The oystercatcher Haematopus ostralegus as a predator of the bivalve Macoma balthica in the Dutch Wadden Sea
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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 m², 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 medi-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:

\[ N(\text{predicted}) = \text{time spent in multiple pecking} \times \text{mean probing rate (probes per second multiple pecking)} \times \text{mean density of the Macoma population within reach of the bill} \times \text{mean effective touch area per available Macoma} \times 10^5 \]

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 (187) approached the number predicted (189). 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 the substrate blow, of multiple pecking is gummed 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...
time required for thick and thin bailed 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 bailed birds opened them
more quickly than thick bailed ones (Fig. 22).

Oystercatchers frequently reject a Macoma, once it has
been opened, suggesting that the birds check the food be-
fore eating it (chapter 5). It was found that rejected Maco-
mas were invariably parasitized by the trematode Parvare-
auma affinis. An infected Macoma can be distinguished from
an uninfected one only when the valves are separated, ex-
posing 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 Maco-
mas, 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 dimin-
ishing 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 di-
rect 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 be-
ing available — it was worthwhile investigating whether Ma-
coma yields obtained in daytime were sufficient for Oyste-
catchers to subsist on, 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
Paasens (Tables 16, 17, 18). It turned out that Macoma can
very well yield 24-hour requirements for Oystercatchers in
springsume in the areas studied (Table 20).

Next a general survey of data from literature is presented
on quantitative food intake by Oystercatchers with Cerat-
derma, 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
equal 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, Cerat-
derma, 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 ef-
fort (Rovana 1970). It is argued that such questions must be
studied by observing individually marked birds for long peri-
dods throughout the seasons. Several factors may influence
prey choice and hence must be taken into account when
studying profitabilities of prey types: bill morphology, on-
togenetic experience, social status, knowledge of the feeding
area, time available for feeding, etc. Besides these char-
acteristics concerning the individual Oystercatchers, char-
acteristics of the prey have to be studied: a measure of the
amount of flesh contained in the shell per Macoma, but also
total quality and particularly the proportion of the popula-
tion 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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