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Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)?

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Abstract. Size selection by oystercatchers (*Haematopus ostralegus*) feeding on the edible mussel *Mytilus edulis* by hammering the ventral side is analysed and compared with the predictions of an optimal diet model. It is found that the oystercatchers select mussels between 30 and 45 mm long which are not overgrown by barnacles and which are thin shelled. However, after including waste handling events in both the profitability and the diet model, and estimating the prey population available to the oystercatchers, a good agreement between the prediction and the data is found. These results are further discussed in the light of optimal foraging theory.

The maintenance of an energy balance sufficient to meet the present needs of an individual and to accumulate energy for the future, is important in the evolutionary success of a genotype. In animals with a close coupling between feeding behaviour and fitness, natural selection should be an important force driving the organization of feeding behaviour, and this can be modelled to show how the animal performs as efficiently as possible. This is the rationale behind optimal foraging theory. This approach has until now been quite successful in explaining several aspects of foraging behaviour (for reviews see Pyke et al. 1977; Krebs 1978; Krebs et al. 1983; Krebs & McCleery 1984). However, as pointed out by Krebs et al. (1983), many papers purporting to test optimal foraging models do no more than refer to some qualitative agreement between observations and one or more assumptions of the model. There is a need for more rigorous quantitative tests of the predictive value of the models (e.g. Thompson & Barnard 1984).

Oystercatchers (*Haematopus ostralegus* L.) occur in winter on estuaries of north-west Europe. Many of them feed on mussels (*Mytilus edulis* L.), which are opened either by hammering a hole through the shell or by stabbing between the intact valves (Norton Griffiths 1967). Stabbing oystercatchers usually select the largest mussels present (Norton Griffiths 1967; Zwarts & Drent 1981; Ens 1982) whereas hammering oystercatchers may not do so, even when a wide range of mussel sizes is present (Drinnan 1958; Norton Griffiths 1967; Ens 1982). The aim of this study was to test whether, by ignoring the largest mussels, hammering oystercatchers increased their energy gain.

METHODS

The data were collected in August and September 1982 on the Slikken van Vianen, a tidal flat in the Oosterschelde (The Netherlands). Extensive mussel beds occur in this area (for a description, see Meire & Kuyken 1984) and some hundred to several thousand oystercatchers use the beds as feeding areas. All observations were made from a hide at approximately 100 m from plots (50 × 100 m) marked out with stakes on the mussel beds. Only birds hammering the mussels through the ventral side of the mussel are considered.

Birds

Throughout the tidal cycle, individual birds were observed for at least 5 min. A focal animal was selected at random and the following recorded.

(1) Pecking.

(2) Handling a prey: pulling a mussel from the substrate, carrying it to a firm place, putting it down, hammering through the shell and swallowing the flesh.

(3) Waste handling: the mussel was attacked but the bird gave up without opening it.

(4) The length of mussels attacked by oystercatchers: this 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.

Mussels

The study plots were located within the most homogeneous parts of the mussel beds. Fifteen core samples (diameter = 15 cm, surface = 176·7 cm^2) were taken to a depth of 5 cm in each plot and preserved in 7% neutral formalin. Mussels were counted and the length and thickness of the shell at the ventral side (near the posterior adductor muscle) were measured with a vernier calliper to the nearest 0·05 mm. A sample of mussels from each plot was used to determine ash-free dry weight (AFDW), by cutting the flesh free from the shell, drying for 12 h at 110°C, weighing and subsequently incinerating at 550°C for 2 h.

To analyse the aggregation pattern we used the b value of the Taylor Power Law, which states that there is a relation between variance (s^2) and the mean (m) of the form $s^2 = am^b$ (Taylor 1969). Parameter b is an index of dispersion and varies continuously from 0 for a regular distribution to infinity for a highly aggregated one. If b is not significantly greater than 1, we can conclude that the population is not aggregated (Taylor 1969). The value b (and its 95% confidence interval) was calculated by linear regression of $\log s^2$ on $\log m$. In addition to the data from the five plots discussed here, we used data from four other mussel plots, sampled in the same area at the same time, for this analysis.

Mussels opened by ventral hammerers are easily recognized, and were collected and measured as described above.

All statistical analyses were performed on the University computer (Siemens BS 2000–VS6) using SPSS (Nie et al. 1975).

