INSTITUTE OF TERRESTRIAL ECOLOGY
(NATURAL ENVIRONMENT RESEARCH COUNCIL)

Report to Commission of the European Communities, Directorate-General for Fisheries

CEC contract: PEM/93/03
ITE project: T08057O5

Models of Shellfish Populations and Shorebirds: Final Report

November 1996

R A Stillman[1], J D Goss-Custard[1], S McGrorty[1], A D West[1], S E A le V dit Durell[1], R T Clarke[1], R W G Caldow[1], K J Norris[2], I G Johnstone[2], B J Ens[3], E J Bunskoeke[3], A v.d. Merwe[3], J van der Meer[4], P Triplet[5], N Odoni[1], R Swinfen[6] & J T Cayford[7]

[1] Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK
[2] Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK
[3] Institute for Forestry and Nature Research (IBN-DLO), P O Box 167, NL-1790 AD Den Burg, Texel, The Netherlands
[4] Netherlands Institute for Sea Research (NIOZ), P O Box 59, NL-1790 AB Den Burg, Texel, The Netherlands
[5] Reserve Naturelle de la Baie de Somme, 40 Rue Carnot, 80550 Le Crotoy, France
[6] Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, UK
[7] Oak Cottage, Langton Green, Eye, Suffolk IP23 7HL, UK

This study has been carried out with financial assistance from the Commission of the European Communities.

CONTENTS

ABSTRACT

(i) The objective of this project was to develop a predictive model to explore the effect of different shellfishery management options on the mortality rates of the shorebirds that feed on the shellfish during their stay on their intertidal wintering grounds in Europe. The model also predicts the effects of these birds on the abundance of shellfish. The model predicts the disturbance effect of people collecting shellfish at low tide and the effect of harvesting shellfish that would otherwise be taken by the birds later in the same winter or in subsequent winters.

(ii) The model is game theoretic but also empirical as its parameter values are derived from the results of many years of field data collection in several European countries. The model was developed by expanding an existing ITE model on the interaction between oystercatchers and mussels on the Exe estuary in south-west England. The main model tests were also carried out in this study system. The tests showed that model predictions were generally in line with the results of field observations. In particular, the model predicted the levels of oystercatcher winter mortality recorded in the field. The model also predicted well the numbers of birds that compensated for failing to achieve an adequate rate of food intake on the estuary at low tide by feeding in the fields over the high water period.

(iii) The range of shellfish policy options that has been explored in this contract has been narrow compared with the range that is possible in principle. For example, the model is capable of exploring the effects on shorebirds of such options as (i) varying the particular shellfishing technique used and the total fishing effort expended; (ii) fishing only at certain times of day, or on particular days of the week, or at certain stages in the neap-spring cycle or times of year; (iii) fishing on some beds but not others; and (iv) regulating the total catch taken in different ways. The report details the predictions of a limited set of example fishing scenarios to illustrate the uses to which the model could be put. But it has also made some predictions that have important implications for shellfishery management and that are likely to apply across a wide range of estuaries and fisheries. The model enables the quantitative effect on shorebird mortality of a wide range of different shellfish policy options to be estimated.

(iv) The main conclusions of the model are:

- It is quite possible to exploit shellfish stocks without increasing the winter mortality of shorebirds as long as certain conditions are met, which are specified.
- The effects of a given intensity of shellfishing depend crucially on local conditions of the climate and the general abundance of food.
- For a given amount of shellfish removal by a fishery, methods that disturb the birds over the low water period can be significantly more damaging to the birds' chances of survival than those that are not disturbing.
- The number of birds using alternative food sources provides an easily-monitored early warning that a change in shellfishery practice is beginning to have an effect on the birds.
- The proportion of the shellfish stock that is affected by shellfishing has a critical influence on predicted mortality rates, this in turn depending on the fishery 'giving-up' density, the minimum allowable fishable shellfish size and how many of the shellfish below the legally-taken size range are killed.
- The cumulative effects of small increases in shorebird mortality in winter can over a period of years greatly affect stable population size because the effects of shellfishing fall disproportionately on the inexeperienced and often subdominant young birds that are the seed corn of the future generations.
- As fishing effort increases, shorebird mortality may be hardly affected initially but then may suddenly increase dramatically once a threshold level of fishing effort has been reached.

(v) The model developed in this contract provides a means for predicting the effects of shellfishery practice on co-dependent shorebird populations and of the effects of the birds themselves on shellfish abundance in both the short- and long-term. As such, it is tool which can be used by decision-makers concerned with shellfish policy throughout Europe, whether they represent governments, fisheries organisations or nature conservation bodies. The model provides a basis for further research into the interaction between shellfish and shorebirds, and could be expanded in a number of directions, including incorporating other species, such as mollusc-eating ducks. The model can also be used to predict the effects on shorebirds of other environmental changes, including habitat loss and change. The model can be used by scientists interested in the reciprocal interactions between vertebrate predators and their invertebrate prey.

KEY WORDS: mussels, *Mytilus edulis*; cockles, *Cerastoderma ed*ule; oystercatchers, *Haematopus ostralegus*; knots, *Calidris canutus*; shellfishing; habitat loss; population dynamics; predator-prey interactions; individual-based modelling.

SUMMARY

(i) The objective of this project was to develop a predictive model to explore the effect of different shellfishery management options on the mortality rates of the migratory shorebirds that feed on the shellfish during their stay on their intertidal wintering grounds in Europe. Member States have signed a number of national and international agreements to maintain the habitats of this group of birds and research is needed to guide policy on how the commercially valuable shellfish stocks can be exploited while at the same time safe-guarding the interests of the birds. The model also predicts the effects of these birds on the abundance of shellfish.

(ii) Fishing affects the birds in two ways. Those methods of harvesting that require people to be present on the intertidal flats over the low water period, such as hand gathering, disturb birds by driving them away from areas that they would otherwise have used for feeding. The disturbance itself costs the birds lost time, because they temporarily stop feeding, and increases their energy requirements if they fly to another place. Disturbance may also increase any competition that occurs between foraging birds because they have been squeezed by disturbance into a smaller foraging space so that the density of the birds increases. Disturbance may thus both directly and indirectly reduce the intake rates of the birds and increase any difficult they may have in obtaining their energy requirements. The second way in which shellfishing affects the birds applies to all fishing techniques. In the winter in which the fishing takes place and in successive winters, fishing may reduce the abundance of the shellfish stocks to the point at which it makes it more difficult for the birds to obtain their energy requirements which, on the wind-swept intertidal flats of Europe, can be very high in winter. Shellfishing may thus have both short-term and long-term effects on the two that also depend on shellfish stocks.

(iii) The model developed in this report includes all of these effects on the birds. The model is based on many years of field data collection in several European countries. A key feature of the model is that it incorporates the realistic responses of birds to the various impacts of shellfishing. For example, birds in the model move from an area that is occupied by shellfishers and attempt to feed in another part of the intertidal flats, with a success that depends on the food abundance and level of competition from other birds that they experience there. The models also allow individuals some measure of compensation for the impact of shellfishing upon their foraging. Thus the birds are able to extend their foraging by feeding upshore on poor quality shellfish stocks as the tide ebbs and flows and also to feed in fields over high tide. In this way, the model tracks the fortunes of individual birds and thus incorporates the vital biological reality of variation between animals in their responses to environmental change. After all, it is individual animals that respond to environemntal change and not populations *per se*.

(iv) The model was tested on the Exe estuary in south-west England, where it had been initially developed. The tests showed that model predictions were generally in line with the results of field observations. Of greatest importance in the present context was the success with which the model predicted the levels of oystercatcher winter mortality that have been recorded on the Exe. The effect of shellfishing on bird mortality is the fundamental issue that arises when its impact on shorebirds is discussed; to be of any practical use, the model had to be able to predict mortality and to predict it with some accuracy. Almost as important, the model predicted well the numbers of birds that compensated for failing to achieve an adequate rate of food intake on the estuary at low tide by feeding in the fields over the high water period. The model would be of little predictive value if it had been unable to allow birds to compensate in realistic ways for any ill-effects of shellfishing on their ability to feed on mussels and cockles.

(v) The range of shellfish policy options that has been explored in this contract has been narrow compared with the range that is possible in principle. The model is capable of exploring the effects on shorebirds of such options as (i) varying the particular shellfishing technique used and the total fishing effort expended; (ii) fishing only at certain times of day, or on particular days of the week, or at certain stages in the neap-spring cycle or times of year; (iii) fishing on some beds but not others; and (iv) regulating the total catch taken in different ways. The report details the predictions of a limited set of example fishing scenarios to illustrate the uses to which the model could be put.

(vi) The report also details some predictions that have important implications for shellfishery management and that are likely to apply across a wide range of estuaries and fisheries. Some of the predictions had been realised before this contract was completed but the important point is that the model enables the quantitative effect on shorebird mortality of a wide range of different shellfish policy options to be estimated. The main conclusions are:

- It is possible to exploit shellfish stocks without increasing the winter mortality of shorebirds. A number of conditions must apply if this is to be true. These conditions include a high abundance of shellfish and the presence of alternative food sources to which the shorebirds can turn when shellfish become scarce.
- The effects of a given intensity of shellfishing depend crucially on local conditions of the climate and the general abundance of food. Shorebirds are most vulnerable during severe winter weather when their energy demands are elevated and, in the case of oystercatchers, their supplementary food souces on the upshore flats and in fields are made inaccessible through freezing.
- For a given amount of shellfish removal by a fishery, methods that disturb the birds over the low water period, such as hand gathering, can be significantly more damaging to the birds' chances of survival than those that are not disturbing, such as the Dutch 'wonderklaw'. Clearly, though, this depends on the fishing effort and therefore on the number of person-days of disturbance.
- The number of birds using alternative food sources provides an early warning that a change in shellfishery practice is beginning to have an effect on the birds. Potentially this is a very important management tool because the numbers of birds using these food sources is usually very easy to monitor, especially as large numbers of amateur ornithologists can be mobilised to help with the counts.
- A key factor determining the impact of shellfishing on shorebirds is the proportion of the shellfish stock that is affected. This in turn depends on such factors as the density of shellfish down to which the stocks can be reduced before fishing ceases to be economic, the minimum size of shellfish allowed to be fished, and how many of the shellfish that are below the legally-taken size range are killed.
- The cumulative effects of small increases in shorebird mortality in winter can over a period of years greatly affect stable population size largely because the effects of shellfishing fall disproportionately on the inexeperienced and often subdominant young birds that are the seed corn of the future generations.
- As fishing effort increases, shorebird mortality may be hardly affected initially but then may suddenly increase dramatically once a threshold level of fishing effort has been reached. This happens when the individuals comprising the population vary only a little in their ability to compensate for increased levels of fishing.

(vii) The model developed in this contract provides a means for predicting the effects of shellfishery practice on co-dependent shorebird populations and of the effects of the birds themselves on shellfish abundance in both the short- and long-term. The model is able to explore by just how much winter mortality in shorebirds would be expected to increase were any of a very wide range of policy options to be introduced by shellfishery managers. As such, it is tool which can be used by decision-makers concerned with shellfish policy throughout Europe, whether they represent governments, fisheries organisations or nature conservation bodies. As part of its Common Fisheries Policy, the EU is committed to maintaining in as good a condition as possible the intertidal feeding grounds of shorebirds, including those that depend on the shellfish that are also commercially exploited on a huge scale. Throughout Europe, conflicts arise between the shellfisheries and the conservation organisations. But as this report has shown, shellfishing does not necessarily affect shorebirds; within limits, the birds do have the capability of compensating for any added difficulties shellfishing might make to their ability to survive the winter. Furthermore, the chances that a given level of shellfishing will affect the birds' chances of surviving the winter depends on the local conditions of shellfish abundance and climate. In order to fulfil the conservation committments of the Policy, there is a need to be able to predict quantitatively how particular shellfish management options affect the number of shorebirds that survive the winter. The model whose development has been described in the report is a contribution towards making the quantitative predictions required if the conservation objectives of the Policy are to be achieved.

Chapter 1 INTRODUCTION

J D Goss-Custard

1.1 POLICY BACKGROUND

The Commission's Research and Development concerning the protection of marine species field of research requires improved knowledge of the impact of fishing activities on the environment in order to achieve a responsible exploitation of marine resources. This study will contribute to meeting this objective by providing a means to predict the consequences for the shorebirds of various policy options for exploiting shellfish populations. It will also enable the effect on the shellfish populations of various conservation policy options, such as limiting fishing in some areas, to be explored. These aims are directly related to the priority area of research concerned with the effects of established fisheries on co-dependent populations.

Two species of bivalve shellfish, the cockle *Cerastoderma edule* and mussel *Mytilus edulis*, that are fished commercially in several European countries are also an important food resource for two species of shorebird, the Knot *Calidris canutus* and Oystercatcher *Haematopus ostralegus*. Young cockles and mussels less than 15mm long, are eaten by Knot, each of which may eat several hundred shellfish per day between autumn and spring. Knot occur in very large numbers during winter, with flocks of tens of thousands of birds being common in the Wadden Sea and in large estuaries and embayments elsewhere in Europe, such as the Wash in east England. Oystercatchers also occur in very large numbers, especially in late summer, autumn and winter, and eat the larger shellfish, just as they begin to enter the size range when they can be fished. Oystercatchers also consume large numbers of shellfish, with each bird eating from 100 to 500 individual shellfish per day, depending on the average size of the shellfish. It is not uncommon for Oystercatchers to remove during winter as much as 40% of the larger shellfish that could otherwise have been fished subsequently (Goss-Custard *et al.* 1996a). As well as affecting the amount of the present stock that remains, Knot and Oystercatchers may also affect the long-term abundance of many shellfish populations (Goss-Custard *et al.* 1996a). The long-term impact of Knot has not yet been evaluated, but Oystercatchers undoubtedly contributed to the low stocks of cockles that occurred over many years in the Burry Inlet, south Wales (Horwood & Goss-Custard 1977). Understandably, commercial shell fisheries are frequently concerned at the numbers of shellfish removed by the birds, especially in years when shellfish stocks are in any case low, and are seeking techniques to reduce the impact of the birds on the shellfish stocks (Spencer 1991).

Migratory shorebirds are, however, also a cause of great concern to conservationists because several aspects of their ecology would appear to increase the vulnerability of their populations to environmental change. The sizes of their populations have been shown to be sensitive to factors that decrease survivorship away from the breeding grounds (Goss-Custard & Durell 1990). Partly because of the exposed nature of their open intertidal habitat (Kersten & Piersma 1987), wintering shorebirds may often have difficulty in maintaining their energy balance, especially in severe weather, as studies on Oystercatchers in the Netherlands (Swennen & Duiven 1983; Hulscher 1989) and the United Kingdom (Davidson & Evans 1982) have shown (Goss-Custard *et al.* 1996b). Shorebirds breed throughout northern Europe and as far north as the Arctic. Because they are specialised feeders, with many species being either entirely or partly dependent on the invertebrates that live in European coasts, the many hundreds of thousands of the birds migrate along or spend the winter on these coasts (Smit & Piersma 1989). This results in very high densities of birds in relatively few sites at particular times of year. Moreover, breeding at high latitudes necessitates the accumulation of large reserves of energy to fuel their onward migration, which may involve flights of thousands of kilometres, as a symposium on the migration of Knot demonstrates (Piersma & Davidson 1992). The loss of one link in the migratory chain may therefore have a disproportionate effect on population viability. For all these reasons, conservationists are understandably concerned that human activities on the estuaries and tidal flats of

Europe may make it more difficult for these birds to survive the winter and to make their long migration flights (Ens *et al.* 1990; 1994). Many Governments have signed agreements to protect this internationally significant group of birds and, in Europe, several important intertidal areas have been designated, or are being considered for designation, as Special Protection Areas.

A conflict of interest often develops between conservationists and commercial fisheries because of this overlap in the resource used by birds and men. Fishermen are concerned that shorebirds, particularly Oystercatchers, might seriously affect shellfish yield. Conservationists are concerned that the commercial exploitation of cockles and mussels, the food supply of Knots and Oystercatchers will be reduced to such an extent that birds are unable to obtain enough food to survive the winter, to migrate and to return in good condition to the breeding grounds, even if they are able to feed on prey other than shellfish before they leave the wintering areas. This concern has increased as more fishing is being done over high water from boats that use suction pumps to dredge up large quantities of shellfish; this is the main method used in the Wadden Sea, which sustains very large numbers of shorebirds. In some areas of Europe, such as the United Kingdom, where shellfish are still collected over low water, conservationists are also concerned that the bodily presence of fishermen on the shellfish beds disturbs the birds and prevents them exploiting the shellfish. This concern has increased in importance following two events. First, the discovery was made that the overwinter survival of Oystercatchers was reduced by a loss of feeding grounds in south-west Netherlands (Lambeck 1991; Meire 1991; Lambeck *et al.* 1996). Second, untypically high numbers of Oystercatchers died on the Wash during the winter of 1992-93, despite the weather being relatively mild. Accusations have been made by some against the shellfish industry (Clark 1993). Conflicts between conservationists and fishermen on this matter arise regularly in a number of European countries (Spencer 1991), and it is timely to develop techniques for evaluating the issues concerned.

1.2 PROJECT BACKGROUND; EARLY MODELS

The need at the beginning of this project was to develop a predictive model which allowed us to explore the consequences of changes in fishing activities and bird numbers on commercial shellfish stocks and on the birds themselves. Prior to the start of the present project, the Institute of Terrestrial Ecology (ITE) had been collecting since 1976 data on Oystercatchers exploiting a population of mussels in south-west England. This made the development of such a model possible at the time this project began in 1994.

A feature of fundamental importance of this system - as in most others - is that the abundance of the prey animals, and so their population dynamics, varies between places, in this case, between the 10-12 (depending on the year) main mussel beds of the Exe estuary (McGrorty & Goss-Custard 1991). Oystercatchers (and fishermen) generally prefer to harvest mussels, and other shellfish, in those areas where the shellfish are abundant and the sediment is firm (Goss-Custard *et al.* 1992). The birds have their greatest impact, of course, in those areas where they congregate. By fishing in the same areas, the fishermen, in turn, disturb the feeding activities, and reduce the food supplies, of particularly large numbers of Oystercatchers. In direct response to disturbance and the declining food stocks over the winter, the birds would be expected to re-distribute themselves over the other mussel beds of the estuary in an attempt to maintain their intake rates, as studies elsewhere on Oystercatchers eating cockles have shown (O'Connor & Brown 1977; Triplet 1984; Goss-Custard *et al.* 1996b; Triplet & Etienne 1991). This re-distribution would result in more birds feeding on the poorer mussel beds where food abundance, and thus their rate of feeding, would be lower. Furthermore, because the birds would now be congregating on a smaller number of mussel beds, and thus in a smaller area, they would be forced to feed together at higher densities. This, in turn, would increase the number of birds whose food intake rate would be reduced by various forms of competitive interactions between individual birds, because such interference increases as the density of Oystercatchers feeding on the mussel beds increases (Koene 1978; Zwarts & Drent 1981; Sutherland & Koene 1982; Ens & Goss-Custard 1984; Ens *et al.* 1996; Stillman *et al.* 1996). The increased bird densities would also increase the rate at which the mussels there would be depleted, with a consequent effect on mussel abundance over the winter and, in some shellfish populations (Goss-Custard *et al.* 1996a), in the long-term. Thus, because the birds can move so readily between mussel beds, increasing human activity on some mussel beds affects the rate of feeding of the birds on many others.

Based on studies of the behaviour of Oystercatchers when severe weather reduces the foraging opportunities in one part of Europe (Hulscher 1989), the increased difficulties faced by the birds, as a result of increased rates of depletion and interference, would be expected to increase the numbers forced to leave an estuary altogether in order to seek better feeding areas elsewhere, or cause more of them to die of starvation. These difficulties would be expected to fall most on the competitively inferior individuals, including the very vulnerable young birds (Goss-Custard & Durell 1987). Since the size of the total population can, in the long term, be reduced considerably if fewer young birds survive the winter (Goss-Custard & Durell 1984, 1990), there can be a disproportionately large impact on the population size of the birds, both locally within one estuary and over a wider geographic scale. Thus the effects on the birds of increasing or decreasing fishing effort in particular localities must be examined at both local and larger scales, and in both the short-term and the long-term, if the full consequences of various policy options are to be evaluated.

Because individual Oystercatchers vary greatly in both their foraging efficiency and susceptibility to interference (Goss-Custard & Durell 1988; Stillman *et al.* in press), the modelling approach has to be able to predict how different individuals would respond to the new circumstances. The theoretical background for doing this has been provided by Sutherland & Parker (1985) and Parker & Sutherland (1986), using a game theory model approach developed by Maynard-Smith (1982) for animal decisions in general. Game theory models enable the effects of the decisions made by individuals, on both themselves and all the other individuals in the population, to be traced. In the present context, this approach enables the intake rate of each bird on each bed to be predicted and hence provides a means to predict where individual birds will feed following any changes in shellfish abundance or disturbance levels due to fishing. Thus the proportion of birds that cannot feed at an adequate rate at each stage of the winter, and so either have to leave the estuary or die, can be predicted. The numbers of birds that can be supported by a feeding area or estuary, or the "carrying capacity" (Goss-Custard 1985), can be predicted for any given circumstances (Goss-Custard *et al.* 1995a; 1996c). Such a model therefore provides a means for estimating the parameters (slope and intercept) of the density-dependent overwinter mortality function which measures how the proportion of birds dying changes as the density of the birds on the feeding grounds increases. This is important because it is the values of these parameters which determine the consequences for population size in Europe as a whole of changes in the carrying capacity of particular overwintering feeding areas (Goss-Custard 1980; Goss-Custard & Durell 1990; Goss-Custard *et al.* 1995b). In short, the approach allows the effects on bird numbers, at both the local and larger scales, of changes in the abundance and accessibility of the food supply - in the present context, of the management of the fishery - to be predicted. A strength of the approach is that predictions are derived from the behaviour of the individual birds that must actually respond to any new circumstances that arise (Goss-Custard et al. 1995a; Goss-Custard & Sutherland in press).

Although long-recognised as a fundamentally sound approach to investigating ecological issues (Ens, Piersma & Drent 1994), studies that deduce the population consequences that arise from the responses of individual animals to environmental change have suffered from a lack of data on the variation in the behaviour of individual animals. It has therefore been difficult in ecology to progress from general theoretical models of no predictive power to empirical models that can be used to make predictions in real situations. ITE has been developing such an empirical game theory distribution model for Oystercatchers foraging on the mussel beds of one estuary, and has tested its predictions with reasonable results (Goss-Custard *et al.* 1995 c,d). This model is based on field estimates of the variation between individual birds (Goss-Custard & Durell 1988) and between age-classes (Goss-Custard & Durell 1987) in the key behavioural parameters concerned. However, version 1 of the model only included interference between birds. The need at the beginning of the present project was to incorporate into this model two further important aspects of the system. The first was the depletion over each winter of the mussels due to the birds' own predation, the magnitude of which varies between mussel beds, according to the abundance of mussels present. This was done in version 2 of the model, as detailed in Clarke & Goss-Custard (1996). The second aspect was the long-term consequences on the mussel abundance on each bed of changed intensity of Oystercatcher predation. This was done in version 3 of the model, the development of which was the principal modelling objective of the present project.

1.3 EXTENDING THE MODEL

Having developed the basic model for this very well studied system, the next aim was to extend it to shorebirds exploiting cockle populations. Much of the background information required for the foraging behaviour of the birds and for the shellfish populations were already available, both in the literature and in unpublished data bases in the United Kingdom, The Netherlands and France. For example, long-term studies of cockle populations in the Wadden Sea had identified predation by crabs *Carcinus maenas* as critically important to spat recruitment (Beukema 1979, 1982, 1991, 1992), an idea which also seems applicable to the mussel populations studied by McGrorty *et al.* (1990). Again, although field studies of Oystercatchers eating cockles had failed to demonstrate directly that interference occurs in this system (Sutherland & Koene 1982), experiments on captive Oystercatchers had suggested that dominant birds feed in the most profitable areas (Leopold, Swennen & de Bruijn 1989), just as do dominant Oystercatchers eating mussels (Goss-Custard *et al.* 1982). Similarly, highly relevant data had been obtained from birds feeding on cockles, including Oystercatchers in Wales (Sutherland 1982a,b & c) and Oystercatchers and Knots on the Wash (Goss-Custard 1977). Research on Oystercatchers and cockles has also been conducted over a number of years in Baie de Somme in France (Desprez *et al.* 1987; Sueur 1987; Triplet 1989, 1994) from where further valuable information could be obtained. Intensive studies of Knot had recently added a great deal to our understanding of their feeding ecology (Zwarts & Blomert 1992; Zwarts *et al.* 1992; Piersma 1994). Most of the extensive data on Oystercatchers and cockles that have been collected in the UK had already been published (Hancock 1967, 1971; Hancock & Urquhart 1965; Dempster 1975; Horwood & Goss-Custard 1977) and so were readily available. It was realised at the beginning of the project that all these data would allow us to go a long way towards deriving the functions that would allow the Oystercatcher-mussel interaction model to be extended to cockle populations exploited by both Oystercatchers and Knots.

Despite the wealth of data available, it was realised before the project began that not all the information required for extending the model to cockle populations was already available. In particular, the model required estimates of the variation between age-classes of birds in their foraging efficiency and susceptibility to interference. Fortunately, extensive data were available in France, where P. Triplet had worked on cockle-eating Oystercatchers from many years, and from the Netherlands, where scientists of the Instituut voor Bos- en Natuuronderzoek (IBN-DLO) had studied both free-living and captive Oystercatchers. But to ensure as reliable a set of parameters as possible for the model, the Royal Society for the Protection of Birds (RSPB) carried out new field studies in the Burry Inlet, south Wales, to obtain additional data that were specifically collected to parameterise the model.

1.4 PROJECT OBJECTIVES

Shellfishing removes a proportion of the prey population that could otherwise be exploited by the birds. Thus the first objective of the model is to predict the direct effect that shellfishing on the winter food supply of the birds and hence on the rate at which the birds can feed and on their chances of obtaining sufficient food to survive the winter in good condition. However, in some places, the physical presence of fishermen may disturb birds and prevent them from feeding in places that they would otherwise exploit and forces them to use time and energy in moving from the disturbed site to another shellfish bed elsewhere. Thus the second objective of the model was to quantify the effect of disturbance from fishermen on the birds. To achieve this, it was necessary to parameterise the model with field estimates of the effects of disturbance. Data with which to do this were obtained from field observations and field experiments in the Burry Inlet and on the Exe estuary to strengthen those already available from The Netherlands (Smit & Visser 1993) and United Kingdom (Goss-Custard & Verboven 1993). By measuring the distance over which the presence of a fishermen stops birds feeding and drives them away to feed on another mussel or cockle bed, these field studies aimed to measure the area of the shellfish beds that are made unusable by birds for every extra fisherman that works there. The model can then predict where the affected birds would go and the intake rates they would achieve in their new feeding areas. The second objective of the models is, therefore, to quantify the effect of disturbance from fishing on the birds.

By eating small cockles, Knots may influence the abundance of larger cockles that are available to Oystercatchers in later years. Indeed, one of the explanations for the high levels of mortality amongst wintering Oystercatchers in the Wash in 1992-93 is that the increased numbers of Knot wintering there has reduced the cockle stocks to such a level that many Oystercatchers can no longer feed at an adequate rate. Oystercatchers themselves may have an influence on the abundance of both kinds of shellfish in the long-term by affecting both population age-structure and recruitment rates although, in the latter case, in quite different ways in different shellfish populations (Goss-Custard *et al.* 1996a). In doing so, shorebirds may affect the long-term abundance of their own food supplies and the interests of the commercial shellfisheries that depend on the same resource. Thus, the third objective of the model is to quantify the effect that the birds themselves have on the abundance of mussels and cockles.

The model also includes field estimates of important population parameters, such as recruitment and mortality rates. It has been designed to include the effects on shellfish abundance of other important factors, such as predation by crabs (Beukema 1982, 1991, 1992). The model can therefore be used to predict the effects of birds and fishery on the shellfish populations and hence on each other, in both the short- and the long-term, and of the consequences for each of various fishery and management policy options. For example, the model can predict the relationship between mortality rate and bird population density under different fishing, and conservation, management options. These functions can then be included in a model of the population dynamics of Oystercatchers throughout Europe which ITE developed in collaboration with 16 other scientists from several Institutes and Universities in Europe (Goss-Custard *et al.* 1995b,e). It had been intended at the beginning of the project to derive density-dependent functions at a larger geographic scale by including the possibility for birds to move between estuaries, but this proved not to be possible in the time available. Nonetheless, Europe-wide predictions can made by inserting the density-dependent functions obtained for a typical site into the global population model.

The main objectives of the project can therefore be summarised as follows:

(i) To develop a predictive model (version 3) of the interaction between Oystercatchers, shellfisheries and mussel populations based largely on existing data.

(ii) To extend the model to cockle populations using existing data and filling major gaps by further field work. This would allow the parameters and functions required to model the interactions between cockles, Knot, Oystercatchers and shellfisheries to be obtained.

(iii) To measure the effects of disturbance associated with fishing activities on the behaviour, distribution and time and energy costs of the birds and, in combination with existing data, to include disturbance in the model.

(iv) To predict the effect on local survival rates and carrying capacity of a variety of shellfish management policy options. By using an existing demographic model of the European Oystercatcher population, to examine in a preliminary manner how predicted changes in the rates of overwinter mortality would affect the size of the European population of Oystercatchers.

Chapter 2 THE MODEL

R A Stillman

2.1 *OVERVIEW*

This chapter describes the shorebird-shellfish model (version 3 of the game theory distribution model) developed under the present contract. A general description of the overall function and structure of the model is given, followed by more detailed accounts of each separate component of the model. This chapter is concerned with the general features of the model that are common to all simulations, and so does not discuss specific details which vary greatly between the Exe estuary and Burry Inlet, oystercatchers and knots, and cockles and mussels. All such details are contained in other chapters. However, the chapter does list general parameter values which vary between the different estuaries and predator-prey systems.

The model simulates the interactions between a single shorebird species and a number of prey species distributed in and around an intertidal shorebird wintering area. The prey include both shellfish and other invertebrates within the intertidal area, as well as species in neighbouring terrestrial habitats. The model incorporates the influence of the tidal cycle and weather factors on the recruitment of shellfish stocks, and on both the energetics of shorebirds and the area available to shorebirds for feeding. Shellfishing may occur within the intertidal area and results in both the depletion of shellfish stocks and disturbance to shorebirds. Simulations may be run over a number of successive years in order to show the long-term consequences of shellfishing management regimes on both shorebird and shellfish populations.

Each year is divided into a ‘winter’ period, during which the interactions between shorebirds and their prey are modelled in detail, and a ‘summer’ period, during which shorebirds leave the wintering area, and in which shorebirds and their prey are modelled independently. Within each winter period, the model continuously follows the location, body condition and survival of each individual shorebird. Simultaneously, the model tracks the associated changes in the abundance and condition of all prey species. During each summer period, the model follows, in a more general way, the reproduction and survival of both the shorebirds, as they migrate to and return from their breeding grounds, and the prey species located in the shorebird wintering area. Shellfishing may occur at any time during simulations.

The model is written in the Pascal programming language and can be run on any IBM-compatible personal computer. In order to simplify the development and subsequent testing of the model it was divided into four separate modules (Fig. 2.1), each of which control a separate aspect of the overall model. The *environment* module calculates all environmental variables, including the day length, weather (temperature, wind speed and solar radiation) and tidal conditions for each day of simulations. The *prey* module controls all modelling of the shellfish and other prey species, including the exposure of intertidal prey by the tide, and the reproduction, survival and condition of prey. The *shorebird* module tracks the energy demands, foraging behaviour, distribution, survival and body condition of shorebirds throughout the winter, and their survival and reproduction between winters. The *shellfishing* module is able to vary fishing intensity throughout the year and tidal cycle, and incorporates both the depletion of shellfish stocks and disturbance of foraging birds. In addition, the model contains an *interface program*, which runs each module and controls the passage of information between modules. The model has been written in a general way such that it may be applied to any estuary and shorebird-prey system for which data are available.

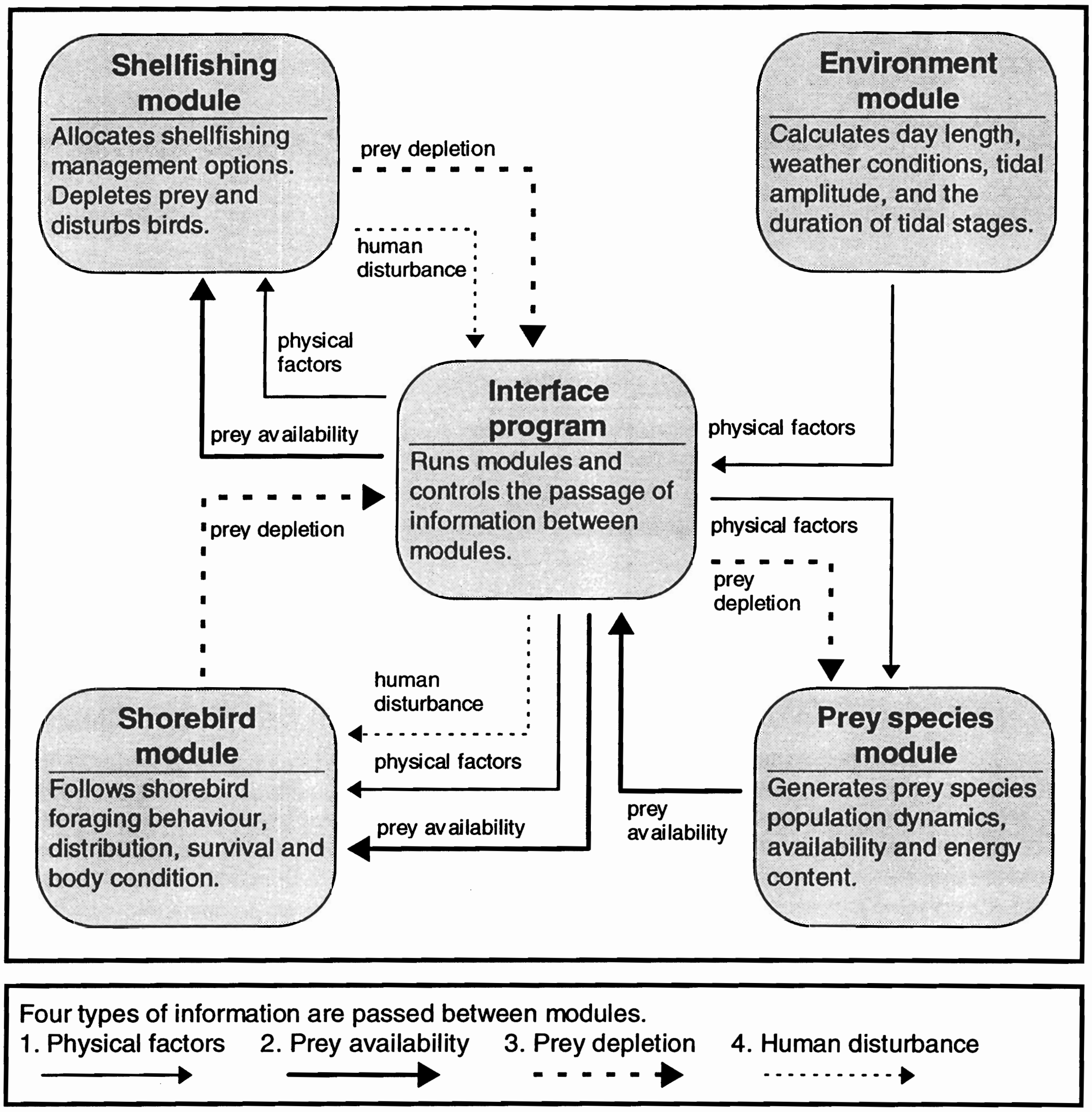


Figure 2.1 Structure of the shorebird-shellfish model developed under the present contract. The model is divided into four separate modules, each controlling a different aspect of the overall model, and an interface program which runs each module and controls the passage of information between modules.

2.2 *TIME*

The model simulates the interaction between shorebirds and their prey over a given number of years (*NumYear*), with each year being divided into an initial 'winter' period followed by a 'summer' period. 'Winter' represents the seasons during which shorebirds occupy their wintering grounds and interact with their prey in these areas, and 'summer' represents seasons when shorebirds occupy their breeding grounds and so do not interact with the prey on their wintering grounds. All time related parameters used in the model are given in Table 2.1.

The passage of time is modelled in a different way during the two periods of each year. In winter, the interaction between shorebirds and their prey is modelled, and so time is followed on a continuous basis, starting on a given day (*FirstDay*), and progressing with the successive ebb and flow of each tidal cycle until a set number of days (*NumDay*) has passed. Throughout this period daily changes in the length of day light, tidal conditions and the weather are incorporated, and the model continuously follows the condition and survival of shorebirds and their prey. In summer, shorebirds and their prey are modelled independently and so time is not followed in such detail. During this period, time simply moves directly from the end of one winter period to the start of the next, with the reproduction and survival of shorebirds and their prey at the end of the period calculated from the numbers at the start.

Table 2.1 Parameters associated with the passage of time. In all simulations, winter runs from 1st September to 15th March.

Parameter	Description	Units	Value
NumYear	Number of years in a simulation	Years	
FirstDay	First day of winter (days since longest day*)	Days	71
NumDay	Number of days in winter periods	Days	196

* 21 June in the northern hemisphere

2.3 *ENVIRONMENTAL CONDITIONS*

During the winter period of simulations, environmental conditions are defined in terms of four cycles, the day length, spring-neap, diurnal and tidal cycles, and three weather variables, temperature, wind speed and solar radiation. Table 2.2 gives a list of parameters associated with environmental conditions, and Figure 2.2 shows the relative duration of each cycle.

Table 2.2 Parameters associated with environmental conditions. Unless otherwise stated, the parameter values apply to both the Exe estuary and Burry Inlet. Although the model reads the values of *WindSpeed* and *Rad* these variables were not used in any simulations.

Parameter	Description	Units	Value
TidalCycleLength	Duration of the tidal cycle	Hours	12.4444
NumTidalStage	Number of stages to a tidal cycle		See Table 2.3
SpringNeapLength	Duration of spring-neap cycle	Days	14
SpringHighWaterTime	Time of 1st high water on full spring tides	Hours	6.25
SpringStageLength	Duration of each tidal stage on full spring tides	Hours	See Table 2.3
NeapStageLength	Duration of each tidal stage on full neap tides	Hours	See Table 2.3
MaxDayLength	Maximum length of daylight	Hours	18.11
MinDayLength	Minimum length of daylight	Hours	9.25
Temp	Mean temperature on each day of winter	°c	See Table 2.4
WindSpeed	Mean wind speed on each day of winter	ms^{-1}	
Rad	Mean solar radiation on each day of winter	W	

2.3.1 Tidal and spring-neap cycles

The major environmental factors influencing the availability of feeding areas for shorebirds in the model are the tidal and spring-neap cycles. The tidal cycle causes the successive exposure and covering of intertidal feeding areas, and the spring-neap cycle influences the amplitude of each tidal cycle and so the duration and extent to which intertidal areas are exposed. In the model, tidal cycles are assumed to start at high water, are of constant length (*TidalCycleLength*) throughout winter, and are divided into a number of tidal stages (*NumTidalStage*), during each of which the tidal height and all other environmental variables are assumed to remain constant. Tidal stages may differ in length, but the total length of all tidal stages must equal *TidalCycleLength*. In the simplest case a tidal cycle could be divided into two tidal stages, high and low water, and as time progresses the tide assumed to switch between these two extremes (Fig. 2.2). A more realistic example would have a number of intermediate tidal stages, for example the receding and advancing tides. The tidal stage is the finest division of time used in the model. Table 2.3 lists the tidal stage parameters values used to model the Exe estuary and Burry Inlet.

Table 2.3 Tidal cycle parameter values used to model the Exe estuary and Burry Inlet.

System	Tidal stage	*SpringStageLength*	*NeapStageLength*
Exe estuary	1 High tide	4.7407	4.1444
NumTidalStage = 4	2 Receeding tide	1.0000	1.0000
	3 Low tide	5.7037	6.3000
	4 Advancing tide	1.0000	1.0000
Burry Inlet	1 High tide	5.9444	5.9444
NumTidalStage = 2	2 Low tide	6.5000	6.5000

Although the duration of tidal cycles remains constant throughout simulations the tidal range of each cycle varies according to the spring-neap cycle. Tidal range is at a maximum on spring tides and a minimum on neap tides. The spring-neap cycle is assumed to have a constant duration (*SpringNeapLength*) and the value of relative tidal range, measured as a proportion of a full spring tide (*PropSpring*), on a given day (*Day*) is calculated from the following equation.

$$PropSpring = 0.5\left(1 + \cos\left(\frac{2\pi Day}{SpringNeapLength}\right)\right) \qquad 2.1$$

This equation produces values which range from 0 to 1 (Fig. 2.2), with a value of 1 indicating a full spring tide (maximum tidal range) and a value of 0 a full neap tide (minimum tidal range). In nature, the spring-neap cycle lasts for approximately 14 days, and consists of approximately 27 tidal cycles. Additionally, at a given stage of successive spring-neap cycles, the timings of high and low water are similar. These natural features are incorporated into the model by setting the value of *SpringNeapLength* to 14 days, and the value of *TidalCycleLength* to 12.4444 hours, so that exactly 27 tidal cycles occur within each spring-neap cycle. This has the effect of ensuring that, as in reality, the timing of tides at a particular stage of the spring-neap cycle is constant between successive spring-neap cycles. One other parameter, the time of the first high water on full spring tides (*SpringHighWaterTime*), is used to determine the timing of tides throughout winter simulations.

The spring-neap cycle has two influences on the tidal cycle. It influences the amplitude of each tidal cycle, so changing the area of intertidal areas exposed (see section 2.4.1), and also the duration of each tidal stage, so changing the time for which intertidal areas are exposed. Changes in the duration of each tidal stage are incorporated by defining the length of each tidal stage on both full spring (*SpringStageLength*) and full neap tides (*NeapStageLength*). The duration of a tidal stage at a given point in the spring-neap cycle (*TidalStageLength*) is then found by interpolation between these two extremes.

$$TidalStageLength = NeapStageLength + PropSpring(SpringStageLength - NeapStageLength) \quad 2.2$$

2.3.2 Day length and diurnal cycles

As time progresses during winter periods, the model incorporates the transition from day to night through the diurnal cycle. Throughout the course of each year, day length (*DayLength*) changes cyclically and is given on a particular day by

$$DayLength = MeanDayLength + \frac{DayLengthRange}{2}\cos\left(\frac{2\pi(Day + FirstDay)}{365}\right) \quad 2.3$$

where *MeanDayLength* is calculated from the mean length of the longest (*MaxDayLength*) and shortest (*MinDayLength*) days, *DayLengthRange* is the difference between the lengths of the longest and shortest days and *FirstDay* is the number of days after the longest day (21st June in the northern hemisphere) on which winter simulations start. For simulations of estuaries in the northern hemisphere this equation generates day lengths with a maximum on 21st June and a minimum on 21st December (Figure 2.2). These dates would be reversed for estuaries in the southern hemisphere. During simulations this equation is used to calculate the length of a given day, from which the times of first (*FirstLight*) and last light (*LastLight*) are obtained by assuming that the hours of light are equally divided either side of midday.

$$FirstLight = 12 - \frac{DayLength}{2} \quad 2.4$$

$$LastLight = 12 + \frac{DayLength}{2} \quad 2.5$$

Once the values of *FirstLight* and *LastLight* are calculated the model calculates the proportion of each tidal stage that occurs during the hours of light (*PropInLight*).

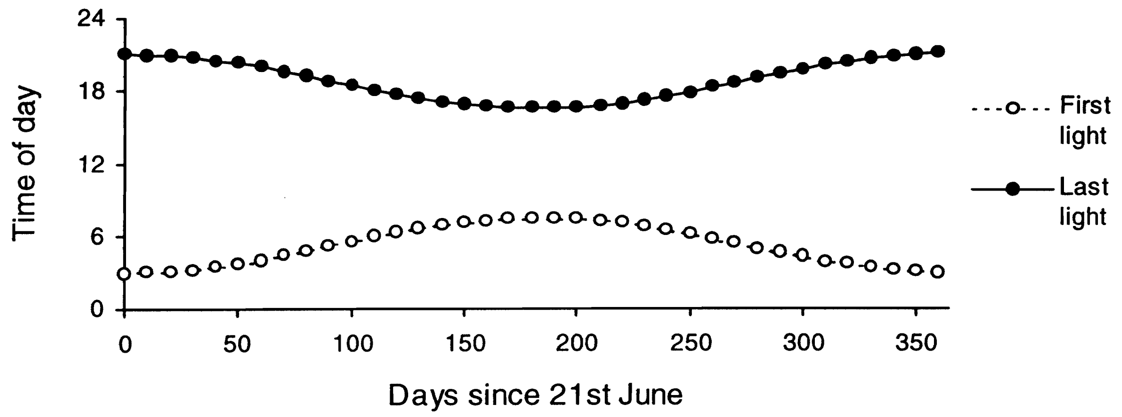
2.3.3 Weather

During each day of winter periods, the model reads three weather variables: mean daily temperature (*Temp*), mean daily wind speed (*WindSpeed*) and mean daily solar radiation (*Rad*). These variables are read for each day of simulations rather than calculated to allow the possibility for real weather patterns to be incorporated into the model. Table 2.4 shows the daily values of temperature used in the simulations.

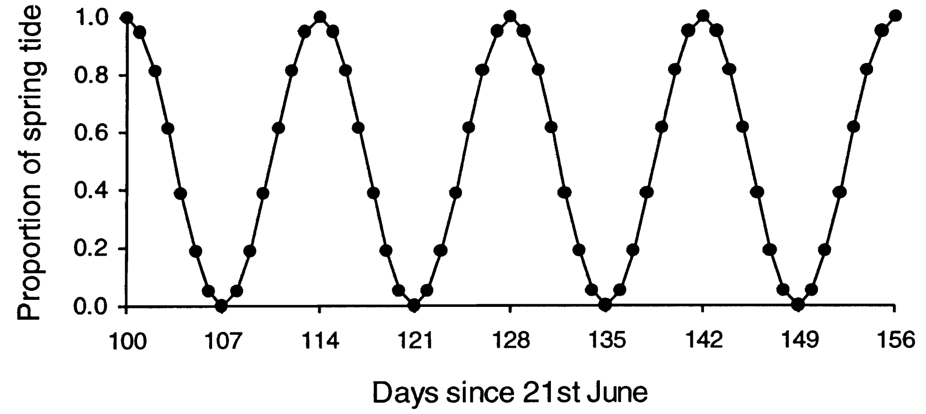
Table 2.4 Mean daily temperature values used in simulations of the Exe estuary and Burry Inlet. The model reads values every day, but for brevity only every 10th value is shown.

Days since 21st June	Temperature	Days since 21st June	Temperature	Days since 21st June	Temperature
71	16.5475	141	8.4230	211	5.3260
81	15.079	151	7.6728	221	5.2939
91	13.7132	161	7.0252	231	5.3645
101	12.4500	171	6.4801	241	5.5376
111	11.2894	181	6.0377	251	5.8134
121	10.2313	191	5.6978	261	6.1918
131	9.2759	201	5.4606		

(a) Day length cycle



(b) Spring-neap cycle



(c) Tidal and diurnal cycles

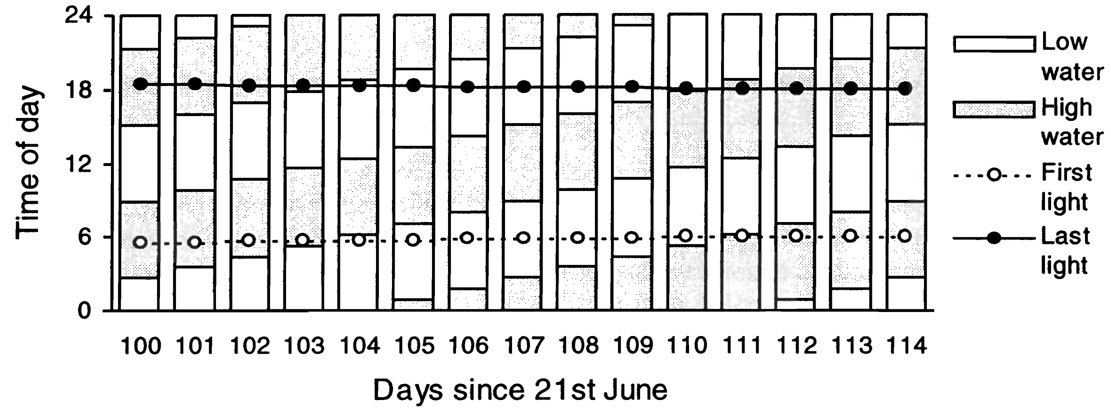


Figure 2.2 Environmental cycles incorporated into the model. (a) day length changes from a maximum on 21st June (day 0) to a minimum on 21st December (day 183). (b) the amplitude of successive tidal cycles varies through the 14 day spring-neap cycle (0 = full neap tide; 1 = full spring tide). (c) the tidal cycle is divided into a number of tidal stages (high and low water in this example) during which the tidal height remains constant. Each tidal cycle last for 12.4444 hours and so the timing of tidal stages advances on successive days, but after 14 days returns to its initial values (i.e. the timing of tides is the same on days 100 and 114). Note that although tidal stages are shown to be divided between days, they are continuous in the model. As the timing of tidal stages advances the proportion of each stage occurring during the hours of daylight changes between successive days.

2.4 *PREY PATCHES*

Shellfish and other shorebird prey are located on a number of patches within a wintering site. Each patch contains only one type of prey. The availability of prey to the shorebirds depends on the exposure of patches under the tidal regime and on the environmental temperature. Shorebirds are able to utilize one other patch, the roost, which is always available but on which no feeding is possible. Table 2.5 shows all parameters used to model the availability of prey patches.

Table 2.5 Parameters associated with the availability of patches of shellfish and other prey during the winter periods of simulations.

Parameter	Description	Units	Value
SpringArea	Area of patch exposed during each stage of the tidal cycle on full spring tides	ha	See Table 2.7
NeapArea	Area of patch exposed during each stage of the tidal cycle on full neap tides	ha	See Table 2.7
Avail	Temperature dependent availability of prey	°c	See chapter 3

2.4.1 Patch exposure

Each patch has a given area exposed at each stage of the tidal cycle on both full spring (*SpringArea*) and full neap (*NeapArea*) tides with the condition that the area on a neap tide must be less than or equal to the area on a spring tide. The model can therefore directly find the area of a patch exposed at each stage of the tidal cycle on either a full spring or full neap tide (i.e. the if value of *PropSpring* is either 1 or 0). For tides between the spring and neap extremes the model calculates the area of a patch exposed (*Area*) for each stage of the tide from the following relationship.

$$Area = NeapArea + PropSpring(SpringArea - NeapArea) \qquad 2.6$$

The model can simulate a number of different tidal exposure patterns using this approach. Intertidal patches that are fully exposed on both spring and neap tides will have equivalent values of *SpringArea* and *NeapArea* for each stage of the tide, whereas those with less exposure on neap tides will have lower values of *NeapArea* than *SpringArea*. Terrestrial patches that are not influenced by the tidal regime will have equivalent values of *SpringArea* and *NeapArea* that do not change for different stages of the tide. Table 2.6 shows some examples of how the model can simulate the tidal exposure of different types of patch assuming that there are four stages to the tide, high water, receding tide, low water and advancing tide. Table 2.7 shows the parameter values used to model mussel beds in the Exe estuary and cockle beds in the Burry Inlet.

Table 2.6 Examples of how the tidal exposure patterns of different types of patch are incorporated into the model. Each patch has a maximum area of 10ha.

Patch exposure details	Tidal stage	*SpringArea* (ha)	*NeapArea* (ha)
Terrestrial patch uninfluenced by the tidal regime	High water	10	10
	Receding	10	10
	Low water	10	10
	Advancing	10	10
Upshore intertidal patch only covered at high water	High water	0	0
	Receding	10	10
	Low water	10	10
	Advancing	10	10
Mid-shore intertidal patch only fully exposed at low water on spring tides.	High water	0	0
	Receding	5	0
	Low water	10	5
	Advancing	5	0
Down-shore intertidal patch not exposed on neap tides.	High water	0	0
	Receding	0	0
	Low water	10	0
	Advancing	0	0

Table 2.7 Parameter values used to model the exposure of mussel beds in the Exe estuary and cockle beds in the Burry Inlet. Mussel and cockle beds are only exposed during low tide stages. The areas of mussel beds are the same as those used in version 2 of the model. All cockle beds are assumed to have the same exposed areas on spring and neap tides.

System	Patch name	*SpringArea* (ha)	*NeapArea* (ha)
Exe estuary	Bed 01	5.49	4.94
	Bed 03	4.45	3.56
	Bed 04	6.31	3.79
	Bed 20	9.41	4.71
	Bed 22	4.06	0.00
	Bed 25	8.30	4.15
	Bed 26	6.52	5.22
	Bed 27	1.27	1.02
	Bed 30	7.64	4.58
	Bed 31	7.79	4.67
Burry Inlet	All patches	50.00	50.00

2.4.2 Temperature and prey availability

The availability of prey on any patch (*PreyAvail*) may be influenced by temperature (*Temp*). Prey availability can range from 0 to 1 and influences the rate at which birds can consume prey items. A value of 0 indicates that no prey can be consumed and a value of 1 indicates that the birds can consume prey at their maximum potential rate. A value of 0.5 would result in birds only being able to consume prey at half their maximum potential rate. See chapter 3 for the temperature dependent availability of different prey species.

2.5 PREY POPULATIONS

The dynamics of shellfish and all other shorebird prey populations are incorporated into the model by using age-structured models derived from empirical relationships. The basic unit of prey abundance in these models is the density of individual prey items in each of a given number of age classes (*NumAgeClass*). As simulations progress, prey populations are followed continuously as prey die, through shorebird predation, shellfishing or other causes, as prey age and move between age classes, and as new individuals are recruited to the population through reproduction. In this way the population dynamics of the prey are modelled independently for each patch. Parameters associated with the dynamics of prey populations are given in Table 2.8. Table 2.9 lists the age distribution of mussels and cockles used at the start of all standard simulations.

Table 2.8 Parameters associated with the prey species populations. Only general parameters which apply to both cockles and mussels are given. The values of *SummerSurv*, *WinterSurv* and *RecrDens* are calculated using further parameters given in chapter 4.

Parameter	Description	Units	Value
NumAgeClass	Number of age classes on each patch		See Table 2.9
AgeClassDens	Density of each age class on each patch	m^{-2}	See Table 2.9
WintSurv	Proportion of each age class surviving to the end of a winter period		See chapter 4
SummSurv	Proportion of each age class surviving to the end of a summer period		See chapter 4
RecrDens	Density of recruits surviving to the end of a summer period	m^{-2}	See chapter 4
NumSizeClass	Number of size classes on each patch		See chapter 4
SizeClassDens	Density of each size class on each patch	m^{-2}	See chapter 4
SizeClassWidth	Width of size classes on each patch	mm	See chapter 4
PreyAFDM	Ash-free dry mass of an average prey item from each size class on each patch	mg	See chapter 3
PreyGrowthRate	Daily proportionate change in the ash-free dry mass content of prey		See text
HighRelAFDM	Ash-free dry mass of highest level prey (i.e. that first exposed by the receding tide) relative to the average of all prey on patch		See text
PreyEnergyDens	Energy density of prey flesh on each patch	KJ g^{-1}	23.5

Table 2.9 The initial age distribution of mussels and cockles used in standard simulations. Each value is the density (m^{-2}) of one age class on one patch on 1st September. The mussel densities are the same as used in version 2 of the model, and those for cockles were measured in the Burry Inlet during the present study (see chapter 3).

		Age class									
System	Patch	1	2	3	4	5	6	7	8	9	10
Exe estuary	Bed 1	221.9	107.9	97.0	108.2	79.0	57.0	23.2	6.6	1.8	0.2
	Bed 3	248.6	61.9	72.3	69.7	62.9	44.7	27.5	10.4	3.1	1.8
	Bed 4	308.9	98.3	72.6	92.9	90.4	60.7	37.5	15.1	6.9	2.3
	Bed 20	93.7	69.3	54.9	54.2	52.8	37.3	18.1	8.3	2.9	1.6
	Bed 22	37.6	15.6	14.3	16.3	20.3	21.1	15.7	7.6	3.9	1.3
	Bed 25	165.7	66.7	62.3	68.0	68.9	72.9	50.0	24.8	10.2	5.1
	Bed 26	217.3	165.4	173.7	182.2	138.6	77.5	40.5	18.6	5.9	2.1
	Bed 27	258.3	144.8	149.0	157.6	127.9	104.6	63.1	29.6	16.2	10.7
	Bed 30	1195.0	202.5	155.4	163.2	54.0	128.6	71.9	28.4	10.4	2.5
	Bed 31	1613.0	222.2	147.2	130.4	103.1	73.3	37.4	14.6	5.8	1.3
Burry Inlet	1	686.7	742.8	39.3	30.7	30.7					
	2	2813.3	799.3	19.9	10.4	10.4					
	3	180.0	73.9	9.2	8.4	8.4					
	4	686.9	66.1	13.9	13.3	13.3					
	5	120.0	38.6	5.2	4.8	4.8					
	6	123.3	112.4	7.8	6.6	6.6					
	7	130.0	127.8	9.5	8.0	8.0					
	8	950.0	197.6	12.3	10.0	10.0					
	9	2686.7	343.5	24.8	20.9	20.9					
	10	175.4	76.3	40.4	40.0	40.0					

2.5.1 Mortality

Throughout the winter period of simulations prey mortality occurs either through shorebird predation, shellfishing or other causes. Shorebird predation and shellfishing are explicitly included in the model and their impact on prey populations depends on factors such as the size of the shorebird population and any shellfishing management practices. Even in the absence of these mortality factors, some prey mortality may occur through the winter periods. The model includes these other mortality factors through empirically derived relationships, which relate the proportion of an age class surviving at the end of winter (*WintSurv*), to a range of factors including its density at the start of winter. These relationships are obtained from data collected in the absence of shorebird predation and shellfishing and so only include mortality due to other causes. Depending on the range of parameter values used in the model, this mortality may either be density dependent or density independent. The precise form of relationships used differ between mussels and cockles, and so are described in detail in chapter 4.

The empirical relationships used to parameterize the model simply provide an overall value of mortality over the whole winter period. However, changes in prey abundance caused by shorebird predation and shellfishing occur on each successive tidal cycle. For compatibility, mortality due to other causes must also be expressed on this time scale. The overall overwinter survival of each age class is converted to that occurring during each tidal cycle (*TidalSurv*), by assuming that such mortality occurs at a constant rate throughout the course of winter.

$$TidalSurv = \exp\left(\frac{\ln(WintSurv)\ .\ TidalCycleLength}{24\ .\ NumDay}\right) \qquad 2.7$$

Throughout winter the density of each prey class at the end of each tidal cycle (*FinalTidalDens*) is calculated from its density at the start (*InitTidalDens*), the loss due to shorebird predation (*PredDens*) and shellfishing (*ShellFishDens*), and the loss due to other causes.

$$FinalTidalDens = (TidalSurv \,.\, InitTidalDens) - PredDens - ShellFishDens \qquad 2.8$$

In the summer period of simulations similar empirical relationships are used to calculate the proportionate survival of each age class by the end of summer (*SummSurv*) from its density at the start. Again these relationships differ for each prey species and are described in detail in chapter 4. During these periods the shorebirds are located on their breeding grounds and so do not interact with their prey. Changes in the density of prey do not need to be followed during each tidal cycle, and so the density of each age class at the end of summer (*FinalSummDens*) can be calculated directly from the density at the start (*InitSummDens*).

$$FinalSummDens = SummSurv \,.\, InitSummDens \qquad 2.9$$

2.5.2 Recruitment

During the summer period of simulations prey populations are aged by moving all prey densities up by one age class. The density of the first age class (*RecrDens*) is then determined by recruitment into the population through reproduction. Empirical relationships are used to relate the density of new recruits to the density of older age classes present and a range of other environmental variables. Depending on the parameter values used, recruitment may either be density dependent or density independent. The actual relationships used differ between mussels and cockles, and are given in chapter 4.

2.5.3 Age-size relationships

The prey population dynamics models are based on age structure, whereas shorebird predation and shellfishing are influenced by the size distribution (not age distribution) of the prey. The model therefore requires a link between the distribution of age classes on a patch and the associated distribution of size classes. A number of size classes (*NumSizeClass*), each representing a range of prey lengths, are defined. Standard growth curves are used to allocate a proportion of each age class to each size classes. These relationships differ between cockles and mussels and so are given in detail in chapter 4, but in both cases provide a means by which the age distribution of a prey population may be linked to its size distribution. The age specific mortality generated by the prey model can therefore act simultaneously with the size specific mortality caused by shorebird predation and shellfishing.

2.5.4 Energy content

The prey population dynamics models simply calculate how the density of individuals in each size class change through time. However, the profitability of a size class to a shorebird depends on the energy content of an individual prey item and not just on its size. The energy content (*EnergyContent*) of an individual prey item is determined by its flesh content, measured as ash-free dry mass (*PreyAFDM*), and the energy content of a unit of flesh (i.e. its energy density; *PreyEnergyDens*).

