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THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS* AS A PREDATOR OF THE BIVALVE *MACOMA BALTHICA* IN THE DUTCH WADDEN SEA

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1. INTRODUCTION

1.1. BACKGROUND

In estuarine areas, birds play an important role in the transfer of energy from one trophic level to another. Many bird species and a host of prey species are involved (Hulscher 1975). In order to truly understand how the vast estuarine resources determine the populations of birds sustained, it is necessary to have precise knowlegde of which fraction of the prey populations is available as food. In the Dutch Wadden Sea area the subject was approached by various workers focusing on individual bird species. Spaans (1971) paid attention to the Herring Gull *Larus argentatus*, Swennen (1976) to the Eider *Somateria mollissima*. Other studies in the Wadden area are reviewed in Smit & Wolff (1980). I myself started a long term study on the Oystercatcher *Haematopus ostralegus*.

Some prey species of Oystercatchers (the Mussel *Mytilus edulis*, *Littorina littorea*) live on the mudsurface, protected against predation by thick shells. Others are buried just beneath the surface, such as the Cockle *Cerastoderma edule*, the Shore Crab *Carcinus maenas* and *Crangon crangon*. A third group of prey species (*Macoma balthica*, *Mya arenaria*, *Scrobicularia plana*, *Nereis diversicolor*, *Arenicola marina*) avoids predation by burying deeply (down to 25 cm) in

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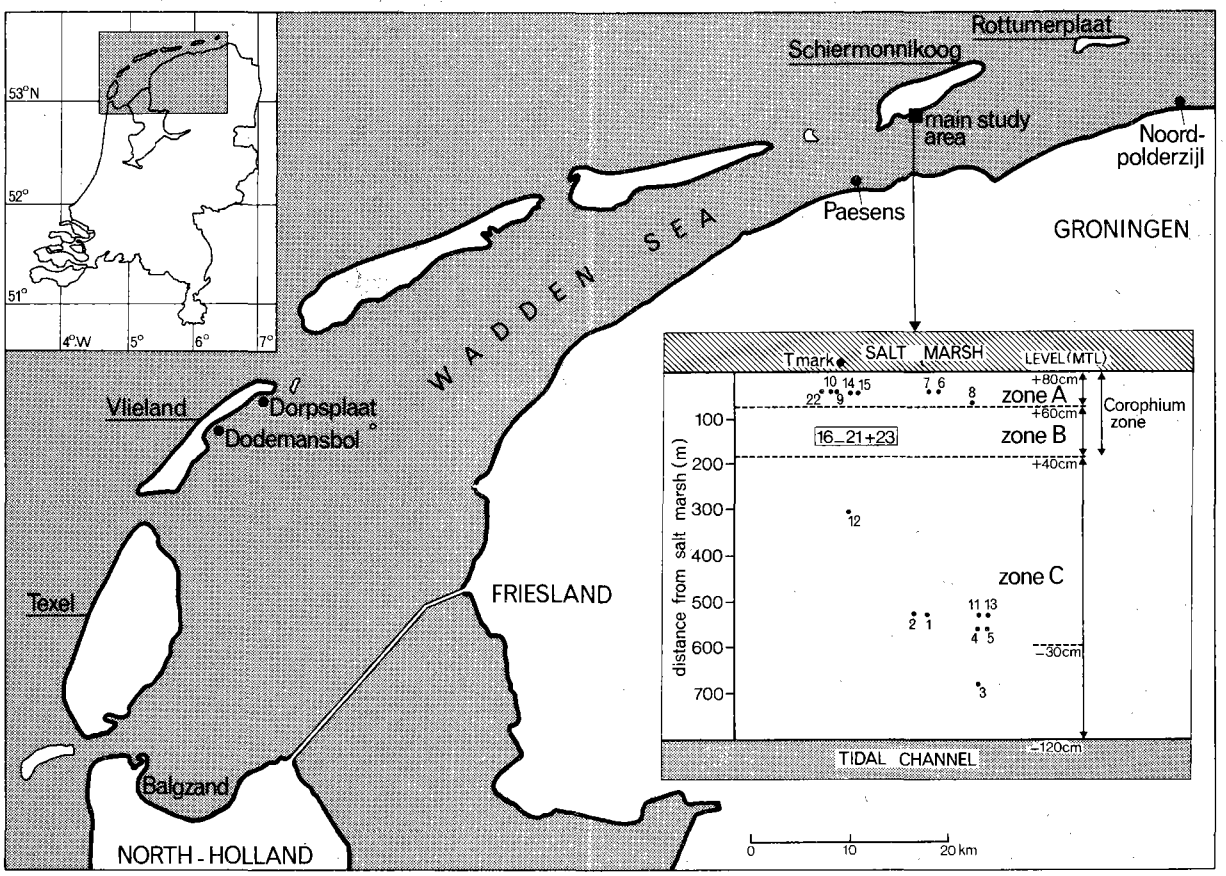


Fig. 1. Situation of study areas in the Dutch Wadden Sea. Inset: main study area at Schiermonnikoog. Observation sites are numbered from 1—23.

the mud (Hulscher 1964 a, b and c). Which part of these prey populations is available as food, is largely contingent on the detection techniques used by the predator. Surface prey are localized visually in daytime. Prey just below the surface are also localized visually in daylight as Oystercatchers directs pecks at surface marks made by Cockles (Hulscher 1976; for Shore Crabs see also Hulscher 1964 a). At night, Cockles are localized by touch. The different localization mechanisms have a large impact on the profitability of prey species in terms of energy gained per unit of time or energy expended (Hulscher 1976).

To understand the role of the deeply buried species as bulk food in the Wadden Sea, I will in this paper analyse the predation by Oystercatchers on the bivalve *Macoma balthica*. Experiments were done to establish whether detection of *Macoma* involves visual cues or only touch (chapter 2). Detection by touch leads to selective predation with respect to burrow depth and further selection for prey size (chapter 3). Profitability of a food source is further affected by the handling of the prey, and observations were made on the technique used by Oystercatchers to open *Macoma* shells (chapter 4). Selection against trematode infected *Macoma* was observed and analysed (chapter 5). The net outcome of searching, selection and handling of *Macoma* leads to estimates of the daily intake of Oystercatchers foraging on this prey. This will be compared with estimates of 24-hour food requirements (chapter 6). On the basis of such calculations, the possibilities presented by *Macoma* as bulk food for Oystercatchers in the Wadden Sea throughout the year can be considered (chapter 7) and a comparative evaluation made

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of the profitabilities of feeding on surface prey (Mussels), shallow-buried prey (Cockles) and deep prey (*Macoma*) (chapter 8). Finally, some prospects for future profitability studies will be outlined connecting the principles of optimal foraging theory with the regulation of animal numbers by their food resources.

1.2. STUDY AREA

The Dutch Wadden Sea (Fig. 1) is a vast estuarine area of 2800 km^2 along the north coast of The Netherlands. To the north and west it is bordered by a chain of islands and to the south by the mainland of the provinces of Groningen, Friesland and the barrier dike, and the tip of the province of Noord-Holland. Forty percent of its area in the western, to 70 percent in the eastern part is exposed during the ebb phase of the tidal cycle leaving extensive feeding areas for birds. Tidal currents enter the shallow sea from the north between the islands, decreasing in strength on their way to the south. Consequently, coarse sandy sediments with little silt are generally deposited along the islands, fine silty deposits along the mainland. The nature of the sediments largely determines the distribution of bivalves and in consequence the distribution of their predators. The areas chosen for the *Macoma* study were:

— Dorpsplaat, an isolated mudflat of 1200 × 130 m^2 at low tide off the south coast of Vlieland, near the village Oost-Vlieland.

— Dodemansbol, half way along the south coast of the island of Vlieland.

— at Paesens, along the north coast of the province of Friesland.

— at Schiermonnikoog, near landmark T[1], the main area of study.

All these areas were characterized by shallow sloping shores with broad intertidal zones. The substrate consisted of fine sand and silt with massive occurrence of *Arenicola marina*, except at the highest levels. Most observations were done at Schiermonnikoog. An outline of this study area and the location of observation sites is given in Fig. 1, inset. The area between the high and low water line is divided in three zones, A, B and C. The substrate consists mainly of fine sand with a decreasing percentage of silt (mud) from A to C. The higher zones A and B are characterized by the amphipod *Corophium volutator*, the lower zone C by *Arenicola*. The infauna of this area has been described by Hulscher (1968).

1.3. FEEDING BEHAVIOUR OF THE OYSTERCATCHER

An Oystercatcher foraging on mudflats displays various movements with its bill, as can be observed upon close and detailed observation. The nature of the movement is correlated with the type of prey the bird is hunting for. When feeding on the *Macoma* fields Oystercatchers generally make tree types of movements with their bill: single pecks, borings and multiple pecks.

A single peck consists of one quick movement of the bill about one to twenty mm into the substrate. The bill is held in an oblique position and is practically closed.

A boring is characterized by a quick movement up and down on the spot while the bill is held in a vertical position and is slightly opened. The bill usually disappears into the substrate up to its base.

A multiple peck consists of a series of probes in the vertical plane with the bill opened a few mm. The number of probes in multiple pecking can vary from three to about seven per sec. While probing the bird walks slowly, moving the bill in the vertical position forward or sideways through the mud. The depth varies from a few mm to the total length of the bill. Every few sec the bird retracts the bill entirely from the mud and a new multiple peck is made a few paces further on.

When observing captive birds from close by, it could be seen that single pecks were invariably directed at surface cues. These cues could be almost anything: small holes, little bumps in the sand, colour differences in the substrate, empty shells, shell fragments etc. Most single pecks were unsuccessful, only in a few instances small prey directly visible on the mud surface were caught like *Corophium*, small Shrimps *Crangon crangon* and small Ragworms *Nereis diversicolor*. Borings were specifically used for catching buried *Nereis*. The presence of *Nereis* is probably perceived at the preceding single peck. The multiple pecking technique is used to locate moderately to deeply buried bivalves as *Macoma*, *Mya arenaria* and *Scrobicularia plana*.

During this study on *Macoma* specific care was taken to chose feeding areas where only *Macoma* and no other buried bivalves occurred. Therefore, in this study, multiple pecking is considered to be directed at finding *Macoma*.

The moment a *Macoma* is located in the substrate can be recognized relatively easily because the bird abruptly stops the movements of multiple pecking and starts with characteristic movements of shell-opening. It may open the shell in situ, deep in the mud, or bring it up to the surface and open it there. After having opened the shell the flesh is removed from the valves and swallowed. Empty shells are left in

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the substrate or on the surface, depending upon where they are opened.

1.4. BIOLOGY OF *MACOMA*

Macoma balthica (Tellinidae) is a bivalve with a somewhat flattened globular shell of up to 24 mm in length. It is common in mudflats and occurs in a large variety of substrates ranging from nearly pure mud to coarse sand. Highest densities occur in sediments with high to moderate percentages of silt (Beukema 1976). *Macoma* lives buried in the substrate to a depth of one to ten cm. *Macoma* shows seasonal variations in burying depth. Observations of Zwarts (pers. comm.) along the mainland coast of the Wadden Sea have shown that *Macoma* reside at their greatest depth between November and March, they rise in April remaining at their minimum depth between May and the first half of September and subsequently drop to deeper levels again in the second half of September and in October, till they reach their winter depth. Seasonal variations in burying depth have also been found in the Wash in England (Reading & McGrorty 1978). Besides seasonal variations there are local differences as well in burying depth depending upon the level of the intertidal zone and the nature of the substrate. At lower levels in the intertidal zone *Macoma* is buried deeper than at higher levels. Furthermore there are differences in burying depth amongst small and large *Macoma* (Hulscher 1973).

Within a *Macoma* population there are usually small variations in mean density, individuals are randomly dispersed (own obs, *cf.* Holme (1950) for *Tellina tenuis*).

Macoma behaves as a suspension feeder as well as a deposit feeder. Suspension feeding is only exhibited during high tide when the mudflat is inundated. Deposit feeding, however, is displayed during high tide and sometimes during low tide too, if the surface is covered with water or, at least, is thoroughly wet. Whilst deposit feeding, the inhalant siphon makes whirling and scraping movements over the mudsurface and sucks in the uppermost layers of the sediment (Fig. 2A). In muddy areas with a coherent film of diatoms on the surface this film is fractured and more or less star-like tracks remain visible during low tide (Fig. 2B). Stars may have a variable number of rays. Sometimes only one or two small holes, the entrances of the siphon tubes, are visible. In the present study area tracks were only seen in zone A and B, the *Corophium*-zone. When the substrate is sandy without such a coherent layer, no such tracks are to be seen. This was the case at Schiermonnikoog in zone C and in Paesens. The absence of marks in these areas possibly is due to the fact that *Macoma* at times behaves purely as a filterfeeder (De Wilde pers. comm.).

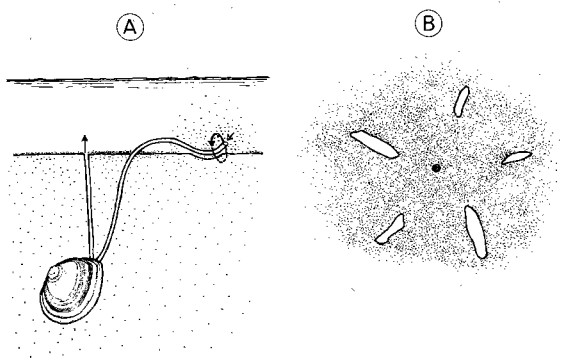


Fig. 2. Position of a buried *Macoma* while deposit feeding (A), and starlike feeding track left on the surface by the scraping inhalant siphon (B) (from Hulscher 1973).

Besides *Macoma* tracks, marks made by other infauna species lavishly decorate the mudsurface. To make the picture more complicated, many marks resemble each other, for instance those of *Macoma*, *Nereis*, *Corophium* and sometimes also those of *Hydrobia ulvae* are hard to distinguish from one another. In order to investigate whether Oystercatchers make use of surface tracks in finding *Macoma* I observed captive Oystercatchers feeding under experimental conditions on the mudflat in daytime — with surface tracks either not erased or erased before starting the observations — and in darkness. There was no difference in feeding behaviour between the captive and free living birds.

1.5. STUDY TECHNIQUES

The feeding behaviour of free living Oystercatchers was studied at Vlieland in August 1963, at Schiermonnikoog in zone C (Fig. 1) in June/July 1966 and at Paesens in May 1978, May 1979 and May 1981. Observations were done with a 30× telescope at distances varying from 100 to 250 m.

Experiments with captive birds were made at Schiermonnikoog, some in zone C in the summer of 1966 on a mixed *Macoma-Cerastoderma* field, the majority in the *Corophium*-zone in the summer of 1967. The *Corophium*-zone was

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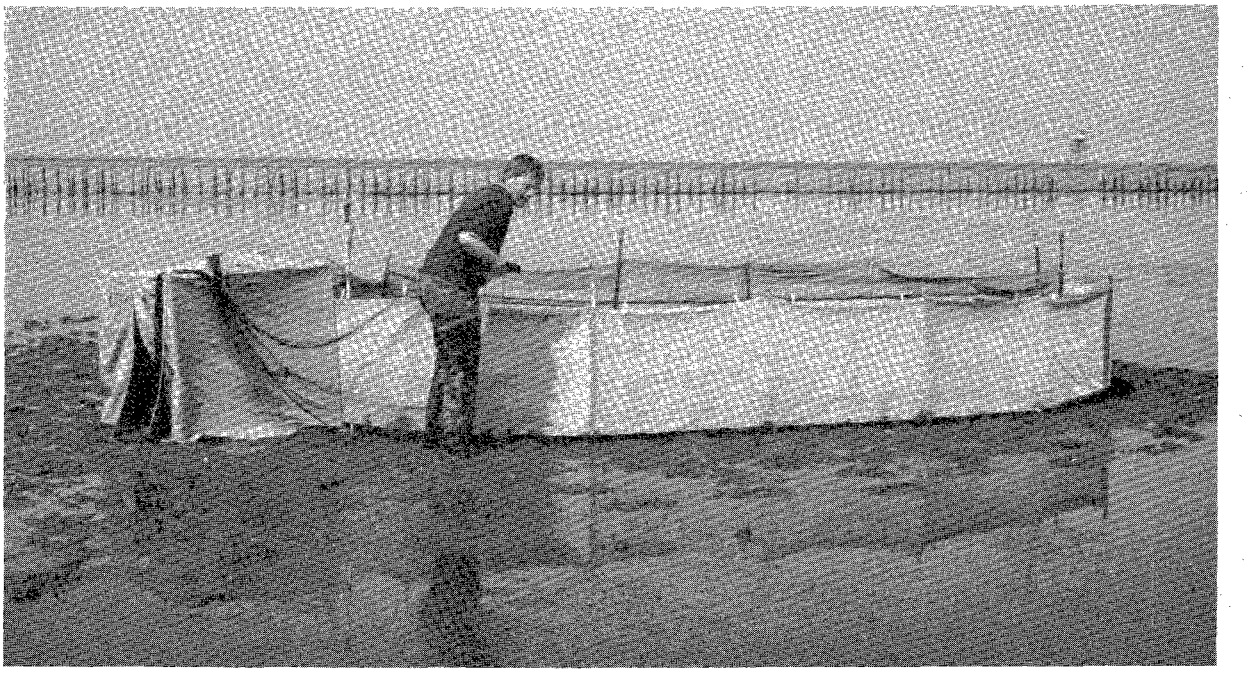


Fig. 3. View of a cage with 20 m^2 floor area, as used in the experiments with the captive Oystercatchers. The cage is made of cloth, height 75 cm, roofed with a net. A hide (one m^3) is seen left of the cage. In the upper right corner an observation tower (height 7 m) is visible from where free living Oystercatchers at Paesens were studied.

the only place where no other bivalve prey for Oystercatchers besides *Macoma* occurred in any appreciable numbers.

The experiments with the captive birds were carried out in fenced-in areas, being cages of 20 m^2 made of cloth (Fig. 3) that could be erected and broken down in a couple of minutes. In the cage the feeding area could be adjusted to any size required by covering the remaining part of the cage floor with cloth. Most observations were made with one adult individual (WR) caught on its nest on Schiermonnikoog in 1965. The behaviour of the bird was observed from a hide at a distance of 1—4 m, no binoculars were required in daytime, at night infrared binoculars were used. The bird fed either on the local natural *Macoma* population or on an experimental population. The latter was obtained by removing the uppermost ten cm-layer of the sediment containing all the bottom fauna, filling the gap with sieved sand and allowing this to settle during a few tidal periods. Then a fixed number of *Macoma* of certain size classes were "planted" in the barren mud and allowed to settle during at least three tidal cycles in which *Macoma* reached its final depth before observations started.

Conditions in the experimental population set-up were simplified since the presence of other species as a complicating factor was ruled out, although a few Ragworms did resettle in the new areas. All species in the bottom fauna of the local natural *Macoma* fields were available for the Oystercatcher when feeding there. Tracks of *Macoma* and of all other infauna species were erased if necessary for the experiment just before the observations started by smoothing the surface area with a board. The bird had always been deprived of food seven hours before the first experiment in any low tide period started. This period corresponds with the average submersion period of the feeding grounds of the free living Oystercatchers.

2. LOCALIZATION OF *MACOMA*

2.1. INTRODUCTION

Oystercatchers seem to be able to catch *Macoma* with ease. How do the birds actually locate these buried bivalves? The technique Oystercatchers use in hunting *Macoma* is always the multiple pecking described above (see section 1.3). The problem of detection of buried shells thus reduces to: "By which sensory stimulus does multiple pecking result in the location of *Macoma*?" Although in principle taste, smell and sound as well as sight and touch might be involved, there is reason to believe that the former three senses are unlikely candidates (see section 2.7.). In this chapter, I will analyse the role of sight and touch. The first obvious question is: can an Oystercatcher distinguish *Macoma* tracks from the large variety of tracks on the mudsurface, and thus locate this prey visually by day? Secondly, the role of touch is analysed by comparing the yield of *Macoma*-hunting birds with a model assuming random probing in *Macoma* populations of different size and density where no surface tracks were apparent.

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2.2. LOCALIZATION OF *MACOMA* BY SURFACE CLUES

In order to test the possibility that Oystercatchers use tracks to locate *Macoma* visually, a variety of experiments was done with the tame bird WR. It was put to feed on plots with known surface area with either an experimental or natural *Macoma* population, in daytime with tracks on the mudsurface either not erased or erased, or at night, no tracks being visible. The recognition of *Macoma* tracks under simplified circumstances was tested first. The captive bird WR was allowed to feed on experimental fields of one m² with 50 *Macoma* each, either with 50 small (shell length 15 mm), 50 large (shell length 19—20 mm) or 25 small and 25 large *Macoma* mixed. The experiments were done in daytime with tracks present or erased and at night. The experiments lasted 30 min. The bird displayed multiple pecking in all the situations. Fig. 4 summarizes the results of these experiments. The success rate of multiple pecking is given as the mean number of *Macoma* found per sec multiple pecking and is calculated over the total time devoted to multiple pecking within the experimental period of 30 min.

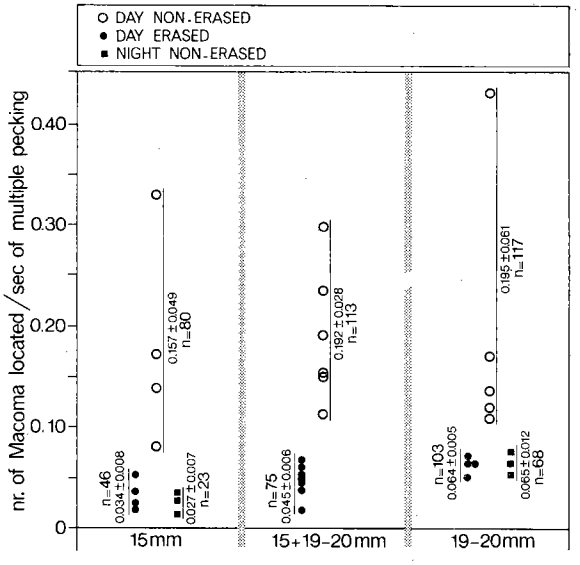


Fig. 4. Location rate of *Macoma* through multiple pecking (*Macoma*/sec) by the captive Oystercatcher WR when feeding on fields of one m² with experimental populations of 50 small (15 mm), 25 small and 25 large, or 50 large (19—20 mm) *Macoma*, when *Macoma* tracks are available (day non-erased), or not available (day erased or at night). Each point represents one experiment of 30 min observation. The mean and the standard error of the mean per series of corresponding experiments are indicated; n = number of *Macoma* located per series.

There was no difference in success rate of multiple pecking in daytime on the non-erased fields with either small, large, or small and large *Macoma* mixed. But the success rate of multiple pecking in daytime was lower when the tracks were erased for each size class of *Macoma*. On erased fields with small *Macoma* the success rate of multiple pecking in daytime was lower than with large ones, while the success rate on the fields with small and large *Macoma* mixed was intermediate. Erased or dark conditions made no difference in success rate of multiple pecking for the fields either with small or large *Macoma*. At night, however, large *Macoma* were found more quickly than small ones.

The results on these experimental *Macoma* populations clearly indicate that WR localized *Macoma* at a higher rate when tracks were available than when tracks were absent or not well visible. The highly simplified situation, in that *Macoma* tracks could not be confused with those of other prey species, since these were absent, may give an inflated notion of the role of *Macoma* tracks in the natural situation. Therefore corollary experiments on fields with natural *Macoma* populations were performed. The captive bird WR was offered a fresh plot of one m², either with or without tracks, to feed upon every new observation period. The density of the whole *Macoma* population in the plot was measured by sieving all the remaining specimens after the experiments. The experiment was carried out ten times both on a non-erased field and on an erased field. The time spent on multiple pecking per min was measured with a stopwatch during the total length of the observations. The results are depicted in Fig. 5, left panel. Data have been split up into successive periods of five min, since the bird possibly blotted out the tracks on the non-erased fields by walking over them, the area of one m² whereupon the bird could walk being very small. Conditions for location by sight could only have been favourable at the beginning of the experiments.

The success of multiple pecking (A) decreased steadily with time in both situations:

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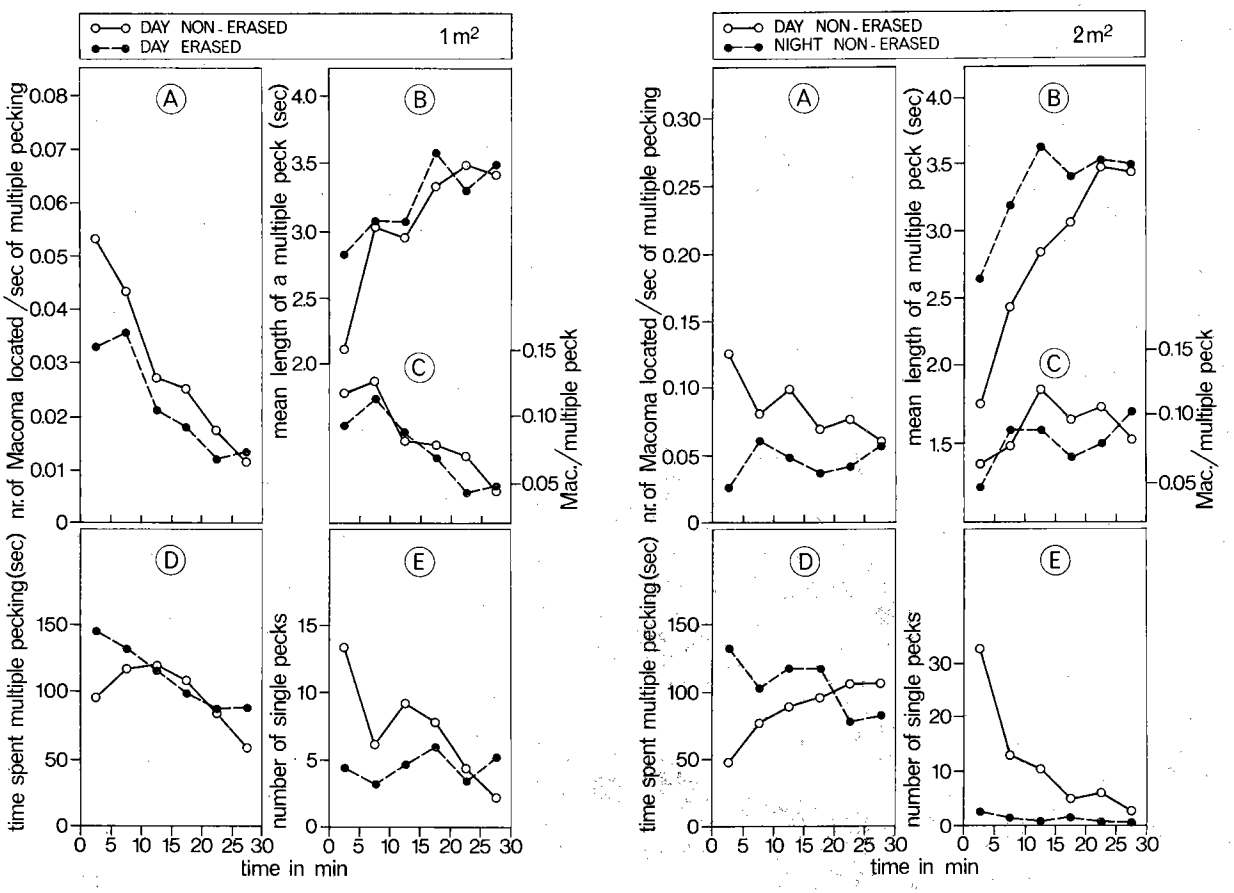


Fig. 5. Results of the captive Oystercatcher WR over successive periods of five min, when feeding on fields with the natural *Macoma* population. Left panel: on fields of one m² in daytime, *Macoma* tracks non-erased or erased. Right panel: on fields of two m², in daytime, *Macoma* tracks non-erased or at night, *Macoma* tracks non-erased.

tracks present or not. During the first five min, however, success was higher on the non-erased fields (Student-t-test, $P < 0.05$). The mean length of a multiple peck (B) increased steadily with time on both non-erased and erased fields, but during the first five min the mean length of a multiple peck was shorter on the non-erased fields ($P < 0.01$). The number of *Macoma* located per multiple peck (C) on the other hand decreased with time, but was higher though not significantly so, on the non-erased fields than on the erased ones in the first five min. The time spent in multiple pecking (D) was only different in the first five min between the two conditions, being shorter on the non-erased fields ($P < 0.01$). Finally the number of single pecks (E) decreased with time on the non-erased fields, but remained constant on the erased fields. During the first five min, however, the frequency of pecking was higher on the non-erased fields ($P < 0.05$).

The higher success rate of multiple pecking during the first five min on the non-erased fields suggests that some *Macoma* were located by sight. This conclusion is also supported by the shorter mean duration of a multiple peck on the non-erased fields. The number of multiple pecks (not indicated in Fig. 5) during the first five min was the same for both types of fields ($P < 0.1$). The higher single peck frequency also indicates that the bird was more intent on searching visually for cues on the non-erased fields during the first five min.

The time spent on non-foraging activities such

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as preening, sleeping etc. was not measured during the experiments. During the first five to ten min, however, the bird practically only indulged in feeding, later on non-foraging activities steadily increased. The time not spent in multiple pecking and handling the prey must have been used for walking between the separate multiple pecks and for single pecking. This means that during the first five min of observations on the average 138 sec were spent in walking and pecking on the non-erased fields and 93 sec on the erased fields. A peck is made in the twinkling of an eye. Goss-Custard & Rothery (1976) estimated that an Oystercatcher makes an unsuccessful peck in 0.4 sec. Assuming the mean value for making a peck to be half a sec, then 13 sec were needed for making pecks (including 12 borings) on the non-erased fields, leaving 125 sec for walking. Four sec were needed for pecks and borings on the erased fields, leaving 89 sec for walking. It follows that 36 sec more were spent in walking and probably looking for surface cues on the non-erased fields. This too indicates the bird had been looking for *Macoma* tracks on the natural mud-surface in the beginning of the observation period.

The experiments imply that the bird only located some *Macoma* by using tracks on the non-erased fields at the beginning of the observation periods. After that it was relying on another locating system, because tracks were no longer available. We can conclude that a visual component plays a role when the Oystercatcher searched for *Macoma*. We shall try to check on this component in another way by comparing feeding results by day and at night on natural fields. The bird was allowed to feed 30 min on fields of two m^2, four times in daytime on non-erased fields and four times in darkness.

Again the results were analysed on the basis of consecutive five minute periods (Fig. 5, right panel). When one compares the left and right hand graphs in Fig. 5, it is evident that the results of night feeding resemble those of daytime feeding without tracks. The initially higher success rate of multiple pecking (A), the shorter duration of a multiple peck (B), the lower multiple pecking time (D) and the higher single peck frequency (E) in daytime with tracks present, all point to the fact that at least some *Macoma* were located by using surface clues at the start of the experiments. After a little while a decreasing number of *Macoma* was located in the non-erased fields, probably because *Macoma* tracks decreased with time, being blotted out by the bird walking over them.