RESULTS

Prey Population

Density and size distribution

The length frequency distributions of mussels present in the plots were compared with a Kolmogorov–Smirnov two-sample test, and found to be significantly different between all plots except between plots 30 and 31 (Table I). As mussels smaller than 12·5 mm were not taken by oystercatchers, the frequency distributions of mussels larger than 12·5 mm were compared in the same way and resulted in the same significant differences (Table I). As there was no difference between plots 30 and 31, and the two plots were situated near each other, the data were pooled in all further analyses and are referred to as plot 30. The density of each size-class of mussels in each plot is given in Table II.

The density of mussels varied between 1637/m^2 in plot 6 and $3183 = m^2$ in plot 30 and is comparable to that found in other studies (Zwarts & Drent 1981; Ens 1982). The mussels in plots 6, 10 and 18 have persisted for several years, so mussels of all size-classes were present. Plots 30 and 31 were situated on a commercial bed where mussels were added and removed regularly, and so contained many mussels of approximately the same size. On

Table I. *H* values of the Kolmogorov–Smirnoff two-sample test comparing the frequency distribution of all mussels present (lower left triangle) and mussels > 12·5 mm (upper right triangle) between each pair of plots.

	Plot				
Plot	6	10	18	30	31
6		1·568*	2·106***	4·558***	3·643***
10	2·227***		2·035**	4·528***	3·571***
18	1·891**	2·372***		4·757***	4·302***
30	4·401***	3·420***	5·466***		1·262NS
31	3·993***	2·770***	4·997***	1·322NS	

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

Table II. Total density and density for each size-class of mussels in each plot

Length (mm)	Plot 6	10	18	30/31
1–4·9	24	60	26	3
5–9·9	275	326	211	42
10–14·9	170	309	124	49
15–19·9	137	309	90	77
20–24·9	101	183	75	91
25–29·9	129	248	64	537
30–34·9	149	204	67	1612
35–39·9	101	248	252	707
40–44·9	234	313	562	56
45–49·9	210	121	252	3
50–54·9	84	17	52	—
55–55·9	20	—	—	—
Total	1637	2342	1780	3183

Densities are given as number of mussels per m^2.

all plots, mussels were free of weed cover, but many of them were overgrown by barnacles (*Balanus balanoides*).

Aggregation

Mussels occur in clumps on the beds and are clearly aggregated. However it is important to know whether the different size-classes of mussels occur at random within the mussel clumps, or whether different sizes occur in different clumps, since then size selection becomes a patch choice problem. To test this, we calculated the index of aggregation (b) from the Taylor Power Law (Taylor 1969). The values of b (+95% confidence interval) are given in Table IV and show that only the 15–20-mm size-class was significantly aggregated. Therefore, most size-classes are scattered randomly over the mussel clumps.

Table III. Relation between mussel length and ash-free dry weight for each plot

Plot	a*	b*	r	N	P
6	−2·131	2·867	0·960	30	<0·001
10	−3·202	3·146	0·968	20	<0·001
18	−2·683	3·010	0·958	30	<0·001
30/31	−1·998	2·743	0·956	20	<0·001

* Ln weight (in g) $=a+b$ ln length (in mm).

Table IV. The b values of the Taylor Power Law (±95% confidence interval) for each size-class of mussels

Length (mm)	b	CI
2·5	0·51	0·83
7·5	1·08	0·51
12·5	0·89	0·05
17·5	1·81	0·49
22·5	1·10	0·33
27·5	1·16	0·39
32·5	1·20	0·26
37·5	1·11	0·24
42·5	2·37	1·70
47·5	1·03	0·66
52·5	1·42	0·57
57·5	1·20	0·75

Biomass

As there is no difference in body composition in mussels of different sizes (Dare & Edwards 1975), we assume that AFDW is a good measure of energy content. The linear relationship between the natural logarithm of mussel length and that of AFDW is given in Table III. The regression equations differ significantly between the plots (Ancova: $F=5·347$; $df=4,124$; $P<0·001$).

Mussel Selection by Oystercatchers

Size-classes preyed upon

The length frequency distributions of mussels present on the bed and those taken by the oystercatchers are compared in Fig. 1a, b. The distributions differ significantly in all plots whether the entire prey population or only the population above 12·5 mm is considered (Kolmogorov–Smirnov two-sample test, all cases $P<0·001$). Oystercatchers tend to select mussels between 30 and 45 mm long.

