Oecologia (Berl.) 27, 75–92 (1977)

Oecologia

Prey Depletion and Foraging Strategy in the Oystercatcher *Haematopus ostralegus*

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Summary. The responses of a population of Oystercatchers to their own depletion of their prey, the edible cockle *Cerastoderma edule*, have been examined in Strangford Lough, Northern Ireland. Cockle stocks were severely depleted each winter as a result of predation by Oystercatchers and about half the birds present in October in the main study area had left by March: the reduction was greater when the initial population of Oystercatchers was high than when it was low. Oystercatchers were initially widespread around the Lough but tended to aggregate by January into a few good sites. Within each site annual differences in the location of feeding effort were correlated with year to year variation in the location of second winter cockles.

Within the feeding areas in a bay the birds apparently hunted in the short-term on the basis of expectation, ceasing to crop the densest cockle beds once an average yield for the area has been removed; this yield was apparently estimated from the local density of the anvils on which captured cockles were broken open. This effect led to marginal areas being depleted of cockles more rapidly than high density areas, so that the birds gradually concentrated their hunting onto an increasingly restricted area of the bay. The birds initially took only second winter and larger cockles but by late winter cockle densities had fallen so much that smaller cockles were accepted: areas previously abandoned or unused for hunting were then economically viable because of the reduced expectations of the birds and were incorporated into the feeding areas.

These results are seen as consistent with Royama's profitability theory.

Introduction

Spatial and temporal variation in the distribution and density of their prey constitute an important ecological problem for predators attempting to maximize the adaptiveness and efficiency of their feeding behaviour. Royama (1970) has

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suggested on theoretical grounds that a predator tries to maximize its hunting efficiency by sampling the food available in different parts of its habitat and spending most time where its success rate is high. Royama's hypothesis was originally developed to account for the behaviour of predators in response to the appearance of new prey species in the habitat. It is, however, also applicable to the situation in which the activities of the predator are responsible for the local depletion of the initial prey species. Here the cost of searching for further prey individuals rises as prey density falls under predation and will ultimately reach a point at which the energetic cost of searching is exactly balanced by the energy content of the prey item found. Royama's profitability hypothesis suggests, however, that before this point is reached a predator might well either move to a new area with a greater prey density present or, alternatively, switch to a new prey species within its current area, if by so doing its rate of food acquisition were to increase relative to its current reward rate. There have been few field studies of such situations, though Goss-Custard (1970) has shown that Redshank *Tringa totanus* will switch to alternative prey when these are as rewarding as the initial prey species. We therefore report here on field observations of two features of feeding behaviour—choice of foraging site and choice of prey size—in a predator whose hunting significantly depletes the one prey species available to it.

Oystercatchers *Haematopus ostralegus* are relatively large waders with high food intake requirements (Heppleston, 1971a; Hulscher, 1974) and can consequently winter in numbers only where there are large resources of one or more prey species readily available. In the British Isles this is the case only on intertidal beds of the molluscs *Mytilus edulis, Cerastoderma edule* and *Macoma balthica.* These species cease growth over the winter (Seed and Brown, 1975; Lammens, 1967) so that their winter predation by Oystercatchers is unmitigated by recruitment of individuals into the size classes selected by Oystercatchers. Thus the mollusc stocks are severely depleted in the course of the winter (Davidson, 1967). Furthermore the intertidal nature of the beds also limits the feeding time available to the birds, particularly when combined with the short day lengths of winter (Heppleston, 1971a). There is thus a high premium on efficient feeding by Oystercatchers, making the species a particularly suitable subject for the present study.

Materials and Methods

Fieldwork was carried out in Strangford Lough, Northern Ireland, principally at Greyabbey Bay on the eastern shore of the lough. Greyabbey Bay is a relatively sheltered sandy bay about a mile in width, sheltered on all sides except the south where it opens onto the lough. We have previously described the area and the behaviour of its Oystercatcher population in some detail (Brown and O'Connor, 1974).

Oystercatcher numbers throughout the winter were obtained as part of the Strangford Wildlife Panel counts of wader and wildfowl numbers in the lough. The distribution of feeding effort by these birds in Greyabbey Bay was assessed from the location of the shells of recently predated cockles: most of the cockles taken by Oystercatchers are broken open by hammering the shells until they fracture along a weak point in the shell, thus leaving a characteristically fractured valve as evidence of the birds activities (Hulscher, 1971). Freshly killed cockles could be distinguished from older kills by the absence of algal staining from the shell. We were, therefore, able to plot the recent feeding activity of the birds at any time by plotting the distribution of such shells along a series of transects through the bay, shell density being recorded in such surveys on a three-point scale at fifty-pace intervals along each transect. Direct observation of the feeding birds confirmed the validity of this approach.

Prey availability was assessed from periodic samples of the cockles actually available to the birds. These samples were of two types: first, a series of regular seasonal samples from the vicinity of fixed points within the bay, thus providing an indication of the impact of oystercatcher predation on the standing crop of cockles, and second, a more extensive annual survey in late winter along a series of five transects through the bay (shown as Fig. 3 in Brown and O'Connor, 1974), to provide information on more widespread changes in the distribution and population structure of the prey population in the area. In both cases each sample was taken by digging a one foot square quadrat to a depth of approximately 5 cm and sieving the sand and cockles through a 2 mm mesh.

Prey selection by the Oystercatcher was assessed from samples of predated shells taken from the vicinity of each samples of living cockles. The heights of all shells collected, both of predated and of living cockles, were measured to 0.1 mm using vernier calipers. Cockle heights at Greyabbey are closely correlated with both the age and the overall size of individual animals (Seed and Brown, 1975; Brown et al., 1976) and height measurements alone therefore sufficed in assessing size selection of prey by Oystercatchers.

