

# Reevaluation of patterns of mussel (*Mytilus edulis*) selection by European Oystercatchers (*Haematopus ostralegus*)

R. Nagarajan, S.E.G. Lea, and J.D. Goss-Custard

**Abstract:** European Oystercatchers (*Haematopus ostralegus*) were highly selective towards mussels between 35 and 50 mm in length, and fewer than 5% of mussels taken were below 35 mm or above 50 mm. The oystercatchers selected ventrally thin-shelled mussels, especially if the length was more than 35 mm, regardless of whether they opened the right or left valve of the mussel. The oystercatchers also took mussels that had few barnacles on the ventral surface. Although brown-shelled mussels were rare in the population, oystercatchers showed a strong preference for them. Generally, oystercatchers consumed ventrally flat mussels, especially in the smaller length classes, particularly the most preferred size class, 30–45 mm. Ventral shell thickness and colour had independent effects on mussel selection. The other two variables, number of barnacles and shape of the ventral surface (flat or curved), apparently had no influence on selection on their own, only by way of their association with colour or thickness.

**Résumé :** Les huîtres pies (*Haematopus ostralegus*) ont montré une préférence marquée pour les moules de 35 à 50 mm de longueur et moins de 5 % des moules capturées au cours de cette étude étaient de longueur inférieure à 35 mm ou supérieure à 50 mm. Les oiseaux ont choisi des moules dont la paroi ventrale de la coquille est mince, surtout parmi les moules de plus de 35 mm, qu'ils attaquaient la valve droite ou gauche. Les huîtres sélectionnent aussi les moules qui portaient peu de balanes à la surface ventrale. Ils ont de plus une préférence marquée pour les moules brunes, bien que celles-ci soient rares dans la population. De façon générale, les huîtres consommaient des moules aplaties ventralement, surtout dans les petites classes de longueur, et cette préférence est particulièrement manifeste dans le cas de la classe de taille de prédilection, 30–45 mm. L'épaisseur ventrale de la coquille et la couleur influencent le choix des moules indépendamment l'une de l'autre. Les deux autres variables, le nombre de balanes et la forme de la surface ventrale, n'ont pas eu d'influence directe sur la sélection des moules; leur effet se fait sentir seulement à cause de leur association avec la couleur ou avec l'épaisseur.

## Introduction

Rate maximizing foraging theory states that animals will make choices which maximize the net rate of energy intake while foraging for some component of their food supply. The simple form of the theory assumes that the animal has full knowledge of the potential rates of intake available from different prey and in different feeding areas. Predators' preferences effectively rank prey according to their profitability, which in optimal-diet models is defined as the intake rate while prey are being handled (energy value/handling time) (Krebs 1978), and predators reject prey whose profitability is below the current average intake rate (Zwarts et al. 1996a). Predators can switch prey, depending upon the availability and activity of prey, to maximize energy intake (Zwarts and Esselink 1989).

Extensive reviews by Goss-Custard (1996) and Blomert et al. (1996) suggest that foraging oystercatchers can increase their intake rate in three broad ways: (1) by choosing the most profitable prey and rejecting the unprofitable ones; (2) by adjusting their searching behaviour to increase the rate of encounter with more profitable prey, and (3) by improving the efficiency of, and thus reducing the time costs involved in, finding and opening prey (Zwarts et al. 1996a). This paper focuses on the first of these three mechanisms and considers how European Oystercatchers (*Haematopus ostralegus*) might maintain their intake rate as high as possible by selecting the most profitable mussels (*Mytilus edulis*). Oystercatchers are extreme specialists in their feeding behaviour and prey selection (Sutherland et al. 1996). They can identify very small differences in the prey environment, even within prey species; for example, they can differentiate between two mussel beds if one bed enables them to achieve an intake rate that is just 3% higher than the alternative one (Goss-Custard et al. 1995). Furthermore, they are able to distinguish the thinner, weaker valve of a mussel shell down to a threshold of 0.036 mm, and therefore attack it; this increases the prey-intake rate by 3% (Nagarajan et al. 2002b). These findings show that in selecting and attacking prey, oystercatchers can be extremely sensitive to prey characteristics.

Ventrally hammering oystercatchers are also highly selective in the mussels they take. In particular, they select those with a thin shell; those that are covered by fewer barnacles (Meire and Eryvncck 1986; Sutherland and Ens 1987; Cayford and

Received 14 August 2001. Accepted 11 March 2002.  
Published on the NRC Research Press Web site at  
<http://cjz.nrc.ca> on 21 May 2002.

**R. Nagarajan and S.E.G. Lea.**<sup>1</sup> School of Psychology,  
Washington Singer Laboratories, Perry Road, University of  
Exeter, Exeter, Devon, EX4 4QG, U.K.

**J.D. Goss-Custard.** Centre for Ecology and Hydrology,  
Winfrith Technology Centre, Winfrith, Dorchester, Dorset,  
DT2 8ZD, U.K.

<sup>1</sup>Corresponding author (e-mail: [s.e.g.lea@exeter.ac.uk](mailto:s.e.g.lea@exeter.ac.uk)).

Goss-Custard 1990; Ens and Altung 1996); those with a brown shell; and those with a ventrally flat shell (Durell and Goss-Custard 1984). These characteristics may all tend to covary across mussels. This being the case, we need to ask whether, in fact, it is a single character, or small subset of characters, that an oystercatcher uses when selecting a mussel. Hence, in this paper we aim to explore the mussel characteristics that independently influence mussel selection by European Oystercatchers.