Selection for shell thickness

The mean ventral shell thickness of mussels opened by oystercatchers was less than that of mussels present on the bed. It seems that, the larger the shell, the more choosey the oystercatchers are for the thinnest ones (Fig. 2), resulting in significant differences (Student t-test) for the larger mussels (Fig. 2). This was also found by Durell & Goss-Custard (1984).

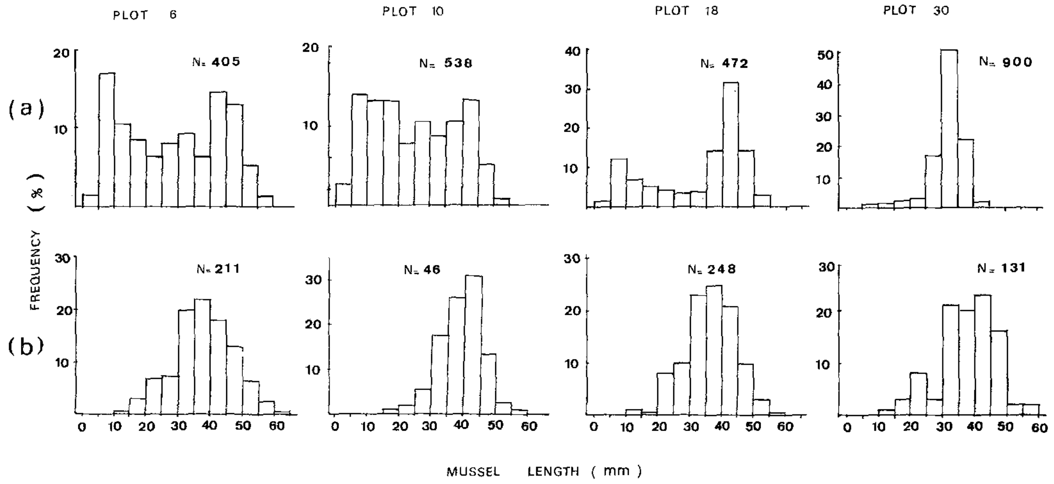

Figure 1. Length frequency distributions of (a) all mussels present and (b) mussels taken by oystercatchers in four different study plots. The distribution of mussels taken by oystercatchers consists of mussels both opened and rejected after a waste handling.

Selection for mussels not overgrown by barnacles

In comparing mussels from the samples with mussels taken by oystercatchers, it was obvious that the birds seldom ate mussels overgrown by barnacles (see below and Durell & Goss-Custard 1984).

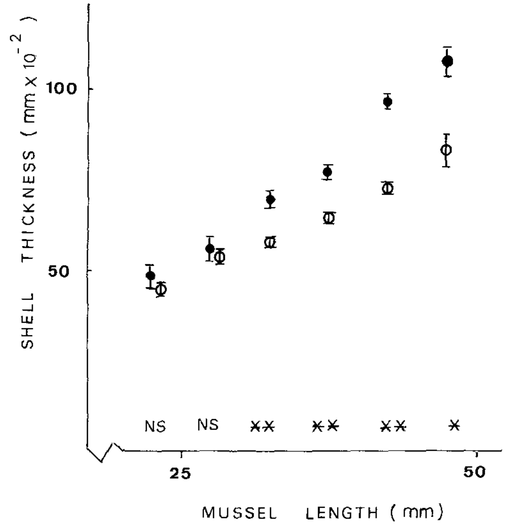

Figure 2. Average shell thickness of mussels present (filled circles) and opened by oystercatchers (open circles). Vertical bars give ±1 SE. Only the results of plot 18 are given since the data from the other plots are very similar. ($^*P<0{\cdot}01$; $^{**}P<0{\cdot}001$; NS not significant; Student *t*-test.)

Costs of Selection

Several costs are associated with this selection of mussels, and will be considered here.