The ash-free dry mass (AFDM) of a size class is related to its length using an empirically derived relationship (see chapter 4 for the actual relationships used for different prey). These relationships calculate the AFDM of an average prey item of each size class on a patch. However, prey at higher levels on the shore usually have a lower flesh content than similar sized prey further down the shore. The model, therefore, calculates the AFDM of prey actually exposed by the tide (*ExpAFDM*), and hence available to shorebirds.

$$ExpAFDM = PreyAFDM\ (HighRelAFDM + (1 - HighRelAFDM)\ .\ (Area\ /\ MaxArea)) \qquad 2.10$$

where *MaxArea* = area of patch exposed on full spring tides, *Area* = area of patch exposed at a given stage of tidal and spring-neap cycles and *HighRelAFDM* = AFDM of prey at highest shorelevel on patch relative to the mean AFDM on patch. The value of *HighRelAFDM* was set to 0.8 for mussel beds and to 1 for cockle beds. The energy content of exposed prey is then calculated from.

$$EnergyContent = ExpPreyAFDM\ .\ PreyEnergyDens \qquad 2.11$$

At the start of a winter period all size classes of prey on each patch are given a fixed value of *PreyAFDM*. Throughout the period of winter simulations the amount of flesh contained within each prey item may decrease with time. This decrease is measured as the proportionate decrease in flesh content occurring on each day of winter (*PreyGrowthRate*). The value of *PreyGrowthRate* was set to -0.00199954 for mussels (value used in version 2 of the model) and to -0.00372743 for cockles (based on measurements made on the Burry Inlet during the present study (see section 3.3)). These values caused the AFDM of mussels to decrease by 30% and that of cockles to decrease by 50% over a 196 day winter. During the summer period of simulations, the flesh content increases so that in each successive winter simulation prey of a given size start with the same value of *PreyAFDM*.

2.6 *SHOREBIRD POPULATIONS*

During the winter period of simulations, the model is individuals-based with respect to the shorebird and continuously tracks the condition, location and survival of each individual. Individuals may differ in their age, feeding method used to capture prey, interference-free intake rate and dominance. Changes in the size of the shorebird population during winter result from the survival or death of each individual within the population. The abundance of shorebirds in the model is determined by the extent of overwinter mortality, and the reproductive rate on the breeding grounds. Parameters associated with shorebird abundance are given in Table 2.10.

Table 2.10 Parameters associated with the survival and reproduction of shorebirds.

Parameter	Description	Units	Value
StarvMass	Mass below which an individual dies	g	See text
MinBreedAge	Minimum age at which shorebirds breed	years	See text
BreedArea	Area of breeding site	ha	See text
a	Density above which competition for territories occurs		See text
b	Intensity of competition for territories		See text
ReproRate	Number of young per pair surviving to return to the wintering area		See text

2.6.1 Mortality

The only factor determining the survival of shorebirds in the model is the balance between energy expenditure and energy acquisition during winter. If energy expenditure exceeds intake, birds compensate for the energy deficit by converting body tissues to energy, and as a consequence lose mass. Birds cannot lose mass indefinitely however, and will die if their weight falls below a minimum value (*StarvMass*).

StarvMass was assumed to be 300g in juvenile oystercatchers, 340g in 2 to 4 year old oystercatchers, 350g in adult oystercatchers (values previously used in version 2 of the model) and 100g in knots (Piersma, Tulp & Schekkerman 1994). It is assumed that no mortality occurs outside the winter period, either when birds are on migration or on the breeding grounds. This assumption, although biologically unrealistic, was made so that all changes in mortality between model simulations could be attributed changes in the simulated winter conditions.

2.6.2 Recruitment

Shorebirds reproduce during the summer periods of simulations when they are on their breeding grounds. The model does not consider each individual shorebird during this period, but simply works on the number of individuals. The recruitment of young is calculated using the model developed by Goss-Custard *et al.* (1995a,b).

The model assumes that all birds in the population migrate to a single breeding site where all mature birds (at least as old as the minimum breeding age; *MinBreedAge*) form pairs which may breed. A 50:50 sex ratio is assumed so that the number of potential breeding pairs (*PotNumBreed*) equals half of the number of mature birds. The model assumes that competition for breeding territories in the site may mean that the number of pairs that actually do breed is lower than the total number of potential breeding pairs. The following relationship (Goss-Custard *et al.* 1995a,b) is used to calculate the proportion of pairs that breed from the number of potential breeding pairs and the area of the breeding site.

$$PropBreed = 10^{b\left(\frac{PotNumBreed}{BreedArea}-a\right)} \tag{2.12}$$

where a is the density of potential breeding pairs above which competition for territories occurs and b measures the intensity of competition for territories above a. The model assumes that those pairs which breed produce a constant number of young which survive to reach the wintering site (*ReproRate*), and so calculates the number of young reaching the wintering grounds using the following equation.

$$NumYoung = ReproRate \;.\; PropBreed \;.\; NumPotBreed \tag{2.13}$$

The parameters for oystercatchers were set to the following values: *BreedArea* = 750; *ReproRate* = 0.64; *a* = 0.1; and *b* = -0.5 (Goss-Custard *et al.* 1995a,b). The model was not used to simulate the reproduction of knot.

2.7 *SHOREBIRD ENERGETICS*

The overwinter survival of shorebirds is solely determined by the relative rates of energy acquisition and expenditure, and so shorebird energetics are modelled in detail. The model incorporates details of shorebird energy acquisition, expenditure and storage. Energy acquisition involves the digestion and assimilation of food in the gut; expenditure, the costs of metabolism and thermoregulation; and storage, the conversion of energy to and from body storage tissues. Table 2.11 lists the parameters associated with shorebird energetics.

Table 2.11 Parameters associated with shorebird energetics. All parameter values given in this table are the same as used in version 2 of the model.

(a) Energy acquisition

Parameter	Description	Units	Value
GutProcRate	Rate at which food ash-free dry mass is passed through gut	g hr^{-1}	see text
MaxGutCont	Maximum amount of food stored in gut	g	see text
PreyAssimEff	Assimilation efficiency of prey on each patch		0.854

(b) Energy expenditure

Parameter	Description	Units	Value
BMR	Basal metabolic rate	W	see text
BMRToGeneral	General energy expenditure relative to *BMR*		see text
LowCritTemp	Temperature below which thermoregulatory costs occur	°c	see text
ThermCost	Rate at which thermoregulatory costs increase below *LowCritTemp*	W $°c^{-1}$	see text

(c) Energy storage

Parameter	Description	Units	Value
StoreEnergyDens	Energy density of bird storage reserves	KJ g^{-1}	23.5
ToStoreEff	Efficiency with which energy is stored		0.884
FromStoreEff	Efficiency with which energy is retrieved from storage		1.000
MaxBodyMass	Maximum body weight that a bird can achieve on a given day	g	see Figure 2.3

2.7.1 Energy acquisition

Energy acquisition occurs through the consumption and subsequent digestion of prey. A simple model is used to follow the digestion of prey based on the results of a study on Oystercatchers (Kersten & Visser in press). The purpose of this model is to calculate, for a given period of time, the quantity of prey mass consumed and the amount of energy assimilated by the shorebird.

The model follows shorebird digestion during each tidal stage. At the start of a tidal stage, the gut contains a given amount of prey (*InitGutCont*), and during the stage, and when the bird is feeding, food mass is passed into the gut at a given rate (*IntakeRate*). The gut of the bird has a set storage capacity (*GutStore*Cap) which limits the total mass of food that can be held in the gut, and a constant processing rate (*GutProcRate*) at which food material is passed through the gut. The model uses these parameters to calculate the proportion of the tidal stage that the bird is able to spend feeding (*FeedProp*), and the amount of food stored in the gut at the end of the tidal stage (which defines the value of *InitGutCont* for the next tidal stage). For example, if the bird's intake rate is lower than its gut processing rate, its gut will not fill to capacity during the tidal stage and it will be able to feed continuously ($FeedProp = 1$). If intake rate is much greater than gut processing rate, the birds gut will quickly fill to capacity and it will not be able to feed continuously ($FeedProp < 1$). In general, the proportion of time spent feeding decreases as intake rate increases. Thus the gut processing rate may constrain the total amount of food that is consumed during a tidal stage.

The model calculates the total quantity of food consumed during the tidal stage (*TotalIn*) given the birds intake rate while feeding, the proportion of time spent feeding and the duration of the tidal stage.

$$TotalIn = FeedProp \,.\, IntakeRate \,.\, TidalStageLength \tag{2.14}$$

The model makes the simplifying assumption that prey are assimilated as soon as they are consumed, rather than there being a time lag between consumption and subsequent digestion. The total amount of energy assimilated during the time interval (*TotalEnergyIn*) can therefore be calculated from the total amount of prey passing into the gut, its energy density (*PreyEnergyDens*) and its assimilation efficiency (*AssimEff*), which measures the proportion of the energy contents of the prey that are assimilated by the bird.

$$TotalEnergyIn = PreyAssimEff \,.\, PreyEnergyDens \,.\, TotalIn \tag{2.15}$$

The following parameter values were used to model digestion in oystercatchers: $GutProcRate = 2.351$g AFDM hr^{-1}; $MaxGutCont = 11.92$g AFDM; $PreyAssimEff = 0.854$; $PreyEnergyDens = 23.5KJg^{-1}$ (Kersten & Visser in press). Digestive constraints were not modelled for knot, but the same values of *PreyAssimEff* and *PreyEnergyDens* were used for this species.

2.7.2 Energy expenditure

The modelling of shorebird energetics is based on laboratory and field experiments on oystercatchers and knots (Kersten & Piersma 1987; Wiersma & Piersma 1994). The model divides the energy expenditure of birds into two components: *general expenditure* is the energy used for activity, digestion and other body functions; *thermoregulatory expenditure* is the energy used to maintain the bird's core body temperature.

The general energetic costs (*GeneralExpRate*) of birds in the model are measured relative to basal metabolic rate (*BMR*), which is the minimum energy expenditure required to keep the bird alive, and excludes the energy required for movement, digesting prey and thermoregulation.

$$GeneralExpRate = BMRToGeneral \,.\, BMR \tag{2.16}$$

where *BMRToGeneral* = the general level of energy expenditure measured relative to *BMR*. For simplicity in the model, *BMR* does not vary between individuals in the population. The model assumes that no thermoregulatory costs occur above a lower critical environmental temperature (*LowCritTemp*), but that below this temperature thermoregulatory costs (*ThermExpRate*) increase by a constant amount per degree reduction in temperature (*ThermCost*).

$$\begin{aligned} ThermExpRate &= 0 && \text{if } (Temp \geq LowCritTemp) \\ ThermExpRate &= ThermCost\ (LowCritTem - Temp) && \text{if } (Temp < LowCritTemp) \end{aligned} \tag{2.17}$$

The daily energy expenditure (*DailyEnergyExp*) is then found from the combined general and thermoregulatory rates of energy expenditure (*TotalExpRate*), and by assuming that these rates are constant throughout a single day.

$$TotalExpRate = GeneralExpRate + ThermExpRate \qquad 2.18$$

$$DailyEnergyExp = 24 \,.\, 60 \,.\, 60 \,.\, TotalExpRate \qquad 2.19$$

The energy expenditure of oystercatchers in the model was based on that measured in oystercatchers held in outdoor cages in the Wadden sea (Kersten & Piersma 1987): *BMR* = 2.91W; *BMRToGeneral* = 2.7; *LowCritTemp* = 10°c; *ThremCost* = 0.7W°c^{-1}. Thermoregulation in knots was not modelled. In this species the total level of energy expenditure was set to the mean value for free living knots in the Wadden Sea between September and March (Poot & Piersma 1994): *TotalExpRate* = 4.3W.

2.7.3 Energy storage

Whenever energy acquisition exceeds energy expenditure, the excess energy (*ExcessEnergy*) is converted into storage tissues and the mass of the bird increases. When the reverse situation occurs and there is an energy deficit (*EnergyDeficit*) the storage tissues are converted to energy and the bird decreases in mass. The increase in mass through energy storage is related to the efficiency with which energy is converted to mass (*ToStoreEff*) and the energy density of the storage tissues (*StoreEnergyDens*).

$$MassGain = \frac{ExcessEnergy \,.\, ToStoreEff}{StoreEnergyDens} \qquad 2.20$$

The storage efficiency measures the proportion of the energy that is lost through the conversion process and the energy density of reserves gives the amount of energy storage per unit mass of storage tissues. When the storage tissue energy density is low, bird mass increases to a greater extent for a given amount of energy storage. The mass reduction required to balance an energy deficit is found using a similar relationship.

$$MassLoss = \frac{EnergyDefecit}{StoreEnergyDens \,.\, FromStoreEff} \qquad 2.21$$

A greater mass loss is required to balance a given energy deficit when either the efficiency of converting tissues to energy or the storage energy density is low.

If energy acquisition exceeds energy expenditure the mass of a bird will increase. It is assumed that this increase cannot be unlimited however and that there is a maximum body mass (*MaxBodyMass*) for a given type of bird at a given stage of the season which cannot be exceeded. This maximum body mass is allowed to change throughout the season. When a bird is at its maximum body mass it will regulate its intake (by reducing the proportion of time spent feeding) to prevent any further mass increase. Figure 2.3 shows the seasonal changes in the maximum body mass of oystercatchers and knots used in the model.

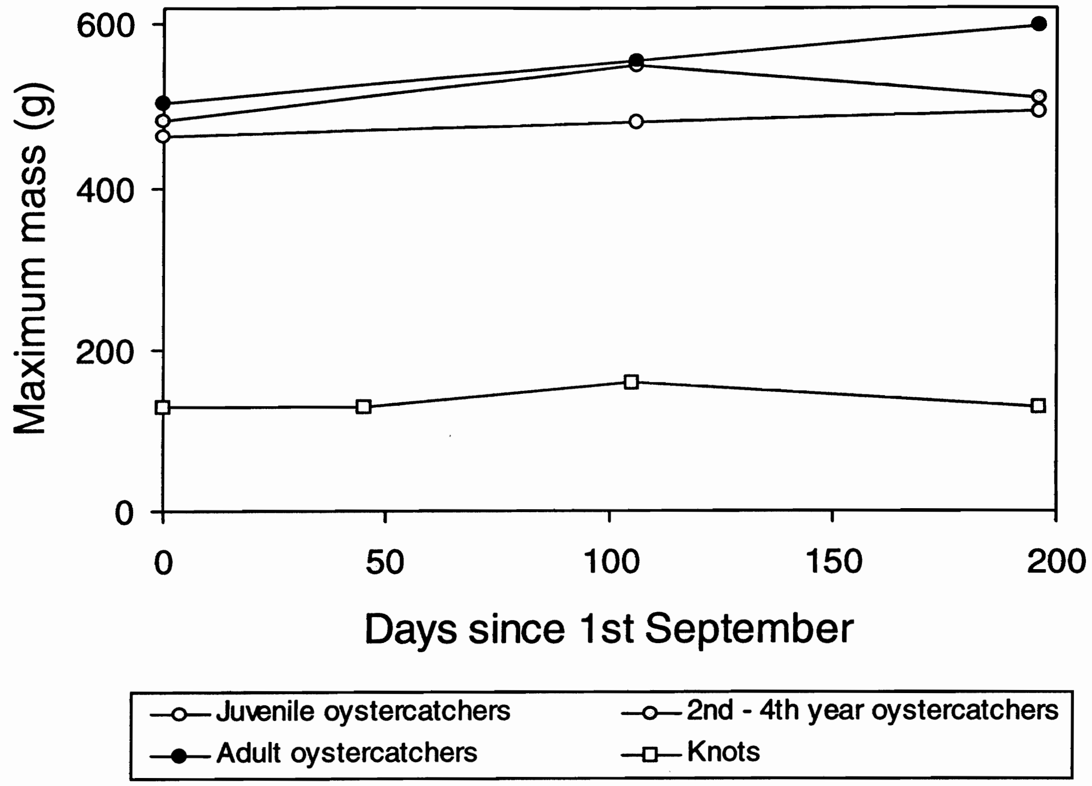


Figure 2.3 The seasonal changes in the maximum body mass of oystercatchers and knots assumed in the model. The values for oystercatchers are the same as used in version 2 of the model, and those for knot are taken from Piersma 1994 (page 195).

2.8 *SHOREBIRD FORAGING BEHAVIOUR*

The foraging behaviour of shorebirds is modelled in detail, and differs for different types of prey. For these reasons, all elements of the model concerned with shorebird foraging behaviour are described separately in chapter 3. Each of these models have some common components however, and all have the same purpose to calculate the energy intake rate a bird will achieve on a particular patch during a given period of time, and the size distribution of prey consumed.

Each model calculates the interference-free intake rate of a bird of average foraging competence foraging in isolation (*MeanIFIR*). This intake rate is calculated in a number of ways in the different models, but basically depends on the density of different prey size classes and the quantity of flesh within each item of prey.

Individuals in the model differ with respect to their foraging efficiency which effects the intake rate they can achieve given a certain availability of prey. Foraging efficiency for each prey type is assumed to be normally distributed with unit mean and a given standard deviation (*ForagingEffSD*). It is assumed that the foraging efficiencies of an individual feeding on different prey species are unrelated. The interference-free intake rate (*IFIR*) achieved by an individual depends on its foraging efficiency (*ForagingEff*) and the intake rate achieved by a bird of average foraging competence.

$$IFIR = ForagingEff \, . \, MeanIFIR \qquad 2.22$$

Apart from varying between individuals, interference-free intake rate may also vary between day and night. Equation 2.22 is used to calculate IFIR during the hours of daylight. IFIR during the night time is assumed to be a set proportion (*NightForagingEff*) of that during the day. If this proportion is one, night time IFIR is the same as day time IFIR. The following values of *NightForagingEff* were used in the model for different predator-prey systems: mussel-feeding oystercatchers using the hammering feeding method = 1; mussel-feeding oystercatchers using the stabbing feeding method = 0.484; cockle-feeding oystercatchers and oystercatchers feeding on upshore prey = 0.615 (Hulscher 1996); oystercatchers feeding in fields = 0; cockle-feeding knots = 1.

Once the value of *IFIR* is calculated for an individual, the influence of other birds on the same patch on its intake rate is taken into account (i.e. interference). Interference has the effect of changing the actual intake rate of a bird from the *IFIR*, and will in most cases decrease intake rate, but it is possible for intake rate to be unaffected or even to increase. The influence of interference depends on the perceived density of competitors (*PerceivedDens*) and the focal bird's dominance relative to these competitors. The perceived competitor density measures the density of competitors encountered by a bird as it forages on a patch and is expressed relative the density of competitors on the patch as a whole.

$$PerceivedDens = RelDens \, . \, (NumComp \, / \, Area) \qquad 2.23$$

where *NumComp* = number of competitors on patch, *Area* = area of patch exposed at current stage of tidal cycle and *RelDens* = the perceived density of competitors relative to the density on the patch as a whole. If in reality birds aggregate into particular areas of patches, *RelDens* will be greater than one. If birds are uniformly distributed over patches, *RelDens* will equal one. The value of *RelDens* was estimated under the present contract to be 8 for mussel feeding oystercatchers using the stabbing feeding method, and 4 for those using the hammering feeding method. Interference in cockle feeding oystercatchers and knots was not modelled (see chapter 3) and so *RelDens* was not measured for these systems.

2.9 *SHOREBIRD DISTRIBUTION*

Throughout the course of winter simulations, the model constantly tracks the location of each individual shorebird. Birds can either occupy one of several feeding patches when they are exposed by the tide, or the roost patch which is always exposed but on which no feeding is possible. During a single tidal stage, each bird remains at one location. Between successive tidal stages birds may move from one patch to another, provided that they are exposed by the tide.

The model assumes that birds attempt to balance their energy expenditure and requirements over the period of two tidal cycles. This time scale was chosen as it has approximately the same duration as a single day. Birds move between different locations in order to meet their energy requirements by feeding for as short a time as possible, and occupy the roost patch during tidal stages in which they do not need to feed. Birds do not show any preference for particular types of prey, but base their decisions purely on the energy intake rates achievable on each patch. The model finds a set of feeding locations for each bird (see below), in which they will feed during the course of the tidal cycles. In finding these locations the model assumes that birds have perfect knowledge of the future conditions, including the density of competitors and any shellfishing activities. Although in reality birds will be able to predict future conditions in such a way, they may still be able use previous experience to assess likely future conditions.

The model attempts to find the ideal-free distribution (Fretwell & Lucas 1970) of birds, such that none can achieve a higher intake rate by selecting a different sequence of feeding locations. This is accomplished using an iterative game theory procedure which is an extension of that used in previous versions of the model (Goss-Custard *et al.* 1995; Clarke & Goss-Custard 1996). Prior to each pair of tidal cycles the model randomly selects the order in which birds are processed, and attempts to find the optimal set of locations for each bird in turn using the following two step procedure.

Step 1: Patch yielding maximum intake rate during each tidal stage

The model calculates the intake rate the bird can achieve on each patch (providing the patch is exposed) at each tidal stage. The model then identifies the feeding patch that yields the maximum intake rate during each tidal stage (Table 2.12). In finding these patches, the model incorporates the bird's limited ability to discriminate between similar intake rates. All patches yielding intake rates within a given percentage (*PercepLimit*) of the maximum rate across all patches at that tidal stage are considered of equal quality. For example, if the maximum intake rate during a tidal stage was 100 KJ hr^{-1}, and *PercepLimit* was 3%, the bird would perceive intake rates as low as 97 KJ hr^{-1} as being exactly equivalent to the maximum value. This process selects the patch yielding the maximum perceived intake rate during each tidal stage. The bird will occupy all or some of these patches during the two tidal cycles.

Step 2: Optimal set of feeding locations

The exact set of patches occupied during a pair of tidal cycles depends on the relative values of the birds energy requirements and acquisition over this period. The model calculates a bird's energy requirements (which will be greater if it is attempting to gain weight or if its thermoregulatory costs are high) and compares this value with the total energy it could assimilate if it was to feed continuously in each of the patches selected above. If a bird's energy requirements are not exceeded by doing so it will feed continuously during the tidal cycle (Table 2.12). If the requirements are exceeded, the model finds the minimum number of tidal stages in which the bird can feed, and still exceed its requirements. This is achieved by sorting all tidal stages by their associated intake rates. The bird is then assumed to feed during the stage yielding maximum intake rate and to roost during all other tidal stages. If its energy requirements are still exceeded the bird will only feed during this one tidal stage. If not the bird is allowed to feed during two tidal stages, those during which it achieves the maximum and second highest intake rates, and its total energy intake calculated once again. This process is repeated until energy requirements are exceeded (Table 2.12). Once this process is completed the bird has a set of target feeding locations such that its demands are just exceeded. Its demands are matched exactly by reducing the proportion of time it spends feeding in the last patch added (i.e. that patch, of those occupied, in which intake rate is minimum).

These two steps are repeated for each bird in the population. If more than 10% of birds change their set of locations between iterations, the model is deemed not to have found a sufficiently stable distribution of birds and so the process is repeated. Up to three iterations of this kind are repeated. A limit of only three iterations is used to reduce the running time of the model, and as trial simulations showed that the model is unlikely to stabilize any more with further iterations. After the model is found to stabilize, or after three iterations, the intake rate of all birds is recalculated based on the final distribution of competitors.

Table 2.12 Example of the process by which birds are allocated to feeding locations. In this example, birds are able to feed in eight patches, divided into three patch types each with different patterns of exposure under the tidal regime: three mussel beds are only exposed at low water; two upshore areas are exposed during the receding and advancing tides in addition to low water; and a terrestrial field is always available. One other patch, the roost, is used during tidal stages in which no feeding is required. During all stages of the tide the model calculates expected intake rate on all patches, and identifies the patch yielding maximum intake rate. At high water this is patch 6, as it is the only one available, on the receding and advancing tides, patch 4, and at low water patch 1. If the birds energy requirements are high it must feed continuously. If not, the model determines which set of feeding locations enable it to meet its energy demands by feeding for the shortest time possible.

		Energy intake on each patch when it is exposed by the tide (non-shaded cells). Bold values show the maximum potential intake during a tidal stage.						Optimal locations (patch numbers) with different energy requirements				
		Mussel bed			Upshore		Field	Target intake				
Tidal cycle	Tidal stage	1	2	3	4	5	6	1000	400	200	100	0
1	high water						**25**	6	Roost	Roost	Roost	Roost
	receding tide				**50**	25	25	4	4	Roost	Roost	Roost
	low water	**100**	75	50	50	25	25	1	1	1	1	Roost
	advancing tide				**50**	25	25	4	4	Roost	Roost	Roost
2	high water						**25**	6	Roost	Roost	Roost	Roost
	receding tide				**50**	25	25	4	4	Roost	Roost	Roost
	low water	**100**	75	50	50	25	25	1	1	1	Roost	Roost
	advancing tide				**50**	25	25	4	4	Roost	Roost	Roost

2.10 *SHELLFISHING*

The influence of shellfishing is incorporated both through the depletion of prey and disturbance to foraging shorebirds. The precise way in which shellfishing is included depends on the exact type of shellfishing being modelled and so is dealt with in chapter 5.

Chapter 3 FORAGING MODULES

3.1 INTRODUCTION

This chapter describes the models used to calculate the intake rates of oystercatchers feeding on mussels, cockles and supplementary prey in upshore areas and fields, and the intake rates of knots feeding on cockles. Although different models are used for the different predator-prey systems, the models can be divided into two categories. (1) Maximum intake rate models: The models of oystercatchers feeding on mussels and cockles, and of knots feeding on cockles each calculate the maximum intake rate that a bird can achieve given the food supply available. (2) Fixed intake rate models: The models of oystercatchers feeding on supplementary prey in upshore areas and fields simply assume that birds feed at a fixed rate independent of the food supply available.

3.2 OYSTERCATCHERS AND MUSSELS

3.2.1 Functional response

J D Goss-Custard, S E A le V. dit Durell, S McGrorty, A D West, B J Ens, E J Bunskoeke & J T Cayford

3.2.1.1 Outline of the Exe estuary model

The role of this model in the shellfish-shorebird model is to predict the quality of a mussel bed for Oystercatchers as a function of the density, size distribution and ash-free dry mass of the mussels present and to predict the sizes of the mussels taken by the birds. Mussel bed quality is defined as the amount, in mg Ash-Free Dry Mass (AFDM), of mussel flesh consumed per 300s by an Oystercatcher of average foraging efficiency (Goss-Custard *et al.* 1995c). The size distribution of mussels taken is defined in 5mm length classes covering the range of 20-70mm within which fall most mussels taken by Oystercatchers between September and March.

The model itself is empirical but based on well-established first principles. The model has been in development since 1988 using data collected on the Exe estuary from the winter 1981-82 until the winter 1995-96. The model contains many empirical relationships, for most of which some field estimates of the parameters were available at the beginning of the present study. The data obtained during the present study allowed some parameter values to be made more precise and some new ones to be estimated and, of crucial importance, model predictions to be tested. Data collected from the Dutch Wadden Sea during the 1980's were processed and analysed as part of the present study and enabled the predictions of the Exe estuary model to be tested in another european area.

The basic principle of the model is that Oystercatchers select the size classes of mussel that maximise their gross rate of intake. A recent review by Zwarts *et al.* (1996a) found much support for this contention from the many studies done on prey size selection in Oystercatchers. In the model, a bird walks across a notional square metre of the mussel bed, searching for mussels within ± 5cm on either side of the midline of its body (Figure 3.2.1); this distance is equivalent to the width of the bird at the shoulders and corresponds to the distance either side to which the birds were observed in the field to peck at mussels. The model calculates gross intake rate by dividing the total dry weight biomass of flesh consumed as the bird traverses the notional metre by the total amount of time it takes to do so. The model calculates in turn the intake rate resulting from the bird taking different combinations of size classes of mussels; in this report, these combinations are referred to as 'size selection strategies'. It first calculates the intake rate that would be obtained if the bird was to take only the most profitable size class of mussel where, following foraging theory (Stephens & Krebs 1986), profitability is defined as *E/T*. The quantity *E* is the energy content of the mussel, defined here in terms of its AFDM. The quantity *T* is the combined 'handling time' (time spent breaking the mussel open and consuming the flesh) and 'waste handling time' (time spent failing to break into mussels in the same size class that it also attacks) (Meire & Erwynck 1986; Cayford & Goss-Custard 1990). The model then calculates the intake rate that would be obtained if the bird was also to take the next most profitable mussel size class. It then repeats the calculation on the assumption that the three most profitable size classes are taken and so on, until all ten size classes are included in the diet. For each size selection strategy, the energy intake (*EI*) obtained as the bird crosses the metre is calculated as the sum of the AFDMs of all the mussels consumed. The total time (*TT*) taken to obtain that energy is the time taken to walk across the metre, including all the time spent in attacking mussels successfully, and in consuming the flesh, and in attacking mussels unsuccessfully. The predicted intake rate for each strategy is, therefore, *EI/TT*.

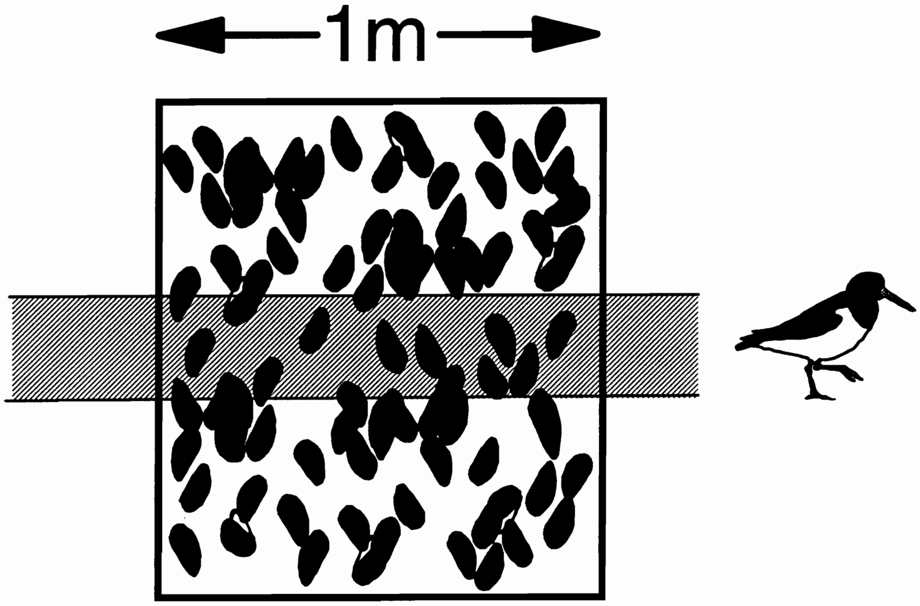


Figure 3.2.1 In the model, an Oystercatcher is assumed to walk straight across a square metre of mussel bed searching a 10cm wide strip (shaded).

Typically, the putative intake rate rises rapidly as more and more size classes are included in the diet until a maximum rate is achieved (Figure 3.2.2). Beyond this point, intake rate declines because the time spent in opening the less profitable mussels is not worth the energy gained from consuming them. The model identifies the maximum predicted intake rate of a bird foraging at maximum gross efficiency. However, in reality, Oystercatchers are not able to discriminate between changes in intake rate of less than *circa* 3% (Goss-Custard *et al.* 1995c). The model therefore takes as its predicted size selection strategy the widest selection of mussel sizes that gives a predicted intake rate that lies within 3% of the maximum (Figure 3.2.2). The intake rate resulting from this strategy is, of course, the predicted intake rate. The model also predicts the frequency distribution of the sizes of the mussels taken, and the mean length, for each size selection strategy.

The time cost in making successful attacks consists of the time spent opening the mussel and in consuming the flesh before resuming searching and varies considerably according to mussel size (Zwarts *et al.* 1996a). The time cost associated with making unsuccessful attacks also varies widely. At one extreme, a mussel is picked up and carried some distance and the bird spends up to five minutes trying to open it. At the other extreme, the unsuccessful attack is a simple rapidly-executed peck directed, it may be presumed, at a mussel or object that the bird very quickly rejects. In the field, the time costs associated with attacking mussels successfully and unsuccessfully were measured separately. The time taken to walk one metre, excluding the delay imposed on searching by attacking mussels either successfully or unsuccessfully, was measured in a further series of observations.

Measurements on the mussel bed provided estimates of the density of mussels in each length class present and visible to the birds. The numbers of mussels of each size class encountered by the bird as it crosses the metre is the density on the mussel bed divided by ten because it is assumed that the bird only searches one tenth of the metre in one pass. However, it quickly became clear that Oystercatchers do not attack every mussel within a size category that lies within this tenth of the square metre. In the model, the birds are assumed to attack mussels with a certain probability (*PROB*) that was estimated using the procedure detailed below.

Two versions of the model were developed which differed in the way in which mussel density was defined. In the simple version of the model, the number of all mussels is used to calculate mussel density. In this case, the many failed pecks made by Oystercatchers are assumed partly to reflect the sometimes high proportion of mussels that is unavailable to the birds. The density of mussels in the complex version of the model refers only to mussels that are actually available to Oystercatchers. In ventrally hammering Oystercatchers, for example, the available proportion comprises those mussels that are free of barnacles and have shells thin enough for the birds to break into (Ens 1982; Durell & Goss-Custard 1984; Meire & Erwynck 1986; Cayford & Goss-Custard 1990; Ens *et al.* 1996b; Meire 1996). This version of the model was only developed for dorsally and ventrally hammering birds as we still do not know how to measure the proportion of mussels available to Oystercatchers that open prey by stabbing. In the complex version of the model, failed pecks are assumed to reflect either mistakes made by the birds in identifying mussels that are available to them or attempts to identify which ones are actually vulnerable.

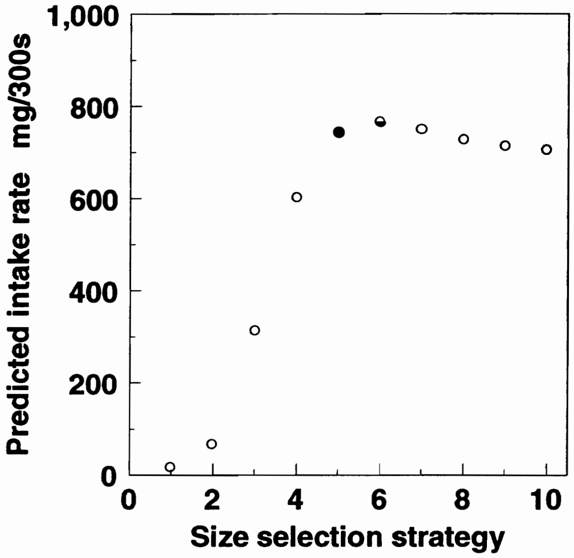


Figure 3.2.2 Example of the model output. Mussel size class are added in decreasing order of their profitability; 1 means only the most profitable size class is taken, 2 means that the two most profitable classes are taken, and so on. As more and more of the mussel size classes are included, the intake rate rises because more and more mussels that bird encounters are taken. However, eventually unprofitable mussel sizes enter the diet and the intake rate begins to fall below the optimum at 6. However, the bird will take the less profitable size classes until the intake rate falls below the optimum by 3%, the minimum difference in intake rates that Oystercatchers can discriminate. In this case, this happens when the top 7 most profitable size classes are being taken.

3.2.1.2 Model details and parameter estimation

Study sites: Data on foraging behaviour and food abundance were obtained from the main mussel beds of the Exe estuary between September and March during the years 1982-83 to 1995-96. The beds studied were numbers 1, 3, 4, 20, 25, 26, 30 and 31 (Figure 3.2.3) on which the majority of mussel-feeders occur. One site was also studied along the adjacent coast at Exmouth. Although the mussels here were on flat rock rather than on a soft sediment, the results from the ventrally hammering Oystercatchers that fed there fell within the range of values obtained from sites within the estuary itself. Data from the Netherlands came from an experimentally-created mussel bed near the island of Schiermonnikoog in 1987 (Ens & Alting 1996) and from natural mussel beds adjacent to Texel in 1983 and 1984 (Ens *et al.* 1996). In all cases, sites were marked out with canes and varied in size from 50x50m to 150x150m.

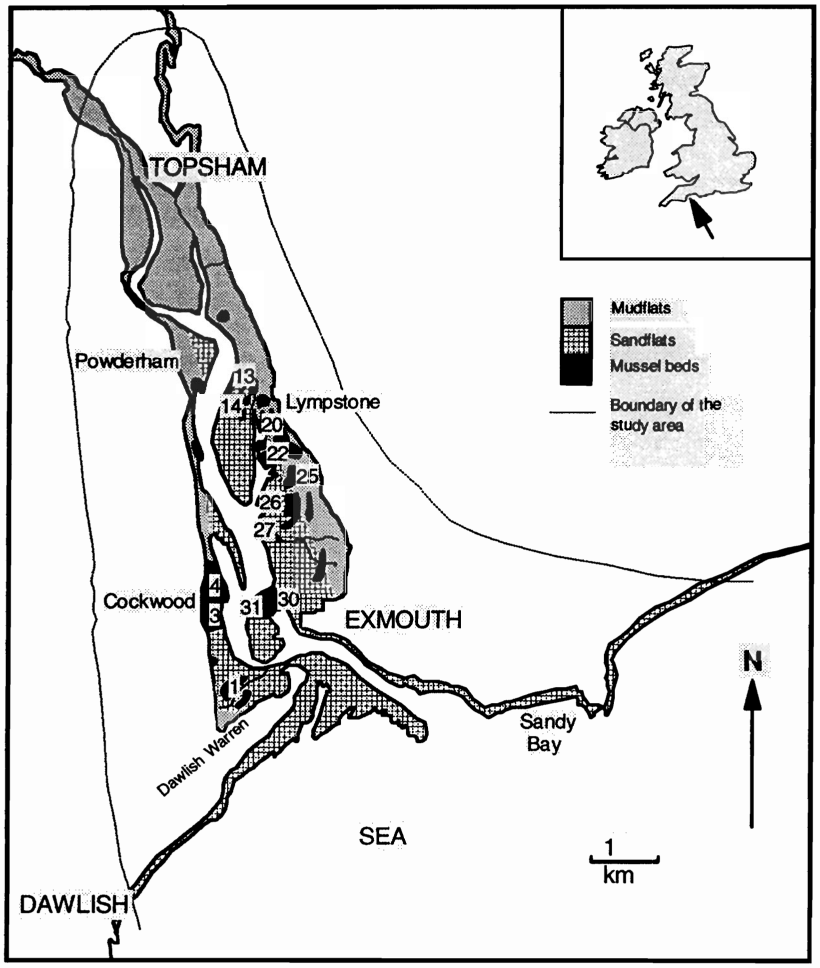


Figure 3.2.3 The Exe estuary, showing in black the main mussel beds used by oystercatchers. The numbers identify the beds.

Energy consumed per metre: Towards the middle of the period during which data on foraging behaviour were obtained, the density (*D*) of each 5mm size class of mussels was measured in each site using standard core sampling procedures; see, for example, Goss-Custard *et al.* (1996f) and Ens *et al.* (1996a). Not all mussels are visible to us, and presumably to Oystercatchers, because many lie beneath other mussels. Following Meire (1991), we determined the proportion visible by spotting ones we could see with white, liquid marker and then taking up the mussels for examination in the laboratory; further details are given in Goss-Custard *et al.* (1993). The proportion of mussels visible to us in each size class (V_i) was related to their size according to the equation:

$$V_i = -0.42476 + 0.05016L_i - 0.0004423L_i^{\ 2} \qquad 3.2.1$$

where L_i is the mid-point of the size class category i. V was also related to the total density of mussels of all size classes combined (Goss-Custard *et al.* 1993). However, this factor was not included in the equation because (i) the fraction of a given size class visible was unrelated to the biovolume of the larger size classes, despite this being the supposed cause of the fraction that is visible (A D West, unpublished information), and (ii) including it did not improve the predictive power of the model. V was also related to whether the sediment was soft and muddy or hard and firm (Goss-Custard *et al.* 1993); on average, V was 9.4% lower in soft and muddy places than in hard places. However, tests with the foraging model again showed that including this variable made little difference to its predictive power and, for simplicity, the effect of sediment on V was omitted from the model.

The AFDM, barnacle-cover and shell thickness on the ventral and dorsal side of a sub-sample of *circa* 40 mussels were also obtained from each site, again using standard techniques (Durell & Goss-Custard 1984). The AFDM of mussels of a given length varied between sites and within sites between seasons; examples are given in Goss-Custard *et al.* (1993) and Ens *et al.* (1996a). Site/occasion specific values of the slope and intercept of the relationship between $\log_{10}$ AFDM and $\log_{10}L$ are used in the model.

The proportion of shells (S) that can be opened by a dorsally hammering or ventrally hammering Oystercatcher is measured as the proportion that are thinner than the thickness below which fell 90% of the shells opened by Oystercatchers based on data collected on several mussel beds between 1976 and 1992. The results in Figure 3.2.4 show that the shell thickness of mussels taken increases with mussel length, as also found by Meire (1996). To calculate the proportion of mussels within each size class that is available to Oystercatchers, it is necessary to know the proportion of mussels in each 5mm size class that have shells thinner than the threshold value plotted size class in Figure 3.2.4. The mean thickness of a shell of given length varied greatly between times and sites (Goss-Custard *et al.* 1993) so it was not possible to assume that a constant proportion of the mussels in a size class fell below the threshold on all beds on all occasions. However, it would have been prohibitively time-consuming to have measured the shell thickness of a large enough sample of mussels from each size class on each occasion to determine how many were thin enough to be taken by Oystercatchers. We assume, therefore, that the distribution of the shell thicknesses of individual mussels within a size class around the mean is the same on all beds on all occasions and that a common frequency histogram of shell thickness variation could be applied on all occasions. To determine the frequency histogram, we re-calculated the shell thickness of all mussels measured between 1976 and 1985 on the Exe estuary by calculating the thickness of each shell as a *mm* deviation from its site/occasion mean. We then pooled all these deviations to produce a frequency histogram of individual mussel deviations for each size class that we assume applies to all site/occasions; as examples, the thickness deviations on the dorsal and ventral sides are shown for one size class of mussels in Figure 3.2.5. The distribution of shell thickness within a size class in a particular site on a particular occasion was then estimated by applying the size-specific frequency histogram to the mean shell thickness of that size class on that particular occasion. From that, the proportion that were thinner than the threshold value was then calculated. Once this had been done for each of the ten size classes for a particular site/occasion, the proportion of mussels with shells thin enough for Oystercatchers to open on that site/occasion was then plotted against size class. Separate calculations and plots were made for dorsal and ventral hammerers, of course. Sometimes the relationship between mussel size class and the proportion with shells that were thin enough for Oystercatchers to open was best described by a linear regression which almost invariably had a negative slope; ie. the proportion of mussels that were vulnerable declined with mussel size. However, more often, the relationship was curvilinear and was best described by a second-order and third-order polynomial. The resulting equation is included in the complex version of the model to calculate the proportion of mussels of each size class present that are available to hammering Oystercatchers on the site/occasion for which intake rate predictions are required.

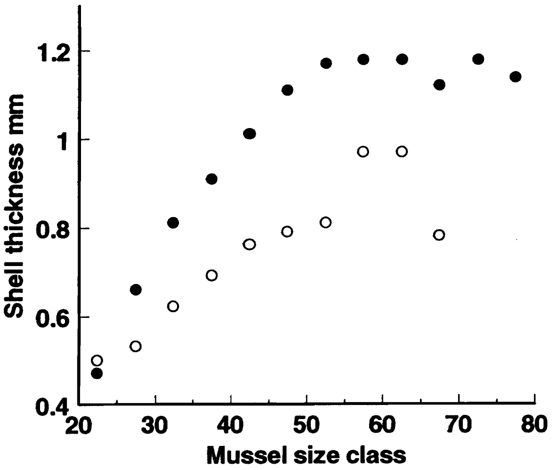


Figure 3.2.4 The thickness of the shell of mussels taken by dorsal (open circles) and ventral (solid circles) hammering Oystercatchers below which 90% of the mussels taken fell. For example, 90% of the mussels 30-35mm long that had been opened by Oystercatchers had shells on the ventral side that were thinner than 0.81mm. Each symbol represents the fraction of a sample of shells ranging in size from 15 to 140.

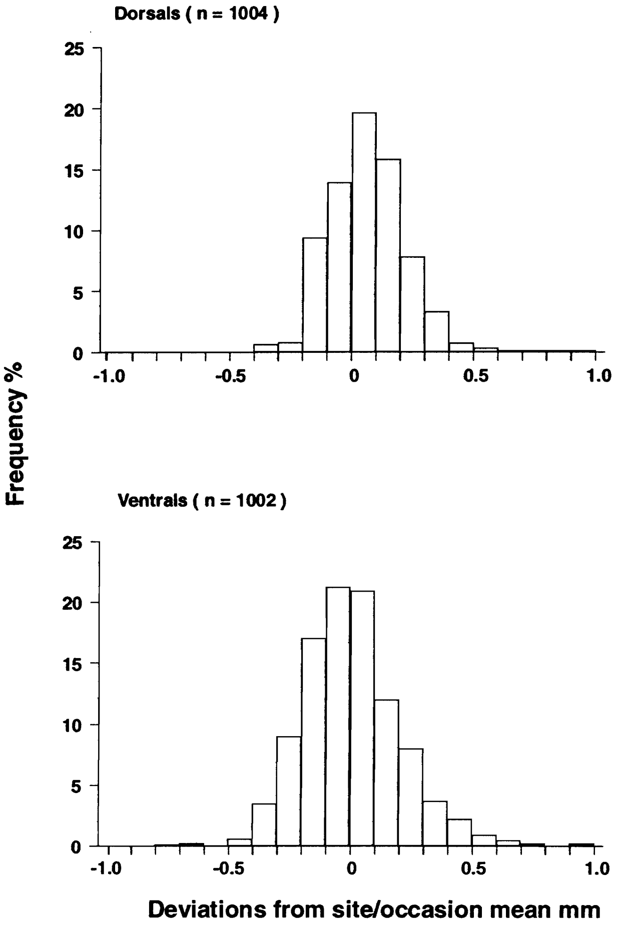


Figure 3.2.5 Frequency distribution of the deviations from the site/occasion mean of the shell thickness of mussels 50-55mm long on the dorsal and ventral side. The data are from all the shell thickness determinations made on the Exe estuary from 1976 to 1994; the sample sizes are shown in brackets.

The proportion of shells with few enough barnacles (<5) for ventral hammerers to open (*B*) was also included in the complex version of the model for ventral hammerers. The extent of barnacle cover was related to mussel length, as the examples in Figure 3.2.6 illustrate. The minimum order of polynomial expression needed for each site to describe the relationship between the proportion of mussels with few mussels and mussel length is included in the complex version of the model.

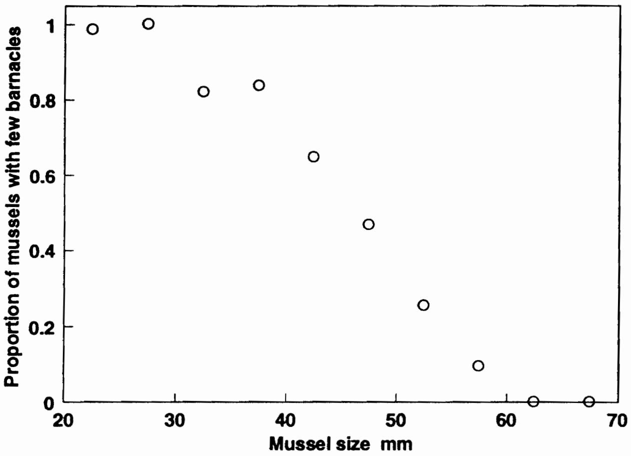


Figure 3.2.6 The proportion of mussels in different size classes that carried few enough barnacles for ventrally hammering Oystercatchers to attack them. Data from bed 31, 1995-96; 30-50 mussels were examined for each size class.

The expression in the complex model for calculating the numbers of each of the ten 5mm size classes of mussels that are attacked successfully (N_i) with probability *PROB* as a bird walks across a metre square of mussel bed, searching one tenth of it, is therefore:

$$N_i = 0.1\ (PROB\ D_i\ V_i\ S_i\ B_i \qquad 3.2.2$$

while in the simple model it is:

$$N_i = 0.1\ (PROB\ D_i\ V_i) \qquad 3.2.3$$

The AFDM (*A*) of each size class taken is then obtained from the equation:

$$\log_{10} A_i = Aa + Ab(\log_{10} L_i) \qquad 3.2.4$$

where *Aa* and *Ab* are site/occasion specific values. The AFDM (*M*) consumed per metre searched from each size class is therefore:

$$M_i = N_i\ A_i \qquad 3.2.5$$

from which the total energy consumed per metre (*EI*) can be calculated for each size selection strategy by summing the M_i values for the size classes that are included in that strategy.

Time expended per metre: The time expended foraging across one metre (T) is comprised of four components:); (i) time spent walking across the metre and searching (*S*), (ii) time spent on making pecks at mussels or other stimuli (*P*), (iii) time wasted on mussels which Oystercatchers made a long attempt to open, but failed (*WHT*), and (iv) time spent handling mussels that were opened and consumed successfully (*HT*).

The methods used for measuring each of these time-cost components of foraging are detailed in the section that follows. Suffice to note that data on each site were obtained, as far as possible, equally throughout the tidal exposure period. When a site was studied throughout the period September - March, we also attempted to obtain data evenly over the months although this was often not possible because weather affected our distribution of effort. We investigated by regression analysis the effect of stage of the tidal cycle and season on many of the parameters detailed below, but the results of this analysis are not given in this report (although they will be published elsewhere). The reasons are: (i) it was often the case that neither variable, either in the linear or in the quadratic, had a statistically significant effect on the dependent variable, and (ii) where a significant effect was detected, the mean values were generally similar to the regression model predictions for the typical values (mid-season and mid-exposure period) of the dependent variable; this suggested that we had been successful in distributing measurements evenly with respect to critical variables. Many of the values differed significantly between birds using different feeding methods for opening mussels. In Table 3.2.1, either the mean of all the site means available are given or the mean of all data collected across all sites. In all cases, data for adults and 'senior' immatures in their third or fourth winter only are given in order to remove any age-dependent effects which will again be detailed in other publications.

Table 3.2.1 The values of the time-cost parameters used in the models and the number of sites from where the mean value shown was obtained (N). Full descriptions of what the parameters represent are in the text. The units appropriate for the parameters are shown in brackets above.

		Stabbers		Dorsal hammerers		Ventral hammerers	
Parameter	Units	Value	n	Value	n	Value	n
S	s	3.781	3	3.595	3	3.957	2
P_S	s	1.191	3	1.313	3	1.112	2
P_L	s	6.390	3	8.050	3	8.130	3
aWHT	s	6.060	1	2.410	1	4.800	3
bWHT	s	0.528	1	0.686	1	0.763	3
aHT	s	-27.17	7	-56.14	3	5.105	4
bHT	s	*2.134*	7	3.401	3	2.746	4
PM	min^{-1}	61.90	5	40.00	5	19.20	4
F_L		0.024	3	0.043	3	0.092	3
cdi		0.016	3	0.016	3	0.602	3

(i) *S*: The time spent in crossing the metre refers just to the time taken to cover that metre, excluding the delay imposed by any time costs associated with decelerating and accelerating, even stopping linked to items (ii)-(iv) above. The value of *S* could not be measured directly as Oystercatchers very seldom walk one metre without making at least one peck and, when they do, their walking rates may not be typical. Instead, we timed how long it took a bird to walk a metre and counted the number of pecks it made as it did so. Plotting the time taken against the number of pecks made allowed two parameters to be estimated

(Figure 3.2.7). The intercept estimates S, the time taken to walk one metre excluding any delays associated with pecking and handling prey. The slope estimates P, the delay imposed by making a peck. Following Cayford (1988), pecks in this study were separated into short pecks of less than 3s duration and long pecks of greater than 3s duration, their durations being denoted by P_S and P_L respectively. For estimating S, only records in which the bird made pecks <3s long were accepted because an occasional long peck can considerably distort the estimates of both the slope and the intercept of the relationships. Often the bird deviated from a path parallel to the many rows of bamboo sticks that we had put out on the mussel bed for measuring these quantities so that the record lasted for less than 1m. In such cases, both the time taken and the number of pecks made were pro-rated up to obtain the metre equivalent values. An example of the data obtained is given in Figure 3.2.8. Table 3.2.1 details the values of the slopes and intercepts obtained for birds using each feeding method in the sites studied and gives the mean value used in the model.

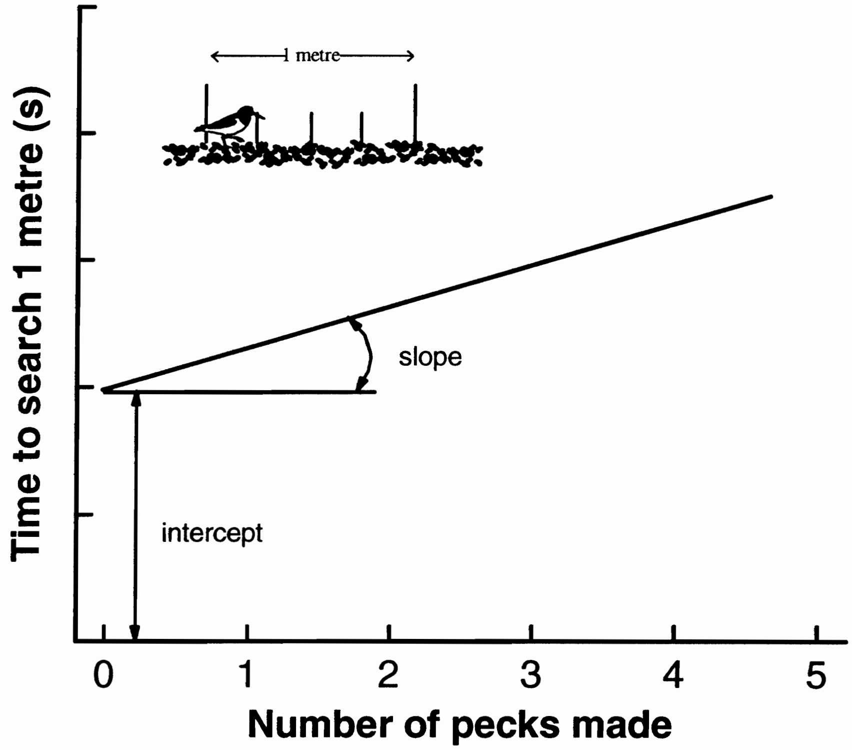


Figure 3.2.7 Hypothetical relationship between the time taken by an Oystercatcher to walk one metre and the numbers of pecks it made while doing so. The inset shows how the data were collected.

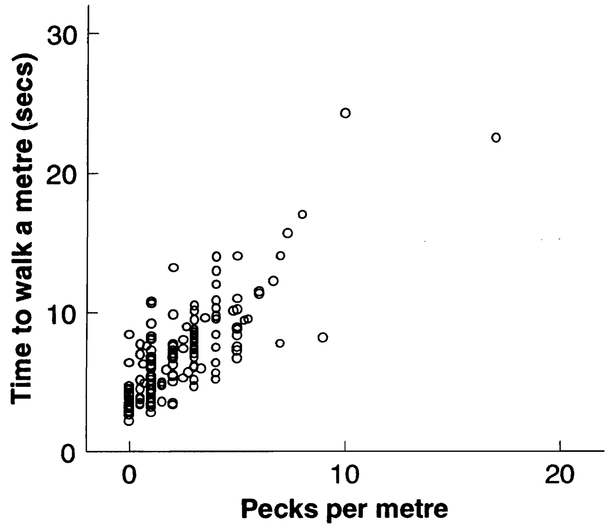


Figure 3.2.8 Relationship between the time taken by a stabbing Oystercatcher on bed 20 in 1991-92 to cover one metre in relation to the number of pecks it made while doing so.

(ii) *P*: We do not know whether a given short or long peck was directed at a small or a large mussel so we could not ascribe the time cost associated with such pecks to a particular mussel size class. We therefore include the time spent on making short and long pecks within the total time spent searching the metre for all size classes of mussels. In the model, the total time spent crossing the metre (*ST*), excluding handling time and waste handling time, was:

$$ST = S + ((NT)(P_SM)(P_S)) + ((NT)(P_LM)(P_L)) \qquad 3.2.6$$

where *NT* is the total numbers of mussels of all size classes taken as the bird traverses the metre, as calculated by the model for the particular size selection strategy under consideration, and P_SM and P_LM are the numbers of short and long pecks respectively made per mussel taken. P_SM and P_LM were measured in the field by counting the total number of all pecks (*PM*) made between resuming searching after consuming one mussel and capturing the next mussel, including the peck that led to that mussel being caught; thus, if the bird successfully opened a mussel with its first peck after consuming the previous one, we recorded that one peck had been made to catch the mussel. The fraction of the pecks that were short (F_S) and long (F_L) were recorded regularly by counting in our heads whether or not the peck lasted longer than three seconds. The products $((PM)(F_S))$ and $((PM)(F_L))$ estimated the number of short pecks ($P_S M$) and long pecks (P_LM), respectively, expended per mussel capture. The duration of short pecks (P_S) was calculated as detailed above. The duration of long pecks (P_L) was measured directly. This was done by counting in our heads up to the first ten seconds in order not to prevent the observer from having to reset a stopwatch continually. Only after a peck had lasted ten seconds was the stopwatch started, the additional ten seconds being added on later. Table 3.2.1 details the values obtained for birds using each feeding method in the sites studied and gives the mean value used in the model.

(iii) *WHT*: Some of the pecks involved the bird in carrying a mussel which subsequently it was unable to open. Such pecks were excluded from the calculation of the number of long pecks made and their duration detailed above. The sizes of these rejected mussels could be estimated in the field and the duration of the failed attempt measured by stopwatch. Examples of the relationship between mussel length and the time wasted in dealing with it for each feeding method are shown in Cayford & Goss-

Custard (1990). Table 3.2.1 gives the slopes and intercepts of all the relationships that we have obtained so far. The *WHT* of each mussel size class was calculated in the model from the following expression:

$$WHT_i = aWHT + bWHT(L_{1i}) \qquad 3.2.7$$

To measure the total amount of time wasted on such rejected mussels, we recorded the proportion (*cdi*) of all the long pecks made per mussel in which mussels were carried and then dropped and ignored ; the results are detailed in Table 3.2.1. For each size selection strategy, the model calculates the total time wasted on carrying and dropping such mussels (*WHTT*) from the expression:

$$WHTT = (NT)(P_L M)(cdi)(WHT) \qquad 3.2.8$$

(iv) *HT*: Details of methods for measuring the time taken to open a mussel and to consume the flesh are given in Goss-Custard et al. (1996f). In that paper, curvilinear relationships between mussel size and handling time were used, but subsequent analysis showed that a simple linear function was as effective at capturing the relationship between mussel length and handling time. The slopes (*bHT*) and intercepts (*aHT*) of all the available linear relationships between mussel size and *HT* are given in Table 3.2.1. The expression used by the model to calculate *HT* of each size class of mussels is therefore:

$$HT_i = aHT + bHT(L_i) \qquad 3.2.9$$

For each size selection strategy, the model calculates the total time spent on opening mussels and consuming the flesh (*HTT*) from the expression:

$$HTT = (NT)(HT) \qquad 3.2.10$$

(v) *TT:* The total time taken to cross the metre and take the mussels resulting from any size selection strategy (*TT*) is calculated by the model as:

$$TT = ST + WHTT + HTT \qquad 3.2.11$$

(vi) *E/T:* The profitability of a particular size class of mussel (E_i / T_i,) which determines the sequence in which size classes are considered in the size selection strategies, is calculated in the model from the expression:

$$E_i / T_i = M_i \,/\, ((HT_i) + ((P_L M)(cdi)(WHT_i))) \qquad 3.2.12$$

Predicted intake rate: The model calculates the intake rate (mgAFDM/300s) for any particular size selection strategy from the expression:

$$\text{Intake rate} = (EI/TT)\text{x}300 \qquad 3.2.13$$

Estimating *PROB*: This variable represents the probability that a mussel which is encountered by a bird within 5cm either side of its midline as it walks across the metre is detected and attacked successfully. As there is no theoretical way in which this value can be derived, *PROB* has to be estimated empirically. It was estimated for a particular site/occasion by running the model with different values of *PROB* until the predicted intake rate, the most important output of the model, matched that which was actually observed in the field. In the early versions of the model, the quantity *PROB* was assumed to be a constant for each feeding method across all site/occasions. Examination of the first results, however, revealed a considerable variation between site/occasions. Since the model output is so sensitive to the value of PROB (see below), it was essential to understand the variation in the values obtained.

The most likely possibility is that *PROB* decreases as mussel density rises. As an Oystercatcher lunges a given distance at a particular mussel to the front or side of its body, the bird inevitably by-passes more mussels when mussels are dense than when they are scarce. Another reason for expecting *PROB* to decrease with mussel density is that the birds may become more selective when prey are abundant (Hulscher 1976; Wanink & Zwarts 1985), especially when a number of size classes are on offer.