2.3. LOCALIZATION OF *MACOMA* IN THE ABSENCE OF SURFACE CLUES

The next step is to find out how the free living birds fare when they hunt on *Macoma*, and compare their outcome with that of the captive Oystercatcher WR. Observations to this purpose were done on Schiermonnikoog in zone C (Fig. 1, inset) in the summer of 1966. The substrate contained mixed *Cerastoderma-Macoma* populations. Some birds fed mainly on *Macoma*, others on *Cerastoderma*. The *Macoma* feeding birds were picked out for observation. In May 1979 *Macoma* eating Oystercatchers were observed near Paesens (Fig. 1). As mentioned in

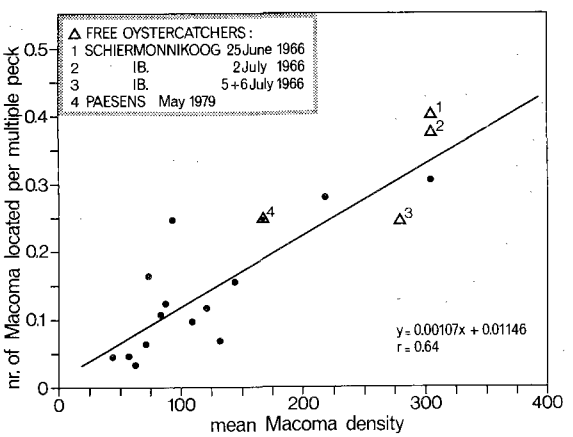


Fig. 6. Success of multiple pecking of free living Oystercatchers compared with that of the captive bird WR when it was feeding in daytime on non-erased fields of two or more m^2 with natural *Macoma* populations. Success is expressed as the number of *Macoma* located per multiple peck. The regression line is calculated through the points (filled symbols) of WR only. Each point represents one experiment of 30 min observation.

section 1.4., no *Macoma* tracks were visible in the areas on Schiermonnikoog and at Paesens where free Oystercatchers foraged. Adult and actively foraging birds were observed only. Individual feeding birds were studied during ten min periods, the number of multiple pecks and the number of *Macoma* located were recorded.

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Table 1. Success rate of multiple pecking by free living Oystercatchers. Adult, actively foraging birds were observed for ten min; (n) refers to the number of birds observed

	Schiermonnikoog (1966)			Paesens (1979)
	site 3 25 June mean ± S.D. (n)	site 3 2 July mean ± S.D. (n)	site 4 5 + 6 July mean ± S.D. (n)	19—27 May mean ± S.D. (n)
Number of multiple pecks/min of observation	4.91 ± 1.07 (9)	5.84 ± 1.33 (17)	7.05 ± 1.60 (11)	8.17 ± 1.93 (86)
Time (sec) of multiple pecking/min of observation	—	10.61 ± 2.90 (13)	—	18.97 ± 4.47 (86)
Number of *Macoma* located/min of observation	1.94 ± 0.72 (9)	2.20 ± 0.45 (17)	1.76 ± 0.87 (11)	2.00 ± 0.70 (86)
Success rate during multiple pecking: number of *Macoma* located/multiple peck	0.394 ± 0.107 (9)	0.385 ± 0.075 (17)	0.244 ± 0.084 (11)	0.245 ± 0.086 (86)
Number of *Macoma* located/sec of multiple pecking	—	0.210 ± 0.055 (13)	—	0.105 ± 0.037 (86)
Mean density (*Mac*/m^2)	353	353	277	168

During the observations at Schiermonnikoog on 2 July and at Paesens the time spent in multiple pecking was determined too. The results averaged per day for all birds observed are given in Table 1.

In Fig. 6 success of multiple pecking of the free living Oystercatchers is compared with that of the captive bird WR when it was feeding in daytime on non-erased fields of two or more m^2 with natural *Macoma* populations. Success is expressed as the number of *Macoma* located per multiple peck. The regression line is calculated through the points (filled symbols) of WR only. Each point represents one experiment of 30 min of observation. This time-parameter was chosen, because WR must have been locating *Macoma* without visual clues, just as the free living birds, having erased tracks himself by walking over them. The results of the free living birds fit in very well with the prediction by the curve of WR, therefore we can accept the experimental method applied, as being a reliable one.

Summarizing, the experiments with the captive bird have shown that a visual component plays a role when tracks are present, since success rate in locating *Macoma* is enhanced in the presence of surface tracks. But when no tracks are available the bird is adept in locating *Macoma* too. The same holds for the free living birds, that fed on *Macoma* in zone C at Schiermonnikoog and at Paesens whilst no *Macoma* marks were present.

All these data point to the fact that since the Oystercatcher is successful in locating *Macoma* when visual stimuli are absent, it must have another locating system at its disposal besides sight. The multiple pecking technique is employed under all circumstances when *Macoma* is eaten, so it is not unconditionally linked with sight. The most likely alternative for the stimulus leading to location of *Macoma* is touch. An attempt to thresh out this possibility will be done now, by constructing a touch model.

2.4. A MODEL FOR LOCALIZATION BY TOUCH

Starting point is that the bill is pierced into the substrate at random and is not directed by any stimulus onto a particular spot, when a multiple peck begins. Each little patch of surface area has the same chance to be touched. Further, the assumption is made that the bill must actually touch a *Macoma* shell before it is found. Given probes do not overlap, the chance to touch a *Macoma* is defined by the proportion of mudsurface that is occupied by *Macoma* shells. Since a *Macoma* shell is invariably

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oriented with its medial plane vertical to the mudsurface and the Oystercatcher's bill always moves vertically downwards, it approaches a *Macoma* straight from above. Therefore it is necessary to know the proportion of the area occupied by *Macoma* shells in the horizontal plane. This can be calculated for any *Macoma* population when the density of the *Macoma* per mm-class and the touchable shell area in the horizontal plane (touch-area) per *Macoma* per mm-class are known. Not all *Macoma* present need be in reach of the bill, this depends both on the burrowing depth of the animals, and probing depth of the Oystercatcher. In the study area there were not only differences locally in the mean burying depth of total *Macoma* populations, but sometimes also between small and large *Macoma* on one spot. In zone A and B (Fig. 1) the small *Macoma* were found to be buried deeper, on the mean, than larger ones (Hulscher 1973). In this situation small *Macoma* will generally be more often unattainable for the bill at a certain probing depth than large ones. In order to put the model into practice we must determine for each case how many *Macoma* per mm-class are in reach of the bill. How this is calculated will be shown later on when the individual cases are discussed.

How the touch area of a *Macoma* can be measured will be explained first. The touch area is defined as the surface area of the largest cross section, in a horizontal plane, that can be made through a buried *Macoma*. The shape of this horizontal section is more or less elliptical. The method of photographing two *Macoma* per mm-class from above, while they were partially inserted in the typical burying position in a tray of mud, was used, just as was done in an analogous case with *Cerastoderma* (Hulscher 1976). The touch areas were measured via the photographs with a planimeter.

In addition the cross section of the billtip is not to be overlooked in the model, as will be shown with a general example next. Suppose the bill is round and the radius of the transverse section at the tip is *a* mm, further, that the horizontal section through a *Macoma* is a circle with a radius of *b* mm (Fig. 7A), then the tip of the bill will touch a *Macoma* when it is placed entirely or partially on the *Macoma*, in the extreme case just touching. Every probe of the bill within a circle with radius $a + b$ mm will be successful. This circle is the effective touch area, and can be found by moving the billtip around the *Macoma*, just touching it continuously. The cross section of an Oystercatcher's bill, near the top however, is not circular, but rectangular. The mean area of the cross section could be determined because of the lucky circumstance that sometimes the imprint of the tip of the bill remains after the bird has pecked in the mud. Usually separate copies of the upper and lower mandible are distinct. The mean measurements of the rectangle of over 100 imprints were 11.0 × 1.4 mm including the minute space between the mandibles.

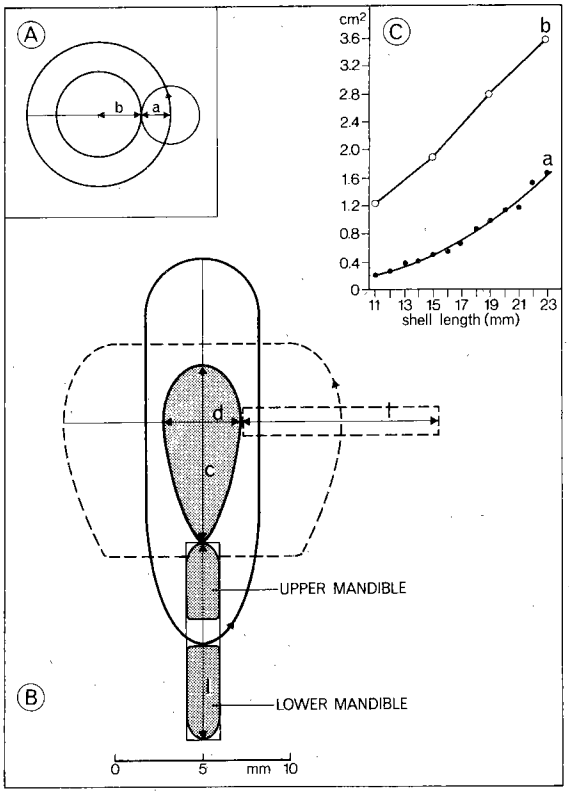


Fig. 7. Scheme to construct the mean effective touch area of a *Macoma*. For explanation see text.

In order to calculate the effective touch area of a *Macoma* the orientation of the billtip towards the shell must be taken into account too. In the drawing of the horizontal section through a *Macoma* two axes can be distinguished (Fig.

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7B): *c* dividing the section in two symmetrical halves and *d*, perpendicular to *c*, corresponding with the greatest thickness of the *Macoma*. The directions of axis *c* of buried *Macoma* are randomly distributed over the compass (own observations). I assume that the bill is moved in a random way in relation to the positions of the *Macoma* in the substrate, in other words, all directions of axis *l* of the billtip in relation to *c* occur equally, lying between the two extremes *l* parallel to *c* or *l* perpendicular to *c*.

In the same manner as in Fig. 7A the effective touch area with these new relations was found by projecting the bill around the *Macoma* in a fixed position either with *l* parallel to *c* or with *l* perpendicular to *c* (Fig. 7B). The mean value of these two areas was taken as the mean effective touch area of that *Macoma*. The touch area was determined for *Macoma* of 11, 15, 19 and 23 mm shell length. The mean value of the effective touch area with *l* parallel *c* was about 72% of that with *l* perpendicular to *c*. For a *Macoma* of 11 mm the mean effective touch area was 4.8 times as large as the actual greatest horizontal section, for a *Macoma* of 23 mm it was 2.5 times as large. The smaller a *Macoma* is the larger the relative effect of the bill on the effective touch area. In Fig. 7C, curve a depicts the size of the greatest horizontal section through a *Macoma* in relation to shell length when in its buried position, curve b indicates the mean effective touch area.

If the density of the *Macoma* within reach of the bill per mm-class in a *Macoma* field is known, the effective touch area of the whole attainable *Macoma* population can be calculated and hence the mean effective touch area per *Macoma* within reach. The chance to hit a *Macoma* at a probe is determined by the proportion of the mudsurface occupied by the effective touch area of the whole *Macoma* population within accessible distance. Provided multiple pecking time and mean probing rate are known, the number of *Macoma* located as predicted by the model (N_p) can be calculated according to the formula:

$$N_p = t \times r \times d \times s/10^4 \qquad (1)$$

where t = multiple pecking time (sec), r = mean probing rate (number of probes/sec multiple pecking), d = density of the *Macoma* population within reach (*Mac*/m^2), s = mean effective touch area per *Macoma* within reach (cm^2).

2.5. APPLICATION OF THE MODEL

Application of the model to field observations is the next step to be taken, to see if it fits in with reality. Data concerning the captive bird WR on fields with experimental and natural *Macoma* populations will be considered first, then those pertaining to free living birds.

The data of WR on the experimental *Macoma* populations will be considered first, bearing upon results of observations when the bird was feeding on fields of one m^2 containing either fifty 15 mm *Macoma* or fifty 19—20 mm *Macoma*, either in daytime with tracks erased or at night. The mean burrow depth in daytime of the 15 mm *Macoma* was 15.6 ± (S.D.) 7.0 mm (n = 14) and the 19—20 mm *Macoma* 15.2 ± 6.9 mm (n = 16), this difference was not significant. No measurements on burrow depth of *Macoma* at night were made, no difference in depth between day and night is assumed. Probing depth of the bird was not measured but it was definitely deep enough to guarantee that all *Macoma* were within reach. The mean density of the *Macoma* (d_m) is calculated as the mean of the densities at the beginning and at the end of the ex-

Table 2. Number of *Macoma* predicted by the touch model and the number found by the captive Oystercatcher WR feeding on 1 m^2 fields with experimental populations of 15 mm or 19—20 mm *Macoma*. There are 4 tests in each category, and in no case does the prediction differ significantly with the experimental results (χ^2-test)

	Day, tracks erased		Night	
	15 mm	19—20 mm	15 mm	19—20 mm
Mean density (d_m; *Mac*/m^2)	44.3	37.1	46.2	38.7
Multiple pecking time (t; in sec)	1438	1643	973	1095
Number of *Macoma* located:				
predicted (N_p)	43.8	95.9	30.9	66.7
found (N_f)	46	103	23	68

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periment. Mean probing rate varied between five and six probes per sec of multiple pecking, 5.5 probes per sec are reckoned with here. The effective touch area (s) of a 15 mm *Macoma* is 1.25 cm^2 and of a 19—20 mm *Macoma* 2.86 cm^2 (Fig. 7C). The number of *Macoma* localized as predicted by the model can now be calculated according the formula:

$$N_p = t \times 5.5 \times d_m \times s/10^4 \qquad (2)$$

For the meaning of the symbols see equation (1).

The results of four experiments of 30 min each per situation are pooled (Table 2). In all four experimental conditions the number of *Macoma* found by the bird (N_f) fitted in with the prediction of the model. This result encourages us to look into the more complex situation of the natural *Macoma* populations.

The captive bird WR was allowed to feed on one m^2 fields with natural *Macoma* populations in daytime with tracks present or erased, and at night (zone B). In this zone small *Macoma* were buried deeper than large ones (Fig. 8A). In connection with the probing depth observed it appeared that part of the *Macoma* present were not in reach of the bill. Because of this the percentage of the *Macoma* that is beyond reach of the bill must be calculated before the model can be applied. It is difficult to measure the probing depth of the bill precisely without the help of cine film. Notes were made in general terms on the mean depth within which probing occurred. This was expressed as the proportion of the bill length (distance from feathers to tip was 77 mm) judged to be inserted into the mud. Within and between sites probing depths varied considerably from about one third to the full length of the bill. The depth taken down in all these notes averaged about half of the bill length (38 mm).

When an Oystercatcher grips a *Macoma* after it has found it, probing depth can be estimated a little more accurately under the circumstances, because at that moment the bird holds its bill, in vertical position, motionless for a short instance before it lifts the bivalve from the substrate to the surface. This gives the observer more time to have a good look at probing depth. In zone B this distance was estimated 33 times, revealing a mean depth of 45.0 ± (S.D.) 15.6 mm. The actual depth these *Macoma* must have been detected at by the bird may have been somewhat less, for after detection of the *Macoma* the bill is pushed downwards a short distance in order to be able to grip the shell. This was estimated to be 5—10 mm by holding a *Macoma* of 15 mm in the bill tip of a dead Oystercatcher. The mean detection depth which is equal to the mean probing depth, must have been about 35—40 mm. In the calculations the probing depth of 38 mm will be applied to all observations in zone B. Burrow depth of *Macoma* and shell length in zone B were negatively correlated (Fig. 8A). For each chosen fixed value of the probing depth (Fig. 8B) the proportion of *Macoma* present that is within reach of the bill can be calculated per mm-class separately, using single tail probability

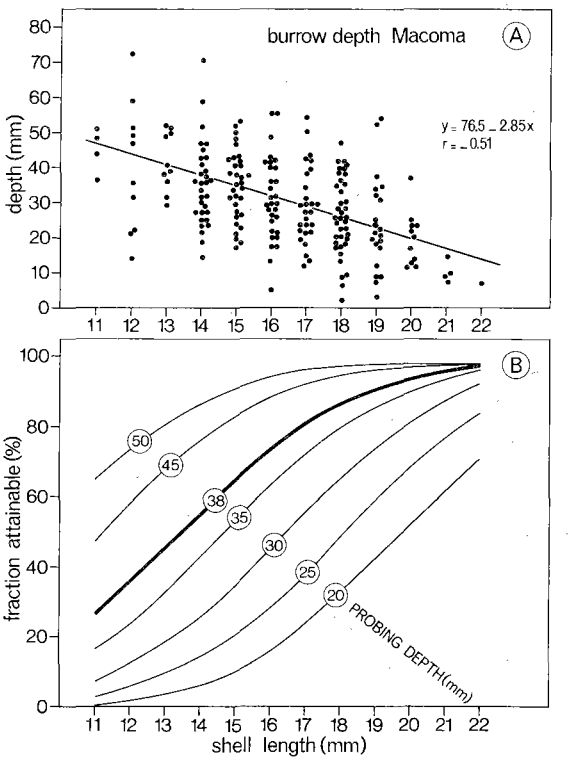


Fig. 8. A: Burrow depth of *Macoma* in relation to shell length, 30 August 1967, Schiermonnikoog, zone B (from Hulscher 1973).
B: Proportion of *Macoma* within reach of the bill at different probing depths.

T = (probing depth − mean burrow depth)/S
S = √ (variance of the burrow depths) of all *Macoma* (11—22 mm shell length), being

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$\sqrt{127.15} = 11.27$. Now the percentage of the number of *Macoma* that is attainable can be calculated for the whole population. The *Macoma* present within reach of the bill at a mean probing depth of 38 mm amounted to 60.0%. Since relatively more large than small *Macoma* are within reach of the bill (Fig. 8A), it will be clear that not only the mean shell length but also the mean effective touch area per *Macoma* of the attainable *Macoma* population will be larger than that of the whole *Macoma* population present. The mean effective touch area per *Macoma* of the total population was calculated to be 1.89 cm^2. When the *Macoma* beyond reach are excluded the mean effective touch area was 2.00 cm^2 at a probing depth of 38 mm.

The mean probing rate of WR on the natural *Macoma* fields in zone B was somewhat lower than on the fields with experimental *Macoma* populations, varying between four to five probes per sec of multiple pecking. A mean rate of 4.5 probes per sec will be used for the calculations in this zone. After this explanation of the computations for each case upon which the model is applied, the experiments with the bird WR on the natural fields in zone b can be worked out.

The density of the accessible *Macoma* population at the beginning of an experiment (initial density) for a probing depth of 38 mm was calculated by taking the known density of the total population into account. The mean density (d_m) of the *Macoma* within reach, as used in the model, was calculated as the mean of the density at the start and at the end of the experiment. The predicted number of *Macoma* located can be found by:

$$N_p = t \times 4.5 \times d_m \times s/10^4 \qquad (3)$$

For the meaning of the symbols see equation (1).

The results over the first ten min of observation of all experiments performed under comparable conditions are pooled and summarized in Table 3. The results of WR fitted in with the model.

2.6. TESTING THE MODEL WITH DATA FROM FREE LIVING BIRDS

The model for localization could be tested with a complete set of data of observations of free living Oystercatchers at Paesens in May 1979.

In this area the burrow depth of *Macoma* was positively correlated with shell length over the range of the 11—19 mm-class ($y = 2.8\ x + 14.33$; $r_6 = 0.74$; $P < 0.05$). With the aid of colour-banded birds, with known bill length it was estimated that the mean depth to which the bill was inserted into the mud at the moment just before a *Macoma* was to be lifted to the surface was 76.4 mm (n = 28), corresponding with a mean probing depth of 66 mm. The mean density of the *Macoma* present (11—20 mm-classes) was measured immediately after the observations and came up to 168/m^2. Accepting the mean probing depth of 66 mm and taking into account the distribution of the burrow depth of *Macoma*, it was computed that 67.7% of the *Macoma* present (11—20 mm-classes) were within reach of the bill. Thus a density of 113.7

Table 3. The number of *Macoma* predicted by the touch model at a probing depth of 38 mm, and the number of *Macoma* found by the captive Oystercatcher WR over the first ten minutes of the observations when feeding during daytime on fields of one or two m^2 with the natural *Macoma* populations. In no case does the prediction differ significantly with the experimental results (χ^2-test)

	Tracks		
Number of experiments × size of field (site nr.)	non-erased 10 × 1 m^2 (16—19)	erased 8 × 1 m^2 (16—19)	non-erased 2 × 2 m^2 (23)
Density (*Mac*/m^2)			
Initial: population present	147.6	99.5	146.0
population attainable	78.9	59.5	87.3
Mean: population attainable (d_m)	67.8	48.6	83.8
Multiple pecking time (t, sec)	1945	2194	494
Number of *Macoma* located:			
predicted (N_p)	118.7	87.0	37.2
found (N_f)	101	96	28

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Macoma/m² is taken as the mean density of the accessible *Macoma* during the observation periods. Effects of the birds on depleting *Macoma* are neglected. The mean effective touch area per attainable *Macoma* at a probing depth of 66 mm was calculated to be 1.93 cm². The mean probing rate was five probes per sec of multiple pecking. The feeding success of each of 99 adult birds was observed during ten min. Together they found 1817 *Macoma* in 17226 sec of multiple pecking. According to the model the birds ought to have localized:
$17226 \times 5 \times 113.7 \times 1.93/10^4 = 1890$ *Macoma*.
The results of the birds approach the prediction remarkably well. ($\chi^2 = 2.82$; n.s.).

Reviewing the results of application of the touch model we can conclude that it holds good for the captive bird WR, as well as for the free living Oystercatchers at Paesens 1979.

2.7. CHOICE OF TECHNIQUE

We have seen that the Oystercatcher has two ways of locating *Macoma* at its disposal: by sight (provided tracks are available) and by touch. The same pertains to location of Cockles. The energy expenditure of the method applied and the final caloric yield per unit searching time must be an important factor in deciding which method to use. The question coming up here is: when is either of the two methods, or a combination of the two, applied in looking for Cockles and *Macoma*? Cockles are located purely by sight in daytime, at least at densities higher than 40/m², and by touch in darkness, when the "sewing" technique is used. Whilst "sewing", the bill is ploughed through the substrate, the tip making little up and down movements. Experiments have shown that more Cockles per time, under otherwise comparable conditions, are located by touch at night than by sight in daytime (Hulscher 1976). Why does not the bird use the touch method in daytime as well? One possibility is that ploughing with the billtip through the substrate costs quite some energy and searching by sight is more profitable, even with a lower success of location per unit time, than by the touch method.

The feeding behaviour of Oystercatchers on *Macoma* is somewhat more complicated than on Cockles. A *Macoma* is always finally located by the multiple peck method, that is by touch. In darkness the bill is put onto the mudsurface, blindly, when beginning a multiple peck; in daytime, however, the starting point can be directed by a visible cue, resulting in a combination of visual and touch methods in locating prey. The differences have been analysed on a time basis. The data were obtained from the captive bird WR feeding during daytime on experimental *Macoma* populations in fields of one m² with 50 *Macoma* of the 19—20 mm-classes, when tracks were either available (non-erased) or non-available (erased) and at night. The observations for these analyses lasted ten min, during which the bird only displayed feeding activities. Fig. 9 gives a résumé of the facts. Feeding time is composed of searching time and handling time. Component parts of searching time are multiple pecking and "rest" activities. These latter consist of displacement of the bird between multiple pecks and, in daytime, a survey of the substrate by the bird, in order to spot surface tracks of *Macoma* and making single pecks. Feeding time was ten min. Handling time was measured, as well as multiple pecking time, therefore searching time and the time for rest activities could be calculated. With these data the number of *Macoma* located per sec searching and per sec multiple pecking can be computed (Table 4). Per sec searching significantly more *Macoma* are located in daytime when tracks are present than at night ($P < 0.05$), and also more, though the difference is not significant, than when tracks are erased in daytime. The number of *Macoma* located per sec multiple pecking is significantly larger in daytime

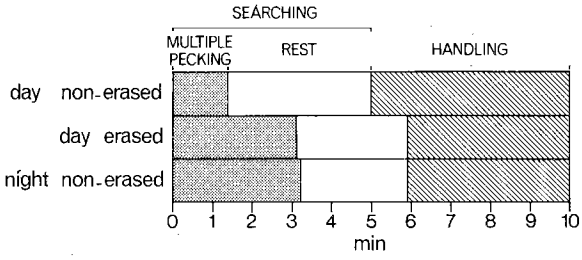


Fig. 9. Mean composition of the time budget of the captive Oystercatcher WR during the first 10 min of observation, when feeding on fields of one m² with 50 *Macoma* of 19—20 mm.

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Table 4. Foraging results of the captive Oystercatcher WR feeding on one m² fields with fifty 19—20 mm *Macoma* during the first ten min of observation. In each case mean and S.D. are given

	Day		Night
	non-erased	erased	non-erased
Number of observations	4	4	3
Number of *Macoma* located/sec:			
searching	0.072 ± 0.018	0.054 ± 0.019	0.049 ± 0.005
multiple pecking	0.307 ± 0.184	0.099 ± 0.032	0.090 ± 0.014
Time (sec)/*Macoma* located:			
multiple pecking	4.0 ± 1.6	10.0 ± 3.5	11.3 ± 1.7
rest time	10.7 ± 2.9	10.3 ± 6.9	9.4 ± 2.4
handling	14.8 ± 1.7	14.3 ± 0.4	14.7 ± 1.5
Number of *Macoma*/10 min feeding:			
located	20.8 ± 3.0	17.8 ± 4.0	17.0 ± 1.0
eaten	16.5 ± 3.9	13.8 ± 1.3	16.7 ± 1.5

with tracks than in the other two situations. Rest time, in sec per *Macoma* located, is similar under the three conditions, but sec multiple pecking per *Macoma* located is markedly shorter when tracks are present. The bird looks for the right spot before starting a multiple peck, whilst walking between two multiple pecks. Since this saves "ploughing" through the substrate, considerable energy must be saved. A combination of visual cues with multiple pecking by day must be more efficient than locating *Macoma* by multiple pecks only.

Table 4 shows another interesting point: more *Macoma* per ten min feeding are located and handled in daytime in the presence of tracks than when tracks are erased or at night, but in both daytime situations some *Macoma* located and handled were not eaten, whereas at night rejection hardly occurred. Here we hit upon the problem to be discussed in chapter 5. As we shall see Oystercatchers discriminate *Macoma* infected with trematodes and tend to reject them. These may well represent the specimens recognised in the daylight situation and subsequently rejected.

In conclusion, the following picture can be drawn on localization of *Macoma* by Oystercatchers. In situations when tracks are formed, the bivalve can be found by sight, this enhances localization success, but usually *Macoma* do not make tracks, therefore localization by touch prevails. This is in harmony with the knowledge that the sense of touch is well developed in waders. Concentrations of Herbst corpuscles occur in the tip of their bills (Schwartzkopff 1973). Bolze (1969) and Heppleston (1970) described them for the Oystercatcher.

The possibility of other touch stimuli besides the shell area aiding in the process is left open. For instance, the Oystercatcher might perceive relative differences in pressure when it probes in the sand above or next to a buried *Macoma*, or it might detect the siphon tubes. Location by touch of immobile (dead) buried prey in an experimental set-up by the Sanderling *Calidris alba* has recently been made plausible by Myers *et al.* (1980).

Any possible localization method by means of the senses of smell, hearing or taste was not investigated in this study. Smell is situated in the nasal cavities, at a distance of five to seven cm from the bill tip in case of the Oystercatchers. The involvement of smell in locating food is thought to be of minor importance for birds in general. The exceptional nocturnal Kiwi very likely proves the rule (Wenzel 1973). Even if *Macoma* would produce some olfactory cue — a fact we do not know — there is little reason to believe that this odour can be operative in such an open and windy area as the mudflats.

Hearing can scarcely be in question in locating *Macoma*. Several plover species are considered to use their auditive senses in locating subterrestrial prey (Lange 1968). It is claimed that the birds hear the rustling of worms when moving in their burrows. The results presented so far, are not convincing. *Macoma*, on the other hand, is immobile in its buried position during

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most of the tidal cycle. A downward, respectively upward, movement might occur at the moment of emersion and submersion of the mudflats. It is doubtful that noises are made herewith, let alone sounds relevant for the Oystercatcher.

The sense of taste is located at the tip of the tongue. An Oystercatcher's tongue only reaches halfway the length of the bill and cannot be protruded. Wenzel (1973) reviewing taste in birds, found that they can discriminate between different types of food after it has been picked up by the bill. It is unknown up till now, if taste stimuli aid in the localisation of food. It cannot be excluded that Oystercatchers savour chemical substances in the mud produced by *Macoma*, for instance mucous, during multiple pecking and that this subsequently may lead to detection of the shell.

3. SIZE SELECTION AS A CONSEQUENCE OF THE LOCALIZATION MECHANISM

3.1. INTRODUCTION

In the foregoing pages we have seen that the free living Oystercatchers located *Macoma* entirely by touch, probably because tracks were absent. For the captive bird WR foraging in zone B localization was more complicated since tracks were present. Here WR located *Macoma* by sight as well as by touch.

Location by touch implies that the chances of encountering *Macoma* of different shell length beneath the substrate are unequal because small and large shells have different surface areas. Large *Macoma* will be contacted more easily than small ones, or put otherwise: there will be passive selection for large *Macoma*. In circumstances when location by sight cannot be totally ignored, we must also take the possibility into account, that the chances to see tracks of *Macoma* of different sizes are unequal. For instance tracks of large *Macoma* could be bigger and therefore more conspicuous. In that case passive selection by sight may be expected likewise.

Before proceeding it is wise to describe clearly what is meant when the word "selection" is used in this study. Selection signifies that the proportion of numbers of *Macoma* of different mm-classes found is not identical to those proportions in the living population, irrespective of the way this is achieved. Passive selection expresses the fact that the proportion of numbers of *Macoma* of different mm-classes found, differs automatically from those in the living population as a consequence of the method of location. To begin with, we shall check, respectively, if the wild birds and the captive birds actually selected the larger *Macoma*. Then we shall examine to what extent the selection found can be attributed to passive selection.