## Materials and methods

### Study area

We studied the oystercatchers wintering in the River Exe estuary in southwest England during winter 1996–1997. The River Exe estuary, and changes in the oystercatcher population, are described in detail in Goss-Custard et al. (1982) and the location of different mussel beds is shown in Fig. 2 of McGrorty and Goss-Custard (1993). For this study the data were collected from McGrorty and Goss-Custard's (1993) mussel bed number 4, which is located on the west side of the River Exe estuary between Starcross and Cockwood (50°37'N, 03°27'W). This is one of the beds that supports a good population of ventrally hammering oystercatchers. It is relatively free from disturbances by people and is also easy to access.

### Mussel population

To investigate the change in the absolute density of different size classes of mussels that occurred because of oystercatchers' predation, mussel frequency and size distribution were sampled three times over the winter, in September 1996, December 1996, and March 1997. Mussels were sampled using stratified random samples in each 25 × 25 m square by taking 9 quadrats, each 0.04 m<sup>2</sup> in area, using an aluminium frame covering an area of 400 cm<sup>2</sup>. Only samples in which 50% or more of the mussels were covered by weed were collected because ventral hammerers mostly take their mussels from under weed; in this study the oystercatchers took 85% of their mussels from under weed. Quadrats that fell in areas where the water depth was more than 10 cm at low tide were also rejected because oystercatchers cannot feed in deep water. When a sample was rejected, another one was taken nearby by throwing the quadrat over the shoulder with eyes shut. This procedure was repeated until the sample met the criteria for acceptance. Mussels collected were sieved and washed immediately using an iron sieve with a mesh size of 4 mm, placed in a polythene bag, transported to the laboratory within 2 h, and stored in a freezer for later analysis. The lengths of the mussels were measured using vernier callipers (to 0.1 mm accuracy), and mussels in different size classes present were counted.

### Opened and comparator mussels

Once a fortnight, towards the end of the low-tide period, a total of 50 fresh mussel shells opened by ventrally hammering oystercatchers were collected. Samples were collected from September 1996 to March 1997, since most oystercatchers arrive in September and remain until March. Freshly opened mussel shells can be identified easily from the fresh flesh remaining inside the shell near the attachment of the

adductor mussel (Durell and Goss-Custard 1984). For each opened mussel, an unopened mussel of the same length was collected from under nearby weed for comparison. Since light and background conditions in the locations where opened and comparator mussels were collected were very similar, there should have been no differences in collection bias between the two samples.

Morphological measurements were made on all mussels, using the procedure of Durell and Goss-Custard (1984). However, Durell and Goss-Custard (1984) and other previous investigators made measurements on only one valve of the mussel shell. Since oystercatchers have subsequently been shown often to have a preference for opening one valve or the other (Sutherland and Ens 1987; Nagarajan et al. 2002b), here we measured many of the characteristics from both valves in opened and comparator mussels. These characteristics were as follows: ventral thickness, dorsal thickness, depth, and number of barnacles on the dorsal surface for both right and left valves, and total number of barnacles on the ventral surface, total number of barnacles on all surfaces, full depth, and width for the whole mussel.

In addition, the length of the shell was measured as noted above. These measurements could not, of course, be made on the mussels that the oystercatchers were eating.

### Length of mussels eaten

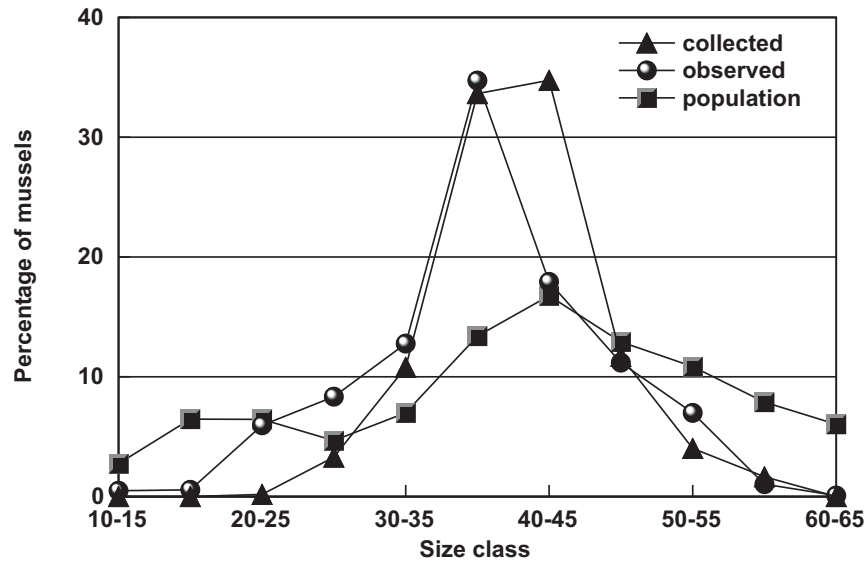
Almost every day during the winter, oystercatchers were watched by R.N. while they were feeding on the mussel bed. The maximum length of the mussels they ate, i.e., anterior to posterior length of the shell, was measured as a percentage of bill length. The bill length of oystercatchers on the River Exe estuary varies from 65 to 85 mm, with a mean of 75 mm (Goss-Custard et al. 1987). On the occasions when a bird with a particularly long or short bill was watched, the observer adjusted his estimate of mussel size accordingly. All observations were made by the first author; tests using a model showed that he tended to overestimate mussel length (Nagarajan 2000), so his mean observation error, 2.06 mm, was subtracted from the observed mussel lengths.