The dependence of *PROB* on the density of all mussels, irrespective of shell thickness and barnacle cover in the case of the hammerers, is shown for all the Exe estuary sites in Figure 3.2.9. Only mussels >45mm long, from which Oystercatchers obtain most of their intake, are included in the estimate of mussel density. A double $\log_{10}$ plot is used as the untransformed relationship is curvilinear. Regression analysis revealed that, as predicted, *PROB* decreases strongly as mussel density increases ($P<0.0001$). The values for ventral hammerers seem generally to be higher than those for dorsal hammerers. However representing the two feeding methods in the regression analysis by a 0/1 dummy variable revealed that the difference between them is not quite statistically significant ($P=0.097$), perhaps because the sample size in ventral hammerers is small. *PROB* is, however, significantly lower in stabbers than in dorsal and ventral hammers combined ($P<0.0001$). The gradients for stabbers and hammers are -1.082 (SE=0.155; N=13) and -1.396 (SE=0.132; N=24), respectively. Essentially the same results as these were obtained in hammerers with the complex version of the model although, of course, the constants and coefficients differed from those obtained with the simple model.

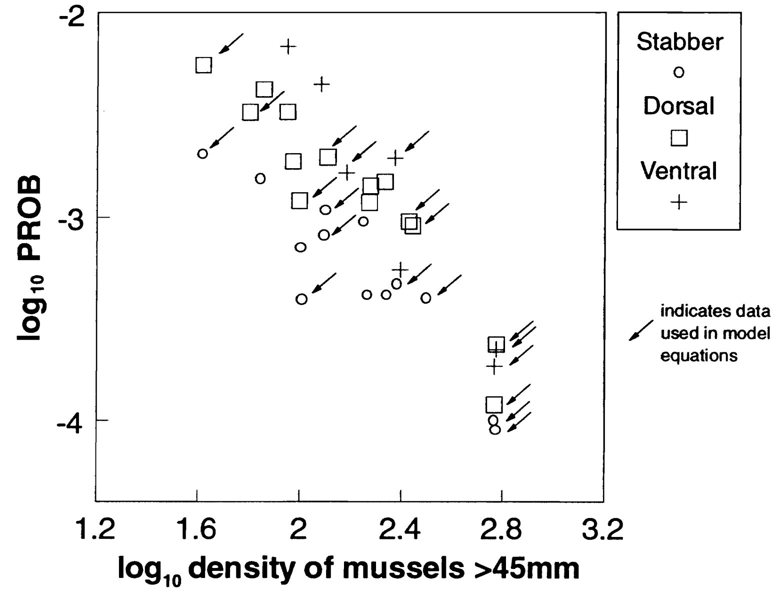


Figure 3.2.9 The parameter *PROB* plotted against the density of large mussels. All available data from the Exe estuary are shown. The symbols refer to the feeding method, as indicated. The small arrows identify data points that were used to calculate the equation used in the model.

A large amount of variation in *PROB* (adj. $R^2=84\%$) is explained by mussel density and by a dummy 0/1 variable which represents stabbers and hammerers. Nonetheless an attempt was made to explain some of the residual variation in *PROB*. One possibility was that *PROB* decreased from September to March as the birds gradually depleted the mussels that were most vulnerable to attack. However, there was no indication from the monthly values obtained in two site (beds 1 and 4) over the winters 1981-82 and 1982-83 respectively that *PROB* decreased significantly ($P>0.05$) as the numbers of days elapsed since September 1 increased and the birds depleted their food supply. Therefore we assumed in the model that variations in *PROB* were associated only with the density of mussels >45mm long.

Figure 3.2.9 shows all the values of *PROB* obtained from the Exe estuary and adjacent coast. However, for the model, we required a subset of data points to calculate the relationship between *PROB* and the density of large mussels so that the model could be tested in sites which did not contribute data to the model equation. We chose for this provisional model relationship the first estimate of *PROB* obtained for each mussel bed; these data points are identified in Figure 3.2.9. We used only one value from each of the mussel beds studied. Although the difference in *PROB* between dorsal and ventral hammerers did not reach the 5% level of significance, separate expressions for calculating *PROB* from the density of mussels above 45mm long were used in the model for the two hammering techniques to improve precision. In the model, the value of PROB for a given site/occasion was calculated for stabbers (equation 3.2.14), dorsal hammerers (equation 3.2.15) and ventral hammerers (equation 3.2.16) from the expressions:

$$PROB = (0.059968)((D_{>45})^{-0.914313}) \qquad 3.2.14$$

$$PROB = (0.369680)((D_{>45})^{-1.135795}) \qquad 3.2.15$$

$$PROB = (0.598068)((D_{>45})^{-1.135795}) \qquad 3.2.16$$

where $D_{>45}$ is the density of mussels greater than 45mm in length.

Comparison of simple and complex model: The predictions for intake rate and mean mussel length of the simple and complex models were compared for sites that were not used to calculate model parameters (Figure 3.2.10). This was done to see whether calculating the proportion of mussels available to hammering birds in each site was justified by a greater predictive power. Across all feeding methods, there is a total of 14 such sites from beds 1, 4, 20 and 26 within the estuary and from Exmouth beach. The values for stabbers are not shown in Figure 3.2.10 as, for this feeding method, there is no complex version of the model. For the hammerers, the relationship between the predictions of the two versions is very close for both intake rates (Figure 3.2.10a) and mean mussel length (Figure 3.2.10b). There is thus little point in using the complex model because its predictive power is not noticeably better than that of the simple version. It was decided to jettison the complex version of the model and use only the simpler version.

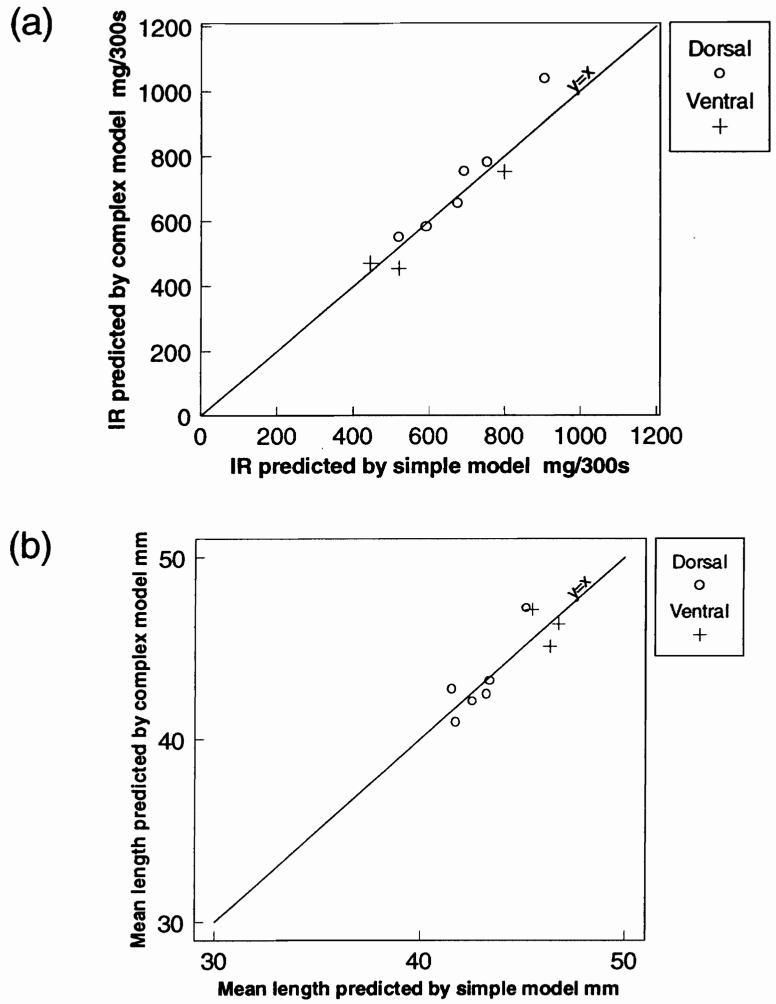


Figure 3.2.10 Comparison between the predictions for sites that did not contribute data to model functions of the simple and complex versions of the model for dorsal and ventral hammerers. The diagonal line shows the line of perfect matching: (a) intake rate; (b) mean length of mussels taken.

3.2.1.3 Model tests and sensitivity

The simple model was tested by comparing its predictions for intake rate and mean mussel length taken for those 14 site/occasions which were not used to estimate parameters in the model. Intake rates and mussel sizes taken by Oystercatchers in each site were measured using standard techniques, as described, for example, in Goss-Custard *et al.* (1996f) and Ens *et al.* (1996a). Only data collected at bird densities <100 birds/ha are used to prevent interference between foraging birds from affecting the results (Stillman *et al.* in press).

The predicted values varied closely with the observed values for both intake rate (Figure 3.2.11a) and mean mussel length (Figure 3.2.11b). With the stabbing and hammering feeding methods represented by a dummy 0/1 variable, regression analysis revealed no significant effect of feeding method on the relationship between predicted and observed values in either case (P=0.785 and 0.590 respectively). Thus the overall relationship between predicted and observed values have been calculated across all feeding methods. In neither case is the intercept significantly different from 0 or the slope significantly different from 1, suggesting the model predicts both intake rate and mean mussel length in these Exe estuary sites quite well (Table 3.2.2). The relationships are reasonably tight, with the R2 values (adjusted) being 49% and 53% respectively. However, measurements of foraging rates in Oystercatchers are notoriously variable and mean values have large standard errors unless the sample size is very large. This undoubtedly accounts for some of the deviations of predicted from observed values. For example, the mean deviation of predicted from observed intake rates is only 88mg/300s, which is less that two times the average SE (49mg/400s; range 32-67) of the observed intake rates in the six sites where this could be calculated. It is concluded that the model predicts the intake rate and mussel sizes taken by Oystercatchers on the Exe estuary quite satisfactorily.

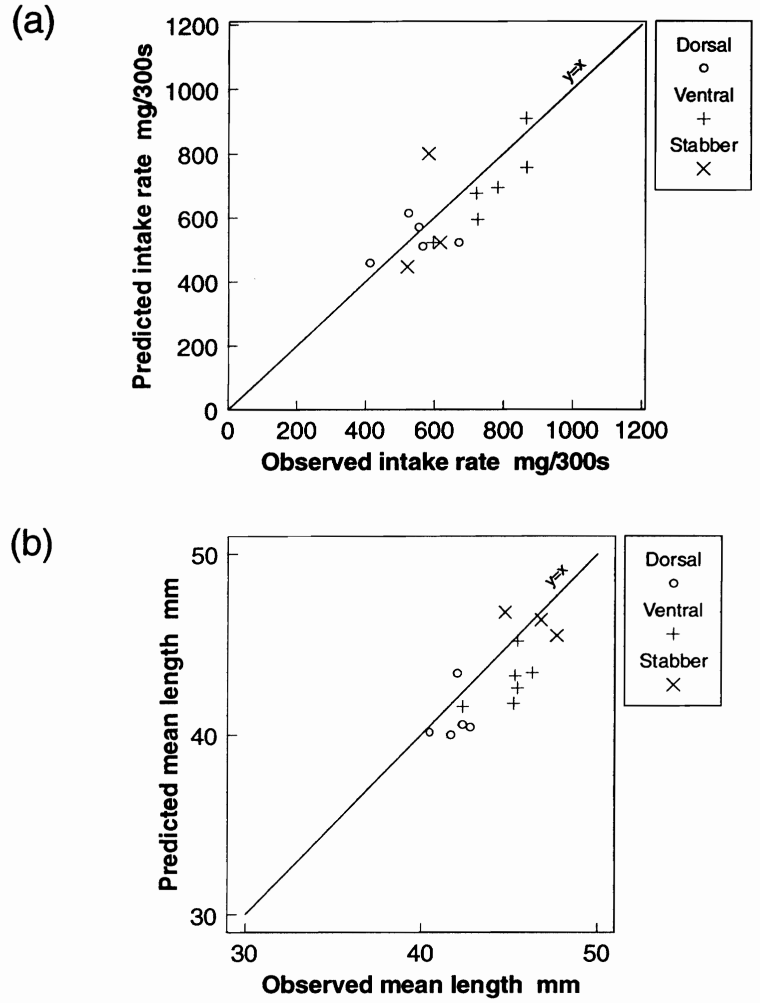


Figure 3.2.11 Comparison between the predictions for sites that did not contribute data to model and observed values for Oystercatchers using the three feeding methods: (a) intake rate; (b) mean length of mussels taken.

The model also predicts the size distribution of the mussels taken. As the examples in Figure 3.2.12 illustrate, it does this quite well except that some of the smaller sizes are under-represented in the predictions. This arises because, in the model, there is an all-or-nothing response to each size class whereas real foragers must sample alternative size selection options and, of course, also make mistakes which involves them taking sub-optimal size categories (Stephens & Krebs 1986). However, because of the small numbers of mussels involved, such model discrepancies are unlikely to have a significant impact on the predicted response of the mussel population to alternative shellfish management options.

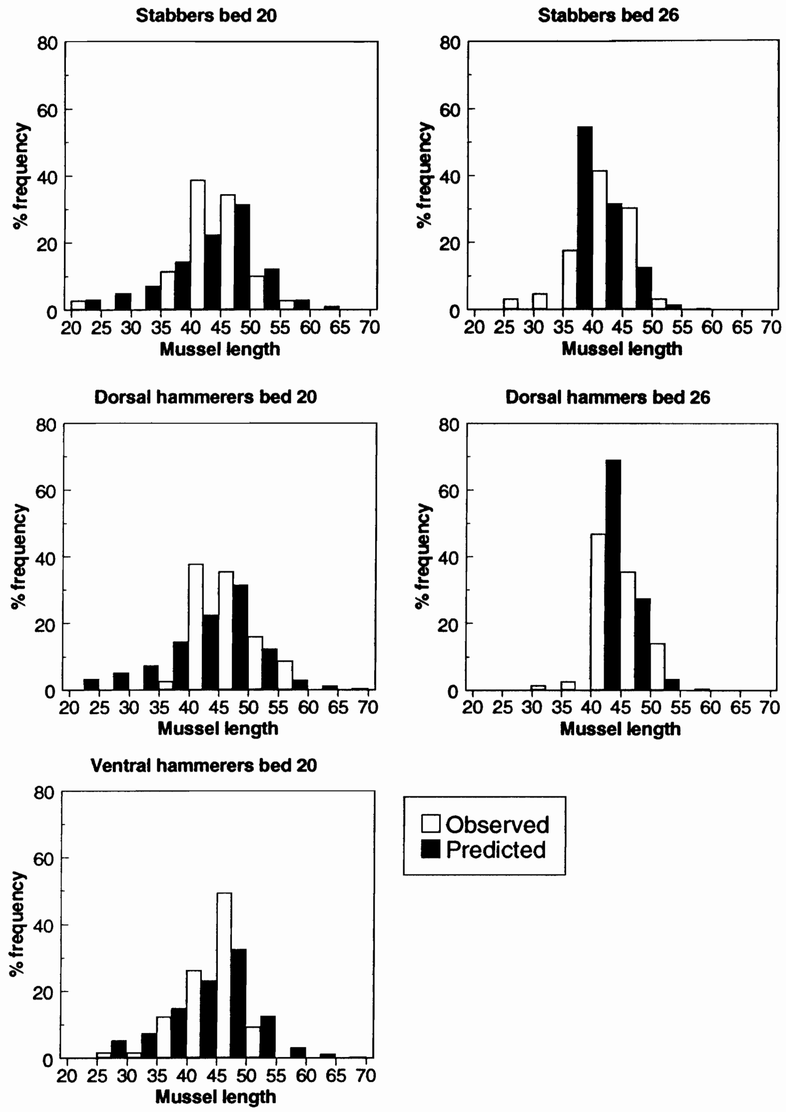


Figure 3.2.12 Comparison between model predictions and observed frequency distributions of the lengths of mussels taken by oystercatchers in a sample of sites and using all three feeding methods.

The ability of the model to predict the foraging of Dutch birds was tested by comparing model predictions with observed values on five site/occasions. Much of the data from the Dutch sites were obtained in spring and summer when many Oystercatchers take small mussels for reasons that are not yet understood (Cayford & Goss-Custard 1990; Ens *et al.* 1996a). As the model does not cater for this shift in size selection strategy, careful selection of the data was necessary. The details of each site/occasion are as follows, the total numbers of minute periods of data available from each being given in brackets. Two site/occasions were provided by the experimental mussel bed described by Ens & Alting (1996) using the data collected from 31 7 87 until 26 8 87, when most birds had clearly stopped taking small mussels. The two site/occasions were (i) two ventrally hammering birds WR200 (154.1 mins) and WR010 (8.7 mins) and a single stabbing bird, WR002 (56 mins). The remaining three site/occasions were the natural mussel beds on Texel studied by Ens *et al.* (1996a). One site/occasion was provided by the data collected during 1983, mainly in August but also in September and October, from a number of stabbers, although mainly LWLY (151.5 mins). Another site/occasion from Texel was provided by the data collected in 1984 from 27/2/84 until 4/4/84 on a variety of stabbers (301 mins). The final site/occasion was provided by data collected from a variety of ventrally hammering birds on Texel over the same two periods in 1983

(125.6 mins) and 1984 (54.6 mins) that the stabbing birds were studied. Sometimes, the mussel food supply had been sampled twice during the period over which the foraging data had been collected; the data collected on Texel in both 1983 and 1984 is an obvious example. Where this occurred, the mussel data were weighted by the number of minutes of observation made on the birds over the intervals represented by the mussel sampling.

Table 3.2.2 Comparison between the model predictions and observed values of intake rate and mean length of mussels consumed by Oystercatchers for the 14 sites on the Exe estuary alone and for the Exe sites and the five sites in the Dutch Wadden Sea combined. The intercept and the slope of the regression equation of the dependence of the predicted vales on the observed values are shown. Intake rate is measured in mg/300s and mean length in mm. The dummy variable is the 0/1 variable representing whether a site was in the Exe (0) or Wadden Sea (1), the coefficient being shown. SE = standard error. The intercepts are not significantly different from 0 and the slopes are not significantly different from 1, except for Length in All sites where P=0.005 and <0.01 respectively.

	Output	Intercept	SE	Slope	SE	Dummy	SE	P	R^2
i) Exe	Intake rate	135.2	133.7	0.74	0.20	-			49
	Length	7.44	9.05	0.80	0.21	-			53
ii) All	Intake rate	136.0	103.6	0.74	0.16	-92.0	50.9	0.09	53
	Length	24.5	7.53	0.42	0.17	3.28	1.06	0.007	36

Although predicted and observed values are clearly related and increase in parallel, the model consistently underpredicts intake rates in the five Dutch sites available (Figure 3.2.13a). However, the discrepancy does not quite reach the 5% level of significance (Table 3.2.2) but, with such a small number of Dutch sites, is nonetheless too large and consistent to ignore. With whether a site was on the Exe or in the Netherlands represented by a 0/1 dummy variable, regression analysis shows that the model underpredicts Dutch intake rates on average by 92mg/300s (Table 3.2.2). This partly occurs because the model underpredicts the length of mussels taken by Dutch birds by a mean value of 3.3mm (Figure 3.2.13b). However, much of this difference arises in one site where some birds seemed already to have switched to small mussels, as Oystercatchers generally do in spring (Cayford & Goss-Custard 1990; Ens *et al.* 1996a). Nonetheless, the model developed on the Exe clearly predicts the foraging behaviour of Dutch birds less well than it does birds feeding on the Exe estuary itself.

The reasons for this discrepancy are not yet known but some clues as to where we might look for possible causes can be obtained by exploring the model sensitivity to the values of its different parameters. This was done by changing one parameter value at a time by one or more orders of magnitude above or below its value in the model. In the case of *PROB*, the site-specific value that gave the observed intake rate was used. Simulations were run for stabbers and dorsal hammerers for the site/occasions used in the model from beds 1, 3, 4, 20, 25 and 26.

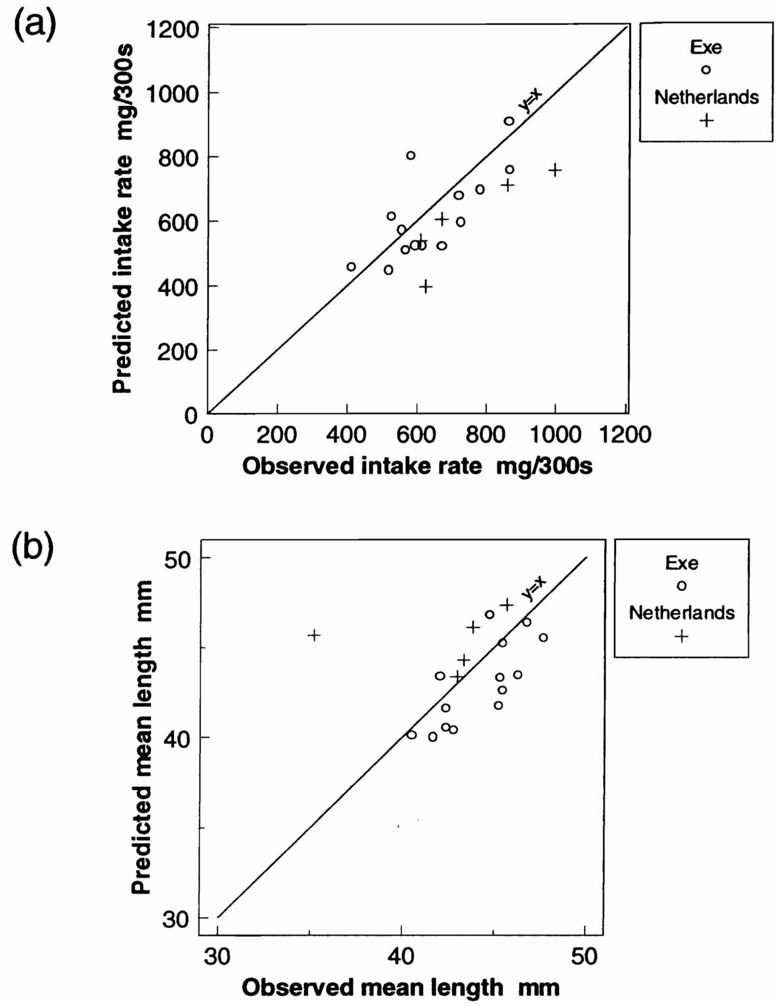


Figure 3.2.13 Comparison between model predictions and observed values for all feeding methods on the Exe and in the Netherlands: (a) intake rate; (b) mean length of mussels taken.

Some illustrative results are given in Figure 3.2.14 on the sensitivity of intake rate to changes in the values of *PROB* and P_S. (the delay imposed on searching by making a short peck). Clearly, the intake rate is affected considerably as each parameter is increased or decreased from its current value in the model. The effect is particularly strong in the case of *PROB*. The results across all the parameters explored are summarised in Table 3.2.3. The values shown are for stabbers and hammerers averaged together across the six mussel beds. The values show the average difference in intake rate or mean mussel length brought about by changing the parameter value from one-tenth to ten times its actual value in the model; in other words, across a range of two orders of magnitude. The effects of changing *PROB* and *S* (the rate of walking over the mussel bed) are equally great because each affects the rate of encounter with mussels in the same way. The remaining parameters are time costs and their effect on predicted intake rates and mean mussel lengths depends on how much they contribute to the existing time costs. Thus, changing the values of *PM* (the numbers of pecks per mussel), *HT* (time spent handling a mussel successfully opened) and P_S has a large effect because all three contribute a lot to time costs. In contrast, changing the values of P_L (the delay imposed on searching by making a long peck), F_L (the fraction of all pecks that were long), *cdi* (the proportion of long pecks in which a mussel was carried but rejected) and *WHT* (time wasted on a rejected mussel) had a much smaller effect because they contribute so little to time costs.

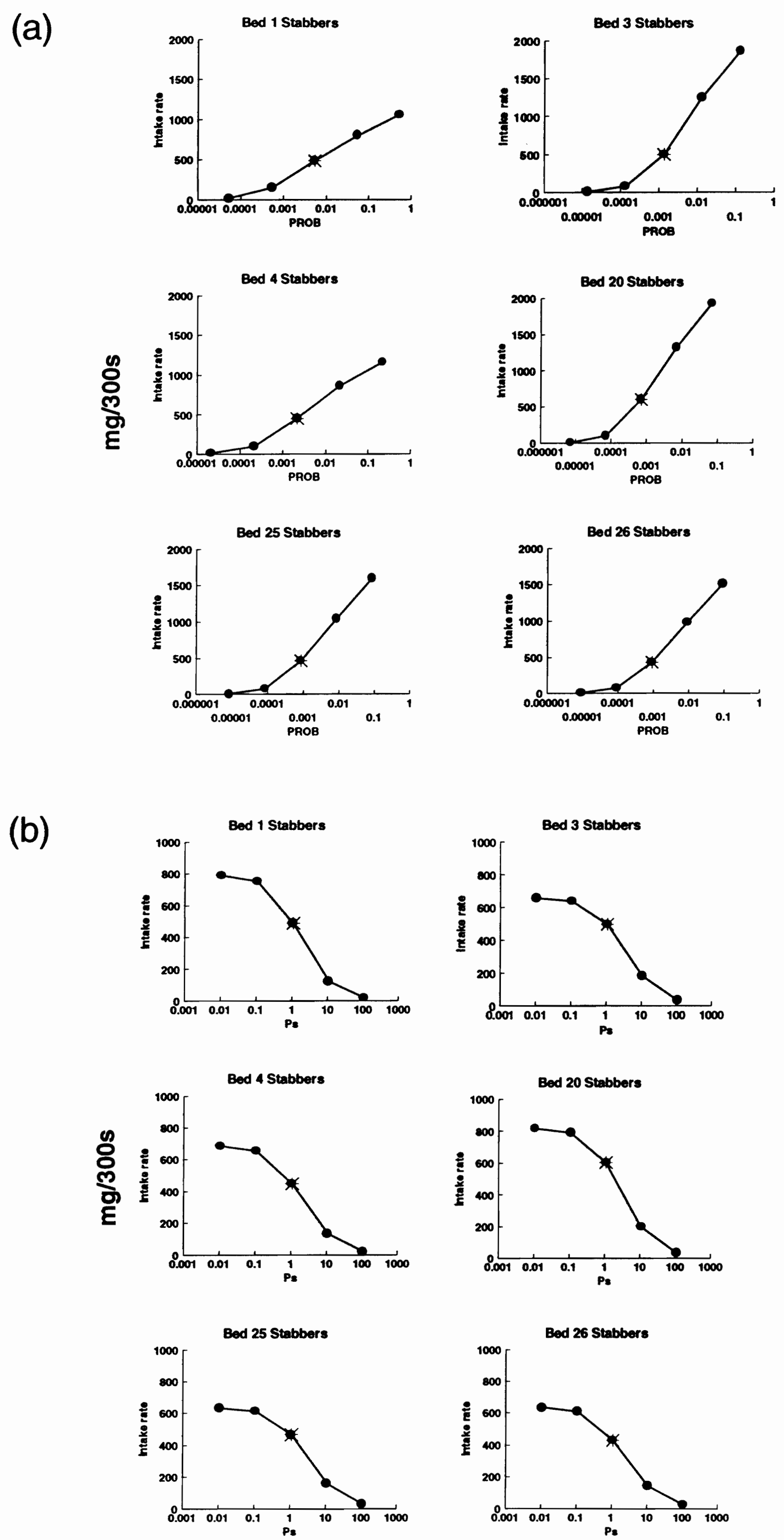


Figure 3.2.14 The sensitivity of model predictions for intake rate to the values of *(a) PROB*, the probability that a mussel encountered by an Oystercatcher will be successfully attacked and *(b)* P_S, the delay imposed on searching by making an unsuccessful short peck. The results from stabbing birds on six mussel beds are shown. The symbols show the outputs when the current model parameter values (shown by the asterisk) are increased or decreased by one or two orders of magnitude.

Table 3.2.3 The sensitivity of the model predictions to the values of the main time-cost parameters. The values show the effect on predicted intake rate and the mean length of the mussels taken by Oystercatchers of increasing or decreasing the parameter value by one order of magnitude above or below, respectively, its current value in the model. In the case of intake rate, for example, the value of 914mg is the average difference between the predicted intake rates when the parameter PROB was decreased or increased by one order of magnitude of the value used in the model in each site. The predictions are averaged for six mussel beds and for dorsal hammerers and stabbing Oystercatchers. Full descriptions of what the parameters represent are in the text.

	Mean difference between maximum and minimum	
Parameter	intake rate (mg/300s)	mussel length (mm)
PROB	914	8.05
S	912	7.80
PM	619	7.15
bHT	546	1.10
P_E	531	6.40
P_L	189	1.95
F_L	173	2.10
cdi	15	0.05
bWHT	9	0.05
aWHT	2	0.00

These results suggest that the first step in investigating why Dutch birds had higher intake rates than predicted by the model is to compare the rates of encounter with mussels of Dutch and Exe estuary birds. It seems unlikely that Dutch birds search much faster than Exe birds because the rates of search measured by Cayford & Goss-Custard (1990) on the Exe are similar to those recorded by Meire & Erwynck (1986) in the Dutch Delta, being 0.083 and 0.085 m/s, respectively. So perhaps mussels are more visible or a greater proportion is available on Dutch mussel beds than on those of the Exe. Alternatively, Dutch birds may have lower time costs by, for example, making fewer unsuccessful pecks. Further field studies comparing the foraging of Oystercatchers within the UK and in other european countries are needed if the cause of the difference is to be established.

Despite the failure of the model to predict the observed intake rates in the Dutch sites, the successful testing of its predictions for 14 site/occasions on the Exe estuary suggested that it captured the main features of the birds' foraging behaviour on that estuary at least. The equations relating *PROB* to the density of mussels >45mm long were therefore recalculated using all the estimates of *PROB* available from the Exe, except for two suspiciously high values that had been obtained very early in the study and not by us. The equations used to calculate *PROB* in the definitive model for stabbers (equation 3.2.17), dorsal hammerers (equation 3.2.18) and ventral hammerers (equation 3.2.19) from the expressions:

$$PROB = (0.056429)((D_{>45})^{-0.891031}) \qquad 3.2.17$$

$$PROB = (0.402582)((D_{>45})^{-1.139920}) \qquad 3.2.18$$

$$PROB = (0.791813)((D_{>45})^{-1.139920}) \qquad 3.2.19$$

where $D_{>45}$ is the density of mussels greater than 45mm in length.

3.2.1.4 Predicted functional response

In models that aim to predict the distribution of a foraging vertebrate over a spatially variable food supply, the change in intake rate with food abundance is adequately described by a simple functional response which relates intake rate to food density. In the case of Oystercatchers feeding on mussels, the most appropriate functional response would be one relating intake rate to the biomass density of large mussels (Goss-Custard et al. 1995c). However, this simple approach is not adequate for present purposes, for two reasons. First, it cannot predict the distribution of sizes - which has such important implications for the population dynamics of the prey - of the mussels that Oystercatchers take. Second, a given biomass density of mussels can lead to very different intake rates depending on whether the biomass is made up of large numbers of small mussels or a small number of large ones. This is illustrated in Figure 3.2.15 in which intake rates predicted by the model over a range of prey biomasses are compared for cases in which the prey population was dominated by either large or small mussels. The two responses are quite different, with a given prey biomass consisting of small mussels generally enabling Oystercatchers to obtain higher intake rates than on the same biomass consisting of large ones. In these circumstances, therefore, a simple functional response cannot even reliably predict mussel bed quality, and thus attractiveness, to the birds. For the purposes of predicting the responses of both Oystercatcher and mussel populations to changes in shellfishery management policy, a model of the kind developed here, which predicts both intake rates and the distribution of prey size classes taken over a wide range of prey population structures, is clearly required.

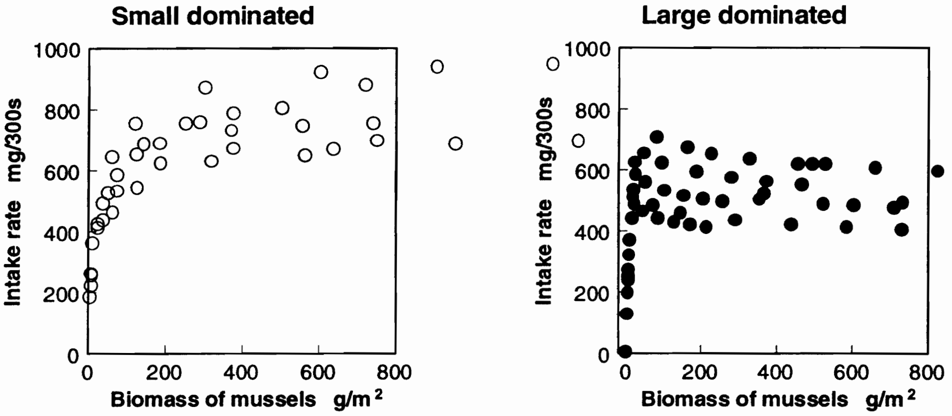


Figure 3.2.15 The functional response of dorsal hammerers as predicted by the model for sites where the mussel biomass is dominated by small mussels and sites where it is dominated by large ones.

Where the prey population is made up mainly of large mussels, the function shape in Figure 3.2.15 is apparently domed . This implies that, above a certain biomass density of mussels, intake rates fall, the trend being particularly evident in hammerers. This arises because the value of *PROB* apparently decreases disproportionately as the density of the larger mussels >45mm long increases (Figure 3.2.9). The reason is unclear, but perhaps Oystercatchers find it increasingly difficult to distinguish for perceptual reasons a vulnerable mussel when it is surrounded by high densities of other mussels. Alternatively, mussels may be relatively less available in sites with high prey biomass so that *PROB* takes a low value; indeed, this could be one of the reasons why the mussels are abundant in a particular site in the first place. There is some evidence for the second possibility because Goss-Custard *et al.* (1993) found that, on the Exe, mussels shells on the dorsal side are thicker where mussels are dense. However, there was no evidence that shells were also thicker on the ventral side and nothing is known about the effect of mussel density on the availability of mussels to stabbing birds. But whether intake rate declined at high prey biomasses for perceptual or prey availability reasons, it is a surprising result. It was therefore necessary to test whether this effect was a misleading property of the model itself or a feature of the real functional response of Oystercatchers feeding on mussels.

This was tested by plotting the observed values of intake rate for all the site/occasions in the present study, irrespective of whether the site contributed to the parameter values used in developing the model; the aim merely was to examine the shape of the functional response using all the data available (Figure 3.2.16). The relationship is negative in stabbers, although not obviously domed, whereas in dorsal and ventral hammerers combined, it is clearly domed. A second order polynomial, in which a dummy 0/1 (hammerers = 1) variable (FM) represents the feeding method, is highly significant, the expression being:

Intake rate =	358	+ 171.6FM	+ 1.20B	$- 0.0019B^2$
(S.E.	68	33.6	0.39	0.0005)
(P		<0.0001	< 0.005	<0.0001)

where B is the biomass density of mussels greater than 30mm long. The negative square term means that the intake rate of mussel-feeding Oystercatchers does indeed decline at high prey biomasses, as the model predicts. The successful testing of this unexpected prediction implies that this model is superior to an earlier and much simpler model which did not predict the decreased intake rates at high prey biomass beyond the empirical range of the data used to construct it (Goss-Custard *et al.* 1996f). While further research is required to find out why intake rate declines at high prey biomass, its prediction by the present simple version of the model raises further confidence in this model itself.

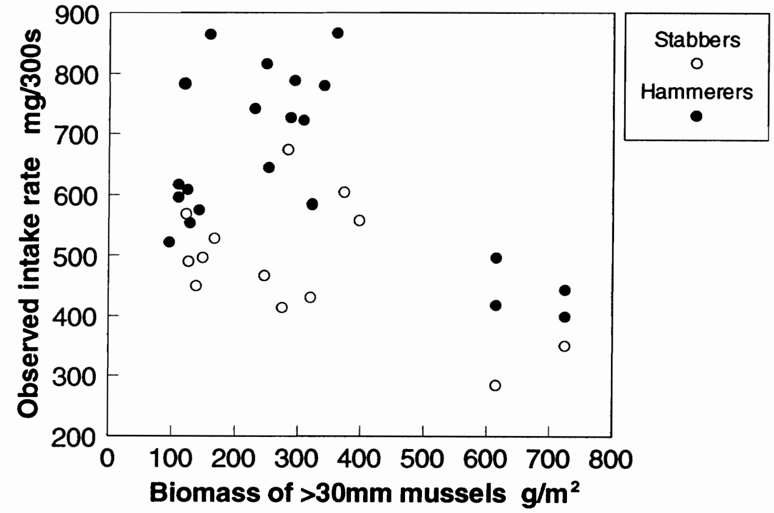


Figure 3.2.16 The functional response of hammering and stabbing Oystercatchers as measured in all the site/occasions in the present study.

3.2.2 Interference function

RA Stillman, J D Goss-Custard, R T Clarke & S E A le V dit Durell

3.2.2.1 Overview

Interference, the short-term reversible decline in intake rate due to the presence of competitors (Goss-Custard 1980; Sutherland 1983), is an important component of intraspecific competition in Oystercatchers (Ens & Cayford 1996) and one of the key factors thought to determine the distribution of foraging animals (e.g. Parker & Sutherland 1986; Holmgren 1995; Moody & Houston 1995). Two key components of interference are its strength, the proportional change in intake rate resulting from a proportional change in competitor density, and the shape of the interference function, the relationship between intake rate and competitor density. Most theoretical and empirical studies have quantified the strength of interference by using the model of Hassell & Varley (1969). This model makes no assumptions about the underlying causes of interference and has been criticised because it assumes that the strength of interference is constant across all competitor densities (Rogers & Hassell 1974; Beddington 1975). Recently, theoretical models based on forager behaviour and possible mechanisms of interference have provided an alternative method of modelling interference (Ruxton et al. 1992; Moody & Houston 1995). These models predict that the strength of interference will not be constant across all densities, but will increase with increasing density.

Previous models based on the Exe Estuary oystercatcher-mussel system have been successful in predicting in a qualitative way the distribution of feeding birds, but have not accurately predicted the quantitative distribution. With this in mind, and given the known importance of interference in determining forager distribution, it was decided that further work should be performed under the present contract in order to further refine the description of this relationship used in the shorebird-shellfish model. This analysis concentrated on accurately describing the shape of the interference function, and in particular testing the hypothesis that interference was insignificant or absent at low competitor densities, and only reduced intake rate to any extent above a threshold value. An extensive amount of suitable data have previously been collected on the Exe estuary, and so the analysis was based on these data rather than on any collected under the present contract. This section simply deals with the use of these data to parameterize the model but a full discussion of the results may be found in Stillman *et al.* (1996).

3.2.2.2 Field data

The field data were collected between October 1982 and March 1987 on mussel beds 4 and 26 of the Exe Estuary, England. Complete details of the field methods used to collect the data are in Goss-Custard & Durell (1987a, 1988) and so are not described in full here. Briefly, direct observation was used to record the number and length of the mussels ingested by a focal bird in 5 minutes of active foraging. From this, intake rate was calculated as the ash-free dry mass (AFDM) of mussel flesh consumed per unit time from a regression equation relating mussel length to AFDM obtained from a sample of mussels taken from bed 4 in 1983. As only one such relationship was used, these intake rates do not reflect the sometimes considerable changes in the flesh content of individual mussels that can take place over the autumn and winter and down the shore. In effect, a standardised measure of intake rate is used which can be thought of as representing the shell volume of the mussels consumed per unit time.

To measure the density of oystercatchers where a focal bird was foraging, mussel beds were marked out with a grid of 25x25m cells. The numbers of oystercatchers feeding in the same cell as the focal bird were recorded at the start and end of the 5min period, the mean density then being calculated and converted for analysis to number of competitors per hectare by multiplying by 16. The time of each record was also noted, both as the stage through the exposure period (minutes since the mussel bed first exposed) and time through the season (days since 1st August). Many of the observations were made on colour-ringed birds of known local dominance, defined as the percentage of encounters won, and so this variable was also available for some of the data.

3.2.2.3 General shape of the interference function

The main aim of the analysis was to find an equation that could accurately describe the shape of the interference function across the whole range of competitor densities observed in the field. In particular, a function was developed to show whether interference was absent, or had a negligible effect on intake rate, at low bird densities, and that interference only reduced intake rate at densities above a threshold value. The function used to model interference needed to provide an accurate description of the interference function and to contain as few parameters as possible. This aided interpretation of the results and increased the likelihood that the model parameter values could be estimated. The model of Hassell & Varley (1969) has been widely applied and has only two parameters and therefore, for consistency with previous studies and for simplicity, we extended this model to incorporate a threshold density below which interference is absent:

$$I = IFIR\left(\frac{D+1}{D_0+1}\right)^{-m} \qquad \text{if } D > D_0 \qquad 3.2.20$$

$$I = IFIR \qquad \text{if } D \le D_0$$

where I = intake rate (mg AFDM/5min), D = density of competitors (/ha), $IFIR$ = interference-free intake rate (mg AFDM/5min), D_0 = competitor density above which interference occurs (/ha) and m = interference coefficient. This model has three parameters, each influencing a different aspect of the interference function. The model has a threshold density, D_o, below which intake rate is independent of density, and above which intake rate is a direct function of density. Below the threshold density, intake rate is given by the interference-free intake rate, *IFIR*. Above this density, intake rate changes with increased density at a rate governed by the interference coefficient, m, with larger values of m indicating that intake rate is influenced to a greater extent by changes in competitor density. This model is almost certainly an oversimplification of the true shape of the interference function, but has the advantage of simplicity, aiding interpretation of results and parameter estimation, and contains only one additional parameter, D_0, to previous interference models.

Non-linear regression was used to fit Equation 1 to nine sub-sets of data in which, from previous work, interference was thought most likely to occur and which, therefore, provided the best chance of testing the hypothesis. These sub-sets were from both mussel beds and from birds of differing age and local dominance. They were also from birds using the three methods used by oystercatchers to break into mussels; stabbing between the valves or hammering a hole in either the dorsal or ventral shell. The estimated parameter values, together with their associated standard errors, are shown in Table 3.2.4.

In all sub-sets, the estimated values of the interference-free intake rates (IFIR) were, of course, significantly greater than zero ($p<0.01$). The values tended to be similar for ventral and dorsal hammerers feeding on the same bed (no significant differences between any paired data sub-sets ($p>0.05$)), but were lower in stabbers than in hammerers (two out of three stabber data sub-sets were lower than all hammerer sub-sets). In eight out of the nine data sub-sets, the estimated value of the interference coefficient (m) was significantly ($p<0.05$) greater than zero, indicating that intake rates were reduced at higher densities of competitors. In five data sub-sets, the threshold for interference (D_o) was significantly ($p<0.05$) greater than zero, indicating that interference only reduced intake rate above a critical density of competitors.

Although the estimated parameters were significant in a majority of the nine data sub-sets, they were not all significant and there was no obvious pattern in significance levels across the sub-sets. For example, D_0 was not significant in dominant ventral hammerers on bed 4, but was in sub-dominant ventral hammerers on the same bed, whereas the reverse was found in dorsal hammerers on bed 26. Oystercatcher intake rates over short feeding periods are highly variable, and very large sample sizes are sometimes required to detect trends. Despite the risk of including birds that were not actually subject to interference, the data from all birds studied over the five years were combined to increase sample size. A previous study using part of the data set (Goss-Custard & Durell 1988) showed that m and IFIR were similar in dorsal and ventral hammerers and that both differed between hammerers and stabbing birds. Therefore, the data were combined into a hammerer and a stabber group, giving very large sample sizes (see combined results in Table 3.2.4).

All three parameter estimates were now highly significant ($p<0.01$) in both data sets, and the fitted functions showed a very close agreement with grouped mean data (Figure 3.2.17). With both axes plotted on log scales, a very clear linear relationship was revealed at competitor densities above the threshold for interference (Figure 3.2.17). The significance of the parameter values estimated from a majority of the data subsets and from the combined data sets, along with the close fit to grouped mean data, suggested that the threshold model provides a good description of the form of the interference function and that a threshold density for interference exists in both feeding methods. Moreover, the threshold density for interference is higher for stabbers (278 vs. 53 competitors/ha) but once interference starts it is more intense (i.e. larger value of m) for stabbers (Figure 3.2.17).

Table 3.2.4 Parameter values obtained using non-linear regression to fit Equation 1 to different sub-sets of the data collected on hammering and stabbing oystercatchers on beds 4 and 26. The table shows for each data set the estimated parameter values and associated asymptotic standard errors.

(a) Hammerers

Data set description	Sample size	Parameters *IFIR*	D_o	*m*
Marked bed 4 sub-dominant dorsal hammerers	348	677.4±29.2**	61.7±13.1**	0.480±0.131**
Marked bed 4 dominant dorsal hammerers	413	673.6±36.2**	50.0±24.3*	0.180±0.055**
Marked bed 4 sub-dominant ventral hammerers	385	630.8±30.6**	105.1±27.4**	0.390±0.111**
Marked bed 4 dominant ventral hammerers	393	610.6±50.3**	34.8±44.7	0.107±0.038*
Marked bed 26 sub-dominant dorsal hammerers	128	785.2±203.0**	1.4±5.7	0.140±0.063*
Marked bed 26 dominant dorsal hammerers	188	509.2±35.4**	52.5±17.6**	0.448±0.171**
All hammerers combined	2176	637.6±14.1**	52.8±9.6**	0.221±0.029**

(b) Stabbers

Data set description	Sample size	Parameters *IFIR*	D_o	*m*
Unmarked bed 4 juvenile stabbers in winter	241	603.1±146.0**	3.6±8.3	0.167±0.076*
Unmarked bed 4 adult stabbers in winter	241	457.7±28.3**	142.9±91.8	0.508±0.337
Marked bed 4 sub-dominant stabbers	451	467.1±19.8**	164.8±57.2**	0.506±0.095**
All stabbers combined	2749	473.9±8.3**	277.7±84.8**	0.352±0.130**

* $p<0.05$ ** $p<0.01$

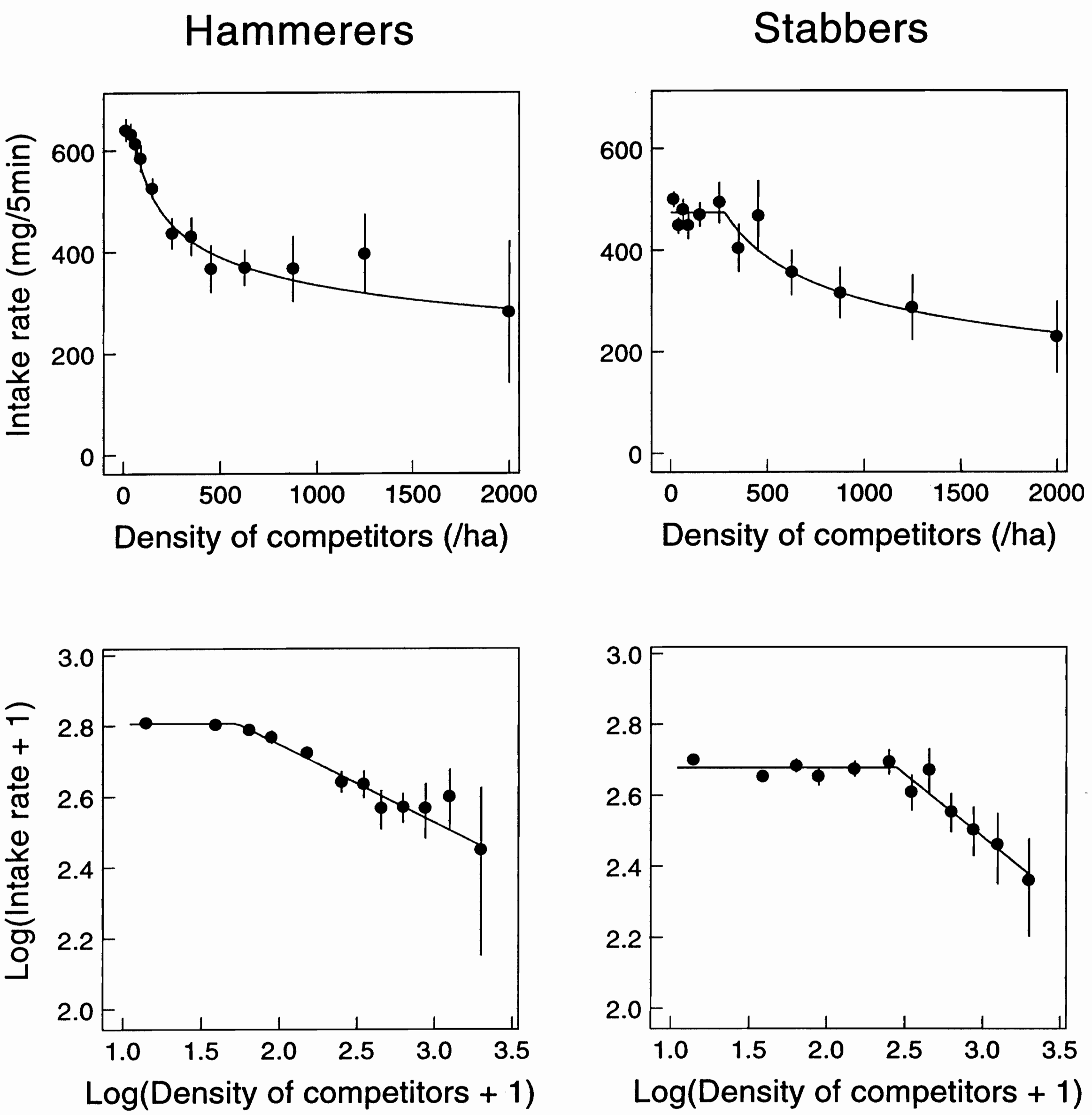


Figure 3.2.17 Interference functions for hammering and stabbing oystercatchers obtained using all data collected on beds 4 and 26. The top figures show the relationships on arithmetic axes and the bottom figures the same relationships on logarithmic axes. The lines show the predicted values of intake rate obtained using Equation 1 with the parameter values given in Table 3.2.4. Observations have been grouped by density of competitors with mean intake rate ± standard errors shown.

3.2.2.4 Individual variation in the interference function

The influence of the local dominance of individual birds on model parameters was investigated using all data collected on marked birds for which local dominance had been estimated. This comprised 13 dorsal hammerers, 12 ventral hammerers and 15 stabbers from bed 4 and 6 dorsal hammerers and 6 stabbers from bed 26. As the results from bed 4 and 26 were rather similar using the threshold model, data from these two beds were combined. This left two data sets of 31 hammering and 21 stabbing individuals.

Interference-free intake rate (IFIR): The influence of local dominance on IFIR was studied without the use of the model by simply calculating the intake rates of individual birds at low competitor densities. Previously, IFIR had been calculated at densities <100 birds/ha (Goss-Custard & Durell 1988), but as threshold densities for interference were often lower than this (Table 3.2.4), we used a lower threshold density in the present study. The lowest density below which IFIR could be reliably calculated across all individuals was found by calculating the IFIR for each bird, first in the absence of competitors, and then at successively higher competitor densities, increasing by steps of 16 birds/ha, or one bird per 25x25m cell. At each stage, the number of data points available to calculate IFIR for each bird was noted. A cut-off density of 64 birds/ha allowed IFIR to be calculated with at least 11 records (mean=28) for all but four birds (3, 6, 7 and 9 records) and yet did not allow competitors to influence by much the intake rates of those individuals whose thresholds for interference were circa 50 birds/ha. For all individuals, IFIR was therefore calculated from all records collected at competitor densities of less than or equal to 64 birds/ha.

Linear regression showed that IFIR was not associated with local dominance (L) in either hammerers (IFIR=644.7(±36.5)-0.237(±0.533)L; r^2=0.0%; p>0.5) or stabbers (IFIR=454.0(±25.6)-0.594(±0.478)L; r^2=0.2%; p>0.2). However, analysis of variance revealed significant differences in the values of IFIR for individual hammerers (F=1.65; df=30,723; p<0.05) and stabbers (F=1.86; df=20,669; p<0.05). For subsequent analysis, the values of IFIR measured in each bird were therefore included in the model to allow for the differing interference-free intake rate of individuals; this effectively scaled each record of a bird's intake rate by its interference-free intake rate. The interference model for marked birds was now re-defined as.

$$I = IFIR_i \left(\frac{D + 1}{D_0 + 1} \right)^{-m} \qquad \text{if } D > D_0 \qquad 3.2.21$$

$$I = IFIR_i \qquad \text{if } D \le D_0$$

where $IFIR_i$ = $IFIR$ of the ith bird estimated as its mean intake rate at densities ≤ 64 birds/ha. This equation is a simple extension of Equation 1 in which only the values of m and D_o are unknown.

Interference parameters, m and D_0: Previous studies of the influence of local dominance on interference have fitted separate interference functions, of various forms but all without a threshold for interference, to the data from individual birds and then regressed model parameter estimates against local dominance (Goss-Custard & Durell 1988; Goss-Custard *et al.* 1995). This could not be done with our threshold model because, in some individuals, intake rate did not change with competitor density, preventing D_o from being estimated. Instead, a single model was built that simultaneously incorporated the influence of competitor density and local dominance on intake rate.

The relationship between local dominance and the interference coefficient was studied by making its value dependent on a linear function of local dominance.

$$I = IFIR_i \left(\frac{D + 1}{D_0 + 1} \right)^{-(m_0 + m_1 L)} \qquad \text{if } D > D_0 \qquad 3.2.22$$

$$I = IFIR_i \qquad \text{if } D \le D_0$$

where L = Local dominance (% of encounters won), m_0 = Interference coefficient of birds with zero local dominance and m_1 = Rate of decline of interference coefficient with increasing local dominance. This equation is able to generate a range of interference functions for birds of differing local dominance. The interference coefficient, m, for birds of zero local dominance is given by m_o, and changes for birds of greater dominance at a rate determined by m_1. Negative values of m_1 mean that birds of higher dominance are less influenced by interference (as they will have lower values of m), and a zero value means that susceptibility to interference is unrelated to dominance.

The parameter values were estimated as above and are shown in Table 3.2.5. The values of D_o exceeded zero in both cases ($p<0.01$), with the value in stabbers being three times greater than in hammerers. In both hammerers and stabbers, m_0 was significantly greater than zero and m_1 significantly less than zero. Therefore, in both feeding method groups, birds with zero local dominance were more susceptible to interference than were those of higher dominance. This is illustrated in Figure 3.2.18 where the interference functions generated by Equation 3, and their fit to grouped mean data, are shown. The figure shows that the influence of local dominance on susceptibility to interference was much smaller in hammerers than in stabbers; indeed, in stabbers, the intake rates of highly dominant birds actually increased with increasing competitor density. In hammerers, values of the interference coefficient ranged from 0.29 for birds of 0% local dominance to 0.16 for those of 100% local dominance. The equivalent values in stabbers were 0.44 for the least dominant birds and -0.28 for the most dominant.

This procedure was repeated for the threshold for interference, D_0, by making its value dependant on a linear function of local dominance and making the interference coefficient independent of local dominance. No association was found between D_0 and local dominance. We conclude that local dominance influenced the coefficient of interference, m, in both feeding methods but did not affect the threshold density at which interference began. In view of the significant influence of local dominance on m, Equation 3 was used as the basis of subsequent analysis.

Table 3.2.5 Parameter values obtained by using non-linear regression to fit Equation 3 to all data collected on marked hammering and stabbing oystercatchers of known local dominance on beds 4 and 26. The table shows the estimated parameter values and associated asymptotic standard errors for each feeding method. The fitted relationships are shown graphically in Figure 3.2.18.

	Sample size	Parameters		
Feeding method		D_0	m_0	m_1
Hammerers	1855	50.1±8.4**	0.285±0.053**	-0.00127±0.00049*
Stabbers	1246	158.0±62.2**	0.437±0.199*	-0.00721±0.00302*

* p<0.05 ** p<0.01

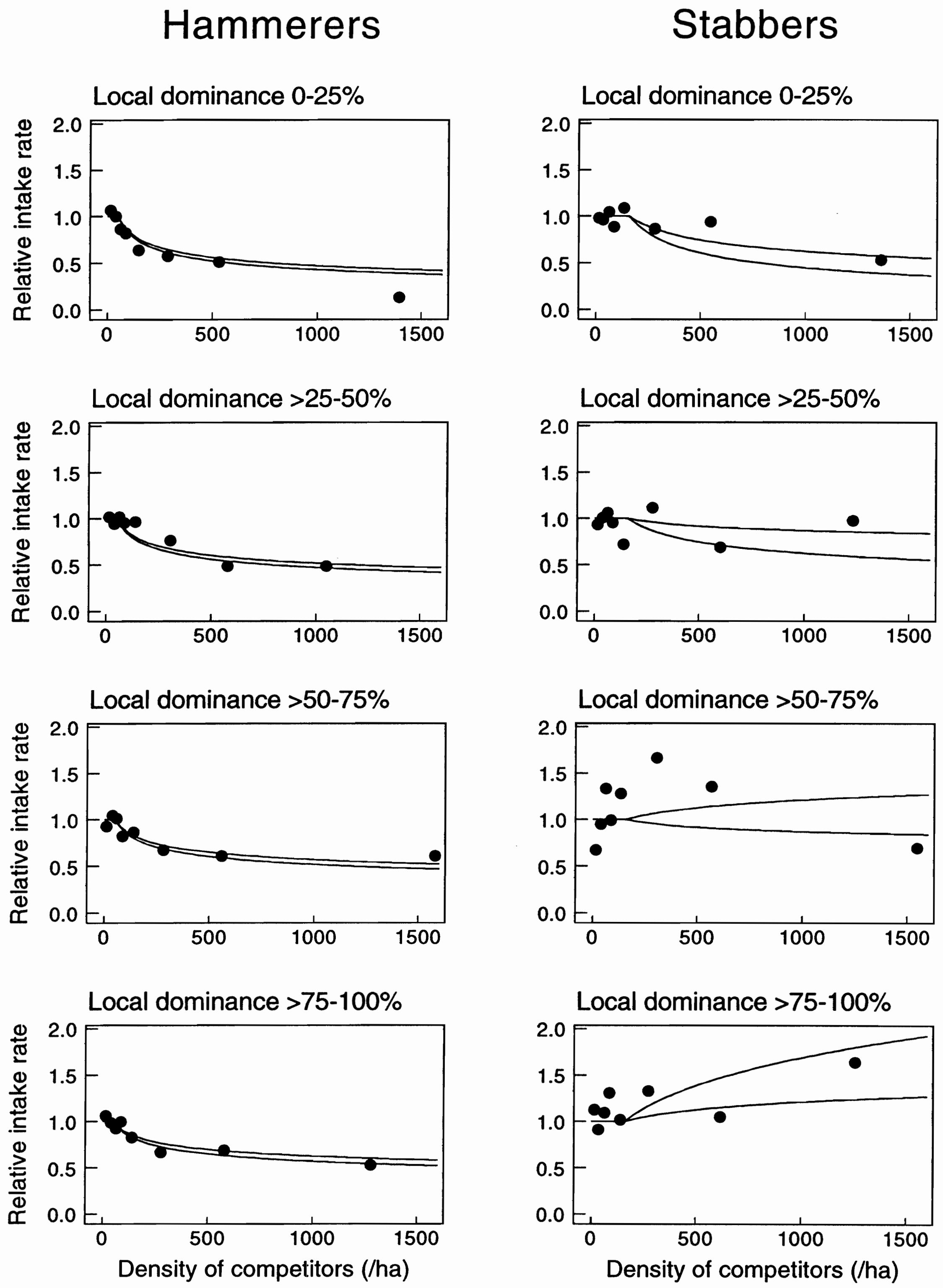


Figure 3.2.18 Interference functions for hammering and stabbing oystercatchers of differing local dominance obtained using all data collected on marked birds. Relative intake rate is the ratio of a birds intake rate and its interference-free intake rate (i.e. $I / IFIR_i$ from Equation 3). The lines show the values predicted from Equation 3 using the parameter values given in Table 3.2.5. In each case, the upper line shows the relationship for the upper end of the local dominance range being used and the lower line the relationship for the lower end of the range. Observations have been grouped by density of competitors with mean intake rate shown.

3.2.2.5 Influence of the feeding conditions

As shown in an experimental field test by Dolman (1995), food abundance, and so the general feeding conditions, can affect the average level of interference amongst competitors. For example, it may only be profitable for dominant birds to steal from sub-dominants when food is scarce. Similarly, birds which have obtained most of their energy requirements may be less likely than birds which are hungry to risk making attacks against others. In either case, the general level of interference might be expected to increase as the feeding conditions deteriorate.

In the present study, factors likely to affect the overall level of interference are the energetic status of the birds and the biomass density of the food supply. Both of these are likely to change through the tidal exposure period and with season. The cumulative food consumption increases over the exposure period so that, by the time the mussel beds are being covered by the advancing tide, most birds will have obtained most or all of their requirements. At the same time, the mussels accessible late in the exposure period are often small and contain low amounts of flesh (Goss-Custard et al. 1993). We might therefore expect oystercatchers to be less aggressive late in the exposure period, with a consequent reduction in the overall levels of interference. Seasonally, the biomass density of mussels decreases by some 30-40% over autumn and winter due to both a decline in the density of mussels and a fall in the flesh content of individual mussels (J.D. Goss-Custard, unpublished information) while the energetic requirements of the birds increase as the weather deteriorates. We might therefore expect competition to intensify over the autumn and winter and interference to increase.

The parameters of the threshold interference model were therefore thought likely to vary both within one day in relation to the time since the mussel bed was first exposed and, perhaps more probably, with the number days elapsed since August 1st. Linear regression was used to study the relationships between the residual intake rates obtained after fitting Equation 3 and both these temporal variables. Two sets of regressions were performed. One used data collected at densities below the estimated thresholds for interference (Table 3.2.6a) to test for any influence of tidal exposure time and season on standardised IFIR. The second used data obtained at densities above the estimated interference thresholds (Table 3.2.6b) to test for the influence of tide and season in situations where there is interference.