Handling costs

Handling time (H) includes both the time to open the mussel and the time to swallow the flesh and is found to be a linear function of mussel length. There was no difference between plots (Ancova: $F=1{\cdot}992$, $df=3{,}33$; $P>0{\cdot}05$), so the data

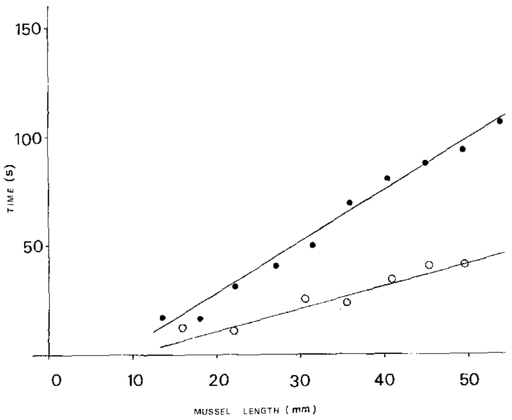

Figure 3. The average handling time (filled circles) and waste handling time (open circles) for each size-class of mussels. The regression lines are $y=2{\cdot}027x-10{\cdot}80$ and $y=0{\cdot}679x-4{\cdot}04$ respectively.

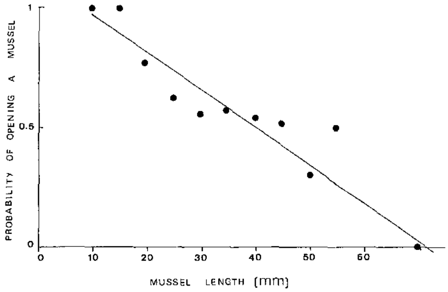

Figure 4. The probability (P) that a mussel is opened, after being taken by an oystercatcher, as a function of mussel length. The regression line ($P < 1\cdot127 - 0\cdot016x$) is plotted.

($N = 389$) were pooled and the regression line was calculated on the basis of the average handling time per size-class (H (in s) $= 2\cdot027 \times$ shell length (mm) $- 10\cdot80$; $r = 0\cdot925$; $df = 9$, $P < 0\cdot01$; Fig. 3). This handling time is short compared with the data given by Ens (1982).

Waste handling costs

About one-third of the mussels attacked were not opened. After handling the mussel for up to 80 s, the birds resumed their searching behaviour without opening it. The proportion of mussels actually opened was calculated for each size-class and is a decreasing function of size (Fig. 4): P (probability of a mussel being opened once taken) $= 1\cdot127 - 0\cdot016$ shell length (in mm); $r = 0\cdot826$, $N = 10$, $P < 0\cdot01$. The waste handling time (WH) was also a linear function of mussel length (Fig. 3) and the regression line was calculated on the basis of the average/size-class (overall $N = 129$): WH (in s) $= 0\cdot679 \times$ shell length (mm) $- 4\cdot04$; $r = 0\cdot825$; $P < 0\cdot05$).

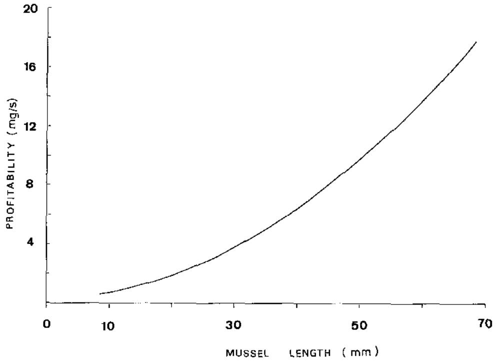

Figure 5. Profitability of mussels, expressed as E/H, as a function of their length.

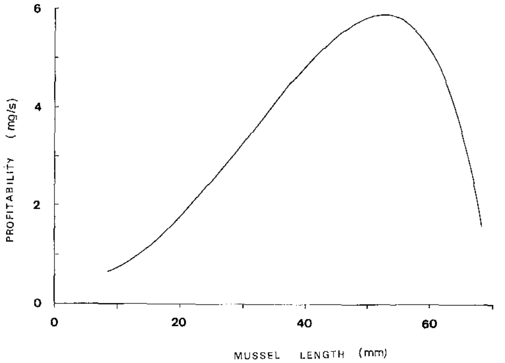

Figure 6. Profitability of mussels (calculated according to equation 1) as a function of mussel length.

Do Oystercatchers Select the Most Profitable Prey?

Once we know the costs and benefits associated with mussel selection we are in a position to calculate an optimal diet and compare this with the data.

