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Oystercatchers and Shellfish: Predator/Prey Studies

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Printed in England by Heffers Printers Ltd, Cambridge, England © Copyright 1977 Published in 1977 by Institute of Terrestrial Ecology 68 Hills Road, Cambridge CB2 1LA ISBN 0 904282 12 0 Dr J. D. Goss-Custard Institute of Terrestrial Ecology Furzebrook Research Station Wareham Dorset BH20 5AS 092 93 (Corfe Castle) 361-2

The Institute of Terrestrial Ecology (ITE) was established in 1973, from the former Nature Conservancy's research stations and staff, joined later by the Institute of Tree Biology and the Culture Centre of Algae and Protozoa. ITE contributes to and draws upon the collective knowledge of the fourteen sister institutes which make up the Natural Environment Research Council, spanning all the environmental sciences.

The Institute studies the factors determining the structure, composition and processes of land and freshwater systems, and of individual plant and animal species. It is developing a sounder scientific basis for predicting and modelling environmental trends arising from natural or man-made change. The results of this research are available to those responsible for the protection, management and wise use of our natural resources.

Nearly half of ITE's work is research commissioned by customers, such as the Nature Conservancy Council who require information for wildlife conservation, the Forestry Commission and the Department of the Environment. The remainder is fundamental research supported by NERC.

ITE's expertise is widely used by international organisations in overseas projects and programmes of research.

Cover photographs reproduced by kind permission of Mr. J. B. Bottomley (Oystercatcher — top), and Mr. P. Ainsworth (Mussels — bottom).

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Predator/Prey Studies on Oystercatchers and Shellfish

This leaflet is one of a series describing research which is currently being done by the Institute of Terrestrial Ecology (ITE), a component body of the Natural Environment Research Council. Each leaflet describes a particular aspect of ITE's research and indicates the nature of the problem, the methods used in the research, and possible practical applications of the results.

In 1976, research was started on the role of the oystercatcher in determining the abundance of the mussel, a common intertidal shellfish. There were two main reasons for undertaking this research. First, we wished to study a fundamental ecological process, namely the interaction between a predator and its prey. Second, we wanted to improve our understanding of the impact which these wading birds have on commercial stocks of shellfish, when compared with other factors such as weather or predation by fish. This impact has aroused considerable controversy in recent years so the research has an immediate and practical value as well as adding to our knowledge of predator/prey relationships generally. The interactions between a predator and its prey are complex, but they can be subdivided into a number of simpler relationships for the purposes of analysis. For example, the feeding rate of a predator in relation to the density of its prey is an important part of the overall predator/prey interaction and one form the relationship may take is shown in Figure 1. In the past, ecologists have been content to describe such relationships qualitatively rather than quantitatively. More recently, attempts have been made to describe these relationships quantitatively through the use of mathematical models. Once the validity of a model has been tested, the role of various factors, singly and in combination, may be explored by changing the parameters of the model. It should also be possible to use the same model to make more precise predictions of the effects of human impact on natural communities.

Collecting data for the construction of models is often difficult. Basically, there are two steps. First, the relationships

Figure 1. The number of prey taken per unit time by a hypothetical predator at different prey densities.

likely to be important in the functioning of the system must be identified. These relationships can be derived from previous studies of the species concerned, from experimental tests of direct effects and from the biological intuition of the individual research worker. Second, these identified relationships need to be described quantitatively over as wide a range of variation as possible. Careful design and execution of the ways in which data are collected are necessary, so that the mathematical expressions of the relationships can be made as precise as possible. While progress has been made for a whole range of species in achieving the first step, the second step may be impossible unless the systems can be studied within the limits of existing field equipment and techniques. Investigations made on estuarine wading birds and a variety of their intertidal prey animals suggest that they may provide realistic opportunities for the quantitative studies of the predator/prey relationship. Furthermore, there is much basic information already available on the oystercatcher and the shellfish on which it feeds, with the result that costly timeconsuming exploratory studies are unnecessary. The oystercatcher is easy to observe in its natural habitats, while the shellfish are easily sampled (see cover photographs). There is, therefore, an opportunity to examine how the oystercatcher responds to variations in the abundance of shellfish, and how these responses, in turn, affect the magnitude of the mortality inflicted on the prey by the birds,

both in space and through time. The contribution of the oystercatcher to the overall population fluctuations of the shellfish can then be modelled and the nature of the interactions explored.