In neither feeding method were any significant associations found between residual standardised intake rates at low densities and either tidal exposure time or season. As the intake rate at low densities of competitors did not change with tide or season, any associations between these variables and intake rate at densities greater than the threshold must have been due to increased interference alone. For hammerers, the residual intake rates at competitor densities above the interference threshold were positively associated with time since first exposure and negatively associated with time through the season. For stabbers, there was again a negative association with season but no significant association with tidal exposure. These results show that for both feeding methods the model underestimated intake rates early in the season and overestimated intake rates late in the season. In hammerers, intake rates were overestimated early in the exposure period and underestimated later in the exposure period. As the influence of these variables on IFIR can be discounted, the results imply that interference decreased during the exposure period in hammerers and increased through autumn and winter in both feeding methods confirming the trend found earlier in stabbers alone (Goss-Custard & Durell 1987a). The results were unchanged when the two variables were used in combination, indicating that there was no interaction between them.

Table 3.2.6 Linear regression of the residual intake rate obtained after fitting Equation 3 to data on marked hammering and stabbing oystercatchers on beds 4 and 26 against tidal and seasonal variables. Two sets of regressions were performed for data collected at densities either (a) below the threshold for interference or (b) above the threshold for interference. The parameter estimates for Equation 3 from which residual intake rates were calculated are given in Table 3.2.5.

(a) Density less than or equal to threshold for interference

Feeding method	Variable	Sample size	Intercept	Coefficient
Hammerers	Time since first exposure	599	-68.8±43.5	0.435±0.244
	Days since 1st August	599	-4.9±40.2	0.067±0.314
Stabbers	Time since first exposure	1011	-0.3±25.3	0.025±0.146
	Days since 1st August	1011	30.1±29.2	-0.214±0.217

(b) Density greater than threshold for interference

Feeding method	Variable	Sample size	Intercept	Coefficient
Hammerers	Time since first exposure	1256	-78.4±20.1**	0.512±0.113**
	Days since 1st August	1256	64.7±25.9*	-0.621±0.223**
Stabbers	Time since first exposure	235	18.2±33.5	0.093±0.181
	Days since 1st August	235	144.0±56.2*	-1.052±0.476*

* $p<0.05$ ** $p<0.01$

3.2.2.6 Interference parameters used in shorebird-shellfish model

The main results of the analysis can be summarised as follows: (1) the threshold model provides a suitable description of the shape of the interference function; (2) interference parameters differ between hammerers and stabbers; (3) the intensity of interference above the threshold is related to a birds local dominance; and (4) the strength of interference is related to the tidal stage in hammerers and season in both feeding methods. Given the importance of interference in determining distribution, it was decided to incorporate into the shorebird-shellfish model as many of these features as possible. In the model, interference is incorporated using Equation 3, with the parameter values given in Table 3.2.5, and *IFIR* calculated from section 3.2.1. Therefore, a threshold for interference is incorporated, susceptibility to interference differs between feeding methods and with local dominance. Changes in the strength of interference during the season are incorporated by adjusting the reduction in intake rate according to the stage of the season using the parameter values in Table 3.2.6b. The shorebird-shellfish model does not incorporate in detail the change in conditions during low tide periods (tidal conditions are assumed to remain constant within a tidal stage), and so the change in interference during the low tide period is not included. One other aspect of interference was incorporated into the model based on a previous study (Goss-Custard & Durell 1988) which suggested that interference in juvenile oystercatchers operated at very low competitor densities. Based on this evidence, the model only incorporated the threshold for interference calculated above in birds older than 2 years; younger birds had a threshold of zero.

3.3 OYSTERCATCHERS AND COCKLES

Ken Norris & Ian Johnstone

3.3.1 Functional response

3.3.1.1 General background

The functional response describes the energy intake rate of a predator in relation to prey density (Holling 1959). This relationship is ecologically very important because it not only describes constraints on the intake rate of the predator as a function of prey density, but also provides a basis for understanding the spatial and temporal dispersion of a predator across a gradient of prey densities (Sutherland 1983; Sutherland & Parker 1985; Parker & Sutherland 1986), and, ultimately, the population dynamic consequences of predation, for both predators and prey (Bernstein *et al.* 1991; Sutherland & Dolman 1994). It is clear, therefore, that an understanding of the functional response is pivotal to understanding how the intake rate of birds dependent on shellfish populations for food might be affected if prey densities are reduced by fishing.

Many theoretical models of the functional response assume that the predator's intake rate increases in relation to prey density, but decelerates to an asymptote (see above and references cited therein). This, so called, type II functional response (Holling 1959) can be described by a simplified version of Holling's disc equation:

$$\frac{N}{T} = \frac{\lambda}{1 + \lambda h} \qquad 3.3.1$$

where N = number of prey taken, T = time predator and prey exposed to one another, h = handling time, and λ = encounter rate with prey.

This simple model assumes that predators take every prey item they encounter, and that all prey are identical in their energy value and time taken to handle an individual item. However, in the wild, predators are usually faced with a range of possible prey items which vary in their profitability (ie. energy gained per unit time spent handling prey). These might include alternative prey species, or different size classes of prey within the same prey population, for example. Under these circumstances, the functional response can be described using a multiple-prey version of the disc equation developed by Charnov (1976). If there are i prey types, the energy intake rate of the predator (E/T) can be described as:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i Q_i}{1 + \sum \lambda_i h_i Q_i} \qquad 3.3.2$$

where E_i = energy content of prey type i, h_i = handling time of prey type i, λ_i = encounter rate with prey type i, and Q_i = probability that a predator would take an individual of prey type i after it is encountered. Charnov (1976) showed that to maximize energy intake, $Q_i = 1$ if $E/T > E_i/h_i$ and $Q_i = 0$ if $E/T < E_i/h_i$, so a predator should take an individual of prey type i if its profitability (E_i/h_i) is above E/T, and ignore it if its profitability is less than this value. If a predator could consume a range of prey types which differ in their profitability, Charnov's (1976) model describes the exact conditions under which prey type i should be included in the predator's diet. In this way, the model not only provides a quantitative basis for describing prey choice by the predator which would maximize its rate of energy intake, but also describes the range of energy intake rates achievable by feeding in different patches of prey, which themselves consist of different prey densities and prey types.

Many wading birds (*Charadrii*) feeding on intertidal invertebrates during winter frequently have to decide whether or not to consume a particular prey species or size class of prey. A number of studies have shown that birds generally take the energetically most profitable prey available (Goss-Custard 1977; Sutherland 1982a; Wanink & Zwarts 1985; Meire & Ervynck 1986; Boates & Goss-Custard 1989; Cayford & Goss-Custard 1990; Zwarts & Blomert 1993). Furthermore, some of these studies used Charnov's (1976) model to predict the optimal prey choice for a bird attempting to maximize its energy intake rate (eg. Wanink & Zwarts 1985; Meire & Ervynck 1986; Cayford & Goss-Custard 1990), and found that most prey consumed by the birds consisted of prey types which the model predicted they should select. However, very few studies have quantified encounter rates with different prey types directly (but see Wanink & Zwarts 1985; Piersma *et al.* 1995). Instead, encounter rates are usually estimated by assuming that λ_i in eq.(2) is a particular function of prey density and searching speed (eg. Thompson 1983; Ward 1993). As pointed out by Wanink & Zwarts (1985), this means that the functional response cannot be predicted quantitatively, even though it is possible to use Charnov's model in this way to assess the *relative* benefits of different prey choice decisions.

Oystercatchers (*Haematopus ostralegus*) feed on a range of bivalves, of which the most important are cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*). Birds consume the soft parts of these prey, and open them by either hammering a hole in the shell ('hammerers') or stabbing their bill between the valves to sever the adductor muscles ('stabbers'). Individuals usually specialize in one feeding method (Swennen *et al.* 1983). The objective of section 3.3.1 is to describe the functional response of oystercatchers feeding on cockles using Charnov's model. To do this, we used the model to address two specific issues: (1) the size classes of cockle oystercatchers select to maximize their energy intake rate using a model of relative encounter rates (section 3.3.1.3), and (2) the development of models which predict the rate at which birds encounter cockles of different size, in relation to their searching strategy, and hence provide a description of how energy intake rates vary in relation to the density of different size classes available to the birds (section 3.3.1.4).

Charnov's (1976) model rests on a number of assumptions which are generally applicable to oystercatchers feeding on bivalves (see Meire & Ervynck 1986), with the exception that prey are assumed to be recognised instantaneously and without error. Oystercatchers do waste time handling prey which they subsequently fail to open (Meire & Ervynck 1986; Cayford & Goss-Custard 1990), so we used an extension of eq.(2) to describe the functional response, developed by Meire & Ervynck (1986), to include this additional time cost, which gives *E/T* as:

$$\frac{E}{T} = \frac{\sum E_i \lambda_i P_i}{1 + \sum \lambda_i (h_i P_i + (1 - P_i) wh_i)} \qquad 3.3.3$$

where wh_i is the time wasted handling a cockle of size i which the bird fails to open, and P_i is the probability that a cockle of size i attacked by a bird will be successfully opened. All other symbols are as defined in eq.(2).

3.3.1.2 Methods

Study site: We studied oystercatchers wintering in the Burry Inlet (51-39°N, 4-10°S) South Wales, during the 1994/95 and 1995/96 winters. The intertidal area of this estuary covers c.6,500 ha, consisting primarily of intertidal sandflats and saltmarsh. The invertebrate fauna of the sandflats is dominated by cockles. The cockle population supports several thousand oystercatchers each winter (see Davidson 1967; Horwood & Goss-Custard 1977), and a commercial cockle fishery throughout the year (Franklin 1976). The estuary is described in detail by Hancock & Urquhart (1966) and Nelson-Smith & Bridges (1976).

We established a number of 20x20m study plots (n = 23) on the sandflats on the south shore of the estuary. These plots were located in areas which were used by feeding oystercatchers, but were also located so as to include a range of shore heights and sediment types in our observations. Most plots were present throughout the winter, although 7 plots were established during late winter (ie. after 16th December) in areas which were used by birds after the removal of fine sediment during winter storms. In addition, we located a number of posts (n = 7) in the sand which were used as reference markers for observations of feeding birds and cockle samples in areas where the topography made the use of a 20x20m plot difficult.

Foraging observations: A vehicle located 100-200m from study plots or reference markers was used as a hide for all observations. Cockle fishermen use tractors and 4x4 vehicles to travel to and from the cockle beds, so oystercatchers regularly encounter vehicles on the sandflats. Observations were made throughout the ebb and flood tide periods, when oystercatchers fed on the cockle beds, using a x60 magnification zoom telescope. Around low tide birds roosted on sand banks adjacent to the river channel. Observations were made of adult (>4 years old) and immature (2-4 years old) birds, distinguished by bill, eye and leg colour (Goss-Custard *et al.* 1982).

Oystercatchers opened cockles by either stabbing their bill between the valves to sever the adductor muscles ('stabbers') or by hammering a hole in the shell ('hammerers'). An individual bird employed only one of these feeding methods during an observation session. Stabbers appeared to search visually for cockles, whereas hammerers searched by 'sewing' (ie. locating buried cockles by touch using rapid sewing movements with the bill in the substrate) on ebb tides and 'probing' (ie. walking slowly while occasionally inserting the bill into the substrate) on flood tides. Individual hammerers did switch between searching methods during an observation session on occasions, but the predominant method used depended on the state of the tide (see section 3.4.1.4.2).

During foraging observations a focal bird was located at random and followed for 268.5 ± 2.03 s on average (range: 155.5 to 367 s, n = 254). This observation period is smaller than used for comparable studies on oystercatchers feeding on mussels (see Meire & Ervynck 1986; Cayford & Goss-Custard 1990), but was necessary because birds frequently left individual study plots. Nevertheless, we obtained data on a reasonable sample of cockles taken by each bird observed (mean ± SE: 10.1 ± 0.32 cockles per bird, range = 2 to 26).

Having located a focal bird a continuous sequence of behaviour was recorded by one of us (IJ) using time-event logging software (Stirling Microsystems, University of Stirling), running on a Psion Organizer, from which the following information was subsequently extracted.
(1) Feeding method: either stabber or hammerer.
(2) Searching method for each bout of searching behaviour: visually for stabbers, and either sewing or probing for hammerers.
(3) Length of each cockle attacked: this was estimated as a percentage of bill-length divided into discrete classes (ie. 0-10%, 10-20%, 20-30%, 30-40%, 40-50%), and later converted into size classes by using the mean bill-length of a sample of oystercatchers caught for banding in the Burry Inlet during winter (73.4mm ± 4.79, n = 120) (ie. 0-7mm, 7-15mm, 15-22mm, 22-29mm, 29mm+). In some cases the size of the cockle could not be assessed because cockles <15mm in length attacked by hammerers were sometimes opened in the substrate, or lifted from the sand but opened without being carried. In these cases the size class was recorded as unknown, and are referred to as 'not carried' hereafter.
(4) Handling time: the time between the first stab or blow to a cockle and the swallowing of the last piece of cockle flesh.
(5) Waste handling time: the time between the first stab or blow to a cockle and the rejection of the cockle by the bird having failed to open it.
(6) Whether or not a particular cockle was successfully opened.
(7) Length of each searching bout, for each searching method.
(8) Number of pecks made per searching bout for hammerers searching by probing and for stabbers.
(9) Other activities, which included preening, resting, displaying or fighting.

Searching speeds were calculated for stabbers, and for hammerers using each searching method (ie. sewing or probing), by measuring the time it took a bird to walk a specified distance across the sandflats. This was achieved by locating small bamboo canes in the sand every 10 cm along the edge of several study plots, and measuring the time taken and distance covered by a bird while walking parallel to the line of canes.

Cockles: We estimated the density of cockles in each size class present in the sand during a 2-3 day period ('sampling period') approximately every spring-spring tidal cycle throughout the winter, starting in September, 1994 and ending in March, 1995. Within each sampling period we sampled cockles within each study plot and within 15m of each reference marker using a 0.10m quadrat. Three quadrats were taken from each study plot or reference marker. All the sand was removed to a depth of 5cm from within each quadrat, sieved using a 4mm mesh size, and the number of cockles present in each size class subsequently counted.

Samples of cockles from a number of the study plots were retained to determine ash-free dry mass (AFDM) and frozen within 24 hours of being removed from the substrate. AFDM was determined by removing the partly thawed cockle flesh from the shell and placing it in a crucible, drying it to a constant mass (measured to an accuracy of 0.0001g), reducing it to ashes in a muffle furnace at 550°C and reweighing it. AFDM was then calculated as the dry mass minus the ash mass.

Prey remains: To quantify the sizes of cockles taken by oystercatchers independently of the foraging observations, we collected a sample of opened shells during each cockle sampling period, from each study plot and reference marker. To collect opened shells we walked a standard route within 1 m of each plot boundary, or at a radius of 15 m from each reference marker, and collected all opened shells we encountered. Cockles opened by oystercatchers during a particular low water period can be easily identified. Hammerers break one of the valves when opening a cockle, so remains consist of an intact and shattered valve, with some flesh remaining in the shell at the adductor muscle scars. Prey remains from stabbers consist of two intact valves, again with some flesh remaining in the shell at the muscle scars. For analysis of size selection, the mean size consumed by hammerers and stabbers was calculated for each spring-neap or neap-spring tidal cycle throughout the winter. Mean sizes were estimated as the product of the relative frequency of size *i* in the prey remains and its size class measured as an integer value between 1 (0-7mm cockles) and 5 (29mm+ cockles), summed across all size classes.

Availability of cockles to birds: Oystercatchers which hammer open mussels select thin-shelled individuals (Durell & Goss-Custard 1984; Meire & Ervynck 1986; Sutherland & Ens 1987; Cayford & Goss-Custard 1990). To assess whether hammerers feeding on cockles showed the same preference we measured the shell mass to the nearest 0.1g of cockles opened by hammerers during each cockle sampling period. Shell mass was measured rather than shell thickness because the curvature of cockle valves and their ridged surface made repeatable measures of shell thickness virtually impossible. To obtain a random sample of shell masses present in the sand we measured the shell masses of unopened cockles from the same size classes opened by hammerers, using the sample of cockles collected to estimate the AFDM of cockle flesh (see above).

3.3.1.3 Size selection

Data analysis: Estimates of cockle size in relation to bill-length are prone to error. To quantify such error we conducted two trials during the winter, in December 1994 and March 1995, in which a sample of cockles of known size (n = 50) were presented for 1 sec at the bill of a life-sized model of an oystercatcher's head, under field conditions (ie. using a telescope at distances of 100-200m between the observer and subject bird). The size of each cockle presented was estimated as a percentage of bill-length, and subsequently converted into a size class (see above). The probability of a cockle estimated to be size *i* actually being the same or a different size class is shown in Table 3.3.1.

To develop parameters for the optimality model from the field data we wished to generate statistical models which described each parameter in the model as a function of cockle size, and other potentially important factors such as feeding method, time during the winter or time during each high water-high water tidal cycle. Such functions could be biased as a result of error in the size estimates made in the field. To circumvent this problem the number of cockles in each size class observed being attacked and consumed by oystercatchers were adjusted for error as shown in Table 3.3.1. For analysis of handling and waste handling times the data from each size class were weighted by the probability that a cockle estimated to be size class *i* was actually size class *i* (ie. using the probabilities shown in bold type in Table 3.3.1). This meant that handling and waste handling times from size classes whose size were estimated accurately had greater influence than data from size classes whose size was estimated less accurately. We considered this approach preferable to using regression models of estimated and actual size to correct for error (see Goss-Custard *et al.* 1987; Meire & Ervnyck 1986; Cayford & Goss-Custard 1990), since the frequency of each size class in the data varied between statistical models and hence the influence of observer error on any fitted function was not constant. All reported analyses used the probabilities from the December 1994 trial, since the results were similar regardless of which set of probabilities were used. Despite these adjustments, the results reported below were similar if the raw handling and waste handling time data were used.

To generate statistical models which described the parameters in Charnov's model, we first constructed simple ANCOVAs which described each parameter in Charnov's model as a function of cockle size and feeding method, assuming a common slope for each feeding method. We then additionally tested whether the rate of change in each parameter with cockle size was similar for birds using each feeding method. For handling and waste handling times, we calculated a mean value for each size class taken by an individual bird during an observation session, and used these means in the ANCOVAs. We then tested whether a simple model containing cockle size class was sufficient, by additionally fitting terms which described the season (ie. winter day, 1st September = 1), and time during each tidal cycle (ie. time after high water), separately for each feeding method. Cockle size class was included in these models as an integer value, ranging from 1 (0-7mm) to 5 (29mm+). These statistical models were then used as the basis for solving eq.(3).

Table 3.3.1 Probability of cockle estimated to be size *i* actually belonging to each size class. Data are based on the trial conducted during December 1994, using a sample of 50 cockles of known size, randomly presented for 1 s at the bill of a life-sized model of an oystercatcher's head to an observer at distances of 100 and 200m. The probability of a cockle of size class *i* being correctly estimated as size class *i* is shown in bold type.

Observer distance = 100m

	Actual size class			
Estimated size class	7-15mm	15-22mm	22-29mm	29mm+
7-15mm	**0.4**	0.57	0.03	0
15-22mm	0	**0.19**	0.81	0
22-29mm	0	0	**0.94**	0.06
29mm+	0	0	0.5	**0.5**

Observer distance = 200m

	Actual size class			
Estimated size class	7-15mm	15-22mm	22-29mm	29mm+
7-15mm	**0.37**	0.58	0.05	0
15-22mm	0	**0.07**	0.93	0
22-29mm	0	0	**0.77**	0.23
29mm+	0	0	0.67	**0.33**

Probabilities can be used to estimate the actual number of cockles observed in size class *i*. For example, the number of cockles in the 15-22mm size class actually consumed by an oystercatcher at a distance of 200m is given by:

$$(NE_{7\text{-}15}*0.58)+ (NE_{15\text{-}22}*0.07)$$

where, $NE_{7\text{-}15}$ = number of cockles estimated to be 7-15mm in length, and $NE_{15\text{-}22}$ = number of cockles estimated to be 15-22mm in length.

Observed size selection: The frequencies of each size class consumed by oystercatchers, based on the prey remains data, and the frequencies of the same size classes present in the sand are shown in Figure 3.3.1. Birds using both feeding methods showed significant selectivity (Stabbers: $\chi^2 = 32.96$, df = 4, $P < 0.0001$; Hammerers: $\chi^2 = 286.79$, df = 4, $P < 0.0001$). Stabbers consumed mainly large cockles > 22mm, whereas hammerers consumed primarily intermediate sizes, ranging from 7 to 22mm.

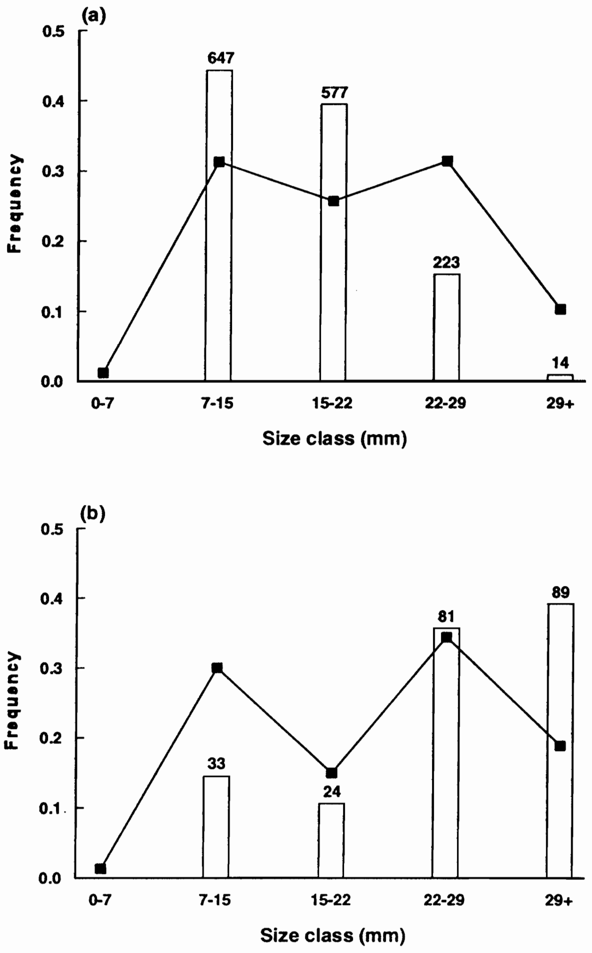


Figure 3.3.1 Frequency distributions of prey remains (bars) and cockles present in the sand (filled squares) for each size class, shown in (a) for hammerers and in (b) for stabbers. The number of cockles in each size class we found opened by oystercatchers is shown on the figure.

In hammerers, the mean size class consumed significantly increased over the winter (Figure 3.3.2a). The mean size class consumed, estimated from the prey remains data, tended to be significantly smaller than the mean size class consumed during foraging observations, at a given point in time (Figure 3.3.2a). This occurred because small cockles (ie. 7-15mm) were sometimes opened in the sand without being lifted, and cockles of 7-22mm were often lifted from the sand but not carried prior to being opened. Both of these factors reduced the likelihood that a cockle could be accurately size-classed during foraging observations. As a result, 7-22mm cockles represented 86.5% of the prey remains, but only 41.3% of cockles carried during foraging observations. However, the percentages were similar if cockles which were not carried during foraging observations were assumed to be 7-22mm in size (ie. 79.4%). Despite these differences, both the prey remains data and foraging observations showed comparable increases in the mean size class consumed over time (Figure 3.3.2a). In contrast, there was no evidence of a significant increase in the mean size class consumed by stabbers over the winter, and the prey remains data and foraging observations provided comparable estimates of the mean size class consumed (Figure 3.3.2b).

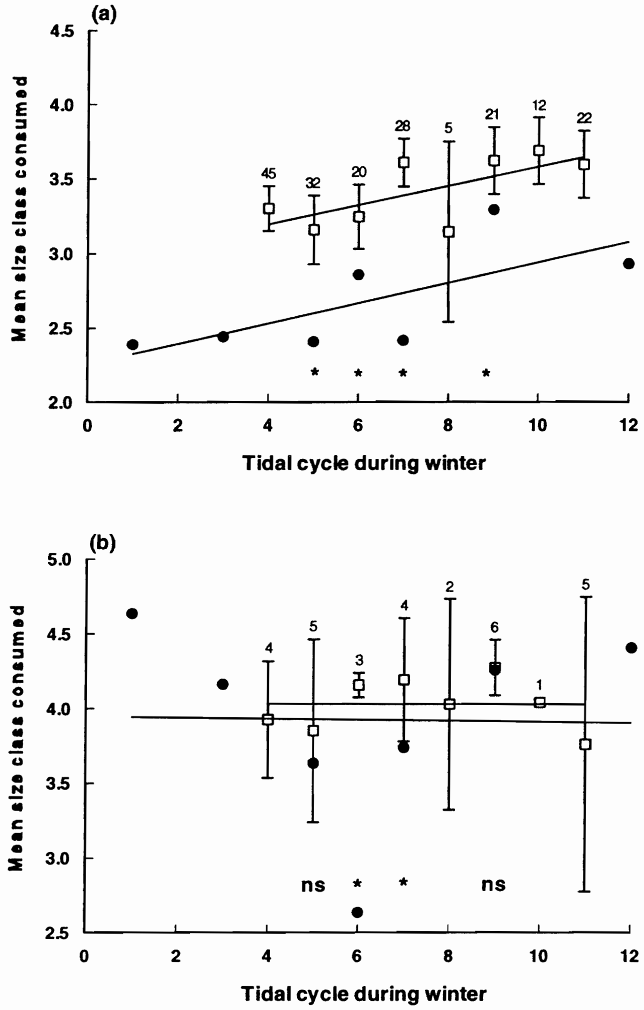


Figure 3.3.2 Seasonal changes in the mean size class consumed by (a) hammerers and (b) stabbers. Mean sizes estimated using prey remains (filled circles) and foraging observations (open squares) are shown. Mean sizes from foraging observations are given ± 95% confidence intervals and the number of birds observed during each tidal cycle shown. Tidal cycle during winter refers to the sequence of spring-neap and neap-spring tidal cycles over the winter. Significant ($P < 0.05$) differences between the mean size estimated using prey remains and foraging observations for a particular tidal cycle ars shown by an *, non-significant comparisons by *ns*. For hammerers, the seasonal trends are described by the linear regression equations, $y = 2.258 + 0.0682x$ (prey remains), and $y = 2.99 + 0.062x$ (foraging observations), which provided a marginally significant fit to the prey remains data ($R^2_{adj} = 39.9\%$, $n = 7$, $P = 0.076$), and a highly significant fit to the foraging observations data ($R^2_{adj} = 7.6\%$, $n = 184$, $P = 0.0001$). For stabbers, there were no significant seasonal trends in either data set (prey remains: $R^2_{adj} = -24.5\%$, $n = 5$, $P = 0.904$; foraging observations: : $R^2_{adj} = -3.4\%$, $n = 30$, $P = 0.92$).

Availability of cockles: The shell masses of each size class of cockle opened by hammerers and the sample of those present in the sand are shown in Figure 3.3.3a. Comparison of the slopes of the regression lines using ANCOVA demonstrated that hammerers opened shells with smaller masses for their size class than those present in the sand (-t = 10.63, P < 0.0001). This difference was most apparent for the 22-29mm and 29mm+ size classes (Figure 3.3.3a). As a consequence, only a fraction of the 22-29mm and 29mm+ cockles present in the sand were available to hammerers. To estimate this fraction we calculated the cumulative percentage of shell masses as a function of shell mass for the sample of cockles opened by hammerers, and for the sample of 22-29mm and 29mm+ cockles unopened in the sand (Figure 3.3.3b). The curve for the opened cockles reached a plateau at a shell mass of c.2.5g. The percentage of unopened cockles with a shell mass of less than this threshold value in the 22-29mm and 29mm+ size classes was 77.3% and 2.4% respectively (Figure 3.3.3b).

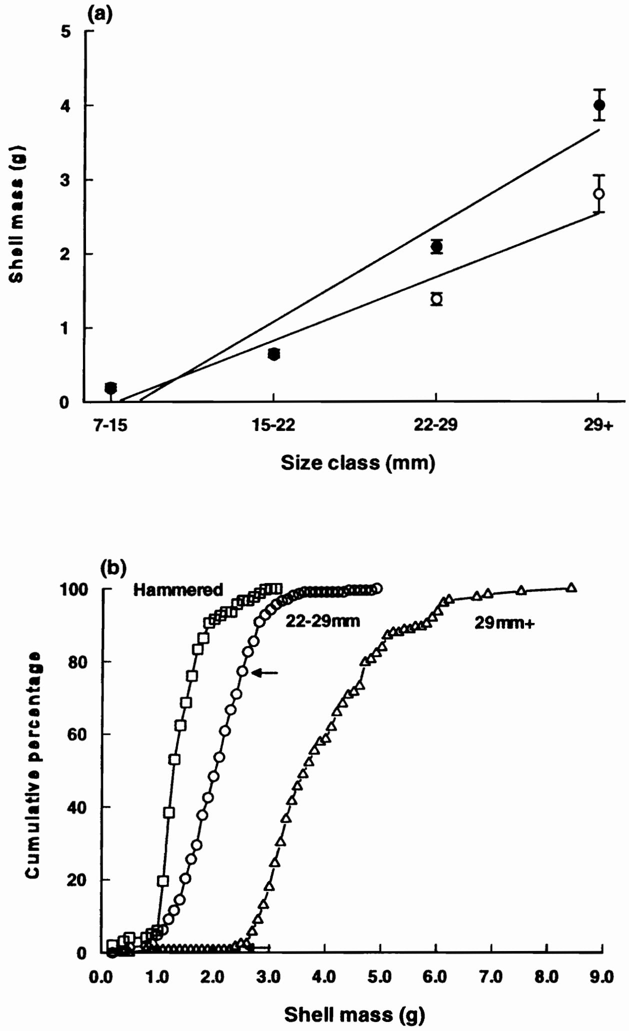


Figure 3.3.3 (a) The relationship between shell mass ± 95% ci's and size class for cockles opened by hammerers (open circles) and a random sample of cockles available in the sand (filled circles). The relationship for opened cockles is described by the linear regression equation: $y = -1.492 + 0.716x$, which provided a significant fit to the data ($R^2_{adj} = 60.6\%$, $n = 387$, $P < 0.0001$). The relationship for cockles present in the sand is described by the linear regression equation: $y = -3.483 + 1.441x$, which provided a significant fit to the data ($R^2_{adj} = 71.7\%$, $n = 477$, $P < 0.0001$). (b) The cumulative percentage of shell masses as a function of shell mass for cockles opened by hammerers (open squares), 22-29mm cockles present in the sand (open circles) and 29mm$^+$ cockles present in the sand (open triangles). The arrows indicate the cumulative percentage at a shell mass of 2.5g for the 22-29mm and 29mm$^+$ size classes present in the sand.

3.3.1.3.1 Model parameters

Energy gains (E_i): The ash-free dry mass (AFDM) of most bivalves increases supraproportionately with shell-length (eg. Zwarts 1991), so both AFDM and size class were transformed by taking the natural logarithm of each variable. Flesh content increased significantly as size increased, and for a given size class, declined throughout the winter, although the rate of the decline decelerated over time (Figure 3.3.4). We found no evidence that flesh content varied in relation to shore-height, measured as the time after high water the study plot, from which the cockle originated, was exposed (t = -0.294, df = 1, P = 0.769), after adding this variable to a regression model of AFDM already including the effect of size class and season.

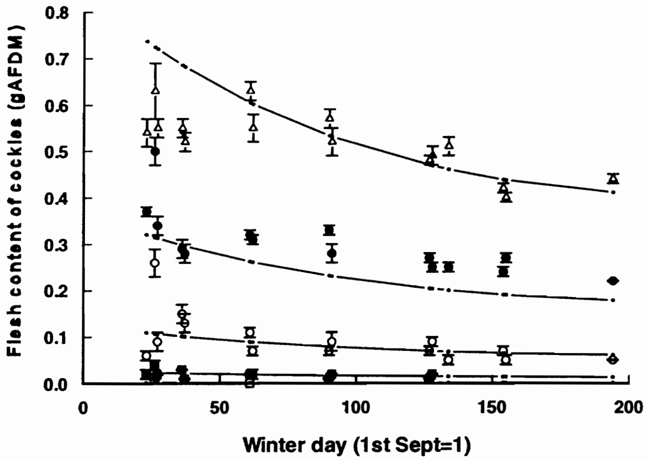


Figure 3.3.4 Seasonal changes in the flesh content of cockles in each size class. The mean flesh content is shown for each size class ± SE for each winter day on which cockles present in the sand were sampled: 29mm$^+$ (open triangles), 22-29mm (filled circles), 15-22mm (open circles), 7-15mm (filled squares), 0-7mm (open squares). The lines on the figure show the fitted values from the regression model: $ln(y) = -6.201 + 3.731*ln(x_1) - 0.0064*x_2 + 1.35E\text{-}05*x_3$, where x_1 = cockle size class as an integer value ranging from 1 (0-7mm) to 5 (29mm+), x_2 = winter day (1st Sept = 1), and x_3 = winter day ^2. This model provided a highly significant fit to the data ($R^2_{adj} = 83.9\%$, $n = 836$, $P < 0.0001$).

Time costs (h_i and wh_i): Handling times were an increasing linear function of cockle size class for both stabbers and hammerers (Figure 3.3.5a), but significantly shorter in stabbers for a given size class (t = -2.27, df = 1, P = 0.019). There was no evidence that the slopes of the regression lines differed between feeding methods (t = -0.886, df 1, P = 0.376). The time wasted handling cockles which were subsequently rejected decreased with size in hammerers, but showed little variation with size in stabbers (Figure 3.3.5b). Waste handling time was significantly shorter in stabbers (t = -2.928, df = 1, P = 0.0039), but the slopes of the regression lines did not differ significantly between feeding methods (t = 0.745, df = 1, P = 0.457).

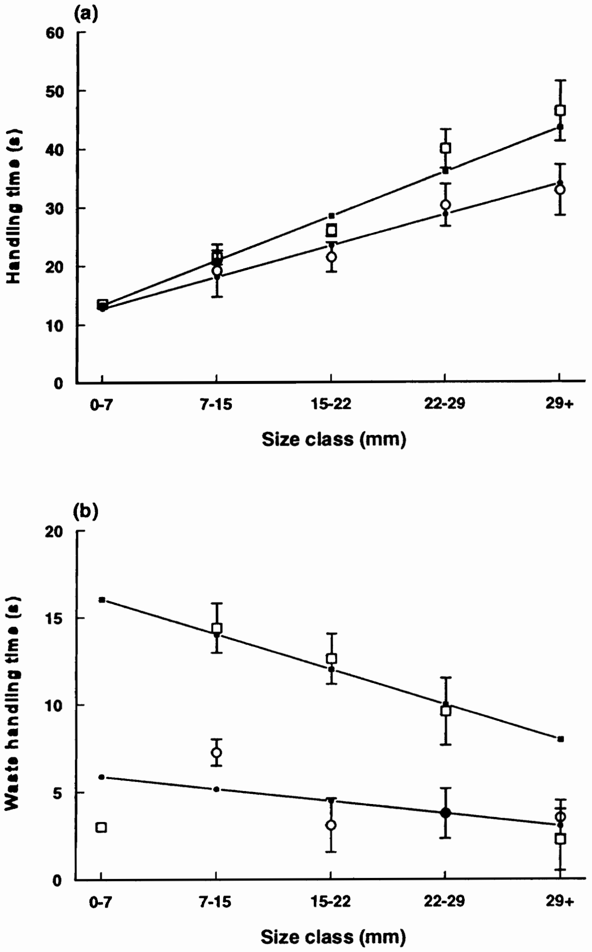


Figure 3.3.5 Time costs of handling cockles of different size when (a) cockles were successfully opened (handling time), and (b) when cockles were subsequently rejected unopened (waste handling time). In each plot hammerers (open squares) and stabbers (open circles) are shown separately. For hammerers, these relationships are described by the linear regression equations: $y = 5.771 + 7.571x$ (handling times) and $y = 18.066 - 2.205x$ (waste handling times), each of which provided a significant fit to the data (handling times: $R^2_{adj} = 18.4\%$, $n = 275$, $P < 0.0001$; waste handling times: $R^2_{adj} = 2.2\%$, $n = 147$, $P = 0.039$). For stabbers, these relationships are described by the linear regression equations: $y = 7.412 + 5.331x$ (handling times) and $y = 6.588 - 0.709x$ (waste handling times). The model of handling times provided a significant fit to the data ($R^2_{adj} = 11.9\%$, $n = 42$, $P = 0.013$), but the model of waste handling times was not significant ($R^2_{adj} = -2.1\%$, $n = 33$, $P = 0.57$). Lines showing the fitted values from the models are shown on the plots (hammerers: small filled squares; stabbers: small filled circles).

There was evidence that handling times in hammerers varied over the winter and during each high water-high water tidal cycle, in addition to the effect of cockle size (Figure 3.3.6a, b; Table 3.3.2a). Handling times decreased significantly over the winter, and showed a negative quadratic relationship over the tidal cycle, being longest at the start of the ebb and at the end of the flood tides. Handling times in stabbers also significantly decreased over the winter, in addition to the effects of cockle size (Figure 3.3.6c; Table 3.3.2b). There was no evidence that waste handling times varied over the winter or with time during a high water-high water tidal cycle, in either feeding method, in addition to the effect of size (additional variance explained when variables x_2 to x_4 in Table 3.3.2a added to a model of waste handling times already containing size class; hammerers: $F_{3,143} = 1.071$, NS; stabbers: $F_{3,29} = 1.167$, NS).

Table 3.3.2 Statistical models of time costs. Handling times (models **(a)** and **(b)**) were modelled using multiple regression analysis, assuming the response variable had a normal error distribution. The probability of successfully opening a cockle (models **(c)** and **(d)**) was modelled using logistic regression analysis, assuming the response variable had a binomial error distribution.

(a) Handling time in hammerers.

Variable	*Coefficient, b*	*SE*	*t-value*	*P*
x_1	7.625	0.975	7.818	0.0000
x_2	-0.050	0.024	-2.085	0.038
x_3	-0.169	0.044	-3.823	0.0002
x_4	2.149E-04	5.610E-05	3.83	0.0002
Constant	36.429	8.337	4.37	0.0000

where x_1 = size class (integer values: 1-5), x_2 = winter day (1st Sept = 1), x_3 = time after high water (mins), x_4 = time after high water ^2.

Overall fit of model: $R^2_{adj} = 22\%, n = 272, P < 0.0001.$

(b) Handling time in stabbers.

Variable	*Coefficient, b*	*SE*	*t-value*	*P*
x_1	5.400	1.983	2.723	0.0095
x_2	-0.0989	0.0479	-2.064	0.046
Constant	19.518	9.81	1.99	0.054

where x_1 = size class (integer values: 1-5), x_2 = winter day (1st Sept = 1).

Overall fit of model: $R^2_{adj} = 18.4\%, n = 41, P = 0.0064.$

(c) Probability of successfully opening cockle.

Variable	*Coefficient, b*	*SE*	χ^2	*P*
x_1	-0.3052	0.1059	8.697	0.0032
x_2	-0.9772	0.2118	20.992	0.0000
Constant	1.7066	0.4198		

where x_1 = size class (integer values: 1-5), x_2 = feeding method (categorical variable: hammerer=1, stabber=2). The coefficient for x_2 shows the linear contrast between levels 1 and 2 of the categorical variable describing feeding method. The probability is significantly lower in stabbers. For both predictor variables, $df = 1$.

Overall fit of model: $\chi^2 = 41.547, df = 2, P < 0.0001.$

(d) Probability of successfully opening a cockle in hammerers.

Variable	*Coefficient, b*	*SE*	χ^2	*P*
x_1	-0.238	0.1108	4.786	0.0287
x_2	0.4257	0.2157	3.906	0.048
x_3	-0.029	0.0129	5.072	0.0243
Constant	0.8042	0.8532		

where x_1 = size class (integer values: 1-5), x_2 = time after high water (mins), x_3 = time after high water ^2. Time after high water was expressed as an integer value which described time as a series of 50 minute intervals (eg. 3=101-150 mins after high water). For all predictor variables, $df = 1$.

Overall fit of model: $\chi^2 = 19.423, df = 3, P = 0.0002.$

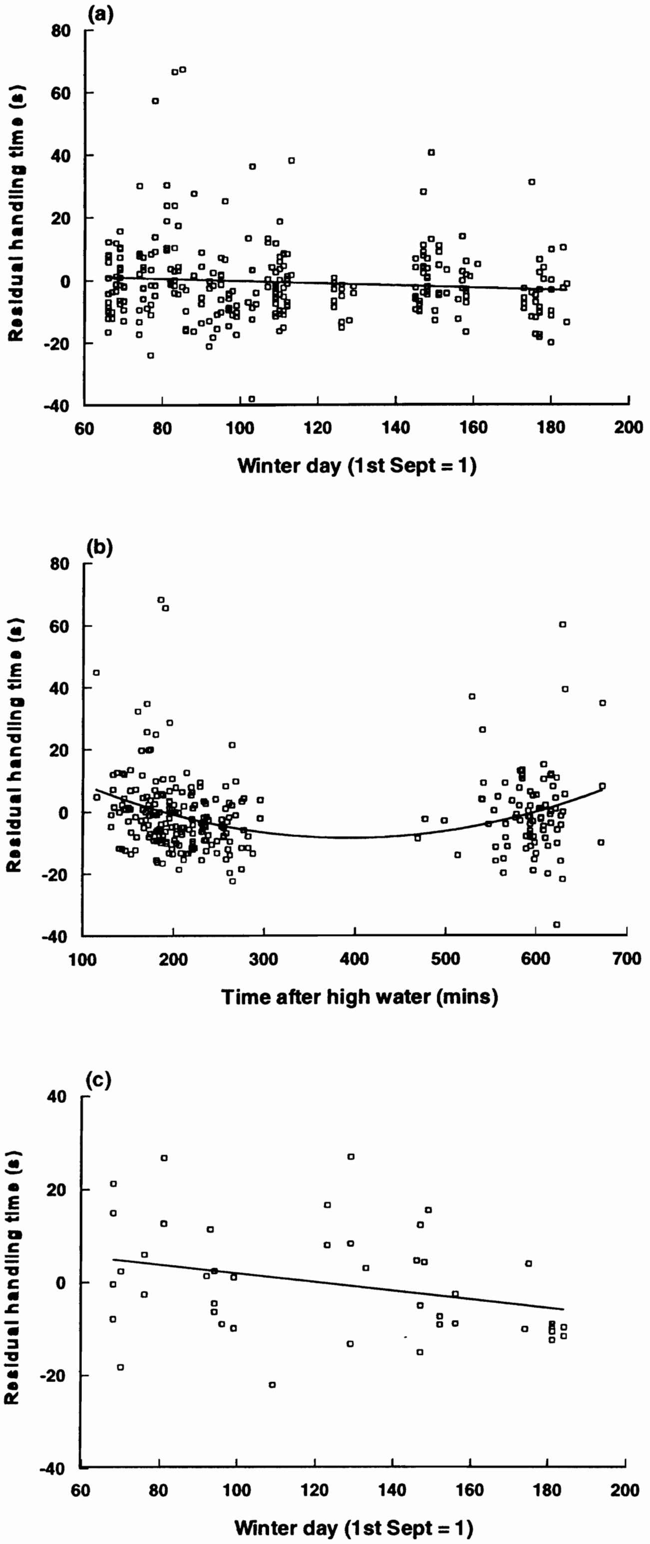


Figure 3.3.6 The relationship between residual handling times (ie. controlling for size class) and (a) winter day in hammerers, (b) time after high water in hammerers, and (c) winter day in stabbers. Details of the relevant statistical models and significance tests of these relationships are given in Table 3.3.2a, b.

Hammerers attacked some 7-22mm cockles without lifting them from the sand, or after lifting them but not carrying them (see above). The handling times and waste handling times of these cockles were shorter than the corresponding time costs observed for cockles of similar size which were lifted and carried before being opened (Handling times: carried = 23.75 ± 0.79 s, n = 239 birds; not carried = 10.3 ± 0.49 s, n = 152 birds; Waste handling times: carried = 13.30 ± 1.04 s, n = 119 birds; not carried = 3.85 ± 0.26 s, n = 126 birds). Handling times were only 43.4% as long, and waste handling times only 29% as long, on average.

Probability of success (P_i): The probability of successfully opening a cockle that had been attacked decreased with size in both stabbers and hammerers, and was significantly lower in stabbers (Figure 3.3.7a; Table 3.3.2c). There was no evidence to suggest that the rate of change in the probability of success with cockle size differed between feeding methods ($\chi^2 = 1.047$, df = 1, P = 0.3062). Among hammerers, 76.4% (1057/1383) of cockles not carried were successfully opened.

There was evidence that the probability of success varied with time after high water in hammerers, in addition to the effect of cockle size (Figure 3.3.7b; Table 3.3.2d). The probability increased over time on the ebb tide, and decreased over time on the flood tide. There were no significant effects of season or time after high water on this probability in stabbers, in addition to the effects of cockle size ($\chi^2 = 1.719$, df = 3, P > 0.10).

Encounter rates (λ_i): To solve eq.(3) we estimated the encounter rate with cockles of size class *i* (λ_i) as the reciprocal of the expected travel time between successive cockles, given by Ward (1993), and derived from Thompson (1983):

$$1 \;/\; 100\sqrt{(1/d_i)} \;/\; s \qquad 3.3.4$$

where s = search speed of an oystercatcher (cm.s^{-1}) and d_i = density of available cockles in size class *i* per m^{-2}. As Meire & Ervynck (1986) point out, this function does not consider the width of the bird's search path. Furthermore, it assumes that a bird would encounter each cockle present in the sand (see also Ward 1993). However, since it seems reasonable to assume that the encounter rate with a particular size class of cockle buried in the sand should be an increasing function of its density, eq.(4) provides a measure of the *relative* encounter rate with each size class.

Densities were adjusted for hammerers by calculating the density of available 22-29mm and 29mm+ cockles as the product of the density and the proportion of cockles with shell masses small enough to be available to these birds (ie. 0.773 and 0.024 respectively). For individual birds, encounter rates with each size class were calculated by assuming that the cockle densities in each size class experienced by each bird we observed were similar to the densities we estimated during each cockle sampling period, for the same spring-spring tidal cycle during the winter and the same plot or reference marker associated with each bird we observed.

Searching speeds were measured for hammerers using both searching methods (ie. sewing and probing), and for stabbers. Hammerers searched at a speed of 0.083 ± 0.0066 m.s^{-1} while sewing (n = 11) and at 0.218 ± 0.0296 m.s^{-1} while probing (n = 40). Stabbers searched at a similar speed to hammerers searching by probing, 0.19 ± 0.058 m.s^{-1}.

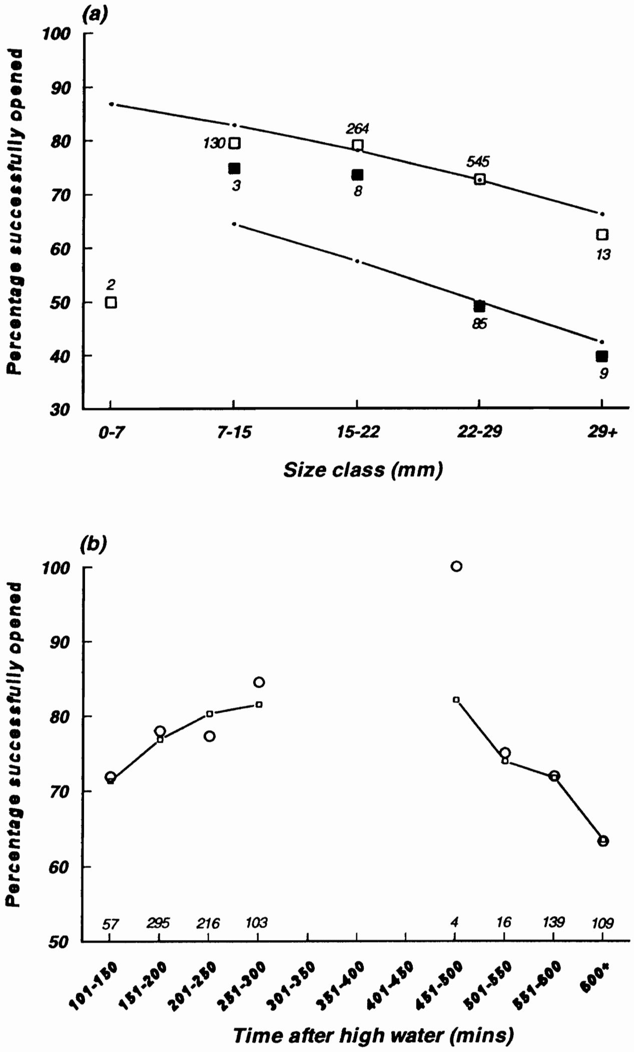


Figure 3.3.7 The percentage of cockles successfully opened having been attacked, in relation to (a) size class, and (b) time after high water in hammerers. In (a) hammerers (open squares) and stabbers (filled squares) are shown separately. The number of cockles observed being attacked in each size class are given on the figure. The lines describe the predicted percentages from the logistic regression model shown in Table 3.3.2c. In (b) the observed percentages (open circles) and predicted percentages (open squares) generated by the logistic regression model shown in Table 3.3.2d are shown. Note that predicted values do not form a smooth curve due to differences in the size classes attacked at different times after high water. Time after high water is shown as a series of 50 minute intervals. The number of cockles attacked during each time interval are shown on the figure.

3.3.1.3.2 Model predictions

The profitability (Z_i) of each size class, to both hammerers and stabbers throughout the winter was estimated as:

$$Z_i = \frac{E_i P_i}{h_i P_i + (1 - P_i) wh_i} \qquad 3.3.5$$

where the definition of the parameters is the same as in eq.(3). Estimating the time costs for hammerers was complex, since parameters varied over the winter, through the tidal cycle and, for cockles <22mm in length, depended on whether or not the cockle was carried before being opened. To incorporate these components for size classes <22mm in length, we estimated the handling time (*h*) and waste handling time (*wh*) of a cockle of size class *i* attacked by hammerers as:

$$h_i = h_c p_c + h_{nc}(1 - p_c) \qquad 3.3.6a$$

$$wh_i = wh_c p_c + wh_{nc}(1 - p_c) \qquad 3.3.6b$$

where h_c = the handling and wh_c = the waste handling time of a cockle of size *i* which was lifted and carried, h_{nc} = the handling and wh_c = the waste handling time of a cockle of size *i* which was not carried, and p_c = the probability that a cockle of size *i* would be lifted and carried. The handling and waste handling times of cockles lifted and carried were estimated from the statistical models in Table 3.3.2a and Figure 3.3.5b respectively, handling times and waste handling times of cockles not carried were estimated as 43.4% and 29% of the value of h_c and wh_c respectively (see above), and the probability of a cockle being lifted and carried was calculated from the foraging observations (mean percentage: 49 ± 3%). For size classes >22mm in length, we estimated time costs directly from the statistical models: handling times (Table 3.3.2a), and waste handling times (Figure 3.3.5b).

For cockles <22mm in length, we estimated the probability of successfully opening a cockle of size class *i* (P_i) after being attacked by a hammerer as:

$$P_i = p_{sc} p_c + p_{snc}(1 - p_c) \qquad 3.3.7$$

where p_{sc} = the probability of successfully opening a cockle of size class *i* that was carried (estimated from the logistic regression model in Table 3.3.2d), p_{snc} = the probability of successfully opening a cockle of size class *i* not carried (ie. 0.764 - see above), and p_c is as defined in eq.(6). For size classes >22mm in length, P_i was estimated directly from the logistic regression equation in Table 3.3.2d.

For stabbers, handling times were estimated using the statistical model in Table 3.3.2b, waste handling times using the model in Figure 3.3.5b, and the probability of success using the model in Table 3.3.2c.

Profitability increased with cockle size for birds using both feeding methods, and tended to be similar in stabbers and hammerers (Figure 3.3.8). This was because although stabbers experienced lower time costs than hammerers when handling a cockle of a given size class (Figures 3.3.5a, b), they also tended to be less successful at opening cockles they had attacked (Figure 3.3.7). Furthermore, time costs for hammerers attacking cockles which were not carried were comparatively small. To determine which size classes each feeding method should include in their diet to maximize their energy intake we solved eq.(2), by calculating predicted energy intake rates for different selection strategies. That is, including only the most profitable size class in the diet, the 2 most profitable size classes, and so on (see also Meire & Ervynck 1986; Cayford & Goss-Custard 1990). For hammerers and stabbers energy intake was maximized if cockles >15mm were included in their diet (Figure 3.3.9).

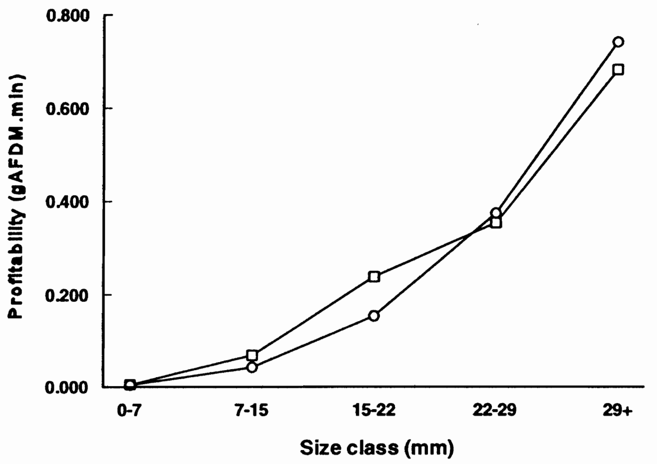


Figure 3.3.8 Profitability (gAFDM.min^{-1}) in relation to cockle size. Hammerers (open squares) and stabbers (open circles) are shown separately. Details of how profitabilities were calculated are given in the text.

Figure 3.3.9 Predicted energy intake rates (gAFDM.min^{-1}) for different size selection strategies. Hammerers (open squares) and stabbers (open circles) are shown separately. The selection strategy which maximized intake rate is shown for each feeding method. Only birds which experienced cockles densities > 0 for all size classes are shown.

3.3.1.3.3 Model tests

To test the model's predictions, we calculated the percentage of cockles consumed by each bird from the size classes the model predicted each should select. Over the entire winter, 47.8% (1334/2790) of cockles in the prey remains from hammerers were >15mm in length. There was a significant seasonal increase in the percentage of cockles consumed by hammerers from the optimal (>15 mm) size classes (Figure 3.3.10a), reaching a maximum of c.80% during late winter (based on prey remains). The foraging observations data from hammerers showed a similar seasonal trend, although, overall, the percentage was higher because small cockles taken by hammerers tended to be missed during our foraging observations (Figure 3.3.10a). In contrast, 87.1% (236/271) of the prey remains from stabbers were >15 mm in length, and this percentage remained high throughout the winter (Figure 3.3.10b), although there was a weak, but significant, trend for the percentage in the prey remains to increase slightly over the winter. There was no such significant trend in the foraging observations data (Figure 3.3.10b).

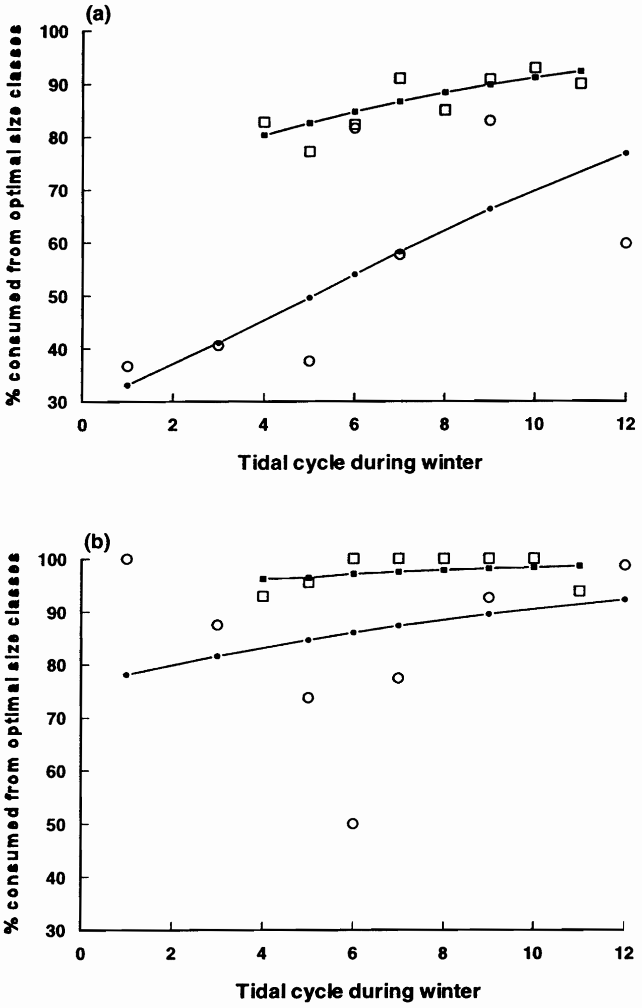


Figure 3.3.10 The percentage of cockles consumed by (a) hammerers and (b) stabbers from the optimal size classes. Foraging observations (open squares) and prey remains data (open circles) are shown. For hammerers, the seasonal increase in the percentage is significant for both prey remains and foraging observations data (logistic regression; prey remains: $y = 1/(1+e^{-(-0.8777+0.1729*\text{tidal cycle})})$, $\chi^2 = 160.1$, $df = 1$, $P < 0.001$; foraging observations: $y = 1/(1+e^{-(0.7844+0.1545*\text{tidal cycle})})$, $\chi^2 = 14.21$, $df = 1$, $P < 0.001$). Fitted values for prey remains (small filled circles) and foraging observations (small filled squares) generated using these models are shown on the figure. For stabbers, there was a weak, but significant, increase in the percentage of cockles in the prey remains >15mm in length (logistic regression: $y = 1/(1+e^{-(1.16+0.1093*\text{tidal cycle})})$, $\chi^2 = 4.67$, $df = 1$, $P < 0.05$), but no significant seasonal trend in the foraging observations data length (logistic regression: $y = 1/(1+e^{-(2.656+0.1422*\text{tidal cycle})})$, $\chi^2 = 0.296$, $df = 1$, *ns*). Fitted values are also shown (prey remains: small filled circles; foraging observations: small filled squares).

3.3.1.4 Searching strategies and encounter rates

3.3.1.4.1 Encounter rate models: theory

Searching strategies: In our study population, hammerers search for cockles using two strategies. Birds search using a 'sewing' technique, during which the bird uses rapid sewing movements with the bill in the substrate ('sewers'). Previous work on oystercatchers, and other waders, feeding on cockles has shown that this searching strategy is based on touch (Hulscher 1976; Piersma *et al.* 1995). Hammerers also search by walking slowly with the bill pointed at the sand, while occasionally inserting the bill into the substrate ('probers'). Stabbers search visually for cues which allow them to stab their bill between the valves of a cockle at the persistent gape. This can be done directly, if part of the cockle's shell is exposed on the sand surface, or indirectly using siphon holes in the sand as visual cues.

Encounter rate models: Hulscher (1976, 1982) showed that an oystercatcher feeding using the 'sewing' technique probed at random in the sand, with respect to the location of buried bivalve prey. This means that the encounter rate with a cockle of size *i* can be described by a simple random search model which predicts the probability that a bird would hit a buried cockle at one probe and the time taken for a single probe as:

$$\lambda_i = \frac{(D_i a_i)\ /\ 10^4}{t_i} \qquad 3.3.8$$

where λ_i = encounter rate with cockle of size *i* (s), D_i = density of size class *i* in the sand (m^{-2}), a_i = mean effective touch area of cockle of size class *i* (cm^2), and t_i = duration of a single probe (s). Data on the duration of single probes while searching by touch are given by Hulscher (1982) and by Wanink & Zwarts (1985).

The mean effective touch area of a cockle of size class *i* (*a*) can be estimated using the equation given by Hulscher (1982) as:

$$a_i = (bl * bw) + (\pi r_i^2) + (2 * bl * r_i) + (2 * bw * r_i) \qquad 3.3.9$$

where *bl* = bill-length, *bw* = bill-width, and r_i = radius of a cockle of size *i*, calculated by assuming its cross-sectional area (touch area) is approximately circular in shape (Hulscher 1982). To solve eq.(9) we needed to calculate the touch area of cockles in each size class, and the dimensions of the bill. To calculate the touch area, we pressed a sample of cockles (n = 50) vertically into plasticine, and measured the area of the largest cross-section (see also Wanink & Zwarts 1985). We used a value of 11mm for bill-length (*bl*) given by Hulscher (1982) for an oystercatcher searching by sewing. Note that the bill gapes while the bird searches. We used a value of 1.79mm for bill-width (*bw*), which is the mean value measured from a sample of 120 oystercatchers captured for banding in the Burry Inlet in January 1995.

