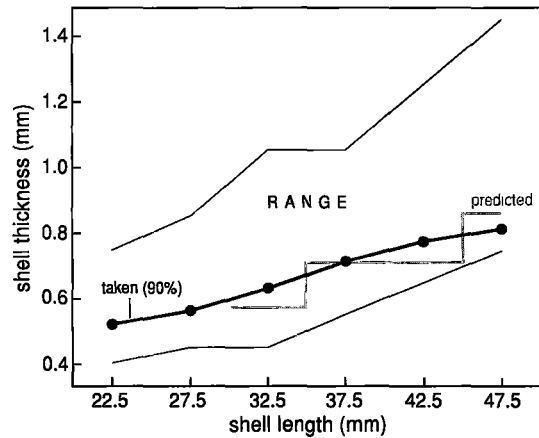


Fig. 5. For each length class, the shell thickness below which 90% of the Mussels taken fell, is plotted with closed symbols. The grey field indicates the range of shell thicknesses observed. The step function indicates the predicted rejection threshold (see text). For the calculation of profitability see text.

ker than 0.8 mm are not taken, whereas this thickness class is taken very frequently in Mussels of 47.5 mm. Oystercatchers are also able to open Mussels which are much thicker (Sutherland & Ens 1987).

Influence of Oystercatchers on the mussel population

As hammering Oystercatchers so strongly select thin-shelled Mussels, one would expect these Mussels to be depleted over the course of the winter and hence that the average shell thickness of Mussels would increase. The average shell thickness of Mussels of different length classes is plotted in Fig. 6. Data from October, December and March are used as during this period no mussel growth occurs (Craeymeersch *et al.* 1986). No trend of increasing shell thickness is obvious. This could be due to hammering Oystercatchers consuming only a small fraction of each size class. Therefore the density of each size class in October, December and March is plotted in Fig. 7. There is a consistent trend of decreasing densities over the winter. Due to the large confidence intervals the decrease was, however, only signifi-

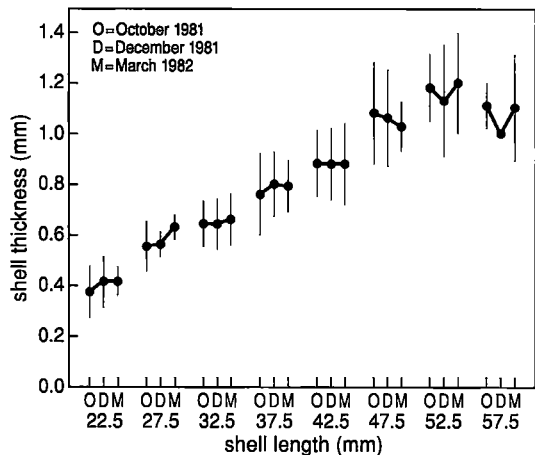


Fig. 6. Average shell thickness ($\pm SE$) of Mussels of different length classes in October and December 1981 and March 1982 on a mussel bed of the Slikken van Vianen.

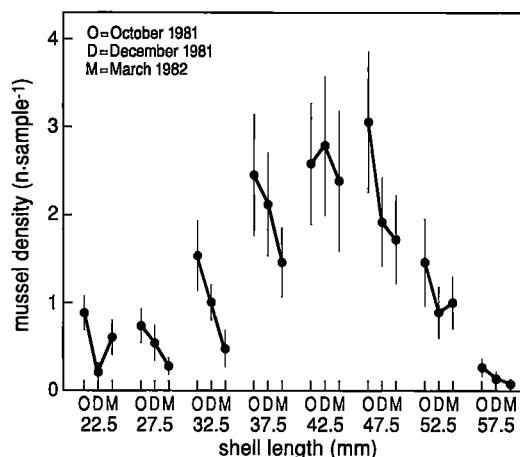


Fig. 7. Average number of Mussels ($\pm SE$) of different size classes per sample (176 cm²) in October and December 1981 and March 1982 on a mussel bed of the Slikken van Vianen.