3.2. EXTENT OF SIZE SELECTION

Samples of *Macoma* shells opened by free living Oystercatchers and of the living populations these *Macoma* were taken from, were collected on several occasions (Fig. 10). On Vlieland this was done at two sites, 560 m apart on the Dorpsplaat (Dorpsplaat-West and Dorpsplaat-East) at the end of August 1963. The population composition at the two sites was the same and the Oystercatchers selected larger *Macoma* to the same extent as compared to the living population (Fig. 10A and 10B). At Paesens, the study area was sampled in May 1978 and in May 1979. Between these dates the living population had increased in mean shell length from 11.27 to 14.77 mm. Again there was selection for the larger *Macoma*, but the size distribution of the opened shells was the same in both years (Fig. 10C and 10D).

On Schiermonnikoog samples of shells preyed upon by free living Oystercatchers could be compared twice with shells opened by captive Oystercatchers at the same place. This concerned site 3 for a sample of three tame birds (Fig. 10E and 10F), and site 5 for one bird (WR) (Fig. 10G and 10H). In neither case was there a difference between samples of the free and the captive birds, suggesting a general trend of size selection under the prevailing circumstances.

Besides the observations on site 3, many more data on size selection are available concerning the tame bird WR, because of the host of experiments performed with him in testing location of *Macoma*. After each experiment with WR in fenced-in areas, when ten or more opened shells were collected, the mean length

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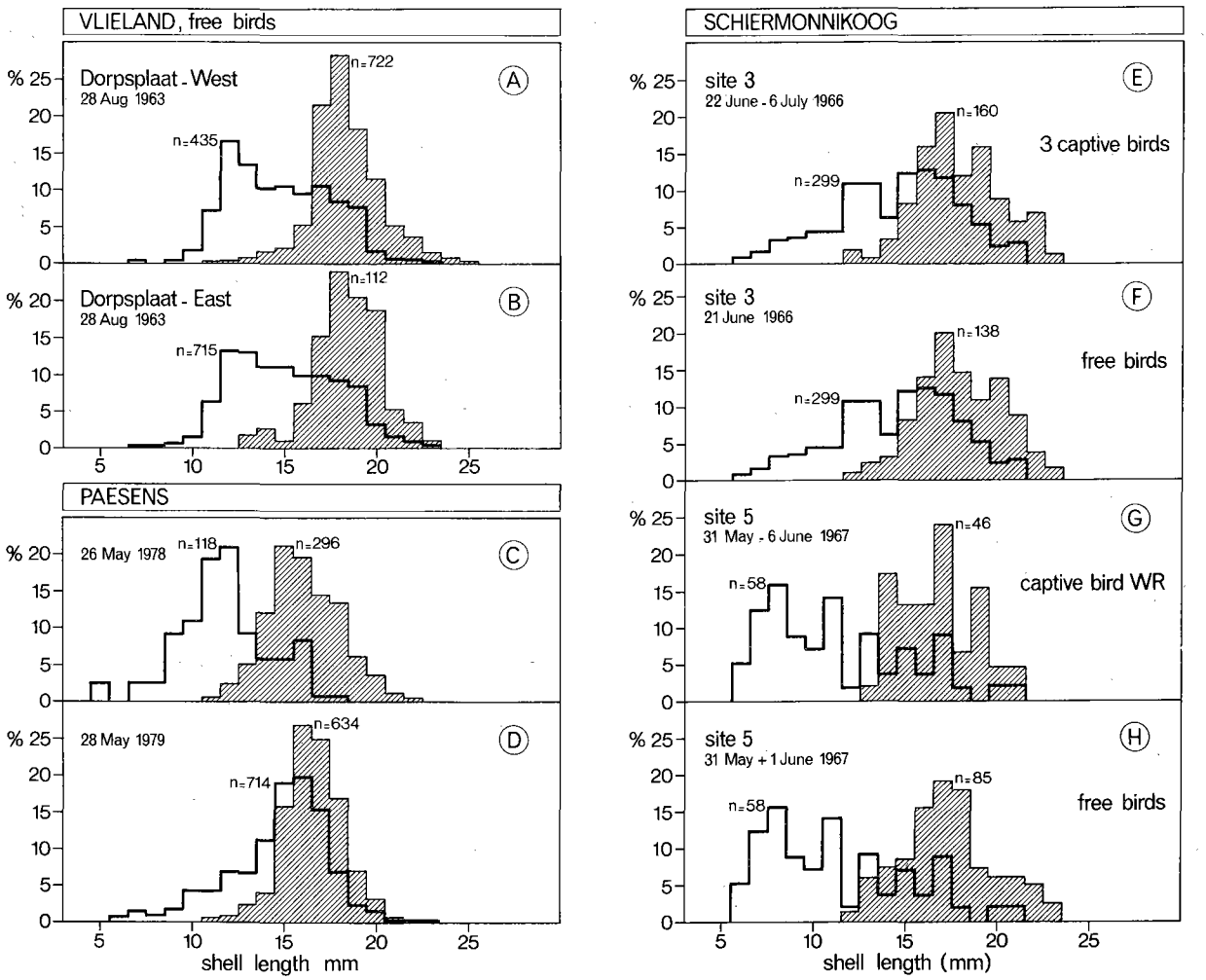


Fig. 10. Selection for size with *Macoma*. Size distributions of shells opened by Oystercatchers (hatched) are compared with samples of the living population (not hatched); n refers to the number of shells measured.

of the opened shells was calculated, as well as that of the living population at the start of the experiment. Fig. 11, left panel, summarizes the results on size selection by the bird. Mean sizes of opened shells and of the living population are compared. It is clear that WR selected the larger *Macoma* in all cases. In Fig. 11, right panel, the results on size selection by free living birds are depicted in the same manner as for WR. Selection by the free birds is similar to that by the captive bird. Since both the free Oystercatchers and captive individuals in fenced-in areas, selected for the larger sizes within the *Macoma* populations, it may very well be that size selection is a general feature in Oystercatchers feeding upon *Macoma*.

To what extent the observed selection can be explained by passive selection by touch will be gone over now. The possibility of passive selection by sight will be considered after that.

3.3. EXPLAINING SIZE SELECTION BY TOUCH

The basic principle underlying passive size selection by touch is that *Macoma* of different sizes have unequal effective touch areas. If the numerical densities of the *Macoma* per mm-class were the same and there were no dif-

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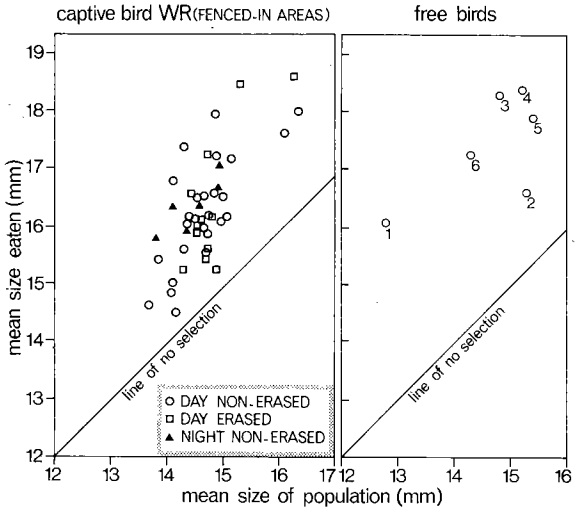


Fig. 11. Selection for size with *Macoma*. The mean size of shells opened by the birds are compared with the mean size of the population on offer (only *Macoma* of 11 mm shell length or more in the population are included).

Left panel: results of the captive bird WR when feeding on fields with natural *Macoma* populations under three different conditions of *Macoma* track availability.

Right panel: results of free living Oystercatchers. Figures refer to the following observations: 1. Paesens May 1978, 2. Paesens May 1979, 3. Vlieland, Dorpsplaat-West August 1963, 4. Vlieland, Dorpsplaat-East August 1963, 5. Schiermonnikoog, site 3 June 1966, 6. Schiermonnikoog, site 5 May/June 1967.

ferences in burrow depth between *Macoma* sizes, the number of *Macoma* per mm-class expected to be found by the bird would be proportional to the effective touch areas of the mm-classes. But if mean burrow depth of *Macoma* of different sizes is unequal, this would influence selection for size too. For instance in the area where the captive bird WR fed on natural *Macoma* fields, the smaller *Macoma* were, on average, buried deeper than the larger ones (Fig. 8A). This means, assuming a certain probing depth, that a greater proportion of the small *Macoma* will not be reached, than of the large specimens. This contributes to the outcome of passive selection. In summary it can be stated that the probability, with which *Macoma* of different size classes will be detected by the Oystercatcher through random searching by touch, is reflected by the total effective touch area per mm-class of those *Macoma* being within reach of the bill. Because Oystercatchers did not eat *Macoma* of less than 11 mm shell length, selection for size will only be analysed for that part of the living population of 11 mm shell length or more. Aspects concerning a possible active selection against undersized *Macoma* will be considered in section 3.6.

3.4. TESTING THE MODEL OF PASSIVE SELECTION BY TOUCH

Captive bird WR. We shall test if the results of WR, foraging on the natural *Macoma* population in zone B (daytime, tracks erased), fit in with the hypothesis of passive size selection by touch. This will be done in three steps. First, the number of shells per mm-class found opened will be compared with the numerical distribution of the mm-classes in the living population without taking accessibility and effective touch area into account. Then depth distribution will be taken into the picture, since some *Macoma* are not accessible because of this, and finally the consequence of the differences in effective touch area between mm-classes will be attended to in combination with the first two procedures. All the separate experiments of WR in zone B are pooled. A total of 295 opened shells were collected.

When one compares the size distribution of the total living population with that of the shells opened by the bird, it is evident that there is strong selection for the larger *Macoma* (Fig. 12, left panel, A). The difference between both size distributions was strongly significant ($\chi^2 = 88.5$; $P < 0.01$). In the next step *Macoma* beyond reach of the bill are excluded. The burrow depth of *Macoma* in this zone is represented in Fig. 8A. A mean probing depth by the bird of 38 mm (*cf.* section 2.5) will be applied in the calculation. The percentage of *Macoma* accessible to the bill at that depth was calculated for each mm-class of the living population (*cf.* Fig. 8B). Then the size distribution of the attainable living population was compared with that of the opened shells (Fig. 12, left panel, B). The result is that the difference between both size distributions has become smaller, but they still are significantly different ($\chi^2 = 22.04$; $P < 0.01$).

In the final step a correction is made for differences in effective touch area of the *Macoma*. The number of *Macoma* within reach of the bill at a probing depth of 38 mm per mm-class was

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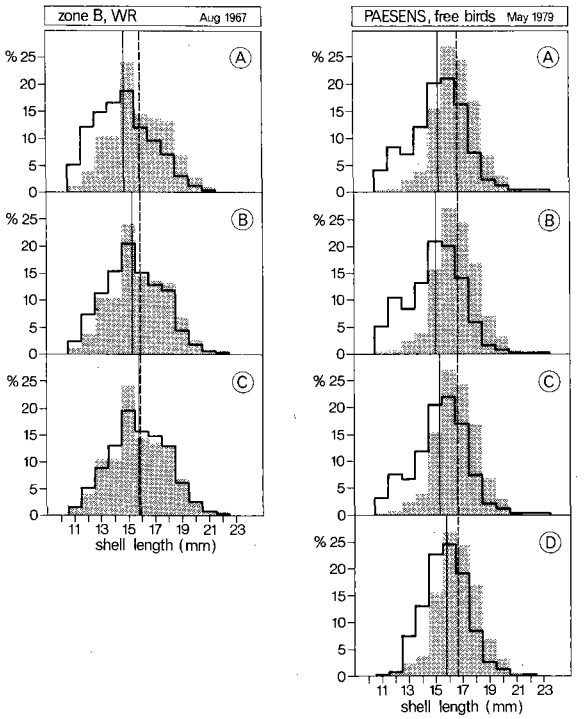


Fig. 12. Appliance of the model of passive selection for size by touch. Left panel: for the captive Oystercatcher WR when feeding in daytime in zone B on erased fields with the natural *Macoma* populations (pooled results). Right panel: for the free living Oystercatchers at Paesens in May 1979. The size distribution of the shells opened by the bird(s) (shaded) are compared with (not shaded). — A. the size distribution of the total *Macoma* population present. — B. the distribution of only the *Macoma* being in reach of the bill at a mean probing depth of 38 mm. — C. the distribution of the effective touch area of the *Macoma* being within reach of the bill at a mean probing depth of 38 mm. — D. as C, accepting that ten percent of the *Macoma* located are rejected, being all the *Macoma* of 11 and 12 mm shell length.

multiplied with the effective touch area of that mm-class. Now the proportion of each mm-class in the total effective touch area of the attainable population can be calculated. The distribution of the effective touch area over the mm-classes was compared with the size distributions of the opened shells (Fig. 12, left panel, C). Both distributions are nearly equal now, statistically there is no difference ($\chi^2 = 8.45$; n.s.). In this example the selection as observed for the larger *Macoma* was in accordance with the model of passive selection by touch.

Free living birds. The hypothesis of passive selection by touch can be tested for free living birds in the Paesens area in 1979 (Fig. 12, right panel). No tracks of *Macoma* were found here, therefore location of *Macoma* entirely by touch can be presumed. A sample of 634 opened shells is at our disposal for the test. The birds selected strongly for the large *Macoma* in comparison with the total living population (Fig. 12, right panel, A) ($\chi^2 = 328.6$; $P < 0.01$). The proportion of the total population within reach of the bill was calculated by applying the burrow depth distribution of *Macoma* and a mean probing depth of 66 mm (*cf.* section 2.6.). When the expected size distribution of the opened shells is calculated after this correction and compared with the distribution found, the difference becomes larger (Fig. 12, right panel, B) ($\chi^2 = 520$; $P < 0.01$). This is due to the positive correlation between burrow depth and shell length of *Macoma*, contrary to the burrow depth distribution on Schiermonnikoog in zone A and B.

When, in the third step, allowance is made for differences in the effective touch area, the bias between the size distributions expected and found diminishes (Fig. 12, right panel, C), but still is significant ($\chi^2 = 311$; $P < 0.01$). The birds find still larger *Macoma* than the hypothesis of random searching by touch predicts. Observations on the free living birds showed that about ten percent of the *Macoma* found were not eaten. Why this happened, is not clear. One reason could be that some were rejected because they were undersized (see chapter 5), another that they were infected with trematodes. As we have seen, the hypothesis of passive size selection by touch, implying that *Macoma* are found by chance, was found to hold good for the captive bird WR. We shall attempt also to explain the size selection by the free birds with our hypothesis, making, by means of the two presumptions just mentioned, a correction for the rejected *Macoma*. From Fig. 12, right panel, C it can be seen that with random searching it may be expected that about ten percent of all *Macoma* found belong to the classes 11 + 12 mm shell length. Suppose that all these small *Macoma* are rejected, then the expected size distribution of the *Macoma* eaten can be calculated anew and compared with the distribution actually found (Fig. 12, right panel, D). It turned out that the samples collected on the grounds where the free

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living birds foraged, still contained larger *Macoma* than were expected according to the hypothesis of passive size selection ($\chi^2 = 207$; $P < 0.01$). Thus the correction does not remove the bias in explaining the size distribution in the samples collected. The samples themselves, however, possibly were not wholly representative for the free birds. It was difficult to collect a sufficient number of empty shells with flesh remains, as being definitely opened by Oystercatchers. The majority of the shells were pushed into the ooze. Flesh remains are only visible for a few hours, since shells are totally cleaned by shrimps and crabs in the following high water period. All empty shells found on the mudsurface, also those containing no flesh remains, were considered as having been opened by Oystercatchers. Possibly not all these shells were actually emptied by Oystercatchers. Some might have ended upon the surface due to other causes, for instance infection with trematodes. Heavily infected *Macoma* crawl up to the mudsurface and die there. This happens relatively more often to large than to small *Macoma* (Hulscher 1973). Perhaps some of the shells collected from the mudsurface at Paesens were not opened and emptied by Oystercatchers at all, but were relatively large sized *Macoma*, that had died of trematode infection. This could have caused the discrepancy between the size distribution of shells collected and expected.

The shells collected after WR had foraged in the experimental cage were definitely opened by the bird. Since the hypothesis held good for this bird and the inaccuracy as described above in collecting samples of shells opened by the free birds, may have occurred, I tend to accept the hypothesis of passive size selection for the free birds too. A strong argument for this view is the fact that the birds located the expected number of *Macoma* according to the model of localization by random searching by touch (see section 2.6).

3.5. SIZE SELECTION WITH THE AID OF SURFACE CLUES

As mentioned in section 3.2. the possibility of passive size selection by sight must be examined too. In case *Macoma* is located by sight, passive selection for large *Macoma* may be expected per definition if the tracks of large *Macoma* are found more easily than those of small *Macoma* even if we postulate that small and large *Macoma* produce tracks equally often.

Selection for size by visual clues was first tested for man. Two samples of *Macoma* collected by man from sites 6 and 23 are available, which can be compared with samples of the captive bird WR feeding on the same sites. The method in track hunting applied was that of crawling on hands and knees, progressing slowly over the mudsurface, scanning the surface for tracks. When a track was found, the presence of *Macoma* was checked by carefully digging upon the spot. Every track thought to be made by *Macoma* was investigated. The results are depicted in Fig. 13. More large and less small *Macoma* as compared to the numbers in the population were found on both sites. In order to determine whether the visual selection for large *Macoma* was a passive one, a census of track formation by small and large *Macoma* must be made first. To study this point, 50 *Macoma* of the uneven mm-classes were marked with nailpolish and replanted at fixed coordinates (the cross points of a grid of 15 cm mesh width) amidst unmarked local *Macoma* on an area of six m^2 at site 23. Five days later the whole field was investigated for *Macoma* tracks. The procedure was as follows. First all *Macoma* tracks found were marked with little sticks, then the presence of *Macoma* was checked by digging them up at the spots indicated by the sticks. After that the whole field was sieved to determine the total number of *Macoma* that was present. It turned out that 23.6% of the *Macoma* marked with nailpolish were retrieved via a surface track, compared to only 8.3% of the unmarked

Table 5. Number of marked *Macoma* found with tracks five days after they were planted at a distance of 15 cm between them, at the crossings of a grid (August, zone B)

Size mm	No. present	No. with track	% with track
11	49	11	22.4
13	49	10	20.4
15	50	16	32.0
17	49	11	22.4
19	43	8	18.6
21	9	2	22.2
Total	249	58	23.3

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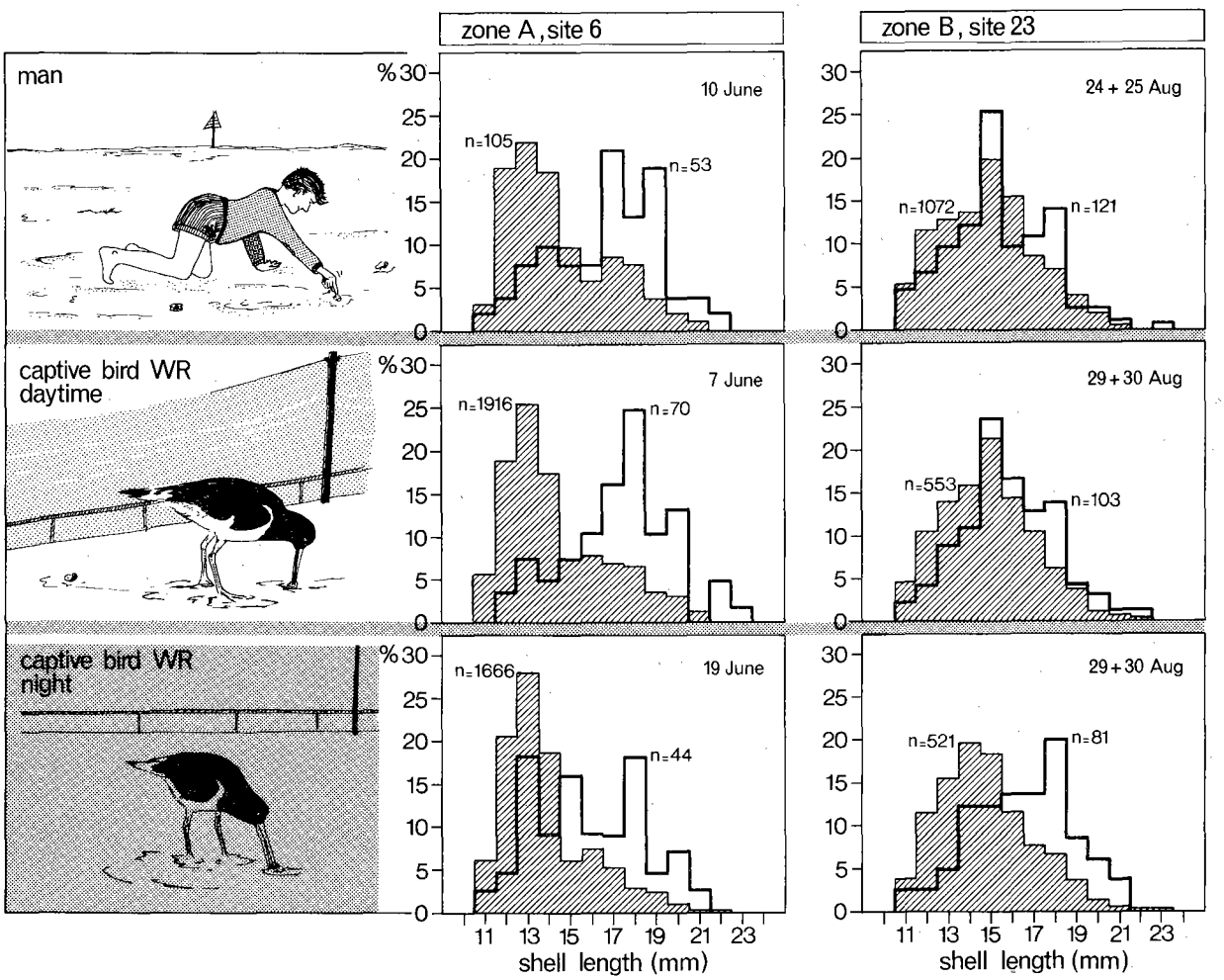


Fig. 13. Selection for size with *Macoma* by man and the captive Oystercatcher WR when both were searching for *Macoma* on the same sites on fields with natural *Macoma* populations. Visual selection by man (top row) in daytime, using surface tracks of *Macoma*, is compared with the selection by the bird when feeding in daytime, tracks not erased (second row), or at night, tracks not erased (third row). Samples of shells, found by man or bird (not hatched) are compared with samples of the living populations (hatched); n refers to the number of shells in the samples.

(local) ones. Moreover, among the marked *Macoma* (Table 5), all mm-classes had produced the same amount of surface clues ($\chi^2 = 2.24$; n.s.), whereas among the unmarked *Macoma* (Table 6) more large than small *Macoma* were retrieved via a surface sign ($\chi^2 = 9.9$; $P < 0.05$). It is quite reasonable to assume that the transplanted and local *Macoma* at site 23 did not differ in frequency of track formation. The difference in proportions of marked and unmarked *Macoma* retrieved via a surface sign, must have been caused by a difference in the way of looking for them. The knowledge that the marked *Macoma* were planted at 15 cm distance from each other must have enhanced the chance to recognize a surface sign of *Macoma* at these spots.

In conclusion we can state that, when the position of a *Macoma* is unknown, large *Macoma* run more risks of being found via surface cues than small ones. Man selects large *Macoma* passively by sight. The mechanism underlying passive selection by sight was not analysed. It may well be that the size of *Macoma* and the size of track it produces are correlated. Probably large tracks are identified more easily as being made by *Macoma* than small tracks, amongst the variety of tracks on the mudsurface. The next ques-

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Table 6. Number of untouched *Macoma* of an area of 8.4 m^2 found with tracks (August, zone B)

Size mm	No. present	No. with track	% with track
11—14	537	18	3.4
15—17	443	44	9.9
18—22	160	32	20.0

tion is whether the captive bird WR also selected for large *Macoma* using surface cues. Before going into this we shall compare size selection by man and bird. Selection by man and WR can be set against one another by direct comparison of the size distribution of the *Macoma* found. In daytime there appeared to be no differences in size selection between man and bird (site 6, $\chi^2 = 7.85$; n.s.; site 23, $\chi^2 = 4.99$; n.s.), at night however, the bird found smaller *Macoma* at site 6 than man did there in daytime ($\chi^2 = 9.95$; $P \sim 0.05$) and larger *Macoma* at site 23 ($\chi^2 = 16.77$; $P < 0.05$). Because of the fairly good conformity in selection for size by man and bird in daytime it is tempting to conclude that the bird also selected for the larger *Macoma* passively by sight as man did. But, since the bird is apt to select for about the same size of *Macoma* in darkness, this view has to be questioned.

As we found earlier (see section 2.2.) WR probably localized but a minority of *Macoma* visually in daytime. With the present data it is becoming quite difficult to settle the question as to how WR selected large *Macoma* passively: visually in daytime and/or by touch in daytime as well as at night. Visual selection for size can only be distinguished from selection by touch if these two activities end up rendering significantly different size classes. In order to dig out any such possibility the results of WR in size selection were screened for the presence or absence of systematic differences between situations when tracks were available against absent or invisible (erased or in darkness).

Table 7 gives a summary of a set of eight paired observations, suitable for analysis. On sites 6 and 8 WR was feeding in the same square during all experiments, for each experiment the initial *Macoma* population was calculated anew. On sites 19 through 23 a fresh feeding area was offered to the bird with each experiment. The results of experiments on squares with comparable situations are pooled per site. Within sites there were no significant differences in size distribution of the initial population between different feeding conditions. Differences in size selection between feeding conditions, therefore, could be tested by comparing the size distributions of the *Macoma* found (χ^2-test). There was no significant difference in the extent of selection between conditions with or without tracks in any case. The mean value of the differences between the mean length of the *Macoma* opened and the populations on offer turned out to be 1.79 ± 0.56 mm ($n = 7$) when tracks were available and 2.05 ± 0.61 mm ($n = 8$) when

Table 7. Selection for size by the captive Oystercatcher WR feeding on natural *Macoma* populations under different conditions of track availability; n refers to the number of shells measured

Site	Time	Tracks	Mean shell length (mm)	
			population on offer (n)	opened (n)
6	day	non-erased	14.09 (1799)	16.73 (90)
	night	non-erased	13.87 (1666)	15.76 (44)
8	day	non-erased	16.32 (298)	17.75 (69)
	day	erased	16.18 (259)	18.58 (26)
	day	erased	15.29 (212)	18.47 (15)
	day	non-erased	14.86 (197)	17.20 (10)
19	day	non-erased	14.67 (392)	16.45 (38)
	day	erased	14.58 (288)	16.86 (29)
20	day	non-erased	14.87 (1054)	16.40 (124)
	day	erased	14.74 (1160)	15.79 (147)
	night	non-erased	14.89 (1189)	16.75 (160)
22	day	non-erased	14.49 (791)	16.33 (111)
	night	non-erased	14.19 (782)	16.20 (80)
23	day	non-erased	14.82 (553)	15.78 (103)
	night	non-erased	14.76 (521)	16.48 (81)

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tracks were not available. The difference is not significant (t = 0.86; n.s.). This means that no conclusions can be made as yet, whether or not WR selected for the larger *Macoma* visually when tracks were available.

There is yet another way to tackle this problem based on the following reflections. If visual localization of *Macoma* actually does occur, it will predominantly be displayed at the beginning of the feeding sessions in our experimental set-ups, when the mudsurface, with all its tracks, is still undisturbed. Whilst the bird is walking about in its relatively small cage, it will blot out more and more surface marks and finally end up with a situation comparable to no tracks available at all. A sample of opened shells collected early in the foraging period can be expected to contain more specimens that were found visually than a sample collected later on. By comparing the size distributions of two such samples one might obtain an indication whether visual selection did occur in effect, assuming that visual selection yields *Macoma* of other size classes than selection by touch. In order to test this hypothesis the following experiment was performed.

The captive bird WR was allowed to feed on the same square of four m² (site 7) during four successive low water periods. Opened shells were collected one and two hours, respectively, after the start of the experiments. Care was taken not to disturb surface marks. The results are depicted in Fig. 14A. WR ate no *Macoma* at all during the second hour of the first low water period on 15 June. In two out of the three cases the *Macoma* found in the first hour were larger than those in the second hour, but the difference was only significant for the sample of 14 June (t = 2.04; P < 0.05). In Fig. 14B the relative frequencies of three sizes of *Macoma* in the population and in the catch are compared for two first hours (samples 1 + 5), two second hours (samples 2 + 6) and two "third" hours (samples 3 + 7). The first and second hours refer to the same low water period, between the second and third hours the feeding area was inundated once during high tide. It can be seen that during the first hours when *Macoma* tracks were still available relatively more large and fewer small *Macoma* were eaten than during the second hours when tracks were partially obliterated, when subsequently new tracks were formed after reinundation the size of the *Macoma* eaten increases again.

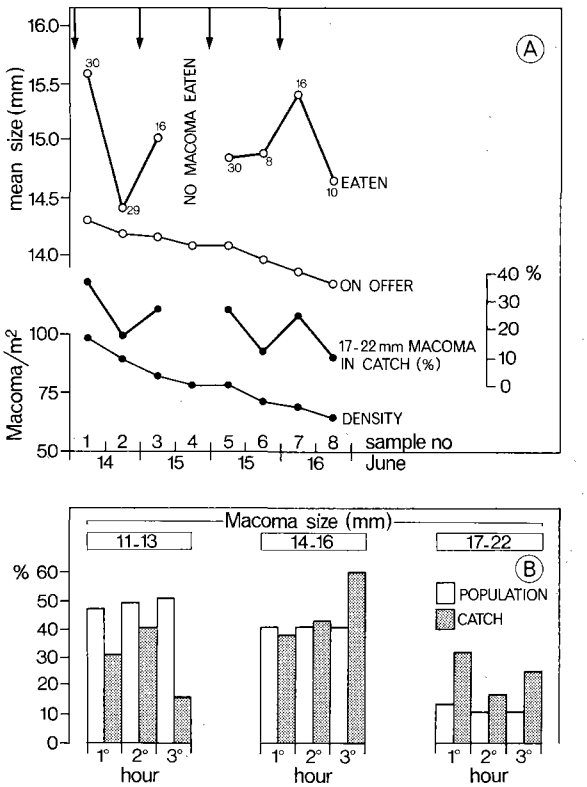


Fig. 14. Visual selection for size: *Macoma* shells emptied by the captive Oystercatcher WR were collected after the first and the second hour of feeding during four successive low water periods on the natural *Macoma* population (the same four m² field throughout).

Panel A indicates the mean size of the *Macoma* eaten by the bird and of those on offer, further the proportion of large (17—22 mm) *Macoma* in the catch and the density of the initial population on offer. Arrows indicate the moment of submersion of the feeding area during high tide, figures near the points the number of *Macoma* eaten.

