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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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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 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* ($\leq$ 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

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 ef-

fort (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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