cant for Mussels of 32.5 mm (ANOVA, $F = 3.2$; $df = 2,42$; $p < 0.05$), one of the most preferred size classes. Can this decrease be attributed to Oystercatchers? To answer this question the number of Mussels taken by the birds was estimated based on field observations. The density of Oystercatchers and their number of feeding minutes in the study plot were measured during the period July 1981-April 1982 (Fig. 8). Density was low in summer and gradually increased as birds arrived in the area during August and September. From January onwards numbers started to decline again. Assuming the birds feed as much during the night as during the day the number of feeding minutes between October and March was estimated at 296 m⁻². However, not all Oystercatchers in the study plot took Mussels by hammering. Based on the feeding observations of birds chosen at random, it was estimated that approximately half of the birds were hammerers, the other stabbers. Therefore the number of feeding minutes must be divided by two to obtain the number of feeding minutes spend in the plot by hammerers. Based on observations in the field the feeding rate of hammering Oystercatchers on Mussels of dif-

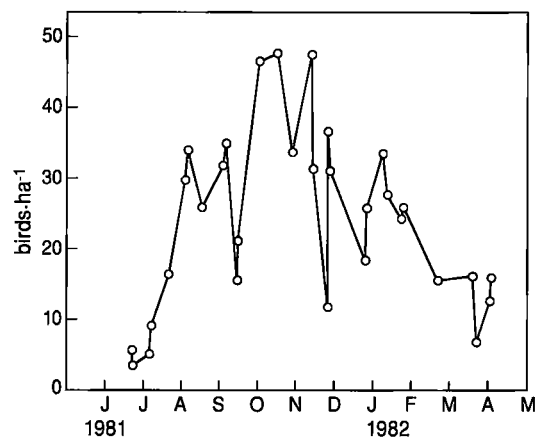


Fig. 8. Density of feeding Oystercatchers (each dot is the average for one low water period) in the study plot during the season 1981-1982.

ferent size classes is known. Multiplied with the number of feeding minutes this gives us an estimate of the number of Mussels removed by the birds. This is summarized in Table 2. During the six months considered, 73 Mussels m⁻² were removed by hammering Oystercatchers, about 27%

Table 2. Impact of Oystercatchers on the mussel population. For each length class of Mussels, the feeding rate (number of Mussels taken per 300 of foraging; 'rate'), the total number of Mussels taken by hammering Oystercatchers between October 1981 and March 1982 ($n\ m^{-2}$; 'taken Oysterc'), the density of Mussels in October 1981 ($n\ m^{-2}$; 'total October'), numbers of Mussels which disappeared between October 1981 and March 1982 ($n\ m^{-2}$; 'total Oct.-Mar'), density of Mussels in October 1981 harvestable for hammering Oystercatchers ($n\ m^{-2}$; 'harvest. October'). The last two columns give predation pressure by Oystercatchers as percentage of the total and harvestable density, respectively. For details about the calculations see text.

| mm | rate | taken Oysterc. | total October | total Oct.-Mar. | harvest. October | total % | harvest. % |
|------|-------|-------------------|------------------|--------------------|---------------------|------------|---------------|
| 17.5 | 0.057 | 2 | 49 | -7.54 | 49 | 4 | 4 |
| 22.5 | 1.171 | 5 | 49 | 15.09 | 49 | 10 | 10 |
| 27.5 | 0.171 | 5 | 41 | 26.40 | 38 | 12 | 13 |
| 32.5 | 0.486 | 15 | 87 | 60.36 | 78 | 17 | 19 |
| 37.5 | 0.429 | 13 | 140 | 56.58 | 74 | 9 | 18 |
| 42.5 | 0.714 | 21 | 147 | 7.54 | 26 | 14 | 81 |
| 47.5 | 0.343 | 10 | 174 | 75.45 | 13 | 6 | 77 |
| 52.5 | 0.057 | 2 | 83 | 22.63 | 1 | 2 | 200 |
| 57.5 | 0 | 0 | 15 | 7.54 | 0 | | |
| sum | 2.428 | 73 | 792 | 271.62 | 328 | 9 | 22 |

of the total number of Mussels which disappeared in this period. Compared with the number per length class, hammerers took between 2.4 and 35 % of the Mussels present, or overall 9%. However not all the Mussels on the bed were harvestable. Indeed due to the selection for thin-shelled Mussels, and the avoidance of Mussels overgrown by barnacles, only a fraction of the population present was harvestable. This fraction was calculated for each length class by multiplying the density with the fraction within the shell thickness classes taken by hammerers and then with the fraction of Mussels overgrown by barnacles (Table 2). If we compare now the number of Mussels taken with the harvestable density we see that, especially for the larger, more profitable Mussels, a large part is removed over winter. However, as this still is a small fraction of the total population this could explain why we did not find a significant increase in shell thickness over the winter.