Panel B summarizes the results on selection; the relative frequencies of three size classes of *Macoma* in the population and in the catch are compared for: two first hours (samples 1 + 5), two second hours (samples 2 + 6) and two "third" hours (samples 3 + 7). The first and second hours refer to the same low water period; between the second and third hours the feeding area was inundated once during high tide. During the first hours when *Macoma* tracks are still available relatively more large and fewer small *Macoma* are eaten than during the second hours when tracks are partially obliterated, when subsequently new tracks are formed after reinundation the size of the *Macoma* eaten increases again.

Summing up it seems there is an indication,

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that visual localization by WR furnishes larger *Macoma* than when the bird localises by touch. It seems likely that the captive bird selected larger *Macoma* visually, just as man, because probably larger *Macoma* make more conspicuous tracks than small ones.

Up till now we have built up the following picture of the localization of *Macoma* by Oystercatchers. Generally speaking Oystercatchers hunt by making multiple pecks in a random way in the mud. When the bill contacts a shell of 11 mm or larger the prey is captured and handled. By this passive method the Oystercatcher obtains on the average *Macoma* which are larger than the average size in the population. When surface tracks of the prey are visible a searching component directed by sight is added to the random touch-hunting system, possibly rendering even slightly larger *Macoma*. In section 3.4. we mentioned we would pay attention to the possibility of active selection against smaller *Macoma* than 11 mm; we shall return to this point now.

3.6. ACTIVE SELECTION AGAINST UNDERSIZED *MACOMA*

The statement that Oystercatchers select larger *Macoma* passively by touch according to the hypothesis of passive size selection might suggest that Oystercatchers never select actively, but take any *Macoma* their bill encounters. This cannot be correct. In the model of random searching by touch *Macoma* smaller than 11 mm were neglected, since such *Macoma* were never eaten (*cf.* Fig. 10). However, when the birds are searching with their bill, multiple pecking in the mud, they must inevitably encounter these small shells. This fact itself is an argument for active selection against undersized *Macoma*. The Oystercatcher probably adapts itself to a certain minimum size class, smaller items being qualified as non-acceptable and ignored. The decision to ignore a small *Macoma* after it has been touched is taken so swiftly, that the observer does not get the chance to ascertain that a *Macoma* has been encountered at all. Only in case a *Macoma* actually is handled, will an observer know one has been found. Every *Macoma* found, larger than the minimum size, indeed is handled. This has been confirmed by the free living birds at Paesens. The number of *Macoma* found by these was in accordance with the hypothesis of random searching.

Swift decisions on taking or ignoring a prey item localized were found for Oystercatchers feeding on Cockles at night (Hulscher 1976). All the Cockles were of the same size class. Only Cockles gaping slightly can be opened with success, and only a small percentage of Cockles gape. When an Oystercatcher finds a Cockle by touch, it must investigate whether the Cockle is gaping or not. At low Cockle densities the number found conformed to the model of random searching by touch, but at higher densities fewer Cockles were found than was expected according to the model. It was reasoned that the bird's actual encounter conformed to the touch model, but that it decided so quickly not to handle closed shells that this escaped detection by the observer.

Turning now back to *Macoma*, the following picture of active selection against small *Macoma* can be constructed. Oystercatchers probably adapt their searching behaviour to local circumstances. In all likelihood they fix a minimum size for *Macoma* worth eating, based upon density, flesh content, size distribution, depth distribution and handling time of the bivalves, furthermore on the nature of the substrate and the energy costs of the depth of probing. They probably determine their criteria from occasion to occasion in order to achieve a most profitable intake. The Oystercatcher has the choice of handling or ignoring every *Macoma* it encounters. The question now arises, when is it profitable to ignore *Macoma* and when to handle it?

3.7. INTAKE IN RELATION TO SIZE SELECTION

In order to get insight in this problem I made the following assumptions and calculations. Let W_e be the flesh weight of the *Macoma* eaten and W_r the flesh weight of the *Macoma* ignored, thus rejected per time foraging. Foraging time (f) consists of searching time (s) that is the time required to detect both eaten and rejected *Macoma*, and handling time (h_e) the time required to open and eat the detected *Macoma* of the preferred size. The food intake per time foraging will be

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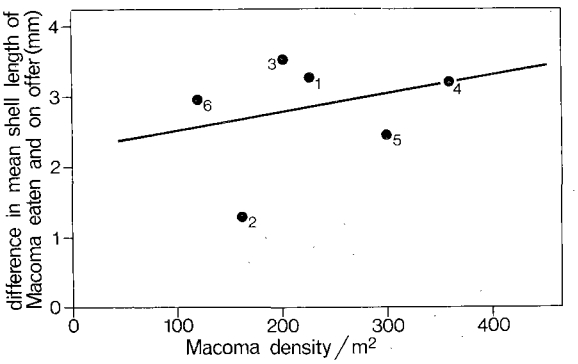


Fig. 15. The extent of selection for size in relation to *Macoma* density by free living Oystercatchers. Selection is measured as the difference (in mm) between the mean length of the opened shells and that of the living *Macoma* of 11 mm shell length or larger. The figures at the points refer to:1. Paesens May 1978, 2. Paesens May 1979, 3. Vlieland, Dorpsplaat-West August 1963, 4. Vlieland-East August 1963, 5. Schiermonnikoog, site 3 June 1966, 6. Schiermonnikoog, site 5 May/June 1967.

$W_e/f = W_e/(s + h_e)$

Suppose h_r to be the handling time of the small *Macoma* in the case they would not have been rejected. In that case the food intake would be

$(W_e + W_r)/(s + h_e + h_r)$

Selection for size will be profitable if

$W_e/(s + h_e) > (W_e + W_r)/(s + h_e + h_r)$

or

$W_e/(s + h_e + h_e) > W_r/h_r$

without advantage if

$W_e/(s + h_e) = W_r/h_r$

and unprofitable if

$W_e/(s + h_e) < W_r/h_r$

If searching time is somehow related to *Macoma* density as might be expected, selection for size is mainly determined by three factors being the relative differences between small and large *Macoma* in 1) flesh content, 2) handling time and 3) density.

The expected positive correlation between *Macoma* density and an increasing selection for size was indeed found for the free birds (Fig. 15). The correlation, however, was weak and not significant ($r = 0.36$; $P > 0.05$). The correlation did not improve when selection was correlated with the densities of only the large *Macoma* in the population. The picture might be different if, instead of total density, only the densities of *Macoma* within reach of the bill would be taken into consideration. This was not possible, because the depth distribution of *Macoma* was not always known. On Schiermonnikoog on site 3 in June 1966 and at Paesens in May 1979, however, the feeding behaviour of the free Oystercatchers was studied in sufficient detail to allow a comparison of the food intake and the extent of selection between both places (Table 8). The food intake $W_e/(s + h_e)$ at Paesens was 83.1/(20.7 + 12.9) = 2.47 mg/sec (ash free dry weight), on Schiermonnikoog 76.0/(18.1 + 10.3) = 2.68 mg/sec AFDW if a general percentage of 13.5 for the ash content of the dry flesh is accepted. The ash content was not determined at Schiermonnikoog. The flesh content of the *Macoma* on Schiermonnikoog was about 2/3 of that of the *Macoma* of the same size at Paesens (Fig. 16B). Nevertheless, the food intake

Table 8. Parameters of the feeding behaviour of free living Oystercatchers feeding on *Macoma*

	Schiermonnikoog (site 3) 3 June 1966	Paesens 19—27 May 1979
Searching time (sec)/*Macoma* located	16.6	18.5
Searching time (sec)/*Macoma* eaten	18.1	20.7
Handling time (sec)/*Macoma* eaten	10.3	12.9
Mean shell length (mm) of living *Macoma* ≥ 11 mm	15.39	15.27
Mean shell length (mm) of *Macoma* eaten	17.88	16.61
Selection for size: difference in length (mm) between *Macoma* on offer and eaten	2.49	1.34
Density (≥ 11 mm, *Mac*/m²):		
population present	305	168
population attainable (probing depth 66 mm)	185	114
Macoma of mean size eaten:		
present	34.9	31.4
attainable (probing depth 66 mm)	21.1	19.5
Flesh (mg, AFDW)/*Macoma* eaten	76.0	83.1

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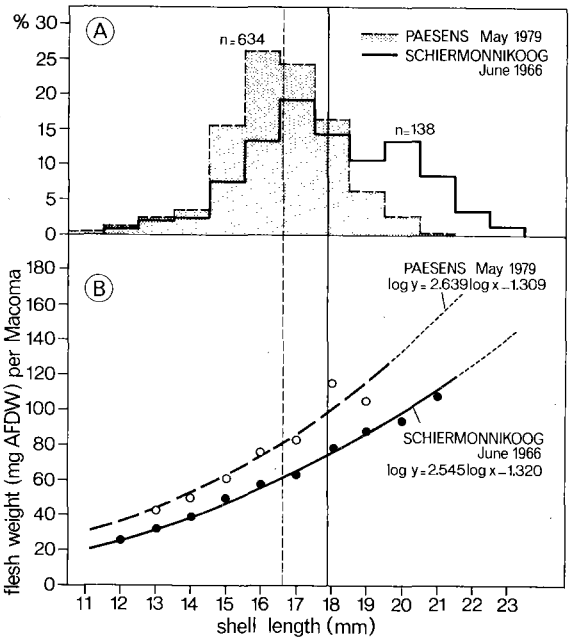


Fig. 16. A. Size distribution of *Macoma* shells opened by free living Oystercatchers; n refers to the number of shells measured. B. Flesh weight (mg AFDW) of *Macoma* in relation to shell length.

at Schiermonnikoog was higher than at Paesens, mainly due to the shorter searching time and shorter handling time at the former place. The higher food intake on Schiermonnikoog was accompanied by a stronger selection (Fig. 16A). I cannot satisfactorily explain why the mean handling time per *Macoma* eaten on Schiermonnikoog (10.3 sec) was lower than at Paesens (12.9 sec) in spite of the larger size of *Macoma* eaten (17.88 on Schiermonnikoog and 16.61 mm at Paesens). Small differences in the technique of opening *Macoma* in both areas may be involved (see chapter 4). The interaction of handling time and selection is difficult to assess for no data on handling time of *Macoma* of a specific size are available for free birds. For the captive bird, WR, such data are at hand in the cases when it was feeding on experimental *Macoma* populations of uniform size, the mean handling time for 15 mm *Macoma* was 12.5 sec (n = 116) and 14.7 sec (n = 137) for 19—20 mm *Macoma*. From the relation $W_e/(s + h_e) = W_r/h_r$ it can be seen that a difference of only a few seconds in handling time between small and large *Macoma* can influence selection significantly.

The density of *Macoma* of 11 mm or more, being in reach of the bill was much higher on Schiermonnikoog (248/m²) than at Paesens (158/m²). However, the densities of the *Macoma* the birds were feeding upon most, that is those with a size corresponding the mean size of the eaten *Macoma*, were pretty well the same, being 21.1 and 19.5/m² for Schiermonnikoog and Paesens respectively. This might explain why searching time at both places was nearly equal. Probably Oystercatchers select *Macoma* of that size giving the highest return per time (or effort) of foraging in each specific situation.

4. OPENING OF *MACOMA*

4.1. INTRODUCTION

Many mollusc eating bird species on the mudflats swallow their prey whole and crush the shells to pieces in their muscular stomachs. But the Oystercatcher, as we already know, opens each bivalve it catches, scrapes the flesh from the innerside and only eats the meat. *Macoma* is rather a small prey species for Oystercatchers. Considering the small yield in flesh, opening and emptying *Macoma* costs relatively much time. Therefore it must be important for the bird to prepare the food in an efficient way. However, especially bivalves can be hard to deal with when they have shut themselves firmly, and it is vital for the Oystercatchers to have a good start by nimbly preventing the shell to close itself. Since the Oystercatcher only eats the flesh, I assume it will try to open bivalves without damaging the shell, because, as I experienced myself, it takes less trouble to loosen the flesh from an intact shell than from one broken to pieces. How efficient is the Oystercatcher in opening *Macoma* and in its turn, how skilful is *Macoma* in resisting the Oystercatcher? Aspects concerning these questions will be considered in this chapter by describing the behaviour of Oystercatchers, the behaviour of *Macoma* and shell damage caused by Oystercatchers when opening *Macoma*.

4.2. THE BEHAVIOUR OF OYSTERCATCHERS OPENING *MACOMA*

Oystercatchers either open *Macoma* directly in the substrate (in situ) after they have located

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them or do so after they have dug them up and displaced them on the mudsurface. It is impossible to see precisely how *Macoma* is opened by observing wild birds, since they push *Macoma* into the substrate, concealing details from the observer. Sometimes birds can be seen hammering *Macoma*, this usually occurs on a firm substrate; on soft substrates biting movements, made with the bill, are seen. I often observed similar biting movements, from quite nearby, in captive birds feeding on *Mytilus* with the stabbing technique. The birds had inserted the bill by means of the "stabbing" technique through the cleft (see on) and subsequently tried to cut through the adductor by simultaneous biting and thrusting movements. Possibly biting in *Macoma* functions in the same way, through cutting the adductor. Biting movements, when attacking *Macoma*, were not accompanied by strong vertical thrusts, as was usual with *Mytilus*, and for this reason I prefer not to use the term "stabbing" here. Biting might be an adaptation to the relatively soft substrate, or to the small size of *Macoma* as compared to *Mytilus*, since less effort is required to cut the adductors of the smaller species.

More detailed observations on the opening procedure could be obtained by watching the captive bird WR from very close quarters whilst it was feeding on the mudflat in the experimental cage. It always handled *Macoma* in a fixed way. When WR located a *Macoma* it pulled the shell out of the substrate vertically upwards, pinching it between its mandibles. Subsequently it placed the shell with the ventral (Fig. 17A)

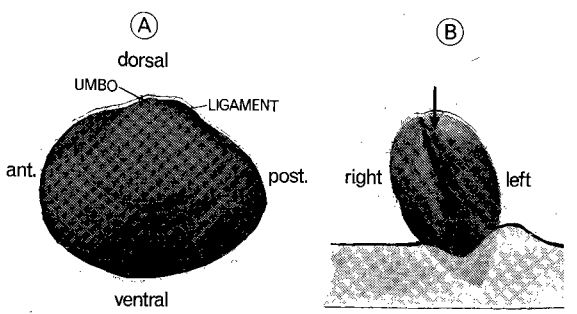


Fig. 17. A. Lateral view of a *Macoma* shell from the left. — B. Position of *Macoma* at the start of hammering by the captive Oystercatcher WR. The anterior end of the *Macoma* is facing to the bird. The arrow indicates the point of attack of the bill.

edge on the mudsurface, slightly at an angle, the right side facing the substrate, the left side upwards, and the anterior end of the shell pointing towards the bird (see Fig. 17B). Having completed this, WR started hammering with closed bill, directing a series of about 2—5 distinct hard vertical blows at one particular spot on the left valve, about two or three mm ventro-anteriorly of the umbo. Sometimes the valve broke, but frequently it was observed that the left valve rotated downwards in the median plane alongside the right valve, causing a small cleft between the dorso-anterior margin of the left valve and the opposite innerside of the right one. The cleft was often large enough to allow the billtip to slip in. Rotation of one of the valves alongside the other in the median plane and slipping the tip of the bill in through the resulting cleft was also observed by Dewar (1913) with Oystercatchers feeding on Mussels.

4.3. BEHAVIOUR OF *MACOMA*

When I excavated buried *Macoma* myself *in situ* during low water, I often found the siphons, mantle edges and foot protruding a short distance from the gaping shell. Gaping of the shell and protrusion of body parts might be necessary for respiration. The gape of the shell is caused by the elasticity of the ligament that draws the valves apart. The shell is closed tightly by the adductors and the cleft is shut only when the animal is disturbed.

When a *Macoma* is dug up and touched, it retracts the protruding body parts into the shell. This process takes a few seconds. At this instant one can slip the blade of a knife between the valves at the ventral side into the shell and the valves can also easily be rotated alongside one another in the medial plane. When a *Macoma* is pressed gently between thumb and index finger the animal closes the shell tightly. In the meantime it tries to retract the protruding bodyparts into the shell. At the final moment, when the last visible parts disappear, the shell reopens again about one mm for an instant, then it is shut firmly. Probably *Macoma* behaves in a similar fashion when it is extracted from the mud, pinched between the mandibles of an Oystercatcher and layed down on the mudsur-

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face. Oystercatchers can only open *Macoma* when the shell is gaping, however slightly. It frequently occurred that WR made another attempt at opening a *Macoma* it had abandoned some time before. Such a new attempt was only successful if the *Macoma* had started to re-bury itself, and in doing so had opened the shell a little bit so as to give the foot opportunity to penetrate into the substrate. Probably the degree of gaping largely contributes to the success an Oystercatcher has in opening a *Macoma*, and possibly it also determines whether a shell will be damaged or not. When the bill has penetrated into the shell, it usually severes the adductors first. By pulling the valves together the adductors in their turn determine the resistence the bill receives. Probably no damage occurs to the valves when the adductors are severed immediately. Any factor influencing gaping in *Macoma*, for instance desiccation of the substrate or its oxygen content, may also affect the success of Oystercatchers and the extent to which shells are damaged.

4.4. PATTERN OF DAMAGE OF SHELLS

The direct observations do not offer enough information to give sufficient insight into the mode and efficiency of the opening procedure of *Macoma* by Oystercatchers. Indirectly additional information may be gathered by analysing damage inflicted upon shells. This method was successfully applied to the Cockle and Mussel by Drinnan (1957, 1958a). The captive bird WR has supplied the most detailed direct information and shell remains left by this bird offer the best samples for further examination. Therefore, how WR fares in opening *Macoma* shall be studied first, in second instance we shall see whether the results fit in with data collected from other birds.

I definitely saw that WR practically always hammered just anterior to the umbo of the left valve. I wondered whether this fixed way of hammering upon the shells would give rise to a characteristic pattern of shell fractures, and also, whether the left valve would be damaged more often than the right one. A few times WR was seen to place *Macoma* shells with the ventral edge on the mudsurface, and the posterior end of the shell pointing towards the bird, slightly at an angle, with the right side facing upwards. In this case the bird hammered on the right valve at the posterior end. It would be interesting to see whether this deviant behaviour is revealed in the fracture pattern of the valves.

The fracture patterns of the shells were studied by dividing the shell margins into six sections (Fig. 18). Each shell was analysed for fractures

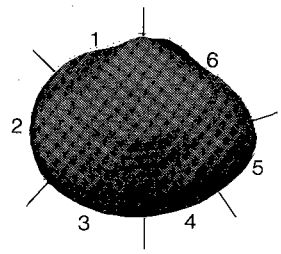


Fig. 18. Codes of sectors distinguished on shell margin.

for each valve separately. Opened shells were first grouped as undamaged and damaged. Damaged shells were classified into three categories:
— left valve damaged
— right valve damaged
— both valves damaged.

4.5. OPENING BY HAMMERING

Fig. 19A and Table 9 present all available data of the captive bird WR on opened shells. Table 9 summarizes the proportions of fracture categories of opened shells, and Fig. 19A depicts for part of the available material (672 left and 7 right valves), the distribution of fractured sections of shells, of which only the left or only the right valve had been damaged. Valves broken throughout all the sections (about 30% of the broken shells) have not been taken into account, because these give no information on the region of attack by the bill. Damage inflicted upon the left valves was particularly concentrated at the anterior end of the shell, while fractures on the right valves were centered round the posterior end of the shell. Table 9 shows that the shells were damaged preponderantly on the left valve. The conclusion is that

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Table 9. Percentage of shell fracture categories of *Macoma* opened by the captive Oystercatcher WR through hammering

Both valves undamaged %	One valve damaged				Both valves damaged %	Number of shells examined
	left	right	left / right	P χ^2-test		
31.5	65.9	0.9	75.6	< 0.01	1.7	2982

the way of hammering is reflected in the fracture patterns of the shells, the left valves nearly always being damaged, with fractures concentrated at the anterior end.

As mentioned earlier another striking feature in the opening procedure I saw, was that, while the Oystercatcher was hammering, the valves were forced to rotate alongside one another in the median plane. The rotation point between the two valves lies posteriorly of the umbo (Fig. 17A), therefore the force exerted by the bill at the point of attack results in a relatively large moment. The ensuing rotation movement is counteracted by the elasticity of the ligament and the adductors. At this instant the teeth of the hinge are not yet interlocked. If the power exercised by the bill is greater than the strain of resistance of the valve, the latter may break. If the shell does not break the bill is forced into the shell through the cleft appearing between the valves, starting in the median plane from the anterior to the posterior end and the bird tries to severe the anterior and posterior adductors, by a combination of cutting and biting movements respectively. During these actions of the bill the valves are forced apart sideways, counteracting the pressure exercised by the adductors. At this moment there is another chance the

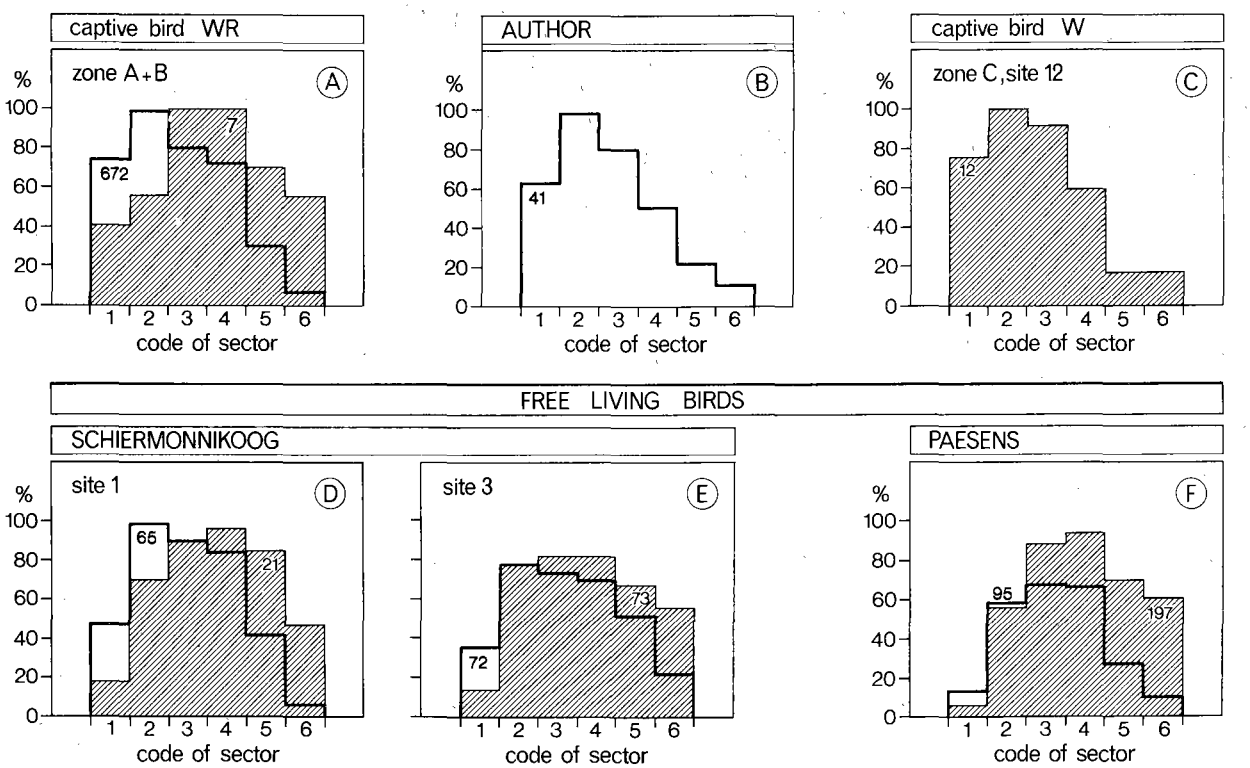


Fig. 19. Fracture pattern of *Macoma* shells opened by captive and free living Oystercatchers and by the author (for details see text). For the code of the shell margin see Fig. 18. Only shells with one valve broken and one intact are considered. The figures on top of the histograms refer to the number of left (not hatched) and right (hatched) valves in the samples.

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shell will break, namely if the power exercised by the bill exceeds the resisting strain of the shell before the adductor gives way. If one of the valves breaks, it is probably the one facing upwards, in the case of WR the left valve, because the other one receives extra support from the substrate. For one thing, the breaking of the shell probably depends largely on the extent to which the anterior adductor is severed by the first thrusts. This in its turn is determined by the degree a *Macoma* has closed its shell at the moment it is attacked.

Since it is not always possible in the field to observe when valves rotate and when not upon hammering, and because the hammering procedure, as applied by WR, in effect seems quite simple, I decided to imitate the bird in opening *Macoma*. Freshly collected *Macoma* kept in a bin with seawater, were slipped into a cleft in a piece of wood in the same position as WR used to place them. With an Oystercatcher bill I directed blows at the same point on the shell as WR did, that is two to three mm anteriorly of the umbo, till the left valve broke. Then I pushed the bill about one centimeter into the shell at the point of fracture, trying to sever the anterior adductor by moving the bill in the median plane forwards and backwards. This phase of the opening process is only a crude imitation of the birds' method. I cut the adductor with the chisel-shaped front edge of the closed bill, whereas the bird reaches the same goal by biting and cutting the adductor between the tip of the upper and lower mandible, both having sharp inner margins. During the phase of cutting the adductor I sometimes damaged the right valve, after the left valve had already been fractured in the hammering phase. Altogether 60 *Macoma* of 14—20 mm (mean 17.3 mm) were handled in this way: 51 shells were damaged to the left valve, nine to both valves. The breach lines I caused by hammering started at the dorsal margin in sector 1 or 2, continued to any place on the ventral margin, either by crossing the growth lines or following these a little way (Fig. 20). They were somewhat more irregular and more angular than those produced by the Oystercatchers. However, the general picture of the fracture pattern of the shells with broken left valves (Fig. 19B) resembled that of WR, and permit the conclusion that the way of attack was about the same in both situations.

There was one main difference between the bird and me. I did not observe the rotation movement of the left valve alongside the right one. Possibly in my efforts the shells were already closed too tightly and the hinge was locked, as it took seconds to place the *Macoma* in the experimental set-up, time enough for *Macoma* to shut up firmly. On this supposition we can explain the difference in the effects of the hammering of WR and myself, in that the bird did not damage all the shells it opened whilst I did. This difference should be expected, if, when the bird was hammering, the teeth of the hinge were usually not yet interlocked, whereas, when I hammered, all *Macoma* had had enough time to shut firmly. This stresses the fact that an Oystercatcher gains advantage if it attacks a *Macoma* it has located as quickly as possible, since when the valves can still be made to rotate, the risk of damaging them is reduced.

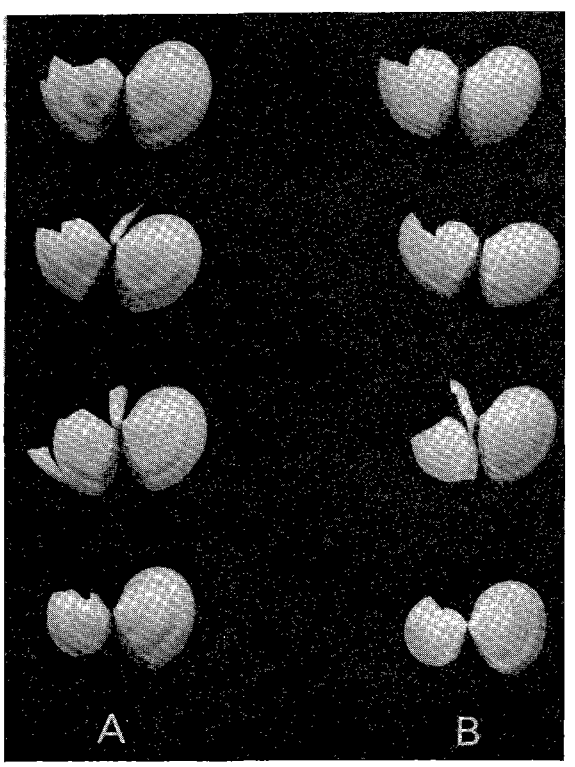


Fig. 20. Examples of *Macoma* shells hammered open by the author (A) and the captive Oystercatcher WR (B) showing similarity in shell damage.

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Table 10. Weight (mg) of left and right valves of *Macoma* shells (doublets) from Schiermonnikoog (zone B) dried at room temperature; n refers to the number of shells examined

Shell length	Left valve	Right valve		$\frac{\text{Left}}{\text{Right}} \times 100\%$
mm	mean ± S.D.	mean ± S.D.	n	
11	42.1 ± 7.9	43.0 ± 7.9	20	98.0
12	52.3 ± 6.8	53.1 ± 7.2	20	98.5
13	71.6 ± 10.7	72.8 ± 11.3	17	98.4
14	104.1 ± 13.2	106.0 ± 14.4	20	98.3
15	131.2 ± 20.4	134.2 ± 20.2	20	97.7
16	182.1 ± 37.2	187.4 ± 38.2	20	97.2
17	227.8 ± 40.7	233.9 ± 42.4	20	97.4
18	271.7 ± 41.3	279.5 ± 44.5	21	97.2
19	307.2 ± 55.4	317.9 ± 56.7	11	96.6
20	469.9 ± 71.4	489.0 ± 68.7	5	96.1
21	502.2 ± 135.6	513.7 ± 137.0	6	97.8
			mean	97.5

The results of WR raise the question whether there is some advantage in general in attacking the anterior part of the left valve, or whether this was a fixed habit, characteristic for this particular bird. The first suggestion can be checked now, the second not until we have examined results of other birds.

In the region of the shell about two to three mm anteriorly of the umbo, the angle between the opposing valves is larger than in the dorso-posterior region and the profile of the shell curves upwards. This feature might prevent the bill from slipping away on the smooth surface of the shell. In contrast, in the dorso-posterior region the profile of the shell curves downwards and no extra support for the bill can be expected here. Another important fact is that, as shown by the course of isopachs (lines connecting points with the same thickness) of valves of *Macoma* in Thijssen's paper (1971), the thickest portion of the valve is just ventro-anterior to the umbo, so this is probably the strongest part too. The chance that the blow of the bill causes rotation of the valves instead of damage is greatest when the blow is aimed exactly at the spot where WR was wont to hammer.

Why did WR deliver blows mainly on the left valves? Possibly left valves are stronger than right ones, so they can receive more battering before they break. A good measure for the resistance of a valve against the force executed by the attacking bill might be its thickness. The topography of the thickness of a *Macoma* valve is complicated (Thijssen 1971), and measuring it is a time consuming affair. The weight of a valve, however, is a good indication for its mean thickness. The weight is proportional to its length × height × mean thickness. Since shell length and height increase isometrically during growth, the mean thickness is related to the cubic root of the weight of the valve.