Working in the present study area, Cayford (1988) showed that there tends to be a collecting bias against smaller mussels, i.e., those in the 25–30 mm length range and below. This implies that observations of mussels being eaten yield a more accurate description of the length distribution of the mussels opened by oystercatcher than measurements of the opened mussel shells that were collected. Nevertheless, determinations of the characteristics of mussels selected by the oystercatchers were based on a comparison of the freshly opened mussels with the comparator mussels that we collected. This is legitimate despite the bias noted above, because our aim was to explore the characteristics in addition to length that influence the selection of mussels. For this reason the lengths of the collected and comparator mussels were carefully matched. So any discrepancy in size distributions between the collected mussels and those observed being eaten should not have introduced any bias into the analyses that follow.

### Statistical analyses

Statistical analyses were performed using standard statistical packages. Values are expressed in the text as the mean ±

**Fig. 1.** Percentages of mussels (*Mytilus edulis*) in each 5-mm length class taken by oystercatchers (*Haematopus ostralegus*) and present on mussel bed 4 between September 1996 and March 1997. The lengths of mussels taken by oystercatchers were obtained in two ways: (1) collection of freshly opened mussels from the mussel bed every fortnight (“collected”) and (2) almost daily observation of mussels being taken by oystercatchers (“observed”).



SD. We used mostly simple and stepwise multiple regression equations. Multiple-regression models were developed using both step-up and step-down procedures. The appropriateness of the regression models was tested as follows. (i) Linearity was tested by plotting the relationship between each response and predictor variable using Minitab's lowess plot. If the figure showed a linear trend then the variable was entered in the regression model in linear form, if it showed an uninflected curve then both linear and quadratic terms were used, and if there was clear inflection then the variable was entered as the linear, square, and cubed form. In the step-up procedure, in the first step, the most influential predictor variable was used and a model was developed by adding further variables successively. (ii) Homoscedasticity was tested by plotting the residuals of a model against fits, after identifying the main variables using the step-up procedure. Whenever we saw evidence of heteroscedasticity, we log-transformed the response variable. (iii) Normality was tested by plotting the distribution of the residuals of each model.

Variables were selected as follows. If the variable was significant on its own ( $t$  test; coefficient significantly different from zero), the variable was retained in the model, otherwise it was eliminated from subsequent models. At the end, the final refined model was derived with variables that were all individually significant.

To investigate the preferences of oystercatchers for different categories of mussels, Jacobs' index of preference ( $D$ ) was calculated as

$$D = \frac{r - p}{r + p - 2rp}$$

where  $r$  is the proportion of a particular category in the diet and  $p$  is the proportion of that category in the population.

Proportions were calculated in terms of number of mussels rather than biomass, since we were concerned with the birds' choice behaviour. The index varies from  $-1$  to  $+1$ ,

with  $-1$  representing total avoidance,  $0$  no preference, and  $+1$  absolute preference for that category, i.e., no other category was consumed (Jacobs 1974).

