THE EFFECT OF AN EXPERIMENTALLY CREATED MUSSEL BED ON BIRD DENSITIES AND FOOD INTAKE OF THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS*

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When an experimental mussel bed was created in 1987 on the mudflats south of Schiermonnikoog, Herring Gulls immediately increased in numbers, consuming starfish and damaged Mussels. The build-up of oystercatcher numbers was more gradual, but persisted for longer. Most Oystercatchers attracted to the mussel bed fed on Mussels. The proportion of Oystercatchers that hammered Mussels was relatively high, which may have been due to the relatively thin shells of the Mussels fished from the subtidal. Intake rates on the experimental mussel bed were on average higher than those achieved by birds feeding on other prey (mainly *Macoma balthica* and *Nereis diversicolor*), but the difference did not reach statistical significance. As the feeding density on the mussel bed increased, intake rates dropped, but it is not known if this relationship has a causal basis. Previous suggestions that the hammering birds substantially depleted the hammerable Mussels seem less likely in the light of our current analysis. The discussion stresses that the experimental creation of mussel beds is a powerful technique to test in the field distribution models derived from ideal free theory and investigates what lessons can be learned from the current pilot experiment that may be of use in the design of future experiments.

Key words: Oystercatcher - *Haematopus ostralegus* - experimental mussel bed - numerical response - feeding technique - intake rate

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INTRODUCTION

Studies of the relationship between waders and their food supply are often motivated by a desire to predict the effects of habitat loss (e.g. Goss-Custard & Durell 1990, Evans *et al.* 1991, Meire 1991). There are two explanations for this. First, much wintering habitat has been lost in the last few decades, or is threatened of being lost in the near future, due to land reclamation, building of marinas, pollution, intensive recreation etc. (Smit *et al.* 1987, Davidson *et al.* 1991). Second, it is generally easier to destroy habitat than to restore it. However, a fundamental understanding of the relationship between bird numbers and their food supply should allow us also to predict what would happen if more, instead of less, habitat became available through the restoration of polders as mud flat areas for instance.

In this paper we will describe the results of a pilot experiment in habitat creation that was closely monitored and we hope that the paper will be of help in the design of future experiments. On 17 June 1987, 20 tons of Common Mussels *Mytilus edulis*, with a length of 10-55 mm, were dumped on a mudflat south of the island Schiermonnikoog in the Dutch Wadden Sea. Over the next two months we studied how local bird numbers were

affected. Though we counted all bird species, we studied in great detail only the feeding behaviour of Oystercatchers *Haematopus ostralegus*, the major predator of large Mussels.

METHODS

Study area

The study was part of a long-term study on the breeding and feeding ecology of the Oyster-catcher on Schiermonnikoog that commenced in 1983. Details on the study area and the population study can be found in Ens *et al.* (1992). For the present purpose, we can suffice with stating that the mudflat study area, which extended 500 m downshore from the edge of the saltmarsh, was divided into squares of 50 × 50 m (Fig. 1). Two observation towers were placed on the edge of the saltmarsh and a very large, 6 m high tower was placed 350 m downshore. From this tower feeding Oystercatchers, many of which were individually colour-marked, were observed with telescopes.

The substrate of the study area is relatively sandy and Lugworm *Arenicola marina* are common. So are, Baltic Tellins *Macoma balthica* and Ragworms *Nereis diversicolor*, the two staple foods for the Oystercatcher during the breeding season. Sand Gapers *Mya arenaria* occur in low densities, while Cockles *Cerastoderma edule* are locally common in some years. Other suitable prey for Oystercatchers are extremely rare.

The experimental mussel bed

On 17 June 1987 approximately 20 tons of Mussels, which had been fished from a tidal channel south of the island of Ameland, were dumped from a fishing vessel in four squares to the west of the mudflat hide over high water. During the following low tide, Mussels that had fallen way outside the four squares were collected and put underneath the hide, where they were safe from bird predation.

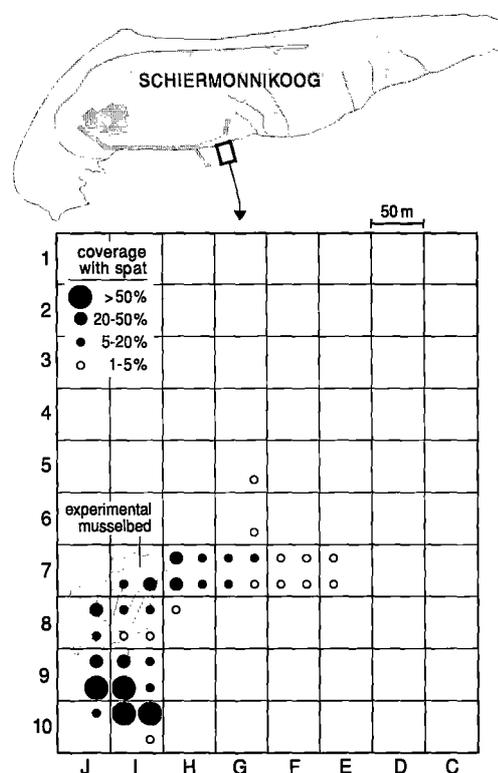In August it became apparent that there had been massive spatfall of Mussels on and around

Fig. 1. (A) Location of the study area on the mudflats of the island of Schiermonnikoog in the Wadden Sea. (B) Map of the mudflat study area, showing the location of the experimental mussel bed and the observation tower. Also indicated per subsquare of 25 × 25 m the coverage with mussel spat as estimated during the survey of 28 August 1987.

the mussel bed. We therefore decided to map this spatfall on 28 August. For each subsquare of 25 × 25 m, we judged by eye if the coverage of spat was less than 1%, between 1 and 5%, between 5 and 20%, between 20 and 50% or over 50%.