Stabbers search visually for cockles. We estimated the encounter rate for these birds as:

$$\lambda_i = aD_i \qquad 3.3.10$$

where *a* = the instantaneous area of discovery ($m^2.s^{-1}$), and, D_i = density of size class *i* in the sand (m^{-2}). The instantaneous area of discovery (*a*) is the product of a number of components: the width of the bird's search path, *w* (m), its search speed, *s* ($m.s^{-1}$), and its probability of detecting a cockle within its search area, P_{det}. The value of *a* cannot be derived directly since it would be extremely difficult to quantify the cues available to a searching bird, and its likelihood of detecting them. However, *a* can be estimated empirically if birds attack all cockles of size *i* encountered, since λ_i can be estimated from observations of feeding birds, and, therefore, a can be calculated by re-arranging eq.(10). We estimated a by assuming that $w = 0.1$ m, and $s = 0.19$ m.s^{-1} (see section 3.3.1.3.1). Therefore, we effectively estimated the probability of detecting a cockle, P_{det}, using observed encounter rates, since the other components of a, w and s, were constants. The validity of this analysis rests on a number of assumptions: (1) birds are maximizing their encounter rate, (2) a is a constant and hence its value is independent of prey density (D_i), and (3) the observed encounter rate is an increasing function of D_i. These assumptions were tested prior to applying the model.

We do not know whether probers search by touch or search visually for cockles. Therefore, we predicted encounter rates with cockles of size i for both possibilities. Encounter rates for a 'prober' feeding by touch were estimated using eqs. (8) and (9), by using the reciprocal of their observed probing rate to estimate the time taken for a single probe, t_i. Encounter rates for a 'prober' feeding visually were estimated using eq. (10), with the exception that $s = 0.218$ m.s^{-1} for probers.

Data analysis: The main objective of our analysis was to compare the predictions of the encounter rate models with observed encounter rates, estimated using our foraging observations data for hammerers searching by touch. For hammerers searching visually, and for stabbers, our objective was to examine the assumptions of the encounter rate model given in eq.(10), and then, provided the model was applicable, compare observed and predicted encounter rates.

For hammerers, comparing observed and predicted encounter rates, and testing the eq.(10)'s assumptions, is complicated by the fact that the number of cockles <22mm in length taken by the birds is underestimated in our foraging observations data (see section 3.3.1.3), and early in the winter birds are including smaller cockles than expected in their diet, resulting in their energy intake rate being less than the maximum possible (see section 3.3.1.3.3). This latter finding raises the possibility that birds might not take every cockle of a given size class they encounter at this time. To circumvent these problems for hammerers (ie. sewers and probers), we used the observed encounter rate with 22-29mm cockles as the basis for comparing encounter rate model predictions with observed encounter rates, and for testing model assumptions. This size class was selected because its frequency in the bird's diet is not under estimated in our foraging observations data, it should always be included in the bird's diet because of its high profitability (see section 3.3.1.3.2), and most cockles in this size class are available to hammerers (see section 3.3.1.3). Too few cockles in the 29mm+ size classes are available to hammerers, and, as a result, this size class is only observed being taken infrequently. Encounter rates with cockles <22mm were not used because their frequency in the diet is under-estimated in the foraging observations data, even though 15-22mm cockles are sufficiently profitable to be taken. We also only used observed encounter rates with 22-29mm cockles collected from January onwards, because birds might not take every cockle in this size class they encountered during early winter, when they were harvesting energy below the maximum possible rate. We tested this possibility explicitly in section 3.3.1.4.2 for birds searching by touch (ie. sewers).

For stabbers and probers searching visually we initially tested the assumptions of the encounter rate model described in eq.(10). First, we tested whether the component of a, P_{det}, was independent of the density of cockles. This was done by estimating the value of P_{det} using observed estimates of the encounter rate and the density of cockles using eq.(10), for each bird we observed. We then plotted the estimated value of P_{det} against cockle density. Second, we examined the correlation between observed encounter rates and the density of cockles, to see whether the encounter rate increased with increasing cockle density. Third, we examined whether the observed encounter rate correlated with any environmental variables which might affect the bird's motivation to feed, in addition to cockle density. These variables were: season (ie. tidal cycle during winter), the density of competitors (see section 3.3.2.2 for a definition), and the degree of energy stress (see section 3.3.1.5.2 for details of how this was estimated). The observed encounter rate was modelled as a linear function of these variables using a multiple regression analysis. This was a crude test of the assumption that encounter rates were being maximized by the birds we observed.

For analysis, we classified each hammerer we observed as a 'sewer' or 'prober', based on its predominant searching strategy. Although birds did switch between strategies on occasions, most birds used predominantly one strategy. We calculated observed encounter rates with 22-29mm cockles as the number of 22-29mm cockles found per second of time spent sewing for sewers. For probers, the encounter rate was estimated as the number of 22-29mm cockles found per second of time spent probing (see above). The number of 22-29mm cockles observed being taken during foraging observations was corrected for observer error as described in Table 3.3.1. All results reported below use the data from the December 1994 trial to correct for observer error, as was used throughout section 3.3.1.3. For stabbers, the observed encounter rate was estimated as the number of cockles >22mm in length taken per second of time spent searching. These size classes were used as the basis for testing the model because their frequency in the diet is adequately represented in the foraging observations data, and most cockles taken by stabbers are from these size classes. Furthermore, since stabbers showed no significant seasonal changes in their size selection, taking predominantly the most profitable size classes, we did not restrict our analysis of observed encounter rates to observation sessions conducted from January onwards, but used data from the entire winter. The number of cockles >22mm observed being taken by stabbers was corrected for observer error as described in Table 3.3.1.

3.3.1.4.2 Encounter rate models: data

Selection of searching strategy by hammerers: Hammerers were more likely to search by sewing on the ebb tide, and by probing on the flood tide. On ebb tides, 88.2% (120/136) of hammerers searched by sewing, whereas on flood tides 32.4% (24/74) of hammerers used this searching strategy ($\chi^2 = 69.25$, df = 1, $P < 0.00001$).

Sewers: The touch area of cockles increased exponentially with increasing shell length (Figure 3.3.11). We used the fitted function in Figure (11) to estimate the touch area of each size class, to solve eq. (9). There was a highly significant relationship between observed and predicted encounter rates (Figure 3.3.12a), and the fitted regression line had a slope not significantly different from 1 ($\beta = 1.639 \pm 0.665$, mean ± 95% ci), and intercept not significantly different from 0 ($\alpha = 0.0124 \pm 0.0465$, mean ± 95% ci). This shows that the encounter rate model based on touch provided a reasonable fit to the observed data, although there is variability in the observed encounter rate for a given predicted value.

We also tested whether sewers were taking 22-29mm cockles at a rate below that predicted by the encounter rate model early in the winter, by examining the seasonal trend in the residual encounter rate (observed - expected encounter rate) (Figure 3.3.12b). If birds were taking fewer cockles than predicted early in the winter, then we would expect residual values to be negative at this time. This analysis showed that birds were observed taking 22-29mm cockles at a rate which was significantly lower than the predicted encounter rate early in the winter (ie. the distribution of residuals had a mean value significantly less than zero). With a single exception, the residual encounter rate was not significantly different from zero during mid and late winter.

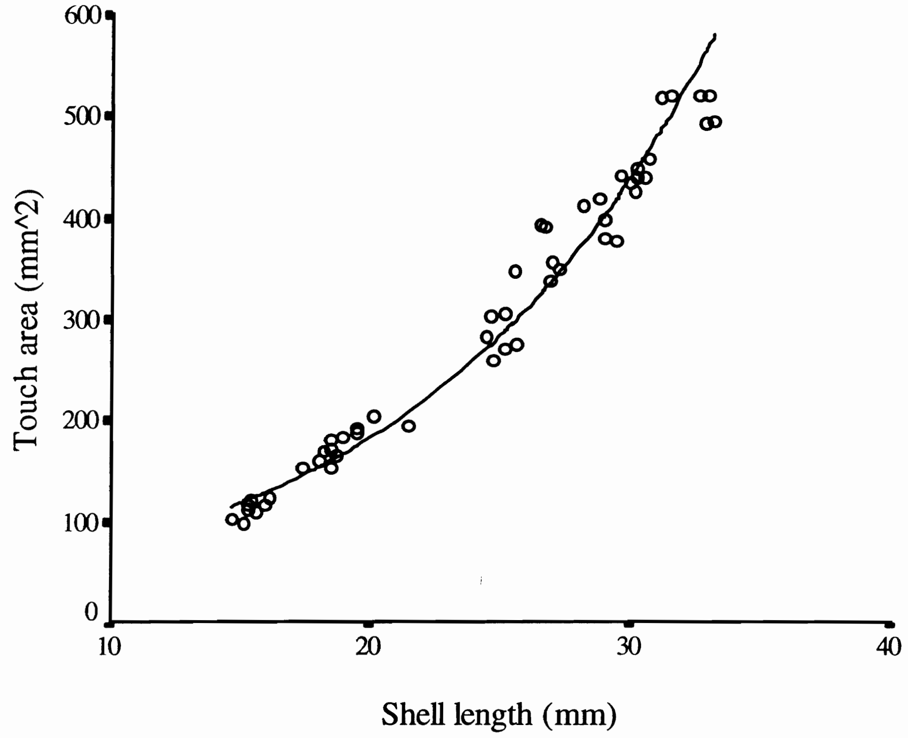


Figure 3.3.11 The relationship between the touch area of a cockle and its size. The fitted line corresponds to the exponential function: $y = 31.88(e^{0.087x})$, which provided a highly significant fit to the data ($R^2_{adj} = 97.2\%$, $n = 50$, $P < 0.0001$). Touch area is related to size class, measured as an integer value between 1 (0-7mm) and 5 (29mm+), by the exponential function: $y = 26.786(e^{0.5905x})$, which provided a highly significant fit to the data ($R^2_{adj} = 82.8\%$, $n = 50$, $P < 0.0001$).

Probers: The observed encounter rate for probers was significantly lower than that predicted by the encounter rate model based on touch ie. eqs. (8) & (9) (paired t-test: t = 4.61, df = 18, P < 0.001). This suggests that probers are unlikely to rely solely on touch to locate cockles. Note that this analysis was limited to observations of probers collected after 1st January, incase probers were also taking fewer 22-29mm cockles than predicted during early winter, as was the case for sewers. However, this restriction does not affect the results.

There was evidence that the value of P_{det} in eq.(10) declined significantly as cockle density increased (Figure 3.3.13a). Furthermore, there was no significant correlation between the observed encounter rate and the density of 22-29mm cockles (Figure 3.3.13b). We also found that birds were able to increase their encounter rate under certain conditions: when feeding in a dense flock and when energy demands were high (competitor density: t = 4.18, P = 0.0001; energy demands: t = 3.31, 0.0019; n = 46 birds) (see also section 3.3.2.3.2). This implies that encounter rates were not always maximized, and could explain the observed density-dependence in the value of P_{det}. This is because, if the observed encounter rate is relatively constant across a range of cockle densities, then eq.(10) can only adequately describe the observed encounter rates if the value of P_{det} decreases with increasing cockle density. These results suggest that hammerers searching by probing did not always attempt to maximize their rate of energy intake, by maximizing the rate at which prey were encountered. Therefore, it is impossible to empirically estimate the relationship between maximum encounter rates and cockle density using eq.(10), since observed encounter rates were not apparently constrained by prey availability.

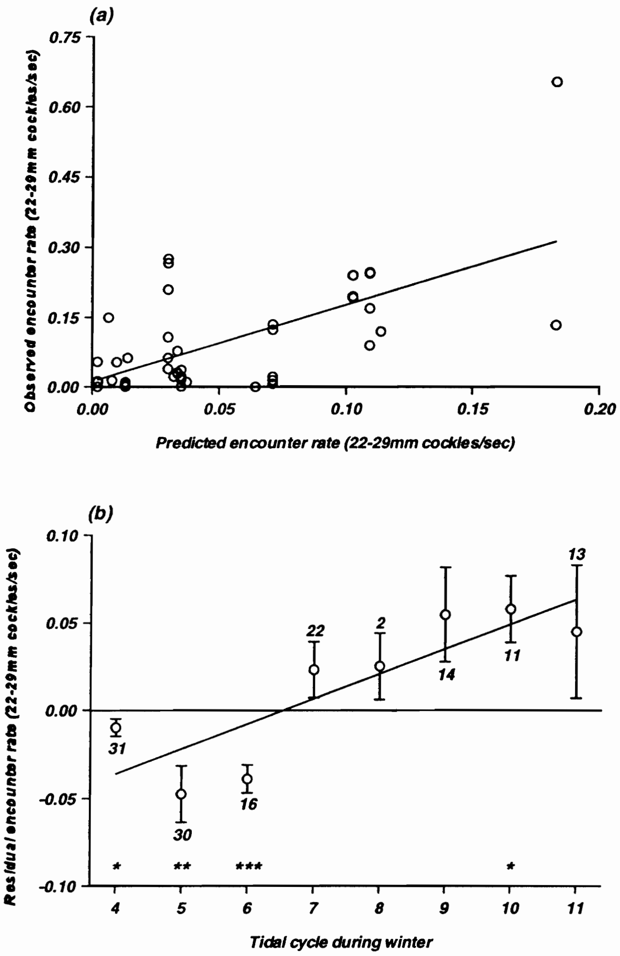


Figure 3.3.12 The relationship between (a) observed and predicted encounter rates with the 22-29mm size class, and (b) seasonal trends in the residual encounter rate (observed - predicted values) with the 22-29mm size class, for hammerers searching by sewing. Predicted encounter rates were generated using eqs.(8) and (9), in which a was estimated from the exponential function in Figure 3.3.11, and $t = 0.1482$ s , which is the time taken for an oystercatcher to probe to a depth of 1.5cm given by Wanink & Zwarts (1985). The relationship in (a) is described by the regression equation: $y = 0.012 + 1.639x$, which provided a highly significant fit to the data ($R^2_{adj} = 36.7\%$, $n = 41$, $P < 0.0001$). Observed data were collected from birds searching by sewing and observed after 1st January. The relationship in (b) is described by the regression equation: $y = -0.088 + 0.0135x$, which provided a highly significant fit to the data ($R^2_{adj} = 13.4\%$, $n = 138$, $P < 0.0001$). Tidal cycle during winter refers to the sequence of spring-neap and neap-spring tidal cycles throughout the winter. The number of birds observed during each tidal cycle is shown on the figure. The asterisks on the figure refer to the significance of the difference between the mean residual encounter rate and an expected mean value of 0, generated by a one-sample t-test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). If the observed mean is significantly less than zero, this indicates that the observed encounter rate was less than that predicted by the model.

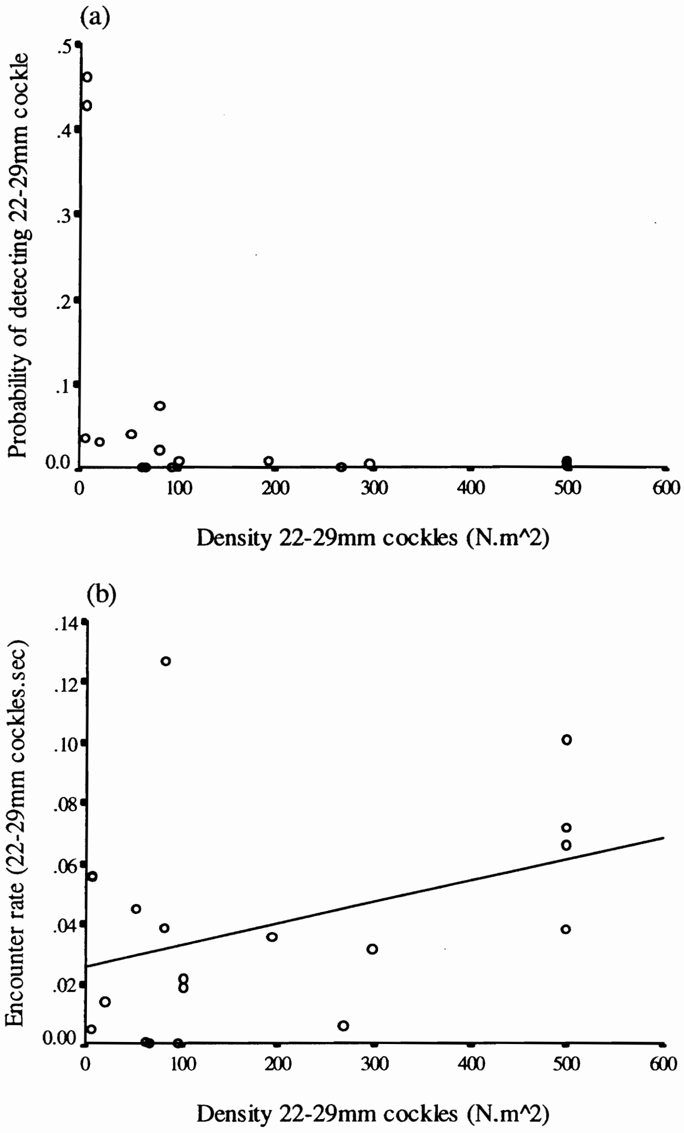


Figure 3.3.13 The relationship between the density of 22-29mm cockles experienced by probers and (a) the probability of detecting a 22-29mm cockle present in the sand, P_{det}, and (b) the observed encounter rate with 22-29mm cockles. The probability of detecting a cockle declines significantly with increasing cockle density (Spearman rank correlation: $r = -0.536$, $n = 18$, $P = 0.018$). The relationship between the encounter rate and cockle density was not significant ($R^2_{adj} = 9.2\%$, $n = 18$, $P = 0.11$). The fitted least squares regression line is shown in (b).

Stabbers: There was evidence that the value of P_{det} also declined significantly with increasing cockle density in stabbers (Figure 3.3.14a). Encounter rates increased significantly with increasing cockle density (Figure 3.3.14b), although the significance of this relationship depends upon a single observation of a bird with a high encounter rate feeding on a dense patch of cockles, the relationship being non-significant if this datum was removed ($R^2_{adj} = 5.2\%$, $n = 28$, $P = 0.13$). We could find no evidence to suggest that encounter rates were correlated with the environmental variables we examined (overall fit of regression model: $R^2_{adj} = -30.2\%$, $n = 9$, $P = 0.93$), even if competitor density was excluded from the analysis to increase the sample size (overall fit of regression model: $R^2_{adj} = -6.6\%$, $n = 23$, $P = 0.77$).

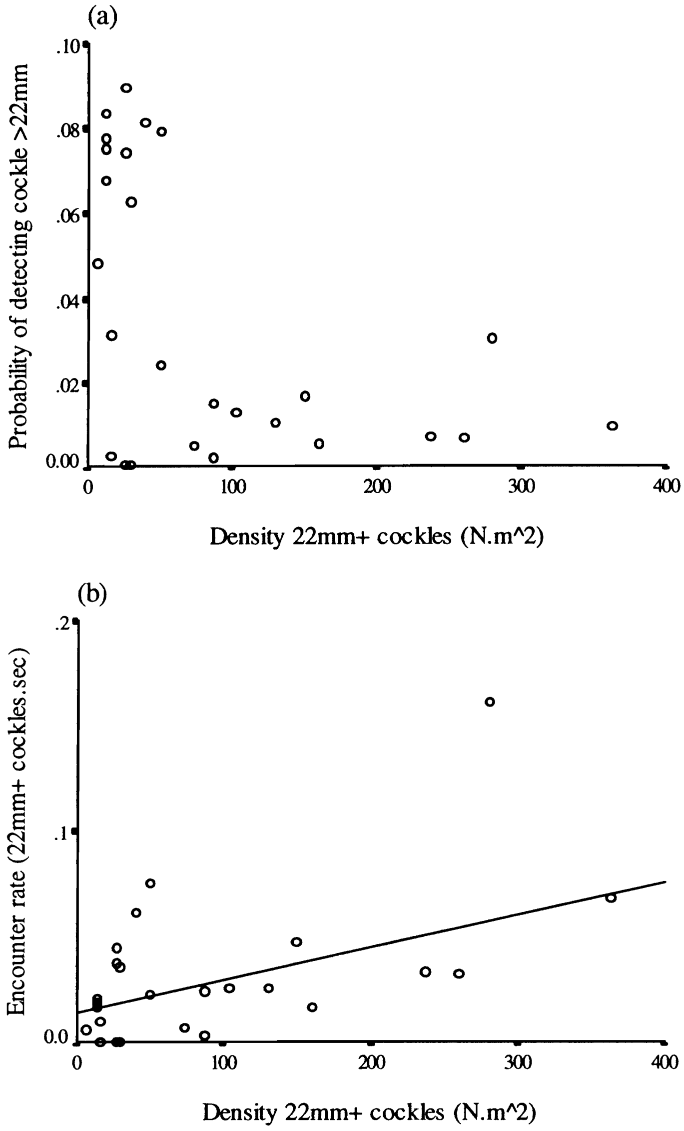


Figure 3.3.14 The relationship between the density of 22mm+ cockles experienced by stabbers and (a) the probability of detecting a 22mm+ cockle present in the sand, P_{det}, and (b) the observed encounter rate with 22mm+ cockles. The probability of detecting a cockle declines significantly with increasing cockle density (Spearman rank correlation: $r = -0.977$, $n = 29$, $P < 0.001$). The relationship between the encounter rate and cockle density was described by the regression equation: $y = 0.0142 + 0.00015x$, which provided a significant fit to the data ($R^2_{adj} = 18.1\%$, $n = 29$, $P = 0.012$).

It is not unreasonable to expect that encounter rates in stabbers might be only weakly correlated with the density of cockles buried in the sand, since birds require visual cues to locate cockles, and tend to concentrate their searching effort in areas with exposed cockles (pers. obs.). Furthermore, we have some data which suggests that the density of cockles visible to us on the sand surface is not significantly correlated with the density of buried cockles of similar size (pers. obs.). If the density of buried cockles is a relatively poor estimate of the density of cockles available to stabbers, then this could account for the density-dependence in the value of P_{det} because, if the observed encounter rate is relatively constant across a range of cockle densities, then eq.(10) can only adequately describe the observed encounter rates if the value of P_{det} decreases with increasing cockle density. Since we are unable to exclude this possibility, we have not applied the encounter rate model to stabbers. Further fieldwork is required to resolve this problem.

3.3.1.5 Predicted size selection and energy intake

Data analysis: We solved the version of Charnov's model described in eq.(3) for hammerers searching by touch (ie. sewers). This was not done for hammerers searching by probing, or for stabbers, because there was evidence that probers did not always attempt to maximize their intake rate by maximizing their encounter rate, and we could not be certain for stabbers that the density of cockles buried in the sand represented a reliable estimate of the density of available cockles. As a result, it was not possible to model the encounter rates of these birds directly. The energy gains and time costs were incorporated in the model for sewers as described in section 3.3.1.3.2. Encounter rates with each size class were estimated using eqs.(8) & (9). Densities of cockles >22mm available to hammerers were adjusted by calculating the density of the 22-29mm and 29mm+ size classes with shell masses <2.5g (see section 3.3.1.3.1).

To test the predictive power of Charnov's model, we compared the predicted energy intake and mean size class taken, with observed data. We used the model to generate predicted intake rates for various size selection strategies, as described in section 3.3.1.3.2. Predicted mean size class taken was estimated as the product of the relative frequency of size *i* encountered and its size class, measured as an integer value between 1 (0-7mm) and 5 (29mm+), summed across all size classes which the model predicted should be included in the diet. For hammerers searching by sewing, comparisons were based on prey remains data, since the frequency of cockles <22mm in the diet were underestimated in our foraging observations data (see section 3.3.1.3). As a result, our foraging observations data would over-estimate the true intake rate and mean size class taken by sewers. The intake rate and mean size taken of individual birds was estimated by assuming that the birds consumed each size class in proportion to its occurrence in the prey remains data for the same study plot or reference marker, and tidal cycle, in which a particular bird was observed. Intake rates were then calculated by estimating the number of cockles consumed per unit of feeding time in each size class as the product of its relative frequency in the prey remains, the total number of cockles consumed and its flesh content (estimated from the fitted function in Figure 3.3.4), divided by the total time spent feeding.

3.3.1.5.1 Model predictions and observed behaviour

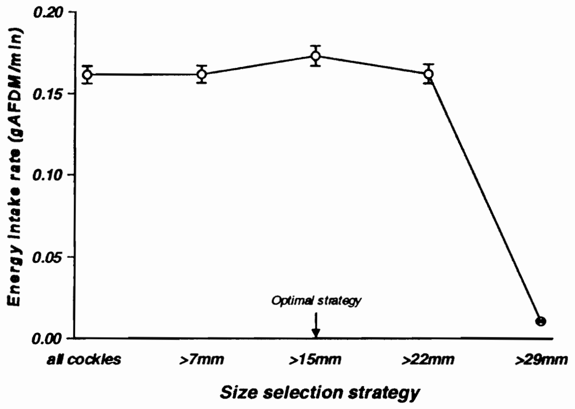


Figure 3.3.15 Predicted energy intake rates for different size selection strategies. The optimal size selection strategy (ie. that which maximizes intake rate) is shown by an arrow.

Energy intake: Energy intake rates for various size selection strategies are shown in Figure 3.3.15. The model predicted that hammerers searching by touch should take cockles >15mm. These predictions are in accordance with those generated using eq.(4) to estimate relative encounter rates (see section 3.3.1.3.2).

Predicted intake rates for sewers consuming only cockles >15mm declined significantly over the winter (Figure 3.3.16), as densities declined due to depletion and probably other sources of mortality, and the flesh content of cockles also declined. The observed intake rates of sewers increased significantly over the winter (Figure 3.3.16). As a result, during early winter (ie. prior to 1st January) the observed rate was significantly lower than the predicted rate for a bird consuming only cockles >15mm (paired t-test: $t = 5.69$, $df = 93$, $P < 0.001$). Analyses were restricted in this way because analysis of encounter rates showed that during early winter birds were not taking as many 22-29mm cockles as the model predicted they could find. At this time, the observed rate was also significantly lower than that predicted for a bird feeding unselectively (ie. including all size classes in its diet) (paired t-test: 4.28, $df = 93$, $P < 0.001$). This is consistent with the finding that sewers do not consume cockles at the maximum rate at which they could be encountered during early winter (see section 3.3.1.4.2). During mid and late winter (ie. after 1st January) there was no significant difference between the observed intake rate and that predicted by the model for a bird consuming only cockles >15mm (paired t-test: $t = -0.60$, $df = 37$, $P = 0.552$). Although this suggests that the model provides a reasonable estimate of the average intake rate of sewers feeding during late winter, it should also be noted that the observed intake rate was not significantly greater than that predicted by the model for a bird consuming all cockles >7mm (paired t-test: $t = -1.43$, $df = 37$, $P = 0.162$).

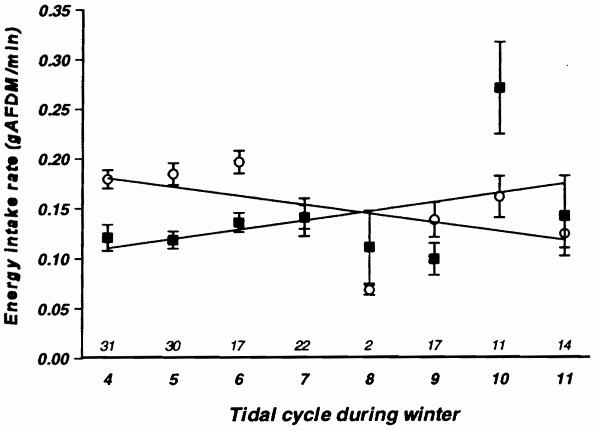


Figure 3.3.16 Seasonal trends in observed (filled squares) and predicted (open circles) intake rates (mean ± SE) for hammerers searching by sewing. Predicted intake rates for birds consuming only cockles >15mm declined significantly over the winter. The trend is described by the regression equation: $y = 0.218 - 0.0082x$, which provided a highly significant fit to the data ($R^2_{adj} = 9.3\%$, $n = 138$, $P = 0.0002$). Observed intake rates showed a significant increase over the winter. This trend is described by the regression equation: $y = 0.086 + 0.0075x$, which provided a significant fit to the data ($R^2_{adj} = 3.4\%$, $n = 131$, $P = 0.02$). Observed intake rates are based on prey remains data.

Since the observed and predicted intake rates of sewers were comparable during late winter, we tested whether the model provided a reasonable estimate of the intake rate of individual birds, feeding on a range of available energy densities (Figure 3.3.17a). There was a highly significant correlation between observed and predicted values, and the fitted regression line had a slope not significantly different from 1 ($\beta = 0.9482 \pm 0.6388$, mean ± 95% ci) and an intercept not significantly different from 0 ($\alpha = 0.0184 \pm 0.1001$, mean ± 95% ci). This suggests that the model provides a reasonable estimate of the intake rate of birds feeding on a given density of each size class present in the sand. The functional response generated using these data is given in Figure (3.3.17b), and shows a good correspondence between observed and predicted mean intake rates for a given density of energy available in the sand. It should also be noted that observed intake rates for individual birds and that predicted by the model for birds consuming only cockles >7mm were also significantly correlated during late winter (r = 0.534, n = 38, P = 0.001).

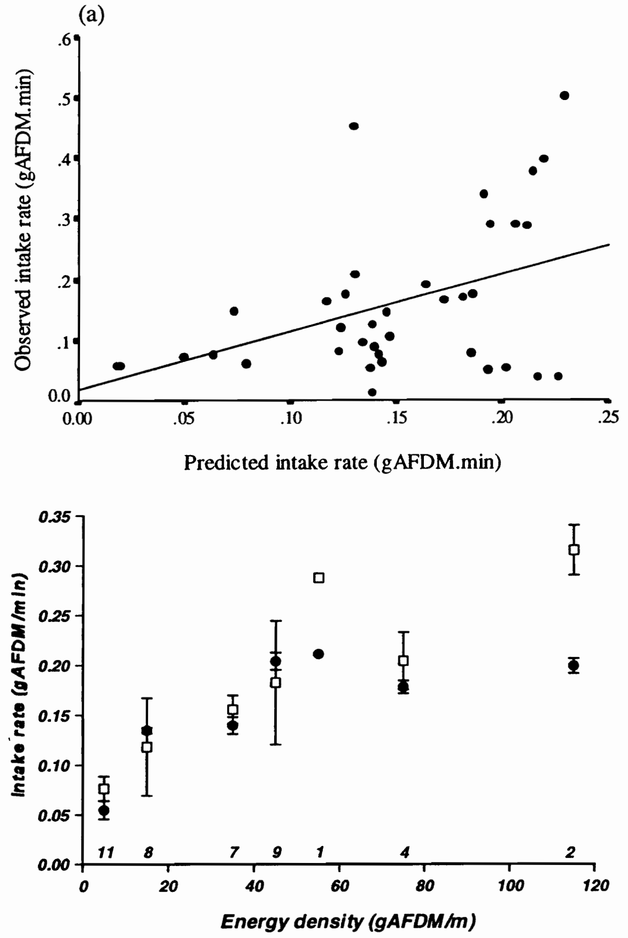


Figure 3.3.17 Observed and predicted intake rates for hammerers searching by sewing. Analyses are based on birds observed after 1st January. Observed intake rates are calculated using prey remains data. Predicted intake rates refer to the intake predicted by the model for a bird consuming only cockles >15mm in length. (a) the relationship between observed and predicted intake rates for individual birds. This relationship is described by the regression equation: $y = 0.018 + 0.948x$, which provided a highly significant fit to the data ($R^2_{adj} = 17.9\%$, $n = 37$, $P = 0.0047$). (b) the observed (open squares) and predicted (filled squares) functional response. Observed and predicted values were grouped into energy density categories of 10 gAFDM.m^{-2}, and are displayed as the mean ± SE intake rate for each category. The number of birds observed feeding on each energy density category is shown on the figure.

Size selection: The predicted mean size for sewers showed no significant seasonal trends, but the observed mean size class taken increased significantly over the winter (Figure 3.3.18a). This resulted in a significant difference between observed mean sizes and the mean size predicted by the model for a bird consuming only cockles >15mm during early winter (ie. before 1st January) (paired t-test: t = 22.66, df = 93, P < 0.001). However, observed and predicted mean sizes were also significantly different during mid and later winter (ie. after 1st January) (paired t-test: t = 6.14, df = 37, P < 0.001). This suggests that birds were consuming more smaller cockles than expected, and is consistent with the finding that observed intake rates were not significantly different from that predicted by the model for a bird consuming all cockles >7mm.

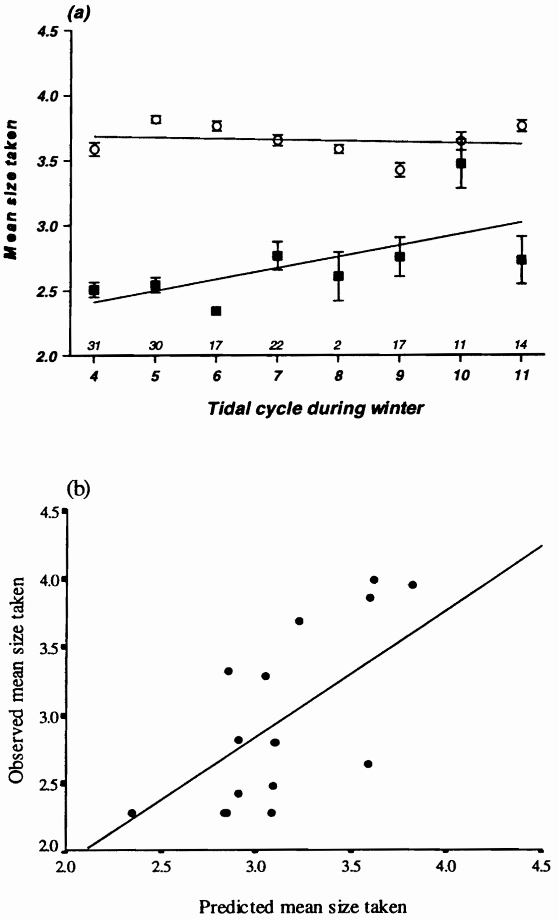


Figure 3.3.18 Observed and predicted mean sizes taken by hammerers searching by sewing. Analyses are based on birds observed after 1st January. Observed mean sizes taken are calculated using prey remains data. (a) seasonal trends in observed (filled squares) and predicted (open circles) mean sizes taken. The predicted mean size showed no significant seasonal trend ($R^2_{adj} = -0.18\%$, $n = 138$, $P = 0.385$). There was a significant increase in the mean size actually consumed by the birds over the winter. This trend is described by the regression equation: $y = 2.158 + 0.0748x$, which provided a highly significant fit to the data ($R^2_{adj} = 12.7\%$, $n = 131$, $P < 0.0001$). (b) the relationship between observed and predicted mean sizes for individual birds. Predicted values are based on model predictions for a bird taking all cockles >7mm. in length. The relationship is described by the regression equation: $y = 0.033 + 0.935x$, which provided a highly significant fit to the data ($R^2_{adj} = 30.4\%$, $n = 37$, $P = 0.002$).

Although there was a tendency for observed mean sizes to be slightly smaller than the mean size predicted by the model for a bird consuming all cockles >7mm during mid and late winter (paired t-test: t = 1.99, df = 37, P = 0.054), observed and predicted values for individual birds were significantly correlated (Figure

3.3.18b). This suggests that the model provides a reasonable description of predation rates on each size class for sewers, but that birds were taking smaller cockles than predicted for a bird attempting to maximize its intake rate.

3.3.1.5.2 Correlates of intake rates

Charnov's model provided a reasonable fit to the observed data for sewers during late winter, when both predicted intake rates and mean sizes taken were comparable to observed values. However, during early winter intake rates were lower than predicted because observed encounter rates were lower than predicted. This suggests that birds were not harvesting energy at the maximum possible rate at this time.

These observations suggest that the intake rates of birds on certain occasions depended on other factors, which dictated the extent to which sewers attempted to harvest energy at the maximum possible rate. Birds might increase their intake rate over the winter in response to increased energy demands. This might be because birds need more energy during late winter immediately prior to spring migration in order to accumulate fat reserves, and/or because energy stress increases over the winter. In addition, intake rates might have been lower during early winter due to interference competition and high competitor densities. All of these factors could potentially increase the degree of time stress experienced by foraging birds, and so increase the likelihood that they would have to maximize their intake rate in order to sustain their energy budgets.

We tested these hypotheses by calculating a residual intake rate (ie. observed - expected intake rate) for sewers, and modelled this as a linear function of (1) tidal cycle during winter, (2) the degree of energy stress, and (3) the density of competitors. Competitor density was assessed by taking the mean value of the number of birds (other than the focal bird we were watching) present at the start and end of our observation period. To obtain a measure of energy stress, we estimated maintenance metabolic costs experienced by the birds using the methods of Wiersma & Piersma (1994; Appendix 2), and using temperature and wind speed data collected during our study. The results of the analysis are given in Table 3.3.3. Birds were more likely to maximize their intake rate as the winter progressed, and this factor accounted for over 40% of the variance in residual intake rate. There was no evidence that the degree of energy stress, or competitor density affected the extent to which birds maximized their intake rate.

Table 3.3.3 Correlates of residual energy intake rate in hammerers searching by touch. In the model, x_1 = tidal cycle during winter (sequence of spring-neap and neap-spring tidal cycles throughout the winter; integer values: 4-11), x_2 = energetic costs of maintenance metabolism (W), and x_3 = number of competitors present in study plot.

Variable	*Coefficient, b*	*SE*	*t-value*	*P*
x_1	0.0249	0.0037	6.77	0.0000
x_2	-5.596E-04	0.006	-0.93	0.927
x_3	3.523E-05	2.61E-05	1.348	0.183
Constant	-0.200	0.041	-4.945	0.0000

Overall fit of model: $R^2_{adj} = 41.7\%, n = 65, P < 0.0001$.

3.3.1.6 General discussion

Model parameters: The predictions of Charnov's model are critically dependent on the validity of the size-specific parameters on which the model is based. In this respect, there were a number of potential sources of error in the estimation of model parameters. First, observer error. Observers estimating the size of bivalves taken by oystercatchers as a fraction of bill-length are prone to error (Goss-Custard et al.

1987; Meire and Ervnyck 1986; Cayford and Goss-Custard 1990; see also Table 3.3.1). However, in estimating the size classes attacked and consumed by the birds we were able to correct for observer error (see Table 3.3.1). Observer error could also affect the estimates of handling and waste handling times in relation to cockle size. However, we found no evidence that this affected the results. The functions which relate handling costs to size class (see Figure 3.3.5) were similar, irrespective of whether they were generated using the raw data, or if handling costs for a particular size class were weighted by the probability that the size class would be accurately estimated by the observer (see Methods for details).

Second, the size classes of cockle consumed by the birds was estimated as a percentage of bill-length, and then converted into a size class based on the mean bill-length of a sample of birds captured in the Burry Inlet (see Methods). This process could affect the results, especially if birds using different feeding methods had different mean bill-lengths. However, there is no evidence to suggest that this was likely. The bill-lengths of oystercatchers which have bill-tips associated with stabbing and hammering cockles have similar bill-lengths (Swennen et al. 1983).

Third, handling costs for a particular size class could be over-estimated if based solely on prey whose size class could be estimated because birds lifted these prey items from the substrate and carried them before opening. Oystercatchers do open prey which are still buried in the substrate, or on the substrate surface close to the point of extraction (eg. Hulscher 1982; Wanink and Zwarts 1985), and these prey tend to have shorter handling costs. This bias would have been present in our optimality model if handling costs were only estimated from prey which were carried, since 7-22mm cockles were often opened either in the sand or on the sand surface close to the point of extraction, and these cockles had much shorter handling and waste handling times than cockles of similar size which were carried by the bird prior to being opened. However, we were able to incorporate these shorter handling costs into the model, since comparison of our prey remains and foraging observations data allowed us to estimate the size class of cockles which were opened by the birds but not carried (see Results). We conclude, therefore, that the model parameters are unlikely to be seriously biased in any way.

The optimality model incorporated a number of observations which have been documented previously in oystercatchers feeding on other bivalve prey. Birds which hammered a hole in the shell tended to select cockles >22mm with shell masses lower than the average shell mass available. Hammerers feeding on mussels avoid attacking individuals with thick shells (Durell and Goss-Custard 1984; Meire and Ervynck 1986; Sutherland and Ens 1987; Cayford and Goss-Custard 1990), a preference related either to the low profitability of hammering open thick shelled bivalves (Sutherland and Ens 1987; Meire 1993), or possibly the risk of bill damage (Swennen and Duivan 1983; Swennen et al. 1983).

The energy content of cockles increased with size and, for a given size class, declined throughout the winter. This is a common pattern among bivalve populations (eg. Beukema 1974; Zwarts 1991). We found no evidence that the flesh content of a particular size class, at a given point during the winter, varied significantly in relation to shore-height. There is evidence that the growth rate of particular age classes of cockle is slower higher up the shore (eg. Sutherland 1982b). However, our results are not contradictory to this general pattern, since we only show that flesh content relative to shell-length is constant across a range of shore heights, for a given time during the winter, not that shell-length, and hence flesh content, is constant across a range of shore-heights, for a cockle of given age.

An increase in handling time with prey size is well documented in oystercatchers feeding on bivalves, for hammerers and stabbers (see Meire and Ervynck 1986; Sutherland and Ens 1987; Cayford and Goss-Custard 1990). Handling times in birds using both feeding methods decreased throughout the winter, and, in hammerers, peaked at the start of the ebb, and the end of the flood tides. For hammerers, one possible explanation for these patterns is substrate hardness. Over the winter, periodic storms removed fine sediments from the sandflats, which could affect the resistance offered by the substrate to a cockle which was being hammered open on it. Furthermore, anvils (areas of firm substrate upon which hammerers open cockles) appeared to become more common over the winter (pers. obs.), increasing the chances of a bird being able to hammer open a cockle on firm sand. As the tide ebbs the sand becomes less penetrable as its water content declines; on the flood tide the sand becomes more penetrable as the tide rises (unpublished data). Again, this could affect the resistance offered by the substrate to hammerers. In addition, this latter process could explain why the probability of successfully opening a cockle increases on the ebb, then declines on the flood tide, among hammerers. Possible explanations for the seasonal decline in handling times in stabbers are (1) the decline in cockle condition over the winter could affect the cockle's ability to hold its valves together after being penetrated by a bird's bill, or (2) cockles possibly gape more often as the winter progresses due to reduced muscle strength. Alternatively, the seasonal decrease in handling times, for birds using each feeding method, could be due to the fact that a given size class contains less flesh during late winter (see Figure 3.3.4), which may take less time to extract from the shell and swallow (see also Ens et al. in press).

Waste handling times decreased significantly with increasing cockle size in hammerers. This contrasts with birds feeding on mussels, when waste handling times were found to increase with prey size (Meire and Ervynck 1986; Cayford and Goss-Custard 1990). A possible explanation for this behaviour is that hammerers feeding on cockles have to lift prey from the substrate and subject it to a blow with the bill in order to determine whether or not it is vulnerable (ie. its shell mass is small enough), but having established that it is not, then waste comparatively little time attempting to open it. In contrast, birds feeding on mussels frequently tap potential prey with their bill, which could establish its shell thickness. In our study, a cockle lifted from the substrate and hammered with the bill would be recorded as being attacked, whereas in studies on birds feeding on mussels a bird only tapping prey while searching would not be considered to have attacked their prey.

Hammerers switched from sewing to probing over the tidal cycle, spending most of their searching time sewing on ebb tides, and probing on flood tides. The most likely explanation for this tendency is sand penetrability. As the tide ebbs the sand is relatively fluid and easy to penetrate (unpublished data). Under these circumstances, it seems possible that a bird could search for cockles whilst 'sewing' with the bill in the substrate. However, on a flood tide the sand remains firm until covered by the tide, which could make 'sewing' impossible. Birds presumably spend less time searching by probing on the ebb tide, because the encounter rate with 22-29mm cockles is significantly lower for probers than sewers, searching on the ebb tide (Mann-Whitney: $z = 1.952$, $n_{sewers} = 36$, $n_{probers} = 5$, $P = 0.0509$).

Model predictions: The functional response model (eq.3)·provided a good fit to observed intake rates and mean size classes taken by oystercatchers which hammered open their prey, and searched by sewing, during mid and late winter. At this time, the data suggested that birds included smaller cockles in their diet than predicted for a bird selecting only those size classes which maximized its intake rate. During early winter, intake rates were lower than those predicted by the model for a bird feeding unselectively ie. including all size classes in its diet, and there was evidence that birds consumed larger cockles (ie. 22-29mm) at a rate below the maximum rate they could have encountered these prey at this time. Therefore, the birds appeared to be consuming energy at a rate below the maximum possible rate, particularly during early winter, and only during mid to late winter were intake rates comparable to those predicted for a bird attempting to maximize its intake rate.

The encounter rate model based on touch has been used to successfully predict encounter rates with bivalve prey in previous studies on oystercatchers (Hulscher 1976; 1982; Wanink & Zwarts 1985), as well as for other waders (Piersma *et al.* 1995). This model provided an accurate estimate of the mean encounter rate for our oystercatchers feeding on a given density of 22-29mm cockles during late winter, but birds observed feeding during early winter took fewer 22-29mm cockles than expected. The functional response model provided a good fit to the data during late winter because the touch model provided a reasonable estimate of the rate at which prey is encountered at this time. During early winter, it seems likely that birds either reduced their searching effort while sewing eg. by reducing their probing rate, or ignored prey they had encountered, and hence had a lower intake rate than the maximum possible rate.

For hammerers searching by probing, and for stabbers, the encounter rate model (eq.10) provided a poor fit to the data. There was evidence that probers increased their encounter rate in response to an increase in energy demands and an increase in bird density. This implies that the intake rate of probers was often below the maximum possible rate, and that birds were able to increase their intake rates when necessary, by encountering prey more often. This makes it impossible to generate a model of encounter rates using empirical observations to estimate the parameter a in eq.(10). This is because unless encounter rates are maximized, it is not possible to determine the constraints on encounter rates imposed by the density of available prey. In the case of stabbers, the encounter rate model in eq.(10) may not be applicable using the density of cockles buried in the sand as a measure of prey availability if this density is only weakly correlated with the density of cockles which are both vulnerable to stabbers and potentially detectable. This is likely given that stabbers rely on visual cues on the sand surface to locate vulnerable cockles, and we have some evidence to suggest that the density of cockles visible to us on the sand surface is not strongly correlated with the density actually buried in the sand. In either case, the development of models which predict potential encounter rates with any accuracy will require the quantification of cues available to searching birds, and also the factors which make cockles vulnerable to attack.

The observation that the intake rate of hammerers searching by touch in the Burry Inlet is often lower than the maximum possible rate implies that selectively consuming only the most profitable size classes involves additional risks, or that accruing energy reserves in the form of fat is costly. Oystercatchers do experience additional risks when handling bivalve prey, such as bill damage which increases their mortality during cold weather (Swennen & Duivan 1983), and infection with parasites (Hulscher 1982). However, we currently lack data to show that these risks are dependent on cockle size, or that the fitness costs associated with these risks are sufficient to outway the fitness benefits of taking only the most profitable prey available. Accruing energy reserves in the form of fat could be costly to oystercatchers, especially if predation risk is an increasing function of body mass (eg. Lima 1986; Witter & Cuthill 1993). Oystercatchers must accrue sufficient energy reserves over each low tide period to survive the intervening high tide period, when food supplies are unavailable. Under these circumstances, the optimal policy for a bird attempting to achieve a target level of energy reserves at the end of the low water period could be to consume less profitable prey, reduce its consumption rate, or both, and thereby reduce the costs of accruing energy reserves. This could be a better alternative to consuming only the most profitable prey, maximizing consumption rates, accruing energy at the maximum rate, but experiencing higher costs.

If accruing energy is costly to oystercatchers, then they should only be prepared to pay the costs of a high intake rate when there are significant benefits. Significant benefits could include accruing energy reserves prior to migration. Such benefits could explain why sewers are more likely to maximize their intake rate during late winter. This is because a seasonal increase in intake rate might be expected in order to accrue fat reserves prior to the birds leaving the Burry Inlet for their more northerly breeding grounds, from January onwards (Davidson 1967), which is when observed intake rates appear to be maximized.

Although there are a number of examples which show that oystercatchers selectively consume classes of bivalve prey which maximizes their energy intake rate (eg. Sutherland 1982a; Wanink & Zwarts 1985; Meire & Ervynck 1986; Cayford & Goss-Custard 1990), there is evidence that birds also consume less profitable prey on occasions, even though their intake rate would have been higher had they only consumed the most profitable classes (eg. Sutherland & Ens 1987; Cayford & Goss-Custard 1990). Furthermore, oystercatchers are capable of increasing their intake rate when time stressed, implying that they sometimes harvest energy below the maximum possible rate (Swennen *et al.* 1989). These observations, together with our own, suggest that costs associated with maximizing energy intake rates might be a general phenomenon among oystercatchers. However, most importantly, these observations show that functional response models based on the assumption that birds attempt to maximize their intake rates is unlikely to provide a general basis for understanding intake rates and the spatial dispersion of predators in the wild.

3.3.2 Interference

3.3.2.1 General background

The presence of competitors causes a reduction in the intake rate of feeding oystercatchers (Ens & Cayford 1996). This process, termed *interference*, has been defined operationally as the short-term reversible decline in intake rate due to the presence of competitors (Goss-Custard 1980; Sutherland 1983). The strength of interference is extremely important in determining the distribution of foraging animals across a food supply gradient (Sutherland & Parker 1985; Parker & Sutherland 1986), and hence has implications for understanding how oystercatchers, faced with a decline in food availability as a result of fishing, might distribute themselves over the remaining food supply. The distribution of birds has important population consequences if individuals particularly sensitive to interference are displaced into poor quality feeding patches, which contain insufficient resources to support them (Goss-Custard & Durell 1990; Sutherland & Goss-Custard 1992; Sutherland & Dolman 1994).

Although a number of empirical studies have documented interference competition in oystercatchers (see Ens & Cayford 1996), none have shown that intake rates increase as the density of competitors increases. Such an effect would not be unexpected, since the presence of competitors could increase foraging efficiency by reducing time allocated to competing behaviours, such as scanning for predators (eg. Mayhew 1987; Diaz & Asensio 1991; Dolman 1994). We showed in section 3.3.1.5.2 that the intake rate of hammerers searching for cockles by probing was positively correlated with competitor density. In the present section we develop a more rigorous analysis of the effects of the density of competitors on the intake rate of oystercatchers feeding on cockles in the Burry Inlet.

3.3.2.2 Methods

A detailed description of our field methods is given in section 3.3.1.2.

Competitor density: Competitor density was assessed by counting the number of birds present in the study plot at the start and at the end of the observation period (excluding the focal bird we were observing). The number of competitors which an individual bird experienced during the time we observed its feeding behaviour was taken as the mean of these two values, expressed as a density (ie. number of birds per hectare) (as in Stillman *et al.* in press). During our foraging observations, we recorded whether or not a cockle was lost to a kleptoparasite.

Data analysis: To investigate the effect of competitor densities on intake rates in hammerers searching by probing and stabbers, we modelled intake rate as a linear function of competitor density. We did not include the density of available energy in these statistical models, since there was a poor correlation between energy density and intake rate in these birds, but we did include additional variables which we found to be correlated with intake rate in section 3.3.1.5.2. We used data from the entire winter for these analyses, since there was no evidence of any strong seasonal trends in intake rate (see section 3.3.1.5.1). For these birds, comparisons were based on intake rates estimated using our foraging observations data.

For hammerers searching by touch (i.e. sewers), we incorporated the effects of competitor density into the functional response model developed in section 3.3.1. We did this because we wished to examine the relative effects of food availability and competitor density on intake rates, and be able to predict intake rates for a given level of food availability and competitor density, for a bird attempting to maximise its intake rate. The functional response model, described in eq.(3) and solved in section 3.3.1.5, effectively describes the intake rate of a sewer feeding on a given energy density of available prey, with an average density of competitors. Within this model, the density of competitors could affect either the time costs associated with handling a cockle of a particular size class, or the rate at which birds encountered a particular size class, or both. Therefore, we tested the extent to which these model parameters were related to competitor density, then re-solved eq.(3), as described in sections 3.3.1.3.2 & 3.3.1.5, to examine the implications of any significant relationships on size selection and intake rates.

3.3.2.3 Results

3.3.2.3.1 Mechanisms of interference

Intake rates in oystercatchers feeding on mussels decline with increasing competitor density because of kleptoparasitism (Goss-Custard 1980). However, among our birds feeding on cockles, kleptoparasitism was rare (Table 3.3.4). This suggests that any negative effect of competitor density on intake rates is mediated by subtle effects on handling costs, or the rate at which prey are encountered.

Table 3.3.4 The frequency of kleptoparasitism

Feeding method	*Searching strategy*	*Cockles lost to parasites*	*Total number found*
Hammerer	Sewer	9	586
Hammerer	Prober	6	357
Stabber		1	130

3.3.2.3.2 Correlations between competitor density and intake rates

The correlation between competitor density and intake rate among hammerers searching by probing was positive, and only marginally significant ($r = 0.252$, $n = 55$, $P = 0.061$), but highly significant if the effects of energy demands on intake rates were also included in a multiple regression analysis (see Table 3.3.5). Encounter rates increased significantly as competitor densities increased, and there was evidence that birds tended to take larger cockles as competitor density increased (Table 3.3.5). However, the effect of competitor density on intake rates was primarily determined by the increased encounter rate, rather than by the change in the mean size taken (encounter rate: $t = 9.4$, $df = 1$, $P < 0.0001$; mean size taken: $t = 0.001$, $df = 1$, $P = 0.998$).

Table 3.3.5 Correlates of intake rates in hammerers searching by probing.

(a) Intake rates

Response variable: gAFDM.min^{-1}

Variable	Coefficient	SE	t-value	P
Competitor density	2.88E-04	9.36E-05	3.079	0.0035
Maintenance metabolism	0.053	0.014	3.895	0.0003
Constant	-0.235	0.0849	-2.765	0.0082

Overall fit of model: R^2_{adj} = *29.2%, n = 47, P = 0.0001.*

(b) Encounter rates

Response variable: 22mm+cockles attacked per second of searching time

Variable	Coefficient	SE	t-value	P
Competitor density	1.36E-04	2.765E-05	4.92	0.0001
Maintenance metabolism	0.0132	0.004	3.277	0.002
Constant	-0.0687	0.0251	-2.737	0.0088

Overall fit of model: R^2_{adj} *=37.7%, n = 47, P < 0.0001.*

(c) Mean size taken

Response variable: mean size class attacked

Variable	Coefficient	SE	t-value	P
Competitor density	9.908E-04	4.271E-04	2.32	0.0258
Maintenance metabolism	0.0959	0.0571	1.681	0.101
Constant	2.656	0.36	7.387	0.0001

Overall fit of model: R^2_{adj} = *11.9%, n = 39, P = 0.034.*

There was no significant effect of competitor density on intake rates, in addition to that caused by this increase in encounter rate (t = -0.895, df = 1, P = 0.38). There was no evidence that the intake rate of stabbers was significantly related to competitor density (r = 0.226, n = 16, P = 0.38).

3.3.2.3.3 Competitor density and the functional response in sewers

Model parameters: There was no evidence that handling or waste handling times, for a given size class of cockle, were significantly related to the density of competitors (Table 3.3.6).

Table 3.3.6 Time costs in hammerers searching by touch.

Handling time

Variable	Coefficient	SE	t-value	P
Size class	7.785	1.423	5.469	0.0001
Competitor density	-0.0021	0.0027	-0.797	0.427
Constant	3.441	4.137	0.832	0.408

Overall fit of model: R^2_{adj} = *23%, n = 98, P< 0.0001.*

Waste handling time

Variable	Coefficient	SE	t-value	P
Size class	-3.28	1.241	-2.644	0.0097
Competitor density	-0.0011	0.0022	-0.51	0.611
Constant	20.47	3.65	5.604	0.0001

Overall fit of model: R^2_{adj} = *5.5%, n = 89, P = 0.031.*

Probability of successfully opening a cockle which was carried

Variable	Coefficient	SE	χ^2	P
Size class	-0.3396	0.19	3.351	< 0.10
Competitor density	-0.00082	0.00025	10.68	< 0.005
Constant	2.7	0.689		

Probability of successfully opening a cockle *in situ*

Variable	Coefficient	SE	χ^2	P
Competitor density	-0.001126	0.00043	6.434	< 0.025
Constant	1.519	0.1296		

Probability of opening a 7-22mm cockle *in situ*

Variable	Coefficient	SE	χ^2	P
Competitor density	-0.0021	0.00035	42.72	< 0.0001
Constant	2.144	0.133		

However, competitor density did affect the probability of successfully opening a cockle which had been attacked (Table 3.3.6; Figures 3.3.19a, b), and the probability that a bird would open a cockle 7-22mm in length *in situ* (i.e. not carry it) (Table 3.3.6, Figure 3.3.19c). In both cases, the probability significantly decreased with increasing competitor density. These analyses provide clear evidence of ***interference***, although it should be noted that the mechanism was not kleptoparasitism.

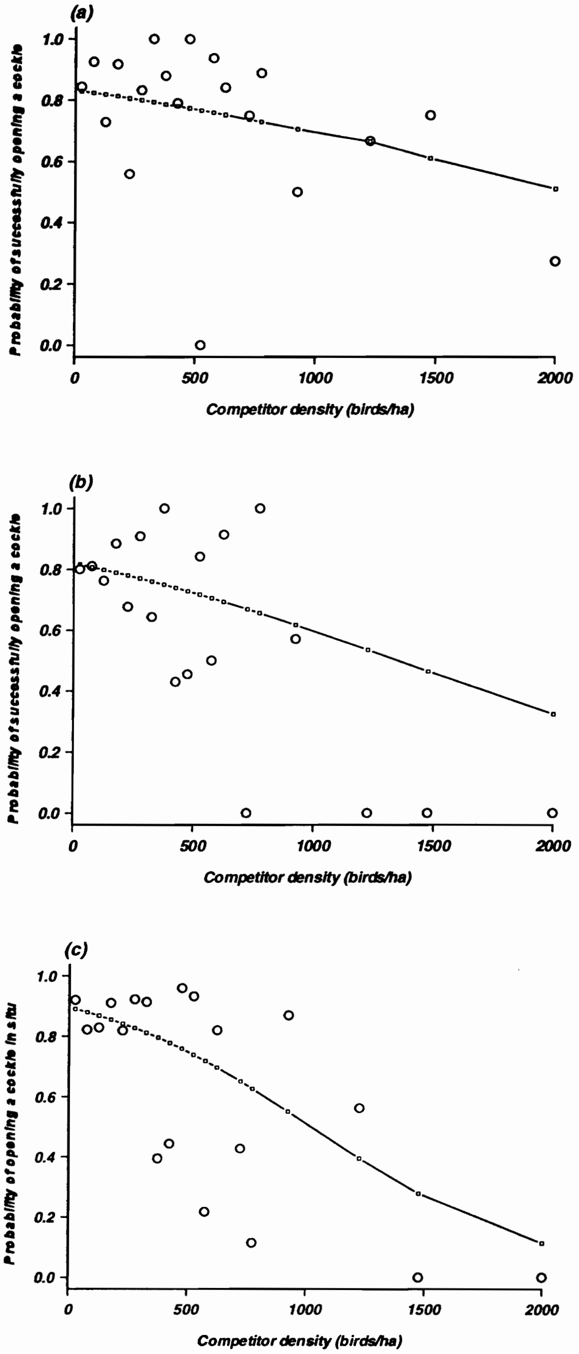


Figure 3.3.19 Probabilities of (a) successfully opening a cockle which had been carried, (b) successfully opening a 7-22mm cockle opened *in situ*, and (c) attempting to open a 7-22mm cockle *in situ*. The open circles represent the observed probabilities for competitor densities grouped into 50 birds.ha^{-1} categories. The lines represent the fitted values from the relevant logistic regression functions shown in Table 3.3.6.

We also examined whether competitor density affected the rate at which prey were encountered. To test this possibility we calculated a residual encounter rate (observed - predicted encounter rate) with 22-29mm cockles based on the predictions of eqs.(8) & (9). We used the observed encounter rate with this size class as the basis for this analysis because this particular size class is accurately represented in our foraging observations data (see section 3.3.1.4.1 for a complete discussion of this problem). We also restricted the analysis to observations of feeding birds conducted during late winter, since the encounter rate model described in eqs. (8) & (9) provides an adequate description of the observed mean encounter rate, for a given prey density (see section 3.3.1.4.2), at this time. There was no evidence that the residual encounter rate with 22-29mm cockles varied significantly in relation to competitor density (Figure 3.3.20). Therefore, we assumed that the maximum encounter rate with all size classes was unaffected by competitor density.

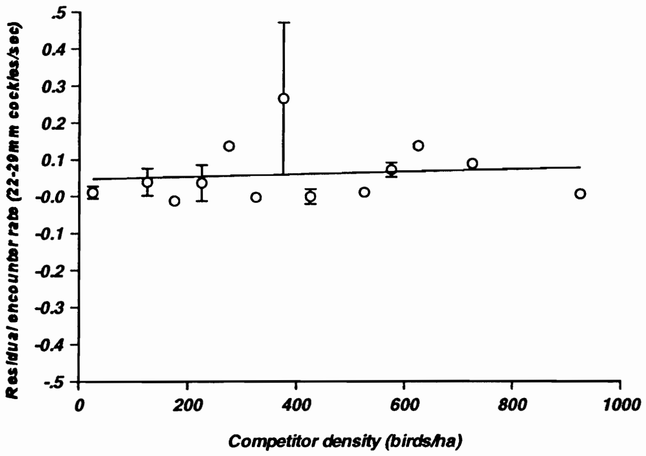


Figure 3.3.20 The residual encounter rate with 22-29mm in relation to competitor density. The residual encounter rate = observed minus predicted encounter rate. Residuals are grouped into categories of 50 birds/ha, and shown as mean values ± SE. The displayed data were collected from birds observed during late winter. The relationship was not significant (*$t = 0.223$, $n = 23$, $P = 0.826$*).