Table 10 shows the proportion of weights of left and right valves of *Macoma* shells at Schiermonnikoog. It turned out that left valves, contrary to expectation, were lighter and consequently slightly thinner than the right valves, though the difference was small (about 2.5%). A higher weight of the right valve of *Macoma* was also found by Lever (1958), this seems to be a general feature of the species. It looks like the bird took the wrong choice by hammering on the left valve, unless the difference of, on the mean 2.5% in weight, corresponding with 0.8% difference in mean thickness, is too small to give a perceivable difference in damaged valves. If this is the case, the bird cannot learn that it is more profitable to hammer upon the right valve. Fig. 21 might throw light upon the problem. The mean thickness of left valves is depicted in its relation to shell length (a), and also to the percentage of undamaged shells (b) of the *Macoma* opened per mm-class. The percentages of undamaged shells are positively related with the shell lengths of *Macoma* of 16 mm or more. No such correlation exists, however, for shells of 11 to 15 mm length. It seems a shell has to be at least as strong as one of the 16 mm class to be able to withstand a blow of an Oystercatcher

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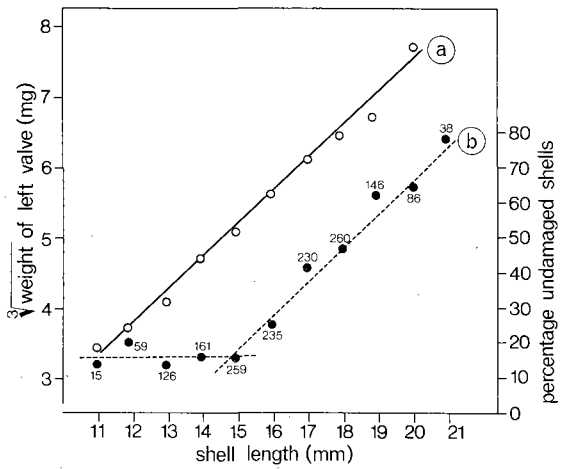


Fig. 21. a. Mean thickness (measured as $\sqrt[3]{}$ weight (mg) of the left valve of *Macoma* in relation to shell length (Schiermonnikoog zone A + B). Twenty valves weighed per mm class. $y(11—20\text{ mm}) = 0.46x—1.76, r = 0.99$.
b. Proportion of undamaged *Macoma* shells opened by the captive Oystercatcher WR by hammering in relation to shell length (zone A + B). Figures refer to the number of shells examined. $y(11—15\text{ mm}) = 0.31x+12.23, r = 0.18$; $y(15—21\text{ mm}) = 9.65x—126.25, r = 0.99$.

bill. The valves of a *Macoma* of 15 mm shell length are on average 1.65 times as thick as those of a *Macoma* of 11 mm, nevertheless the percentages of unbroken shells of both size classes are the same. It is not very likely that the bird profits from hammering mainly upon the right valve, since the proportional difference in mean thickness between the two valves is small. On account of this one would expect that the bird would hammer just as often on the one valve as on the other. The question remains, why WR hammers upon the left valves. Possibly data on the behaviour of other birds can aid in solving this problem.

A few data on opening *Macoma* are available for four other captive birds, with the colour banding codes Yellow (Y), Yellow Green (YG), Green (G) and White (W). They were observed hammering on *Macoma* shells, and the results are collected in Table 11. WR, YG and G fed together in the same cage on site 3, leaving 26 shells with the left valve and 21 with the right valve damaged, respectively. WR once fed alone on the same site, and left eight damaged shells, each one with the left valve fractured, in correspondance with its habit. YG or G or both birds did inflict damage to the right valves. The birds W and Y mainly caused damage to right valves. Only of the bird W a few notes were taken down on the exact way it attacked *Macoma*. It placed the shells in front of itself, with the anterior end nearest, ventral side on the substrate, left valve facing downwards, right valve upwards, thus contrary to WR. Fig. 19C shows that the right valves were damaged preponderantly at the anterior end, corresponding with the point of attack by the bill. This outcome is analogous to the data obtained from WR. Evidently valves are fractured most severely in the region where blows strike them, when birds hammer. Looking over the data, so far, I have the impression that individual Oystercatchers have the habit to handle *Macoma* shells in a fixed way, causing damage either mainly to the left or mainly to the right valve.

The observation of habit formation leading to individual differences is by no means new in Oystercatchers. Mussels for instance are opened either by hammering or stabbing. Upon hammering a hole is made in one of the valves by the bill, upon stabbing the bill is pushed into the shell through the cleft between the slightly gaping valves, severing the adductors (Dewar 1908). Norton Griffiths (1967, 1968) has shown that individual Oystercatchers practice one of the two techniques; they are either hammerers

Table 11. Number of fracture categories of *Macoma* shells opened by five captive Oystercatchers through hammering

Birds (colour-code)	Site	Both valves undamaged	One valve damaged			Both valves damaged	Total
			left	right	left / right		
WR, YG, G together	3	41	26	21	1.2	1	89
WR	3	4	8	—	—	—	12
W, Y together	21	4	2	18	0.1	3	27
W	12	3	2	13	0.2	—	18

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or stabbers. According to him the complicated behaviour of attacking a Mussel, opening the shell and loosening the flesh from the shell is gradually learned by the bird during the period it is still reared by the parents. The young eventually adopt the same technique of attacking Mussels as their parents and they keep to this method for the rest of their lives.

Oystercatchers who open Mussels by hammering, probably also handle them in a constant way. One of our captive birds, when feeding on a natural musselbed, opened the Mussels by hammering a hole in the shell at the mid ventral side; 48 out of a total of 50 shells were damaged at the left and only 2 at the right valve. Individual habits have been observed on other bird species too: individual Jays *Garrulus glandarius* open peanuts in a particular fashion (J. de Heer pers. comm.) and Vince (1964) reports that individual Great Tits *Parus major* use their feet in their own way when handling food.

I consider it likely that the way Oystercatchers open *Macoma* also develops through learning during their ontogeny. It would be interesting to investigate whether the birds learn that it is of benefit to aim blows at the convex anterior side of the valves, and whether the habit of either attacking the left valve or the right one starts off by some chance encounter. Another aspect of interest would be to find out if the time required for, and/or energy spent in, opening shells is reduced by keeping to one technique, thus maximising the skill in opening the bivalves.

4.6. OPENING BY BITING

Let us now see how free living Oystercatchers damaged *Macoma* shells and compare their results with those of the captive birds. Shells opened by wild Oystercatchers have been collected from the mudflats at Schiermonnikoog (site 1 and 3), at Paesens (1979) and at Vlieland. Opening behaviour was not uniform in these areas. At site 1 on Schiermonnikoog the hammering technique dominated, though biting occurred too. The substrate was rather sandy here, and therefore firm. At site 3, in the direct vicinity of a musselbed, more birds were seen biting than hammering, the substrate was relatively soft. At Paesens biting was the general technique applied, the substrate was soft. No observations were done on the opening procedure by Oystercatchers on Vlieland; the substrate was sandy and firm.

On the ground of the preceding conclusions on the correlations between the hammering technique and patterns of damage inflicted upon the valves, we need not necessarily expect a similar fracture pattern when shells are opened by biting. Therefore we shall go over the results on shell damage at Schiermonnikoog site 1 first, where the wild birds predominantly hammered. Subsequently we shall analyse the shells collected at Paesens where biting predominated, and lastly those from Schiermonnikoog site 3 where hammering and biting occurred simultaneously. The shells opened at Schiermonnikoog on site 1 were collected from an area of 20 m^2. Only a small number of wild birds could have foraged there, for individual Oystercatchers usually feed on the same restricted area day after day. In Table 12 and Fig. 19D a summary is given of the shell fracture categories of *Macoma* opened by these Oystercatchers. In my view the biased left-right ratio of damaged valves is due to the ratio of "left-damaging" to "right-damaging" birds present at the time. Fig. 19D shows that left valves were damaged relatively more at the anterior end, right valves more towards the posterior. The patterns correspond closely with those of WR (Fig. 19A). These data suggest that the wild birds tackled *Macoma* when ham-

Table 12. Percentage of shell fracture categories of *Macoma* opened by free living Oystercatchers

	Both valves undamaged %	One valve damaged				Both valves damaged %	Number of shells examined
		left %	right %	left / right	P χ^2-test		
Schiermonnikoog site 1	25.1	50.6	11.9	4.3	< 0.01	12.3	243
site 3	32.7	21.7	28.3	0.8	< 0.05	17.3	614
Paesens (1979)	30.4	12.3	33.8	0.4	< 0.01	23.5	829
Vlieland	56.7	19.4	15.5	1.3	< 0.05	8.4	1361

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mering in a similar fashion as the captive bird WR did.

Now we shall consider the results offered by the samples of shells opened by birds generally seen biting at Paesens (Table 12 and Fig. 19F). The shells were collected from a relatively large area, so we can assume they were opened by a large number of different birds. Relatively more right valves were damaged than left ones, with fractures preponderantly concentrated at the posterior end of the right valve. Left valves were damaged most often along the mid-ventral margins. This suggests that a different general fracture pattern is caused when *Macoma* are opened by biting than by hammering.

Details of the opening procedure of *Macoma* when Oystercatchers utilize the biting technique could not be seen directly, because the shells vanished from view in the ooze. But observations on free living colour-banded Oystercatchers revealed quantitative information on the time required to handle *Macoma* in different situations, which might be helpful in understanding the opening procedure of *Macoma*. It turned out that 36% of all *Macoma* found were opened *in situ*, the rest after displacement onto the surface. The mean time to handle a *Macoma in situ* was 8.9 ± 3.3 sec (about 1000 *Macoma* opened by 132 birds), for a displaced *Macoma* 15.1 ± 5.3 sec (about 2000 *Macoma* opened by 178 birds). This difference is highly significant ($P < 0.0001$). Measurements of bill characteristics of the colour-banded adult birds were known. With these data a new correlation turned up: Fig. 22 shows that the thickness of the distal four mm of the billtip was positively related to the handling time of *Macoma* opened successfully after displacement ($y = 0.434\ x + 7.159$ (n = 91); r = 0.27; $P < 0.02$). This relation did not hold when *Macoma* were opened *in situ* ($y = 0.001\ x + 7.879$ (n = 76); r = 0.01; n.s.). The odds are that *Macoma* eaten *in situ* were gaping widely, giving thick- and thin-billed birds equal chances to open them, but that *Macoma* displaced onto the mudsurface were gaping less, so thin-billed birds had a greater chance to penetrate into them more quickly than thick-billed birds. No doubt the extent to which a *Macoma* is gaping at the moment it is localized largely determines the chance that it will be opened successfully by the Oystercatcher.

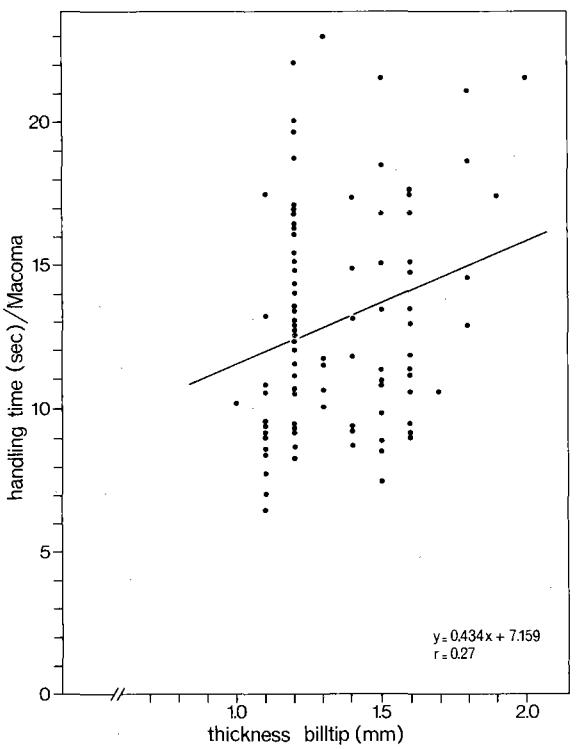


Fig. 22. The time required by free living Oystercatchers in May 1979 at Paesens to open and eat *Macoma* that had been extracted from the substrate and deposited on the mudsurface in relation to the thickness of the billtip. Each point refers to the mean value of a sample of five or more *Macoma* opened by one particular bird.

The fact that the fracture pattern of shell margins shows relatively more damage to the mid-ventral and posterior half than to the anterior may be another cue in interpreting the opening procedure. The gape of the shell is most likely widest at its posterior end where the siphons protrude, and the billtip probably penetrates into the shell somewhere in this region, along the ventral margin. The following tentative reconstruction of the method of opening a *Macoma* by biting can be made.

After the Oystercatcher has lifted a *Macoma* from the substrate and put it with one valve flat on the mudsurface, it immediately tries to slip its closed billtip into the slit at the ventral-posterior end of the shell. As soon as it succeeds, it raises the bivalve into a vertical position, pushing its bill farther into the shell and cleaving the

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valves apart at the same time. The valve initially lying underneath is buttressed by the mudsurface at the beginning of these actions, while the upper valve is wrenched upwards, till the vertical position is reached and both valves are supported by the substrate. In the meantime the bird tries to sever the posterior adductor muscle with its billtip. Now two things can happen: the adductor is cut before the upper valve gives way, so it does not break when it is wrenched upwards, or, on the contrary, the upper valve gets fractured before the posterior adductor is fully severed. In most cases the shell is pressed completely down into the substrate as a result of this way of handling. If the chance that a shell is damaged should be minimized, it is better to buttress the weakest left valve and tackle the stronger right one, speculating that it will not break. And this is what actually was found at Paesens (Table 12).

At this point it may be useful to review the relevance of the difference in mean thickness between left and right valves for the Oystercatcher attempting entrance by hammering or biting. When hammering the aim of the Oystercatcher is to rotate the two valves of a *Macoma* in relation to each other in the medial plane. A maximum force and probably often an overdose of impetus will be applied to the shell surface. The small difference in thickness of left and right valve is not relevant. When opening a *Macoma* by biting, however, one can expect that the Oystercatcher, once the bill has penetrated into the shell, will use just enough force to sever the adductor muscles, more force will only add to the risk of breaking the bivalve. The thickness of the shell is proportional to the size of the adductor muscles, and also proportional to the size of the shell. Therefore we can expect that the force with which the billtip is pushed into the shell will be proportional to shell size. This also means that the chance to break the shell must be similar for all sizes. Fig. 23 shows that indeed there was no correlation between the proportions of undamaged shells and shell length for the shells collected at Paesens.

Now we return to Schiermonnikoog, site 3, where Oystercatchers were seen opening *Macoma* by hammering and by biting. More right valves were broken than left ones (Table 12).

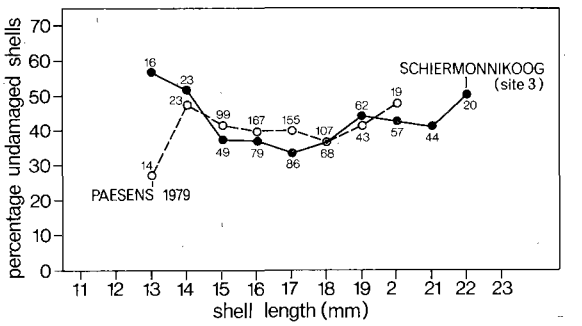


Fig. 23. Proportion of undamaged *Macoma* shells, opened by free living Oystercatchers in relation to shell length. Figures refer to the number of shells examined.

The fracture pattern of the valves (Fig. 19E) is more or less intermediate between those of the samples collected from site 1, where the birds predominantly hammered, and from Paesens where they were generally seen biting. There was no correlation between the proportion of undamaged shells and shell length (Fig. 23), as was found at Paesens, suggesting that biting was the technique applied most often on Schiermonnikoog at site 3.

From Vlieland no information on the behaviour of the Oystercatchers when opening *Macoma* is available. The substrate was rather firm, probably permitting opening by hammering. Left valves were slightly more often broken then right ones (Table 12). If hammering was the method applied most, this probably means that more left- and less right-damaging birds were represented in the population.

4.7. CHOICE OF TECHNIQUE

Summarizing our observations on the way Oystercatchers open *Macoma* we come to the following picture. Opening of *Macoma* can be achieved by two techniques: hammering and biting. When hammering, blows of the bill are directed at the anterior region of one of the two valves. Access into the shell is gained when the valve breaks or loses its apposition with the opposing valve. When biting the bill is pushed into the shell in the gape between the valves at its ventral-posterior margin. Shell damage occurs at the point of attack of the bill and is largely determined by the degree the shell is gaping. Hammering requires a firm substrate, biting can

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be performed on a rather soft substrate, but not in very soft mud, since some resistance of the substrate is required to counteract the forces exercised by the bill on the shell.

On sites where hammering is possible, hammering and biting Oystercatchers feed together, but individual birds keep to one of the two techniques. Individuals which open *Macoma* by hammering do this in a characteristic and constant way, they always put the *Macoma* in the same position and hammer on the same valve, left or right depending on the individual, producing a fixed pattern of shell damage. Habit formation in opening *Macoma* is probably determined during ontogeny. The question remains open if Oystercatchers learn to open *Macoma* by hammering as well as by biting, applying the method that is most appropriate under the prevailing conditions. To me it seems likely that Oystercatchers do learn both techniques, otherwise the hammerers would not be able to exploit the rich *Macoma* populations occurring over vast areas in the Wadden Sea in soft substrates, like those at Paesens.

The question arises which is the most profitable way of opening *Macoma*. We shall try to answer this question by considering handling in the different situations. The mean time the captive bird WR needed to open *Macoma* by hammering was 13.8 sec (435 *Macoma* timed). The wild birds at Paesens, that opened *Macoma in situ* needed 8.9 sec on the average to handle the bivalve and 15.1 sec after displacement by biting. Because in the mean 36% of all *Macoma* were opened *in situ* and 64% after displacement, the mean handling time per *Macoma* eaten at Paesens was 13.1 sec, nearly equal to that of the hammering of WR. Opening *in situ* apparently is the more profitable way. The birds gain time because they do not dig up the bivalves. Probably they do not need to do this because the shells are gaping and the birds do not really open them, but simply loosen the flesh from the valves. Second in line is hammering. Opening by biting after removing the shells onto the substrate takes most time; evidently piercing the bill into the shell and opening it in the soft ooze is a time consuming method.

The degree to which a *Macoma* is gaping probably largely determines if it can be opened *in situ*, and consequently the time that is required to open it. Factors influencing gaping of *Macoma* may be important in determining the time Oystercatchers have to spend in opening *Macoma*. In this respect one may ask if visual location of *Macoma* using surface tracks is profitable for Oystercatchers. *Macoma* located by sight are found more quickly than by touch. It is conceivable that a *Macoma* found by sight has less time for drawing its valves together than one approached by the multiple pecking method of searching by touch. This point was not investigated but deserves further study.

The next question we may ask is why did all the five captive birds studied extract the *Macoma* they found from the substrate and why did they not handle at least some *in situ*? The answer probably is that *Macoma* gape less to avoid desiccation in the fairly firm substrates prevailing in these tests.

Last we shall summarize and discuss what is known about differences in extent of left and right damaged valves of two other Oystercatcher prey, the Mussel and the Cockle (Tabel 13).

Table 13. The ratio in numbers of shells with either the left or the right valve damaged of *Mytilus* and *Cerastoderma* opened by free living Oystercatchers

Prey	Locality	Left / Right	P χ^2-test	Number of shells examined	Reference
Mytilus	Forth	> 1	?	?	Dewar 1908
	Morfa	1.4	< 0.01	440	Drinnan 1958a
	Pensarn	0.7	< 0.01	276	
	Ythan A	1.0	n.s.	255	Heppleston 1971
	B	1.2	n.s.	113	
	D	1.0	n.s.	157	
	Montrose	0.7	n.s.	88	
Cerastoderma	Morecambe Bay	1.0	n.s.	> 2000	Drinnan 1957
	Rottumerplaat	1.3	< 0.05	157	Hulscher unpubl.

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No consistent picture emerges. Only Dewar (1908) discusses the possible factors causing dissimilarity in the numbers of left and right broken valves. When describing the opening of Mussels this author states that, after an Oystercatcher has inserted its bill into the shell between the valves in the medial plane, the bird tries to prize the valves apart by lateral movements of head and bill or by rotating the bill through 90° around its longitudinal axis. According to Dewar both lateral and rotational movements of the bill are performed preponderantly to the birds left side, and, because the bird approaches the Mussel more often at its anterior than at its posterior end, more left than right valves are broken. Dewar gives no information on the number of birds he has observed. Baker (1974) also observed the rotation of the bill around its vertical axis in three different species of New Zealand Oystercatchers when opening bivalves. All three species rotated their bills significantly more often to their left than to their right sides. Neither from Dewar's paper nor from that of Baker is it clear whether these authors actually have seen the valves being prized apart by the bill movements described.

When watching captive Oystercatchers feeding on Mussels myself from nearby, I have often seen similar lateral and rotational movements of the bill as described by Dewar, but never did I see that the valves of the Mussel were prized apart during these actions. The movements in question were simple reorientation movements of the bill following upon changes in the position of the Mussel, caused by the bill itself when it was penetrating into the shell by vigorous thrusts in the medial plane. Prizing the valves apart also occurred but in a different way. In the first place the bill was entirely retracted from the shell, then the bill was closed, turned 90° and only the tip inserted again into the shell perpendicularly to the valve margins. By subsequently forcibly opening the bill the valves were separated (see also Norton-Griffiths 1968). Prizing bivalves apart as described by Dewar can only be successful when the shell is firmly anchored to the substrate, as is usually the case with Mussels. The method can never successfully be applied to Cockles. This can easily be demonstrated using a loose Oystercatcher's bill. Even when buried in a firm sandy substrate, the Cockle shells follow the vertical rotation movements of the bill; this happens also when the adductors have been heavily impaired before. In my opinion prizing with Mussels does not occur either, because the bird runs the risk of dislocating its mandibles and certainly cannot exert a force that can break the valves at the same time.

5. OYSTERCATCHERS AND TREMATODE INFECTED *MACOMA*

5.1. INTRODUCTION

After an Oystercatcher has located and opened a *Macoma*, one can ask the question whether it inspects the quality of the prey. Some observations suggest that the bird checked its food before eating it. Free living Oystercatchers as well as the captive bird WR when feeding on fenced-in areas, frequently rejected some *Macoma* they had found and opened. The basis upon which the wild birds rejected the prey could not be seen, but it turned out that the *Macoma* rejected by WR were invariably parasitized by a trematode. It may well be that this behaviour serves to reduce infection. This section will report on the extent to which infected *Macoma* were rejected by the captive bird WR in experimental set-ups, and discuss the selective value of this behaviour.

5.2. LIFE CYCLE OF THE TREMATODE

Swennen & Ching (1974) identified the trematode in question to be *Parvatrema affinis*. These authors also studied the life cycle of the parasite. According to them an infected *Macoma* cannot be distinguished from an uninfected one when the valves are closed. Upon removing a valve of an infected specimen small white sausage-shaped bodies with a mean length of 612 by 350 μm become visible. These are the sporocysts, full of metacercariae (40 on the average). Sporocysts fill up the entire interstitial space in the gonads and the digestive gland. Within the sporocyst cercariae rapidly develop into metacercariae, so *Macoma* serves both as first and second intermediate host for *Parvatrema*. The final host of the parasite is a bird. For instance in the southern part of the North Sea, Common

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Scoter *Melanitta nigra*, Velvet Scoter *M. fusca*, Herring Gull *Larus argentatus*, Eider *Somateria mollissima* and Oystercatcher have been found infected (Loos-Frank 1971, cited by Swennen & Ching 1974). The birds become infected by eating parasitized *Macoma*. Infection experiments with uninfected newly hatched Mallard ducklings *Anas platyrhynchos* showed that metacercariae developed into mature flukes in the course of a single day. Egg production already started four hours after infection (Swennen 1969, Swennen & Ching 1974). Repercussions for the host are not yet known.

Infected *Macoma* are virtually confined to the upper reaches of the intertidal zone (Swennen & Ching 1974). Sometimes *Macoma* leaves its protected position deep in the mud. It moves up to just beneath the mudsurface and starts crawling in a horizontal direction making conspicuous crawling tracks on the way. The *Macoma* can be found at the end of those trails, betraying their presence by a slight elevation of the mudsurface. All such *Macoma* are infected with *Parvatrema affinis* (Swennen 1969). Hulscher (1973) experienced the same on Schiermonnikoog, and found that some parasitized *Macoma* dug themselves out upon the mudsurface and remained there. The high oxygen demand of the dense metacercariae-clump probably causes oxygen shortage in the bivalve and compels it to crawl to the surface. Swennen (1969) hypothesized that the crawling behaviour of *Macoma*, induced by the parasite, enhances the chance of the infected *Macoma* to be eaten by the final host of the parasite, so its life cycle is ensured.

Other examples of parasites altering the behaviour of the intermediate host and thus increasing the chances of predation by their final hosts are reviewed by Holmes & Bethel (1972). Another example, the Dogwhelk *Nucella lapillus*, an inhabitant of rocky sea shores, has been discussed by Feare (1971). This species is an important prey of Oystercatchers throughout the summer, but disappears from the menu in the winter, when the Dogwhelks withdraw into clefts and pools where they are safe from Oystercatcher predation. Adult Dogwhelks infected with the trematode *Parorchis acanthus*, a species that castrates its host, go into winter aggregation later and thus undergo increased risk of being ingested by Oystercatchers who serve as one of the final hosts.

5.3. OBSERVATIONS ON THE CAPTIVE OYSTERCATCHER WR

In the beginning of the summer of 1967, when the observations with the captive Oystercatcher WR on natural *Macoma* fields started, it was seen several times that some *Macoma* found in the sand and brought to the surface were actually opened, but that the flesh was not swallowed by the bird. Sometimes it was repeatedly taken into the bill but finally rejected altogether, or the shell was only opened without taking the flesh into the bill at all.

Upon inspection it turned out that all the *Macoma* refused where infected with *Parvatrema*. Usually the flesh had been loosened from the shell and tossed away, occasionally it remained in the opened shell. Free living Oystercatchers have been seen to refuse *Macoma* flesh, but in such cases it is more difficult to prove that rejection was caused by *Parvatrema*. However, at Paesens in May 1979 the flesh of an infected *Macoma* was found twice just a few centimeters from an empty shell on an area where many Oystercatchers had been feeding on *Macoma*. Recently (May 1981) at Paesens during observations from an observation tower, two birds feeding on a permanent spot were seen to reject *Macoma* regularly after having opened them. Once I found the loose flesh of five infected *Macoma* on the mudsurface immediately after the observations.

Most likely it is not exceptional that Oystercatchers discard parasitized Macoma. The question arises to what extent this takes places. To answer it choice experiments have been carried out with WR. Non-infected and infected *Macoma* were simultaneously offered in a cage on a grass field near the field laboratory. Subsequently, observations were made with this bird on the number of *Macoma* it rejected when it was feeding on fenced-in areas on the mudflats with natural and experimental *Macoma* populations.

5.3.1. Choice experiments near the field laboratory

In a first experiment seven large (17—20 mm)

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Table 14. Choice experiments with simultaneously offered non-parasitized and parasitized *Macoma* to the captive Oystercatcher WR near the field laboratory. Test 1: intact shells; test 2 flesh only. See text for scoring method

Test	Supply	Scores	Non-infected		Infected	
			eaten	rejected	eaten	rejected
1	7 non-infected *Macoma* 7 infected *Macoma*	18	5	—	2	11
2	9 non-infected *Macoma* 9 infected *Macoma*	16	9	1	1	5
Total		34	14	1	3	16

non-infected and seven large infected *Macoma* were mixed and offered to the bird on a plate. The shells had been opened but the flesh was left intact inside. The bird had been deprived of food for 8½ hours before the session started. How often non-infected and infected *Macoma* were eaten or rejected was determined by watching the bird from a hide. Each time the bill touched a *Macoma* was scored as a choice. After 18 choices the test was discountinued because some *Macoma* had been thrown out of the plate and could not be located any longer. The results are given in Table 14.

In a second test, one hour after the first, detached flesh of nine non-infected and nine infected large *Macoma* was offered in two separate plates placed next to each other. The results from 16 choices of the bird were recorded (Table 14). If the results of both tests are combined we see that the bird ate significantly (χ^2-test) more non-infected *Macoma* ($P < 0.01$) and rejected significantly more infected ones ($P < 0.01$).

5.3.2. Field observations

The observations were done as described above. The number of *Macoma* consumed and refused was noted. It was impossible to see from the hide whether the discarded *Macoma* were indeed infected, but the number of items seen to be rejected was generally in fair agreement with the number of infected *Macoma* found on the mudsurface after the experiment. In all cases some infected *Macoma* could not be retrieved because the flesh had been loosened from the shell, thrown away and trampled upon by the bird. The infection rate per size class of the local *Macoma* population was determined.

By comparing the proportion of infected *Macoma* expected within the sample of opened shells with the proportion actually rejected the extent to which infected *Macoma* were refused can be calculated. The assumption was made that no *Macoma* were rejected upon localization underground. Only observations in daytime are considered.

Natural Macoma populations. Infection rates of the *Macoma* population were determined in zone A (10—20 June) at the sites 6, 7 and 8 and on 25—26 August at site 22; in zone B on 30 August—2 September at site 23, this site was also representative for the sites 16—21 (Hulscher 1973).

The data are summarized in Table 15. It is evident that less *Macoma* were rejected than was

Table 15. Proportions of rejected *Macoma* by the captive Oystercatcher WR in relation to the proportions of infected *Macoma* in the populations

	Number of *Macoma* opened	Rejected		*Macoma* infected in the population
		number	%	%
Natural populations:				
zone A, 10—20 June, site 6, 7, 8	669	42	6.3	18.7
25—26 Aug., site 22	214	10	4.7	15.5
zone B, 30 Aug.—2 Sept., site 16—23	480	21	4.4	18.7
Experimental populations:				
small *Macoma* (15 mm)	456	17	3.7	20.6
large *Macoma* (19—20 mm)	656	121	18.4	23.9

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anticipated according to the ratio of infected animals in the populations: WR must have eaten about 70% of the infected *Macoma* found.

Experimental Macoma populations. *Macoma* collected for building up experimental populations during 26 June—5 August were found to be infected in 20.6% of the small (15 mm) *Macoma* individuals (131 specimens examined), and in 23.9% of the large (19—20 mm) *Macoma* (163 specimens examined). The results of WR when feeding in daytime on fields with *Macoma* of one size (either 15 mm or 19—20 mm) are pooled in Table 15.

Assuming that all rejected *Macoma* were infected, this would mean that about 82% of the small and 23% of the large parasitized *Macoma* had been eaten. Large infected *Macoma* were rejected significantly more often than small ones ($\chi^2 = 53.6$; $P < 0.001$). In this connection it is interesting to note that large *Macoma* contain on the average more sporocysts than small ones (Swennen & Ching 1974). The results of both the choice experiments near the laboratory and the field observations indicate that WR can discriminate parasitized *Macoma*, but does not always reject them.