On 14 July and 6 August, Mussels of varying sizes were selected at random to determine the relationship between biomass and shell length following standard procedures. After the length of the shell was measured, the flesh was removed and dried for 48 h at a temperature of 60°C and subsequently weighed. Then the flesh was burned for 4 h at a temperature of 550°C and the remain-

ing ash was weighed. Subtracting the ash mass from the dry mass yielded the ash-free dry mass (AFDM). This yielded the following relationships between biomass (mg AFDM) and shell length (mm):

14 July:
$\ln(mg) = 2.308\ln(mm) - 2.233$, $r = 0.94$, $n = 47$

6 August:
$\ln(mg) = 2.769\ln(mm) - 4.025$, $r = 0.94$, $n = 29$

combined: $\ln(mg) = 2.51 \ln(mm) - 3.04$

On 14 July, random clumps of Mussels were picked from the mussel bed and the length of all Mussels was taken to determine the length frequency distribution. We also measured the thickness of the shells (see below). On the same date, the same procedure was applied to the Mussels that had been stored under the hide. This allowed a comparison of the size distribution of Mussels that had been safe from Oystercatcher predation, with Mussels from the bed where Oystercatchers (and other birds) had been free to consume Mussels from 17 June onwards.

Shell collections

Oystercatchers that hammer Mussels on the ventral side carry these to a hard sandy patch that serves as an 'anvil' for hammering. Because of this, it is possible to collect the shells on these anvils and such shell collections are not biased towards shells of large size, in contrast to shell collections of Mussels opened by stabbers or dorsal hammerers, which often open their prey *in situ* (Ens 1982, Goss-Custard *et al.* 1987, Cayford 1988). On 14 July, 6 August and 11 September, we collected all hammered shells from the anvils. Thus, shells from the sample of 14 July were hammered between 17 June and 14 July, while shells collected on 6 August must have been hammered between 14 July and 6 August etc. All shells were classified as very recently opened if there was still some flesh attached to the shell, as recently opened when the ligament was stiff and

as not recently opened when the ligament was highly flexible. The length and the thickness of the shell were measured in a random subsample of the collected shells.

We used a micrometer on a stand to measure shell thickness. With this device we searched the edge between the black and white on the ventral inner margin for the lowest thickness value. Not surprisingly, this leads to a lower thickness value compared to studies where a single 'random' instead of minimum value is reported. However, the minimum value (*MINTHICK*, mm) is closely correlated with the mean value of four measurements on the same valve (*MEANTHICK*, mm):

$MEANTHICK = 0.043 + 1.000 \times MINTHICK$, $r = 0.97$, $n = 565$

Thus, simply adding 0.04 mm to the shell thickness values reported here will yield values that can be compared to other studies. For Mussels hammered ventrally, we chose the undamaged valve to measure shell thickness. We chose the left or right valve at random for live Mussels. There is a reasonable correlation between the thickness of the right and the left valve and neither valve is systematically thinner than the other (Sutherland & Ens 1987). Since individual hammerers often specialize on either the left or the right valve, they seem to lack a procedure to identify the weakest valve (Sutherland & Ens 1987).

Bird counts

To study the effect on local bird numbers, we selected eleven adjacent squares of 50 × 50 m out of the 80 squares comprising the study area (Fig. 1). Due to the unexpected massive spatfall of Mussels, these eleven squares were distinguished in three, instead of two, types of square (in brackets the identification codes of the square):
– squares with Mussels added on 17 June (I7, I8, J7 and J8); spatfall occurred in all these squares
– control squares with no Mussels added on 17 June, but with heavy spatfall in August (I9, I10, J9 and J10)
– control squares with no Mussels added on 17

June and without heavy spatfall in August (H8, H9 and H10).

We counted the numbers of all bird species feeding in the squares on 12, 13, 16, 17, 18, 19, 22, 25 June, 6, 11, 22 July and 4, 8 August. In the graphs, 17 June is indicated as day 0 of the experiment. Counts started when the first square became exposed on the receding tide and were continued each half hour until the last square was covered again by the advancing tide. Since the differences in tidal height between the squares were small, there was only a short period during which some squares were exposed while other squares were still covered. For all squares, the average number of birds feeding in the square during a tide were then calculated. The next step in the analysis was to lump similar squares, i.e. squares with Mussels added and control squares with or without spatfall.

Observations on feeding behaviour of Oystercatchers

On average once a week we spent a whole low tide period scanning the mudflat study area for marked Oystercatchers from the downshore observation tower. When a marked individual was spotted we noted its colour code, the square in which it was feeding, its choice of prey species and its method of attacking the prey. These observations allowed us to calculate the prey choice and feeding specializations of individuals in a given site in the course of the study.

To measure intake rate we recorded the behaviour of marked Oystercatchers feeding on the mussel bed. With the use of an electronic event recorder we noted to the nearest second the amount of time spent searching, handling, in aggression and in other activities. Furthermore, we registered the method of handling the prey, the prey species and the size of the prey. In the case of Mussels, the length of the shell was estimated in quarters of the length of the code-ring; in effect, this provides a ruler of 2.5 cm long conveniently attached to the leg of the bird. The previously established relationships between shell size and biomass were then used to transform the sizes
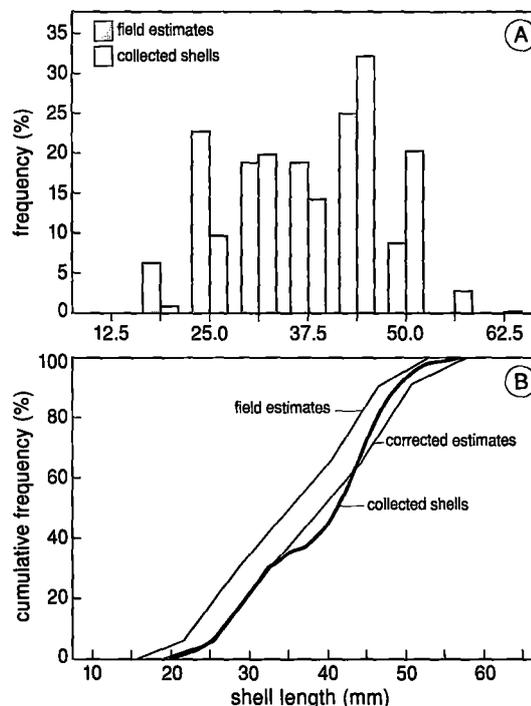

Fig. 2. (A) Size distribution of hammered Mussels as estimated during the focal animal observations (all records lumped, $n = 80$) compared to the size distribution of hammered Mussels from shell collections (all periods lumped, $n = 1990$). According to the Kolmogorov-Smirnov two-sample test, the two distributions differ significantly ($p = 0.002$), using the same size categories. (B) Cumulative distribution of the distributions depicted in (A), as well as the cumulative distribution of the corrected size estimates. According to the Kolmogorov-Smirnov two-sample test the distribution of the corrected size estimate does not differ significantly from the shell collections ($p = 0.66$), using the same categories.

of captured Mussels into biomass ingested. Since the difference between the relationships for July and August was small we took the combined value.