Model predictions: To generate predicted intake rates we solved eq.(3). Energy gains and time costs were incorporated as described in section 3.3.1.3.2, with the exception that eqs.(6a), (6b) and eq.(7) were solved using parameter values derived from Table 3.3.6.

Profitabilities, calculated by solving eq.(5), increased with size, but tended to decrease with increasing competitor density (Figure 3.3.21). This occurred because birds became progressively less likely to successfully open a cockle they had found as competitor density increased. This decrease was most pronounced in the 15-22mm size class, because its profitability was high only when cockles could be opened *in situ*, the probability of which decreased as competitor density increased (see Figure 3.3.19c). Having to carry the cockle prior to opening it substantially increased its handling costs (see section 3.3.1.3.1). This cost was in addition to the decrease in the probability of successfully opening 15-22mm cockles, *in situ* or after being carried, with increasing competitor density (Figures 3.3.19a, b).

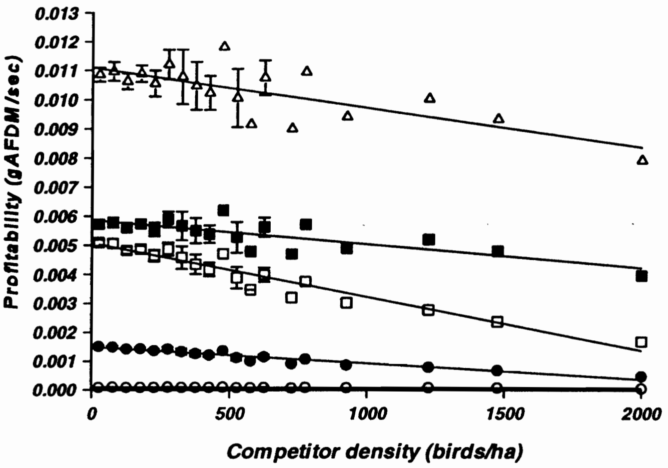


Figure 3.3.21 Profitabilities of each size class in relation to competitor density. Profitabilities are grouped into categories of 50 birds/ha, and shown as mean values ± SE. The least squares regression line is shown for each size class, which are displayed as: 29mm+ (open triangles), 22-29mm (filled squares), 15-22mm (open squares), 7-15mm (filled circles), and 0-7mm (open circles).

The predicted mean intake rate for different size selection strategies is shown in Figure 3.3.22, and shows that birds should take only cockles >15mm in length to maximize their intake rate.

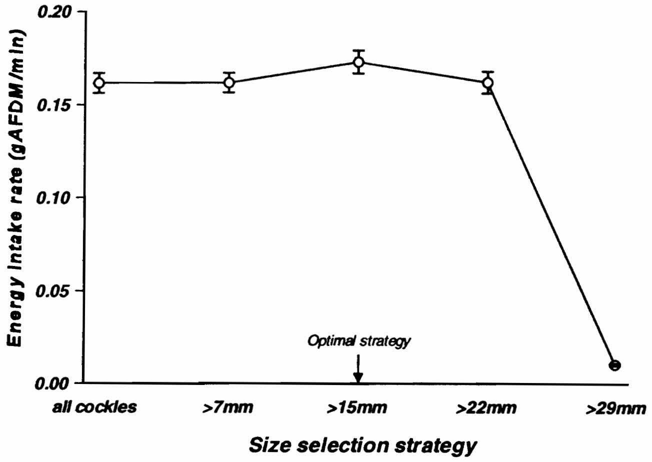


Figure 3.3.22 Predicted intake rates (gAFDM.min^{-1}) for different size selection strategies. The optimal strategy is that which maximizes the rate of energy intake, and is indicated by an arrow.

This result is similar to the predicted size selection generated using the functional response model which did not include any effects of competitor density (see section 3.3.1.5.1), and is to be expected since both models should provide comparable estimates of the mean intake rate for a particular size selection strategy. There was weak evidence to suggest that competitor density affected the size selection strategy predicted by the model (Figure 3.3.23).

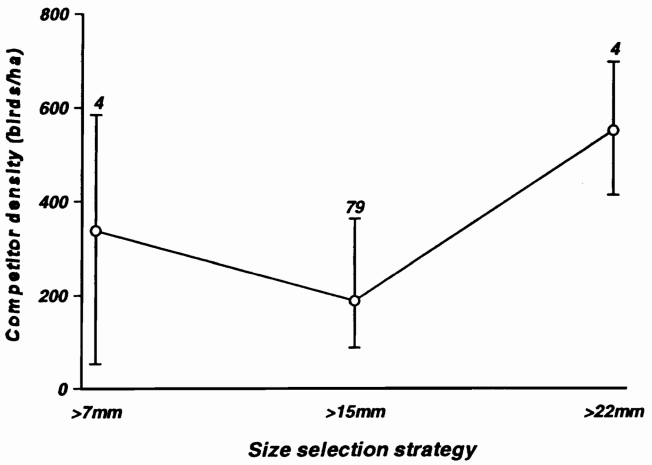


Figure 3.3.23 Competitor densities associated with different predicted size selection strategies. Densities are given as the median ± quartiles, and show significant differences between selection strategies (Kruskal Wallis: $\chi^2 = 6.38$, df = 2, P = 0.041, corrected for ties). Note that most birds (91%) were predicted to take only cockles >15mm.

This process results from the rapid decline in the profitability of 15-22mm cockles, with increasing competitor density. At low densities, the profitability of this size class is sufficient for birds to include it in their diet, whereas at the highest competitor densities, the model predicts birds should only take cockles >22mm, and hence drop the 15-22mm size class from their diet. However, the majority of birds were predicted to take only cockles >15mm, irrespective of the density of competitors they experienced.

The functional response, for a range of competitor densities, is shown in Figure 3.3.24.

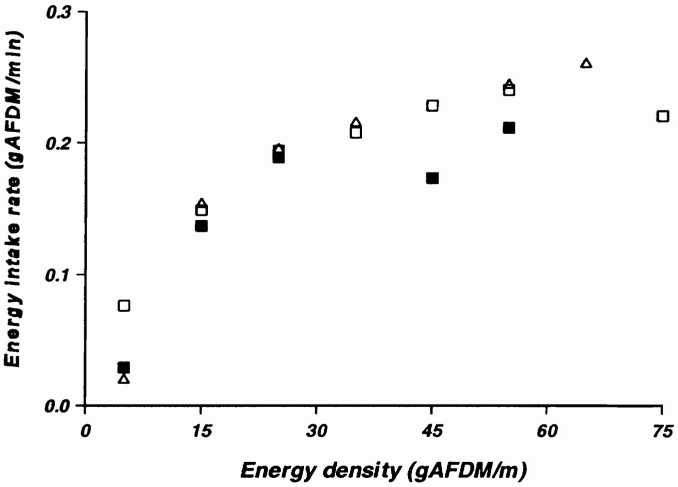


Figure 3.3.24 Functional responses for a range of competitor densities. Displayed data are the predicted mean intake rate for energy densities grouped into 10 gAFDM.m^{-2} categories. Functional responses are shown for competitor densities <100 birds/ha (open triangles), 100-500 birds/ha (open squares), and 500+ birds/ha (filled squares).

This shows that interference has an impact on intake rates, but that this impact is small in comparison with the variation in intake rates generated by differences in the density of available energy in the sand. We quantified this by comparing the predicted maximum intake rates generated using the functional response model which did not include the effects of competitor density (***functional response model***), with the predicted maximum intake rates for the model including these effects (***interference model***). Both models should provide comparable predictions of the mean intake rate for a given energy density, but any variance in the intake rate around this mean value due to interference would not be predicted by the functional response model. As the effect of interference on intake rates becomes stronger, we would expect the correlation between the predicted values of the two models to decrease from a value of 1 (i.e. no effect of interference on intake rates) towards 0. In fact, the correlation is 0.923 (Figure 3.3.25), suggesting that the variance in intake attributable to interference is small compared to that attributable to the density of energy available to the birds in the sand. Under these circumstances, it is not surprising that there is a weak and non-significant negative correlation between the predicted maximum intake rate generated by the interference model and the observed density of competitors (r = -0.142, n = 86, P = 0.19).

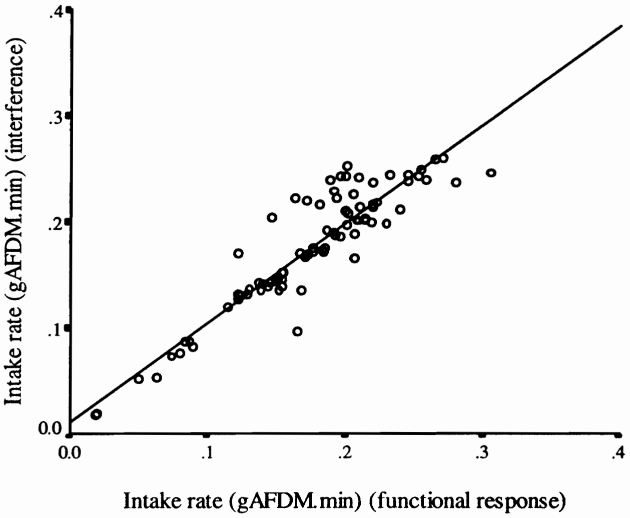


Figure 3.3.25 The relationship between intake rates (gAFDM.min^{-1}) predicted by the interference and functional response models. The relationship is described by the regression equation: $y = 0.013 + 0.925x$, which provided a highly significant fit to the data ($R^2_{adj} = 84.9\%$, $n = 86$, $P < 0.0001$).

Model tests: To test the functional response model we used prey remains data to estimate observed intake rates for birds feeding in particular locations, during each tidal cycle during the winter (see section 3.3.1.5). Whilst the prey remains data provide an estimate of the mean intake rate of birds feeding over a particular ebb tide period, they do not necessarily provide an accurate estimate of how intake rates change in response to a change in competitor density, especially as competitor densities differed between birds we observed. Therefore, to test the predictions of the interference model we used the foraging observations data. Our analysis was limited to observations of birds conducted during late winter, when observed intake rates were close to the maximum predicted by the functional response model. In using the foraging observations data we implicitly assume that these data provide a reliable estimate of intake rate, which seems a reasonable assumption given that intake rates based on the foraging observations and prey remains data were significantly correlated during this period (r = 0.472, n = 22, P = 0.027), and there was no significant difference in the mean intake rate, estimated using the different data (paired t-test: $t = 0.59$, $n = 22$, $P = 0.56$).

Comparisons of observed and predicted intake rates, using predicted values for both the functional response and interference models, are given in Figure 3.3.26. If the interference model provided an improvement in the description of observed intake rates we would expect that the model's predictions should provide a better fit to the observed data than the predicted values from the functional response model. However, this was not the case, both models providing a comparable fit to the observed data.

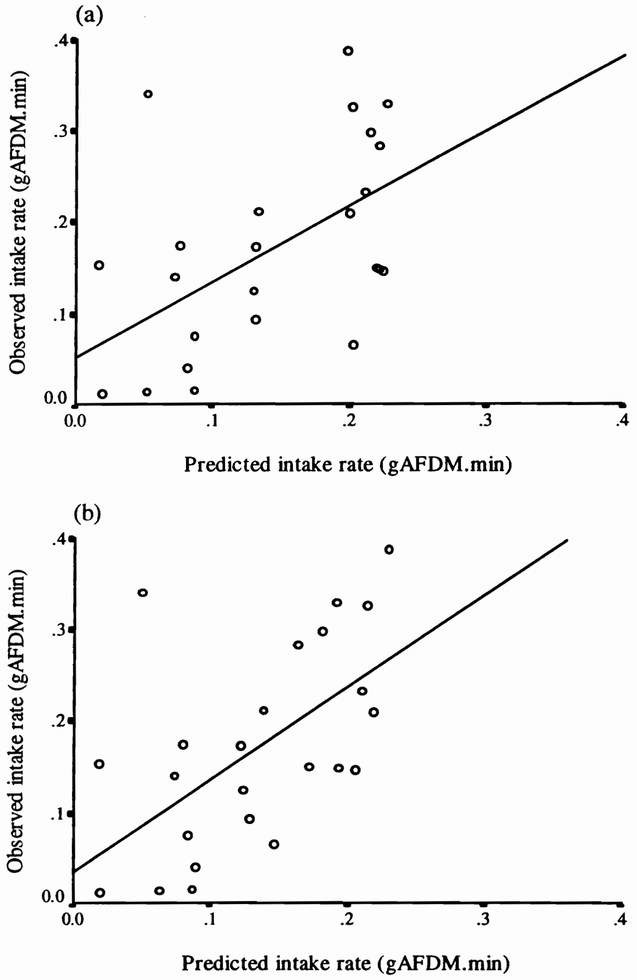


Figure 3.3.26 The relationship between observed intake rates and (a) predicted values from the interference model, and (b) predicted values from the functional response model. The relationship in (a) is described by the regression equation: $y = 0.052 + 0.825x$, which provided a highly significant fit to the data ($R^2_{adj} = 27.1\%$, $n = 24$, $P = 0.0045$), and in (b) by the regression equation: $y = 0.0363 + 0.1005x$, which provided a highly significant fit to the data ($R^2_{adj} = 33\%$, $n = 24$, $P = 0.0016$).

3.3.2.4 Discussion

Intake rates in hammerers searching by probing increased with increasing competitor density, as well as being significantly greater when energy demands were high. These increases were the result of the encounter rate i.e. the number of cockles found per unit of searching time, increasing as competitor density increased. These results suggest that these birds often harvested energy below the maximum possible rate (see also section 3.3.1.6). Why do intake rates increase with increasing competitor density?

The fact that birds are able to increase their intake rates, implies that maximizing their intake rate involves costs, in addition to those associated with searching for and handling prey. One possible cost is that searching for food and searching for predators are conflicting behaviours i.e. cannot be conducted simultaneously. Under these circumstances, it may only be beneficial to incur such costs when energy demands are high, or when the risk of being predated is reduced, as might occur, for example, when a bird is feeding in a relatively dense group (see also section 3.3.1.6).

For hammerers searching by touch, there was evidence of interference as competitor density increased, which acted by (1) reducing the probability of successfully opening a cockle, and by (2) increasing the handling costs of cockles by reducing the likelihood that they could be opened *in situ*. It should be noted that these effects were not the result of kleptopararsitism, since few cockles were stolen by either other oystercatchers or common gulls (*Larus canus*). Birds were simply more likely to abandon cockles they had found as competitor density increased. Although the effect of interference was significant, its impact on intake rates was small compared with the importance of the density of available energy in the sand. As a result, there was no significant negative correlation between the intake rate predicted by the interference model, and competitor density, for the range of energy densities experienced by the birds we observed. This contrasts with the situation in oystercatchers feeding on mussels, in which intake rates significantly decline in the presence of competitors (Zwarts & Drent 1981; Sutherland & Koene 1983; Stillman *et al.* in press). Furthermore, there was little difference between the predictive power of the functional response and interference models, again suggesting that the effects of interference on intake rates was relatively weak.

Why does the effect of competitor density differ between hammerers using different searching strategies? It is worth noting that the probability of successfully opening a cockle also decreases as competitor densities increase in hammerers searching by probing, for a given size class (logistic regression: $\chi^2 = 6.41$, df = 1, $P < 0.025$), but this effect is more than compensated for by the increased rate at which birds encounter prey as competitor densities increase. Furthermore, there was evidence that the encounter rate of birds searching by touch during early winter increased as competitor density increased (encounter rate with cockles 22-29mm per second of searching time vs competitor density: $r = 0.751$, $n = 62$, $P < 0.0001$), although the encounter rate with prey was significantly lower than that predicted by the encounter rate model based on touch at this time (see section 3.3.1.4.2). In this respect, therefore, birds using different searching strategies experience a similar mechanism of interference as competitor density increases, as well as comparable effects encounter rates. The only difference is that birds searching by touch do not increase their encounter rates as competitor density increases during late winter. However, this is not surprising given that these birds are encountering cockles at the theoretical maximum rate possible, whereas birds searching by probing and birds searching by touch during early winter are, apparently, capable of increasing their intake rates when necessary, and hence have the potential to adjust their intake rates to environmental conditions.

Under these circumstances, the relevant distinction is that birds searching by touch on an ebb tide do attempt to maximise their intake rates under certain conditions eg. during late winter, whereas birds searching by probing on flood tides adjust their intake rates in response to changes in energy demands and competitor densities. Understanding this difference requires a more complete understanding of the tidal routine of oystercatchers wintering in the Burry Inlet. Birds show a distinct tidal feeding pattern, with large numbers of birds feeding on the ebb tide, and fewer birds returning to feed on the subsequent flood tide. Birds roost over the low water period i.e. about 2 hours either side of low water. McNamara *et al.* (1993) show that foraging birds could show a variety of daily routines (= tidal routines) in their feeding behaviour depending on the costs and benefits of different decisions. For oystercatchers, benefits are determined by energy demands which tend to peak during mid-winter, and costs might include a mass-dependent energy or predation cost, or a predation cost associated with searching for and handling prey. A more complete understanding of these costs is likely to provide an insight into (1) seasonal changes in intake rate observed in hammerers searching by touch; (2) the relationship between intake rates, energy demands, and competitor density observed in hammerers searching by probing; and (3) tidal routines in feeding behaviour.

3.4 OYSTERCATCHERS AND SUPPLEMENTARY PREY

J D Goss-Custard, R W G Caldow, S E A le V dit Durell, R Swinfen & A D West

3.4.1 Introduction

From October onwards, Oystercatchers on the Exe estuary that feed on mussels at low tide frequently feed on prey other than mussels before the receding tide has exposed the mussel beds and after the advancing tide has covered them. Some feeding is done by mussel-feeding birds on the upshore flats where a variety of supplementary prey is taken. Many mussel-feeders also use the fields over high tide, when all the intertidal flats are inaccessible. Here, they feed mainly on earthworms (Goss-Custard & Durell 1983). It is believed that in many parts of their winter range such supplementary food supplies enable Oystercatchers, that might otherwise lose condition and starve over the winter, to survive for longer (Goss-Custard *et al.* 1996c). It is also likely that Oystercatchers prevented from feeding on shellfish at low tide by disturbance would compensate for lost time by feeding on these supplementary foods at other stages of the tidal cycle, unless frozen ground prevents them from doing so (Goss-Custard & Durell 1987). This response could reduce the impact of shellfishing on the body condition and survival of Oystercatchers. It was therefore very important to incorporate an option in the model which allowed birds to feed on supplementary food supplies.

3.4.2 Use made of supplementary supplies by mussel-feeding Oystercatchers

Prior to the start of this contract, an intensive study was made on the Exe estuary over the winters of 1989-90 and 1990-91 to quantify the use made by mussel-feeding Oystercatchers of upshore and terrestrial supplementary food supplies. From mid-September to mid-March, we searched for individually colour-ringed Oystercatchers feeding during the low-tide exposure period on the main mussel beds of the estuary (beds 3, 4, 20, 26, 30 and 31). When an individual was located, its age and main feeding method were recorded; although individuals do switch between hammering and stabbing into mussels, most individuals rapidly demonstrate a clear preference for one or other technique. Between early December and early February, when most use is made of the supplementary food supplies, regular searches for these marked individuals were made on all the main upshore feeding areas as the tide receded and advanced and, over high water, in all of the fields where Oystercatchers fed. The upshore areas (and their predominant sediments) were (i)the Bite (muddy sand), in the south-west corner; (ii) Cockle Sand (muddy sand), in the south-east corner; (iii) Sowden End (mud for clam-eaters; rock for mussel- and winkle-eaters), just south of Lympstone on the east side, and (iv) Lower Halsdon (mud), also on the east side. The fields were located all around the estuary, the boundaries of the study area being given in Goss-Custard & Durell (1983). Marked individuals were watched until it became clear whether they were feeding rather than roosting. This work enabled the use made of upshore and terrestrial food supplies by birds of different age and feeding method to be established.

Birds of all ages and both feeding techniques fed in the upshore feeding areas and fields at some stage during the winter (Table 3.4.1). Sixty-eight per cent of all ringed mussel-feeders made use of supplementary food supplies at some point. Approximately 40% of individuals were only seen in the fields and 14% were only seen in the upshore areas while 13% were seen in both. Juveniles, of which almost all stab into mussels (Goss-Custard *et al.* 1993), were most likely to be seen feeding in fields at high tide, confirming an earlier finding (Goss-Custard & Durell 1983). However, even amongst older birds, a substantial proportion, especially of immatures, used one or both of the supplementary food supplies, apparently irrespective of the feeding method they used to open mussels at low tide. It is therefore assumed in the model that birds of all ages and feeding methods are able to utilise supplementary food supplies in both upshore intertidal and terrestrial habitats.

Table 3.4.1 Numbers of mussel-feeders involved in supplementary feeding in the fields over high water (HWF) and in upshore intertidal areas on the receding and advancing tide (TR/TA), or both. The data are sub-divided by bird age and according to whether the bird opened mussels by hammering (either dorsally or ventrally) or by stabbing.

age	feeding method	HWF only	TR/TA only	both	neither
adult	hammerer	5	2	1	15
	stabber	3	0	1	4
immature	hammerer	20	5	4	11
	stabber	15	6	9	6
adult & immature	hammerer	25	7	5	26
	stabber	18	6	10	10
juvenile	stabber	7	1	0	2

3.4.3 Intake rates on upshore supplementary prey

3.4.3.1 Prey species taken

The prey species taken during the winters 1989-90 and 1990-91 on the upshore flats by individually-marked mussel-feeding Oystercatchers of known feeding method are detailed in Table 3.4.2. The data were obtained in the Bite, in the south-west corner of the estuary, and at Lower Halsdon, on the east side, two very important upshore feeding areas. No data are available from Cockle Sand, where many Oystercatchers also feed as the tide recedes and advances because we were unable to find any marked individuals there. Observations on unmarked birds on Cockle Sand in later years revealed that most birds fed on cockles or winkles, with a large minority also taking mussels, mainly using the ventral hammering technique.

Many individually marked Oystercatchers were seen in the Bite and at Lower Halsdon on several occasions through a winter and each bird always took the same type of prey whenever it was seen. The Table shows the numbers of individuals that took each of the five prey types recorded. All five species were taken by birds of each feeding method and were mussels *Mytilus edulis*, cockles *Cerastoderma edule*, winkles *Littorina* spp., clams *Scrobicularia plana* and ragworms *Hediste diversicolor*. There were apparent tendencies for (i) more hammerers (six dorsal hammerers and seven ventral hammerers) than stabbers to eat ragworms; (ii) more hammerers (four dorsal hammerers and five ventral hammerers) than stabbers to eat winkles, and (iii) more stabbers than hammerers to eat cockles. However, the sample size is too small, and the representativeness of the data too uncertain, to draw such conclusions with confidence at this stage. Therefore, in the model, we assumed that both hammerers and stabbers were equally likely to take each of these prey species as the tide ebbed and flowed.

Table 3.4.2 Prey species taken by Oystercatchers feeding on upshore areas on the receding and advancing tides. Data are the number of marked individuals seen taking each prey species, according to their age and whether they opened mussels at low tide by hammering or stabbing. No individually-marked juveniles were seen feeding upshore.

	adults		immatures		both ages	
	hammerers	stabbers	hammerers	stabbers	hammerers	stabbers
mussels	1	4	1	0	2	4
cockles	4	17	0	3	4	20
winkles	7	1	2	0	9	1
clams	2	4	4	4	6	8
ragworms	9	2	4	0	13	2

3.4.3.2 Intake rate on each prey species

Unmarked individuals were watched between mid-December and mid-February during 1994-95 and 1995-96 in the four main areas used by mussel-feeding Oystercatchers as the tide ebbs and flows. Data were collected over a period of 1-1.5 hours before and after the main mussel beds were exposed and covered by the tide; this was the period during which most individuals were seen on these upshore supplementary areas. A bird was selected at random and watched for five minutes. Depending on the variability of the data, 20-44 such five-minute data points were collected for each prey-type/site on both the receding and advancing tides. At Sowden End, data on winkle- and mussel-feeders could only be collected on the advancing tide. The identity and length of each prey taken were recorded, using standard techniques. Thus prey length was measured against bill length in birds eating cockles, clams and, at Sowden End, mussels. These estimated lengths were later corrected for individual observer bias (Goss-Custard *et al.* 1987). For mussel-eaters on Cockle Sand, samples of empty mussels recently opened by Oystercatchers were collected because the birds were feeding at too great a distance for prey size to be assessed visually. The size of winkles taken was also measured from samples of opened prey because the prey were too small to judge their length accurately. Most cockle-eaters were stabbers, most mussel-eaters were ventral hammerers and most winkle-eaters were hammerers. No birds consistently ate ragworms during the present study so the upshore intake rate on this prey species was not determined.

Samples of 40 living prey were taken from each area in the middle of the one-two month period during which data for one prey species/site were collected. The relationship between AFDM and length were obtained using standard techniques (eg. Durell & Goss-Custard 1984) and were used to calculate the dry ash-free mass of each prey item taken by Oystercatchers. The intake rates of the birds were then calculated from the number and lengths of each prey taken per five minute observation period. Virtually all birds took only one prey species over the five minute period they were watched.

The procedure in the statistical analysis of the data was to regress intake rate against the date (days elapsed since January 1) and the time (minutes elapsed since the last high water). Data collected on the receding and advancing tides were analysed separately in case some variables were correlated with intake rate at one stage of the exposure period but not the other. Of the 18 data sets analysed, intake rate changed with date in only one case (cockle-eaters, Lower Halsdon, tide advancing). The general absence of a seasonal trend probably reflects the short period (1-2 months) over which data were collected. Intake rate changed with time over the period during which the tide was either receding or advancing only twice (cockle-eaters, Lower Halsden, tide advancing; clam-eaters, Sowden End, tide advancing); as an example, the trend against time in cockle-feeders at Lower Halsdon is shown in Figure 3.4.1. In all three cases, the crude mean intake rate was virtually the same as the rate predicted by the regression equations from the median values of the independent variables. Therefore it made little difference to use the crude mean values to compare these intake rates with those obtained from the other 15 data sets.

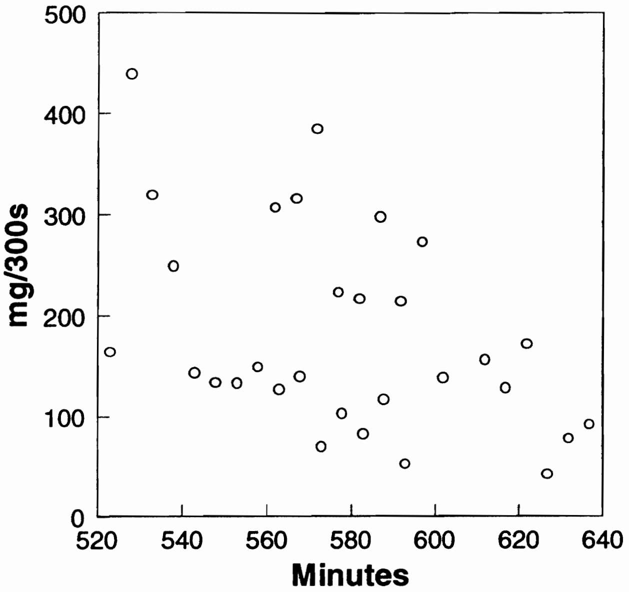


Figure 3.4.1 The intake rate (mgAFDM/300s) of Oystercatchers feeding on cockles on the advancing tide at Lower Halsden in January and February 1995 in relation to the time elapsed since the preceding high tide.

Intake rate differed between the periods when the tide was receding and when it was advancing in only two out of the eight prey-type/sites for which data were available. At Cockle Sand in 1995, the intake rates (mgAFDM/300s) on the receding and advancing tides were: 108 (SE=13.5, n=24) and 182 (SE=18.4, n=30) respectively, with P=0.0023 (t-test); in clam-eaters at Sowden End in 1995, the rates were: 231 (SE=21.4, n=24) and 285 (SE=19.3, 40) respectively, with P=0.005 (t-test). None of the other comparisons were significant at the 5% level.

As the differences between mean rates in the two periods were generally either not significant or quite small, and as the sample sizes were the same or very similar, data for both periods were combined to estimate the mean intake rate per prey type/site (Table 3.4.3). Mean rates varied from 65 to 403 mg/300s, with an overall mean of 178 mg/300s. This mean is biased towards cockle-eaters, however. The mean of the mean values for each prey type are therefore also shown in Table 3.4.3. The mean of the means for cockles and mussels were similar as were those for winkles and clams, although only one mean was available in the latter case. The limited data thus suggest that, in the upper shore-levels, there may be a difference between the intake rates of birds eating cockles or mussel eaters and birds eating winkles or clams. But clearly, with the sample size as yet so small, this conclusion may be premature. Furthermore, the difference between the prey types taken in upshore areas by birds that hammer and stab mussels over low tide is as yet too indistinct to ascribe particular supplementary prey types to birds with a particular feeding method. It is therefore assumed in the model that Oystercatchers supplementing their low tide consumption of mussels by taking other prey at higher shore levels as the tide recedes and advances achieve an intake rate in winter of 202mg/300s (SE=31.4, n=4), the mean rate recorded on the four prey types studied during this contract. Encouragingly, this is close to value of 178mg/300s (SE = 20.9, N = 22) obtained in adult Oystercatchers feeding in upshore ares in winter on ragworms in the Baie de Somme, France (P. Triplet, unpublished information).

As the birds studied on the receding and advancing tides were unmarked, we were unable to ascertain whether they included many individuals that fed on mussels at low tide. In fact, it is likely that many of them specialised throughout the entire exposure period on the prey species they were seen taking as the tide receded and advanced. Probably, such birds fed faster on upshore prey than did birds that were mussel-feeders over low tide. Accordingly, the value used in the model of 202mg/300s for the upshore intake rate of mussel-feeders is probably rather high, although by an amount that cannot be estimated at present.

Table 3.4.3 Intake rate (mgAFDM/300s) of Oystercatchers eating four kinds of prey in upshore areas as the tide recedes to, and advances from, the mussel beds. (A) The mean values for each site/prey type/year. (B) The means for each prey type of the site/year means shown in section (A).

	prey	year	site	mean	se	n
(A)	Cockles	1995	Lower Halsden	148.9	12.8	54
		1995	Cockle Sand	101.1	6.7	61
		1995	Bite	159.7	14.1	70
		1996	Cockle Sand	97.9	8.7	79
		1996	Bite	220.1	24.1	80
	Mussels	1995	Sowden End	64.7	13.3	20
		1996	Cockle Sand	236.1	14.3	84
	Winkles	1995	Sowden End	90.8	10.8	20
		1996	Cockle Sand	403.3	24.3	30
	Clams	1995	Sowden End	264.6	14.8	64
(B)	Cockles			145.5	22.4	5
	Mussels			150.4	85.7	2
	Winkles			247.5	156.3	2
	Clams			264.6	-	1

3.4.4 Intake rates feeding on earthworms in fields

3.4.4.1 Study area and methods

Oystercatchers feeding in fields over high water were watched in January and February 1985 and, under the present contract, in January and February 1996. In both periods, observations were made in a field at Cockwood, on the west side of the estuary, where mussel-feeding birds from the nearby beds 3 and 4 have regularly fed in the short, heavily-grazed grass, since before 1976. Oystercatchers were watched from a hide placed on an elevated platform at the edge of the field. The hide was entered before the birds arrived from the estuary as high water approached. Individuals were picked at random. Most birds studied were not individually known and so their feeding method and diet at low water on the estuary was unknown. However, many of the birds that fed in the field were seen to come over the sea wall from the adjacent mussel beds, so many of the birds would have been mussel-feeders.

Intake rate was measured by assessing against bill length the size of each worm taken during observation periods of five minutes duration. No observer bias correction was applied as studies of Oystercatchers eating ragworms on the estuary found no observer bias with visual estimation of worm length (Durell *et al.* 1996). A number of variables thought likely to affect intake rate in fields were measured. As rain brings earthworms to the surface where they may be more easily caught by Oystercatchers, we recorded whether it was raining during the observation period. As the temperature of the soil affects worm activity, and probably their availability to Oystercatchers, soil temperature was read from the hide using a telescope from a mercury thermometer pushed 2cm into the soil. As the density of competitors may also affect intake rate in Oystercatchers (Ens & Cayford 1996), we took three alternative measurements of competitor density at the beginning and end of each five minute observation period: (i) the distance from the subject bird to the nearest neighbour, in bird lengths; (ii) the numbers of feeding and resting birds within 2m of the subject, and (iii) the numbers of feeding and resting birds within 5m. Field tests had previously shown that all three measurements can be judged by eye with reasonable precision (Cayford 1988). The number of aggressive encounters between the subject bird and other Oystercatchers, and which bird in the dyad initiated the attack, was also noted.

Regression equations relating the AFDM of a worm to its length were used to calculate the intake rate in each five minutes from the numbers and sizes of worms taken. Forty worms over a wide range of sizes were collected and processed to derive the regression equation. Worms were dug from the surface soil and manipulated until they were elongated. We measured this stretched length, as this seemed most closely to approximate the state of the worms as they were pulled from the soil by Oystercatchers. Samples were collected in 1995 to estimate AFDM in 1986 as a reliable worm sample from that earlier study period was not available. Another sample was taken in 1996 to estimate AFDM of the worms in that year. The AFDM of worms of a given length in the two samples were not statistically different (Figure 3.4.2). Nonetheless, the separate equations were used to calculate intake rates in 1986 and 1996.

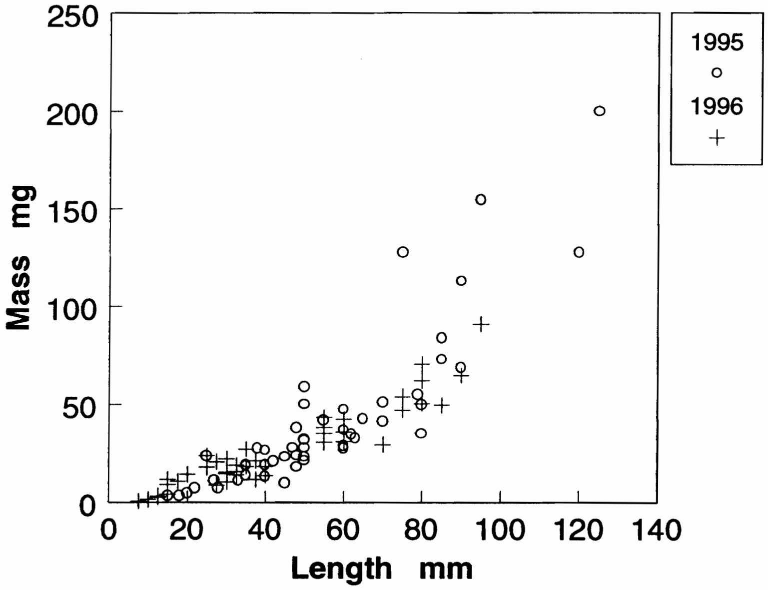


Figure 3.4.2 The ash-free dry mass of worms of different length collected from Cockwood field, adjacent to the Exe estuary, in February 1995 and February 1996.

3.4.4.2 Intake rate in relation to Oystercatcher age

In 1986, observations were made in 85 matched pairs in which an adult and then a juvenile feeding in the same place were watched in succession; one juvenile record was lost, so the total sample size was 169. There were no significant differences between the two age classes in any of the measurements made (Table 3.4.4). The data for the two age classes were therefore combined. In a multiple regression analysis of all the data, intake rate was significantly correlated with temperature in the quadratic and with a 0/1 dummy variable expressing whether or not it was raining as the data were being collected. When added to this suite of variables, none of the variables measuring competitor density added significantly to the regression, although all took the expected sign: for nearest neighbour distance, $P = 0.510$; for feeding bird numbers within 2m, $P = 0.332$; for total bird numbers within 2m, $P = 0.303$; for feeding bird numbers within 5m, $P = 0.138$; for total bird numbers within 25m, $P = 0.128$. There is no evidence, therefore, of any significant effect of competitor density on intake rate once the effect of soil temperature and rainfall had been taken into account.

All the observations made in 1996 were of adult birds. As we had found no difference between the intake rates of adults and juveniles in 1986, all the data from all birds watched in both 1986 and 1996 were combined. In a multiple regression in which intake rate was regressed against temperature in the quadratic and the dummy variable for rain, a further 0/1 dummy variable expressing whether the data were collected in 1986 or 1996 was not significant ($P = 0.141$). Therefore, the data for both years could be combined to calculate the regression between intake rate and temperature and rainfall. The equation is detailed in Table 3.4.5.

Table 3.4.4 Comparison between the foraging behaviour of adult and juvenile Oystercatchers feeding in Cockwood field in 1986.

	Adults		Juveniles	
	mean	SE	mean	SE
Intake rate (mg AFDM/300s)	112.6	14.4	113.5	12.9
Worms/300s	5.4	0.3	5.6	0.5
Nearest neighbour	40.0	5.6	34.3	4.2
Birds within 2m	1.7	0.2	1.8	0.2
Birds within 5m	4.7	0.5	5.1	0.5
Attacks against others/300s	0.29	0.06	0.32	0.07
Attacks on subject/300s	0.32	0.07	0.20	0.05
Total encounters/300s	0.61	0.10	0.52	0.08

Table 3.4.5 Multiple regression equation relating Oystercatcher intake rates in fields to soil temperature, its square, and, in the left-hand column, whether or not it was raining. In the right-hand column, only data from dry days were included in the analysis.

	Wet and dry days	Dry days only
Intercept SE, P	-1.15 18.29, 0.950	-1.98 17.69, 0.911
Temperature SE, P	61.16 9.24, 0.000	64.67 9.09, 0.000
Temperature^2 SE, P	-5.95 0.94, 0.000	-6.50 0.93, 0.000
Wet=1; dry=0 SE, P	78.03 18.44, 0.000	-
adjusted R^2 (%)	20.2	16.8
Number observations	288	243

We had expected intake rate to increase with soil temperature since at low temperatures worms are less active and, probably, more deeply buried (Rabe, Prince & Goodman 1983). But is was a surprise that, as the temperature rose above 4-5^{o}C, intake rate again began to fall (Figure 3.4.3). We do not know the cause of this but can speculate that earthworms retreat deeper into the soil as the surface layers became warm.

For the model, it was decided that the equation for dry days, though usually wet ground, should be used as this was typical of most winter days. It is assumed in the model that there is a close relationship between the average daily air temperature, which is used in the model, and the average daily temperature of the surface of the soil. This is very likely to be the case as the grass where Oystercatchers feed is usually very short.

As we were unable to distinguish between stabbing and hammering birds as we watched them in the field, it is necessary to assume that birds using either feeding method forage on earthworms equally efficiently. In fact, this is rather unlikely as the sharper bill-tip of mussel-stabbing birds would be expected to give them an advantage in capturing earthworms. At present, the magnitude of this potential advantage cannot be determined, and measuring it remains a priority for future field research. In the meantime, the equation for dry conditions in Table 3.4.5 describes the effect of ambient temperature on intake rate in the fields. It is used to predict the intake rates of Oystercatchers that feed in fields at high tide to supplement their inadequate consumption of mussels over the low water exposure period.

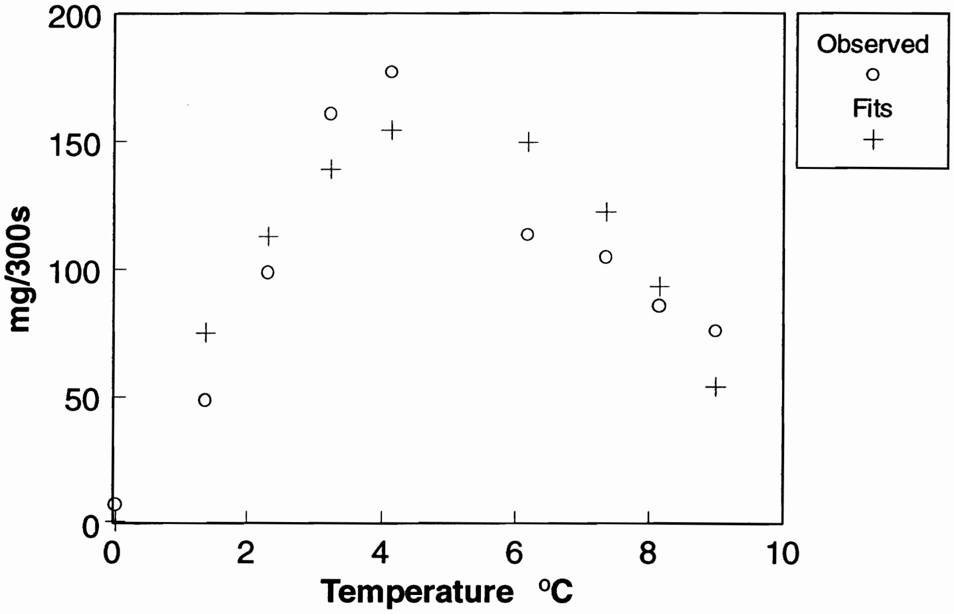


Figure 3.4.3 The intake rate of Oystercatchers (mgAFDM/300s) feeding on earthworms in Cockwood field, adjacent to the Exe estuary, in relation to the surface temperature of the soil. Circles show the observed mean for the data collected within a one degree temperature range (eg. 0-0.99°C). Crosses show the predicted intake rate using the 'dry' equation from Table 3.4.5.

3.5 KNOTS AND COCKLES

R A Stillman

3.5.1 Introduction

This section describes the knot functional response model, which predicts the size selection and intake rate of knots feeding on cockles. The foraging behaviour of knots has been studied intensively previously, and so the model is based on published studies rather than any work performed under the present contract. In particular, we use the models developed by Zwarts & Blomert (1992) and Piersma *et al.* (1995). These models are based on fundamental aspects of knot foraging behaviour and have successfully predicted the intake rates of knots feeding on cockles under a range of conditions (Piersma *et al.* 1995). They should therefore produce reliable predictions under any situation arising in the shorebird-shellfish model.

The knot foraging model shares many features with that developed for oystercatchers feeding on cockles (section 3.3), but differs in two major ways due to differences in the foraging behaviour of knots and oystercatchers. First, oystercatchers and knots differ in the method used to consume bivalve prey; oystercatchers either open or break into shells, and then consume the flesh (Hulscher 1996), whereas knots swallow the prey whole with the shell intact (Prater 1972). As a consequence, the maximum size of prey consumed by knots is limited by the width of their gape. The knot foraging model therefore limits the maximum size of prey consumed. Second, interference has frequently been observed in oystercatchers (see Ens & Cayford 1996 for an overview), but has not been observed in knots (Goss-Custard 1970; Piersma *et al.* 1995). Therefore, the knot foraging model does not incorporate interference; intake rate is determined solely by the food supply available and is independent of competitor density.

3.5.2 The model

The functional response of an animal consuming prey of uniform size may be modelled using Holling's disk equation (Holling 1959a,b).

$$\frac{E}{T} = \frac{aDE}{1 + aDH} = \frac{\lambda E}{1 + \lambda H} \qquad 3.5.1$$

where E/T = energy intake rate, E = energy content of the prey, a = instantaneous area of discovery (i.e. the rate at which the animal searches the habitat for prey), D = prey density, H = handling time, and λ = prey encounter rate = aD. Two assumptions of this model are that both the instantaneous area of discovery and handling time are unrelated to prey density. Piersma *et al.* (1995) has shown that both of these assumptions hold for knot feeding on cockles across the full range of densities observed under natural conditions. The disk equation therefore provides a valid description of knot foraging behaviour.

Foraging knots will encounter a range of cockle sizes, and so the simple disk equation (in which all prey are assumed to be of equal size) is too limited. Therefore, and following Zwarts & Blomert (1992), we use the multiple size class version of the disk equation (Charnov 1976).

$$\frac{E}{T} = \frac{\sum \lambda_i E_i}{1 + \sum \lambda_i H_i} \qquad 3.5.2$$

where λ_i = encounter rate with cockles of size class i, E_i = energy content of size class i, and H_i = handling time of size class i. As maximum prey size is limited in knots, equation 3.5.2 is only applied to a limited range of size classes. All size classes of greater length than the maximum consumable length (L_{max}) are excluded from calculations.

3.5.2.1 Encounter rate (λ)

Knots search for prey by rapidly probing the substrate with their bill (Prater 1972). Prey are then detected either by touch, or some other sensory mechanism. Piersma *et al.* (1995) showed that models assuming that touch is the only detection mechanism, accurately predict observed encounter rates with cockles, which are usually shallow buried (Zwarts & Wanink 1989). In contrast, touch models under predict encounter rates with more deeply buried prey, indicating that other sensory mechanisms must be used to detect these prey. We therefore use a touch model (Piersma *et al.* 1995) to predict encounter rates with cockles, but note that the model will not be applicable to more deeply buried prey species.

The touch model assumes that each time the bill is inserted into the substrate, prey will be detected within a given area. Encounter rate with a given size class of cockle (λ_i) can then be found from

$$\lambda_i = (1 - v)pA_iD_i \tag{3.5.3}$$

where v = the proportional overlap between the area covered by successive probes, p = the probing rate, A_i = the area within which a cockle of a given size class i can be detected and D_i = the density of cockles of size class i. A_i can be expressed in terms of cockle surface area in the horizontal plane (touch area) and the knot bill tip area, by assuming a circular touch area and a rectangular bill tip (Zwarts & Blomert 1992).

$$A_i = \pi r_i^2 + 2yr_i + 2xr_i + xy \tag{3.5.4}$$

where r_i = the radius of the cockle surface area in the horizontal plane (touch radius), x = the width of the bill tip, and y = the depth of the bill tip. Encounter rate can therefore be expressed in terms of knot behaviour and the dimensions of cockles and the bill tip.

All parameter values needed to calculate encounter rate have been estimated in previous studies (Table 3.5.1). Probing rate and probe overlap in cockle-feeding knot were estimated by Piersma *et al.* (1995). Zwarts & Blomert (1992) related cockle touch area to length using an allometric equation, and calculated r_i by assuming a circular touch area. Zwarts & Blomert (1992) estimated the width and depth of the knot bill tip. The predicted encounter rate derived from these parameters increases as both the density and size of cockles increase (Figure 3.5.1a).

3.5.2.2 Handling time (H)

Piersma *et al.* (1995) estimated the relationship between handling time and cockle size for five individual knots. Handling time increased with increased cockle size, but at different rates for each of the experimental birds. We use the mean rate of increase observed in these birds (Table 3.5.1). The smallest cockles used by Piersma *et al.* (1995) measured 6mm and had handling times of approximately 1s. The handling time-size equation used by Piersma *et al.* (1995) assumes that handling time decreases to zero for prey items below this range. In reality, handling time must always be greater than zero and so we use an extension of their relationship in which handling time has a lower limit (H_{min}). Following Zwarts & Blomert (1992), this lower limit is taken as the time taken for a knot to transport a small piece of flesh up its bill (Gerritsen 1988; Table 3.5.1). Handling time therefore decreases with decreasing cockle size until the lower limit is reached (Figure 3.5.1b).

3.5.2.3 Maximum size of cockle consumed (L_{max})

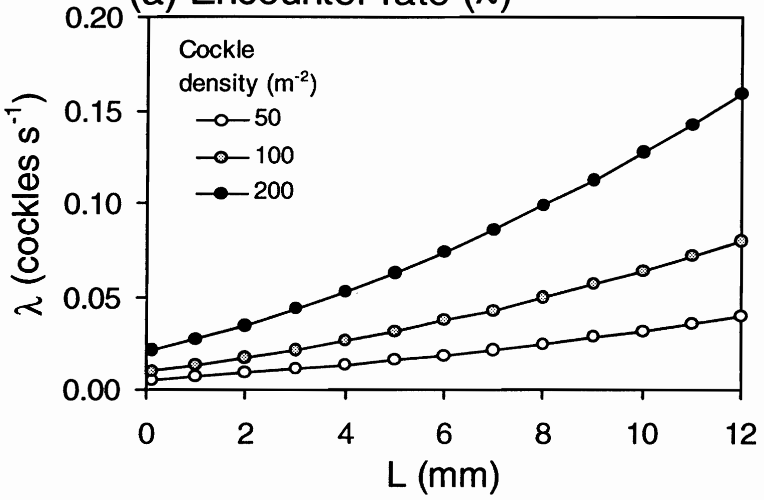
Zwarts & Blomert (1992) estimated the maximum size of cockle consumed by knots under field conditions (Table 3.5.1).

3.5.2.4 Cockle energy content (E)

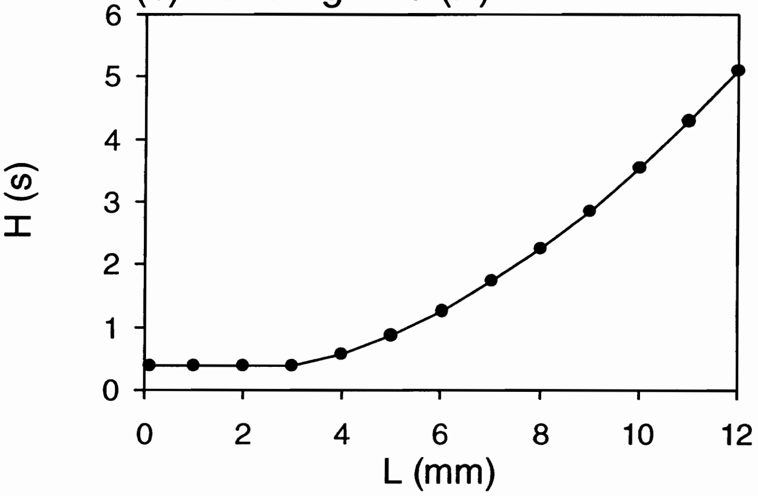
It is assumed that the energy density of cockle flesh is not related to cockle size. Therefore, for the purpose of calculating intake rate, energy content can be expressed as cockle flesh content measured as ash-free dry mass. In the shorebird-shellfish model, the relationship between flesh content and size will vary during the course of simulations (see chapter 4), but for presentation a standard relationship, referring to September in the Wadden sea (Zwarts 1991), is used here (Table 3.5.1; Figure 3.5.1c).

Table 3.5.1 Parameter values used to model the foraging behaviour of knots feeding on cockles. L_i = length of a cockle in size class i.

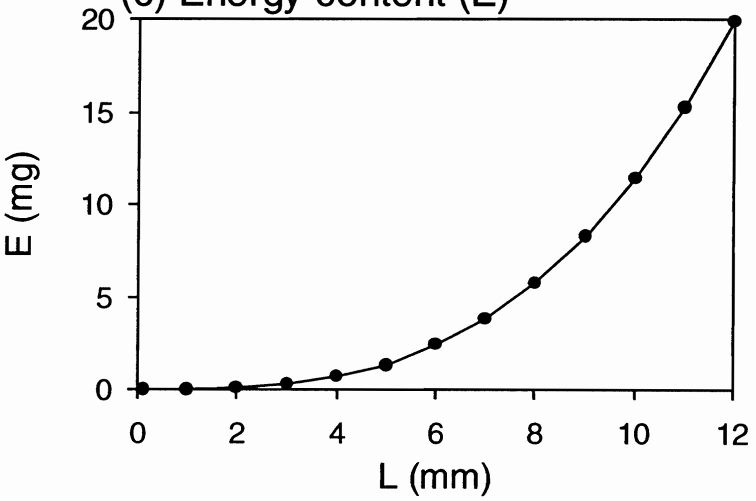
Parameter	Value	Units	Source
Bill tip width (x)	3	mm	Zwarts & Blomert 1992
Bill tip depth (y)	7	mm	Zwarts & Blomert 1992
Cockle touch area (A_i)	$0.340L_i^{2.07}$	mm^2	Zwarts & Blomert 1992
Cockle touch radius (r_i)	$(A_i/\pi)^{0.5}$	mm	Zwarts & Blomert 1992
Probing rate (p)	9.6	s^{-1}	Piersma *et al.* 1995
Probe overlap (v)	0.5		Piersma *et al.* 1995
Maximum size of cockle consumed (L_{max})	12	mm	Zwarts & Blomert 1992
Handling time (H)	$0.03536L_i^2$	s	Piersma *et al.* 1995
Minimum handling time (H_{min})	0.4	s	Gerritsen 1988
Cockle energy content	$0.012L_i^{2.97}$	mg	Zwarts 1991



(a) Encounter rate (λ)



(b) Handling time (H)



(c) Energy content (E)

Figure 3.5.1 Parameters used to model the foraging behaviour of knots feeding on cockles. L = cockle length. See text and Table 3.5.1 for equations and source references.

3.5.2.5 Profitability

The initial step in calculating prey size selection is to find the profitability (P_i) of a cockle belonging to each size class.

$$P_i = \frac{E_i}{H_i} \qquad 3.5.5$$

The profitability of a size class is dependent on its energy content (E_i), which will decline during the course of winter as cockles lose condition (see chapter 4), and its handling time (H_i), which will be constant (Table 3.5.1). The profitability of a size class will therefore change during simulations over the winter. However, as an example, profitability is calculated using the energy content-size relationship given in Table 3.5.1 (Figure 3.5.2). Profitability is proportional to length in cockles longer than 4mm because E_i is proportional to length cubed and H_i to length squared (Table 3.5.1). The relationship differs for cockles shorter than 4mm because these size classes all have the minimum handling time (Figure 3.5.1b). Although the precise form of the relationship will vary during and between simulations, the general trend that larger cockles are more profitable than smaller ones will not change. This is because flesh content tends to be related to shell volume (i.e. to length cubed) whereas handling time is related to length squared.

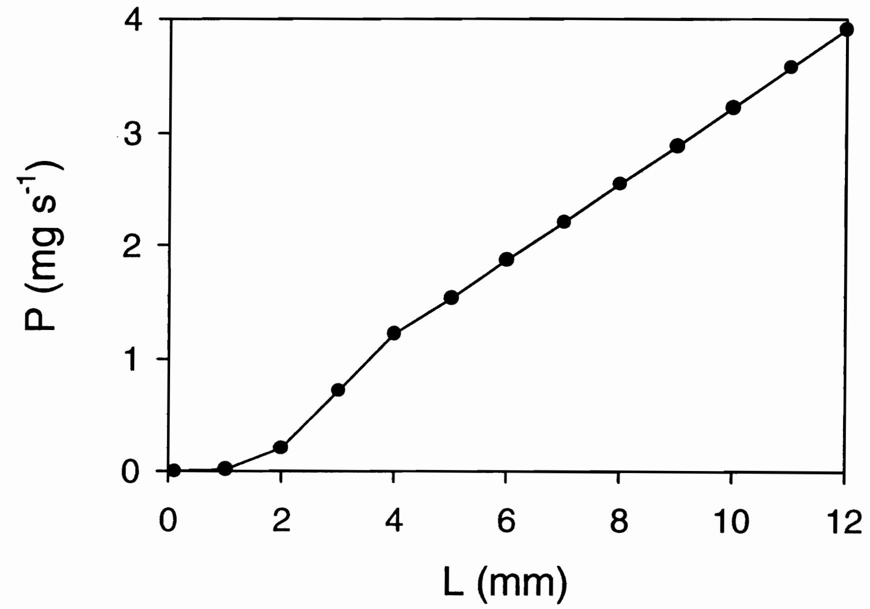


Figure 3.5.2 Example of the relationship between profitability (P) and cockle size (L) across the range of cockle sizes consumed by knots. See Table 3.5.1 for parameter values used to calculate profitability.

3.5.2.6 Size selection and the functional response

Optimal size selection and intake rate are found using equation 3.5.2. The size classes are ordered by profitability and successively added to the diet (starting with the most profitable) until predicted intake rate is maximized. This process yields the optimal set of size classes in the diet and the associated intake rate. As large size classes are more profitable, and are therefore added to the diet first, size selection may simply be expressed as the minimum size class included in the diet. It is assumed that the selected size classes are always consumed when encountered, and so the frequency of each class in the diet (f_i) is equal to its relative encounter rate.

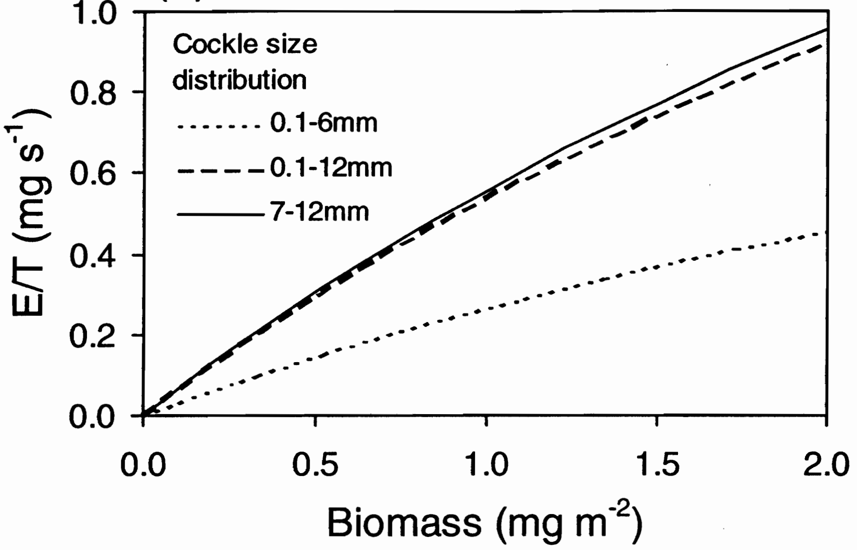
$$f_i = \frac{\lambda_i}{\sum \lambda_i} \qquad 3.5.6$$

The precise size selection and functional response generated in the shorebird-shellfish model will vary according to the size distribution, abundance and energy content of cockles in a given simulation. As an example, three possible alternatives, based on notional cockle size distributions, are shown (Figure 3.5.3). Cockle sizes are assumed to be uniformly distributed within three size ranges: 0.1-12mm; 0.1-6mm; and 7-12mm. Intake rate, for a given cockle biomass, clearly depends on the size distribution of cockles present (Figure 3.5.3a). When cockles are small, intake rate is much lower than when the full size range is present because small cockles have low profitability. When they are large, intake rate is only slightly above that with the full range of sizes. This occurs because when the full range is present, it is the large cockles that are selected. The minimum size of cockle included in the diet increases with overall intake rate, and therefore, for a given biomass, tends to be larger when cockles are large than when they are small (Figure 3.5.3b). Minimum size class increases with intake rate as size classes with a profitability lower than overall intake rate are excluded from the diet (Charnov 1976).

3.5.3 Conclusions

The model assumes that touch is the only mechanism used to locate prey. Whilst this is valid for location of cockles which are shallow buried, it is not for more deeply buried prey. Therefore, the model may not simply be extended to such prey species. The model is derived solely from previous studies. These studies have shown that the major model assumptions hold for knots feeding on cockles (Piersma *et al.* 1995), and have used the model to successfully predict the intake rates of individual birds over a wide range of cockle densities and the observed distribution of knots in the Wadden sea (Piersma *et al.* 1995). Confidence may therefore be placed in the accuracy of the model predictions across the full range of situations that will be generated in the shorebird-shellfish model.

(a) Intake rate



(b) Size selection

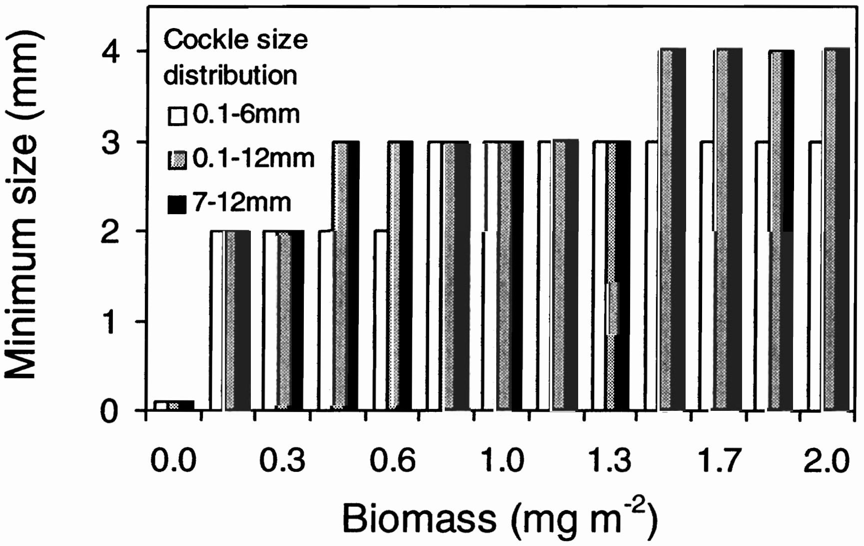


Figure 3.5.3 Predicted functional responses and size selection of knots feeding on three different size distributions of cockles. In each size distribution, cockles sizes are uniformly distributed between the upper and lower limits. Size selection is measured as the minimum size class included in the diet.