Results

Changes in Prey Availability

More than three-quarters of all cockles taken by Oystercatchers in Greyabbey Bay are 15 mm or larger in height (Brown and O'Connor, 1974) and the seasonal variation in numbers of cockles of this size therefore closely reflects the total stocks available to the birds through the winter (Fig. 1). Numbers were highest in autumn following summer recruitment to the size class; this recruitment occurs as the spatfall of the previous year resume the growth interrupted in their first winter. Numbers declined steadily through the winter, largely as a result of predation by Oystercatchers but rose again in late spring and summer as growth resumed (below).

Figure 2 displays the pattern of growth shown by cockles in Greyabbey Bay. Growth was rapid during the warm summer months but ceased during winter. The winter populations of cockles thus consisted of largely discrete size classes, each a year older than the next smallest. Measurements made of tissue dry weight of cockles of constant size in November 1974 and March 1975 showed that there was no increase in biomass to compensate for the decline in cockle numbers noted above (Fig. 1). The net weight of shellfish available to the birds as food therefore declined throughout the winter.

Changes in Predator Numbers

Seasonal changes in the number of Oystercatchers wintering in the bay are shown in Figure 3. The population increased between September and October, presumably as a result of passage birds temporarily stopping in the bay to

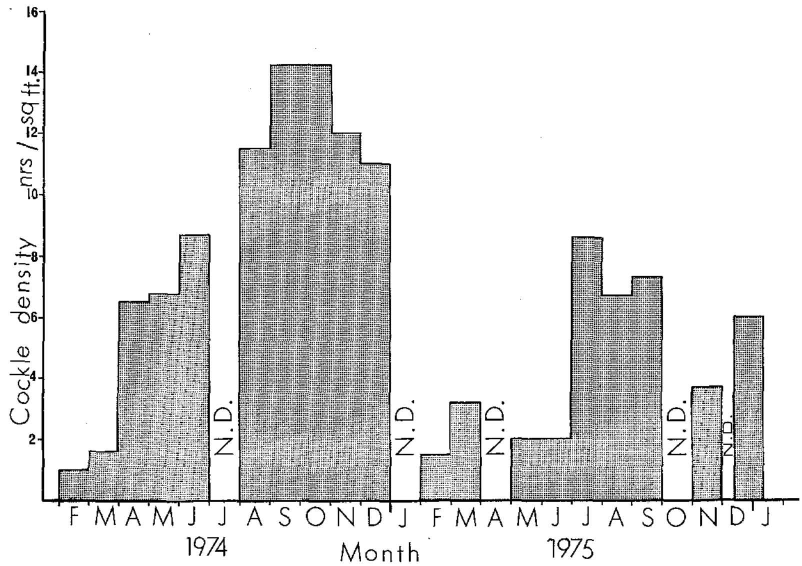


Fig. 1. Seasonal changes in the numbers of second winter and older (heights above 15 mm) in Greyabbey Bay. Samples were pooled for counting but typical variation was about 22% (*N.D.* no data)

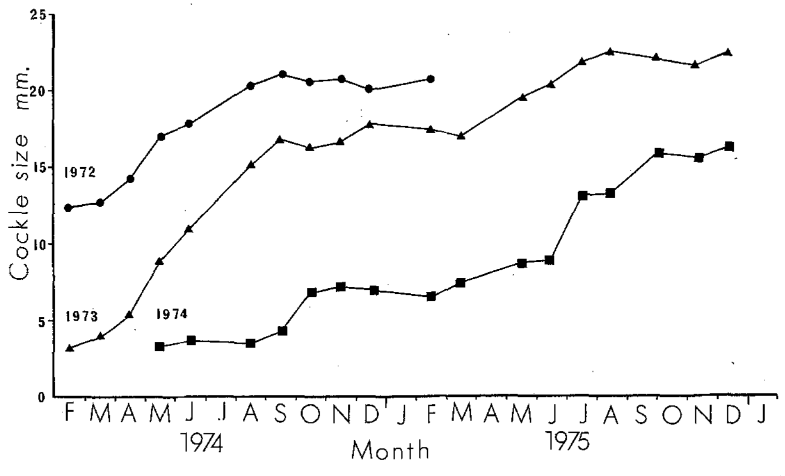


Fig. 2. Growth curves for individual cohorts of cockles in Greyabbey Bay. Cohorts identified by year of settlement. Sample size for each point was at least 20, except in six cases, and maximum variation about the mean was 10%

feed (Hutchinson, 1974), but then declined throughout the rest of the winter, steeply at first, more slowly after January. Oystercatcher numbers thus varied roughly in parallel with the cockle stocks in the bay (Fig. 1), suggesting that some birds might have moved out of the bay in the course of the winter in response to falling food levels. This possibility was examined further by