The collections of hammered shells allowed us to check our size estimates. The two distributions were roughly similar, but gave an indication that the field observations underestimated the real length (Fig. 2A). We therefore added 4 mm to the
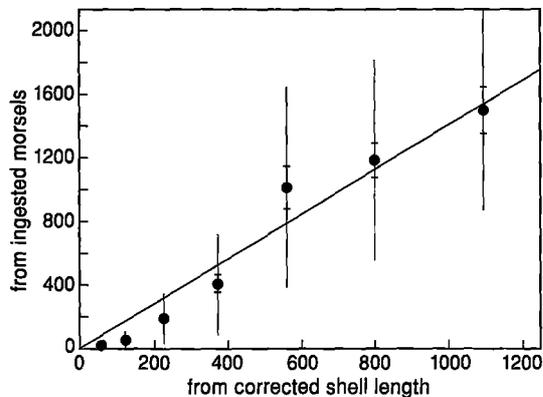
Fig. 3. Ingested biomass (mg AFDM) as estimated from food morsels plotted against the biomass as estimated from the corrected shell length. Plotted are mean values for each length class; uncapped bars denote 1 *SD*, while capped bars denote 1 *SE*. The regression line was forced through the origin and relates to the individual data points. When not forced through the origin the regression equation was $Y = -125.5 + 1.60X$, $r = 0.79$, $n = 236$, $p < 0.0001$.

field estimates and the cumulative distribution of the corrected estimates did no longer differ significantly from that of the shell collections (Fig. 2B). We assumed that a similar correction was necessary for shell length estimates of Mussels taken by stabbers.

Sometimes we could not estimate the length of the shell, or the bird cleaned out a shell opened by another bird. In these cases, we estimated the biomass ingested from the sizes of the pieces of flesh swallowed by the bird (see Table 1 in Kersten & Brenninkmeijer (1995) for conversion values). We could calibrate these estimates in a sample Mussels from which all the flesh was taken and where we had also estimated the size of the shell. The two estimates were correlated, but estimates on the basis of food morsels were too high (Fig. 3). For the calibration we forced the regression through the origin and found that biomass estimated from food morsels was 1.40 times the biomass calculated for the corrected estimate of the shell length.

Individuals sometimes switched between feed-

ing on Mussels and feeding on other prey. In the analysis we therefore separated search time preceding the capture of a Mussel from the search time preceding the capture of another prey (a similar procedure was adopted by Bunskoeke *et al.* 1996 and de Vlas *et al.* 1996). When the remaining feeding time (search time plus handling time of Mussels) was less than two minutes, the record was discarded for the calculations on intake rate of mussel feeders.

In the same period the feeding behaviour of Oystercatchers feeding on other prey was studied outside the study sites affected by the experiment (Bunskoeke *et al.* 1996, de Vlas *et al.* 1996, Ens *et al.* 1996a and Hulscher *et al.* 1996). Methods were similar, except for the details specific for each prey species of estimating prey size and converting the size estimates into biomass ingested. These studies allowed us to compare the intake rate of Oystercatchers attracted to the mussel bed to the intake rate of Oystercatchers continuing to feed elsewhere.

RESULTS

Effect on spatfall of Mussels

When the study on Schiermonnikoog was started in the year 1983, a mussel bed bordered the tidal channel to the south of our study area. The Mussels were attached to a shellbank. In the years that followed, the density of Mussels steadily declined and in 1987, hardly any Mussels remained. In the summer of 1987 an exceptionally massive spatfall of Mussels occurred throughout the entire Wadden Sea (Beukema *et al.* 1993) and our study site was no exception. During the survey of 28 August there were hardly any 25 × 25 m subsquares which did not contain some spat, ranging in size from a few mm up to a cm, attached to a shell, a tube of *Lanice*, or a piece of seaweed. In fact, it was only in the very sandy squares in the south-east that not a single sign of spat was found. Nonetheless, the pattern of coverage suggested that the experimentally created mussel bed had greatly influenced the location of

Table 1. Densities (birds ha⁻¹) for all species whose density exceeded at least once one bird ha⁻¹, separated for sites with Mussels, control sites with spat and control sites without spat.