Chapter 4 SHELLFISH MODULES

4.1 INTRODUCTION

S McGrorty

The identification and modelling of density-dependent regulatory processes in animal populations has advanced rapidly over recent years. Insects, for example, have frequently been studied (Crowly *et al.* 1987; Stiling 1988), but comparable studies on marine benthic invertebrates are rare (Hancock 1973; Dempster 1975). Long-term studies are required to detect and measure density dependence (Hassell, Latto & May 1989) in field populations. The practical problems of sampling large, highly aggregated (sub)populations in difficult terrain may explain the paucity of long-term studies of marine benthic species (Hancock 1973; Vahl 1982; Bowman 1985; Barnett & Watson 1986; Beukema & Essink 1986). However, another particular problem of studying inshore marine benthic communities is that they tend to be dominated by a few species (Levin 1984; Paine 1984) with free-living, and often widely dispersing, planktonic larvae. In effect these are 'open' systems, in which individual species form metapopulations (Roughgarden & Iwasa 1986), consisting of many local subpopulations, whose distribution, size and density may be 'limited' (Doherty 1983) or 'regulated' (Hughes 1990) by the supply of larvae from the plankton rather than by local fecundity. In contrast, the dispersal phase in insect metapopulations is usually the final adult stage.

In these open populations of marine invertebrates there is, therefore, the particular problem of detecting local density-dependent recruitment within subpopulations against a background of a potentially much greater supply of planktonic larvae, which originate from other places. The relative importance of the density of settling larvae and of the post settlement density-dependent and density-independent processes in determining adult density has been the subject of recent debate (Holm 1990). However, this is difficult to resolve, because marine ecologists have tended to concentrate on short-term and experimental studies of factors which structure communities (Menge & Farrell 1989) and operate within small patches (Frid & Townsend 1989). Nevertheless, several density-related phenomena have been described, including density-dependent mortality (Hancock 1973; Beukema 1982), self-thinning (Hughes & Griffiths 1988), density-limited growth (Morrisey 1987; Okamura 1986) and density-related emigration (Ambrose 1986). Long-term studies should, therefore, be able to measure the strength of any density-dependent regulatory processes acting on local populations. Studies of these metapopulations at a scale at which movements have only trivial effects, and numbers are determined mainly by the interplay of birth and death rates, would involve huge geographical areas and are generally impractical. The EC COST 647 programme was a rare attempt to describe variations in population processes in selected species throughout their geographical range in western Europe (Lewis 1986).

Despite the paucity of long-term population studies of inshore benthic marine invertebrates in general, there have been two estuary-wide studies of commercially important shellfish, which are also important sources of food for shorebirds, in particular the Oystercatcher, *Haematopus ostralegus*. These are a study of the dynamics of the common blue mussel, *Mytilus edulis*, population in the Exe estuary in England (McGrorty *et al.*1990) and of the cockle, *Cerastoderma (= Cardium) edule,* population in the Burry Inlet in Wales (Hancock 1973). Though similar in many ways, there are important differences in the population dynamics of these two species, for example, in their recruitment strategies. In the Exe estuary, mussel larvae appeared to settle and survive only within the byssus threads of the adults already present, thus those beds with most adults attracted most recruits. By contrast, in the Burry Inlet, because of cannibalism and competition between spat and adults, more settling cockle larvae survived in areas with few adults than within the dense adult beds. The dynamics of these two populations are described in detail, and modelled, in the following sections of this report.

4.2 MUSSEL POPULATION DYNAMICS

S McGrorty

4.2.1 Background

The common blue mussel, *Mytilus edulis*, has a wide geographical range in northern temperate and arctic waters (Seed 1976). It is widespread in the littoral and shallow sublittoral in any habitat which provides a secure anchorage, but is generally most abundant at or below the mean tide level. On rocky shores it is often the dominant species within a distinct band, or zone, with upper limits set by physical stress and time available to filter feed, and lower limits set by predators, eg crabs and starfish, which migrate up and down-shore with the tide. Though not so obvious in estuaries and on open soft-sediment beaches (Raffaelli, Karakassis & Galloway 1991), these limits still pertain, but mussels usually occupy distinct patches or beds.

Mussels usually release their reproductive products into the seawater in several batches during spring and summer. The larvae grow in the plankton before a primary settlement phase onto finely divided substrata, eg algae and hydroids (Bayne 1964). After growing to *circa* 1 mm the larvae migrate and settle for a second time, approximately 6 weeks after spawning, as plantigrades, either onto unoccupied substrata to form new beds, or onto existing mussel beds among the adults. This strategy of primary and secondary settlement is generally believed to keep larvae and adults apart until most of the larvae are too big to be filtered out of the water and eaten by the adults. Mussels are gregarious (Seed 1976), and spat distributions usually highly aggregated, resulting in wide spatial variations in density, often at several scales. Likewise, plantigrade settlement, and spat survival, often varies widely from year to year. Settlement is often particularly large, and successful, after cold winters (Beukema 1982). This is partly because the frequently high levels of predation on shellfish spat by, for example, shore crabs, *Carcinus maenas,* (Reise 1985; Sanchez-Salazar, Griffiths & Seed 1987) is reduced. Low seawater temperatures delay crab larval development (Beukema 1991) and the onset of juvenile and adult inshore/intertidal migrations in spring (Atkinson & Parsons 1973; Dare & Edwards 1981), allowing the mussel spat to become established. By contrast, after warm winters (Beukema 1992), predators may already be established inshore, when plantigrade settlement begins, resulting in poor survival of spat mussels.

Typically, mussel populations in large exposed, soft-sediment embayments resemble those on rocky shores in that large densities of larvae (up to 10^5 m^{-2} in Morecambe Bay, Dare 1976) settle onto 'clean' substrata to form new beds. Wide variation between years in the number of settling larvae is carried through to the adult population, which is usually short-lived; winter gales and ice (Dare 1976; Sousa 1985) strip mussels from the beds and cause catastrophic mortalities. By contrast, small sheltered estuaries are less prone to such disturbances and mussel larvae generally settle only onto existing, long-lived, beds in hydrographically suitable areas (Verhagen 1982), but their densities are generally lower than in Morecambe Bay (personal observation and up to 10^3 m^{-2} in the Exe estuary, McGrorty *et al* 1990). Since more larvae were collected in 'Hairlock' traps suspended 30 cm above the substrate than settled on the beds in the Exe (unpublished data), and Dare, Edwards & Davies (1983) collected up to 10^6 larvae m^{-1} of rope suspended in the water column in another sheltered estuary in Devon, it is likely that there are always more larvae available to settle in such sites than actually do so. This suggests that these sheltered populations must be regulated, and adult density therefore determined by some factor operating on the beds themselves and not, as in exposed populations, by the supply of larvae of uncertain origin. Therefore, unlike open coast populations, the regulatory processes acting on mussels in small sheltered estuaries, such as the Exe, are amenable to study.

4.2.2 The Exe estuary mussel population

4.2.2.1 Description of the area and methods

The River Exe forms a small, mainly muddy, sheltered estuary protected from the sea by twin sand spits which reduce the entrance to a narrow channel. The study population consisted of the 12 large intertidal mussel, *Mytilus edulis,* beds which between them contained >90% of the adults and >95% of the spat. In 1976 when the study began, there were 31 beds scattered throughout the seaward half of the estuary, but many were either very small or consisted of only a few scattered clumps of mussels, and most of these disappeared during the study through natural causes. There was no commercial fishing of mussels in the estuary during the study. There was a considerable variation between the 12 beds in the densities and sizes of mussels they supported. The beds also occurred on a range of substrata, varying from gravel near the sea to very soft mud further up the estuary. Only 2-4 beds with gravel substrata are probably natural, the others were all laid originally by man for the culture of 'winkles' (*Littorina littorea).*

Each bed was sampled in March and September from September 1976 to September 1983. The methods used are detailed in McGrorty *et al* (1990); in brief, 600 samples, 0.04 or 0.02 m^{-2} in area according to mussel density, were collected from the 12 beds using a stratified random scheme, which allocated samples to strata chiefly in proportion to area. Mussels were counted, measured and aged from growth rings on the shell. Bed areas were calculated from maps based on a series of parallel lines measured across the beds each time it was sampled.

4.2.2.2 Mussel development

The life cycle begins in the autumn and early winter when adult females achieve their maximum weight and primary oocytes develop. Females spawned from late winter through spring and by July most were spent. Plantigrade settlement began, and in most years reached peak densities in spring and continued in lower numbers throughout the summer. Spat were considered to be recruited to the population in the autumn and by the following spring, having developed a gonad, were classed as adults. Thus, eggs within females in September 1976 gave rise to the 1977 cohort, which were sampled as recently settled plantigrades in March 1977 and as spat recruits to the population in September 1977. By March 1978 they had a single ring on the shell and were considered to be one year old. Another ring was added to the shell in spring each year and adults lived up to 10 or more years, though few survived beyond their eighth year.

4.2.3 The whole estuary population

4.2.3.1 General trends 1976-83

There were no significant trends over the 8 years in either the highly variable numbers of settling plantigrades/spat, or the remarkably stable numbers of adult mussels (Figure 4.2.1). However, the difference between the 17-fold annual variation in spat numbers and the 1.5-fold variation in adults implies that a very strong regulatory process was operating during the first year. There was a small increase in adults in 1979 following the dense spatfall of 1978, but the even larger spatfall in 1979 did not result in a further increase in adults. The increase in adults in 1983 was almost entirely due to storm-driven immigrants into the estuary observed at the beginning of September. At the estuary scale, therefore, the study showed that the mussel population between 1976 and 1983 was tightly regulated and so stable.

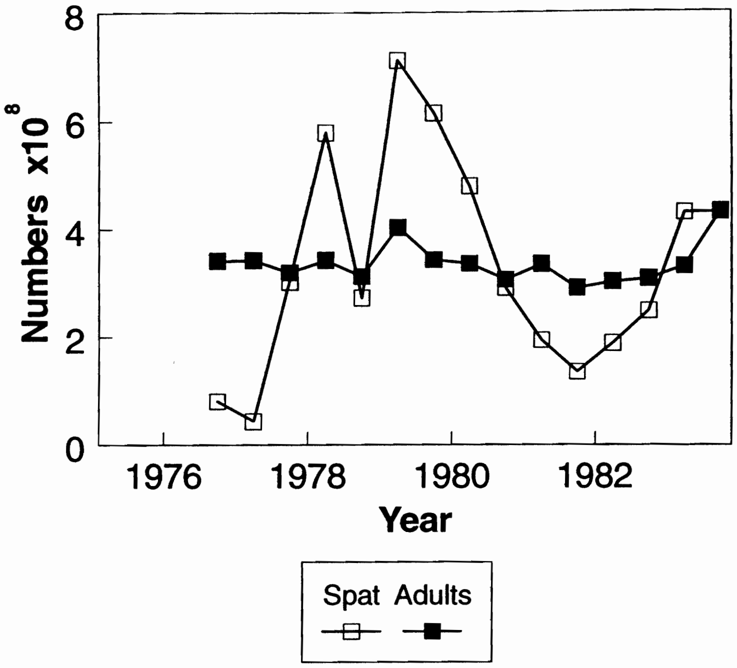


Figure 4.2.1 Changes in the total numbers of spat (0 year; open symbols) and adult mussels (>1 year old; closed symbols), on all twelve beds of the Exe estuary combined, between 1976 and 1983. There were no significant trends with time in either set of data, but the 17-fold variation in the numbers of spat between years compared with the 1.5-fold variation in adults implies strong damping, or regulation, during the first year of life.

4.2.3.2 Changes in density between ages

The largest losses of mussels undoubtedly occur in the plankton and primary settlement phases. On average the density of plantigrades/spat on the beds in March represented only 0.0002% of the potential egg production by the adult population (McGrorty *et al.* 1990). However this is only a notional loss, since we are uncertain of the fate of eggs spawned in the Exe, or the origin of those larvae settling on the beds. There was a large reduction in the density of spat mussels during their first year on the beds in the estuary (Figure 4.2.2). Following the highly variable rates of settlement in spring and subsequent small losses in the first summer (March to September), there was a mean loss of 68% of the spat during the first winter (September to March). For the next 4 years there was little change in density; small gains in summer were countered by small losses in winter. From their sixth year onwards, there were increasingly large losses each year in summer (mean 39%) after spawning (Worrall & Widdows 1984) and in winter (mean 24%) as mussels entered the size range most eaten by Oystercatchers (Cayford & Goss-Custard 1990). So, by far the largest losses of mussels, produced in the Exe as eggs, occurred outside the estuary in the early planktonic and settlement stages; thereafter, once established in the estuary, the largest single loss occurred during their first winter on the beds.

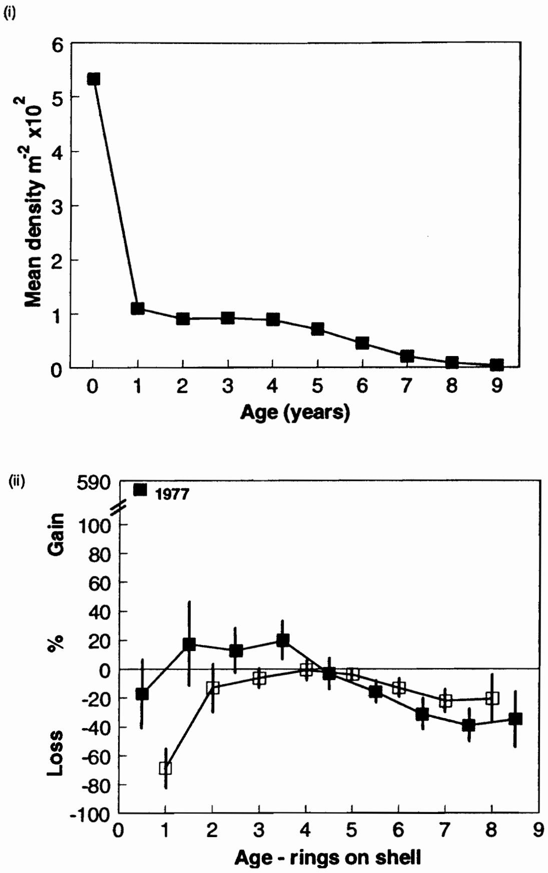


Figure 4.2.2 Changes in density of the whole estuary mussel population by age. (i) The mean density of mussels at each age from 0-9 years as determined by annual growth rings on the shell and measured in March and September each year from 1976 to 1983. (ii) Mean % gains and losses in summer (March - September; solid symbols) and winter (September - March; open symbols) at each age up to the tenth summer, averaged over 8 years. The bars represent two standard errors. The 0-year summer value for 1977 is shown separately because the twice normal rainfall in the winter and spring of 1976-77 covered the beds in liquid mud and prevented spat settlement until it had been dispersed later in the summer. Thus, instead of the usual small loss, in that year there was a large summer gain of newly settled spat. As indicated by both graphs, the largest changes in density occurred in the first winter of the mussels life and in summer and winter from the fifth year onwards.

4.2.3.3 Density dependence

Within the first year of life only the first winter loss was closely and positively density-dependent (McGrorty *et al.* 1990; major axis (Smith 1973) and reversed axes (Varley and Gradwell 1968) tests). Regardless of the wide variation in the density of recruits in September between years, the density of survivors in the following March was very similar (Figure 4.2.3a). When the density of survivors is plotted against the initial density of spat in September (Figure 4.2.3b), the curve rapidly approaches an asymptote of 128 m^{-2}. This implies that, however large the recruitment of spat to the population in a particular autumn, the numbers entering the adult population in the following spring will not exceed this upper limit. Plotting these data again as mortality, expressed as a k-value (Varley & Gradwell 1960), against the logarithm of the initial density in September (Figure 4.2.3c) produces a linear relationship which explains 93% of the variance in the mortality from year to year. Whatever the cause or agent of this overwinter density-dependent mortality, few spat died of other density-independent causes. The slope of the relationship indicates the strength of the density dependence compared with perfect compensatory density dependence which has a slope of 1. The intercept on the x-axis indicates the density of spat at which there is no mortality ('critical density', Hassell 1975), but above which density dependence process operates. Because this relationship is logarithmic, an increasing proportion die as density increases above the critical density. Thus, in years of high recruitment few extra spat survive their first winter to become adults compared to years of low recruitment.

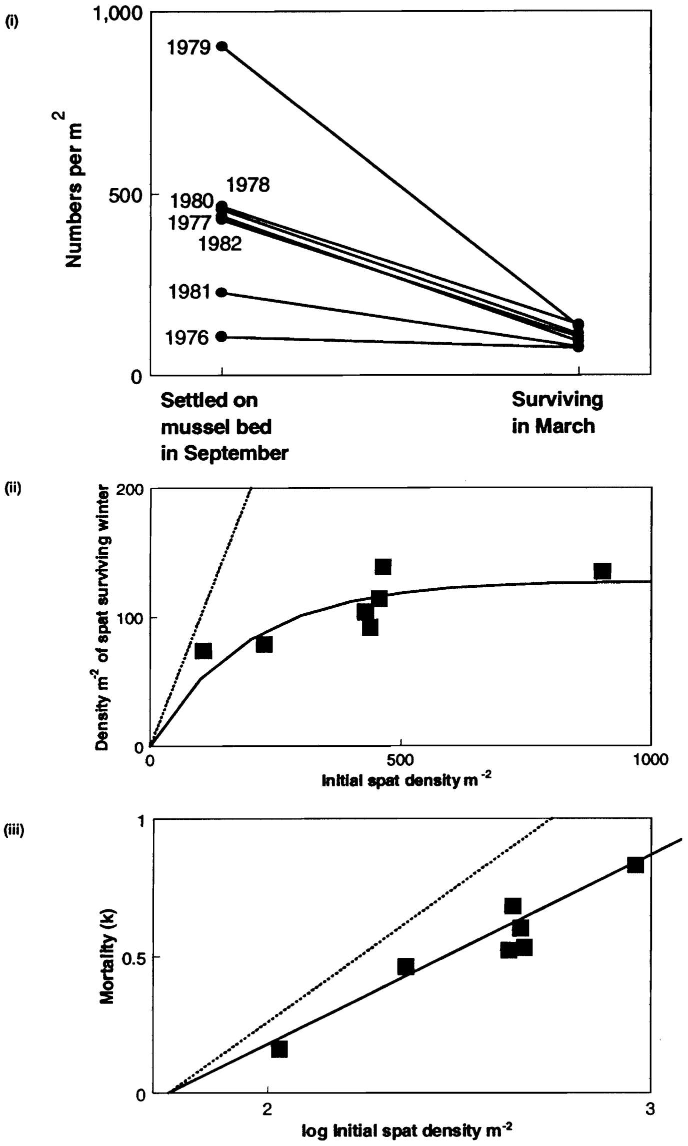


Figure 4.2.3 Density dependence in the first winter mortality of spat mussels for all twelve beds combined. The graphs are based on the results of surveys of the whole mussel population in the Exe in September and March in each of seven successive years and express the mortality in three ways: (i) The change in spat numbers in the estuary from September to March in each of the seven winters studied. This illustrates how the variable spat settlement between years in September was evened out by March. (ii) Survivors in March as a function of initial spat density m^{-2} in the previous September. The dashed line represents 100% survival. The asymptotic regression equation is: $y = 127.9\ (1\text{-}e^{-0.0052x})$, $r^2 = 58\%$. Regardless of the density of recruits in September, the density of young mussels in March did not exceed 128+/-18 m^{-2}. (iii) Mortalities, expressed as k-values, plotted against the logarithm of the initial densities. The dashed line represents perfect compensatory mortality with a slope, b = 1. The linear regression equation is: $k = 0.69 \log_{10}$ Initial density - 1.20, $r^2 = 93\%$. The line intersects the x-axis at the critical density of spat (57 m^{-2}); the density above which the density-dependent mortality process operates.

There was little evidence of density dependence in the adult population. Density-dependent mortality was detected only in the second winter and the tenth summer. Strong density dependence (slope = 0.7) in the second winter further reduced the small variation in density remaining after the first winter. The density dependence in the tenth summer is of little significance, since by this age densities were very low. Clearly, the main process regulating the density of the mussel population in the Exe estuary, and the main cause of the remarkable stability in the numbers of adults, was the strong density-dependent mortality operating on the recruits in their first winter, just before they became adults. Following this, the second winter mortality could only 'fine tune' the density of particularly abundant year-classes.

4.2.3.4 Density-independent losses

Though unrelated to density, some adult mussels died at all ages and seasons, and especially from their sixth year onward when they died in increasing numbers each year. Some of these density-independent mortalities were related to annually varying weather variables. In the second summer, mortality was negatively correlated with temperature (r = -0.77) and the incidence of gales (-0.80), while in the second winter mortality was positively correlated with temperature (0.80). Thus, more of the youngest adults died in cooler than average summers with few gales and in warmer than average winters. Since it is unlikely that these conditions would kill mussels directly, but would favour crabs foraging in intertidal areas, it is probable that the weather only indirectly affects the mortality of young adult mussels. The mortality of middle-aged adults was not related to the weather, but from the sixth to the eighth summer, more of these old adults died in cooler than average summers (r = -0.87, -0.79 & -0.72) and, in the eighth to the tenth summer, more died in years with few gales (r = -0.90, -0.85 & -0.76). Since gales can dislodge clumps of mussels from the beds or bury them in sediment, the negative correlations are counter intuitive. Perhaps, in reality gales wash mussels into the estuary, thereby partly offsetting losses due to physiological stress after spawning. After the second year none of the mortalities in winter were related to the weather. While these mortalities account for some of the variation in population density from year to year, they play no part in the regulation of the population density in the estuary, because they are unrelated to the density of mussels,.

4.2.4 Spatial variation between beds within the estuary

The processes described in the preceding paragraphs relate to the population at the estuary scale and are, in effect, the sum of the processes acting on the 12 beds. However, the beds were not identical replicate subpopulations. Indeed, they varied widely in the density of the adult mussels living on them and in their position along the environmental gradients within the estuary. Both of these are closely linked and have an influence on the settlement and recruitment of spat, which also varied widely between the beds.

4.2.4.1 Spatial variation in mussel density

The density of adult mussels varied widely between the 12 beds (McGrorty & Goss-Custard 1991; McGrorty, Goss-Custard & Clarke 1993). On average over the 15 surveys, adult density varied by three orders of magnitude from 10^1 to 10^3 m^{-2} and declined up-estuary (Figure 4.2.4). The density of young adults (second - fourth years) declined by up to 25% on the large down-estuary beds and increased by up to 50% on the small muddy up-estuary beds, suggesting the possibility of an up-estuary migration at these ages. The density of old mussels (>5 yr) declined up-estuary, but the proportion of older mussels on the beds increased, thus the mean age of mussels on the beds increased up-estuary. However, beds higher up the estuary tended to occur at lower levels on the shore, and multiple regression analyses revealed that the most important environmental gradient along which adult densities varied was not the up-estuary gradient itself, but the up-shore gradient, as measured by the percentage of the tidal cycle for which the beds were exposed to the air. The relationship between density and exposure was domed; the highest densities occurred on beds which lay between 30 & 40 % exposure time, and declined at higher and lower shore levels (Figure 4.2.5). The position of the beds along this gradient explains 71% of the variance in adult density, and determines the time available for the mussels to feed over high tide, their exposure to physiological stress over low tide and their relative exposure to bird and aquatic predators, such as crabs.

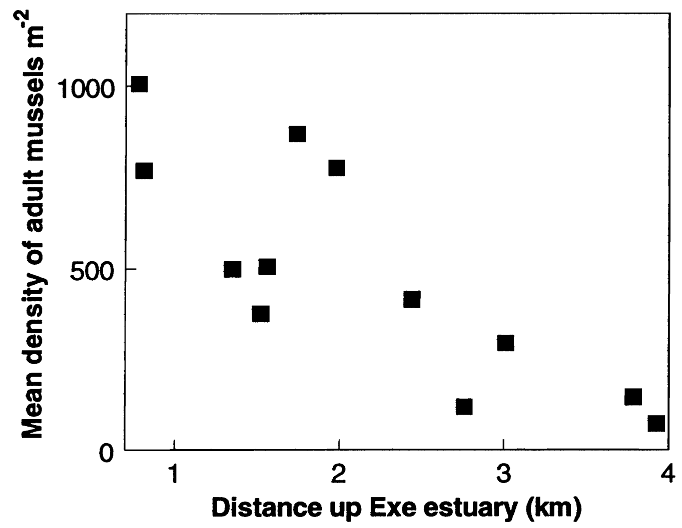


Figure 4.2.4 Spatial variation in the densities of adult mussels (>1 year old) on the 12 main beds in the Exe estuary plotted for illustration against their distance up-estuary from the sea. Densities, averaged over 15 surveys, varied across the beds from 10^1 - 10^3 m^{-2}. The relationship is described by the equation: Mean adult density (m^{-2}) = 985.2 - 235.4 Distance up-estuary (km), r = -0.81, p<0.01.

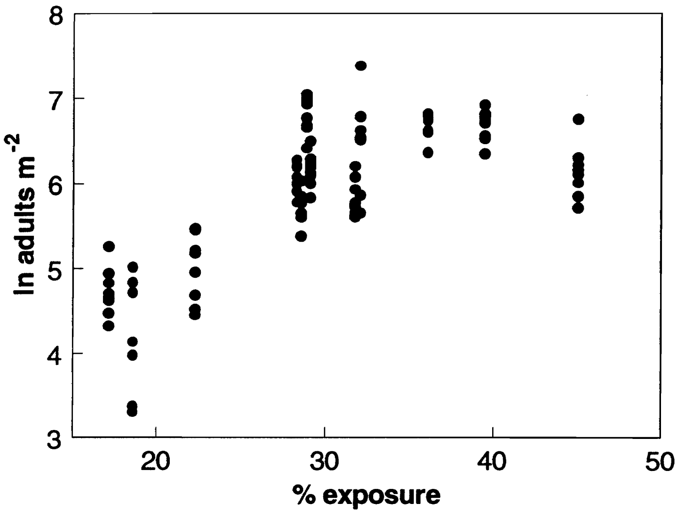


Figure 4.2.5 The variation in adult mussel density (>1 year old) along the up-shore environmental gradient within the estuary. The regression equation describing the relationship is: ln Adults (m^{-2}) = 0.40 Exposure - 0.0053 $Exposure^2$ - 1.08, R^2 = 71%. The data are 12 beds sampled each September for eight successive years. Adult mussels were most numerous between 30 & 40% exposure and densities declined at higher and lower levels on the shore. There were no mussel beds centred above 50% exposure.

The density of mussel plantigrades and spat also varied widely between beds by four orders of magnitude, from 10^0 to 10^3 m^{-2} . There was a huge preponderance of spat, on average 71%, in March and September on just 2 beds (30 & 31) near the mouth of the estuary. Between March and September in most years, the density of plantigrades and spat on the six down-estuary beds declined, but on the six up-estuary beds it increased. Thus, settlement occurred in spring on some beds and in both spring and summer on others. However, since on average 87% of spat occurred on the down-estuary beds, overall spring settlement was the dominant process at the estuary scale. The observation that spat mussels in the Exe only seemed to settle and survive deep within the byssus of the adult mussels was confirmed by partial regression and correlation analyses. This showed that the main determinant of spat density across the beds was the density of the adults already present on the beds and not the exposure of the beds which determines the density of adults. The only other environmental variable which influenced spat density was the softness or muddiness of the substrate. Fewer spat settled on muddy than on 'clean' beds. The relationship:

$$\ln \text{spat m}^{-2} = 2.80 + 0.85 \ln \text{adult density m}^{-2} - 1.13 \text{ substrate softness}$$

explained 76% of the variance in spat density between the 12 beds. In conclusion, the density of adult mussels varied along the up-shore gradient, being most numerous just below the mid-tide level. More spat settled and survived on beds with more adult mussels and where the substrate was firm. Thus, although densities varied widely between the beds, they were all self-sustaining from year to year because spat aggregated where mussels were already present.

4.2.4.2 Spatial variation in mortality

Over half of the 'mortalities' in the first summer were negative, that is settlement/immigration, but in the first winter there were only losses of spat. There was a wide variation in first year mortalities, in summer and winter, both between the beds and between the years. An analysis of variance also showed that there was a large interaction between beds and years, suggesting that the magnitude of the mortalities across the beds did not all change to the same extent, or even in the same direction, from year to year (McGrorty & Goss-Custard 1993). However, there was synchrony between beds in the magnitude and direction of changes in extreme years; for example, after cold winters and in the winter and spring of 1976/77 when there was twice the normal rainfall.

Over a third of the estimates of adult 'mortalities' took negative values. Although many of these were wholly or partly the result of errors in density estimation, there was widespread evidence of immigration of adults onto beds (McGrorty & Goss-Custard 1995). This is surprising since mussels attach byssus threads to each other in addition to the substrate. Whatever the mechanism involved, immigration was common especially in young adults moving onto up-estuary beds in summer and onto down-estuary beds in winter. Immigration was, therefore, an important component of the density dependence at many ages on many beds. But losses on some beds were countered by gains on others within and between years. This had two main effects. First, density variation on individual beds between years was much reduced at the estuary scale and resulted in the remarkable stability in the numbers of the whole adult population in the estuary. Second, although there was evidence that density dependence was widespread among adult age-classes at the bed scale, at the estuary scale density dependence was only detected in the second winter and tenth summer.

Statistical tests for density dependence could be applied to the eight years data for each bed at each stage (age x season) separately, or globally across all of the data for each stage while allowing for differences between beds. The first approach applied 'traditional', conservative tests (McGrorty *et al.* 1990) and was regarded as direct evidence of density dependence. The second approach applied three regression models; (i) a common slope and intercept, (ii) a common slope, but separate intercepts for each of the beds, and (iii) separate slopes and intercepts for each bed, and compared the proportions of the variance in mortality explained by each of them (McGrorty & Goss-Custard 1993, 1995). This second approach was less rigorous statistically than the first and was regarded as indirect evidence of density dependence.

There was direct evidence of density dependence in the first summer on the six down-estuary beds (slope, b = rate of mortality = 0.87 - 1.21) and in the first winter on three down-estuary beds (b = 0.69 - 0.96). These strong to near perfect compensatory density-dependent mortalities on beds which between them supported >80% of the spat settling in the estuary dominated the dynamics of the population at the estuary scale and resulted in strong density-dependent regulation of the whole estuary population in the first winter, but not in the first summer. In the first summer, losses on some beds in some years were countered by gains on others and overall density dependence was not detected at the estuary scale, despite strong evidence for its presence on half of the beds. The lack of density dependence on some beds in the first year was probably due to a failure to detect it using 'traditional', conservative tests, rather than to its absence. Less rigorous, indirect evidence suggested that density dependence was widespread across beds in both seasons. The best model explaining variation in mortalities across all beds and years in each season had a common slope across all beds (b = rate of gain/loss = 0.95 in summer and 0.60 in winter), but separate intercepts or critical densities, above which there was density-dependent mortality and below which there was density-dependent settlement/recruitment. The most important factor explaining variation in the critical densities across the beds in both the first summer and winter (Figure 4.2.6) was the density of adult mussels on the beds (McGrorty, Goss-Custard & Clarke 1993). Thus, the density of spat in March and September and the critical densities, about which density-dependent immigration and mortality processes operated, were both closely and positively related to the density of adult mussels already present on the beds.

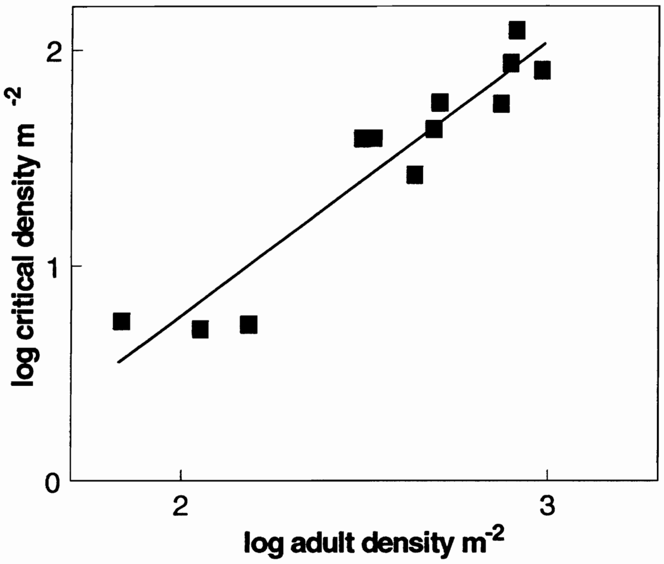


Figure 4.2.6 The critical density of spat recruits in September, above which the first winter density-dependent mortality operates, varies with adult density across the 12 beds. The linear expression: log Critical density = log Adults (m^{-2}) - 1.77, r^2 = 90%; describes the relationship. The greater the density of adults on a bed the greater the density of spat that can be recruited before the mortality operates.

There was direct evidence of density dependence in only 21% of adult mortalities (McGrorty & Goss-Custard 1995), but this was four times the number expected by chance. Density-dependent mortality was most often related to the initial density of the particular age-class, but other adults probably also influenced the mortality in many cases. There was no clear pattern of density dependence (as determined by these direct tests) across all the bed, age and season combinations of adult mortalities, but it was more common among young than old adults, and on large muddy up-estuary beds in summer and on down-estuary beds in winter.

As in the first year, indirect tests suggested that density dependence was more widespread across beds and among adult age-classes than suggested by the more stringent direct tests, but probably did not occur at all ages on all beds. Once again the best model explaining the variation in mortality across all beds and years at each age and season had a common slope, or rate of mortality, across all beds, but separate intercepts, or critical densities, for each bed. The critical densities, above which the density-dependent mortalities operated declined with age. However, at each age for which there was evidence of density dependence the factor which best explained the variation in critical density between beds in summer and winter was exposure time, or the level of the bed up the shore.

4.2.5 Discussion

4.2.5.1 Mussel population regulation

Two distinct life strategies have been identified in the common mussel. In open coast populations, larvae generally settle at high densities onto bare ground to form new short-lived beds. The density of adults is closely correlated with the density of spat, which probably originated wholly or partly from other unknown populations, and varies widely from year to year. It has not yet been possible to directly measure losses in the planktonic and primary settlement stages, or to study these metapopulations at a sufficiently large scale to determine at what stage, and how, these populations are regulated. By contrast, mussels in small sheltered estuaries have more stable, self-sustaining populations that occupy long-lived beds. Although the larvae settling in the estuary are also of uncertain origin, new beds are formed only rarely and larvae generally settle only onto existing beds. The population is subject to density-dependent processes acting on the beds, and is, therefore, amenable to study during the important regulatory stages.

At the scale of the whole Exe estuary, population density was chiefly regulated during the mussels' first winter on the beds following settlement in spring and summer. The powerful first winter density-dependent mortality reduced the wide variation in autumn spat recruitment between years to within very narrow limits by spring, when they first became adults, and the total adult population was remarkably stable over 8 years. The cause of this density-dependent mortality was probably shore crabs, which are well known predators of shellfish spat, and were present in large numbers on the mussel beds. In the Exe estuary, spat mussels only seemed able to settle in spring when juvenile crabs were least abundant (unpublished data), and to survive to recruitment in the autumn, deep within the byssus threads of the adult mussels. Thus, spat densities across the beds were closely associated with adult densities. In an unpublished experiment, 96% of spat were eaten by crabs when alone, but only 53% were eaten when adults were present. However, by autumn and through the winter, many spat outgrow the byssus protection and were again vulnerable to crab predation. This first winter density-dependent mortality reduced spat numbers to close to the critical density, which again varied between beds mainly in relation to adult density. Elsewhere, mussels inside clumps were less likely to be eaten by crabs than those on the outside (Okamura 1986). The number of survivors is, therefore, probably determined by the availability of refuges within the matrix of spaces between adults in the mussel clumps, though the tangle of byssus threads is undoubtedly still important. As a result of this density-dependent loss, few extra spat survive to adulthood even after very dense spatfalls, but because the density dependence is not perfectly compensatory, some do. These abundant cohorts are further reduced during the second winter, but thereafter no other density dependence was detected at the estuary scale until their tenth summer when the few remaining adults died. Clearly, at the estuary scale, the most important regulatory process acting upon the population was the first-winter mortality due chiefly to crab predation.

Although the population dynamics at the estuary scale was the sum of the processes acting on the 12 beds, the mussel subpopulations on the individual beds did not all follow the same pattern as each other and as the estuary population as a whole. There was direct evidence of strong to near perfect compensatory mortality during the first winter on only three large, dense, down-estuary beds. However, these three beds contained on average >80% of the spat recruited to the whole population. So, the density-dependent process on these three beds dominated the changes in first winter density within the whole population in the estuary. By contrast, during the first summer and subsequently in many of the adult stages, there was evidence of density dependence on many of the beds, yet this was not apparent at the estuary scale. This was because both recruitment/immigration and mortality played a part in the density dependence and losses on some beds countered gains on others, reducing variation in density and masking density dependence at the larger estuary scale. It is clear, however, that while the main regulatory process acting on the mussel population was the first winter mortality, density on all of the beds was closely regulated by density-dependent processes at several stages throughout their maximum 10 years of life.

4.2.5.2 The effect of oystercatchers on mussels

Oystercatchers undoubtedly eat many large adult mussels, but they do not regulate the mussel population. Regulation in sheltered estuaries occurs at a much earlier stage in the mussels life and the main predator responsible is most likely the much less conspicuous shore crab. Nonetheless, there are ways in which Oystercatchers can affect the mussel population.

As mussels increase in length they become more profitable to most Oystercatchers (Cayford & Goss-Custard 1990) and are increasingly likely to be eaten by the birds in winter. Within one winter, Oystercatchers removed up to 30% of the larger mussels (>40 mm long) in the places where mussels had initially been most abundant and where the birds tended to congregate (Goss-Custard, Caldow & Clarke 1992). Over a succession of winters, predation by Oystercatchers could have two negative and one positive effect on secondary settlement. By eating large mussels, Oystercatchers deplete the reproductively most productive mussels and reduce the refuge space available to spat. But they may also reduce competition between mussels for food and space (Seed 1976; Okamura 1986) and allow younger ones to grow more quickly, so replacing some of the lost spat refuge.

Egg production by female mussels increases with length and flesh content, and therefore can be calculated for each age class in the estuary population (McGrorty *et al.* 1990). The most productive mussels are those between 4 and 7 years old, and over 50% of the eggs are produced by the age classes eaten by Oystercatchers (Goss-Custard, McGrorty & Durell 1996). By removing up to 30% of these mussels in winter before they spawn, Oystercatchers reduce the potential mussel egg production by up to 10-15% each year.

This is unlikely to have an effect on mussel abundance in the long-term, however. During the planktonic and primary settlement phases larvae from the extensive populations in the English Channel probably swamp the effect of any reduction due to Oystercatchers in the numbers of eggs produced in the Exe. Even if this is not the case, the ability of the beds in the estuary to attract and support settling larvae at up to 10^3 m^{-2} was substantially less that the average production of 10^8 eggs m^{-2}, and there is some reason to believe that there may always be more plantigrades available in the water than settle in sheltered estuaries. Furthermore, the powerful first winter density-dependent mortality would ensure that any small annual variations in spat supply due to Oystercatcher predation would have rather little effect on subsequent adult density. It seems most unlikely that the impact of Oystercatchers on egg production could have an effect on mussel abundance.

As plantigrade larvae only settled successfully within the byssus threads of adult mussels, more spat established themselves in spring and summer where adults were numerous. This trend is particularly apparent with adults <40 mm long, and so too small usually to be eaten frequently by Oystercatchers. The variation in spat densities across the 12 mussel beds in September (Figure 4.2.7) was significantly correlated with the densities of adults <40 mm in six of the seven years of the study when the effect of the densities of adults >40 mm was taken into account using multiple regression analysis. In contrast, the densities of adults >40 mm long, eaten by Oystercatchers, had a significant partial regression coefficient in only three of the seven years. However, the densities of spat surviving the over-winter, density-dependent mortality until March was related to the densities of adults both above and below 40 mm long in most years. By removing large adult mussels over the winter, Oystercatchers may thus reduce the densities of 1-year old mussels surviving until March, and thus the numbers reaching adulthood.

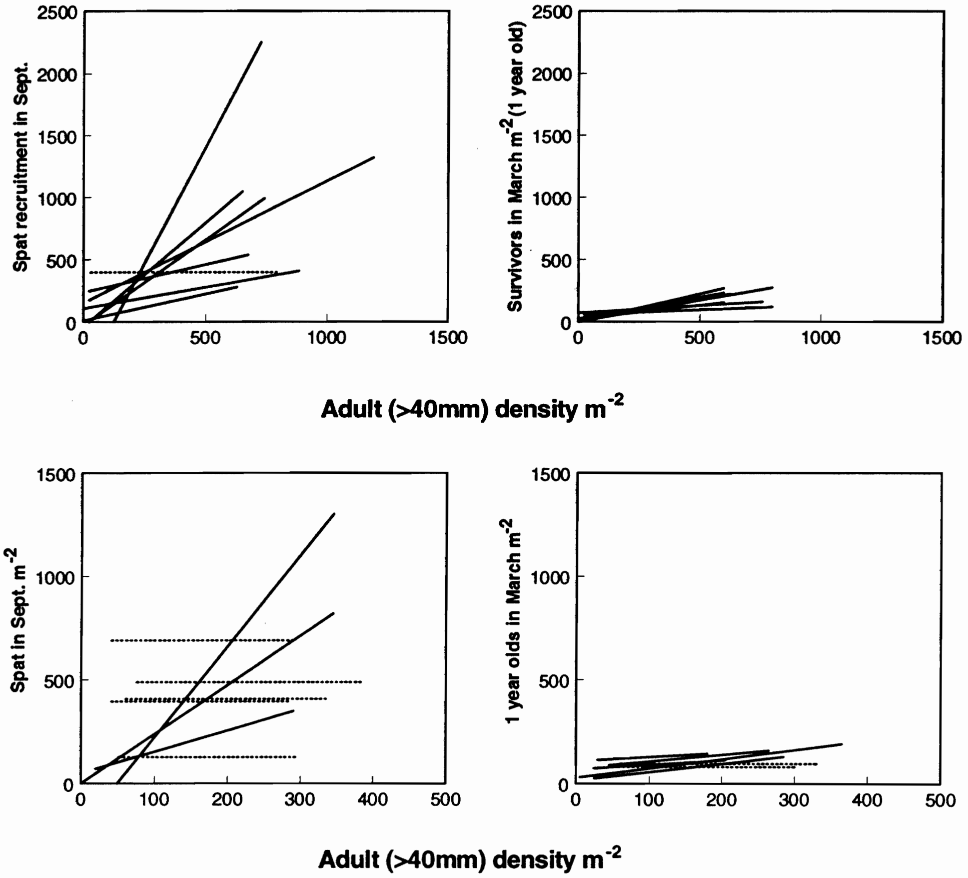


Figure 4.2.7 The relationship between the densities of spat mussels in September and March and the density of adult (>1 year old) mussels either <40 mm or >40 mm long. Oystercatchers prey mainly on adult mussels >40 mm long. Regression lines are plotted for each of the eight successive years in which measurements were made on each of the 12 beds studied. The lines are based on multiple regression equations in which the logarithm of spat density was regressed against the densities of adults both <40 mm and >40 mm long. The lines were calculated across the actual range of the x-axis recorded in the year in question by inserting the maximum and minimum values into the multiple regression equation. The value of the density of adults of the size class not used in the x-axis was the mean of all the years studied. Dashed lines indicate years in which the relationships were not significant at the 5% level of probability. The graphs show that the number of spat recruited to a mussel bed in September increased with the density of adults, particularly those <40 mm long. The numbers surviving their first winter also increased with the density of adults, including those >40 mm long.

The precise effect Oystercatchers have on mussel numbers will depend, however, on the extent to which any reduced competition between the mussels that remain in summer leads subsequently to increases in their growth rate. The regressions in Figure 4.2.7 show that, on average, each adult >40 mm long supported by March 31% more spat/1-year olds than each adult <40 mm long. Although no work has yet been done on the Exe itself, studies elsewhere suggest that the food supply over beds of mussels may be limited (Frechette & Bourget 1985a) and that competition reduces both shell growth rates (Seed 1976, Okamura 1986, Gentili & Beaumont 1988) and the flesh content (Seed 1976, Frechette & Bourget 1985b). The mussels that escape predation may therefore grow so much faster that the loss of spat refuge space resulting from the reduction in adult numbers is compensated by the greater space provided by each adult that remains. But to what extent any such increase in growth rate could compensate for the loss of refuge space is unknown. The problem can only be solved by field experiments which control for environmental variables, such as exposure/submergence, which affect growth and vary adult density at both the local clump/patch scale and at the wider beds scale.

In conclusion, in the absence of commercial fishing the mussel beds on the Exe estuary are long-lived and self-sustaining because mussel larvae only settle, and growing spat survive, deep within the byssus threads of the adults already present. The population is regulated by crab predation of spat during the first winter, just before they become adult. But the critical density above which the mortality operates is set by the density of adults. Oystercatchers mainly eat large adults, hence they do not directly regulate the density of the mussel population. However, they do depress the density of the larger and older adults and probably, therefore, the density of the whole population. The interaction between Oystercatchers and mussels is complex. While the birds' effect on mussel reproductive output is probably insignificant, they reduce refuge space for spat by reducing adult density which, in turn, will depress recruitment to the next generation. This could partly be offset, however, if reduced competition between mussels results in increased growth of the survivors, so that individually they subsequently provide more space for spat to find refuge from crabs.

4.3 WINTER GROWTH OF MUSSELS

S McGRORTY

4.3.1 Introduction

The studies reported in this section were carried out for the contract and arose out of a concern that estimates of oystercatcher mussel food density at the beginning of winter in September might underestimate the food actually available to them over the winter. If large, this could be important in the model. In an unpublished study over the winter of 1990-91, we attempted to measure directly the decline in density of the size class of mussels eaten by oystercatchers and, by using bird exclusion cages, to differentiate between those eaten and those lost through other causes. The pattern of density changes and the extent of the losses were not as high as expected, given the large numbers of birds present on the selected beds (20, 30 & 31). A possible explanation was that overwinter losses were to some extent countered by the growth of smaller individuals into the size class eaten by oystercatchers.

In temperate waters growth is seasonal (Seed 1976), being rapid in spring and summer and slow or absent in winter. This pattern has been recorded many times, but few authors have specifically commented on growth in winter. Dare (1976) reported that growth virtually ceased between December and February, while Bayne & Widdows (1978) found that the 'scope for growth' was negative for 4-5 winter months. Creameersch, Herman & Meire (1986) recorded >90% of shell growth between April and September and very low, or even negative, growth rates from September to March or May, according to the size of the mussels. Likewise, Sukhotin & Kulakowski (1992) reported a positive correlation between seasonal growth and temperature, with 7% of the annual growth occurring between November and April. It seems possible therefore that, given adequate food (Frechette, Aitkin & Page 1992, Frechette & Grant 1991, Muschenheim & Newell 1992, Page & Richard 1990, Smaal & van Stralen 1990) and suitable temperatures (Mallet *et al.* 1987, Sprung 1984, Sukhotin & Kulakowski 1992, Theissen 1973), mussels in the Exe estuary could grow in winter, especially early and late in the season.

Within a particular location, exposure/submersion, or level on the beach (Faldborg, Jenson & Maagard 1994, Rodhouse *et al.* 1984, Wanink & Zwarts 1993), and mussel density (Newell 1990, Svane & Ompi 1993) have been identified as important determinants of growth, being measures of the time available to feed and of intraspecific competition for food and space respectively. Other environmental variables have also been shown to influence growth, for example distance up-estuary (Essink & Bos 1985), sediments (Wanink & Zwarts 1993), commensals/parasites (Bierbaum & Ferson 1986) and pollution (Widdows & Johnson 1988, Lapota *et al.* 1993). Given the wide distribution of mussel beds within the Exe estuary, it is probable that the likelihood of there being winter growth, and its magnitude, would vary from bed to bed along environmental gradients.

Seed (1976) commented that growth in mussels was highly variable, not only between localities and sizes/ages of mussels, but also between individuals within populations, and even within the same patch or clump of mussels. This may imply a strong genetic influence on growth strategy (see, for example, Beaumont, Abdul-Mutin & Seed 1993, Newkirk 1980, Rodhouse *et al* 1986, Gentili & Beaumont 1988, Zouros & Mallet 1989) in addition to environmental controls. This wide variation in growth between individuals at one place could be important for oystercatchers. Even if, on average, growth over the winter is very small, a proportion of faster-growing individuals might still grow sufficiently to enter the oystercatcher food size-range and replenish some of those eaten.

The aims of this study were to determine :

i. whether mussels in the Exe estuary grow over the winter period; and, if so

ii. whether growth varied between beds and which factors were responsible for the differences,

iii. whether growth was density-dependant, so that oystercatchers by eating larger mussels allowed smaller ones to grow into their preferred food size category, and

iv. whether growth could offset depletion arising from oystercatcher predation.

The experimental strategy was to place different densities of individually labelled mussels, 25-50 mm long, in cages on several beds, which varied both in the number of mussels living on them and in their position along the environmental gradients which are known to influence growth. The expectation was that some mussels would not grow during the winter, while others would grow by widely different amounts, and not that all mussels would grow by a similar amount. Counting the number of individually labelled mussels actually growing into the Oystercatchers preferred range was, therefore, likely to give a much better estimate of the magnitude of food replenishment than would be obtained from estimates based on the mean growth increments of particular size-classes. The chosen size-range of mussels varied from the smallest eaten by Oystercatchers to the largest that previous experience suggested was likely to show any detectable overwinter growth.

The mussels were contained within cages to protect them from predators, and to prevent their dispersal by waves and currents, both of which could have changed their local density substantially overwinter and prevented us from finding them. Mussel density varies at two scales; the local scale within clumps/patches within a bed and the wider between-bed scale. Hence, it was necessary to vary cage density within beds, and to establish replicate sets of cages on beds with a wide range of mean mussel densities. In addition, beds were chosen to give sites with a wide range of exposure times, from close to the level of low water on spring tides to mid-tide level.

Unfortunately, persistent wet weather over spring tides in September 1994 prevented mussels from being individually labelled in the field. Removal of mussels to the laboratory for labelling was not possible because the physiological stress imposed could have interfered with growth and increased the risk of mortality. Instead, three size bands of mussels (28-32, 38-42 & 48-52 mm long, hereafter referred to as 30, 40 & 50 mm mussels) were selected and growth determined by following changes in group mean lengths. The aims of this winter's experiment were modified accordingly; (i) to compare mean growth increments at different local (cage) densities, (ii) to determine if bed density had an effect by comparing growth increments of mussels on a large dense bed with that on bare sediment (ie bed density = 0 m^2) nearby, holding exposure level constant and (iii) to compare mean growth increments of mussels growing on different sediments.

In the following year, the cages were set up in late-August/early-September when it was possible to label individual mussels. Because the 1994-95 data indicated that local (cage) density and substrate had no effect on mean growth increment, all replicate cages had the same number of mussels and were placed on mussel beds. The 1994-95 results also indicated that the location of the bed, rather than the density of mussels on it, was the most important variable determining mean growth increment; thus, cages were placed on a selection of beds lying at different levels on the shore.

In both winters the numbers of mussels dying in the cages were noted. This gave an estimate of overwinter mortality due to factors other than Oystercatcher predation.

4.3.2 Methods

Winter is defined as the period from mid-September, when the oystercatcher population has stabilised, to mid-March, when the adult birds leave the estuary to breed elsewhere.

4.3.2.1 Winter 1994-95

Four 20*20*20 cm 13 mm mesh galvanised wire cages were sited 2 m apart at each of 8 sites. The cages were held in place on the substrate by 4 canes (1.5 m long) to which they were attached by synthetic twine. This system allowed flexibility to withstand gales and fouling, while causing little, if any, additional scour or deposition of sediment. Three sites were located in the central part of large mussel beds (Beds 20, 26 & 31), three on bare sand adjacent to each of these beds (offshore) and two on bare mud adjacent to Beds 20 & 26 (inshore). There was no mudflat near Bed 31. The beds chosen were widely separated within the estuary and at different levels on the beach. At each bed, the sites that were on and off the mussels were all set at the same exposure / submergence level.This on-bed and off-bed design was employed to test for a large, bed scale density effect and a sediment effect on mussel growth. At each site, 30 mussels, 10 of each size band, were placed in 2 cages and 120 mussels, 40 of each size band, placed in the other 2 cages to test for the effects of local density on growth. The lower density represented the usual pattern on the beds of a single layer of mussels within patches or small clumps. The higher density represented the highest observed patch densities with mussels 2-3 layers deep. The lengths of all of the mussels in the cages were measured to the nearest 0.1 mm using vernier callipers in September, November, January and March and any mortalities noted.

It was not possible to measure all of the experimental mussels 'instantaneously'; nor, because of the weather and tidal conditions, on a particular date, or even over a single spring tide series. It took a minimum of one week to cut the byssus, measure all 2,400 mussels in the 32 cages with the minimum of disturbance, and service the cages. The mean length of each size group (30, 40 & 50 mm) in each cage on, for example, the first (16/9/1994) and last (15/3/1995) days of winter were, therefore, estimated from regression analyses of length against the dates when measurements were actually made. These values were used to calculate mean overwinter growth increments.

4.3.2.2 Winter 1995-96

Five cages, constructed and secured as in 1994-95, were placed in a line at 2 m intervals in the central part of 5 'flat' mussel beds (Beds 27, 26, 25, 22 & 20), which lie in a line up the eastern side of the estuary. A further 3 sets of cages were placed at high, mid- & low levels on Bed 30, a steeply sloping bed near the mouth of the estuary with mussels extending from mid-tide level to the low water level of spring tides. 20 mussels collected haphazardly at each site, and ranging from 25 to 45 mm long, were placed in each cage. The mussels were individually labelled, using numbered self-adhesive coloured plastic tapes from a Brother P-touch 2000 system and cyanoacrylic 'superglue' applied to the shell for extra security. All the cages were set up by the end of August and the mussels measured to 0.1 mm using vernier callipers in September, November, January and March. On each occasion, mortalities were noted and any lost labels replaced. To check the accuracy of measurements in the field 100 mussels haphazardly selected in the muddiest part of Bed 26 were measured twice, at the beginning and end of the low water period, on a cold wet, windy and dull day in October. 90% of the paired values were within +/- 0.2 mm, but the remainder varied by up to +/- 0.5 mm.

Together the 8 sites covered the full range of conditions in which mussels occur in the Exe estuary: from 10-50% aerial exposure, 0.78-3.93 km up-estuary from the mouth, gravel to muddy sediments (measured as substrate softness, 0.38-17.4cm penetration by a standard rod dropped from a height of 1 m; McGrorty & Goss-Custard 1991), bed areas from 1.11-9.49 ha and adult mussel densities of 143-896 m^{-2}. Bed areas and mussel densities were estimated from a survey of the whole intertidal population made in September 1995. 500 samples (0.04 or 0.02 m^2 in area) were collected from the 10 mussel beds using a stratified random sampling scheme (McGrorty *et al* 1990). Sample quadrat size varied according to mussel density and the number of samples in each stratum according to bed area.

4.3.3 Results

4.3.3.1 Winter 1994-95: Overwinter trends in mussel length

Of the 96 regression analyses (3 size categories * 32 cages) of mussel length against time, 92 had positive slopes (b = growth rate in $mm.d^{-1}$) indicating overwinter growth had occurred. However, the growth rate was significantly greater than zero (t-test, $p<0.05$) in only 33 cases. The majority of these significant relationships (22 cases) were for the smallest mussels (30 mm: Table 4.3.1). The number of cages in which there was significant growth declined with increasing size of the mussels such that, for 50 mm mussels, there was only a single significant relationship. The mean growth rate across all cages approximately halved with each 1 cm increase in initial mussel length, so that the mean growth increment for the winter period varied between 2.0 mm for 30 mm mussels and 0.5 mm for 50 mm mussels. Given these results, it is extremely unlikely that any larger mussels grew out of the size class eaten by oystercatchers (upper limit 65 mm), but clearly some smaller mussels could have grown through the 40 mm lower limit of the birds' preferred class of prey.

4.3.3.2 Winter 1994-95: Variation in overwinter growth of mussels

The influence of the four variables 'bed', 'substrate', clump 'density' and mussel 'length' on overwinter growth was investigated by analysing the variance in growth increment between 16/9/94 and 15/3/95, using cages as replicates. Unfortunately, the absence of a muddy site near Bed 31 prevented a fourway multiple analysis of variance (ANOVA) from being performed. This would have identified those variables having a significant effect on growth and also any interactions between them. Instead, oneway ANOVAs were used to test for the effect of each variable on its own on growth (Table 4.3.2). A multiple regression analysis was then used to test for their effects in the presence of each other (Table 4.3.3). Finally, bed and substrate were combined to give 8 sites and a threeway ANOVA performed (Table 4.3.4), which allowed some of the interactions between variables to be examined.

Table 4.3.1 Overwinter trends in mussel length: summary of regression analyses of length in mm against days after 15/9/1994 for 32 cages. The slope, b, of the regression is the growth rate in $mm.d^{-1}$; $p<0.05$ indicates the number of cases in which the relationship was significant at the 5% level of probability.

Length class	mean slope, b, in $mm.d^{-1}$	minimum b	maximum b	$p<0.05$	mean growth increment in mm.
30 mm	0.0112	0.0021	0.0215	22	2.02
40 mm	0.0059	-0.0014	0.0143	10	1.05
50 mm	0.0029	-0.0019	0.0120	1	0.51

Table 4.3.2 Oneway analyses of variance (ANOVA) on mussel overwinter (1994-95) growth increment against each of four variables on their own. F = F-test, p = probability; ns. = not significant at the 5% level of probability, se = standard error.

Analysis variable	F	p	Mean increments (mm) +/- se		
Length	46.06	0.0001	30 mm 2.02+/-0.14	40 mm 1.05+/-0.11	50 mm 0.51+/-0.08
Bed	10.68	0.0001	Bed 20 1.12+/-0.11	Bed 26 0.85+/-0.13	Bed 31 1.83+/-0.22
Substrate	5.13	0.008	Sand 1.55+/-0.18	Bed/mussels 1.00+/-0.12	Mud 0.94+/-0.14
Density	0.08	0.779 ns	30/cage 1.22+/-0.13	120/cage 1.17+/-0.13	

The oneway ANOVAs (Table 4.3.2) indicated that mussel length, bed and substrate on their own each had a significant effect ($p<0.05$) on growth increment, whereas local cage/clump density did not. As indicated above, mean growth increment across all beds and substrates decreased with increasing length of the mussels. Mean growth across all lengths and substrates was greatest on Bed 31 and least on Bed 26. Mean growth across all lengths and beds was greatest off the mussel beds on bare sand (1.6 mm) and least off the beds on bare mud (0.9 mm). However, there was little difference between the growth increment of mussels on mud and those on the mussel beds (1.0 mm). Indeed, when the effect of each of the four variables was tested in the presence of the others (Table 4.3.3), substrate was not significant. Only bed and mussel length had a significant effect on growth increment, explaining between them 54% of the variance in overwinter growth. The results therefore suggest that there was a difference in growth between beds, but that the difference was not related to bed differences in the density of mussels or the sediments. Thus, the difference must be related to the location of the beds within the estuary, and most probably to the length of the exposure/submergence period. This could not be tested effectively with only 3 beds, but growth was greater on Beds 31 and 20 (overall means = 1.83 & 1.12 mm), sited just above the low water mark of spring tides, than on Bed 26 (0.85 mm), which lies above the low water mark of neap tides.

The threeway ANOVA using site as a variable (Table 4.3.4) allowed some of the interactions between variables to be examined. It confirmed that mussel length and site had a significant overall effect on growth increment, but local density did not. However, there was a significant interaction between site and density, indicating that, despite the general pattern of no difference, at some sites growth did vary with density. The best example of this was off Bed 26 on sand where the mean growth in the low density cages was clearly less than in the high density cages (30 mm mussels; low density = 1.68 & 1.74 mm, high density = 2.21 & 2.28 mm: 40 mm mussels; low density = 0.40 & 0.33 mm, high density = 1.12 & 1.27 mm). Observations suggested that this might have been due to 'sand blasting'; the shells of most of the low density mussels were eroded over the winter, whereas in the high density cages most were not affected. There was also a significant interaction between site and length, indicating that at some sites, despite the general trend for smaller mussels to grow more than larger ones, large mussels grew more than smaller ones. Again the clearest example was at a sandy site, off Bed 20, where in two of the cages 40 mm mussels had a larger mean increment than the 30 mm mussels (1.47 *vs.*1.23 mm & 1.95 *vs.* 1.85 mm), though the differences were small and in the other two cages the normal pattern prevailed. There was no obvious explanation for these differences, though individual or local (genetic) variation in growth strategy may have played a part.

Table 4.3.3 Multiple regression analysis of overwinter (1994-95) growth increment on four explanatory variables. (ns = not significant at the 5% level of probability, p)

Predictor	Partial regression coefficient	Standard deviation	t-ratio	p
Constant	2.749	0.539	5.10	0.0001
Length	-0.076	0.008	-9.93	0.0001
Bed	0.054	0.015	3.70	0.0001
Substrate	0.080	0.082	0.98	0.328 ns
Density	-0.00057	0.0014	-0.41	0.680 ns
$R^2 = 54\%$				

Table 4.3.4 General linear model: threeway analysis of variance on overwinter (1994-95) growth increment. (Bed and substrate are combined into 8 sites; F = F-ratio test, p = probability)

Source of variance	F	p
Length	145.03	0.0001
Site	24.89	0.0001
Density	0.49	0.487 ns
Length*Site	2.36	0.014
Length*Density	1.44	0.246 ns
Site*Density	2.31	0.041
Length*Site*Density	1.29	0.248 ns

Clearly, many mussels grew during the 1994-95 winter on the three beds selected for the experiment. This was particularily true of the smallest mussels, but there was little evidence of growth among the largest. It is possible, therefore, that small mussels could grow into the Ostercatchers preferred prey size-class, but most unlikely that large mussels would grow out of it during the winter. The analyses indicate that of the four variables tested only mussel length and bed had a significant effect on mean growth increment. However, the significance of the bed was not related to either the substrate or the density of mussels, suggesting that its location within the estuary must influence mussel growth.