DISCUSSION

Mussel selection

The influence of the shell thickness of Mussels on the feeding behaviour and prey selection of Oystercatchers was first discussed by Norton-Griffiths (1967). In an experiment, very similar to the one described here, he found differences in the force needed to open Mussels from different beds. Although not measured, he attributed this result to differences in shell thickness between Mussels from the two beds. This difference was reflected in the size selection of hammering Oystercatchers. On the lower part of the Ravenglass mussel beds, where the shells were thicker, no Mussels longer than 40 mm were hammered, whereas on the Pensar beds, where shells were thin, all sizes were hammered (Norton-Griffiths 1967). Shell thickness does, however, not only influence size selection. More recently, it has been shown that, even within one length class of Mussels, there is a strong selection for the thin-shelled Mussels (Durell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford &

Goss-Custard 1990, Ens & Alting 1996).

The results of our experiment show a supraproportional relation between the number of blows needed to open a Mussel and its shell thickness. As Norton-Griffiths (1967) also showed, no relation with mussel length or indeed any of the other measures such as the height or breadth of the shell and the force necessary to open the shell is found. Consistent with this is that Durell & Goss-Custard (1984) did not find any difference in shell width, depth and volume between shells taken by ventral hammerers and shells taken at random from the mussel bed.

The effect of shell thickness on the profitability of Mussels is considerable. I do not have data to test directly whether handling time increases with increasing shell thickness for Mussels of a given size, as assumed in calculating profitability, but Sutherland & Ens (1987) did find such a relationship between shell thickness and handling time for Mussels of 35–40 mm. The estimate of profitability remains qualitative, as it was not the real force to open a Mussel that was measured. However, the results convincingly show a decreasing profitability with increasing shell thickness, a profitability which differs between length classes. The now well documented selection for thin-shelled Mussels and the acceptance of thicker Mussels within the larger length classes (Fig. 3) are clear evidence that the prey selection of Oystercatchers is in accordance with an energy maximization foraging strategy.

From this results we can easily predict that, if the intake rate declines, for whatever reason, hammerers should accept thicker Mussels in their diet. No field data are available at present to test this possibility convincingly, but Sutherland & Ens (1987) found in an experiment with captive birds that, once the preferred prey had been depleted, birds took the thicker-shelled Mussels.

From the results presented in this paper and from previous studies we can conclude that the selection of Mussels by ventral hammerers depends on several factors: the coverage by barnacles (Ens 1982, Durell & Goss-Custard 1984, Meire & Ervynck 1986), shell thickness (Norton-

Griffiths 1967, Durell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987), how firmly the Mussels are attached to the substrate (Norton-Griffiths 1967) and, of course their density (Meire & Ervynck 1986). The flesh content of the Mussel is also important. This is not only highly variable on one mussel bed (Durell & Goss-Custard 1984) but also shows distinct seasonal variations with the lowest flesh-content occurring in spring (Craeymeersch *et al.* 1986, Cayford & Goss-Custard 1990).

Ecological consequences of prey characteristics

As so many different characteristics of the Mussels present on a bed influence prey selection and hence intake rate we would expect differences in these parameters to influence the distribution of Oystercatchers between beds. Indeed Goss-Custard *et al.* (1981) found a significant partial correlation between shell thickness of the Mussels on a bed and the density of Oystercatchers.

Food supply and Oystercatcher densities

Predation by shorebirds can substantially reduce prey populations over the winter (Goss-Custard 1980, Baird *et al.* 1985, Meire *et al.* 1994). As only a small proportion of the prey are actually available and harvestable to the predators (see e.g. Zwarts & Blomert 1992, Zwarts *et al.* 1992), the depletion of their food resource is much more important than suggested by the depletion of the population as a whole. For the mussel bed studied in this paper this is clearly shown by the data in Table 2. The estimate of the harvestable fraction is without doubt subject to much error. The shell thickness classes taken by the birds were determined by shell collections in September. It is well possible that in the course of the winter thicker shells are taken. No data are available to test this. The division of Mussels as edible or not, based on the barnacle cover, is subjective, especially in Mussels not extensively covered. On the other hand, Meire (1990) showed that of the total population only a small proportion of Mussels is vis-