bird species	site	\-5	-4	-1	0	1	2	5	8	19	24	35	48	53
Shelduck	Mussel					0.6	0.4				1.5			
	spat	0.2												
	control			0.2										
Mallard	Mussel	2.0		0.4	0.4	0.8	0.1		0.6				0.1	
	spat	0.3												0.4
	control													
Eider Duck	Mussel	0.5		0.2	1.1	3.2	0.1	1.4	0.9	1.9		1.18	0.1	
	spat	9.9		5.6	2.9	3.4	2.4	1.7	3.6	5.8	4.0	0.6	1.5	1.5
	control	2.3					0.3	0.3	0.4	1.7	0.1			
Oystercatcher	Mussel	0.9	0.2	0.7	1.1	4.2	7.4	4.7	7.4	7.8	10.2	13.0	17.0	5.8
	spat	1.9	1.2	1.5	1.1	1.6	1.4	1.8	1.7	4.6	6.4	6.9	9.1	12.3
	control	1.2	0.2	1.1	0.9	1.6	0.3	0.4	0.9	0.4	0.7	0.7	1.8	1.0
Golden Plover	Mussel												0.3	3.7
	spat											1.0	5.1	7.5
	control												1.5	6.9
Dunlin	Mussel												0.9	1.6
	spat												1.1	6.6
	control												0.2	10.4
Redshank	Mussel	0.2								2.2	2.8	5.8	2	3.9
	spat	0.8	0.5	0.2		0.5	0.5	0.6	0.1	3.8	3.6	4.8	6.6	11.6
	control	0.2		0.2						0.7	2.8	3.3	0.3	3.2
Greenshank	Mussel										0.4	1.4	0.3	
	spat									0.2	0.4	1.8	0.4	
	control										0.1	0.6	0.3	
Curlew	Mussel	0.1				0.3		0.2		1.9	0.3	1.3	0.2
	spat	0.3		0.1		3.6	0.2	1.9	1.3	0.4	2.5	0.7	1.5	1.5
	control	0.6	0.2			0.4			0.8	0.1	3.2	0.6	0.5	0.4
Black-headed Gull	Mussel	0.3	0.8	0.4		0.2	5.2	1.0	0.9	0.3	4.4	5.1	3.3	2.6
	spat	0.3	0.2	0.2	0.1	0.2	0.5	1.0	0.2	0.4	5.4	1.6	6.8	9.6
	control	0.3	0.2	0.2	1.3	0.8	0.4	0.5	0.4	0.3	3.2	1.5	4.8	6.4
Herring Gull ad.	Mussel	0.3	0.5	0.2		14.5	9.7	2.3	1.3	1.1	0.9	1.1	4.6	0.5
	spat	0.5	0.2	0.2	0.4	0.8	0.5	0.3	0.3	0.2	0.6	0.5	2.9	1.7
	control	0.4		0.1		1.4		0.4		0.1	0.4	0.2	1.0	0.1
Herring Gull juv.	Mussel												1.1	0.4
	spat												10.6	5.9
	control												0.3	0.2
Common Gull	Mussel			0.2		0.3			0.1			0.3	2.4	0.4
	spat	0.5		0.2		0.3					1.0	0.6	2.6	3.1
	control	0.7	0.2	0.1	0.2	0.2					0.1	0.4	0.3	0.7
number of counts		12	6	17	9	12	10	10	10	16	10	11	8	11

the spatfall (Fig. 1). Coverage exceeded 50% in several subsquares between the experimental bed and the main gully, i.e. on the shell bank to which the old mussel bed had been attached. Yet, the old mussel bed had covered a much larger area and it was only close to the experimental mussel bed that massive spatfall had occurred.

Effect on bird numbers

Before the experiment, densities of birds were low in all sites (Fig. 4A). But even by the day after Mussels were laid, bird densities were very much higher in the mussel sites, where they remained high throughout the rest of the study period. After a month bird numbers began to increase in the control sites with spat (Fig. 4A). It was only after two months, i.e. near the very end of the study period, that bird numbers increased substantially in the control sites, due to the influx of migrants, such as Golden Plovers *Pluvialis apricaria*, Dunlin *Calidris alpina* and Black-headed Gull *Larus ridibundus* (Fig. 4A, Table 1).

Of the species listed in Table 1, only Eider Duck *Somateria mollissima*, Oystercatcher and Herring Gull *Larus argentatus* regularly prey on Mussels. Eider Ducks only visited the squares during the short periods that these were covered with a few cm water and there was no evidence that their numbers were affected by the experiment (Table 1). In contrast, Herring Gulls were present on the experimental mussel bed in large numbers the very next day (Fig. 4B). They consumed damaged Mussels and starfish, crabs and some fish that had been transported inadvertently with the Mussels. When this food supply had apparently been depleted, the numbers of gulls dropped again, but numbers remained higher than before: some gulls continued to feed on small Mussels that they swallowed whole. Though Oystercatcher numbers were also higher in the experimental sites immediately upon the addition of Mussels, their numbers continued to increase throughout the study period (Fig. 4C). At the very end of the study period in early August, the numbers on the mussel bed dropped. Visits to the hide made for other purposes in August and September
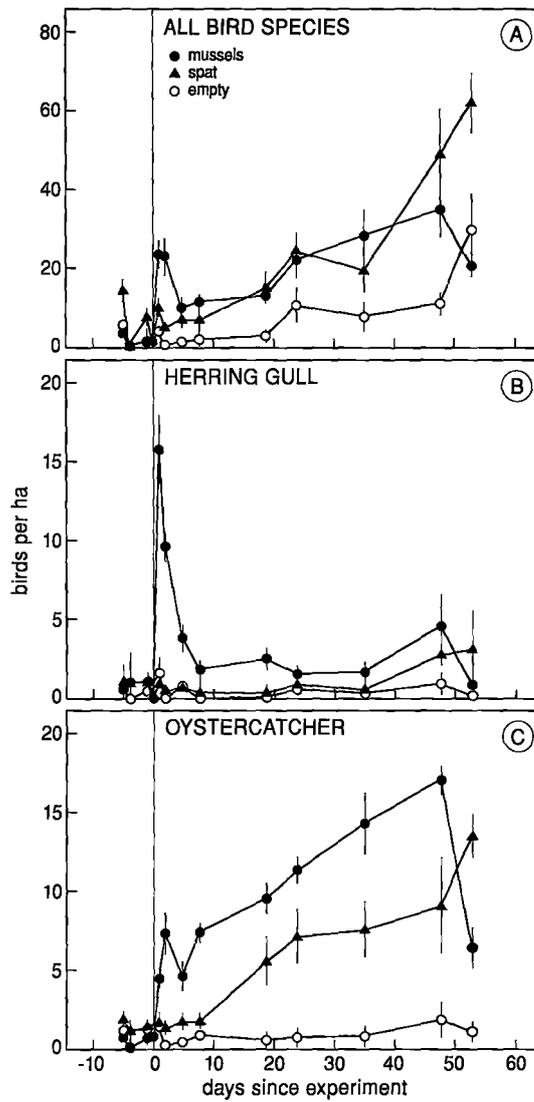

Fig. 4. Bird densities (n ha^{-1}), separated for sites with Mussels added, control sites with heavy spatfall and control sites without spatfall on different days before and after the creation of the experimental mussel bed. Dots indicate the mean value for a given observation day, while bars represent 1 SE. (A) All bird species lumped, (B) Herring Gulls and (C) Oystercatchers.

confirmed that this last count with low numbers was not an accident but indicative of a sustained

drop in numbers. Oystercatcher numbers in the control sites with spat were not immediately affected by the experiment (Fig. 4C). It was only in July that numbers started to increase. The numbers in the control sites without spat remained low throughout the study period.