5.4. DISCUSSION

In all likelihood WR discriminated between infected and non-infected *Macoma* after having opened the shell on the mudsurface. In view of the many parasitized *Macoma* dug up it is quite improbable that the bird noticed the difference when the bill localized the buried shells, or if it did this must have been quite imperfect.

Often infected *Macoma* were taken into the bill several times and nibbled at before final refusal. Prime cause of the rejection either is the bad taste of the flesh or a touch stimulus, the sporocysts being hard and granular. Some *Macoma* were discarded immediately after opening the shell. These must have been recognized as foul by taste, touch or sight during the opening procedure. The whitish conspicuous colour of the well developed sporocysts may have served as cue. Large *Macoma* contain more sporocysts in absolute numbers than small ones and can more easily be recognized as being infected. This might be the reason why WR refused more large than small *Macoma*. Also the findings that relatively more *Macoma* were rejected in daytime than in darkness points to visual recognition of infected *Macoma* (see above).

No data upon the role of the crawling tracks of parasitized *Macoma* in the infection cycle were collected in these experiments. It may well be that Oystercatchers have learned that *Macoma* with crawling tracks are parasitized and therefore avoid them. In that case the chance of ever seeing them eating such a specimen is negligible. Other birds feeding upon surface-*Macoma* have never been seen either. On the other hand I have found fresh pellets of Herring Gulls exclusively containing remains of *Macoma*. Apart from shell fragments the pellets all contained a few to maximally ten empty, but undamaged doublets of large *Macoma* (18—21 mm). Since healthy *Macoma* are beyond reach of Herring Gulls the specimens in the pellets must have been on or just under the surface and were most likely parasitized.

Predators specializing upon one prey species for long periods and acting as final hosts for the parasite of the prey run the risk of infecting themselves to a harmful level. Cases of mortality among gulls and terns after experimental and natural infection with trematodes (*Cotylurus* spp.) have been described (Swennen *et al.* 1979). The detrimental effects of parasites on their hosts may largely depend on the general condition of the latter. Among Eiders, who perished shortly after the breeding season, most likely due to a heavy infection of the Ancantocephalan worm *Polymorphus botulus*, more females than males were involved (Swennen & Van den Broek 1960). Females fast during the incubation period (Korschgen 1977), so their general body condition must have been inferior to that of the males.

During most winters one or more cold spells of varying length occur in the Wadden Sea. In such periods feeding conditions are usually bad. When temperatures drop below zero Oystercatchers do not immediately react by leaving the area when feeding has become totally impossible; many try to tide over the adverse time, relying upon their fat reserves. In the course of their long life span Oystercatchers have to cope repeatedly with such conditions. The effect of a parasitic load may be detrimental to the birds

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throughout such periods of famine. Therefore each response of the host preventing infection or lowering its levels may be advantageous. Physiologically homoioterms (including birds) usually respond to parasitic infection by building up immune systems. The immune response may result in elimination of the parasite that provoked it and/or make the host refractory to reinfection (Kennedy 1975, Swennen *et al.* 1979).

Indirectly birds may lower their parasitic load by changing to other diets. This happens more or less automatically when a species shows seasonal migrations.

Studies on gulls (Threlfall 1967, Bakke 1972 cited by Kennedy 1975) suggest that the parasitic levels in wild birds are for the most kept at low levels because of dietary changes of the host in relation to its ecology. The seasonal movements of the Oystercatchers in the Wadden Sea are an example of such a negative feedback system: those birds leaving the Wadden Sea during the breeding season and changing to another diet escape further infection; at the same time the low numbers of Oystercatchers in the Wadden Sea prevent the infection of the *Macoma* population rising to extraordinary high levels.

To my knowledge the direct behavioural response of refusal of a parasitized prey by a potential host of the parasite, as observed in this study, has not been described before.

6. QUANTITATIVE FOOD INTAKE WITH *MACOMA*

6.1. INTRODUCTION

As pointed out earlier, the information available at present on the bulk diet of Oystercatchers in estuarine areas points to *Cerastoderma* and *Mytilus* as main food items. But as we have seen, in the Wadden Sea Oystercatchers at times feed solely on *Macoma*, at least in daytime. No data were available for the night. In this section we shall try to answer the question whether *Macoma*-yields obtained in daytime are sufficient for the Oystercatchers to subsist upon, or whether additional feeding at night is essential for the birds solely feeding on *Macoma* to meet their needs. For this purpose we shall compare the daytime yields with an estimation of the daily food requirements.

6.2. METHOD

Birds exclusively feeding on *Macoma* were observed on the mudflats of Vlieland, Schiermonnikoog and Paesens. It was ascertained that the birds did not feed on the roosts. Drinnan's method (1957) was followed in broad lines to estimate the mean food intake per low water period per bird.

Feeding rate per individual was determined for periods of seven or of ten min feeding throughout the observations. The individual prey items could be discerned. The mean number of *Macoma* eaten per min feeding per bird was calculated subsequently (= average feeding rate). The percentage of feeding birds was determined by making counts at fifteen min intervals of Oystercatchers feeding and not feeding. This made it possible to calculate the mean percentage of feeding during the observation period. This figure is used to indicate the time spent in feeding. The mean number of *Macoma* eaten per observation period per bird is found by multiplying the total time spent in feeding with the average feeding rate. The overall feeding rate is the number of *Macoma* eaten per min observation per bird. The size distribution of *Macoma* eaten was found by measuring samples taken of the shells left opened by Oystercatchers on the mudsurface. Food intake, expressed in milliliter *Macoma* flesh per bird per low water period, was calculated by means of curves relating meat content with shell length in *Macoma* taken from the living population. Incinerating, so that ash free dry weight can be determined, is the most reliable method for calculating food and energy intake. Field circumstances, however, did not always permit this. For the Vlieland samples the volume of fresh flesh per *Macoma* was determined by water displacement after the surface of the flesh had been drained with filterpaper. For the Schiermonnikoog samples the volume of the flesh per *Macoma* was determined, as well as the dry weight (DW) after desiccating for 72 hours at 90°C. For the Paesens samples finally DW was determined and ash free dry weight (AFDW) by incinerating desiccated flesh for two hours at 500°C.

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6.3. RESULTS

Vlieland. Observations were done on the Dorpsplaat (Fig. 1) during five low water periods from 26—30 August (Fig. 24 left). The length of the exposure periods of the Dorpsplaat was registered by an automatical tide recorder, situated at a distance of 500 m from the observation site.

On August 26 during the morning low water period observations started about one hour before the moment of low water. A constant number of about 100 Oystercatchers was present till they were driven away by the incoming tide. During the late afternoon low water period that same day, observations started one hour after the highest part of the Dorpsplaat became exposed. Several Oystercatchers were already present at that moment, their numbers increased during the subsequent 15 min. From then on there was a continuous decrease in numbers because of birds leaving for other feeding areas. This lasted till about 45 min before submersion of the Dorpsplaat. By this time the other feeding areas had been flooded again, and the birds came flying back from those grounds. During the last half hour before complete submersion the birds left the Dorpsplaat gradually one by one.

On August 27 observations started whilst the feeding grounds were still completely inundated. The first Oystercatchers arrived 20 min after the first parts of the Dorpsplaat became exposed. The number of Oystercatchers increased steadily during the first hour because of the continuous arrival of birds from the high water roosts. In the meantime other feeding areas had become exposed and little groups of birds moved to these grounds, so the numbers on the Dorpsplaat receded. About half an hour after the moment of low water the number of Oystercatchers began to increase again, just as was seen the day before. Now the birds remained till the Dorpsplaat was practically submerged. The

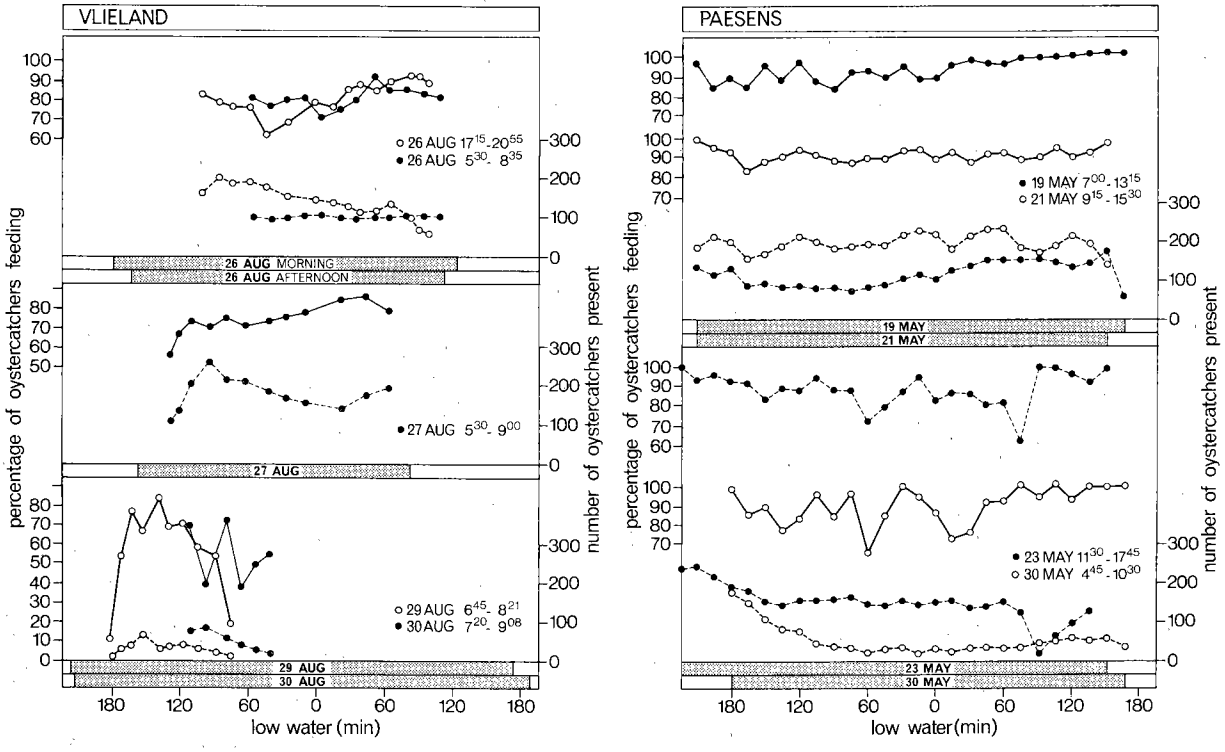


Fig. 24. Feeding of free living Oystercatchers on *Macoma* during daylight low water periods on the Dorpsplaat at Vlieland and at Paesens (1979). The number of birds present on the feeding areas and the percentage birds feeding were determined every 10—15 min period. The length of the shaded horizontal bars indicates the exposure time of the feeding areas.

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last birds departed when the water actually reached their belly feathers.

The picture was different during the early morning low water periods on August 29 and 30. The number of birds visiting the Dorpsplaat was quite low and steadily decreased till all birds had left, one hour before the moment of low water. Why did the Oystercatchers leave so early? The weather was quite warm and sunny on August 29 and 30. This was not so on August 26 and 27, when it was cold, with some light rainfall, but on August 31, when Oystercatchers in higher numbers (about 88 birds around the moment of low water) were present again the weather was fine. High temperatures and sunshine may have caused a drop in the availability of *Macoma* for Oystercatchers, since *Macoma* probably reacts to these environmental conditions by shutting up tightly in order to avoid desiccation.

Table 16 summarizes the data on food intake for the days 26—30 August. Two observers, A (R. H. Drent) and B (J. B. Hulscher), watched one group of Oystercatchers, concurrently but independently, on 27, 29 and 30 August in order to test the reliability of the method practised in estimating food intake. Feeding rate varied among individual birds from 0—3.36 *Macoma* per min, independently of the moment in the low water cycle. The percentage Oystercatchers actually feeding was quite stable during the low water periods. After an initial high level in the first hour, whilst the mudflat became exposed, the percentage of feeding birds became a little lower. On August 26 and 27 the percentage of birds feeding increased slightly in the second half of the exposure period. It was relatively low on the warm sunny days 29 en 30 August. These circumstances did not seem to affect the average feeding rate as is seen in column 4 Table 16. Observer A found a mean feeding rate of 1.36 *Macoma*/min (208 *Macoma* eaten in 9197 sec of feeding by 27 birds); 66.2% of the available time was spent in feeding. Thus the overall feeding rate was calculated to be 0.898 *Macoma*/min. Observer B, concurrently, found a mean feeding rate of 1.33 *Macoma*/min (206 *Macoma* eaten in 9318 sec feeding by 27 birds); 64.5% of the available time was spent feeding, so the overall feeding rate was calculated to be 0.856 *Macoma*/min. The difference between the estimate of A and B was less than five percent, which gives confidence in the reliability of the observation method.

The mean number of *Macoma* eaten per low water period per bird has been calculated for the three low water periods of 26 and 27 August. The food intake, during those parts of the low water periods of 26 August, when no observations were done, was extrapolated. The data

Table 16. Food intake of free living Oystercatchers with *Macoma* at Vlieland

Date and observation period (A) observer A (B) observer B	Feeding period sec	*Macoma* eaten (birds observed)	Average feeding rate *Mac*/min	% of birds feeding (number of counts)	Overall feeding rate *Mac*/min	Feeding area exposed/low water period min	*Mac* eaten/ low water period /bird
26 August 5.30—8.35	4391	123 (12)	1.68	82.1 (12)	1.38	305	421
26 August 17.15—20.55	4298	107 (12)	1.49	81.6 (14)	1.22	280	342
27 August (A) 5.30—9.00	3651	72 (11)	1.18	78.1 (12)	0.92	240	230
27 August (B) 5.30—9.00	4466	98 (13)	1.32	75.0 (11)	0.99	240	
29 August (A) 6.45—8.21	2394	59 (6)	1.48	59.1 (6)	0.87	390	—
29 August (B) 6.45—8.21	2505	61 (6)	1.46	56.3 (5)	0.82	390	—
30 August (A) 7.20—9.08	3152	77 (10)	1.47	60.9 (7)	0.90	405	—
30 August (B) 7.20—9.08	2347	47 (8)	1.20	58.2 (8)	0.70	405	—

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collected simultaneously by A and B on 27 August have been averaged. No calculations could be made for 29 en 30 August because no birds were present on the Dorpsplaat in the second half of the low water period.

A sample of *Macoma* shells opened by Oystercatchers was collected on the Dorpsplaat on 28 August. The size distribution of the living *Macoma* population was determined at the same time (Fig. 11). The mean volume of wet flesh of *Macoma* consumed was found to be 0.35 ml per specimen. The intake during the three low water periods on 26 and 27 August respectively was 147, 120 and 180 ml wet flesh.

Schiermonnikoog. Observations were done from 25 June to 7 July 1966; see Fig. 1, inset for the diagram of the local situation. The daily routine will be described first. The first Oystercatchers reached the feeding grounds after leaving the high tide roosts, when the waterline had receded to about 250 m off the salt marsh. They started feeding immediately, following the waterline downshore till the main feeding areas with *Cerastoderma* and high density *Macoma* fields were uncovered. These were situated at levels off the shoreline, ranging from site 5 to site 3. Most birds kept on feeding there, some crossed the tidal channel for more remote feeding grounds.

The birds fed steadfastly till the incoming tide forced them to leave. This time they did not follow the waterline towards the shore but flew directly to the high tide roosts. The highest densities of *Macoma* were to be found at the level of site 3, densities declined steadily towards the shoreline.

During the first phase of the low water period, before the main feeding areas were exposed, only a few Oystercatchers fed exclusively on *Macoma*, most birds took to a variety of prey species. At site 3, however, the majority of Oystercatchers did confine themselves to *Macoma*. The observations have been worked out separately for the phases I and II of the low water period described. In both cases adult birds solely feeding upon *Macoma* were considered.

Phase 1 (July 5, 6 and 7). The duration of phase I, from the moment the first Oystercatchers reached the feeding area till site 3 was exposed, lasted 140, 147 and 144 min for the three observation days respectively. The mean percentage of feeding birds was found to be 94.2%, 90.1% and 78.5%. The time spent feeding therefore was: 132, 132 and 113 min; that is on the average 125.7 min in phase I. The feeding rate of seven actively feeding birds was estimated in periods of six to seven min, on the three days. Seventy-two *Macoma* were eaten altogether, in 2800 sec, which adds up to a mean feeding rate of 1.54 *Macoma*/min feeding. Mean food intake during phase I of the low water period, therefore, was 125.7 × 1.543 = 193.9 *Macoma* per bird.

Phase II (25 June and 7 July). The duration of the exposure time of site 3 was 156 and 219 min on these two days respectively, on the average 187.5 min. The mean percentage of feeding birds was determined on 7 July only; it amounted to 83.3%. If we take this percentage as representative for both days, 187.5 × 0.833 = 156.2 min were spent in feeding during phase II. Feeding rate of 26 actively feeding individuals was estimated on 25 June and 7 July, revealing a mean feeding rate of 1.957 ± (S.D.) 0.57 *Macoma* per min. This means that on the average 156.2 × 1.957 = 305.7 *Macoma* were caught per bird during phase II. Thus during the whole low water period (phase I plus phase II) a bird caught on the average 499.6 (500) *Macoma*.

A sample of *Macoma* shells opened by Oystercatchers was collected on 21 June at site 3. The mean flesh content per *Macoma* consumed was 0.0879 g DW. The mean food intake therefore is 499.6 × 0.0879 = 43.91 g DW per low water period per bird. The dry weight of the flesh was 29.1% of the wet weight, the specific weight of the wet flesh was found to be 1.11. An intake of 43.19 g DW therefore is equivalent with 150.9 g wet weight or 136.1 ml *Macoma* flesh.

Paesens. Observations were done in the second half of May 1979 (Figs. 24 and 25). The daily routine was as follows. When the highest parts of the feeding grounds became exposed, birds started arriving immediately from their high tide roosts. Two groups of Oystercatchers, the breeders and non-breeders, visited the

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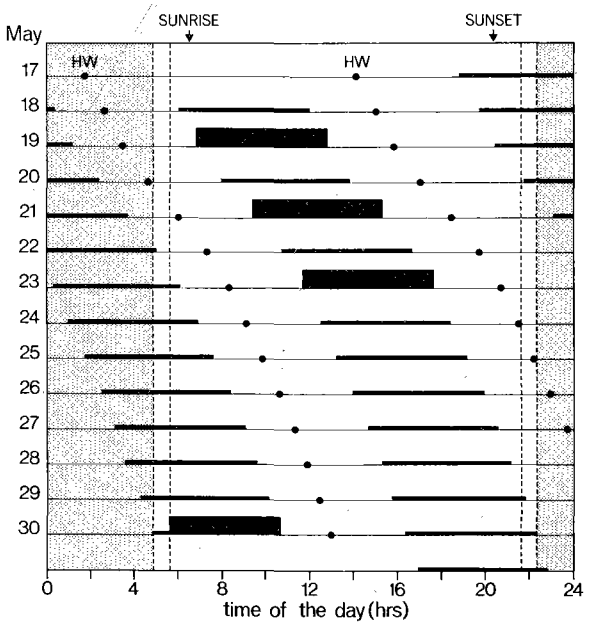


Fig. 25. Exposure schedule of the feeding area at Paesens from 17—30 May 1979 in relation to the daylight and dark hours of the daily cycle. Broken lines indicate the periods of civil twilight. Observation periods are indicated by thick black bars, low water periods without observations by thin bars.

mudflats in order to feed. Some representatives of these groups could be distinguished because they had been colour-banded, either in 1978 after having been caught on their nest, or between October 1977 and April 1979 after having been caught by cannon netting on the high water roost. Probably the birds caught on their nest in 1978 were breeders in 1979 as well; there is no certainty as to the status of the members of the cannon-netted party. Some will have been breeders in May 1979, others not. The number of Oystercatchers present (Fig. 24 right) was fairly stable throughout the low water periods. The sudden fall on 30 May at 16.40 h was caused by a Honey Buzzard, which flew at low height and passed right over the study area. Every single bird, irrespective of species, flew up and disappeared. The waders gradually returned within the next 45 min. All through the exposure period small numbers of Oystercatchers were arriving on, or leaving the feeding grounds. Probably these were local breeders which had territories on the salt marsh and the adjoining coastal strip of farmland.

The number of Oystercatchers was markedly low during the low water period of May 30. Probably local breeders did not visit the intertidal feeding areas very early in the morning (*cf.* Fig. 25), but preferred to stay in their breeding territories, where incubation had just started. Own unpublished observations on an inland breeding population indicate that the birds have a diurnal rhythm in this phase of the breeding cycle. Especially in the early morning much time is devoted to territorial behaviour and less to feeding. Time spent feeding increases from the mid-morning hours onwards. In coastal birds a tidal rhythm is probably superimposed upon the diurnal rhythm. This may explain the fact that the mean number of Oystercatchers present on the feeding area per low water period is negatively correlated with the total hours of exposure in daylight in the preceding low wa-

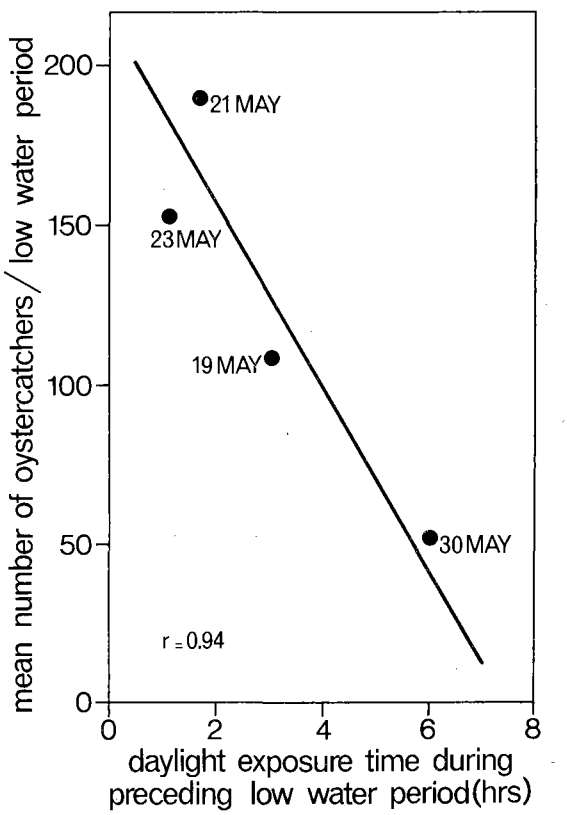


Fig. 26. Mean number of Oystercatchers present per low water period on the feeding area at Paesens in relation to the number of daylight hours of exposure of the feeding area during the low water period preceding that when observations were done.

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Table 17. Food intake of free living Oystercatchers with *Macoma* at Paesens in May 1979

Intake rate (*Macoma*/min feeding):	
breeding birds	1.93* ± (S.D.) 0.32 (n = 80)
non-breeding birds	1.51* ± 0.48 (n = 72)
Mean exposure time (min/low water period)	364
Mean percent of birds feeding/low water period	90.9
Mean feeding time (min/low water period) (364 × 0.909)	331
Mean shell length of consumed *Macoma* (mm)	16.61
Mean flesh content/*Macoma* consumed (mg) dry weight (DW)	96.1
ash free dry weight (AFDW)	83.1
Intake/low water period/bird (non-breeders):	
number of *Macoma* (331 × 1.51)	499.4
flesh (gDW) (499.4 × 96.1 × 10^{-3})	47.98
flesh (gAFDW) (499.4 × 83.1 × 10^{-3})	41.51

* Difference, t = 4.97; P < 0.001

ter period (Fig. 26). Or put otherwise, low water periods starting at early dawn were not attended by many breeders. Fig. 24 shows on the right how the number of Oystercatchers grew after 9.15 h on May 19.

The data on food intake are summarized in Table 17. Feeding rates of individually colour-marked adults were determined throughout the daylight hours of most of the low water periods between May 19 and May 27. The feeding rate of (potential) breeders and that of (potential) non-breeders differed strongly.

The mean percentage of feeding birds was fairly constant throughout the low water period. No distinction between breeders and non-breeders could be made during counts. Therefore, no distinction was made in calculating the mean time spent on feeding between the two groups, even though we know that non-breeders remained on the feeding grounds throughout the exposure period and breeders flew to and from the territories. The mean intake per low water period for the non-breeders was calculated to be 47.98 g (DW), or 41.52 g (AFDW) flesh per bird.

Table 18 summarizes the food intake with *Macoma* in the three study areas. The following conversion factors were used for comparison: the dry weight as percentage of the wet weight: for May and June/July 29.1%, for August 19.2%. Ash content of the dry flesh for May and June/July 13.5%, for August 11.6%. Specific weight of the wet flesh 1.11.

Food intake per low water period did not differ very much for the different localities and days except for the low water period on 27 August on Vlieland which, however, was quite short. Were these yields of *Macoma* in daytime sufficient for the Oystercatchers to subsist upon, or were they forced to feed at other times too, either on the intertidal mudflats at night or in the fields during high tide? No measurements of nocturnal feeding on the mudflats were made. We can, however, approach an estimation of daily food requirements of free living birds in an indirect way.

6.4. A CALCULATION OF THE 24-HOUR FOOD REQUIREMENTS

Daily gross energy intake of captive Oystercatchers has been investigated by various authors. The data available are summarized in Ta-

Table 18. Food intake of free living Oystercatchers per daylight low water period with *Macoma* flesh

	Wet ml	Wet g	DW g	AFDW g
Vlieland, 26 August (morning)	147	163.2	31.33	27.70
(afternoon)	120	133.2	25.57	22.61
27 August	80	88.8	17.05	15.07
Schiermonnikoog June/July	136.1	150.9	43.91	39.56
Paesens May	148.5	164.9	47.98	41.50

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Table 19. Daily (24 hour) gross energy intake of captive Oystercatchers in relation to Basic Metabolic Rate (BMR) when fed with *Cerastoderma* and/or *Mytilus*

Month		Number of birds	Experimental period days	Body weight g mean ± S.D.	Gross intake kcal/24 h/bird mean ± S.D.(1)	Gross intake times BMR (4) mean ± S.D.	Reference
June—Aug.,	outdoor	9	46—98	460.7 ± 10.5	152.4 ± 26.6	3.40 ± 0.57	Hulscher 1974
March,	outdoor	4	25	504.5 ± 26.0	196.3 ± 26.7	4.09 ± 0.43	Koene 1978
October,	outdoor	7 or 8	36	521.6(2)	219.1(2)	4.46(2)	Hulscher, unpubl.
December,	outdoor	2	6	461.5 ± 14.9	243.5 ± 13.9	5.42 ± 0.18	Drinnan 1958b
13 °C,	indoor	1	28	420	148.5(3)	3.85	Heppleston 1971

(1) *Cerastoderma* and *Mytilus* flesh 5.3 kcal/g (ash free dry weight)
(2) Averaged figures of all 7 or 8 birds
(3) *Mytilus* flesh in December 0.921 kcal/g (wet weight, Heppleston 1971)
(4) BMR according to Aschoff & Pohl (1970) for non-passeres

ble 19. Gross energy intake is calculated in relation to Basic Metabolic Rate (BMR). The birds were fed with *Mytilus* and/or *Cerastoderma*. Body weights of the birds remained constant. The formula for non-passeres as derived by Aschoff & Pohl (1970) was taken to calculate BMR. The energy content of the flesh of *Cerastoderma* and *Mytilus* were taken equal, 5.3 kcal/g AFDW. The food intake in summer (June—August) 3.40 ± 0.57 BMR was lower than in winter (March—December) 4.53 ± 0.77 BMR, ($t = 3.28$; $P < 0.005$).

Energy expenditure of captive and free birds is not equal. Both categories have to open shells and clear them from flesh. Free birds, however, walk greater distances while searching for food and they fly at least eight to sixteen km per day between feeding areas and roosts. Weather conditions can be quite harsh for them, whereas captive birds are more sheltered, even in outdoor cages, against hard winds, rains etc.

The ratios of energy requirements for humans during sedentary, light, middle-hard and hard work are taken to be 1 : 1.2 : 1.3 : 1.5 (Swennen 1976). For want of something better, I shall qualify feeding of free Oystercatchers as middle-hard work and fix their food requirements on 1.3 times that of captive birds. According to Table 19 the gross energy intake of free birds in summer is therefore estimated to be 1.3 × 3.40 = 4.4 BMR, and in winter 1.3 × 4.53 = 5.9 BMR.

6.4.1. Daytime food intake with *Macoma* in relation to 24-hour requirements

How yields on food intake with *Macoma* in daylight low water periods in the months May—August at Vlieland, Schiermonnikoog and Paesens relate to the 24-hour requirements will be reviewed next, in order to determine whether these daytime yields are sufficient to subsist upon by the birds, or whether feeding at night must be essential too.

In Table 20 the food per daylight hour, the number of daytime hours available for feeding, that is the total exposure time between dawn and dusk including the periods of civil twilight, and the daily food requirements are compared. Notice that on the average 1.91 low water periods per 24 h occur. The data on food intake for

Table 20. The food intake with *Macoma* per daylight hour and the number of daylight hours available for feeding in relation to daily food requirements

		Required/ 24 h g AFDW	Intake/h g AFDW	Hours feeding required day	Hours feeding available day	Hours feeding available night
Paesens	May	40.7	6.83	6.0	8.7	3.0
Schiermonnikoog	June/July	40.7	7.17	5.7	7.9	2.4
Vlieland	August	41.3	4.74	8.7	7.0	3.8

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the three low water periods in August on Vlieland are averaged.

The mean rate of food intake per bird per daylight hour is sufficient to cover the daily requirements in May and June/July, since the exposure time of the feeding grounds during daylight is longer than the amount required. In August, however, the birds suffer a deficit of 1.7 h of daylight feeding time on the average. This means that they must feed at other times too. Further field data on *Macoma* in other months of the year in the study area are not available, but data on food intake in daytime with other prey species do exist. First we shall review these data on daytime food intake in relation to 24-hour requirements and subsequently enter into the general question as to whether Oystercatchers only feed intertidally in daytime or if intertidal nightly feeding sessions or terrestrial feeding are common too.

6.4.2. Daytime food intake with *Cerastoderma*, *Mytilus* and *Macoma* in relation to 24-hour requirements

Various authors have estimated food intake of *Cerastoderma* and *Mytilus* by Oystercatchers during daylight low water periods. The analyses of these studies can now be set side by side with the *Macoma* data. Since in these studies different parameters for measuring food intake have been used, conversion factors (Appendix 1) will be applied to make the studies comparable.

The nutritional value of bivalve flesh (AFDW) does not significantly differ between species and over the year its caloric value varies only within very small limits (Dare & Edwards 1975, Beukema & De Bruin 1979). We may therefore compare the food intake for *Cerastoderma*, *Mytilus* and *Macoma* irrespective of species expressing it in grams AFDW.