Basic Biology of the Species Involved

Oystercatchers are numerous around the coasts of Britain, particularly on estuaries. They breed in many areas of the British Isles, especially in the north, but occur in the greatest numbers in autumn and winter outside the breeding season. Counts made by teams of volunteers as part of the joint British Trust for Ornithology/Royal Society for the Protection of Birds/Wildfowl Trust Estuaries Enquiry have shown that up to 185,000 of these birds may be present in Britain at any one time. Ringing studies have shown that these wintering flocks contain British birds and many individuals that breed to the north in the Faeroes, Iceland and Norway.

Oystercatchers feed on several kinds of intertidal invertebrates and in some areas of the country feed in fields as well. On the shore, ragworms (Nereis diversicolor) and crabs (Carcinus maenas) are often taken, but the bulk of the diet in most areas seems to be shellfish. Of these, the edible mussel (Mytilus edulis), cockle (Cerastoderma edule) and Baltic tellin (Macoma balthica), are the most important. Mussels lie on the surface and are easily detected by the birds once the receding tide has exposed them. Cockles may also be detected by sight, even though they are buried just below the surface: presumably, the birds are able to detect the short syphon tubes with which the cockles maintain contact with the surface. Oystercatchers often use their bills to detect cockles and the deeper-burrowing Macoma by touch. Once found, the birds may swallow the smaller shellfish whole, but open the larger ones with their powerful beaks either by cracking the shell open or by prising the two halves apart. The birds then cut the flesh away from the shell and swallowit. Normally, oystercatchers do not simply take all the shellfish they encounter, but select particular size classes. For example, they select large Macoma and medium-sized cockles (Figure 2) and only take other size classes in large numbers when the preferred ones are scarce. This selection implies that it is important to distinguish between size classes of shellfish when the role of oystercatchers in the population dynamics of their prey is being studied.

The main shellfish prey of oystercatchers in this study is the mussel. In the summer, each female, depending on its size, produces several thousand eggs which are fertilised in the sea. After a few weeks of growth in the plankton, the ciliated larva develops a bivalve shell and sinks to the bottom where it may settle on one or more substrates before settling on an established mussel bed. By delaying final settlement in this way, many larvae are sufficiently large to avoid being consumed by the adult mussels. The growth rate and

Figure 2. The sizes of cockles and Macoma (solid line) taken by oystercatchers in one area on the Wash compared with the sizes of animals (dotted line) in the sand where the birds were feeding.

survival of the young mussels varies enormously from place to place and will depend upon the density and size of its neighbours and on a variety of abiotic factors, such as the period of tidal immersion, and hence time available for feeding. Little is known about the planktonic phase of the larval mussel, but, on the beach, small mussels are eaten in large quantities by crabs and fish, and large mussels are eaten by birds, notably the oystercatcher, and fished by man. Many mussels of all ages may be destroyed by winter storms. Populations of mussels in estuaries are often characterised by low recruitment but good growth rates, with a relatively high proportion surviving for 5 or 10, or even more, years. This high rate of survival is in contrast with that of populations on rocky shores. At high levels on exposed rocks, there is low recruitment and poor growth potential, but, in the absence of predators, a high proportion may survive even up to 20 years. At low levels on the shore, recruitment may be very heavy and growth rate extremely fast, but few mussels survive beyond 1 or 2 years because of intensive predation by a wide range of species which penetrate the lower levels of the shore from , the sublittoral when the tide is in. These findings on rocky shores suggest that predators can have a profound influence on the performance of mussel populations, and that a study of the interactions between one predator, the oystercatcher, and its mussel prey would be worthwhile.

The Study Area

An important consideration in the choice of study area was the efficiency with which the prey population could be sampled. Accordingly, a small estuary was selected in preference to a large embayment such as the Wash or Morecambe Bay. This decision to some extent determined the prey species, because, in general, oystercatchers feed mainly on mussels in the smaller estuaries. The Exe estuary in South Devon was chosen because several features made it particularly suitable for study. Most oystercatchers in this estuary feed on mussels, although a variety of other prey is also taken. The mussel beds on the Exe are extensive (Figure 3) and are protected from storms which, in more exposed sites, may destroy entire beds.

Figure 3. The Exe estuary, showing mussel beds.