Bird species, like Curlew *Numenius arquata* and Redshank *Tringa totanus* that do not feed on Mussels, but feed on the animals living on the mussel bed, like Shorecrab *Carcinus maenas*, were not noticeably affected by the experiment (Table 1). Curlew numbers were low in all study sites and remained so throughout the study period. Redshanks only increased in numbers beyond two weeks after the experiment, but there was no substantial difference between mussel and control sites without spat. In control sites with spat, numbers were clearly higher, but this was the case throughout the study period.

Diet, feeding specialization and intake rate of Oystercatchers

Before the experiment *Macoma* and *Nereis* were the main prey of Oystercatchers in all three types of site (Ens *et al.* 1996a). When the mussel bed was created, Mussels were immediately an important component of the diet of Oystercatchers feeding on the bed (Fig. 5). Expressed in numbers of prey, Mussels never contributed more than 50% to the diet. But because Mussels are so much heavier than the other prey species, it was the dominant prey in terms of biomass. Mussels were almost never eaten in the control sites without spat, but became an increasingly important component of the diet of Oystercatchers feeding in the control sites with spatfall.

Of course, it came as no surprise that the experimental mussel bed attracted many Oystercatchers which came there to feed on Mussels. What did come as a surprise was that a substantial number of the attracted Oystercatchers were observed to open Mussels via hammering, instead of stabbing, the dominant feeding specialization in previous studies of mussel-feeding Oystercatchers on Schiermonnikoog (Zwarts & Drent 1981). In all cases hammerers attacked the Mussels from
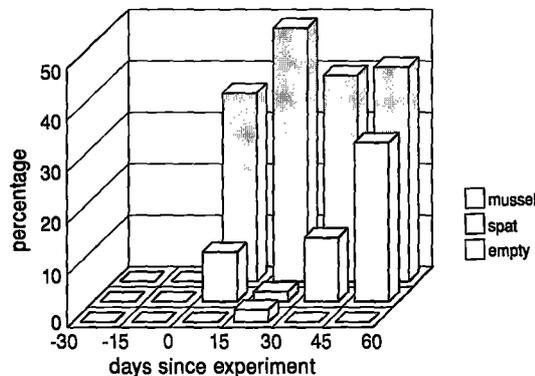

Fig. 5. Proportion of Mussels in the diet, as determined from scan observations, in relation to the number of days since the beginning of the experiment for Oystercatchers feeding in sites with Mussels (665 scans), control sites with spat (300 scans) and control sites without spat (142 scans).
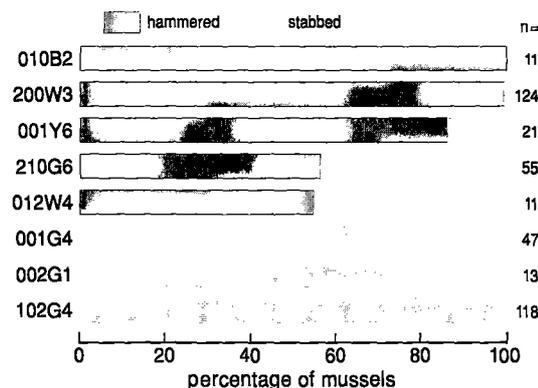

Fig. 6. Proportion of Mussels that were either hammered or stabbed for all marked individuals that took at least ten Mussels. Numbers of prey taken by each individual are indicated on the right.

the ventral side. The majority of marked individuals feeding on Mussels could be classified decisively as either hammerer or stabber, though two individuals used both feeding specializations equally frequently (Fig. 6). Judged from Fig. 6, hammerers and stabbers seemed equally common and the few scan observations where feeding specialization was noted ($n = 79$) yielded the same
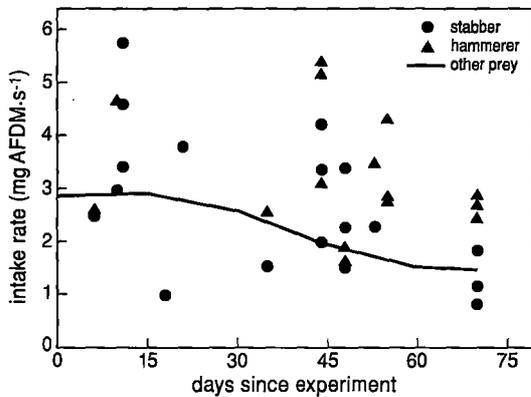
Fig. 7. Intake rate (mg AFDM s^{-1} feeding) of hammering and stabbing Oystercatchers feeding on the experimental mussel bed in relation to the number of days since the bed was created. The line indicates the intake rate of birds feeding nearby on other prey, mainly *Macoma balthica* and *Nereis diversicolor*, in the same period (Bunskoeke *et al.* 1996). The line is based on 80 records of individuals followed throughout the entire low water period and these were treated as independent data points together with the much shorter feeding records of birds preying on Mussels in a two-way ANOVA testing the effect of food type and month on intake rate. Neither variable significantly affected intake rate (food type: $p = 0.33$, month: $p = 0.16$).

result: 46.8% hammering and 53.2% stabbing. There was some suggestion in these scan observations that the proportion hammerers declined over three consecutive fifteen-day periods (63%, 42%, 32% respectively), but this was not significant ($\chi^2 = 5.75$, $df = 2$, $p = 0.056$).