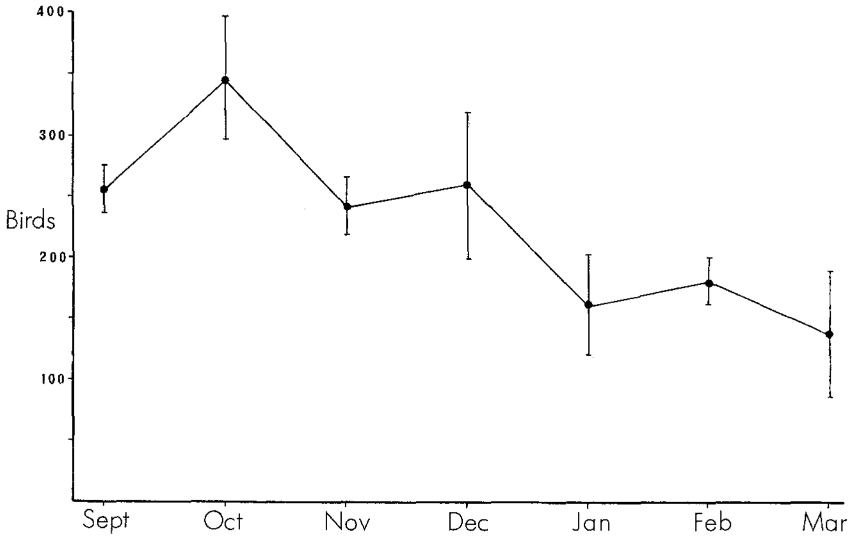
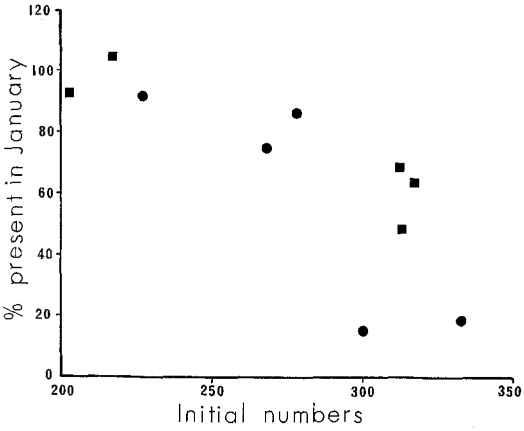


Fig. 3. Seasonal variation in the number of Oystercatchers feeding in Greyabbey Bay, autumn 1970 to spring 1975. Vertical bars indicate ± one standard error

Fig. 4. The proportion of the early winter population of Oystercatchers still present in January in relation to the size of the early winter counts. Early winter numbers taken as the mean of the October to December counts. Data for two sites (Greyabbey Bay ●, Boretree Islands ■) in Strangford Lough for the five winters 1970–1975



comparing the January Oystercatcher population against the average population previously present in the bay that winter (Fig. 4). The data show that when many Oystercatchers fed in the bay in early winter the January numbers were relatively lower than was the case when smaller numbers were initially present. The same effect is apparent in data for Oystercatchers feeding around the Boretree Islands in Strangford Lough (Fig. 4). Hence if cockle stocks are approximately constant from year to year these data may be interpreted as indicating that when birds are present in early winter in large numbers they reduce their food supplies sooner than when they are present in early winter in lower numbers, thus forcing some birds to leave the bay early.

An alternative explanation of the results just described would be that the birds remaining in January were residents, the others being passage migrants present in Greyabbey for only some weeks. This possibility can, however, be dismissed on further examination. Table 1 shows the December and January totals for Oystercatchers feeding over Strangford Lough as a whole during the winters of 1970 to 1975. These show that the net change in Oystercatcher numbers between these two months was, on average, less than 12%, only a third of the 38% decrease observed in Greyabbey Bay (Fig. 3). Hence either the birds from Greyabbey moved elsewhere within Strangford Lough or the Greyabbey birds showed relatively more movement than birds feeding elsewhere round the lough, e.g. because the depleted their food supplies more rapidly or because birds on passage had settled differentially into Greyabbey Bay. Table 2 shows that most sites containing significant (at least one hundred) numbers of Oystercatchers in December held fewer birds in January, but that some areas held more. The size of this concentration effect is shown in Figure 5: here the January counts are plotted against the early winter averages for the sites and the regression between the two variables calculated. The regression slope (1.68 ± 0.37) was greater than unity, though not quite significantly so ($t = 1.83$, $0.05 < P < 0.10$) indicating that sites more attractive to Oystercatchers in early winter had become even more attractive by January.

In summary, therefore, these results show that some Oystercatchers moved out of their early winter feeding grounds as the cockle stocks there were depleted, some birds going to join flocks feeding at better sites round Strangford Lough, others moving even further afield.

Choice of Feeding Locations

Although cockles were present in varying numbers throughout the bay the Oystercatchers concentrated their foraging into a small number of intensively searched areas or feeding grounds: this effect is illustrated in Figure 6. Table 3 shows that this effect was due mainly to annual differences in the location of most second winter and older cockles: in each year examined sample sites within the feeding grounds tended to have high densities of cockles present whilst those outside the feeding areas tended to have below average cockle numbers. The Oystercatchers were, therefore, concentrating their hunting into areas with the highest probability of success.

The location of these feeding grounds changed from year to year, so areas heavily hunted one year were largely ignored twelve months later (Fig. 6). This reflects the year to year variation in the position of high densities of second winter cockles, since settlement of young cockles tends to be more successful in the less crowded parts of the beds, that is, in those areas in which older cockles provide less intraspecific competion (Kristensen, 1957).

Within each winter shorter term changes in the location of the feeding grounds took place (Fig. 7). In December 1974 the birds were using fairly large reaches of the bay for hunting but in February 1975 only a fraction of this area was still in use and few additional areas had been incorporated into the

Table 1. Numbers of Oystercatchers present over the whole of Strangford Lough in December and January in different winters

	1970–1971	1971–1972	1972–1973	1973–1974	1974–1975
December	3939	3962	2416	1892	1489
January	2647	3628	2816	1715	1291

Table 2. The number of sites round Strangford Lough showing changes in Oystercatcher population size between December and January each winter. Only sites with at least 100 birds present in December are included. Decreases are statistically more frequent than increases ($P < 0.002$, Sign Test)

Change	1970–1971	1971–1972	1972–1973	1973–1974	1974–1975	Totals
Decrease	6	5	3	3	4	21
No change	0	1	0	2	0	3
Increase	1	0	1	1	1	4