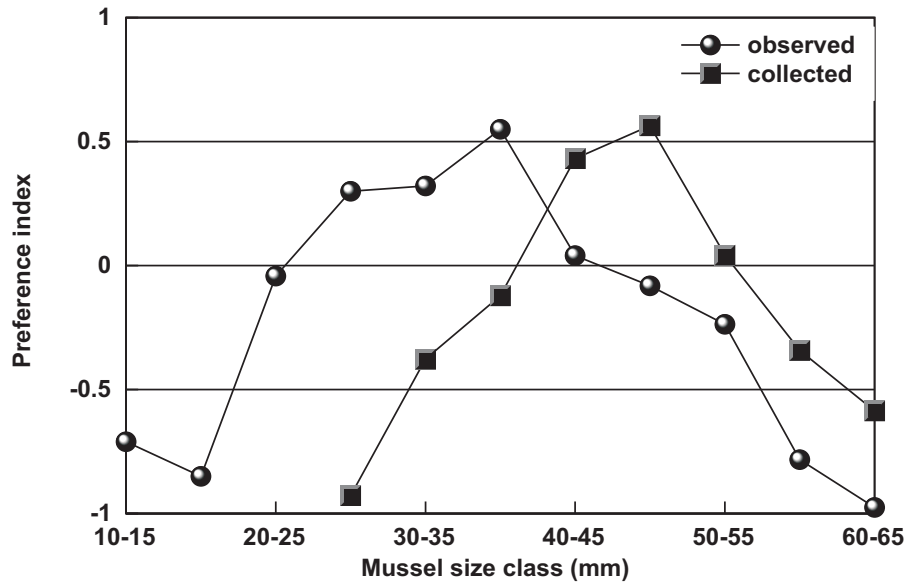
## Results

### Length of mussels

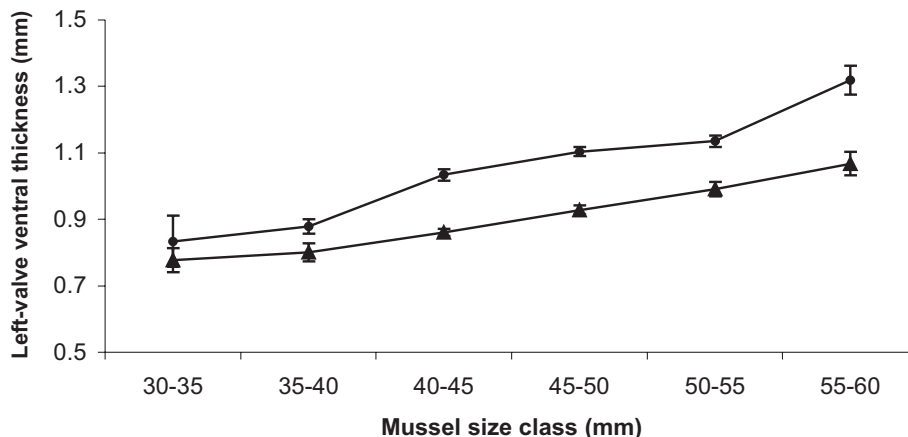
Figure 1 shows the length distributions of mussels collected at random from the bed, collected from the bed when freshly opened by oystercatchers, and observed being eaten by oystercatchers. The lengths of mussels collected at random from the bed ranged from 8.0 to 77.7 mm, with a mean of  $41.9 \pm 0.2$  mm ( $n = 6335$ ). The modal length class was 40–45 mm, which included 16.7% of the mussels. In total, 53.9% were between 35.0 and 55.0 mm in length. Fewer than 2.9% of mussels were less than 15 mm long and fewer than 4.7% were more than 70 mm long. The lengths of the freshly opened mussels collected ranged from 29.3 to 61.4 mm ( $45.2 \pm 0.3$  mm;  $n = 545$ ). Of these, 90.9% were between 35 and 55 mm in length; the modal length class was 45–50 mm and included 34.8% of the mussels. Of the remaining 9.1% of mussels, 3.5% were small (25–30 mm) and 5.6% were large (55–65 mm). The estimated length of the mussels that the oystercatchers were observed eating was  $38.0 \pm 0.2$  mm, with a range of 12.9–61.7 mm ( $n = 1261$ ); 70.8% of mussels were estimated to be between 35.0 and 55.0 mm in length. The modal length class was 35–40 mm and included 34.7% of the mussels. Only 1% of mussels were more than 55.0 mm or less than 20.0 mm in length (Fig. 1).

The size distribution of the mussels eaten, based on both collected and observed samples, differed significantly from that of the population according to the Kolmogorov–Smirnov two-sample test (see Siegel and Castellan 1988):  $D_{\max} = 3.49$ ;  $m = 546$ ,  $n = 4739$ ,  $P < 0.001$ , and  $D_{\max} = 5.47$ ;  $m = 1260$ ,  $n = 5644$ ,  $P < 0.001$ , for collected and observed samples, respectively. This indicates that oystercatchers were significantly selective towards particular length classes of

**Fig. 2.** Jacobs' (1974) preference indices for different length classes of mussels taken by oystercatchers on mussel bed 4, measured from collected and observed mussels.



**Fig. 3.** Left-valve ventral thicknesses (mean  $\pm$  SD) of mussels in length classes spanning those eaten by oystercatchers, freshly opened mussels collected from the mussel bed ( $\blacktriangle$ ) and comparator mussels collected close to them ( $\bullet$ ).



mussels. The preference index shows that their selectivity took the form of a strong preference for mussels between 35 and 45 mm in length (see Fig. 2).

Figure 2 shows a discrepancy in the length distributions of the opened mussels that were collected and those that the oystercatchers were observed to eat. The preference index showed that the most preferred length class was 35–40 mm for in the observed mussels and 45–50 mm for the collected mussels. We observed 27.1% of mussels eaten by oystercatchers to be between 20 and 35 mm long, whereas only 3.5% of the freshly opened mussel shells collected from the bed fell into this length class.

**Comparison of characteristics between opened and comparator mussels**

**Shell thickness**

For both opened and comparator mussels, the left valve of the shell in all size classes was slightly thicker than the right valve. We discuss the significance of this asymmetry and the

birds' response to it elsewhere (Nagarajan et al. 2002b). However, the oystercatchers always selected thin-shelled mussels across all length classes, whichever side they opened. Figure 3 shows left-valve ventral thickness for opened and comparator mussels grouped by length class; trends for the other three measures (right-valve ventral thickness, left- and right-valve dorsal thicknesses) were very similar. Regression lines for shell thickness against length were calculated separately for opened and comparator mussels for all four measures of thickness. The regression line for opened mussels fell wholly below that for the comparator mussels in all four cases, confirming that hammering oystercatchers select the thinner shelled mussels from those available (Durell and Goss-Custard 1984). However, the differences between the slopes of the relationships for the opened and comparator mussels were significant in all four cases: for left-valve ventral thickness the slopes were 0.0129 and 0.0187 for opened and comparator mussels, respectively ( $t = 2.56, P < 0.05$ ), while for left-valve dorsal thickness they were 0.0080 and 0.0111 ( $t = 3.47, P < 0.05$ ). Results for right valves were very similar

(Nagarajan 2000, p. 104). This means that the difference between the thicknesses of the shells of opened and comparator mussels increased with the length of the mussel considered. In other words, the similarity between the thicknesses of the shells of opened mussels and the shells of those present on the mussel bed was greater for small mussels than for large mussels.