In most of the studies food intake has been calculated for a daylight low water period. A comparison of summer (May to August) and winter studies (October to March) showed the intake per low water period to be different (Table 21). However, these data cannot be directly compared since the exposure time varies between study areas. A comparison of food intake must be based on the intake per hour, subsequently an estimate of food intake in daytime can be made by multiplying the intake per hour with the amount of daylight hours in which the feeding areas are exposed. Finally one can check whether food intake in daylight is sufficient for 24-h food requirements, by calculating the theoretical energy requirements in the specific circumstances (Appendix 1). As is seen in Table 21 the intake per hour expressed in grams AFDW varies only slightly and was not different between summer and winter.

We can now compare the yields throughout the year in daytime. The summer studies show that the daylight exposure time was — on the average — not quite sufficient, falling short by 45 min, for collecting all the food required in the period. In winter, the daylight low water period is generally too short for gathering the daily rations. Supposing Oystercatchers also feed on the mudflats during the nocturnal exposure hours, with the same feeding rate as in daytime, the total time per 24 h is usually sufficient. We can conclude that the observed feeding rates during daytime hours are insufficient in most areas during most parts of the year to meet the daily requirements only during the daylight exposure hours.

Table 21. Food intake of free living Oystercatchers during intertidal feeding with bivalve flesh (g AFDW ± S.D.) of *Cerastoderma*, *Mytilus* or *Macoma*. Intake per daylight low water period (l.w.p.) and per daylight hour and the deficit or surplus in feeding time calculated when the total daily food requirements are collected during a) only the daylight hours or b) during daylight and night hours available for intertidal feeding

	May—August	October—March	P t-test
Intake per daylight l.w.p./bird	28.4 ± 10.5 (n = 6)	38.2 ± 11.8 (13)	< 0.05
Intake per daylight hour/bird	5.09 ± 1.28 (6)	4.27 ± 1.47 (13)	n.s.
Feeding time (h) deficit (−) or surplus (+) when feeding:			
a) only during the daylight hours	−0.78 ± 2.79 (6)	−7.7 ± 10.9 (14)	< 0.1
b) during daylight + darkness hours	+2.35 ± 2.34 (6)	+2.11 ± 5.14 (14)	n.s.

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The next thing to do is to look for arguments that additional nocturnal and/or terrestrial feeding is taking place.

6.5. ARGUMENTS FOR ADDITIONAL NOCTURNAL AND TERRESTRIAL FEEDING

Experiments with captive birds on natural mudflats indicate that Oystercatchers can feed there perfectly well in darkness when feeding mainly on *Cerastoderma*. The captive bird WR fed at the same intake rate by day and by night on the mudflat (Hulscher 1974). When captive birds in the laboratory were provided with food 24 h per day, their intake rate during the dark period of the day was about half that in daytime. (Drinnan 1958b, Heppleston 1971, Hulscher 1974). But if food was only available during five hours in daylight and five hours at night, there was no difference in intake rate between light and dark periods (Hulscher 1974). Data from various sources point to nocturnal intertidal feeding of free birds too, as will be shown below.

On Vlieland roosts were always abandoned during nightly low water periods (August observations). Oystercatchers were present on the feeding grounds when the author made nocturnal walks there. Fresh faeces found on the high water roosts immediately after such low water periods indicate that the Oystercatchers had been feeding on the intertidal grounds.

On Schiermonnikoog in October by means of infrared binoculars Oystercatchers were observed in darkness when feeding on *Mytilus*. The scarce observations indicate that the intake rate at night was lower than during the day. At Morecambe Bay in December, Drinnan (1958b) concluded from stomach analyses of birds netted or shot during nocturnal and daylight low water periods, that the intake rate in darkness was half of that in daylight.

In the Burry Inlet in February Davidson (1968) found no difference in feeding rate on *Cerastoderma* in a very bright night with a full moon, compared to the daylight ratio. Heppleston (1971) concluded from counts of the number of Oystercatchers present on the intertidal feeding grounds at the Ythan Estuary that Oystercatchers feed at night on a limited scale in winter, relatively more birds being involved in midwinter than in October of February, and more birds in bright than in dark nights. On the other hand Goss-Custard (1977), studying Oystercatchers in the Wash, found, that most Oystercatchers did not feed there in darkness in January and February. According to his data there was no need to feed at night, since daylight intake was sufficient for 24-h requirements, notwithstanding the fact only five foraging hours were available. The intake rate of Oystercatchers was amazingly high, 11.50 g AFDW/h, surpassing all other observed feeding rates considerably (range 2.20—7.58 g AFDW/h, Appendix 1).

Terrestrial feeding in coastal meadows during high tide in daylight was observed frequently on Schiermonnikoog and at Paesens. It only occurred from late autumn to early spring, particularly during periods of stormy weather with reduced exposure of the intertidal feeding areas. At Vlieland no opportunity for terrestrial feeding exists. On Texel terrestrial feeding was observed in October during a period of short exposure times of the musselbeds (Koene 1978). On the Ythan Estuary a variable proportion of the Oystercatcher population showed terrestrial feeding at high tide, to a lesser extent at low tide and more birds were involved in terrestrial feeding in midwinter than in autumn (Heppleston 1971). At Morecambe Bay terrestrial feeding did not occur during the period in which Drinnan was carrying out his study (1954/55), but it did occur in daytime during the winters after the Cockle crash in the 1962/63 winter. Dare (1966) states that terrestrial feeding in daytime in coastal areas increased in Great Britain from that time onwards. Neither he nor Heppleston (1971) observed terrestrial feeding at night. They suggest the birds leave the inland fields for the coast before dark, where they are supposed to utilize the mudflats when the tide is out. From Heppleston's paper it can be calculated that the intake rate with *Mytilus* in October was 2.15 and in December/January 1.27 as high as during terrestrial feeding with earthworms. This may explain why terrestrial feeding during daylight low tide only occurred on a limited scale.

Dare & Mercer (1973) report for Morecambe Bay that at one particular place a group of Oystercatchers spent the whole day feeding on

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coastal fields, even when the tide was out. Terrestrial feeding might have been more profitable for these birds than intertidal feeding. Terrestrial feeding may be expected to occur in at least three of the areas mentioned by the various authors. In these areas time available for intertidal feeding calculated per 24 h was too short to satisfy food requirements (Texel, Burry Inlet and Grey Abbey). At Texel, as has been mentioned, terrestrial feeding did occur. No data are available for the other two areas. At Grey Abbey the calculated deficit of feeding time was very pronounced and the observed food intake probably was hardly sufficient to sustain normal body weights. Eight birds in August weighed only 484 g, whereas the normal body weight of adults at that time of the year is about 525 g (Dare 1977).

According to the field data presented in this chapter *Macoma* can very well yield 24-h requirements for Oystercatchers in springtime in the areas studied. The question remains, whether this holds for the rest of the year too, and for the Wadden Sea in general. A tentative answer might be obtained by investigating the possibilities for *Macoma* as bulk food in the Wadden Sea by means of making an estimate of the biomass distribution of *Macoma* throughout that area.

7. THE ROLE OF *MACOMA* AS BULK FOOD FOR OYSTERCATCHERS IN THE WADDEN SEA

7.1. INTRODUCTION

The relative importance of *Macoma* for Oystercatchers in the Wadden Sea cannot be assessed directly since no long term observations on the menu and the quantitative intake have as yet been done. We know that Cockle and Mussel play a large role in the diet of Oystercatchers too. The question when *Macoma* will be chosen and when not depends on the accessible amount of other prey species and the relative profitability of all species (see later) consumed. In this section we shall first review *Macoma* stocks in the Wadden Sea and then enter into the question whether these stocks suffice to sustain Oystercatchers throughout the year. Next we shall compare biomass values of *Macoma* with those of *Cerastoderma* and *Mytilus*.

7.2. THRESHOLD DENSITIES OF *MACOMA*

When the density of a prey is gradually reduced in time the moment arrives that the predator is no longer able to find enough prey to satisfy its requirements within the time available for feeding. Therefore it is essential to ascertain the threshold density of *Macoma* necessary for Oystercatchers in order to exploit this prey with success. The minimum density required is not constant throughout the year, because of the different developmental phases of *Macoma*. The growing season extends from the end of March till the end of June. The ash free dry weight of the flesh of individual *Macoma* steadily decreases with 5% per month throughout the eight to nine months of the non-growing season (Beukema & De Bruin 1977). This means that the weight of ash free dry flesh of a *Macoma* of 16.6 mm shell length — the mean size of the *Macoma* eaten in Paesens in May 1979 — will decrease from 68.4 mg in June tot 37.6 mg in March. In June the daily food requirements per Oystercatcher are estimated to be 41 g bivalve flesh (AFDW Apendix 1), this corresponds with 41 : 0.0684 = 600 *Macoma* of 16.6 mm shell length.

Assuming the feeding areas are exposed 12 hours per 24 hours and the birds use all their time for feeding at the same rate by day and at night, their rate of intake would be 600 : (12 × 60) = 0.83 *Macoma* per min. A *Macoma* of 16.6 mm is opened and consumed in 10 sec on the average, so per min feeding 8.3 sec are used for handling and 51.7 for searching. Of searching time 54% is used for multiple pecking and 46% for walking. That means that 0.83 *Macoma* must be found in 0.54 × 51.7 = 27.9 sec multiple pecking, or 0.030 *Macoma* per sec multiple pecking. But, on the average 10% of the *Macoma* localized are not eaten for what reason soever. Therefore localization rate should be 100/90 × 0.030 = 0.033 *Macoma* per sec multiple pecking. The average length of a multiple peck is 1.91 sec. Localization rate in June can thus be expressed as 0.033 × 1.91 = 0.063 *Macoma* per multiple peck. The localization rate in March can be calculated in the same way. The daily food requirements in March are estimated to be 60 g (Appendix 1) bivalve flesh. This represents

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1595 *Macoma* of 16.6 mm shell length and 37.6 mg of flesh (AFDW). If 12 hours feeding time is available, the localization rate in March must be 0.230 *Macoma* per multiple peck.

We can compare the calculated localization rates in June and March with those observed for the captive Oystercatcher in relation to *Macoma* densities next (chapter 2, Fig. 6). If (Fig. 27)

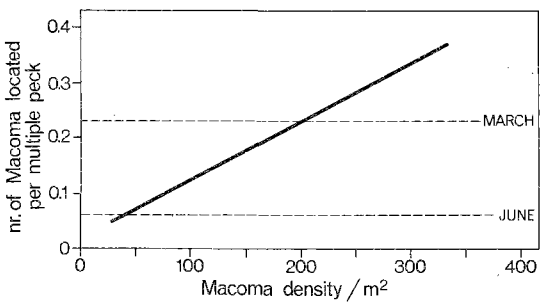


Fig. 27. Threshold densities of *Macoma* (shell length 11 mm or more) in March and June (for their derivation see section 7.2.). *Macoma* populations with below threshold densities cannot be exploited by Oystercatchers without sufficient return in food.

the localization rate in June is 0.063 *Macoma* per multiple peck, the minimum density must be about 50 *Macoma* per m^2, if the localization rate in March is 0.230 *Macoma* per multiple peck, the minimum density must be about 200 *Macoma* per m^2. These densities refer to *Macoma* of 11 mm shell length or more, because Oystercatchers do not eat *Macoma* below this size. The conclusion from Fig. 27 is that Oystercatchers cannot successfully exploit *Macoma* populations of over 11 mm shell length in June unless the density is 50 or higher and in March 200 *Macoma* per m^2 or more. The June value can be illustrated by the following observations of the captive bird WR foraging on natural fields of mixed *Cerastoderma*/*Macoma* populations in fenced-in areas of 20 m^2 (Table 22). Here the number of *Cerastoderma* and *Macoma* eaten per hour by the bird is given for two sites with different densities of the two bivalves. Prey size of *Cerastoderma* on offer was 25—35 mm, that of *Macoma* 11—22 mm. On site 3, where *Macoma* density was 305 and that of *Cerastoderma* 450/m^2, predominantly *Macoma* was taken (12 *Macoma* versus 1 *Cerastoderma*); on site 1, on the contrary, with 140 *Macoma* and 62 *Cerastoderma*/m^2, *Macoma* had practically vanished from the menu (1.4 *Macoma* was taken versus 1 Cockle). It looks like WR preferred *Macoma*, but the density on site 1 was so low, that the bird supplemented with Cockles.

Table 22. The number of *Cerastoderma* and *Macoma* eaten per hour feeding by the captive Oystercatcher WR in June when feeding in fenced-in areas of 20 m^2 on a mixed *Cerastoderma*/*Macoma* field at two sites having different *Cerastoderma* and *Macoma* densities on offer. Shell length: *Cerastoderma* 25—35 mm, *Macoma* 11—22 mm

	Schiermonnikoog, zone C	
	site 1	site 3
Observation period (min)	527	312
Prey density/m^2 *Cerastoderma*	62	450
Macoma	140	305
Number of prey eaten/h feeding		
Cerastoderma	10.4	6.1
Macoma	15.0	73.4

Supposing the time for feeding is less than 12 hours, for instance because the mean exposure time of the feeding areas is less, and/or the birds do not exploit the available time for the full 100% for feeding because of other activities, then the intake rate and of course localization rate must be speeded up, with correspondingly higher minimum densities of *Macoma*.

7.3. PREDATION UPON TWO *MACOMA* POPULATIONS

We have enough data available for two areas, one on the Dorpsplaat at Vlieland in August 1963 and the other at Paesens in May 1979, to determine predation pressure exerted by Oystercatchers upon the local *Macoma* populations and to relate these data to minimal densities.

Vlieland. The feeding area was 12.3 ha, the mean density of one year old or older *Macoma* was 166/m^2 (0.83 m^2 mudsurface sampled), the whole *Macoma* population came up to 20.4 million. The number of *Macoma* consumed per observation period is summarized in Table 23. During altogether 819 min of observation 102, 288 *Macoma* were removed, or 7494 *Macoma*/h, being 0.04% of the momentary population. The average density of Oystercatchers on the feed-

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Table 23. Predation of Oystercatchers on the *Macoma* population (age one year and older) in two areas: the Dorpsplaat at Vlieland in August 1963 and at Paesens in May 1979

	Mean number of birds	Overall intake *Macoma*/ min	Observation period in min	Number of *Macoma* eaten/ observ.p.	% of initial living population
Vlieland 26 Aug. morning	106	1.38	185	27062	0.13
afternoon	118	1.22	220	31671	0.15
27 Aug.	180	0.96	210	36288	0.17
29 Aug.	52	0.85	96	4243	0.02
30 Aug.	35	0.80	108	3024	0.01
			819	102288	
Paesens 19 May	111	1.22	375	50783	0.23
21 May	191	1.22	360	83888	0.38
23 May	155	1.22	375	70913	0.32
30 May	55	1.22	345	23150	0.10
			1445	228734	

ing area in this period was 11 per ha and the biomass of *Macoma* about seven g/m² (AFDW).

On December 29, 1963 Vlieland was visited again. At that time only five Oystercatchers were seen on the Dorpsplaat eating newly settled Cockles. The bottom fauna was not sampled because of bad weather. Meanwhile about 1000 Oystercatchers were foraging nearby at Dodemansbol. They represented about 10% of all Oystercatchers on Vlieland at that time. The birds at Dodemansbol were feeding exclusively upon *Macoma*, which were present in densities of 400—600/m². It is evident that the already marginal *Macoma* density on the Dorpsplaat in August must have dwindled to below the threshold value a short time afterwards.

Paesens. In May 1979 the feeding area covered 12.8 ha, the mean density of one year old or older *Macoma* at the end of the month (28 May) was 168/m², thus the *Macoma* population added up to 21.5 million. The overall intake rate averaged 1.22 *Macoma* per min per bird. The daily observation periods covered complete low water periods (Table 23). Predation rates varied between 0.11 and 0.39% of the momentary *Macoma* population per daylight low water period, or 0.04%/h. Throughout the month of May the number of Oystercatchers feeding in the area was stable. Assuming the birds only ate in the daylight phase of the day (8.7 h) they removed 2.5 million *Macoma* in May, or 10.4% of the *Macoma* population present at the beginning of the month.

The predation pressure exerted by the Oystercatchers upon the *Macoma* population on the Dorpsplaat at Vlieland in August 1963 and at Paesens in May 1979 was similar, 0.04%/h, whereas also the mean density of feeding Oystercatchers and *Macoma* biomass were more or less the same on both areas. This may mean that the number of feeding Oystercatchers was probably set to capacity by the food density.

We can conclude from this section that locally Oystercatchers can deplete *Macoma* populations to densities beyond which the birds cannot satisfy requirements any longer, but new sources may be tapped in consequence.
We shall turn to biomass distribution of *Macoma* throughout the Wadden Sea area next, in order to determine whether or not *Macoma* is able to sustain the Oystercatcher population in general, or when and where the bivalve can function as bulk food.

7.4. BIOMASS DISTRIBUTION OF *MACOMA* THROUGHOUT THE WADDEN SEA

Biomass density values for the most important macrobenthic animals in the Dutch Wadden Sea have been assessed by Beukema (1974, 1976, 1979, Beukema *et al.* 1978). An extensive sampling programme over the whole area made a survey of *Macoma* distribution possible (Table

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Table 24. Zonal distribution of averages of some environmental characteristics and of the biomass of *Macoma balthica* at tidal flats in the Dutch Wadden Sea (from Beukema 1976, Table III)

	Area km²	No. of transects	Mean level cm MTL	Mean % silt	*Macoma* g (AFDW)/m²
Coastal zone: 0—1 km Mainland	100	12	+ 19	34.2	5.1
Islands	100	8	+ 14	3.1	1.8
Transitional zone:					
1—3 km Mainland	200	18	− 38	5.8	4.8
Islands	200	17	− 45	1.6	1.1
Off shore: 3—6 km Far	400	25	− 54	1.4	1.1
≥ 7 km Farthest	200	19	− 62	0.6	0.8
Total or average	1300	99	− 36	6.2	2.2

24) from Beukema (1976, Table III). Biomass values were much higher for the inner parts of the Wadden Sea along the mainland, than for the outer parts along the island. This coincided with a high silt content of the sediment and with relatively high littoral levels with correspondingly long exposure times.

From Table 24 it will be clear that *Macoma* eating Oystercatchers can be expected particularly along the mainland up to about three km from the coast. Biomass figures in Table 24 can roughly be converted to average numerical densities because one gram of *Macoma* flesh AFDW corresponds with about 25 adult *Macoma*, as can be calculated from Beukema *et al.* (1978, Table IV). Beukema (pers. comm.) also provided further information on *Macoma* densities for the coastal strip along the mainland. Between zero and one km from the coast adult *Macoma* densities exceeded 100 per m² in 45%, between one and two km in 36% and between two and three km in 18% of the total area of the mudflats exposed there. For densities exceeding 200 adult *Macoma* per m² these percentages were 15, 21 and 0, respectively.

Two other studies on the macrobenthos along the mainland coast have been performed, one by Essink (1978) and the other by Zwarts (in prep.). Essink studied an area of 6.4 km² along the coast at Noordpolderzijl (Groningen), situated between one and two km from the coast, between 1969—1975. From Fig. 33 in his paper it can be calculated that mean adult *Macoma* densities were between 0 and 100 per m² in 67% of the area, between 100 and 400 per m² in 29% and over 400 per m² in 4%.

Since 1976 Zwarts has been studying two areas: two squares of 400 and 17 ha respectively along the Friesland coast and one square of 14 ha along the coast of Groningen. These areas are situated between 0.5 and 1 km from the coast. Densities of adult *Macoma* (shell length 10 mm or more) in summer (August/September) varied between 228 and 410, mean about 300 per m², whereas densities in winter or early spring came to about 75% of the summer densities (pers. comm.).

Summarizing we can state that in the coastal strip along the mainland of about a half to three km breadth and maximally 100 km length, *Macoma* density is high enough to allow Oystercatchers to feed solely on this prey with sufficiently high returns to satisfy requirements. In roughly 100 km² of this coastal strip adult *Macoma* density exceeds 100 per m² and within this area 36 km² stores more than 200 per m². In other parts of the Wadden Sea comparably high *Macoma* densities only occur locally, restricted to small sheltered areas.

In order to know whether these *Macoma* stocks suffice for all the Oystercatchers in the area throughout the year, we shall have to know how many birds have to be fed.

7.5. *MACOMA* STOCKS IN RELATION TO OYSTERCATCHER NUMBERS

The mean number of Oystercatchers occurring in the Dutch Wadden Sea varies between a maximum of about 220,000 during the winter (January) and a minimum of 26,000 in summer (June). The daily mean, calculated over a whole year works out at 130,000 birds (Hulscher 1980). Mean daily food requirements over the year of an Oystercatcher can be put at 55 g (AFDW) bivalve flesh (Appendix 1); the mean flesh content of an adult *Macoma* of the size

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range consumed by Oystercatchers is 53.5 mg. Therefore, the daily consumption of the individual bird can be calculated to be 1028 *Macoma* (55 : 53.5) × 10^3. Thus, the total Oystercatcher population consumes about 5.10^{10} *Macoma* (1028 × 365 × 130000) per year. On average over the whole year, Oystercatchers can only successfully exploit areas having densities of over 175 *Macoma* per m^2 (see section 7.2 and Fig. 27). The extent of the area with such densities cannot be calculated, since the sampling programme does not provide sufficient resolution. Suppose Oystercatchers would extract 100 *Macoma* per m^2 above the minimal density of 175, then they would need an area of about 500 km^2 (5.10^{10} : (10^2 × 10^6)). As we have seen above, the actual area with exploitable *Macoma* densities is a little more than 36 km^2 and much less than 100 km^2.

What is more, Oystercatchers are not the sole predators of *Macoma*. Other avian *Macoma* eaters are the Shelduck *Tadorna tadorna*, the Mallard *Anas platyrhynchos*, the Knot *Calidris canutus*, the Bar-tailed Godwit *Limosa lapponica*, the Curlew *Numenius arquata* and the Redshank *Tringa totanus* (Smit & Wolff 1980). Amongst fishes there are siphon eaters: small Plaice *Pleuronectes platessa* and complete *Macoma* eaters: Plaice, Flounder *Platichtys flesus* and Dab *Limanda limanda* (Kühl & Kuipers 1978).

In conclusion we can state that the amount of *Macoma* in exploitable densities in the Wadden Sea is by no means sufficient as bulk food for Oystercatchers. At best this bivalve offers bulk food locally and temporarily. Therefore we shall go over biomass distribution of the other two important prey species for Oystercatchers in the Wadden Sea, the Cockle and the Mussel, and compare these data with those of *Macoma*.

7.6. COMPARISON OF BIOMASS DISTRIBUTION OF *MACOMA*, *CERASTODERMA* AND *MYTILUS*

The results of the sampling programme along 99 transects throughout the Dutch Wadden Sea by Beukema (1976) are given for *Macoma*, *Cerastoderma* and *Mytilus* in Table 25, and the annual biomass figures during late winter and early spring of these species on the Balgzand in the Western Wadden Sea for the period 1971—1981 in Fig. 28 (Beukema 1979 and pers. comm.). The mean biomass of *Mytilus* was three times, that of *Cerastoderma* twice as high as the biomass of *Macoma* (Table 25). *Macoma*, however, was a much commoner species, occurring in 93% of all transects, *Cerastoderma* in 62% and *Mytilus* only in 25%. *Macoma* is not only a very common species but fluctuations in its biomass were between narrow limits over the years too (Fig. 28). The biomass of both *Cerastoderma* and *Mytilus* varies over much wider ranges. The relatively low biomass figures for *Mytilus* on the Balgzand are not fully representative for the

Table 25. Mean (and 95% confidence limits) biomass over the year and commonness (percent occurrence among the transects) of three main Oystercatcher prey. Results of the sampling of 99 transects throughout the whole Dutch Wadden Sea (Beukema 1976, Table I)

	Biomass g AFDW/m^2	Commonness %
Mytilus	6.2 (0—12)	25
Cerastoderma	4.3 (2.3— 6.3)	62
Macoma	2.2 (1.7— 2.8)	93

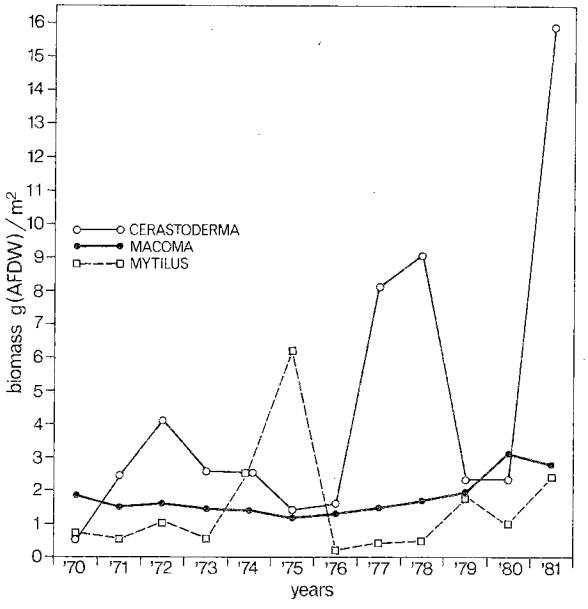


Fig. 28. Biomass of three main Oystercatcher prey during late winter or early spring on the Balgzand in the western Wadden Sea over the years 1970 to 1981 (from Beukema 1979 and pers. comm.).

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whole Wadden Sea, due to aggregations of *Mytilus* that complicate sampling.

Cerastoderma stock in the Wadden Sea is characterized by heavy fluctuations caused by high variability in both success of spatfall and subsequent survival (Beukema 1979). Particular survival over the winter half year period was highly variable and correlated with mean winter temperatures. *Mytilus* stock also fluctuates pronouncedly between years. In this species winter survival was not found to be correlated with temperatures in at least about 90% of the winters. Only during very severe winters heavy losses occur. *Macoma* survival over the winter is independent of winter temperatures. The species can withstand severe cold weather for quite long periods on end.

The biomass and commonness of the three main prey species of Oystercatchers, as depicted in Table 25, give an impression of their distribution under average conditions. *Cerastoderma* and *Mytilus* may be less common than *Macoma*, but where they do occur, they are frequently amassed to high densities, sometimes of several thousands per m^2. The aggregated distribution of both species, particularly that of *Mytilus*, enable Oystercatchers to find sufficient prey within the limited time that is available for feeding. The relatively few birds in relation to prey biomass taking *Mytilus* may be a consequence of the very high densities of the Mussels all clumped together on restricted areas. Densities of 50—100 Oystercatchers per ha musselbed are noted frequently, as compared to 10—15 birds per ha on cocklebeds (Zwarts 1980). Koene (1978) observed that when density of foraging Oystercatchers increased, their food intake decreased because of an augmenting number of interactions between the birds. The available space probably limits the number of birds that can feed with sufficiently high success.

Total *Cerastoderma* and *Mytilus* stocks are usually high enough to sustain large populations of Oystercatchers for some time. If *Cerastoderma* should collaps after a short cold spell or after some years without recruitment, the majority of Oystercatchers can switch over to *Mytilus* and *Macoma* and locally to other prey: *Scrobicularia*, *Mya* and *Nereis*. If both *Cerastoderma* and *Mytilus* fail after a very severe winter, the birds have to rely on *Macoma* as their main prey.

Such a situation can only be expected to occur from late winter to the end of summer, that is from March through August. During these months — the breeding season — minimal numbers of Oystercatchers forage in the Wadden Sea. So comparatively few birds need to rely on *Macoma* as the main prey, and for only a short period. This indeed was observed by Dare & Mercer (1973), examining stomach contents of birds shot in Morecambe Bay during 1961—1966. A switch from Cockle to *Macoma* feeding was apparent after the severe winter of 1962/1963, and also but less pronounced, in the early spring of 1964, 1965 and 1966. They reasoned that Cockle stocks had dwindled to too low levels to maintain all the Oystercatcher flocks. However, a change to *Macoma*, particularly in spring (April/May) can be expected, since then the accessible amount of biomass increases. This is caused by the fact that it lives closer to the surface at that time (see section 1.6.) and practically all individuals end up within reach of the Oystercatcher's bill.

After severe winters spatfall and subsequent growth of *Cerastoderma* is usually high in the Wadden Sea (Kristensen 1957, Beukema 1979). Following the icy winter of 1962/1963 young Cockles born in 1963 had reached sizes of 14—27 mm, mean 20.5 mm, on the Rottumerplaat (Fig. 1) already by the end of September (own observation). Here I watched thousands of Oystercatchers eating them. Probably they had started exploiting these Cockles weeks before.

8. PROSPECTIVE STUDIES

As we have seen *Macoma* can play an important role locally and temporarily in the Oystercatcher diet, especially in springtime. However, usually other prey, like *Cerastoderma* and *Mytilus* are available too in exploitable densities. When, then, will an Oystercatcher take *Macoma*, *Mytilus*, *Cerastoderma* or perhaps some other prey? It would be worthwhile investigating whether the prey choice of the individual Oystercatcher is the most profitable one the bird can make at a certain moment. According to the theory of optimal foraging predators hav-

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ing a choice of different prey types, will take the most profitable type. Royama (1970) defined this as the type giving the highest reward in food for a given amount of hunting effort (see also Krebs 1978). Different factors influence the effort a bird has to take at capturing food, as will be illustrated below.

First, one cannot simply expect, that each individual can feed upon each prey type with equal ease. Field observations show, that even when different prey species are available, many individual birds keep to one prey type for long periods on end, at least during one low water period. At Paesens I have seen Oystercatchers feeding side by side, some taking only *Macoma*, others *Scrobicularia*, again others restricting themselves to siphons of *Mya*, whereas some individuals were only eating *Nereis*. On Schiermonnikoog, in zone C, I saw free living birds foraging either on *Cerastoderma* or *Macoma*, though a few birds took both prey species (see section 2.3.). Dare and Mercer (1973) give corresponding results by means of stomach analysis. They found that most birds, they had shot, contained only one prey type in their stomach. They conclude that the birds had been either *Mytilus* feeders, *Cerastoderma* feeders or *Macoma* feeders. A minority of the birds had fed on two or three types of prey at a time (see also Goss-Custard *et al.* 1980). Some findings suggest that morphological traits of the bill are linked with the success with which different prey can be opened, and therefore are linked with choice of prey.