Interactions

For the purposes of study, the interaction between predator and prey can be subdivided naturally into two maior components and a mathematical model constructed for each:—

- (i) variation in the abundance of each age and size class into which the total mussel population may be divided;
- (ii) the responses of the oystercatchers to variations in the abundance of particular age and size classes of mussels, and their impact on them.

As is shown schematically in Figure 4, the output from one model comprises the input for the other. In the simplest form of the model the birds respond to variations in the abundance of the preferred age and size classes of their prey by taking fewer or more of these prey in the various age and size classes and, indeed, of other species. The predation on the mussels affects the settlement and growth potential of the small animals and the reproductive output of the population as a whole. These prey responses, in turn, determine the future food supplies of the birds. Because factors other than the abundance of mussels affect the predatory activities of the birds and, similarly, factors other than the birds affect the behaviour of the mussel population, extrinsic variables must also be incorporated into both models, if a proper understanding is to be obtained.

Figure 4. Simplified diagram of the predator-prey interaction between oystercatchers-and mussels.

Each of these models will itself comprise a series of submodels which describe the behaviour of particularly critical parts of the system. Space does not permit more than a cursory examination of this point, but an indication of the procedures and methods employed may be gained by describing aspects of the model of bird predation in more detail.

Model of Bird Predation

It has proved useful in studies of predator/prey interactions to distinguish between (a) the behavioural responses of individual predators to variations in the abundance of prey, and (b) the numerical response to prey abundance of the predator population as a whole through survival and reproduction. The combined behavioural responses of all the oystercatchers present on the estuary determine the mortality that they inflict on the mussels. Some of the basic relationships that comprise one of these categories of response, the behavioural response, may be illustrated with data obtained from oystercatchers eating cockles on the Wash. The birds are presented with a food supply which varies in density from place to place. Direct observation of birds on the feeding grounds suggest that both the number and weight of prey taken per unit time is related to the abundance of prey

Figure 5. The relationship between (1) the number of cockles, and (2) the weight of cockles eaten per minute by oystercatchers in relation to the abundance of the prey in the substrate. The birds took larger food items as the abundance of cockles in the substrate increased.

in the substrate (Figure 5). It is likely that the birds prefer to feed where feeding is easiest and so will go where their prey are most abundant. Indeed, oystercatchers on the Wash were most numerous where cockles were most abundant (Figure 6).

Figure 6. The relationship between the density of oystercatchers and the abundance of cockles in nine areas on the Wash.

Figure 7. The proportion of oystercatchers feeding in the preferred part of their feeding area in relation to the total numbers present.

However, this tendency to congregate in the most profitable feeding areas may, in turn, be counteracted by the birds becoming increasingly intolerant of each other as their own density rises, so that some birds feed in the less preferred areas (Figure 7). Such a tendency would depress the impact of the oystercatchers on their prey where these are most abundant. These behavioural responses by the oystercatchers to each other and to their common food supply would result in their impact on their prey during autumn and winter varying in magnitude from place to place according to the density of prey at the start. One possible form which the relationship might take is shown in Figure 8. The aim of the studies on the birds' feeding behaviour is to build a sub-model which describes the relationship between the density of the prey and the impact of the oystercatchers on it while, at the same time, incorporating the effects of any other relevant variable.

Future development

It is, of course, only possible to describe a small part of the research as it is envisaged at the moment. However, once the models have been constructed and tested, it will be possible to explore how the oystercatcher-mussel system would respond to disturbances of various kinds. This exploration should contribute to the understanding of how predator-prey

Figure 8. Possible form of the relationship between the density of the prey in autumn and the percentage eaten by oystercatchers by the following spring.

systems function, and, at the same time, yield insights to the solution of practical problems. Currently there are two main applications.

First, there are a number of proposed schemes for developing parts of major estuaries for water-storage and industry. Birds displaced by such schemes would presumably attempt to settle in the remaining feeding grounds, with a consequent increase in bird density. The long-term quantitative effect on both predator and prey populations of an increase in the density of predators that feed preferentially on particular size and age class of prey cannot be predicted easily without a mathematical model based on a firm understanding of the system. Second, it is often claimed that oystercatchers are a major pest of commercially exploited shellfish populations. The effect of varying numbers of oystercatchers on the performance of the mussel population will be explored by the models derived from this research. Although the models will be constructed for a particular estuary, their properties should enable reasonable predictions to be made for other areas.

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