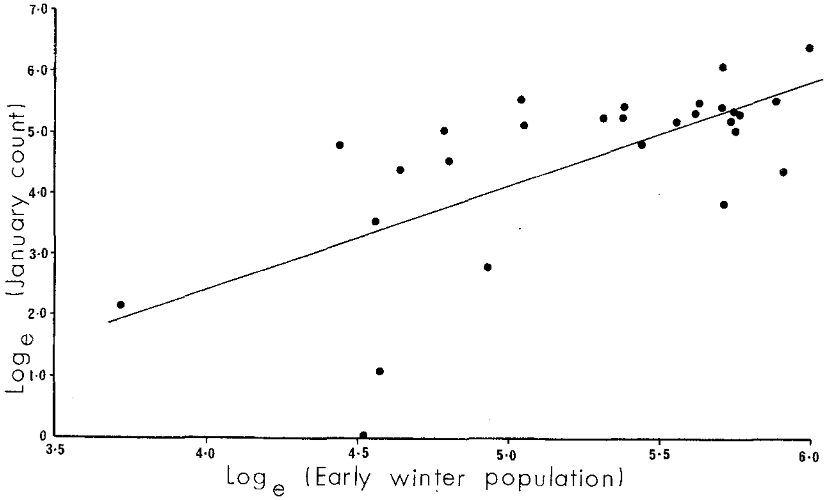


Fig. 5. The relationship between Oystercatcher numbers in January and those for the earlier part of the winter (October to December average). Data for all sites in Strangford Lough with at least 100 birds present in December that year, for winters 1970–1975. The regression equation is: Log_e (January count) $= 1.68 \log_e$ (early winter population) -4.28, $t=4.50$, $P<0.001$. The slope differs from unity by an amount just short of significance ($t=1.83$, $P<0.10$)

feeding grounds (Fig. 7a). These results can be attributed to local depletion of the cockle stocks within the abandoned areas (Fig. 8). Samples from sites still hunted over in February contained more cockles in November than did samples from sites abandoned by February, and these cockles were also slightly larger than those from the sites subsequently abandoned ($t=2.47$ for cockles above 10 mm, $P<0.02$). Comparison of the February samples from abandoned

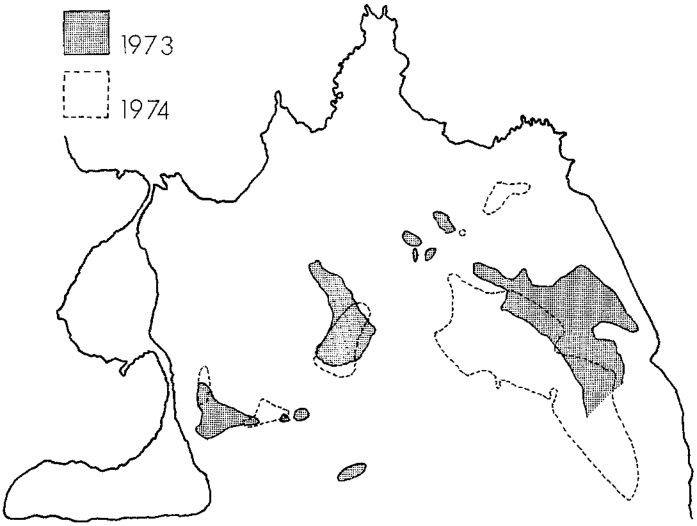


Fig. 6. The location of the March feeding grounds of Oystercatchers in different years, showing the relatively small overlap between years. Compare also with the March data in Figure 7. Feeding grounds were identified by the presence of recently predated cockles at points along transects through the bay

Table 3. The location of feeding areas with respect to cockle density. Samples were collected in March each year. Significance testing by Fisher's exact probability test or χ^2 test as appropriate. "Average" refers to the average cockle density in all samples for that March

Year	Cockle density	Number of samples with cockle density specified In feeding areas	 Outside feeding areas	Significance level
1973	Above average	11	2	
	Below average	10	27	$P=0.0004$
1974	Above average	10	4	
	Below average	2	13	$P=0.0021$
1975	Above average	13	6	
	Below average	7	18	$P<0.025$
Combined	Above average	34	12	
	Below average	19	58	$P<0.001$

and non-abandoned sites shows also that the latter sites still held some cockles in February, but cockles of small size, normally not taken by Oystercatchers in Greyabbey (Brown and O'Connor, 1974). That these small cockles were now being cropped is suggested by the results of the March survey of the feeding grounds (Fig. 7b), which showed that, far from having continued to shrink in area, the feeding grounds had actually increased in extent, once more taking in parts of the bay abandoned in February but also, and more significantly, incorporating some new areas not previously hunted that winter.