Profitability

Profitability in optimal diet models is defined as

Table V. Assumptions of the optimal diet model (after Krebs & McCleery 1984), and their validity in this study

Assumption	Valid?
(1) Prey value is measurable in terms of net energy content or some other comparable simple dimension	Yes
(2) Handling time is a fixed constraint	Yes
(3) Handling and searching cannot be done at the same time	Yes
(4) Prey are recognized instantaneously and with no errors	No
(5) Prey are encountered sequentially and randomly	Yes
(6) Energetic costs per s of handling are similar for different prey	Yes
(7) Predators are designed to maximize rate of energy intake	Yes

Table VI. Percentage of mussels per size-class that are edible* for oystercatchers

Length (mm)	Plot 6	 10	 18	 30/31
10–14·9	100	100	66	100
15–19·9	100	100	78	100
20–24·9	100	100	100	100
25–29·9	100	94	55	42
30–34·9	100	70	50	44
35–39·9	73	47	30	53
40–44·9	31	30	20	100
45–49·9	36	30	20	—
50–54·9	12	1	25	—
55–59·9	1	—	—	—

* Not extensively covered by barnacles.

the amount of energy (E) gained per unit time spent in handling (E/H) (e.g. Krebs 1978). For mussels, we found the profitability increases supraproportionally with mussel length (Fig. 5). However this is not, we feel, the profitability the oystercatchers are experiencing. Indeed, if they take 10 mussels of 50 mm they can open only about three of them (see Fig. 4). We can account for this in calculating the profitability by using the energy gained after taking N mussels (E_iP_i) and the time spent handling these N mussels ($H_iP_i+\mathrm{WH}(1-P_i)$), or

$$\text{Profitability of size-class i} = \frac{E_iP_i}{H_iP_i+\mathrm{WH}\,(1-P_i)} \qquad (1)$$

The profitability curves now show a peak around 50–55 mm (Fig. 6), but this is still much larger than the average taken (30–45 mm). However, the diet not only depends on the profitability of the prey but also on the density of the different prey types (Charnov 1976; Krebs 1978). In order to test the optimal diet model, it is therefore necessary to use a more rigorous formulation.

The model

The model used is a multi-species version of Hollings' disc equation (Charnov 1976)

$$\frac{E}{T} = \frac{\Sigma E_i\lambda_i}{1+\Sigma\lambda_iH_i} \qquad (2)$$

in which λ_i is the encounter rate for size-class i, and T is the foraging time.

The assumptions of the model and their validity for this study are listed in Table V. To correct for the fourth assumption, the probability of opening a mussel once taken (P) is included in the same way as was done for the profitability

$$\frac{E}{T} = \frac{\Sigma E_i\lambda_iP_i}{1+\Sigma\lambda_i(H_iP_i+(1-P_i)\mathrm{WH}_i)} \qquad (3)$$

Encounter rate

Before calculating the optimal diet based on equation (3) we only need to know the encounter rate (λ_i) for each prey class. This can be estimated from equation (4) given by Thompson (1983)

$$\lambda_i = 1/100\sqrt{(1/d_i)}/s \qquad (4)$$

where s is the search speed and d_i the density of size-

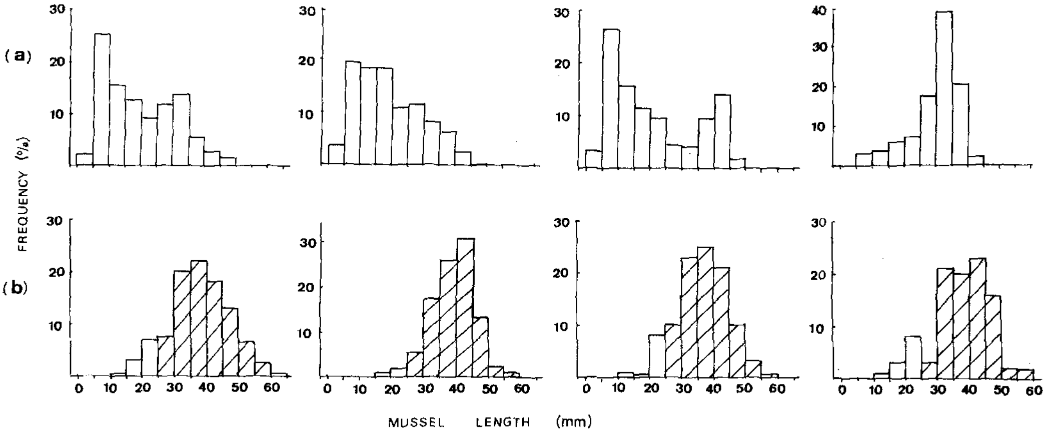

Figure 7. Length frequency distributions of (a) mussels available to oystercatchers (see text) and (b) mussels taken by oystercatchers. The hatched bars show the predicted optimal diet.