There was also no significant difference between the intake rates of hammerers and stabbers when averaged over the whole study period (Student-$t = -1.29$, $df = 31$, $p = 0.21$). The intake rate of birds feeding on the mussel bed tended to exceed the average intake rate of birds that continued to feed on other prey, but the difference was not significant (see Fig. 7 and its legend). Intake rates of mussel-feeders were high a few days after the mussel bed was created and steadily declined thereafter (Fig. 7). This decline did not result because the condition of captured Mussels declined
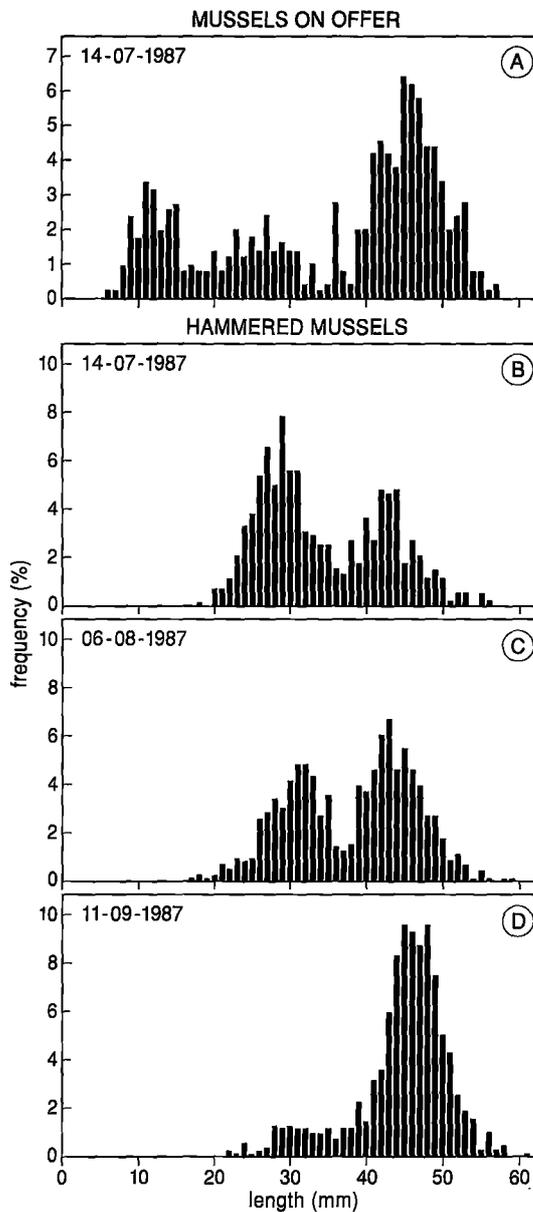

Fig. 8. (A) Size distribution of Mussels on the experimental mussel bed as sampled on 14 July, compared to the size distribution of hammered Mussels collected on (B) 14 July, (C) 6 August and (D) 11 September.
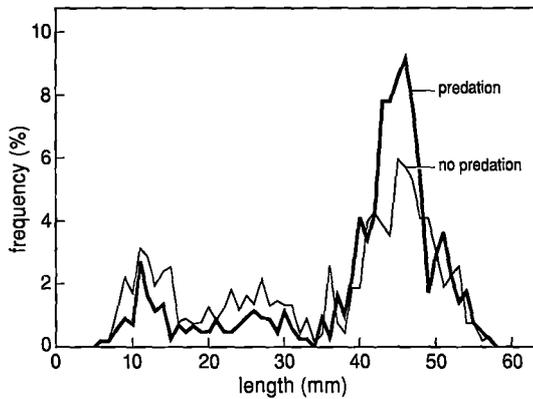
Fig. 9. Size distribution of Mussels from the experimental mussel bed that had been exposed to predation ($n = 437$), compared to the size distribution of Mussels that had been protected from predation by storing them under the observation tower ($n = 539$). Both samples were taken on 14 July 1987. The distributions differed significantly according the Kolmogorov-Smirnov two-sample test: $p < 0.001$.

Fig. 10. Distribution of shell thickness of hammered Mussels collected on 14 July and 11 September (A) for Mussels from the medium size class and (B) for Mussels of the large size class. Using the slope of the relationship between shell thickness and shell length, the thickness values of individual shells were standardized to conform to Mussels with a length of 35 and 45 mm for Mussels from the medium and large size class respectively.

over the course of the season, since we assumed that the condition was constant during the study period (see methods). When the pattern in intake rate was analysed separately for hammerers and stabbers, it was negative in both, but significant only for the latter (hammerers: $r = -0.23$, $n = 15$, $p = 0.42$; stabbers: $r = -0.55$, $n = 18$, $p = 0.02$). However, there were no feeding observations on hammerers in the first month after the start of the experiment.

Possible evidence for depletion of hammerable Mussels

The size distribution of the Mussels on the experimental mussel bed was measured halfway through the observation period when the spat had not yet grown to an appreciable size. Three size classes could be distinguished among the older Mussels: small Mussels of around 10 mm long, medium-sized Mussels of between 20 and 30 mm long and large Mussels with a length exceeding 40 mm (Fig. 8A). Probably due to their low profitability, hammering Oystercatchers consistently ignored the smallest Mussels and fed exclusively on
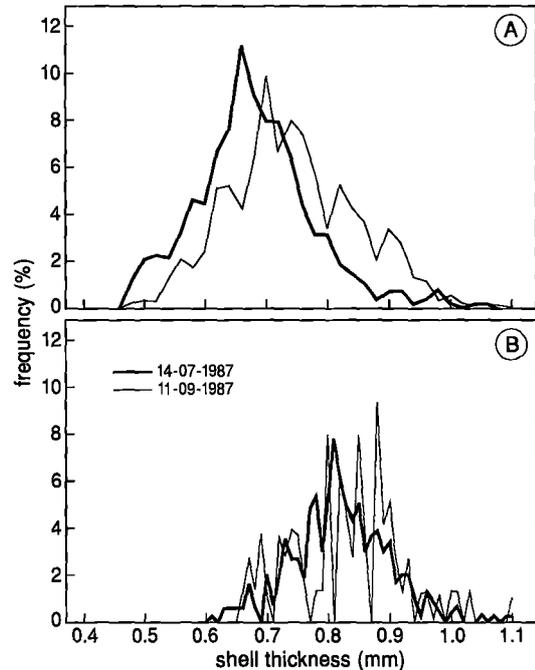
Mussels of the medium and large size class (Fig. 8B). Initially, medium-sized Mussels predominated in the shell collections, but at the end the birds fed almost exclusively on Mussels in the large size class (Fig. 8D). This may have happened as the medium-sized Mussels were gradually depleted. This suggestion seems substantiated when the size distribution of Mussels on offer on the mussel bed is compared to the size distribution of Mussels protected from predation by Oystercatchers: medium-sized Mussels were more abundant when the Mussels had been protected from predation (Fig. 9). Disappearance of the small Mussels may have been due to the Her-

ring Gulls, which were observed to swallow these Mussels whole (pers. obs.). Further evidence that hammering Oystercatchers may have depleted the hammerable Mussels comes from the change in shell thickness of hammered Mussels (Fig. 10). Mussels of a given size that were hammered before 14 July had thinner shells than Mussels that were hammered between 6 August and 11 September.