To investigate the length at which oystercatchers began to show a preference for thinner shells, the lengths of opened and comparator mussels were grouped into 5-mm length classes over the range 5–10 to 60–65 mm. The difference in thickness between opened and comparator mussels was tested in each length class by using Student's *t* test. Regardless of which measure of thickness was used, the difference between the opened and comparator mussels did not become significant until length class 30–35 mm was reached, while the difference was significant in all the remaining length classes. Hence, the oystercatchers did not show a significant preference for thinner shells in mussels less than 35 mm long, but did so increasingly (and as an increasing proportion) as mussel length increased above 35 mm.

### Depth

Depth was  $18.4 \pm 0.2$  mm ( $n = 357$ ) for opened mussels and  $19.6 \pm 0.2$  mm ( $n = 368$ ) for comparator mussels. The difference between the depths of the opened and comparator mussels was examined by comparing the regression equations of depth against mussel length for the two samples. The slopes did not differ significantly, so the intercepts were tested and there was no significant difference. Hence, depth had no influence on mussel selection. These results were found for both right and left valve depths.

### Width

The widths of opened and comparator mussels were  $24.7 \pm 0.02$  mm ( $n = 373$ ) and  $25.1 \pm 0.02$  mm ( $n = 371$ ), respectively. The difference between the widths of opened and comparator mussels was again investigated by comparing the regression equations of width against shell length for the two samples. The slopes were not significantly different, so the intercepts were tested and there was again no significant difference. From this analysis it was inferred that the width also had no influence on mussel selection.

### Number of barnacles on the mussels

The barnacles were attached either on the dorsal or ventral side of the mussels. Overall, 34% of comparator mussels were completely free from barnacles; 47% of right valves and 49% of left valves did not have barnacles on the dorsal surface, while 88% of the mussels in the comparator population and 93% of opened mussels did not have barnacles on the ventral surface. So overall, 66% of mussels on the mussel bed did have barnacles attached.

Total numbers of barnacles on the whole sample of comparator mussels ( $5.6 \pm 9.84$ ;  $n = 486$ ) and whole sample of opened mussels ( $4.7 \pm 7.95$ ;  $n = 486$ ) did not differ significantly ( $F_{[1,970]} = 2.74$ ,  $P = 0.098$ ). The numbers of barnacles attached to the dorsal surface of the right valve ( $F_{[1,1008]} = 2.12$ ,  $P = 0.146$ ) and left valve ( $F_{[1,1036]} = 2.11$ ,  $P = 0.146$ ) of opened and comparator mussels also did not differ. In contrast, a higher proportion of the mussels taken by oyster-

catchers were without barnacles on the ventral surface. The number of barnacles observed on the opened mussels was  $0.17 \pm 0.73$  ( $n = 535$ ), significantly fewer ( $F_{[1,1069]} = 6.67$ ,  $P = 0.010$ ) than occurred on the ventral surface of the comparator mussels ( $0.34 \pm 1.30$ ,  $n = 535$ ). Ventrally hammering oystercatchers selected mussels that had fewer barnacles on the ventral side, whereas they were indifferent to the number on the dorsal surface and on the mussel as a whole.

To test whether the numbers of barnacles differed between the opened and comparator mussels by different amounts across length classes, mussels were again grouped into 5-mm length classes and the mean numbers of barnacles were compared between the groups in each length class. There was no significant difference between the groups in any length class, so selectivity for barnacles was not specific to any length class.