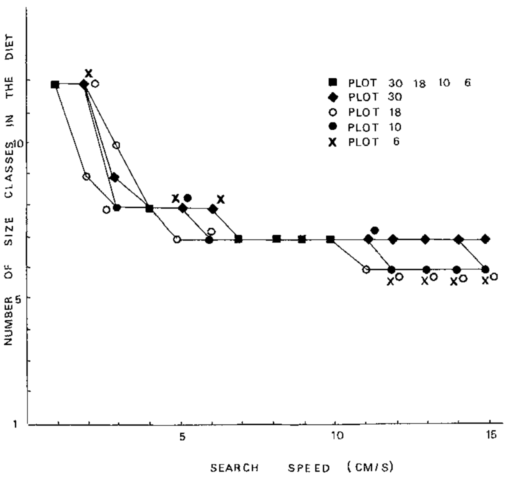

Figure 8. Sensitivity of the model to variations in *S* (search speed). The number of size-classes in the optimal diet is given as a function of *S*.

class i (number of mussels per m^2). On the basis of observations of walking speed and step length (measured on mud flats), the search speed can be estimated at 0·085 m/s (Meire, unpublished data). This is a relative measure of the encounter rate since it does not take any width of the search path into account. For estimating the mussel density, two additional factors must be taken into account. First mussels taken by oystercatchers are almost free of barnacles (Durell & Goss-Custard 1984; present study), yet many mussels on the bed are covered extensively by barnacles. The mussels from the samples were therefore redesignated as edible (with no or only a few barnacles) and inedible (for the greater part overgrown by barnacles): the difference was usually very obvious as few mussels with intermediate coverage were present. The percentage of edible mussels varied between plots and particularly with size-class (Table VI).

Second, only thin-shelled mussels are taken (Durell & Goss-Custard 1984; present study). For each size-class the fraction of mussels available was estimated as the cumulative percentage of mussels occurring within the range of shell thicknesses taken by the oystercatchers. The density of mussels actually available to the birds was then obtained by subtracting the proportions of mussels overgrown by barnacles and with shells that were too thick. The frequency distributions obtained in this way are given in Fig. 7a. Now it can be seen that oystercatchers are selecting for the largest mussels of the available population.

Table VII. Spearman rank correlation coefficients (r_s) between feeding rate and mussel density, for different ranges of mussel size

Mussel length	r_s	N	P
10–60	0·077	40	0·637
15–60	0·2276	36	0·182
20–60	0·3351	32	0·061
25–60	0·4592	28	0·014
30–60	0·6792	24	<0·001
35–60	0·7734	20	<0·001
40–60	0·8576	16	<0·001
45–60	0·7144	12	0·009

Optimal diet

All the variables of equation (3) are now known and the optimal diet can be calculated. In Fig. 7b the hatched columns are the optimal size-classes and we see that the diet model predicts most of the diet taken (between 90 and 97%). We can ask, however, how sensitive the model is to variations in our estimates of the various factors. Therefore we calculated the number of size-classes in the diet for various values of *s* (Fig. 8). As *s* increases, the encounter rate increases and obviously fewer size-classes should be added to the diet. However, for a large range of values near the estimated value of 0·085 the diet breadth is identical.

Feeding rate

In accordance with the prediction of the optimal diet model, a correlation between feeding rate and density should be found. We calculated therefore the Spearman rank correlation coefficient between feeding rate and available mussel density based on data from the 10 size-classes taken by oystercatchers for all plots ($N=40$), and several subsets of size-classes by dropping each time the smallest mussels. The results are given in Table VII. For all data together no significant correlation was found; however, for the mussels within the optimal set (>25 mm) a significant relation emerged. Dropping more of the smaller mussels improved the correlation even more, indicating a stronger preference for the larger ones.

DISCUSSION

Though optimal foraging models have been quite successful in predicting some aspects of foraging behaviour (see review by Krebs et al. 1983), many difficulties remain. Zach & Smith (1981) argue that optimal foraging theory is very useful in simple laboratory experiments but that most feeding problems in the wild are complex, so that in practice it is difficult to define optima. We originally thought that the oystercatcher–mussel situation would be a simple system, but it is now clear that mussel length selection is not the only factor involved (Durell & Goss-Custard 1984; present study). Each large size-class should be divided into at least thin- and thick-shelled groups.