DISCUSSION

Effect on bird numbers

Differences between species According to our counts, the experiment most clearly affected the numbers of Oystercatchers and Herring Gulls, which both feed on Mussels. In contrast, the numbers of two other species that also feed on Mussels, the Eider Duck and the Knot *Calidris canutus*, did not change as a result of the experiment. In the case of the Eider Duck, this may have been due to a counting error, since the Eider Ducks only used the mussel bed when it was covered with a thin layer of water. In retrospect we think that more intensive counts during these ephemeral stages of the tide would have revealed an increased use of the mussel squares and, later on, the squares with spat. In the case of the Knot there may have been too few Mussels of a harvestable size (i.e. measuring between 5 and 20 mm, Zwarts & Blomert 1992) on the experimental mussel bed. When the density of these small Mussels is low, they tend to be hidden in the clump. That the spatfall did not attract Knots later in the season is not surprising either, as huge areas of the Wadden Sea were covered with spatfall of Mussels in that year (Beukema *et al.* 1993). Finally, the experiment did not affect the number of bird species that do not feed on Mussels themselves, but on benthic animals that live on the mussel bed. Possibly, many of the mussel bed-dwelling organisms, such as the Shorecrab, did not survive the transport, or were consumed by the Herring Gulls during the first days of the experiment, when the new mussel bed and its inhabitants were still in a state of turmoil.

Why was the build up of Oystercatcher numbers so slow? Whereas Herring Gulls responded immediately to the newly created mussel bed, the increase in Oystercatcher numbers was more gradual. This may have been due the timing of the experiment in the middle of the Oystercatcher breeding season. The area where the mussel bed was put out was divided up between several breeding pairs defending feeding territories (Ens *et al.* 1992), the remaining space being taken by pairs of nonbreeding birds attempting to gain a nesting territory (Ens *et al.* 1995). The increase in numbers was due both to territorial birds changing their site-use in favour of the squares with Mussels and to an influx of new birds (Ens unpubl.). Thus, if the territorial birds ended their territorial behaviour only after some time as part of their normal annual cycle and/or in response to the heavy intruder pressure, this may have slowed down the influx of new birds. Alternatively, the initially high numbers of Herring Gulls, which regularly stole Mussels from the Oystercatchers, may have retarded the build up of Oystercatcher numbers. Finally, instead of new birds being prevented from entering, there may have been an initial lack of new birds trying to enter. Especially adult birds are often extremely faithful to their feeding grounds (see reviews in Goss-Custard 1996), which may prevent them from learning that new profitable feeding areas have come into existence elsewhere.

Why did Oystercatcher numbers not increase further? Since Oystercatchers achieved much higher intake rates on the experimental mussel bed than in the immediate surroundings, it comes as no surprise that Oystercatchers numbers increased. As numbers increased, intake rates dropped, but we have no evidence, other than the correlation itself, that the higher bird densities themseles caused the lower intake rates through interference. It may well have been the case though, since many Oystercatchers employed the hammering technique and such birds tend to be especially susceptible to interference (Goss-Custard & Durell 1988). Alternatively, intake rates may have dropped because

birds became less stressed for time as the breed-
ing season came to an end (Ens et al. 1996b). Re-
grettably, we did not collect sufficient data on
marked individuals, their intake rates and the bird
densities at which they fed in the course of the ex-
periment, to test the suggestion that the build-up
of numbers stopped when intake rates were equal
to that which birds could gain elsewhere.

Did Oystercatchers seriously deplete the ham-
merable Mussels?

From a preliminary analysis of the data we
concluded that the hammering Oystercatchers
significantly depleted the harvestable thin-shelled
Mussels from the experimental mussel bed during
the study period (Alting & Ens 1992). We will
now describe why we no longer think that this
interpretation of the data is correct.

Why were hammering Oystercatchers so common?
Before we do this, we first examine why hammer-
ing Oystercatchers were so common on the ex-
perimental bed, whereas very few hammering
Oystercatchers were observed in previous studies
on nearby natural mussel beds (Zwarts & Drent
1981). There are at least two explanations. First,
the substrate where the mussel bed was laid out
was rather sandy and ventral hammerers need a
hard substrate to serve as an anvil (Norton-Grif-
fiths 1967, pers. obs.). Natural mussel beds in the
Dutch Wadden Sea are often soft, in part because
of the continued accumulation of silt by the mus-
sel bed itself (e.g. Flemming & Delafontaine
1994). Second, the Mussels that were fished from
the tidal channel may have been especially thin.
Within the size range of interest, the Mussels
studied by Meire & Ervynck (1986), Cayford &
Goss-Custard (1990) and Ens & Alting (1996)
were definitely thicker than the Mussels on the
experimental bed. Indeed, with the exception of
Rao (1953), the majority of authors report that
Mussels that live lower in the tidal zone have
thinner and less heavy shells (Baird & Drinnan
1957, Dare 1976, Seed 1980, Galbraith 1987 quoted
by Bustnes & Erikstad 1990, Peterson & Black
1987, Goss-Custard et al. 1993, Cadée in press).3

Shell collections There is no doubt that our shell
collections mimic the results of Sutherland & Ens
(1987) on ventral hammerers kept in captivity that
preferred to feed on small and thin-shelled Mus-
sels, but gradually switched to larger and thicker-
shelled Mussels when the preferred prey was de-
pleted. However, the switch from smaller to lar-
ger Mussels that we observed could also have
been due to the, as yet unexplained but well-es-
tablished, seasonal switch from a preference for
small Mussels in spring and early summer to a
diet dominated by larger Mussels (and more in
line with predictions from optimal foraging) at
other times of the year (Cayford & Goss-Custard
1990, Ens et al. 1996b). Can we also account for
the observed increase in shell thickness of the
Mussels that were taken if it is not due to deple-
tion of thin shells? Yes. We noted before that
Mussels living high in the tidal zone grow thicker
shells, so the change in shell thickness might be
due to a growth response of the Mussels adapting
to their new conditions.