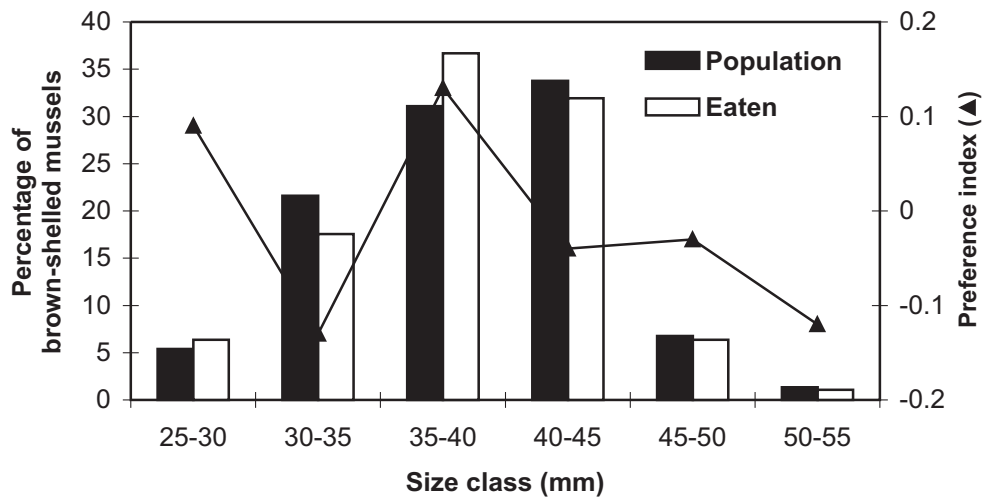
### Shell colour

The results of previous studies (e.g., Durell and Goss-Custard 1984) had suggested that ventrally hammering oystercatchers might take a greater proportion of brown- than black-shelled mussels. Nagarajan et al. (2002a) used the present dataset to test this suggestion, and confirmed it: the preference index in favour of brown-shelled mussels was found to be +0.54, with 34.4% of the freshly opened mussels being brown compared with only 13.6% of the comparator mussels. Since the proportions of brown-shelled mussels varied between length classes, we calculated Jacobs' preference index for colour in each length class (these calculations were not reported by Nagarajan et al. 2002a). The preference for brown-shelled mussels was positive in length classes 25–30 and 35–40 mm and highest in length class 35–40 mm ( $D = 0.13$ ; see Fig. 4). The significance of the colour preference was investigated using a three-way  $\chi^2$  test, taking as factors colour, size class, and sample (opened mussels vs. comparator mussels). The proportions of brown-shelled mussels differed between length classes (colour  $\times$  length:  $\chi^2_4 = 68.5$ ,  $P < 0.001$ ) and samples (colour  $\times$  opened mussels/comparator mussels:  $\chi^2_1 = 64.7$ ,  $P < 0.001$ ). The interaction between the three factors was not significant (colour  $\times$  opened mussels/comparator mussels  $\times$  size:  $\chi^2_4 = 3.8$ ,  $P > 0.05$ ), showing that the observed changes in preference with length class could have been due to chance.

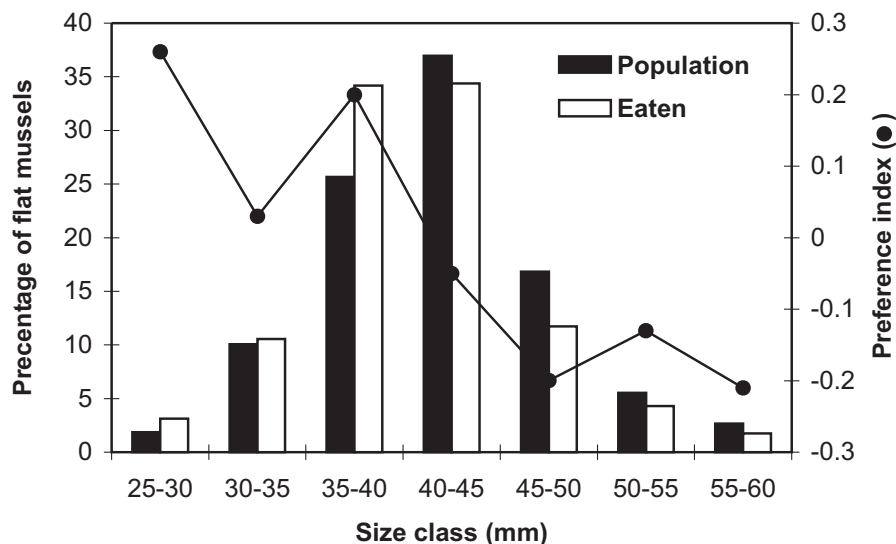
### Shape of the ventral surface

The ventral surface of a mussel tends to appear either flat or curved. In total, 89.4% of mussels in the comparator population were flat on the ventral surface, whereas 91.4% of those taken by oystercatchers were flat. The preference index of +0.27 suggests that the oystercatchers preferred to open ventrally flat mussels. Since the proportion of ventrally flat mussels changed across length classes, we calculated Jacobs' preference index for shape in each class. The preference index showed that preference was positive for length classes between 25 and 40 mm, being particularly high for the smallest size class, 25–30 mm (Fig. 5). The significance of this preference was also investigated using a three-way  $\chi^2$  test. In general, the oystercatchers significantly selected flat mussels (shape  $\times$  opened mussels/comparator mussels:  $\chi^2_1 = 6.4$ ,  $P < 0.05$ ). The proportion of flat mussels changed

**Fig. 4.** Proportions of brown-shelled mussels in different size classes in the population and among those eaten by oystercatchers, together with Jacobs' index of preference for brown-shelled mussels in each size class.



**Fig. 5.** Proportions of ventrally flat mussels in different size classes in the population and among those eaten by oystercatchers, together with Jacobs' index of preference for flat mussels in each size class.



across length classes (shape × size:  $\chi^2_3 = 8.05$ ,  $P < 0.05$ ), but preference did not (shape × opened mussels/comparator mussels × size:  $\chi^2_1 = 1.5$ ,  $P > 0.05$ ).

**Effect of individual characters on mussel selection**

The results so far have shown that the oystercatchers preferred mussels that were ventrally thin, on both the right and left valves, had fewer barnacles, and were brown-shelled and ventrally flat. But it is likely that these characteristics all covary across mussels. We therefore need to ask whether, in fact, it is a single character, or small subset of characters, that an oystercatcher uses when selecting a mussel. The necessary analysis was carried through by Nagarajan et al. (2002a, Table 2) in an investigation of the origins of the preference for brown-shelled mussels. They compared mussel shells that had been attacked by oystercatchers with comparator mussels, using a binary logistic regression model. In the binary logistic regression the dependent variable was condition of

the mussel (opened or comparator) and the independent variables were the measured characteristics, viz. length, ventral shell thickness, number of barnacles, colour, and shape (the last two being entered as dummy variables). Nagarajan et al. (2002a) found that the regression coefficients for ventral shell thickness, colour, and length differed significantly from zero, but those for number of barnacles on the ventral surface and shape of ventral surface did not. This suggests that only ventral shell thickness and colour had independent effects on mussel selection. The other two variables, number of barnacles and shape of the ventral surface, apparently had no influence on selection on their own, only by way of their association with the other characteristics.