Male Oystercatchers have shorter and higher, and therefore probably stronger bills, than females. From sightings of colour-banded birds belonging to an inland breeding population at Drachten in Friesland we have found that the sexes distribute themselves differently over the Wadden Sea during the winter. Relatively more males reside on the Wadden islands and more females along the mainland coast. It may well be that this difference in distribution pattern of the sexes is linked with differences in profitability to exploit different food sources. The strong bill of the male may be better adapted to opening large Mussels, these occur in large quantities along the islands, whereas the longer bill of the females may be better adapted to feed on moderately to deeply buried prey, such as *Macoma*, *Mya* and *Scrobicularia*, predominantly occurring along the mainland coast. Sightings of colour-banded birds of known sex in the area of Paesens indicate that this assumption is true. More males were seen feeding on the musselbeds and more females on the mudflats (Zwarts pers. comm. and own obs.). Dare's (1977) observations point to the same: males predominated among Oystercatchers shot whilst feeding on musselbeds. The author, however, does not stress this point himself. A long bill, on the other hand, may be favourable in exploiting terrestrial prey, as is suggested by Dare and Mercer (1973). These authors studied Oystercatchers at Morecambe Bay. A proportion of the birds supplemented insufficient intertidal food intake by feeding on terrestrial prey, mainly earthworms, in coastal fields. More females than males were involved in terrestrial feeding. As mentioned above females have longer bills, on the average, than males. Furthermore, the males implicated in terrestrial feeding had longer bills than the males keeping to estuarine feeding.

Another finding pointing to a link between bill morphology and skilfulness in opening a prey is the example given in section 4.6. Oystercatchers with thin billtips opened and handled *Macoma* after these were extracted from the mud and brought to the surface in less time than thick-billed birds (Fig. 22). All the same, linkage between bill morphology and choice of prey probably is not a very strict one. The sole fact that many birds make a change of diet from wintering areas to breeding grounds confirms this.

It is likely that ontogenetic experience takes part in determining prey choice. Individuals residing in one population, but of different ontogenetic background, need not to make identical choices in identical situations (Norton Griffiths 1968, thesis). Another factor to keep in mind is knowledge of the feeding area. Marked birds have shown that Oystercatchers usually feed in a restricted part of a feeding area, which they frequent days, weeks or even months on end. An individual profits by a long stay at one site, because it gathers thorough knowledge of the dispersion pattern of its prey and the stimulus situation leading to detection of the prey. It can

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adapt its searching strategy to the behaviour of the prey by exploring the area systematically. Obtaining this knowledge costs time and effort. Therefore an individual will tend to a temporary conservation in feeding strategy. Once it has started feeding upon a certain type of prey, above threshold value, it will keep on eating it. Quite some changes must come about before it will switch to another prey type. With experiments we might be able to determine how big the change must be before switching; this may well take several days.

Another point that may make an individual reluctant to change its feeding area is its social status. Among Oystercatchers feeding on a particular site, for instance on a musselbed or part of a musselbed, there usually is a rather strong social hierarchy among the members of the party. Dominant individuals may steal Mussels from subdominants, the reverse seldom happens (Ens & Goss-Custard in prep.). Individuals know each other, and this may aid them in adjusting their feeding strategy. A change of one type of prey to another is likely to often imply a change of feeding site. Finding one's way in a new area and establishing a new social position within a community of unknown fellow birds will cost quite some energy.

A last point worth mentioning in evaluating observations on profitability of prey types is the time the individual bird has at its disposal for feeding. Table 17 showed that on the feeding area at Paesens the intake rate with *Macoma* of non-breeding birds was 1.51 *Macoma*/min feeding, whereas for breeders it was 1.93 *Macoma*/min feeding. Non-breeders foraged during the total time span of the emersion period of the feeding area, breeders only a few hours, the rest of their time they spent in the breeding territory, where they did not feed. In May 1981 we followed the feeding habits of a mated male during two weeks, at the end of which period the couple had completed a four-egg clutch. The bird always fed at the same site, solely on *Macoma*. As the breeding season proceeded, the bird remained shorter and shorter on the mudflat, but speeded up its feeding rate (Fig. 29).

When testing the profitability hypothesis all considerations mentioned above must be taken into account. What we need are long series of

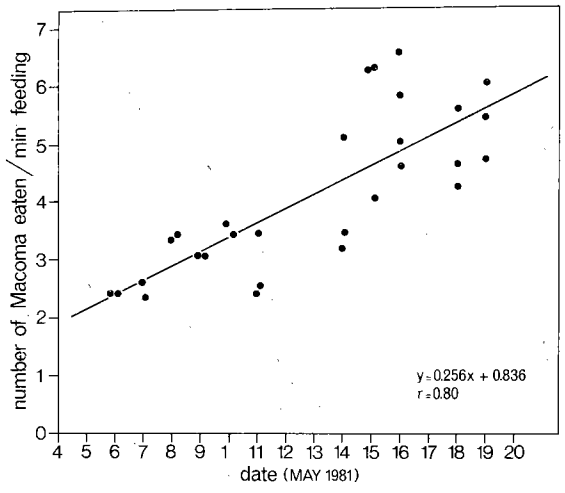


Fig. 29. Feeding rate with *Macoma* of an adult male Oystercatcher constantly feeding at the same site at Paesens in May 1981. During the two weeks preceding the date the clutch was completed (about 19 May) the feeding rate steadily rose. In the mean time the total time spent feeding on the mudflat decreased, but to what extent was not determined.

observations of marked birds in different areas at different times of the year, and with some luck, with individual birds feeding on different types of prey. Pure feeding bouts on one prey type must be isolated and analysed on searching time, handling time and intake rate, together with other factors such as density of the prey, size of the prey eaten, etc.

So far no observations of sufficient length of single individuals coming up to the conditions are available for testing the profitability hypothesis. However, data of a series of observations, all dating from the month of May, are at hand, concerning mean food intake of groups of Oystercatchers, which had been foraging constantly on one prey type (Table 26, Hulscher unpubl.). It seems that feeding on large Mussels gives a high yield per time unit feeding. Possibly the intake of large *Mytilus* is somewhat overrated because some of the smaller Mussels opened may not have been found (Ens in prep.).

Before being able to compare the true profitability values of these prey species, we must make an estimation of the amount of energy spent in foraging. Probably energy spent per time unit on searching and handling the prey is different per prey type. During searching pacing

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Table 26. Mean food intake and the time costs of feeding of groups of Oystercatchers feeding on one prey type in May

	Prey type			
	Mytilus		*Cerastoderma*	*Macoma*
Area	Schiermonnikoog		Vlieland	Paesens
Mean prey size eaten (mm)	26.4	50.0	14.4	16.6
Observation period (min)	330	2840	720	600
Density (prey/m^2)	?	780	680	168
Intake (g flesh AFDW/h feeding)	6.0	13.7	7.1	7.5
Time costs/g flesh consumed (min):				
searching	5.46	2.72	5.45	4.79
handling	4.50	1.66	3.04	3.17

rate and step length may differ. *Mytilus* and *Cerastoderma* are detected visually by single pecks, buried prey like *Macoma* by multiple pecks. Peck frequencies and probing depth may all vary between prey types.

The effort spent on handling the different prey types may be expected to vary widely too. This can be attributed to a variety of factors. Once, for instance, I saw an Oystercatcher attempting to pull a large *Scrobicularia* out of the mud with all its might, but in vain. Other Oystercatchers, however, did succeed in extracting large *Scrobicularia*. Factors influencing the energy required in opening the prey probably vary because of shell size, bivalve structure, thickness of the valves, degree of gaping of the shell, technique of opening practized by the bird (stabbing, biting, hammering).

The energy costs of these components of the feeding behaviour are hitherto unknown. The challenge for future study is to make the components of the profitability concept measurable.

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10. SUMMARY

The Oystercatcher is a specialised feeder on bivalves in estuarine areas. Among the different prey species taken *Macoma* can be considered to be an important one. In this study some relations between Oystercatchers and this prey are described: the method of localization of *Macoma*, the consequences the way of localization has for the sizes of *Macoma* that are taken (selection for size), the way *Macoma* is opened and the role *Macoma* plays as bulk food for Oystercatchers.

Research was done in different parts of the Dutch Wadden Sea (Fig. 1) with captive birds which were allowed to feed on the mudflats within fenced-in areas up to 20 m^2, and by observing free living birds.

Feeding behaviour of the Oystercatcher was described first. Oystercatchers invariably use the multiple pecking technique when hunting on *Macoma*. A multiple peck consists of a series of probes in the vertical plane with the bill opened a few millimeters. Probing rate can vary from 3 to 7 probes per second of multiple pecking.

Details of the biology of *Macoma* relevant for this study are reported next. *Macoma* lives buried in the substrate to a depth of 1—10 cm. It feeds by stretching its inhalant siphon up to the mudsurface. Where the substrate is somewhat muddy and covered with a coherent film of diatoms, the bivalve makes star-like tracks by sucking in the uppermost layers of the sediment. When the substrate is more sandy, no such tracks are seen. The question was posed, whether Oystercatchers use surface tracks to locate *Macoma*.

This point was studied in chapter 2 by observing a captive Oystercatcher (WR) feeding on experimentally made and natural *Macoma* populations in daytime, with surface tracks either left intact or erased, and in darkness. It turned out (Fig. 4 and 5) that *Macoma* was localized at a higher rate when tracks were available than when tracks were absent or not clearly visible. However, the captive bird could also localize the prey in absence of tracks, pointing to the fact that it must have had another locating mechanism at its disposal besides sight. This was confirmed by results with free living birds, which located comparable numbers of *Macoma* in areas without surface tracks, under comparable population densities of *Macoma* (Fig. 6).

The most likely alternative besides sight, for the stimulus leading to location of the bivalve is touch. A model for localization by touch was constructed, based upon the assumption that the bill must actually touch a *Macoma* shell before it is found. A *Macoma* shell is always oriented with its medial plane vertically to the mudsurface and the Oystercatcher bill moves vertically downwards. Therefore the proportion of area in the horizontal plane occupied by *Macoma* shells in reach of the bill can be calculated when the density of *Macoma* and the effective touchable area (Fig. 7) per mm-class are measured as well as the burrow depth of the bivalves and the probing depth of the bill (Fig. 8). The number of *Macoma* to be located according to the model could be predicted by the formula:

N(predicted) = time spent in multiple pecking × mean probing rate (probes per second multiple pecking) × mean density of the *Macoma* population within reach of the bill × mean effective touch area per available *Macoma* × 10^{-4}.

The model was first tested on the results of the captive bird WR. These fitted in with the model (Tables 2 and 3). Next the model was applied to data from free living birds. Again the number of *Macoma* found (1817) approached the number predicted (1890). It was concluded that in the absence of surface tracks the stimulus for locating *Macoma* was touch. Localization by means of the senses of smell, hearing or taste are not considered relevant. The captive Oystercatcher WR, and free living Oystercatchers always select for the large *Macoma* within a population (Fig. 11). This size selection was hypothesized to be generated passively as a consequence of the location mechanism by touch; since small and large shells have different surface areas the chances of encountering *Macoma* of different size underground are unequal (chapter 3).

The expected passive selection by touch can be calculated by taking three prerequisites into account: the numerical distribution of the mm-classes in the living *Macoma* population, the depth distribution of the mm-classes (some *Macoma* are beyond reach because of depth), and the differences in effective touch area between mm-classes in combination with the first two prerequisites.

The results of size selection of the captive bird WR were in accordance with the hypothesis of passive selection by touch (Fig. 12, left panel), the free birds at Paesens, however, found larger *Macoma* than predicted by this hypothesis (Fig. 12, right panel). In this case it could not be concluded that the hypothesis of passive selection should be rejected, because among the *Macoma* in the sample of the Oystercatchers some, particularly large ones, probably were not opened by the birds, but had died of trematode infection.

Visual size selection with the aid of surface clues could also be demonstrated for the captive bird. Probable large *Macoma* make more conspicuous tracks than small ones (Fig. 14). In all likelihood Oystercatchers select actively against undersized *Macoma* (≤ 11 mm), which they never take, but must inevitably encounter during multiple pecking. Probably they decide so swiftly not to handle a small *Macoma* just encountered, that this escapes detection by the observers.

After having localized a *Macoma*, an Oystercatcher has to open it, since it only swallows the flesh. It is assumed that the bird will try to open the shell without damaging it, since it takes less trouble to loosen the flesh from an intact shell, than from one broken to pieces (chapter 4). The behaviour of Oystercatchers opening *Macoma* is described as well as the behaviour of *Macoma* resisting being opened. The following picture emerges. Opening of *Macoma* is achieved either by hammering or biting. Hammering requires a firm substrate. When hammering, blows of the bill are directed at the anterior region of one of the two valves, which is where the valves are thickest (Fig. 17). Access into the shell is either gained because the two valves rotate alongside each other and the bill enters through the cleft emerging between them, or because one valve breaks. Shell damage occurs mostly at the point of attack and is largely determined by whether the hinge is fastened tightly or not. Individual Oystercatchers hammer *Macoma* in their own way, fracturing mainly only the left or the right valve (Table 11).

Biting occurs where the substrate is rather soft. *Macoma* often gape in soft and wet substrates. When biting, the slightly opened bill is pushed into the shell in the gape between the valves at its ventral-posterior margin. Shell damage occurs at the point of attack and is largely determined by the degree the shell is gaping. This also holds for the time required to open and eat a *Macoma*. When gaping widely *Macoma* is, as a rule, opened underground (*in situ*). The free Oystercatchers at Paesens used 8.9 sec on the average to handle a *Macoma in situ*, and there was no difference in

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time required for thick and thin billed birds. When *Macoma* is only slightly gaping, it is extracted from the mud and opened on the surface. Then, on average, the birds needed 15.1 sec per *Macoma*, but thin billed birds opened them more quickly than thick billed ones (Fig. 22).

Oystercatchers frequently reject a *Macoma*, once it has been opened, suggesting that the birds check the food before eating it (chapter 5). It was found that rejected *Macoma* were invariably parasitized by the trematode *Parvatrema affinis*. An infected *Macoma* can be distinguished from an uninfected one only when the valves are separated, exposing the sporocysts with a whitish conspicuous colour. Choice experiments and field observations on natural and experimental *Macoma* populations with the captive bird WR showed that it discriminated between infected and non-infected *Macoma* after having opened the shell. On average one third of the infected *Macoma* found were rejected, the others were eaten (Table 15). Relatively more large *Macoma*, having more sporocysts in absolute numbers than the small ones, were rejected. Bad taste or a touch stimulus, the sporocysts being hard and granular, were considered to be the prime cause of rejection. Sight might have played a role too. It was reasoned that the behaviour of the bird to reject at least part of the infected *Macoma* may serve in diminishing the chance to infect the bird to a harmful level. A high parasitic load may be particularly harmful in situations of physiological stress. To the knowledge of the author the direct behavioural response of refusal of a parasitized prey, as observed in this study, has not been described before.

Since it was found that at times Oystercatchers feed solely on *Macoma*, at least in daytime — no data for the night being available — it was worthwhile investigating whether *Macoma* yields obtained in daytime were sufficient for Oystercatchers to subsist upon, or whether additional feeding at night would be essential too (chapter 6). Estimates of the mean food intake with *Macoma* per low water period were made for the three study areas Vlieland, Schiermonnikoog and Paesens (Tables 16, 17, 18). It turned out that *Macoma* can very well yield 24-hour requirements for Oystercatchers in springtime in the areas studied (Table 20).

Next a general survey of data from literature is presented on quantitative food intake by Oystercatchers with *Cerastoderma*, *Mytilus* and *Macoma* (Appendix 1). It looks like daylight food intake on mudflats is sufficient in general in the months May to August, but insufficient from October to March (Table 21) when nightly feeding excursions to the mudflats, or terrestrial feeding in coastal fields, must make up for the deficiency.

Further it was considered whether or not *Macoma* could be bulk food for Oystercatchers in the Wadden Sea (chapter 7). First, threshold densities of *Macoma* were determined, below which *Macoma* cannot be exploited successfully (Fig. 27). A quantitative survey of the biomass distribution of *Macoma* in the Dutch Wadden Sea (Table 24) in above-threshold densities (Beukema 1976) revealed that *Macoma* can only offer bulk food locally and temporarily, especially in springtime. In most places the Oystercatcher has to rely on other food species, especially Cockles and Mussels, their abundance usually being much higher in the Wadden Sea (Table 25).

Finally (chapter 8) the question is discussed under which set of conditions an Oystercatcher will take *Macoma*, *Cerastoderma*, *Mytilus* or perhaps other prey and whether the choice it makes is the most profitable one in terms of giving the highest reward in food for a given amount of hunting effort (Royama 1970). It is argued that such questions must be studied by observing individually marked birds for long periods throughout the seasons. Several factors may influence prey choice and hence must be taken into account when studying profitabilities of prey types: bill morphology, ontogenetic experience, social status, knowledge of the feeding area, time available for feeding, etc. Besides these characteristics concerning the individual Oystercatchers, characteristics of the prey have to be studied: a measure of the amount of flesh taken by the birds per food item, the nutritional quality and particularly the proportion of the population that is continuously available to the birds. Prey types are not only localised in different ways, but also handled in an individual way. Not only the time but also the amount of effort that must be spent in feeding per unit of food ingested must be measured.

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12. SAMENVATTING

De Scholekster is een zeer algemeen voorkomende vogel in het Nederlandse Waddengebied. Eén van zijn belangrijkste prooidieren is het Nonnetje *Macoma balthica*, een klein tweekleppig schelpdier. In dit artikel wordt nagegaan welke betekenis het Nonnetje heeft voor de Scholekster door een aantal betrekkingen tussen de vogel en zijn prooidier te bespreken en wel: hoe vindt de Scholekster Nonnetjes, hoe komt het dat de vogel steeds de grotere exemplaren vindt, hoe wordt de schelp van het Nonnetje geopend en welke rol speelt het Nonnetje als stapelvoedsel voor de Scholekster. Waarnemingen werden gedaan zowel aan vrij levende als aan gevangen Scholeksters op het wad.

Eerst wordt het gedrag beschreven van Scholeksters die naar Nonnetjes zoeken. De vogels bewegen hun snavel op een karakteristieke manier: samengesteld pikken genoemd. Hierbij wordt de snavel in het slik snel op en neer bewogen, terwijl de vogel langzaam doorloopt, zonder dat de snavel iedere keer in zijn geheel uit de modder wordt gehaald.

Het Nonnetje leeft ingegraven in de wadbodem (Fig. 2). Met een lange uitstulpbare instroomsifo zuigt het het allerbovenste laagje van het wad op. In zachte modder ontstaan hierdoor stervormige sporen, is de bodem zandig dan worden geen sporen gevormd.

We vroegen ons af of Scholeksters gebruik maken van sporen om Nonnetjes te vinden. Dit bleek inderdaad zo te zijn, hetgeen kon worden geconcludeerd uit waarnemingen aan gevangen Scholeksters. Hierbij werd de snelheid waarmee de Nonnetjes gevonden werden, wanneer sporen beschikbaar waren, vergeleken met die wanneer sporen afwezig waren door ze weg te wissen, of de vogels 's nachts te laten foerageren (Figs. 4, 5).

Aangezien de Scholekster ook Nonnetjes kan vinden in afwezigheid van sporen, moet er naast een visuele methode ook een andere zijn waarmee de Nonnetjes gevonden worden. Localisatie op de tast leek aannemelijk. Uitgaande van de veronderstelling dat de snavel de schelp van een Nonnetje moet aanraken om deze te kunnen vinden, konden we berekenen hoe groot de kans was om een Nonnetje toevallig te raken, als de vogels willekeurig zouden pikken (Fig. 7). Deze kans wordt bepaald door het deel van het oppervlak van een stuk wad van bekende grootte dat, van boven bekeken, door de schelpen van de Nonnetjes die binnen snavelbereik zitten wordt ingenomen. Door nu de berekende aantallen te verwachten Nonnetjes te vergelijken met de aantallen die de vogels werkelijk gevonden hadden, blijkt dat inderdaad Nonnetjes op de tast worden gevonden als er geen sporen aanwezig zijn (Tabellen 2, 3).

Scholeksters blijken uit een populatie van Nonnetjes steeds de grotere exemplaren te nemen (Fig. 11). De vraag werpt zich dan op of dit een gevolg kan zijn van de manier waarop de Nonnetjes gevonden worden, namelijk op de tast. Immers een Nonnetje met een kleine schelp heeft een kleinere kans toevallig door de snavel geraakt te worden dan één met een grote schelp. Inderdaad blijkt dat, wanneer men rekening houdt met de verschillen tussn de mm-klassen

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in schelpgrootte en aantallen Nonnetjes binnen snavelbereik, de waargenomen selectie voor grote Nonnetjes geheel passief tot stand komt (Fig. 12). Het is dus niet zo dat kleine Nonnetjes, nadat ze gevonden zijn, vaker geweigerd worden dan grote Nonnetjes. Hierbij moet wel aangetekend worden dat Nonnetjes kleiner dan ongeveer 11 mm door Scholeksters actief worden geweigerd.

Na het vinden van een Nonnetje moet de Scholekster de schelp openmaken teneinde het vlees te kunnen opeten. Het openen van een nonnetjesschelp gebeurt op twee manieren: door hameren of door bijten. Hameren vereist een stevige ondergrond. D.m.v. een aantal harde pikken op één van de beide kleppen (Fig. 17) wordt deze óf t.o.v. de andere gedraaid waardoor een spleet ontstaat en de snavel in de schelp geschoven kan worden, óf de klep breekt. Individuele Scholeksters hameren meestal op dezelfde klep, waardoor zij min of meer vaste breukpatronen veroorzaken. Het openbijten van Nonnetjes vindt plaats in zacht substraat. Belangrijk hierbij is de mate waarin de kleppen wijken op het moment dat de vogel het Nonnetje vindt. Wijken de kleppen sterk uiteen dan wordt het Nonnetje ondergronds leeggegeten. Dit kost weinig tijd. Wijken de kleppen minder ver dan wordt het Nonnetje eerst naar het wadoppervlak gehaald waarna de vogel probeert zijn snavel tussen de kleppen te wringen. Dit kost veel meer tijd en vogels met een dunne snaveltop doen het sneller dan vogels met een dikke top (Fig. 22). Zowel bij het hameren als bij het openbijten wendt de Scholekster een methode aan, waarbij de kans op breuk van de kleppen zo gering mogelijk is, hetgeen de efficiëntie van het losmaken van het vlees uit de schelp ten goede komt.

Nonnetjes worden vaak geparasiteerd door een trematode *Parvatrema affinis*. Het Nonnetje fungeert als tussengastheer, een vogel (deze kan een Scholekster zijn) als eindgastheer van de parasiet. Geïnfecteerde Nonnetjes zijn herkenbaar aan witte, bolvormige sporocysten die zichtbaar worden wanneer de schelp geopend is. Waargenomen is dat Scholeksters althans een deel van de geïnfecteerde Nonnetjes niet opeten nadat ze deze geopend hebben (Tabel 15). Verondersteld wordt dat dit gedrag als functie heeft te voorkomen dat de vogels te zwaar besmet worden. Een hoge besmettingsgraad met parasieten kan gevaarlijk zijn, bijvoorbeeld bij hongertoestanden die in strenge winterperioden regelmatig voorkomen.

Vervolgens willen we weten hoeveel Nonnetjes per Scholekster worden gegeten over een hele laagwaterperiode die in het daglicht valt en als er geen andere prooien dan Nonnetjes worden gegeten. De resultaten zijn voor de waarnemingsgebieden Vlieland, Schiermonnikoog en Paesens afzonderlijk weergegeven (Tabellen 16, 17, 18). Het blijkt dat in het voorjaar het aantal gegeten Nonnetjes in de daglichturen dat het wad droog ligt groot genoeg is om de dagelijkse voedselbehoefte te dekken. De vogels hoeven niet ook 's nachts nog te eten (Tabel 20).

Uit een literatuuroverzicht van de voedselopname van Scholeksters met Kokkels, Mossels en Nonnetjes (Appendix 1) blijkt dat van maart tot augustus het aantal daglichturen waarin gegeten kan worden voldoende hoog is om de dagelijkse voedselbehoefte te dekken, maar in oktober tot maart is deze periode te kort. Dan moeten de Scholeksters bij laag water 's nachts ook foerageren op het wad, of eventueel bij hoog water overdag op de weilanden langs de kust (Tabel 21).

Verder is nagegaan in hoeverre het Nonnetje stapelvoedsel voor Scholeksters in het Nederlandse gedeelte van de Waddenzee kan zijn. Eerst werd bepaald bij welke minimale dichtheden (Fig. 27) van het Nonnetje de Scholeksters deze prooi nog net met succes kunnen exploiteren. Uit een overzicht van de verspreiding van de biomassa van het Nonnetje in de Nederlandse Waddenzee in dichtheden hoger dan de minimum dichtheden (Beukema 1976) blijkt dat het Nonnetje alleen plaatselijk en tijdelijk als stapelvoedsel voor Scholeksters kan dienen, vooral in het voorjaar. Op de meeste plaatsen is de Scholekster dus afhankelijk van andere prooidieren, zoals Kokkel en Mossel, die in de Waddenzee meestal in veel grotere hoeveelheden aanwezig zijn (Tabel 25).

In de laatste tijd staat nog al in de belangstelling de vraag of dieren al of niet optimaal voedselzoeken, dat wil zeggen of zij in een keuzesituatie steeds die prooi nemen welke de hoogste opbrengst (energie) geeft per eenheid geleverde inspanning. Onderzoek aan Scholeksters leent zich heel goed voor dit soort vragen. Daarom wordt in het laatste hoofdstuk nog een aantal opmerkingen gemaakt waarmee men bij toekomstig werk rekening zal moeten houden om in dit veld van onderzoek tot vruchtbare resultaten te komen.

ERRATA ARDEA 70 (2) 1982: 89—152

p. 97 Table 1. For 353 read 305 (twice)
p. 113. In the fourth formula from top, delete the second h_e
p. 114. For *Macoma* densities read 185 for 248 and 114 for 158 (*cf.* Table 8)
p. 131 line 15. For fine read cold with rain
p. 132 line 14. Read 80 for 180 (*cf.* Table 18)
p. 133 line 14. Read 23 May for 30 May (*cf.* Fig. 24)
p. 136 line 64. For 45 min read 35 min
p. 136 Table 21 line 4. Should read −3.58 ± 3.02 (6) −5.58 ± 5.23 (14) < 0.05
line 5. Should read +2.55 ± 2.60 (6) +2.59 ± 5.17 (14) n.s.
p. 142 line 9 and 15. For 175 read 100
p. 152 Appendix 1 first textline. BMR should read 49.0

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Appendix 1.

Month	Locality	Prey (16)	Observ. period h	Intake/ h g AFDW	Body weight g (1)	BMR kcal/ 24 h (2)	Food req./ 24 h gAFDW	Hours feeding requi- red	Hours feeding available day	Hours feeding available night	Food intake per daylight low water period wet ml (3)	wet g (4)	DW g (5)	AFDW g (6)
May	Vlieland (7)	Ce	12.0	5.11	520	29.0	40.7	8.0	8.0	2.8	*155.0*	*165.8*	35.7	30.8
	Paesens (8)	Ma	6.1	6.83	520	49.0	40.7	6.0	8.7	3.0	148.5	164.9	*48.0*	*41.5*
June/July	Schiermonnikoog (8)	Ma	5.5	7.17	520	49.0	40.7	5.7	7.9	2.4	*136.1*	*150.9*	*43.9*	39.6
July	Vlieland (7)	Ce	3.7	4.59	520	49.0	40.7	8.9	7.8	3.0	*81.0*	*86.7*	18.6	16.8
Aug.	Vlieland (7)	Ce	6.1	3.29	533	49.8	41.3	12.6	7.0	3.8	*97.0*	*103.8*	22.3	20.0
Aug.	Vlieland (8)	Ma	13.8	4.74	533	49.8	41.3	8.7	7.0	3.8	*116.0*	128.4	24.7	21.8
Sept./Nov.	Texel (9)	My	4.7	4.57	552	51.1	56.9	12.4	4.7	4.4	91.1	97.5	*23.9*	*21.4*
Oct.	Morecambe Bay (10)	Ce	7.5	5.35	583	53.2	59.2	11.1	7.2	7.3	*194.6*	208.2	44.8	40.2
Oct.	Ythan (11)	My	11.2	5.30	*500*	47.6	53.0	10.0	10.8	10.8	414.0	*443.0*	*66.2*	*59.2*
Oct./Nov.	Burry Inlet (12)	Ce	8.5	4.58	558	51.5	57.3	12.5	8.0	8.4	188.3	*202.0*	43.4	39.0
Oct./Feb.	Morfa (13)	My	7.0	6.74	583	53.2	59.2	8.8	6.0	7.6	*200.9*	215.0	52.7	47.2
Nov.	Vlieland (7)	Ce	5.7	7.58	571	52.4	58.3	7.7	4.6	6.2	*208.0*	*222.6*	47.9	42.9
Dec.	Ythan (11)	My	9.2	4.49	*500*	47.6	53.0	11.8	6.9	10.9	225.2	*241.0*	*46.2*	*41.4*
Dec./Jan.	Burry Inlet (12)	Ce	8.5	3.32	589	53.8	59.9	18.0	6.4	10.0	139.3	*149.0*	32.0	28.2
Jan.	Morecambe Bay (10)	Ce	7.5	4.05	589	53.8	59.7	14.7	6.0	8.5	*151.2*	161.8	34.8	30.4
Jan.	Wash (14)	Ce	?	11.50	*555*	51.3	57.1	5.0	5.0	7.9	—	—	—	—
Jan./Mar.	Greyabbey Bay (15)	Ce	10.0	2.20	605	54.6	60.8	27.6	9.2	10.1	110.7	118.5	*25.5*	22.0
Feb./Mar.	Burry Inlet (12)	Ce	8.5	3.45	615	55.3	61.6	17.8	8.3	8.1	148.6	*159.0*	34.2	29.3
Mar.	Brancaster (10)	Ce	8.0	4.93	615	55.3	61.6	12.5	8.5	6.9	*201.6*	215.7	46.4	39.5
Mar.	Pensarn (13)	My	9.0	6.22	615	55.3	61.6	9.9	10.1	7.3	*251.1*	268.7	65.8	56.0

(1) body weights according to Dare (1977)
(2) BMR according to Aschoff & Pohl (1970) for non-passeres
(3) parameters italicized given by the authors
(4) specific weight of wet flesh of *Cerastoderma* and *Mytilus* = 1.07; of *Macoma* = 1.1 (Hulscher, unpublished; Drinnan 1958b)
(5) % dry weight of the wet weight (Hulscher, unpublished; Drinnan 1957)
(6) % ash of the dry flesh for *Mytilus* and *Cerastoderma* from monthly figures of *Mytilus* (Dare & Edwards 1975), for *Macoma* corrected with a factor 1.5 when *Macoma* was not cleaned with sea-water (Beukema & De Bruin 1977
(7) Hulscher, unpublished
(8) this study
(9) Koene (1978)
(10) Drinnan (1957)
(11) Heppleston (1971)
(12) Davidson (1967)
(13) Drinnan (1958a)
(14) Goss-Custard (1977)
(15) Brown & O'Connor (1974)
(16) Ce = *Cerastoderma*, Ma = *Macoma*, My = *Mytilus*

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