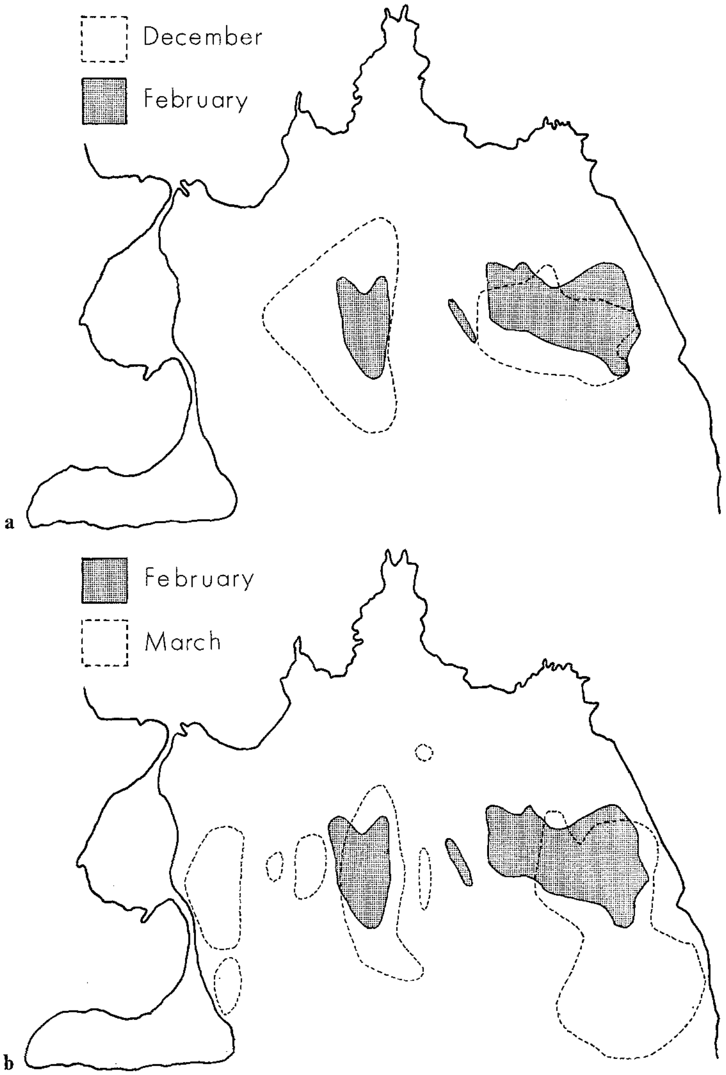


Fig. 7 a and b. Changes in the location by Oystercatcher feeding grounds in the course of the 1974–1975 winter. **a** Feeding areas in December 1974 and February 1975, showing the mid-winter contraction in area. **b** Feeding areas in February and in March 1975, showing the expansion of hunting back onto areas previously abandoned and the incorporation of new areas into the feeding range

This pattern cannot be attributed to still further concentration onto the "best" areas but can be explained if the birds had relaxed their previous size criteria for prey acceptability, thus being able to exploit areas previously offering an unacceptably low reward rate for hunting effort. Analysis of the sizes of cockles actually taken supports this explanation (below).

Given that Oystercatchers concentrated their hunting onto the densest parts of the cockle beds (Table 3) one can ask how this came about. Gibb (1962) suggested that titmice (Paridae) hunting eucosmid larvae in pine cones hunt

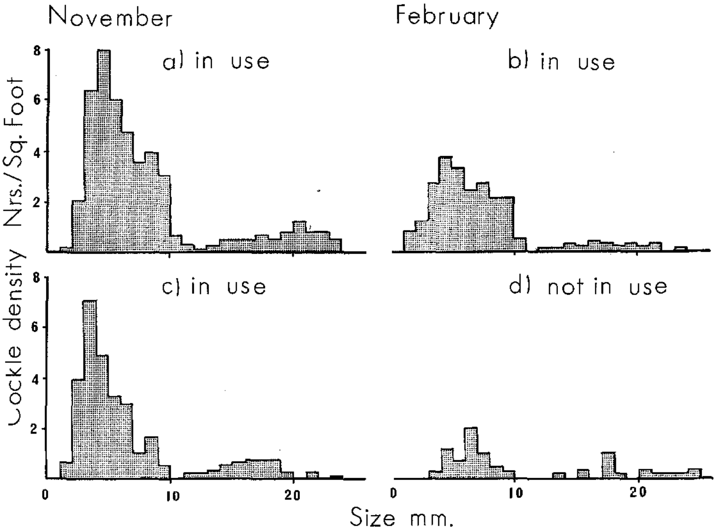
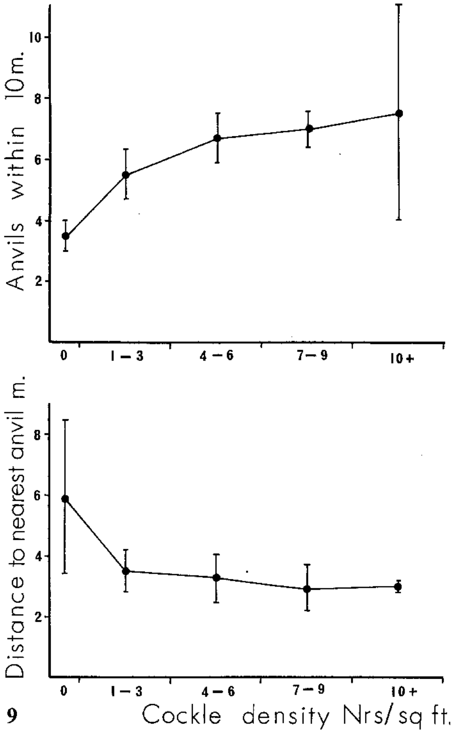


Fig. 8a–d. Size-frequency histograms of cockles available to the Oystercatchers in different parts of Greyabbey Bay. Each transect station was sampled for cockles in November and again in February, and each November sample was classified in February according to whether or not that station was still hunted over in that month. Top row shows cockle sizes **a** in November and **b** in February, for areas still hunted over in February. Bottom row shows equivalent data for **c** November and **d** February for samples from areas hunted in November but abandoned by February, and show that depletion effects were already apparent at these stations the previous November

by "expectation", forming a value for their likely reward rate with a potential prey species on the basis of sampling its abundance over their foraging area as a whole and locally ceasing to hunt that particular prey species when their actual yield reaches this level. Gibb suggested that the tits assessed the total yield achieved on the basis of the damage done to the pine cones in extracting larvae; he suggested that waders might similarly hunt by expectation on the basis of the probe marks left on mudflats. In the case of Oystercatchers the presence of anvils piled with cockle shells is a more conspicuous clue to the hunting intensity in the area, since each bird carries the cockles it finds to the nearest anvil to break open the shell there. We examined this possibility in November 1974 by taking nineteen samples of cockle density from 20 m grid points within a 100 m square in the main feeding ground at the time, and counting the number of anvils within 10 m of each sample point; Oystercatchers carrying captured cockles do not normally move greater distances than this in walking to an anvil; we also recorded the distance from each sample point to the nearest anvil, as a second measure of anvil density. Both measures showed the same trend with cockle density (Fig. 9): anvil density rose with cockle density when cockles were relatively scarce, but levelled off at higher densities. These results clearly fit the hunting by expectation model if anvil density is a valid measure of hunting intensity by the Oystercatchers and seem to indicate, therefore, that the birds do respond to this evidence of their own activity.