**Discussion**

The results confirm a number of trends in oystercatchers' selection of mussels. Some of these are well established,

such as preferences for the medium size class (e.g., Ens 1982; Cayford and Goss-Custard 1990), thinner shells (e.g., Durell and Goss-Custard 1984; Meire and Ervynck 1986; Sutherland and Ens 1987; Cayford and Goss-Custard 1990; Ens and Alting 1996), and shells with less barnacle cover (Durell and Goss-Custard 1984; Meire and Ervynck 1986; Sutherland and Ens 1987; Cayford and Goss-Custard 1990). In addition, however, the present results confirm some trends that have only been reported once or twice before, including the absence of any thickness selectivity for the smaller size classes (Sutherland and Ens 1987) and the preference for the less common brown-shelled mussels over black-shelled mussels (Durell and Goss-Custard 1984). Finally, on a methodological note, the discrepancy between the length distributions of freshly opened mussels and those the oystercatchers were observed to eat (Fig. 2) confirms Cayford's (1988) observation of a collection bias against small mussels on the part of the experimenters. As explained in the Materials and methods section, this should not have affected the results of the present study but would need to be controlled for in some other kinds of research.

It can be argued that all these trends in the oystercatchers' selectivity are consistent with rate maximizing foraging theory. The effects of length and shell thickness are easily understood. Mussels in the medium length class are most profitable for oystercatchers (Meire and Ervynck 1986; Ens and Alting 1996; Zwarts et al. 1996a and 1996b Appendix), and thinner shells obviously break more easily (Meire 1996), so reducing handling time (Sutherland and Ens 1987). However, the difference will be minimal for the small size classes, for which handling times are minimal: length and shell thickness are correlated, and small mussels often break after the bird has made only a few blows, so rejecting a thicker shelled small mussel and searching for even thinner shelled mussels would take more time than it was worth.

High barnacle cover might provide a clue that either the shell is thicker (Durell and Goss-Custard (1984) found that the two variables were correlated) or the flesh content lower, as suggested by Ens and Alting (1996). Alternatively, the barnacles themselves may pose an extra barrier to the opening of the mussel, and this idea receives some support from our data. In an attempt to distinguish between the influence of shell thickness and that of barnacle infestation, we used four different measures of infestation: the total number of barnacles on the whole mussel and the numbers on the dorsal surfaces of the right and left valves and on the ventral surface separately. The only measure to vary significantly between opened and comparator mussels was the number of barnacles on the ventral surface. If barnacles merely provide a clue to shell thickness, the birds should respond to the number on the dorsal side, since they cannot see the ventral side until after they have attacked the mussel and torn it from the bed. Hence, we suspect that barnacles could be a barrier when the oystercatcher is hammering on the ventral surface, since the barnacles must be hammered before the bird can break the shell. Such mussels would therefore be harder to break and so unprofitable.

Nagarajan et al. (2002a) investigated possible reasons for the oystercatchers' preference for brown-shelled mussels and showed that black-shelled mussels had wetter flesh. By selecting brown-shelled mussels, oystercatchers consumed less

water while expending a given amount of energy than they would have done by taking black-shelled mussels. Those authors noted that the oystercatcher's limited oesophageal capacity (Kersten and Visser 1996) means that they must stop feeding during foraging bouts, when their intake rate exceeds their gut processing rate (Zwarts and Dirksen 1990). Nagarajan et al. (2002a) therefore argued that by selecting mussels with lower water content, the oystercatchers might be able to increase daily energy consumption enough to have survival value, especially in the winter, when many oystercatchers die of starvation (Goss-Custard et al. 1996).

Accounts of the oystercatchers' preference for flat-shelled mussels can only be speculative. It could be that ventrally flat mussels have a larger flat surface at which a hammering bird can direct its blows, this advantage perhaps being particularly strong in the smaller mussels (for which the shape preference was highest) whose flat area is necessarily smaller than in the larger mussels.

However, although reasons can be found why all these variables might influence profitability, we found that they do not all have an independent impact on choice. With length, shell thickness, and colour taken into account, the effects of the other variables fall into insignificance. This means that the observed effects of barnacle cover and shell shape must be assumed to arise either accidentally or because these variables provide the birds with a clue that helps them select mussels which are more profitable for other reasons, such as shell thickness. However, the interaction noted above between the location of barnacles and the birds' preference suggests that there may be a small direct effect of barnacle cover. However, ventral shape did not have a significant independent effect on mussel selection, and until it has been demonstrated that such an effect is independent, it would be premature to consider its origin: based on the present data we must conclude that it is a by-product of the preference for thinner, brown shells, perhaps because shell shape provides the birds with a clue that helps them locate their preferred mussel types.

## Acknowledgements

R.N. gratefully acknowledges the Commonwealth Commission, U.K. and the Ministry of Human Resources Development, Government of India, for a Ph.D. fellowship. We are grateful to Arie van der Lugt for making the figures, Catriona Ryan, Ian Hocking, Avril Mewse, and Jane Barnfield for comments, Rachel Kirby for computer assistance, Britta Osthaus and Jacqueline Hill for some field assistance, and David Taylor and Peter Goodes for arranging the supply of field equipment.