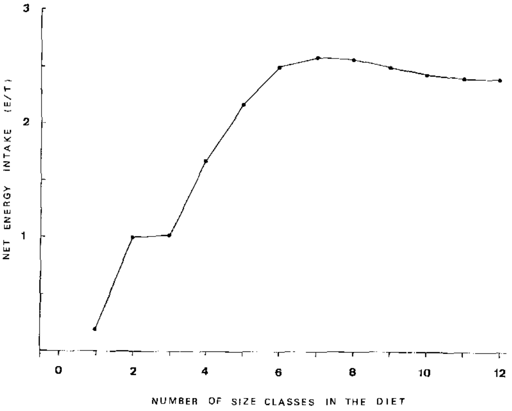

Figure 9. The intake rate (*E*/*T*) as a function of the number of size-classes included in the diet. The size-classes are ranked according to their profitability. Only data from plot 6 are shown since they are very similar in all other plots.

Moreover mussels overgrown by barnacles are seldom taken, perhaps because they are not recognized by the oystercatchers or because the presence of barnacles on the ventral side makes it impossible to hammer the shell. It is also important to incorporate the waste handling times into the model.

Ideally we should be able to predict both selection for shell size and for shell thickness. However, because the relation between handling time and shell thickness has not been measured in the field, this is actually impossible. Then if our measures of prey density do not include those prey categories (thick and overgrown shells) that are not actually consumed, we can predict the optimal mussel sizes.

Do our results confirm the optimal diet model? The predictions can be summarized as follows (after Krebs & McCleery 1984). (1) The highest-ranking prey should never be ignored. (2) Low-ranking prey should be ignored following equation (2) and this exclusion should be all-or-nothing. (3) The exclusion of low-ranking prey does not depend on their own values of λ. From the first prediction it is obvious that prey within the optimal set should be taken proportional to their density (Goss-Custard 1977; Sutherland 1982; Thompson & Barnard 1984). For the optimal size-classes we indeed found a significant correlation between density and feeding rate.

Prediction 2 is violated in most studies, and many explanations have been offered to account for it (discrimination errors, long-term learning, inherent variation in the animal, runs of bad luck, simultaneous encounters, averaging across individuals: Krebs & McCleery 1984). Oystercatchers in this study also took some prey outside the optimal set though it was only a small proportion of the total (5–10%). The most likely explanation might be that adding sub-optimal size-classes to the diet decreases intake rate only by less than 5% (Fig. 9). In addition, given the enormous variation in handling time and profitability, it is not surprising that some sub-optimal mussels are taken. The fact that the smallest prey are the most abundant, yet very scarce in the diet, is in accordance with prediction 3. The optimal diet is the same in the four plots. Therefore we could not prove that, if the density of more profitable mussels increased, fewer size-classes would be taken. But overall, the selection for the thin-shelled and most profitable mussels does suggest that oystercatchers are optimizing their intake rate and, within constraints that must be taken into account, the diet model is successful in predicting diet breadth.

The importance of including additional factors (selection against thick-shelled mussels and mussels overgrown by barnacles) and constraints (waste handling) are obvious when comparing the predictions of equations (2) and (4). On the basis of the original model (equation 2) and the overall densities of mussels present, the optimal diet consists only of mussels larger than 40 mm or between 40 and 80% of the actual diet.

In this paper we discussed some factors that may explain why oystercatchers do not take the largest mussels. Obviously there are other possible explanations in addition to those considered here.

Larger mussels may be harder to pull from the bed (Norton Griffiths 1967). Handling time may be greater for larger prey (contradicting assumption 6, Table V), or large mussels may involve the risk of damaging the bird's bill, but this is very difficult to measure. The risk of having food stolen may increase with mussel size. This is likely and has already been found for other birds (Thompson & Barnard 1984) but, in our study area, both inter- and intraspecific aggression and robbing is very rare. Parasite infections are almost absent and are not size dependent (Dijkema, personal communication). Incorporating any of these factors could improve the fit to the data but we believe we selected the most important ones.

These results also have some ecological implications. Since the prey population measurable in the field and the one experienced by oystercatchers are very different (which is likely to be true in many other predator–prey systems), one should be extremely cautious when calculating functional and numerical responses based on measured prey densities.

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