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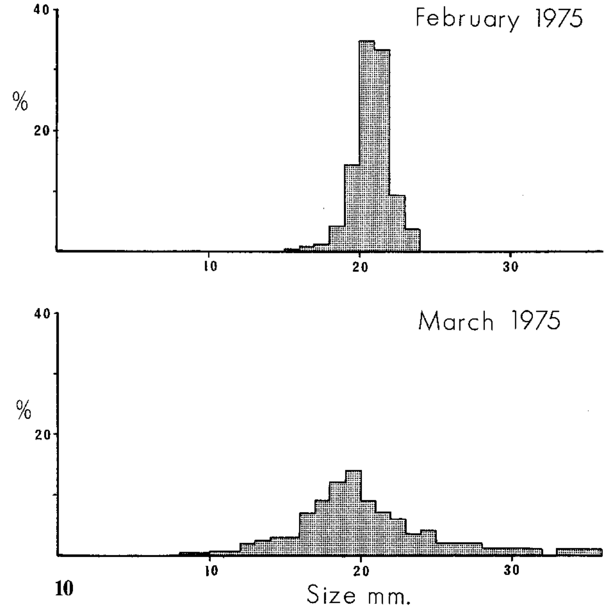

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Fig. 9. The distribution of "anvils" in relation to cockle density. Above, density of anvils, below, distance to nearest anvil. Vertical bars indicate ± one standard error. Figures below each point indicate the number of cockles in that density class

Fig. 10. Size-frequency distribution of cockles taken by Oystercatchers in February and in March 1975. The increase in variance in March is significant ($F = 14.6$, $P < 0.001$)

It is interesting to note that the two curves levelled off at cockle densities of 5–8 per quadrat, since the mean density of all nineteen samples proved to be 5.0 per quadrat. This result would fit quite nicely with the idea of an expectation value based on the bird's experience of prey densities in the feeding grounds, though it is no doubt coincidental here in view of the relatively few samples taken.

Choice of Prey Size

Table 4 summarizes data on the mean size of second winter and older cockles available to the Oystercatchers in different years. Cockle size varied substantially between years but these differences were essentially independent of the time of sampling within the year, being attributable largely to year to year variation in the length of the summer growth season: a long growth season enabled cockles in that year to grow to a larger size at which to overwinter (Seed

Table 4. The size of cockles available to, and actually taken by, Oystercatchers on various dates. Only cockles above 15 mm in height included. Figures given are mean ± standard deviation (sample size) in mm

Date	Size (mm) of cockles which were	
	Available	Actually taken
November 1972	16.7±1.3 (122)	16.2±1.1 (374)
January 1973	16.6±0.8 (63)	17.5±2.2 (317)
April 1974	16.6±1.5 (26)	15.8±2.1 (192)
November 1974	21.0±1.9 (24)	20.6±1.4 (728)
February 1975	19.4±2.6 (71)	20.8±1.2 (299)
March 1975	18.6±2.1 (16)	19.7±4.6 (1080)

and Brown, 1975). Comparison of the mean size of cockle available on each date with the mean size of cockle actually taken by Oystercatchers at that time shows a close correlation between the two (Table 4) and the dispersions of the samples from each date show no bias in favour of a smaller size range for the predated cockles. These results indicate, therefore, that there was relatively little selection of prey on the basis of size, at least within the older age groups of cockles. We have previously noted the exclusion of the smallest, first-winter, cockles from the diet of Oystercatchers at Greyabbey (Brown and O'Connor, 1974) and these cockles have therefore been omitted from the analysis here.

Figure 10 shows the size spectrum of cockles taken by Oystercatchers in February and in March in 1975. Although the mean size taken varied little over the winter (Table 4) the March spectrum was significantly broader than in the February sample ($F=14.6$, $P<0.001$). This increase extended to both smaller and larger cockles, though more so towards the former (Fig. 10). We noted above that the feeding grounds increased in area between the dates of these two samples (Fig. 7b). These parallel increases suggest that the birds may have relaxed a previous bias against the smallest cockles so that they could once more economically hunt over areas abandoned in February, though now with a lower reward rate from the still numerous but small cockles of lower biomass. Some large cockles previously missed in the feeding areas would probably be found under this more intensive searching, particularly in those parts of the bay now incorporated into the feeding grounds for the first time (Fig. 7b), and thus account for the presence of some cockles above 24 mm in the March samples.

In the course of a brief visit to Greyabbey in early April 1976 we obtained additional information pertinent to size selection by Oystercatchers. The birds were present on this occasion in lower than usual numbers, though it was not possible to obtain a proper count. A survey of the bay revealed cockles were also considerably scarcer than usual and measurement of a sample showed them to be of only average size (Table 5). Cockle biomass was thus considerably down on previous years and food must have been extremely scarce for Oystercatchers feeding in the bay. In keeping with this the scattered mussel scars throughout the bay showed considerable evidence of attacks by the birds, princi-

Table 5. The availability and size of spring populations of cockles in Greyabbey Bay. Figures given are mean ± standard deviation

Date	Density of second year or older cockles (nrs/m^2)	Size of second year cockles (mm)
21 March 1973	67.0±178.1	15.6±1.3
3 April 1974	191.0±296.1	12.7±1.8
20 March 1975	69.7± 63.0	16.9±2.9
8 April 1976	38.5± 48.1	15.3±1.6

pally on mussels in the 20–40 mm size range (mean 28.2±6.1 mm). This size range is equivalent in tissue content to the 10–17 mm range of cockles (Brown et al., 1976) which suggests that mussels are at best a poor substitute for cockles. The coincidence of tissue content for the smaller shellfish taken in the two species suggests that this was a limit imposed by energetic considerations. Larger mussels were available on many of the rocky scars but were always heavily encrusted with barnacles: this presumably strengthened the mussel shell against attack by the birds, as predated shells were relatively free of such encrustation.