## References

- Blomert, A.-M., Ens, B.J., Goss-Custard, J.D., Hulscher, J.B., and Zwarts, L. (Editors). 1996. Oystercatchers and their estuarine food supplies. *Ardea*, **84A**: 1–538.
- Cayford, J.T. 1988. A field test of the accuracy of estimating prey size-selection in oystercatchers from recovered mussel shells. *Wader Stud. Group Bull.* No. 54. pp. 29–32.
- Cayford, J.T., and Goss-Custard, J.D. 1990. Seasonal changes in the size selection of mussels, *Mytilus edulis*, by oystercatchers,

- Haematopus ostralegus*: an optimality approach. *Anim. Behav.* **40**: 609–624.
- Durell, S.E.A. le V. dit, and Goss-Custard, J.D. 1984. Prey selection within a size-class of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*. *Anim. Behav.* **32**: 1197–1203.
- Ens, B.J. 1982. Size selection in mussel-feeding oystercatchers. *Wader Stud. Group Bull.* **34**: 16–20.
- Ens, B.J., and Altung, D. 1996. Prey selection of a captive oystercatcher *Haematopus ostralegus* hammering mussels *Mytilus edulis* from the ventral side. *Ardea*, **84A**: 215–220.
- Goss-Custard, J.D. (Editor). 1996. The oystercatchers from individuals to populations. Oxford University Press, Oxford.
- Goss-Custard, J.D., Durell, S.E.A. le V. dit, McGrorty, S., and Reading, C.J. 1982. Use of mussel bed *Mytilus edulis* beds by oystercatchers *Haematopus ostralegus* according to age and population size. *J. Anim. Ecol.* **51**: 543–554.
- Goss-Custard, J.D., Cayford, J.T., Boates, J.S., and Durell, S.E.A. le V. dit. 1987. Field tests of the accuracy of estimating prey size from bill length in oystercatchers, *Haematopus ostralegus*, eating mussels, *Mytilus edulis*. *Anim. Behav.* **35**: 1078–1083.
- Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. le V. dit, and Sutherland, W.J. 1995. Deriving population parameters from individual variations in foraging behavior. 1. Empirical game-theory distribution model of oystercatchers, *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *J. Anim. Ecol.* **64**: 265–276.
- Goss-Custard, J.D., Durell, S.E.A. le V. dit, Goater, C.P., Hulscher, J.B., Lambeck, R.H.D., Meininger, P.L., and Urfi, J. 1996. How oystercatchers survive the winter. *In* The oystercatchers from individuals to population. *Edited by* J.D. Goss-Custard. Oxford University Press, Oxford. pp. 133–154.
- Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologica*, **14**: 413–417.
- Kersten, M., and Visser, W. 1996. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Funct. Ecol.* **10**: 440–448.
- Krebs, J.R. 1978. Optimal foraging: decision rules for predators. *In* Behavioural ecology: an evolutionary approach. *Edited by* J.R. Krebs and N.B. Davies. Blackwell Publications, Oxford. pp. 2–63.
- McGrorty, S., and Goss-Custard, J.D. 1993. Population dynamics of the mussel *Mytilus edulis* along environmental gradients: spatial variations in density-dependent mortalities. *J. Anim. Ecol.* **62**: 415–427.
- Meire, P.M. 1996. Using optimal foraging theory to determine the density of mussels *Mytilus edulis* that can be harvested by hammering oystercatchers *Haematopus ostralegus*. *Ardea*, **84A**: 141–152.
- Meire, P.M., and Ervynck, A. 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Anim. Behav.* **34**: 1427–1435.
- Nagarajan, R. 2000. The foraging behaviour of oystercatcher (*Haematopus ostralegus*) in relation to food depletion during winter on the River Exe estuary, England. Ph.D. thesis, University of Exeter, Exeter, England.
- Nagarajan, R., Goss-Custard, J.D., and Lea, S.E.G. 2002a. Oystercatchers use colour preference to achieve longer term optimality. *Proc. R. Soc. Lond. B Biol. Sci.* **269**: 523–528.
- Nagarajan, R., Lea, S.E.G., and Goss-Custard, J.D. 2002b. Mussel valve discrimination and strategies used in valve discrimination by oystercatchers *Haematopus ostralegus*. *Funct. Ecol.* **16**.
- Siegel, S., and Castellan, N.J. 1988. Nonparametric statistics for the behavioural sciences. McGraw-Hill International, New York.
- Sutherland, W.J., and Ens, B.J. 1987. The criteria determining the selection of mussels *Mytilus edulis* by oystercatchers, *Haematopus ostralegus*. *Behaviour*, **103**: 187–202.
- Sutherland, W.J., Ens, B.J., Goss-Custard, J.D., and Hulscher, J.B. 1996. Specialization. *In* The oystercatcher from individuals to populations. *Edited by* J.D. Goss-Custard. Oxford University Press, Oxford. pp. 56–76.
- Zwarts, L., and Dirksen, S. 1990. Digestive bottleneck limits the increase in food intake of whimbrels preparing to migrate from the Banc d'Arguin, Mauritania. *Ardea*, **78**: 257–278.
- Zwarts, L., and Esselink, P. 1989. Versatility of male Curlews *Numenius arquata* preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availability. *Mar. Ecol. Prog. Ser.* **56**: 255–269.
- Zwarts, L., Cayford, J.T., Hulscher, J.B., Kersten, M., Meire, P.M., and Triplet, P. 1996a. Prey size selection and intake rate. *In* The oystercatchers from individuals to populations. *Edited by* J.D. Goss-Custard. Oxford University Press, Oxford. pp. 30–55.
- Zwarts, L., Ens, B.J., Goss-Custard, J.D., Hulscher, J.B., and Durell, S.E.A. le V. dit. 1996b. Causes of variation in prey profitability and its consequences for the intake rate of the oystercatcher *Haematopus ostralegus*. *Ardea*, **85A**: 229–268.