ible at the surface and thus available to Oystercatchers. This was not accounted for in this study. Therefore, although the estimate of the harvestable fraction is subject to error, it is certain that the fraction is small. It is probably even much smaller for the smaller Mussels than estimated here, as especially these are covered by others (Meire 1990). Hammering Oystercatchers remove a substantial part of the harvestable fraction. For the stabbing birds no estimates of the harvestable fraction can be made yet as no information on the gaping behaviour of the Mussels is available.

Populations are limited by their food supply only if their consumption equals the production of the harvestable fraction (Piersma 1987). No studies are available yet where this was measured although the work of Zwarts and coworkers give very detailed estimates of the harvestable fraction of different prey for several wader species (Zwarts & Wanink 1984 & 1989, Zwarts & Blomert 1992, Zwarts *et al.* 1992). Craeymeersch *et al.* (1986) estimated for the same study plot on the Slikken van Vianen in the same period the annual production of the entire mussel population to be about 156 g AFDW m⁻² y⁻¹. By multiplying, for each size class, the production with the percentage Mussels harvestable, the total production of the harvestable Mussels in the preferred size classes (25-60 mm) can be estimated at 46 g AFDW m⁻² y⁻¹. The total consumption by Oystercatchers on a yearly basis can not be estimated based on the feeding rates measured in autumn (see Table 3) since it is known that in spring the birds tend to feed on much smaller Mussels (Cayford & Goss-Custard 1990). The yearly consumption of hammerers, estimated by multiplying the total number of feeding minutes m⁻² y⁻¹ with an average intake of 150 mg AFDW min⁻¹, is 32 g AFDW m⁻² y⁻¹, or about 70% of the production. Taking in account the fact that not all smaller Mussels are visible and hence not harvestable for the birds, the consumption by hammerers is near to the production. This could indicate they are limited by their food supply. There is also other circumstantial evidence for this conclusion. Indeed, in 1987 a huge biomass of second year cockles occurred in the

same study plot and the numbers of Oystercatchers did increase quite substantially (Meire 1990).

Conclusions

The results presented in this paper, along with those from other papers, clearly show that the mussel selection by hammering Oystercatchers can be well understood and modelled within the framework of the optimal foraging theory. Without a detailed knowledge of the foraging behaviour of the predator it is not possible to give an adequate estimate of the harvestable prey density. This is essential in order to solve the problem of carrying capacity, a question often asked by conservationists. Ultimately one should succeed in modelling habitat distribution of birds on the basis of foraging models as done for example by Werner *et al.* (1983) for fish.

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SAMENVATTING

Meire & Ervynck (1986) toonden aan dat Scholeksters die Mossels openhaken de grootteklassen selecteerden die het meeste opleverden. In het model dat ze daarbij gebruikten werd aangenomen dat de vogels Mossels met een dikke schelp niet konden openen. In dit artikel

wordt onderzocht of deze selectie het resultaat is van het niet kunnen openkrijgen van de dikschalige Mossels of van de onevenredige hoeveelheid tijd, die het een Scholekster kost om de Mossel te openen. Om dit te onderzoeken werd een kunstmatige scholekstersnauvel gemaakt en werd gemeten hoe vaak er moest worden gehakt om Mossels van verschillende schelpdikte te openen. De tijd die nodig was om een Mossel te openen nam zeer sterk toe met de schelpdikte. Dit gegeven werd gecombineerd met veldmetingen om uit te rekenen hoeveel Mossels van verschillende grootte en schelpdikte opleverden. De waarde van een Mossel voor Scholeksters nam toe met de grootte en nam af met de schelpdikte. De vogels selecteerden de grote Mossels met een dunne schaal. De verwachting was dat dunschalige Mossels in de loop van de winter steeds zeldzamer zouden worden, maar dit werd niet gevonden. De verklaring is dat waarschijnlijk slechts een klein deel van de Mossels voor Scholeksters werkelijk oogstbaar was, dat wil zeggen niet te klein of te dikschalig. Van die oogstbare Mossels werd jaarlijks 70% van de productie door Scholeksters weggegeten.