Intake rates In the course of depletion, intake
rates are expected to drop. Though the intake rate
of stabbers declined in the course of the experi-
ment, we did not have definitive evidence that this
was also true for the hammerers. Furthermore, as
suggested above, the decline in intake rate could
also have been due to an increase in interference
as a result of the increase in the density of conspe-
cifics: many studies have shown a negative rela-
tionship between intake rate and bird density for
Oystercatchers feeding on Mussels (Zwarts &
Drent 1981, Ens & Goss-Custard 1984, Goss-Cus-
tard & Durell 1987, 1988).

Estimating the extent of depletion Perhaps most
damaging to the idea of depletion is the following
calculation that seeks to estimate the extent of de-
pletion. The fishermen dumped 20 tons of Mus-
sels. According to L. Zwarts (pers. comm.) to-
tal weight of live Mussels (mg) is related to
shell length (mm) in the following way: $mg = \exp(-2.485 + 3.09\ln(mm))$. In combination with
the size distribution of Mussels we find that 2.7

million Mussels exceeding a length of 6 mm were dumped. Of these, 0.5 million belonged to the medium size class (i.e. within the size range of 20-35 mm) and 1.6 million to the large size class (i.e. larger than 35 mm). During the first month of the experiment on average eight Oystercatchers fed on the mussel bed for approximately five hours in each tide. Intake rate during the first month amounted to 5 Mussels per 10 min. If intake rates and feeding densities were similar during the night as during the day, a maximum of 72 000 Mussels would have been consumed. If we take into account that not all birds fed on Mussels (75% seems a maximum estimate) and that a maximum of 65% of Mussels was hammered, we find that only 4% of the medium-sized and 1% of the large-sized Mussels were consumed during the first month; this cannot explain the difference between the two distributions in Fig. 10.

Thus, alternative explanations can be found for each of the phenomena that so neatly fitted together as due to depletion of the hammerable Mussels in the interpretation of Alting & Ens (1992).

Designing future experiments

A primary aim of experiments like these can be to test the distribution models proposed by Ens & Goss-Custard (1984), Sutherland & Parker (1985) and Parker & Sutherland (1986), which can be seen as further refinements of the theory of animal distributions proposed by Fretwell & Lucas (1970), generally known as 'ideal free theory'. This study shows that the experiment is feasible, but also suggests some improvements in the design.

Timing Adding a large amount of food will always disrupt the local social organization of the Oystercatchers, but doing it closer to the end of the breeding season would have been better. Also, had this been done, it would not have induced spatfall of Mussels. Early September would have been a better date.

Scale The scale of the experiment was clearly sufficient to get a measurable response, but, in a way, only barely so. Mean low-tide densities on the ex-

perimental bed only once exceeded 15 birds ha^{-1}, implying that there were rarely more than 15 birds present on the experimental bed. Even more important than a somewhat larger bed, however, would be the creation of more than one bed so that the beds could be made to vary in quality and or size.

Manpower However, implementing this last suggestion would exacerbate the problem of sufficient manpower. Lack of an adequate database, ultimately due to lack of manpower, prevented us from performing several obvious analyses. Thus, anybody contemplating facing the many logistical and bureaucratic hurdles that must be dealt with before an experimental mussel bed can be created, should make sure that sufficient manpower is available to fully monitor the situation in case of success.

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SAMENVATTING

Op 17 juni 1987 werden er, bij wijze van experiment,
20 ton Mosselen gestort op het wad onder Schiermon-
nikoog (Fig. 1). Deze Mosselen waren eerder opgevist
uit een geul onder het wad van Ameland. De aantallen
Zilvermeeuwen namen direct spectaculair toe, maar de
meeuwen verdwenen weer snel toen de meegevoerde
zeesterren en de door het transport beschadigde Mosse-
len opraakten (Fig. 4B). De aantalstoename van Schol-
eksters was meer geleidelijk en duurde voort tot meer
dan anderhalve maand na de aanleg van de bank (Fig.
4C). Andere vogelsoorten leken nauwelijks te zijn
beïnvloed door het experiment (Tabel 1). Later in het
seizoen namen de Scholeksters eveneens toe in vakken
buiten de experimentele mosselbank waar een grote
broedval van Mosselen had plaatsgevonden (Fig. 1B).
Zoals te verwachten was, bestond het dieet van de
Scholeksters die op de mosselbank foerageerden voor
een belangrijk deel uit Mosselen (Fig. 5). Een opval-
lend groot deel van de mosseletende Scholeksters
opende de schelpen door ze kapot te hameren in plaats
van open te steken (Fig. 6). Dit had waarschijnlijk te
maken met de relatief dunne schelpen van de opgeviste
Mosselen. De mosseletende vogels hadden gemiddeld
een grotere opnamesnelheid dan de dieren die in de
omgeving op andere prooidieren, met name Nonnetjes
en Zeeduizendpoten bleven fourageren, maar dit ver-
schil was statistisch niet significant (Fig. 7). Terwijl de
dichtheid fouragerende vogels op de mosselbank toe-
nam, nam de opnamesnelheid van voedsel af (Fig. 7),
maar het is niet zeker dat het hier om een causale rela-
tie ging. Eerdere suggesties dat de veranderende selec-
tie van prooigrootte (Fig. 8) en schelpdikte (Fig. 10)
van de hamerende Scholeksters het gevolg waren van
uitputting van de 'hamerbare' Mosselen lijken minder
waarschijnlijk op grond van de huidige analyse. Het
experimenteel uitleggen van een mosselbank is een
krachtige techniek om theoretische modellen over de
verspreiding van dieren in het veld te toetsen. In de dis-
cussie wordt daarom aandacht besteed aan de vraag hoe
de door het experiment verkregen inzichten en ervarin-
gen van nut kunnen zijn bij de uitvoering en het ont-
werp van nieuwe experimenten in de toekomst.