Discussion

A predator faced with a declining prey population has essentially three options open to it. First, it can move elsewhere to hunt for its preferred prey. These movements may be either local or long-distance in character, depending on how local the depletion of prey actually is. Second, the predator may change its diet, turning to some other prey not previously taken for some reason, for example, because this prey is of lower palatability, or because it requires greater capture effort. Finally, the predator may exploit its current prey more intensively, taking individuals it previously ignored for any of a variety of reasons, e.g. small size, difficulty of capture, and so on. The exact response adopted depends in a complicated way on the relative sizes of searching, pursuit and capture times (MacArthur, 1972). Our results suggest that several of these considerations influenced the hunting behaviour of the Oystercatchers in Strangford Lough.

Food Shortage and Movement

Several of the results reported here indicate that Oystercatchers in Strangford Lough are subject to food shortages in mid-winter. First, the number of birds feeding in Greyabbey Bay varied through the winter roughly in parallel with the cockle stocks (Figs. 1 and 3). Secondly, the changes in the location of the feeding grounds within the bay were associated with local depletion of the cockle stocks (Fig. 8). Thirdly, most of the small bays round the Lough were abandoned by Oystercatchers between December and January, the period of severest depletion of cockle populations at Greyabbey (Table 2). Fourth, in those years when large populations of Oystercatchers were present at Greyabbey or at the Boretrees relatively fewer remained beyond December (Fig. 4), corresponding to the earlier depletion of the cockles under the heavier predation of those years. These results thus indicate a reduction in Oystercatcher numbers correlated with food shortages in mid-winter.

The observed changes in Oystercatcher numbers could be due either to mortality or to movement. However, some sites in Strangford Lough showed increases rather than decreases between December and January (Table 2), and the overall change in the Strangford population was markedly less (Table 1) than that observed in the individual sites studied in more detail (Figs. 1 and 4). Hence a large part of the changes in Oystercatcher numbers at Greyabbey can be attributed to the birds moving elsewhere in Strangford Lough to feed; the analysis of Figure 5 suggests that this movement and that of birds from other sites depleted of cockles in the course of the winter (Table 2) involves the concentration of Oystercatchers into those sites already heavily used by conspecifics, presumably because these sites hold larger stocks of cockles. This behaviour thus parallels on a large scale the concentration of those birds remaining in Greyabbey Bay onto the areas of greatest cockle density within the bay (Fig. 7).

Evidence of a mid-winter food shortage amongst Oystercatchers has been obtained in several other studies (Drinnan, 1958; Hancock and Urquhart, 1965; Davidson, 1967; Heppleston, 1971 a) and in some cases local movement onto alternative food sources, as in the present study, has been noted (Heppleston, loc. cit.). The possibility that these movements may predominately involve young and immature birds needs to be borne in mind here: Heppleston found that weight losses and mortality occurred amongst immature birds rather than amongst adult birds, whilst some chance observations of our own suggest that immature birds may be confined to the poorer parts of the feeding grounds through behavioural interactions with adults.

Change of Prey Species

An alternative strategy open to the birds in meeting the effects of prey depletion may be to switch their diet to a prey species not previously exploited. The use of this strategy is correlated with weak, rather than strong, initial prey preference (Murdoch, 1969), but the evidence as to prey preference strength in Oystercatchers is equivocal. Weak prey preferences are indicated by Heppleston's (1971 b) study and by opportunist feeding of birds in other studies (Norton-Griffiths, 1967; Dare and Mercer, 1973), but strong prey preferences are suggested by intra-population specialists being identified in some areas e.g., specialists on periwinkles (Dare and Mercer, 1973) and on polychaetes (this study). We found Oystercatchers at Greyabbey to exploit mussels only during extreme cockle scarcity (Table 5): this, with the low tissue content of mussels (Brown et al., 1976) and their availability (because of their position) only towards low water, suggests that mussels are only marginally profitable as prey at Greyabbey. There must, therefore, have been rather little scope for prey switching by Oystercatchers as a response to cockle depletion in the course of the winter.

Changes in Prey Acceptability

Predators feeding over a range e.g., in size—of prey items should extend their diet to include the next adjacent category (whether of smaller or larger items) if the energy content of the prey thus obtained relative to the cost of doing so is at least as great as the average for the current prey spectrum (MacArthur, 1972). Oystercatchers at Greyabbey showed little evidence for size selection except for a bias against the smallest cockles (Brown and O'Connor, 1974; Table 4). This is presumably because the meat content of third year and older cockles has increased with size in proportion to shell thickness (Brown et al., 1976), leaving relative reward rates unchanged. Norton-Griffiths (1967) argues thus in respect of Oystercatcher predation on mussels, in which size-age relationships are broadly similar to those in cockles (Seed and Brown, 1975; Brown et al., 1976). Thus there is little scope for seasonal switching between size classes as a response to prey depletion.

A seasonal increase in the *range* of prey sizes taken can, nevertheless, be predicted on theoretical grounds (MacArthur and Pianka, 1966). Seasonal prey depletion should require a reduction in the criteria for acceptable densities and individual size of prey in late winter, leading to an expansion of hunting area over parts of the bay previously depleted to the original criterion level (Fig. 7b) and to the acceptance of smaller cockles than hitherto (Fig. 10). In addition the wider-ranging more intensive hunting of late winter should reduce the effectiveness of the protection by dispersion (Tinbergen et al., 1967) previously obtained by third year cockles as a result of the competitive spatial segregation of cockle age-classes at spat-fall (Kristiansen, 1957): disproportionately more third year cockles should therefore be taken in late winter, and this was in fact observed (Fig. 10).

Davidson (1967) and Drinnan (1958) have previously noted that Oystercatchers observe a size threshold in taking prey. In addition, Lind (1965) found that adult Oystercatchers feeding nestlings consumed the smaller size classes of prey for their own maintenance and brought large items to their young: since Hulscher (1974) found that food intake by non-breeding captive Oystercatchers in summer was about 59% of winter intake the presence of young nestlings probably leaves the adults in much the same energy crisis as in late winter, and the results of Lind (loc. cit.) thus parallel those found here. Finally, Hartwick (1976) has also found prey-spectrum differences between adult and chicks of the Black Oyster Catcher *Haematopus bachmani* in British Columbia, differences related to variations in the profitability of each item and the cost of transporting them to the nest.

Location of Feeding Effort

The annual and seasonal changes in the location of feeding grounds within Greyabbey Bay were well correlated with the corresponding variations in cockle densities (Table 4, Figs. 7 and 8), showing that the Oystercatchers concentrate their feeding efforts onto the areas of greatest prey density currently available. Heppleston found that Oystercatchers in Aberdeen also concentrated their feeding onto areas of high prey density, both when feeding on *Macoma* on mudflats (Heppleston, 1971 a) and when taking earthworms in fields (Heppleston, 1971 b). The same phenomenon has been reported in other shore birds (Goss-Custard, 1970; Prater, 1972; Krebs, 1974) and in passerines, both in the field (Bryant, 1973) and in the laboratory (Smith and Dawkins, 1971; Smith and Sweatman, 1974).

Smith and Sweatman (1974) found that Great Tits *Parus major* faced with changes in the pattern of prey distribution from that they had previously experienced required time to learn the new distribution of the prey, and tended to hunt over areas adjacent to the previously "best" area rather than fly to a more remote high density area. These results are paralled by the behaviour of the Oystercatchers in the present study. Thus the birds hunting in February continued to concentrate their efforts onto areas that were either already in use in December or that were immediately adjacent to December areas (Fig. 7a). Again, the expansion of the feeding grounds which took place between February and March largely involved sites adjoining those in use in February (Fig. 7b), even though some ten per cent of our sampling points with above average cockle densities remained unexploited outside these areas (Table 3). Alcock (1973) has experimentally demonstrated a similar conservatism in hunting location in Red-winged Blackbirds *Agelaius phoeniceus*.

Croze (1970) found that Carrion Crows *Corvus corvone* concentrated their further hunting in the immediate vicinity of a find, a response which will tend towards the aggregation of birds in areas of high food density. This effect is enhanced in Oystercatchers by their habit of moving to and from the feeding grounds in small groups (Brown and O'Connor, 1974). This feature has also been noted of Great Blue Herons *Ardea herodias* by Krebs (1974) who suggested it to be part of a complex of adaptations to ephemeral food supplies. A recent simulation study (Thompson et al., 1974) suggests that an important consequence of aggregations of this type is to minimize the risk of doing badly, of failing to find any prey at all. Although the molluscan prey of the Oystercatchers in Greyabbey is far from ephemeral the marked concentration of birds onto relatively restricted areas of the bay clearly points to there being "best" areas for foraging. Heppleston (1971 a) found that the food intake of individual birds over a low tide cycle dropped from 443 g wet weight in October to only 241 g in December, and that feeding was more intensive on short than on long tide cycles. Such figures suggest a high premium on feeding in mid-winter on the densest prey available and this presumably underlies the concentration of Oystercatchers onto such areas reported here.

Finally, we suggested above that Oystercatchers might be hunting by "expectation" (Gibb, 1958), using the anvils with recently predated shells as cues to the intensity of hunting to which that particular part of the bay has recently been subjected. An alternative explanation of the relationship found between prey taken and prey available (Fig. 9) might be a functional response (Holling, 1959), since the data resemble the response functions of many predators limited at high prey densities by prey handling times. This is unlikely to be so here since the feeding rates of Oystercatchers in the bay are fast enough (Brown and O'Connor, 1974) for handling time to be negligible at the cockle densities involved in Figure 9. Krebs et al. (1974) have recently shown experimentally that Black-capped Chickadees *Parus atricapillus* do not hunt by expectation but rather in a manner consistent with an optimal foraging model developed by Charnov and Orians (in press; cited by Krebs et al., 1974). However, their test set-up differed from our field situation in lacking cues to the intensity of hunting effort to which each patch had already been subjected, so that it is not clear whether the chickadee results are strictly applicable to the hunting of Oystercatchers. Certain parallels between the two species are nevertheless apparent. Chickadees hunting in rich environments took fewer prey from patches of given prey density than they did when patches of this density occurred in a poor environment, whilst Oystercatchers feeding in a rich environment in December ignored prey they were subsequently willing to take in March, when the bay had become a "poor" environment (Fig. 7). Charnov and Orians' (loc. cit.) model predicts that when birds are allowed deplete the prey in their environment predation should become intensity dependent with respect to patches of different prey density within the environment as a whole, and thus result in a constant number of prey left in each patch. The seasonal contraction and expansion of feeding areas within Greyabbey Bay is clearly consistent with this prediction.

In summary, therefore, Oystercatchers locate much of their hunting activity with respect to prey density, concentrating onto areas of high density. As their hunting reduces the density of cockles of the normal size taken the birds either move to other cockle beds or relax their size criteria, thereby changing the relative economies of hunting in different parts of the cockle beds. Their hunting is thus broadly in accord with Royama's profitability hypothesis, that predators seek to maximize their hunting efficiency within their limited abilities to locate the prey.

Acknowledgements. The manuscript was read in draft by Jim Gilliam, John Krebs and Ray Seed and we are grateful for their time and comments. We thank Patrick Mackie and the Strangford Wildlife Panel for allowing us use of wader counts for Strangford Lough.

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Received September 8, 1976