4.3.3.3 Winter 1994-95: Mortality

The mussels in the cages were protected from oystercatcher predation, but some still died of other unknown causes. The proportion dying ranged from 0 to 0.23 in individual cages, but analyses failed to reveal any discernible pattern in relation to bed, substrate, mussel density or mussel length. Overall, 5.8% of the adult mussels in the cages died during the winter period.

4.3.3.4 Winter 1995-1996: Overwinter changes in mean length

Regression analyses of length against time for each of the 8 sites gave growth rates (positive coefficients) varying between 0.0035 $mm.d^{-1}$ and 0.0229 $mm.d^{-1}$ (Table 4.3.5), equivalent to overwinter growth increments of, on average, 0.6 - 4.2 mm. However, at Sites 1 & 2, the regression coefficients were not significantly greater than zero (at $p<0.05$), indicating that on average mussels at these two sites did not grow over the winter. At the other 6 sites, mussels did grow, but at different rates. This difference was confirmed by an analysis of variance of overwinter growth increment (Table 4.3.6), which indicated that there were significant differences between sites, but not between cages within sites.

4.3.3.5 Winter 1995-96: Growth of individual mussels

While there was no overall trend in mean length over the winter on two beds, it was evident from the individually labelled mussels that even on these beds some had grown. Table 4.3.7 shows the percentage of individuals at each site that had increased in length by >1 mm, equivalent to twice the maximum measurement error of +/-0.5 mm. Using this criterion of growth, 13% of individual mussels at Site 1 grew overwinter and 43% grew at Site 2. On the other 6 beds, between 76 and 91% of individuals grew by >1 mm. Table 4.3.7 also shows the percentage of individuals that grew during early, mid- and late winter periods. On average over all 8 sites, over half of the mussels (54%) grew during the early winter (September to November), but very few (4%) grew during late winter (January to March). Although growth varied from site to site, some mussels could have grown into the oystercatcher food range at all of the sites to replace some of those eaten. However, the likelihood of this happening declined through the winter.

Table 4.3.5 Overwinter (1995-96) changes in mean mussel length with date. (sd = standard deviation, p = probability). 301, 302 & 303 represent upper-, mid- & low-level sites on Bed 30 respectively

Site	Bed	Regression coefficient, b.	+/- sd	t-ratio	p	Mean increment, mm.
1	301	0.0035	0.0043	0.81	0.418 ns	0.6
2	27	0.0055	0.0042	1.31	0.190 ns	1.0
3	26	0.0104	0.0037	2.81	0.005	1.9
4	25	0.0132	0.0033	4.07	0.000	2.4
5	302	0.0181	0.0035	5.11	0.000	3.3
6	303	0.0214	0.0038	5.61	0.000	3.9
7	20	0.0193	0.0032	6.03	0.000	3.5
8	22	0.0229	0.0033	7.05	0.000	4.2

Table 4.3.6 Twoway analysis of variance on overwinter (1995-96) growth increments: General linear model. (df = degrees of freedom, F = F-ratio test, p = probability)

Source	df	F	p
Site	7	75.91	0.000
Cage	4	0.96	0.431
Error	732		
Total	743		

Table 4.3.7 Growth of individually labelled mussels: the percentage growing by >1 mm during winter (1995-96) periods. Sep.= September, Nov.= November, Jan.= January, Mar.= March.

Site	Sep.-Nov.	Nov.-Jan.	Jan.-Mar.	Sep.-Mar.
1	0	6	3	13
2	8	5	1	43
3	49	29	2	83
4	61	30	1	76
5	67	44	9	90
6	80	62	6	89
7	81	24	2	84
8	84	35	7	91
Mean	54	29	4	71

4.3.3.6 Winter 1995-96: Variation in growth between sites.

The effect of 6 possible explanatory variables on overwinter (September - March) growth was first tested on their own by simple regression analyses, using the growth increments of all 800 labelled mussels, and then together by a stepwise multiple regression procedure. The variables were: initial length of the mussel; the bed-wide mean densities of small (25 - 39 mm), and large (40 - 65 mm) mussels; percentage aerial exposure (= level on the beach); distance up the estuary from the sea, and substrate softness (= muddiness). The logarithmic transformation of the two measurements of density were used to stabilise the variance. The square of exposure was used as the relationship with growth increment was curvilinear.

Overwinter growth increment was significantly ($p<0.001$) related to all six variables (Table 4.3.8). The regression coefficients for initial length, the two mussel densities and exposure were negative, while those for distance up the estuary and substrate softness were positive. Thus, growth increments were largest in small adult mussels, on low density, low level, muddy beds up the estuary away from the sea. Although growth increment increased down the beach with decreasing percentage exposure, the maximum mean increment was not at the lowest site (6, Bed 303) at 10% exposure, but at Site 8 (Bed 22) at 17% exposure; hence the squared relationship. Exposure was the most important variable, explaining on its own 36% of the variance in growth increment. In comparison, the remaining variables explained on their own rather little of the variance (1.5 - 10.2 %). When the effects of the explanatory variables were tested in the presence of each other in a stepwise multiple regression, these four variables explained only a further 15.5% of the variance after the effect of exposure had been taken into account (step 1, Table

4.3.9). Of this, initial length (step 2) explained 9.7% and the density of large adults, eaten by oystercatchers (step 3), only a further 0.4%. In the presence of the other variables, the relationship with substrate softness changed sign and became negative. In other words, although in general mussels grew best on the muddiest beds, it was not muddiness *per se* that was responsible. After the effect of exposure, initial length and adult density had been taken into account, growth increments were actually largest on the firmest, and so least muddy beds. Only the density of small adult mussels was not chosen in the stepwise procedure, but this was not surprising since it was so highly correlated (r = 0.88) with the density of large adults.

Table 4.3.8 Simple regression analyses of overwinter (Sep.1995-Mar.1996) growth increments (mm.) on 6 explanatory variables separately. p = probability, r^2 = variance explained by the variable.

Variable	Constant	Regression coefficient	t-ratio	p	r^2 %
Initial length (mm)	6.505	-0.105	-7.84	0.000	7.6
log density 25-39 mm (m^{-2})	6.985	-1.918	-9.20	0.000	10.2
log density 40-65 mm (m^{-2})	8.616	-2.604	-7.88	0.000	7.7
Exposure^2 (%)	4.391	-0.00172	-20.59	0.000	36.4
Distance up-estuary (km)	1.754	+0.521	6.34	0.000	5.1
Substrate softness (cm)	2.201	+0.0421	3.36	0.001	1.5

Table 4.3.9 Stepwise multiple regression analysis of overwinter (1995-96) growth increment (mm) on 6 explanatory variables. Values are partial regression coefficients: R^2 = variance explained by the selected variables together. (N=800, F-to-enter or remove = 4.0)

Step	1	2	3	4	5
Constant	4.391	8.760	10.097	12.253	12.211
Exposure^2 (%)	-0.00172	-0.00177	-0.00170	-0.00170	-0.00152
Initial length (mm)		-0.119	-0.118	-0.120	-0.128
log density 40-65 mm (m^{-2})			-0.630	-1.350	-1.400
Substrate softness (cm)				-0.040	-0.261
Distance up-estuary (km)					1.590
R^2 %	36.4	46.1	46.5	47.3	51.94

Thus, the 1995-96 experiment confirmed the 1994-95 finding that mussels grew overwinter in the Exe estuary, but there was a significant increase in mean length at only 6 of the 8 sites (beds). However, even at those sites, where there was no overall trend in mean length, some individuals did grow. Some small mussels could, therefore, have grown into the Oystercatchers preferred prey range at all sites to replace some of those eaten. Growth increments varied between sites and the most important explanatory variable was exposure time (= level on the beach); with growth increasing downshore. Other variables tested explained rather little of the variation in growth increment, either on their own, or in the presence of each other. After the effect of exposure was taken into account, initial length of the mussel was the next most important variable; small mussels growing more than large ones. The density of large mussels, eaten by Oystercatchers, explained <1% of the residual variance; thus, any positive density-dependent effect on the growth of small mussels, resulting from the depletion of large mussels by the birds, is also likely to be small compared to the effect of exposure.

4.3.3.7 Winter 1995-96: The numbers of mussels growing into the size-range taken by Oystercatchers over the winter

At the beginning of the experiment, 25% of the mussels in the cages were within the size-range (40 -65 mm) taken by Oystercatchers. As the main purpose was to determine whether smaller mussels could grow into this range, mussels >40 mm were removed from the data set and the stepwise regression repeated. This resulted in some small changes, but the same 5 variables were selected and in the same order. The main differences were: (i) that the effect of exposure increased, explaining on its own 44% (+7.4%) of the variance in winter growth increment, while (ii) as expected, the effect of initial length declined (-6.7%), explaining only an additional 3% of the variance after the effect of exposure had been taken into account. The effect of adult density also increased, but was still very small as it explained only an additional 1.2% of the variance. Between them, the 5 variables explained 55% of the variance in growth increment. Exposure was clearly the most important variable determining winter growth of mussels, followed by their length.

This multiple regression analysis provided a predictive equation which could be used to estimate the mean growth increment for those beds not used in the experiment, and hence the numbers of mussels in September 1995 that would have grown into the oystercatchers' range over the winter on all of the beds in the estuary. However, the equation explained only a little over half of the variance in growth and another method was used which explained a greater proportion of the variance. The proportion of mussels in the 30 - 34 mm and 35 - 39 mm categories, which grew to >40 mm over the winter, were estimated directly from the basic data (Table 4.3.10). These proportions were regressed against exposure, the bed mean densities of small (30 - 40 mm) and large (40 - 65 mm) adult mussels in September 1995, the distance of the bed up the estuary and the substrate softness (= muddiness). Only the square of exposure had a significant effect ($p = 0.009$), on its own, or in combination with the other variables, and explained 70.6% of the variation in the proportion of 35 - 40 mm mussels growing into the oystercatchers' food range overwinter. This gave the equation:

$$\text{proportion} = 0.810 - 0.000327\ \text{exposure}^2$$

This equation was then used to calculate for those beds not included in the experiment the proportion of small mussels that grew over the winter into the size-range eaten by Oystercatchers. Table 4.3.10 lists these proportions, mean bed densities (m^{-2}) from the September 1995 survey and the numbers (m^{-2}) growing into the oystercatchers food range on each of the 10 beds in the Exe. These numbers varied from 2.8 m^{-2} to 61.4 m^{-2} and represent an overwinter increase in food supply for the birds of 4 - 25%. Clearly, September surveys of adult mussels underestimate the potential winter food supply for oystercatchers, especially on Beds 20, 30 & 31, where over 50 m^{-2} grow into their range replacing those already eaten and where on average 41% of the Oystercatchers fed over the winter between 1976 and 1983.

Table 4.3.10 The proportions and numbers of smaller size-classes of mussels growing into the 40-65 mm class eaten by oystercatchers over the winter of 1995-96. * denotes beds not used in the experiment, values were calculated from the equation relating proportion to exposure; ** values are means of sites 301, 302 & 303 (upper, mid- & low level sites on Bed 30).

	Proportion growing into 40+mm class from:		Densities from September 1995 survey (m^{-2})			Numbers (m^{-2}) growing into 40.0-64.9 mm	% increase in initial Sept. density
Bed	30.0-34.9 mm	35.0-39.9 mm	30.0-34.9 mm	35.0-39.9 mm	40.0-64.9 mm		
1	0	0.133 *		66.7	114.7	8.9	8
3	0	0.465 *		6.0	53.5	2.8	5
4	0	0.531 *		31.3	196.8	16.6	8
20	0.143	0.909	47.4	52.3	220.7	54.3	25
22	0.313	0.700	10.2	9.4	57.0	9.8	17
25	0	0.469		22.9	183.9	10.7	6
26	0	0.407		52.4	184.4	21.3	12
27	0	0.069		106.3	193.8	7.3	4
30	0.010 **	0.426 **	119.9	141.3	278.2	61.4	22
31	0	0.475 *		56.6	113.4	26.9	24

4.3.3.8 Winter 1995-96: Mortality

As in the 1994-95 winter, the experimental mussels were protected from predation by the wire cages, but some still died of unknown causes. Within cages the mortality ranged from 0 - 25% and within sites from 3 - 17%. However, there was no detectable pattern to the mortality, either between beds / sites or during the winter. Overall, 7% of the mussels (25 - 45 mm) died overwinter.

4.3.4 Discussion

4.3.4.1 Do mussels grow in winter?

The first aim of this experiment was to determine whether adult mussels in the Exe estuary grew over the winter period, September to March. Many mussels, but not all, did grow over both winters. In 1994-95, there were significant increases in length, indicating that growth occurred in 69, 31 & 3% of the 32 replicate cages for 30, 40 & 50 mm mussels, respectively. In 1995-96, there were significant increases in 25 - 45 mm mussels at 75% of the sites and overall 71% of individuals grew by more than 1 mm. Given the rapid decline in growth increment with increasing length, it is very unlikely that any mussels could have grown out of the oystercatchers upper limit of 65 mm. However, small mussels could have grown into the size-range taken by Oystercatchers (40 - 65 mm) on all of the beds.

4.3.4.2 Are there bed differences in mussel growth rate?

Given that winter growth occurred, the second aim was to determine whether growth varied between beds, and if so, to determine the factors responsible. There were clear differences in mean growth increments between beds / sites in both winters, but this is best illustrated by the larger range of beds / sites studied in 1995-96. Mean increments varied across the 8 sites from 0.6 mm (Bed 301, range 0 - 3.8 mm) to 4.2 mm (Bed 22, range 0 - 9.6 mm). Likewise, the percentage of individuals growing by more than 1 mm varied between sites from 13 to 91%. The results indicated which factors were and were not responsible for this variation in growth increment The results from the first winter confirmed the expectation that small mussels would grow more than large ones. However contrary to expectation, local density did not affect winter growth. There was a difference between beds, but this did not appear to be strongly related to the substrate, including the presence or absence of mussels.

This suggests that another aspect of location within the estuary was more important. This was confirmed by the results from the second winter when aerial exposure (or level on the beach) and distance up the estuary from the sea were both found to be significant correlates of growth. Mussel length, the bed-wide density of large, mussels and the softness (or muddiness) of the substrates had an additional, but much smaller effect. Together these variables explained 55% of the variance in overwinter growth increment for 25 - 40 mm mussels. However, exposure was by far the most important, explaining on its own 44% of the variation.

4.3.4.3 Was growth density-dependent?

On their own, the bed-wide densities of small (25 - 39 mm) and large (40 - 65 mm) adult mussels had a significant effect on growth, but in the presence of the other variables only the density of the larger mussels had a significant effect and, after the effect of exposure and mussel length had been taken into account, explained only an additional 1.2% of the variance. While this suggests that the effect of large adults on the growth increment of small adults is likely to be small, compared with, for example, the effect of exposure, the actual size of the effect is determined by the regression coefficient, and the range of values over which the variable has its effect; not by the r^2 value. To compare the actual effects of each explanatory variable on the mean growth increment, the maximum and minimum value of each variable, measured at the 8 sites, were inserted in turn into the following multiple regression equation, while holding the other variables constant at their mean values. The equation was:

Mean growth increment (25-40 mm) = 12.918 - 0.00167 Exposure^2 - 0.113 Initial length
- 1.918 log Adults (40-65mm) - 0.307 Substrate softness + 1.960 Distance-up-estuary.

The results of this analysis are presented in Table 4.3.11, which shows for each explanatory variable, (i) the range of values measured over the 8 sites, (ii) the calculated range of mean growth increments, (iii) the size of the effect of each variable, in terms of the percentage reduction in growth increment over its range, and (iv) the direction, along each of these environmental gradients, in which growth declined. Clearly, small mussels grew more on beds with low densities, than on those with high densities of large adults. However, a 4.7-fold increase in adult density resulted in only a 33% reduction in growth increment, compared to a 99% reduction in growth with a similar (5-fold) increase in percentage exposure time.

So, the third aim of the study, to determine whether growth was density-dependent at the bed scale, was confirmed. (Note that this is a bed-wide effect; there was no significant effect of local, within-bed, density on growth increment in the 1994-95 winter experiment.) However, compared to the effect of aerial exposure, distance up-estuary or the softness of the substrate, the effect of oystercatchers eating large mussels, and thereby allowing smaller ones to grow into their food range, was small.

Table 4.3.11 The effect of five explanatory variables, chosen by multiple regression analysis (Table 4.3.9), on mean growth increment of small (25 - 39 mm) adult mussels over the 1995-96 winter. The mean growth increment is shown for the maximum and minimum values of each variable, and were calculated while holding the other variables constant at their mean value. These values are used to calculate the effect of each variable, as the percentage reduction in mean growth increment, over its range. The direction along the environmental gradient, over which the effect reduces growth, is also included.

Explanatory variable	Range of variable across the 8 sites	Calculated range of growth increment (mm)	% reduction in mean growth increment	Direction of reduction in growth
Exposure (%)	10 - 50	4.05 - 0.04	99	upshore
Substrate Softness (cm)	3.9 - 17.4	4.63 - 0.49	89	increasing muddiness
Distance up-Estuary (km)	0.63 - 3.01	0.77 - 5.43	86	down-estuary
Initial Length (mm)	25 - 39	3.52 - 1.83	48	small to large mussels
Large Adults (40-65mm: m^{-2})	58 - 275	4.00 - 2.70	33	low to high density

4.3.4.4 Does growth of mussels offset depletion?

Bivalve mollusc growth is well known to be seasonal in temporate areas and few authors have specifically referred to the growth of mussels in winter. Shell growth has generally been regarded as predominantly a summer process, which declines through the autumn. Certainly, to our knowledge, winter growth of prey has not prevoiusly been considered as a factor affecting the food supply of birds overwintering in intertidal areas.

The final aim of the study was to assess whether overwinter growth of small mussels could offset the depletion of large ones due to oystercatcher predation. To some extent this was the case on all of the beds in 1995-96. However, on half of them, the effect was small (<10 m^{-2} or <10% increase), either because on high level beds very few of them grew (eg Beds 301 & 27), or because bed-wide densities were low (eg. Beds 3 & 22). Any increase could, of course, be important to the oystercatchers; even the minimum value of 2.8 m^{-2} (+5%), estimated for Bed 3, implies a substantial addition of new mussels. However, on the other 5 beds with up to 25% increase (Bed 20, +54 m^{-2}) and up to 61 m^{-2} (Bed 30, +22%) mussels growing into the oystercatcher range, growth must be considered to have had a substantial effect on overwinter food supply for the oystercatchers. Indeed, on the three beds (20, 30 & 31) with >20% increase, small mussels growing into the size range may have equalled, or even exceeded, depletion. So, the density of mussels derived from September surveys did underestimate the potential overwinter food supply for the oystercatchers.

While the proportion of small size-classes of mussels growing into the larger size-classes preferred by Oystercatchers (Table 4.3.10) is a good illustration of the potential importance of this process on the different beds, it was not used as a 'correction factor' in the model. Instead, a more direct approach was used (see Section 4.4.4), which applied a winter growth curve, fit to the 1995-96 data for each bed, and calculated the length of each individual mussel on a particular day in winter.

4.4 THE MUSSEL MODEL

S McGrorty & R A Stillman

4.4.1 The model strategy

The main aim was to produce a model which was structurally simple and compatible with the oystercatcher model. It is, therefore, based on 10 mussel patches, or beds. During the Exe mussel population study (1976-83; McGrorty *et al.* 1990), there were 12 main beds, or subpopulations, but the two smallest declined in area and density during the final years and disappeared soon afterwards, probably due to disturbance associated with the many boats moored in the area. These two beds were, therefore, omitted from the model. In the model, each of the ten subpopulations has a separate suite of relationships which describe the processes of recruitment and mortality.

The fate of the eggs spawned in the Exe, and the origin of the plantigrade larvae that settle there, is uncertain (McGrorty & Goss-Custard 1993), therefore only 'notional' mortalities could be calculated for the early planktonic and primary settlement stages. Secondary settlement on the mussel beds occurs predominantly in spring at the estuary scale (McGrorty *et al.* 1990), but continues at a low rate through summer on some beds in most years and on all beds in some years (McGrorty & Goss-Custard 1993). The first process in the model is the recruitment of spat to the subpopulations in September. By this date settlement is complete, and the main overwinter regulatory mortality just beginning. This decision avoids the period of uncertainty and complex interplay of settlement and mortality during the preceeding spring and summer.

In the Exe estuary, mussels lived up to 10 years and the population has been surveyed biannually in March and September. The model, therefore, contains 10 age-classes (0 - 9 years) and two seasons, winter (16th September to 15th March) and summer (16th March to 15th September) and so 18 periods during which mortality occurs. The first mortality in the model, after recruitment, occurred during the first winter. This was followed by second summer and winter mortalities, and so on until the 10th summer.

At each stage in the model, alternative strategies can be used. Separate relationships can be derived for spat recruitment on each of the patches, or beds. Alternately, spat density at recruitment can be calculated for the whole estuary, with spat then being allocated to beds on the basis of their individual adult densities and substrate softness (McGrorty & Goss-Custard 1991). Likewise, there are two strategies for calculating density-dependent losses at each stage in the mussels life. The first strategy is to apply density-dependent relationships to each bed only during those stages for which there was direct evidence that density-dependent mortality actually occurs. The second strategy is to apply a general model, which applies to all beds, and in which all beds have a common slope, but each bed has a separate intercept (McGrorty & Goss-Custard 1993, 1995).

The first strategy used only the data for each bed at each stage in turn, while the second strategy applies the model to the combined data for all beds and years at each stage. Both strategies have advantages and disadvantages. Though the first strategy applied more rigorous tests, significant relationships were detected in only 45% of the stages, probably because we only have eight years data. It is probable that density dependence occurred at some of the other stages, but was not detected. Such failure of detection could occur either because the range of variation in mortality between years was too small, or because the errors in density estimation on the smaller beds with few samples was too large. The general regression model tests across all beds used in the second strategy, only provide indirect evidence of density dependence and density-dependent mortality may not occur on all of the beds to which it is applied at each stage. Furthermore, while a common slope and separate intercepts for each bed was the best overall model in summer and winter (McGrorty & Goss-Custard 1993, 1995), it was not the best at some stages. In the 5th-7th summer and 8th-9th winter, it failed to explain a significantly greater proportion of the variance than a single slope and intercept model across all beds. At yet other occasions (6th,7th summer

& 3rd winter), a model with separate slopes and intercepts for each bed explained a significantly greater proportion of the variance in stage mortality than did the model applying a common estuary-wide slope. On balance we decided on the first strategy, largely because it represents a more cautious approach.

At some stages, annual variations in the rates of density-independent mortality were related to weather variables (temperature, incidence of gales and rainfall) in summer and winter, but there was no clear pattern to these mortalities across beds or ages. With only eight years data, it was important to minimise the number of variables in the relationships used in the model. Each additional variable reduces the degrees of freedom for statistical tests and increases the possibility of statistical significance arising by chance. Density-independent losses due to weather effects were not, therefore, included in the model.

In keeping with the aim of producing a structurally simple model compatible with the bird model, the mussel population model uses separate relationships for each of the 10 patches, or beds, at each stage. The model begins with spat recruitment to the beds in the autumn, when the bird model begins, rather than with the earlier larval settlement stages. It then applies winter, or summer, mortalities to each of the year-classes present and calculates the densities of each at the beginning of the next 6-month period.

4.4.2 Recruitment

It is well known that spat settlement and survival in bivalve mollusca, including mussels, varies widely from year to year. Spat are often particularly abundant after colder than average winters and scarce after warmer than average winters (Beukema 1982, 1992 and see section 4.2.1). To produce predictive equations of this phenomenon for each bed, spat density at recruitment in September was regressed against the mean air temperature for the previous January to March, the coldest months of the year. This is also the period when spawning begins and the main spat settlement in the estuary occurs. Because the relationship with temperature was curved - mainly as a result of 1979 when very high densities of spat followed a very cold winter - the square of temperature was also included. In contrast to this approach, McGrorty & Goss-Custard (1993, 1995) used the difference in temperature from the 30 year average rather than the actual temperatures. This approach is appealing because it is the extreme variations in temperature which have the most noticeable effects on spat recruitment. However, in practice, there are only slight differences in the proportion of the variance in spat density explained by the two approaches. As direct measures of temperature are likely to be more widely and readily available, we decided to use direct temperature mearures in the model.

Spat in the Exe only settled where adults were already present, and only survived in the safe refuge provided by their byssus, therefore adult density was forced into the regression. Between them, temperature and adult density explained between 52 and 92% of the variation in spat recruitment between years on the 10 beds. After calculating the regressions, the standard deviation of the residual variation was used to set limits within which a randomly chosen number of recruits was added to the number predicted by adults and temperature. The regression coefficients for each of the 10 beds are shown in Table 4.4.1.

4.4.3. Mortality

There are 18 stage mortalities in the model between the first winter and the 10th summer.The first mortality in the model is the major regulatory process (see section 4.2.5) acting during the first winter after settlement on the beds, and before the mussels become adult in the following spring. The last mortality is the tenth summer, during which in the model all of the remaining mussels died, though in reality occasional mussels did survive beyond this age on some of the low-shore beds.

Table 4.4.1 Spat recruitment to the mussel beds in September. The table shows the constants and partial regression coefficients for each variable. R^2 % = the proportion of the variation in recruitment between years explained by adult density and temperature. sd residual = the standard deviation of the residual variation.

Bed	Constant	Adults	°C (J-M)	°C^2 (J-M)	sd residual	R^2 %
1	-1740.2	0.1004	877.7	-91.1	38.4	90
3	-177.4	2.0724	-42.3	0.0	66.3	83
4	780.4	0.2149	-93.0	0.0	40.4	86
20	-1088.8	0.8357	358.3	-33.0	10.1	92
22	-201.4	-0.2772	125.2	-13.0	9.9	60
25	485.6	0.1251	-61.8	0.0	37.7	79
26	-805.8	0.3760	361.9	-39.1	58.3	52
27	367.3	0.4435	-76.3	0.0	45.9	84
30	2314.0	2.2030	-538.8	0.0	399.0	66
31	4983.0	1.3479	-723.2	0.0	360.0	89

The model uses density-dependent relationships only for those stages, in which the mortality, expressed as k-values (Varley & Gradwell 1968), has been shown to be related to the logarithm of the initial density of the particular age-class. The criteria for acceptance were (i) support by major axis (Smith 1973) and reversed axes (Varley & Gradwell 1968) tests of $\log_{10}$ initial density *versus* $\log_{10}$ final density and (ii) the logarithm of the density of other competing adults explained a significant proportion of the residual variation in mortality after the effect of their own initial density had been taken into account in a multiple regression analysis. Since these relationships did not explain all of the variation in mortality between years, a value for additional density-independent mortality is chosen at random within limits set by the standard deviation of the residual variation after the effect of the density-dependent relationship has been taken into account. For those stages in which there is no direct evidence of density dependence, a value for the density-independent mortality is chosen randomly within limits set by the mean and standard deviation of the actual mortalities calculated for the particular bed during the study. The partial regression coefficients used in the model to calculate each stage mortality are set out in Table 4.4.2 for a typical bed (30).

4.4.4 Linking the mussel and Oystercatcher modules

4.4.4.1 Mortality

In the absence of any commercial mussel fishing during the mussel study, it is assumed that most of the winter mortality of large mussels was due to Oystercatcher predation. This is supported by the observation that, in a typical winter on the Exe, oystercatchers on average across all of the beds ate 10-15% of mussels 40-50 mm long and 15-30% of mussels >50 mm long (Goss-Custard, McGrorty & Durell 1996). When the mussel model was run in conjunction with the bird modules, therefore, mussel mortality from the third winter onwards, when many were big enough to be eaten by the birds, was calculated from the Oystercatcher - mussel functional response module (Chapter 3). In addition to those eaten, an additional 6% are assumed to die of unknown causes. This value was derived from the winter growth experiments (section 4.3) and was the number dying in cages, designed to protect them from predators.

Although there are small numbers of immature, non-breeding Oystercatchers feeding in the Exe during the summer, their effect on mussel density is assumed to be small compared to the stress-related mortalities after breeding and is, therefore, not specifically included in the model. Thus, summer mortalities remain the same as shown, for example, in Table 4.4.2 for Bed 30.

Table 4.4.2 An example of how mortality was calculated at each stage. The table shows the partial regression coefficients for stage mortalities, expressed as k-values, for Bed 30. The coefficients are for mortality against the initial density of the particular age-class (own ID) and, when they had a significant ($p<0.05$) effect, the density of all other adults on the bed. sd residuals = standard deviation of the residual variation in mortality. Where there is no density dependence, the means of the actual stage mortalities on the bed between 1976 & 1983 are entered under 'constant', and their standard deviation under 'sd residual'. R^2 % = the proportion of the variance in the stage mortality explained by the relationship. w = winter, s = summer, hence 1w = first winter, 2s = second summer etc of the mussels life.

Stage Mortality (k)	Constant	log own ID	log other Adults ID	sd residuals	R^2 %
1w	-1.5307	0.7311	0	0.0463	97
2s	0.0042	0	0	0.1732	
2w	-2.2395	1.0108	0	0.0705	86
3s	-5.4250	0.8672	1.1930	0.0714	62
3w	-4.2202	0.7639	0.8923	0.0344	95
4s	-0.0304	0	0	0.0910	
4w	-1.0951	0.4962	0	0.0451	75
5s	0.0033	0	0	0.1257	
5w	-0.0007	0	0	0.1012	
6s	-2.4431	1.1600	0	0.1038	60
6w	0.5307	0.6187	-0.6165	0.0603	62
7s	-5.1570	0.6077	1.3768	0.0654	74
7w	0.0369	0	0	0.0932	
8s	0.3508	0	0	0.0791	
8w	-0.0496	0	0	0.1877	
9s	0.5417	0	0	0.2194	
9w	14.3240	2.0050	-5.399	0.5020	67
10s	0.8300	0	0	0.8110	

4.4.4.2 Mussel growth

Oystercatchers select their prey by size, preferring mussels >40 mm long, but also take some smaller ones. The mussel model, however, operates on the basis of age-classes, as determined by annual growth rings on the shell (McGrorty *et al.* 1990). In order to make the bird and mussel modules compatible, therefore, mussel growth rates in September on the 10 beds had to be included in the model to convert the age-based mussel module to the length-based Oystercatcher module. Table 4.4.3 shows the growth curve equations, based on the von Bertanalaffy model, in which

$$L_t = L_{max}(1 - \exp^{-k(t-to)}) \qquad 4.4.1$$

and L_t = the mussel length at time t, L_{max} = the asymptotic (maximum) length, k = the specific growth rate and t_0 = the time when length is zero. These equations were calculated using age (years) / length (mm) data obtained by aging at least 40% of the mussels collected from each bed during each of the eight September surveys. These subsample data were weighted in proportion to the length frequency distribution of mussels in the whole sample before the growth model was applied.

Mussel growth was very variable between beds: the specific growth rates vary by a factor of 2.5 from 0.12-0.30 and the asymptotic length from 54-86 mm. The specific growth rates were highest on the lowest beds on the shore (20 & 22) and lowest on high-level beds (1 & 26). Although the beds with the lowest specific growth rates had the highest asymptotic lengths, these lengths were not actually reached. Mussels on these high-level beds rarely exceeded 65 mm before dying. This variation in growth between beds was expected, since mussel growth is known to be extremely variable, not only between sites, but even within small clumps of mussels (Seed 1976; section 4.3). It was not surprising, therefore, that there was a wide spread of data around the growth curves. In the model, this variation about the line was assumed to be normally distributed, and a mean standard deviation of 4.5 was applied across all ages and beds. In the model these relationships were used to convert the predicted number of mussels within each 5 mm length category eaten by the birds, to the number within each age class.

Mussel growth is seasonal and fastest in summer, but does not stop in September (section 4.3), continuing in at least a proportion of the smaller mussels up to 50 mm to December/January. The cessation of growth for a time between then and March leads to the annual growth ring appearing on the shell. Thus, some of the mussels, which in September were smaller than 40 mm and so below the lower limit of the preferred food of the Oystercatchers, grew into the preferred range during the winter. The proportions of smaller mussels growing over 40 mm on each bed was determined in a winter growth experiment, as described in section 4.3.1, and are set out in Table 4.3.10. the results indicate the relative importance of this continued growth to the potential winter food supply of the birds.

In the model, the size distribution of mussels on a bed on a particular day in winter is calculated as the September distribution, obtained from the von Bertanalaffy model, plus a growth increment for the interval in between. The growth increment was calculated from the lengths of individually marked mussels, 25-45 mm long, in the winter of 1995-96 and expressed using the following relationship:

$$G_d = G_{max} (1 - \exp^{-ad}) \qquad 4.4.2$$

where $G_{max} = (G_1 - G_2 L_{Sept.})$, and $L_{Sept.}$ is the length of mussels in September, G_d is the growth increment on day d, G_1 is the maximum growth increment of a 0 mm mussel, G_2 measures the rate at which maximum growth declines with length in September. a is the specific growth rate in winter.

Table 4.4.3 Annual mussel growth: parameter values for a von Bertanalanaffy model (equation 4.4.1) calculated using the September samples collected in each of the eight years of the study from each bed. L_{max} = the asymptotic (maximum) length, k = the specific growth rate and t_0 = the time (or age) at which length was zero.

Bed	L_{max}	k	t_0
1	77.4	0.13	-1.00
3	65.1	0.27	-0.52
4	76.5	0.18	-0.73
20	65.5	0.30	-0.54
22	69.4	0.28	-0.44
25	70.3	0.19	-0.86
26	86.3	0.12	-1.20
27	54.3	0.26	-0.71
30	60.5	0.27	-0.40
31	72.9	0.17	-0.58

Equation 4.4.2 describes the growth increment on a given day in winter in terms of mussel size in September and days since the start of winter. G_{max} is a function of September length because smaller mussels grew by more than larger mussels during the winter growth experiment. Each of the parameters, G_1 , G_2 & a, were estimated for each of the mussel beds using non-linear regression analysis, and are shown in Table 4.4.4.

Table 4.4.4 Overwinter mussel growth: parameter values for the winter growth model (equation 4.4.2) calculated using the growth increments of all of the mussels measured in the 1995-96 winter experiment (Section 4.3). G_1 = the maximum growth increment of a 0 mm mussel, G_2 = the rate at which maximum growth declines with length in September, and a = the specific growth rate in winter. G_{max} the maximum overwinter growth increment is calculated using G_1 and G_2.The average growth increment of a 40 mm mussel is included as an illustration of the differences between the beds. sd residuals is the variation in growth increment remaining after the model has been fitted.

Bed	G_1 (mm)	G_2	a	Growth increment of a 40 mm mussel by the end of winter	sd residuals
20	11.4	0.204	0.023	3.2	1.27
22	14.2	0.268	0.024	3.5	1.60
25	10.0	0.210	0.017	1.5	0.99
26	6.4	0.112	0.011	1.6	0.82
27	3.8	0.071	0.007	0.7	0.45
30	6.4	0.091	0.009	2.3	1.37

Also shown in the table is the average winter growth increment for a 40 mm mussel calculated using equation 4.4.2. The 5-fold range in average winter increment clearly demonstrates the large differences in winter growth between high- (27) and low-shore (22) beds. In the model, it is assumed that the actual increments about the mean value on a particular bed is normally distributed with the standard deviation given in Table 4.4.4. Thus, in the model, the length of a particular mussel of known age on a day in winter is calculated as the length in September, derived from equation 4.4.1, plus the mean growth increment derived from equation 4.4.2, plus, or minus, a randomly selected value within limits set by the standard deviation of the residuals. The four beds, not included in the winter growth experiment, were each allocated the same parameter values in the model as the bed with the closest exposure/ submergence value, since this was the most important determinant of variation in winter growth between beds. Bed 1 was paired with Bed 27 and Beds 3, 4 & 31 with Bed 30.

4.5 COCKLE POPULATION DYNAMICS IN THE BURRY INLET

J D Goss-Custard

The biology and dynamics of the cockle population in the Burry Inlet were intensively investigated by the Ministry of Agriculture, Fisheries and Food during the period when oystercatchers in that area were regarded by many as being a serious pest of the cockle fishery. The population dynamics model developed during the present contract obtained its parameter values from that study.

The main cockle beds in the Burry Inlet were sampled in November and May, when cockles spawn, between 1958 and 1972 (Hancock 1971). The total numbers of cockles of all ages fluctuated enormously over the course of the study, but two periods could be recognised. Before the severe winter of 1962-63, numbers fluctuated without trend and only small numbers survived their first two years because of a combination of predation by oystercatchers and harvesting by the cockle fishery. At this time, the population was characterised by a high rate of turnover and a relatively stable recruitment to a population consisting of relatively young cockles. The severe weather in 1963 killed most of the adults, as frequently occurs in cockles (Beukema 1979, 1985, 1989, Jensen & Jensen 1985, Dorjes, Michaelis & Rhode 1986, Beukema & Essink 1986, Sueur 1987), in contrast to mussels (Beukema 1989). As has been recorded elsewhere (Kristensen 1957, Beukema 1979, 1982, Jensen & Jensen 1985), an enormous number of spat subsequently became established in the intertidal zone, perhaps having spent part of the summer drifting in the water column (Armonies 1992). The massive settlement of cockle spat after severe winters occurs because of a combination of two factors. First, the competition from established adults (Kristensen 1957, Beukema 1982, Moller & Rosenburg 1983, Andre & Rosenberg 1991) is reduced. Second, and sometimes more importantly (Beukema 1982), the frequently high levels of predation by crabs (Reise 1985, Sanchez-Salazar, Griffiths & Seed 1987) is reduced because the larval development (Beukema 1991) and migrations into the intertidal zone over high tide (Dare & Edwards 1981) are delayed by low sea water temperatures (Naylor 1962, Atkinson & Parsons 1973), allowing the cockle spat to become established. Following the 1963 cold spell in the Burry Inlet, large numbers of recruits survived to become adults the next year because the mortality of young cockles over the intervening 12 months was density-independent. The severe winter thus began a sequence in which years of high spatfall were generally followed by years of high adult numbers and low spatfall, and *vice versa*. But gradually, the cycle smoothed out so that, by the early 1970's, the numbers of adult cockles had drifted down towards the consistently low numbers that had been typical before the 1962-63 severe winter. As had occurred in the earlier phase, very few cockles then survived more than three or four years, despite being capable of living for much longer.

The gradual return to previous adult numbers after the major perturbation in 1962-63 implies regulation, and thus density dependence, in the population. In contrast to mussels on the Exe estuary, the numbers of adults, especially those in their second winter, did fluctuate sufficiently to test for density dependence directly. The spatial pattern in the mortality of second-winter cockles in most years showed that the overwinter loss slowed down, or stopped, once cockle densities had reached a threshold level of *circa* 50-100 m^2, causing the loss to be spatially density-dependent. By congregating where cockles were initially most abundant, oystercatchers and fishermen grazed the initially spatially variable cockle stocks down to a uniform stand by May. Oystercatchers must then have turned to other size-classes of cockles, or to other prey species, while fishermen presumably switched to other places or alternative pursuits. In most years, when the initial density of second-winter cockles in November was less than 600 m^2, the cockle stocks were reduced to the threshold density over the whole bed, irrespective of the numbers present at the start of the winter. Hence, the mortality over the whole bed was also density-dependent over time, at least across most of the winters studied. The density dependence only broke down in the two winters when there were so many cockles in November that even the combined consumption capacity of the birds and harvesting by fishermen could not reduce numbers everywhere to the threshold level.

In contrast to the mussels on the Exe, there was no evidence of density-dependent mortality amongst spat cockles during their first year on the beds. Instead, there was a fairly constant and density-independent mortality during their first winter and second summer after settlement. Again in contrast to the mussels on the Exe, the numbers of spat cockles that had settled by November was inversely, rather than positively, related to the density of older cockles. To the extent that the numbers of adults reflect the severity of the preceding winter, this relationship may have arisen because, after mild winters, more spat were eaten by sub-littoral predators or adult cockles were in poorer condition and so produced fewer spat (Zwarts 1991, Beukema 1992). Alernatively, high densities of established cockles may have directly reduced settlement either because adults and young compete directly for food or space (Hancock 1971) or because adults inhale and kill larvae and newly settled young (Kristensen 1957), just as may adult mussels (Bayne 1964). Whatever the reason, whereas low adult abundance was followed by low recruitment of spat in mussels on the Exe, it was followed by high recruitment of young cockles in the Burry Inlet.

The enormous spatfall in 1963, when adults in the Inlet were so scarce, demonstrated that there was a local super-abundance of recruits. In common with mussels on the Exe estuary, it is therefore unlikely that oystercatcher predation on adult cockles significantly affected the supply of recruits. However, by removing adult cockles, oystercatchers probably allowed more spat to settle. As discussed above, the extent to which it was the density of adults, rather than the influence of other factors that co-varied with adult density, that actually determined the level of spat settlement in cockles is not clear. However, both early (Kristensen 1957) and recent (Andre & Rosenberg 1991) experimental evidence suggest that high densities of adult cockles would have caused part of the reduction in the success of spat settlement. We therefore assume in the cockle population model that oystercatchers have exactly the opposite effect on spat recruitment in cockles in the Burry Inlet as they do in mussels on the Exe. This reduction in cockle spat recruitment as adult cockle densities increase is, in fact, the only source of density dependence for which convincing evidence has been found in the Burry Inlet population (Horwood & Goss-Custard 1977). Without introducing this density dependence, the cockle population dynamic model would not stabilise and would frequently go extinct were random fluctuations in its parameters to be introduced. Some density dependence had to be included in the model if its dynamics are to match those of the Burry Inlet cockle population to any degree in a realistic fashion and, given the available evidence, it was best introduced at the recruitment stage.

4.6 THE COCKLE MODEL

R A Stillman & K Norris

The cockle population dynamics model follows the approach used by Horwood & Goss-Custard (1977) and is largely based on the data presented by Hancock (1971, 73). The model works in a very similar way to that applied to mussel population dynamics, being divided into four components: recruitment, overwinter mortality, over summer mortality and growth. One key difference between these models is that cockle population dynamics are assumed to be the same on all cockle beds (as studies of the Burry Inlet have been at the whole estuary scale), rather than differing between beds as in the mussel model.

4.6.1 Recruitment

The density of spat at the start of a winter period (D_{spat}) is calculated from the density of adults at the end of the previous winter period (D_{adult}) using the stock-recruitment curve derived by Hancock (1973).

$$D_{spat} = a\, D_{adult}\, e^{(-bD_{adult})} \qquad 4.6.1$$

where a = 30 and b = 0.0075 (Hancock 1973). Figure 4.6.1 shows the shape of relationship generated by these parameter values. This relationship assumes that the Burry Inlet is a closed system, with recruitment falling to zero at very low adult densities, reaching a maximum at a density of approximately 150 adults m^{-2}, and then decreasing at high densities.

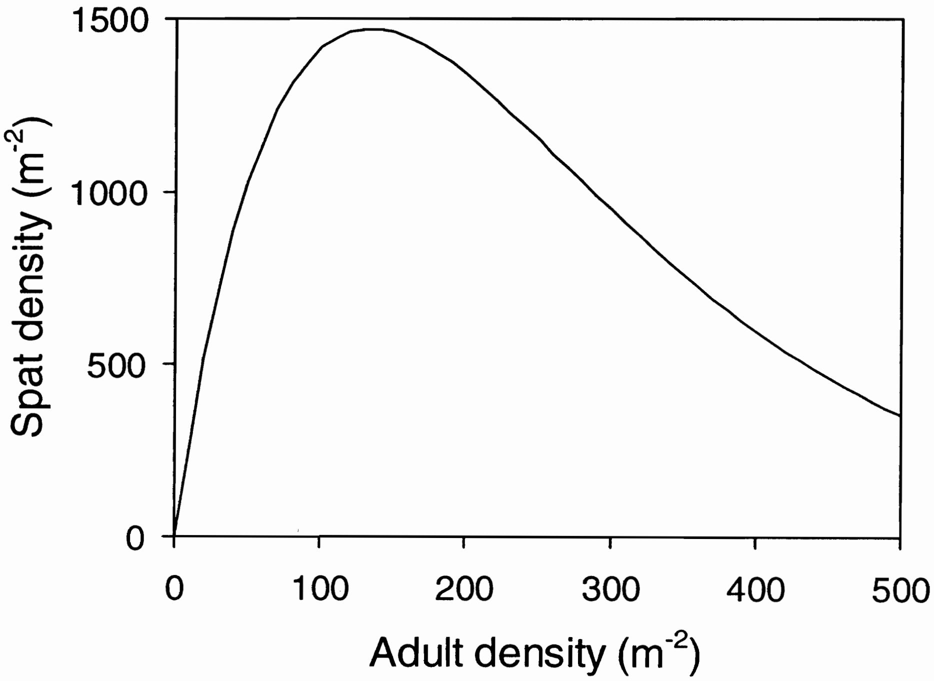


Figure 4.6.1 The stock-recruitment curve used in the cockle population dynamics model. Spat density at the start of a winter period is predicted from adult density at the end of the previous winter. See text for parameter values.

4.6.2 Winter mortality

Overwinter mortality is caused by shorebird predation, shellfishing and other cause (e.g. crab predation). The mortality due to shorebirds and shellfishing is automatically incorporated into the model and will be either density dependent or density independent in different simulations. Other sources of mortality are assumed to be density independent, and to vary between different cockle age classes. First winter mortality due to other causes is set to 60% (Hancock 1971), and that of second winter and older cockles set to 10% (Horwood & Goss-Custard 1977). The mortality rates due to other causes are assumed to be independent of winter temperature.

4.6.3 Summer mortality

Cockle mortality during summer periods of simulations is caused by shellfishing and other causes. Second summer cockles are assumed to have a mortality rate of 42% (Hancock 1971), and older cockles a mortality rate of 10% (Horwood & Goss-Custard 1977). As in the winter, these mortality rates are independent of both cockle density and temperature.

4.6.4 Growth

The cockle population model is based on age classes, whereas shellfishing depletion and shorebird predation are size dependent. The model therefore needs to link age to size through a growth curve as in the mussel model. This link was provided by fitting the von Bertanalaffy model to a sample of cockles of known age and length collected from the Burry Inlet during the study period.

$$L_t = L_{max}(1 - \exp^{-k(t-to)}) \qquad 4.6.2$$

where Lmax = 33.9 , b = 0.807 and t0 = -0.730 (Figure 4.6.2). This equation was used to generate the size distribution of cockles on each patch during each day of winter from their age distribution. No winter growth occurred in the model.

Figure 4.6.2 The relationship used to model cockle growth in the Burry Inlet. See text for equation and parameter values.

Chapter 5 SHELLFISHING MODULES

5.1 SHELLFISHING PRACTICES

B J Ens, K J Norris, I G Johnstone & J van der Meer

5.1.1 Introduction

To employ the shellfish-shorebird model as a useful tool to predict the effect of different shellfishing practices on the shorebirds, it is necessary to describe how shellfishing is currently practised in the EU. We restrict our survey to fishing for mussels and cockles in the intertidal, the primary feeding habitat of the shorebirds. Shellfishing may directly affect the birds through disturbance, or indirectly affect them through a temporary or sometimes even permanent change in the food supply. This requires that we measure for each shellfishing practice the associated disturbance of the birds and the changes in the shellfish stock. A distinction is made between the methods used to collect the shellfish and the regulations imposed on the fishery.

5.1.2 Methods used to fish for mussels

Mussel fishing on the Exe estuary currently occurs by hand, at low tide, on spring tides during the hours of daylight, and can be divided into two methods:

1. stripping: all mussels are removed from the substrate and later sorted into saleable (40 mm or greater in length) and non-saleable size ranges;

2. thinning: only mussels with the saleable size range are removed.

The two methods differ in the way in which they deplete the mussel stock. Stripping removes sections of mussel beds and so reduces their area, the mussel density in the remaining bed area being unchanged. Thinning reduces the density of mussels over 40 mm in length, but not of those below this range, and does not reduce the total area of the bed. As both methods occur at low tide, they both influence birds through disturbance.

An alternative method, which does not occur currently on the Exe estuary, is dredging mussels from submerged beds at high water. This method, which we term high tide stripping, will deplete mussels through a reduction in bed area, as does low tide stripping, but will not disturb birds. High tide stripping also differs from that at low tide as it is not possible to completely remove mussel beds using dredges. Continued dredging will cause a mussel bed to become fragmented. The fragments will become increasingly difficult to relocate (as they are submerged), and eventually dredging will become impractical. In contrast, low tide stripping can potentially remove complete beds as they are exposed and hence visible.

5.1.2.1 Hand gathering

When fishermen collect mussels by hand over low tide, they disturb some birds but not necessarily all. For example, as only mussels above a certain size are commercially valuable, mussel beds with small mussels will not be exploited. Since the mussels occur in clumps on the surface of the mud, the fishermen are effectively able to remove the entire mussel bed. Even if some mussels remain, these may then be washed away by storms. When the entire mussel bed is depleted, recruitment of new mussels may be impaired, since the larvae prefer to settle between old mussels (Chapter 4). However, even though the fishermen are able to remove the entire mussel bed, this does not mean that they will necessarily do so.

Sometimes, as in the Exe estuary, mussels are fished from the subtidal and laid out in the intertidal to grow and be harvested only later. Once in place, these mussel beds are also used to "grow" and collect periwinkles.

5.1.2.2 Mechanical dredging

Mechanical dredging of mussels occurs over high tide, so no disturbance of the birds will occur. Shallow draft boats operate big mechanical dredges that scrape the mussels from the bottom. After fishing, many damaged individuals remain, causing a temporary feeding bonanza for the birds. Like hand gathering, mechanical dredging may lead to the complete demise of the mussel bed and the associated impairment of recruitment. When the fished mussels are directly sold, only mussel beds with large mussels will be fished, as in Denmark, when the yield from culture plots is low (N. Dankers, pers. comm.). However, mussels may also be fished as seed to be laid out in subtidal culture plots. In this case, small mussels of one year class will be preferentially fished.

5.1.3 Methods used to fish for cockles

5.1.3.1 Hand gathering

Typically, fishermen collecting cockles by hand work as solitary individuals, employing a rake or other device to extract the cockles from the sediment. Since fishing is mostly done at low tide, this may lead to extensive disturbance of the birds. It is almost certainly the case that, when shellfishing methods are compared, the amount of human disturbance of the birds per collected cockle is highest for this kind of fishery. Probably, hand gathering causes little additional damage to other benthic organisms and it is not expected to have long-lasting effects other than depletion of the cockle stock. This depletion will be localized as this method of gathering is only economically viable when cockle density is relatively high. As a result, only dense cockle beds are exploited.

Cockle fishing in the Burry Inlet occurs by hand gathering at low tide. The relationship between the rate at which fishermen collect cockles and the density of fishable cockles in the sand (the functional response of hand gathering) was measured under the present contract (Figure 5.1.1):

$$y = \frac{x}{350.82 + 5.44x} \qquad 5.1.1$$

where y = rate at which standard sized sacks (each containing 25kg of cockles) are filled (sacks min^{-1}) and x = density of fishable cockles (cockles m^{-2}). At the present time, each fishermen is restricted to a maximum daily catch of 100kg of cockles (4 sacks). They remain on the sand flats until this daily quota is reached and then leave. As the rate at which cockles are collected increases with increased cockle density (Figure 5.1.1), the time taken to collect the quota decreases with increased density. As fishing occurs at low tide, it can potentially disturb foraging shorebirds. The duration of disturbance depends on the time taken for fishermen to collect their daily quota of cockles, and hence is longer when cockle densities are low.

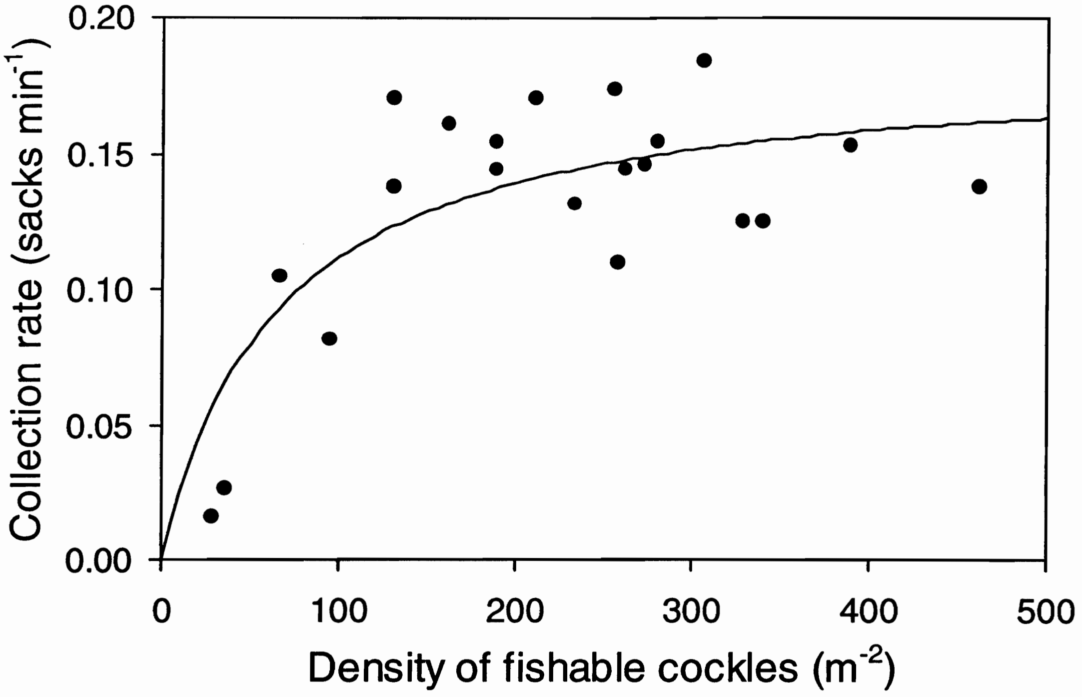


Figure 5.1.1 The functional response of cockle gathering by hand in the Burry Inlet.

Much of the above is true for a particular technique of hand gathering employed in the Netherlands except that the dredge, which is called a "wonderklauw", is pulled by hand through the sediment when the sediment is still covered with shallow water. Between 10 and 80 cm water is needed, so that fishing is only possible during ebb and flood (Oord 1992). Disturbance of the birds during the actual fishing is therefore expected to be minimal, but some disturbance will occur when the fishermen scout for profitable fishing sites. Depending on the area between 1.5 and 4 hours can be fished per tide, during which ca. 100 m^2 can be covered (Oord 1992). Within one tide, fishing is very systematic so that only a few cockles remain on the small ridges between the fishing tracks. One might expect fishing to become less systematic when the same cockle bed is fished for a large number of tides. Steehouwer's (pers. comm.) estimate that on a bed with 35 ton only 20 ton can actually be exploited supports this suggestion. Economical factors determine at which initial cockle densities the technique can be profitably employed. According to Oord (1992), densities of fishable cockles must be at least 600 to 800 cockles per m^2. Steehouwer (pers. comm.) takes 500 cockles per m^2 as the minimal density; only when the price is very good can densities of 250 cockles per m^2 be fished.

5.1.3.2 Tractor dredging

Instead of pulling the dredge by hand, a tractor may be used. Since this allows more cockles to be collected per unit time, this will cause less disturbance of the birds per collected cockle compared to hand gathering, especially when dredging is done when the mudflats are still covered with water (Cooke 1988). The tractor and the dredge may cause some damage to the cockles that remain, which will create a temporary bonanza for the birds. Comparing three samples of 0.1 m^2 per wheel track, dredge path and undisturbed control area, Cooke (1988) concludes that the damage to the cockles is minimal. From the absence of large cockles in the dredge path, Cooke (1988) concludes that nearly all large cockles are retained by the dredge, whilst undersized cockles are rejected with 100% efficiency. The minimally exploitable density of cockles is probably lower than with hand gathering, so that a greater range of cockle beds can be exploited to a greater degree. However, it is clear that the technique cannot be used in very muddy areas. Finally, some effect on the sediment is possible, which would have long-lasting consequences on the benthic fauna.

5.1.3.3 Suction dredging

Suction dredging is done over high tide so that disturbance of waders does not occur. In former times, a dredge was pulled over the bottom by a boat and the cockles were washed out of the sediment at the front of the dredge by a stream of water. Undersized cockles passed through the dredge, which had to be emptied on board of its fishable cockles every now and then. Nowadays, the catch is continuously pumped on board via a hydraulic device. On board, some extra sorting is done. Damage to both caught and discarded cockles and other fauna is noticeable. This sudden high availability of damaged animals will create a temporary bonanza for the birds, as with tractor dredging. The extent of the damage to the discarded animals will depend on the intensity of fishing, i.e. how often the fishermen go over an area and discard the same individual animals. According to Franklin & Picket (1978), discarded as well as fished cockles are much less likely to survive after suction dredging than after hand raking or blowing out: only 60% of hydraulically dredged and apparently undamaged cockles survived 10 days. In the mean time, techniques may have improved to comply with the Dutch regulation that no more than 12% of landed cockles are allowed show signs of shell damage (J. Holstein, pers. comm.), but no published data seem available. However, the extraction technique is quite efficient. The large majority of undersized first year cockles pass through the dredge and only few are discarded later on, while virtually all cockles older than two years are retained (Table 3.3 in Huggett 1993, based on Bailey et al. 1991 and unpublished Solway Cockle Surveys 1991). Low retention of spat was only observed by De Vlas (1982) when the densities of spat were high (Table 5.1.1). The apparent tendency that, of the very large cockles, only between 8 and 10 per m^2 remain after fishing has stopped (termed here the ***remaining density***) would only apply if fishing was very systematic. In fact, the average remaining density established by De Vlas (1982) for intertidal areas in the Netherlands for the years 1979 and 1980 is ten times as high as this (Table 5.1.2). The following theoretical analysis of the functional response of suction dredging explains why. In the analysis, we also provide estimates of the parameters as they currently apply to The Netherlands.

Table 5.1.1 Estimation of efficiency (in %) of suction dredging in retaining cockles of particular ages from a comparison of densities (cockles per m^2) inside (in) and just outside (out) fishing tracks. Data from De Vlas (1982).

		Age class 0			Age class I			Age class II		
Location	Date	in	out	%	in	out	%	in	out	%
Inschot	02/09/1980	3	0	100	1033	69	93	0	0	-
Rottumerplaat	15/11/1979	6876	4698	32	0	0	-	0	0	-
Piet-Scheve Plaat	29/11/1979	435	382	12	0	0	-	36	10	72
Rottumerplaat	15/11/1979	243	73	70	7	3	57	55	8	85
Balgzand	15/11/1980	4	1	75	126	21	83	0	0	-
Balgzand	25/08/1980	0	0	-	179	21	88	0	0	-
Zuid Meep	21/11/1980	0	0	-	717	61	91	0	0	-

Table 5.1.2 Average overall densities of fishable cockles (number per m^2) on cockle beds before and after suction dredging, providing an indication of the giving up density, i.e. the density at which fishing is stopped, and the proportion fished. Based on De Vlas (1982) and communications with the author.

Location	Year	Cockle density before fishing (m^{-2})	Cockle density after fishing (m^{-2})	% fished
Balgzand - Amsteldiep	1980	152	68	55%
Balgzand - Vangdam	1980	340	128	62%
Hooge Kraayer	1979	320	90	72%
Zuid Meep	1980	717	163	77%
Rottumerplaat	1979	62	12	80%
Inschot	1980	1033	114	89%
Neeltje Jans	1979	950	86	91%

The following parameters are defined.

t = total time (h) the suction dredge has operated; in The Netherlands, fishing only takes place during daylight in the first four working days of the week; each vessel is allowed a maximum of three or four hours of fishing per day.

A = total area (m^2) of the cockle bank; judging from Figure 26 in De Vlas (1982), cockle beds average 1.5 km^2 in size; however, according to Dankers (pers. comm.), 0.5 km^2 may be a more reasonable estimate.

v = speed (m h^{-1}) of the fishing vessel; according to J. Holstein (pers. comm.) cockle fishing boats in The Netherlands currently sail at an average speed of between 3 and 4 km h^{-1}, even though speeds of 7 km h^{-1} are possible under good conditions.

w = total width (m) of the dredges; in the Netherlands one dredge on each side of the boat is allowed and each of these dredges is allowed a maximal width of 1 m (an alternative is one dredge of 1.25 m width); according to J. Holstein (pers. comm.) most fishing vessels in the Netherlands have 2 dredges of 1 m, so w equals 2 m.

a_s = search rate (m^2 h^{-1}), i.e. the area dredged per unit time; clearly a_s=w.v.

$a_d(t)$ = area of discovery (dimensionless), i.e the probability that a fishing vessel will fish a particular unit of space during time t; by definition: $a_d(t)=a_st/A$.

d_f = density (m^{-2}) of fishable cockles before fishing has started; in The Netherlands the legal minimal size of cockles is 15 mm.

d_{min} = density (m^{-2}) of fishable cockles at which fishing is no longer profitable, i.e. this is the "giving up density" and this will depend on many economic factors (the supply of cockles, the demand for cockles, the price of gasoline etc.). According to both J. De Vlas and J. Holstein (pers. comm.), this currently varies in The Netherlands between 30 cockles per m^2 for large and therefore highly valuable cockles (ca. 2 gram wet flesh weight per cockle) to 60 cockles per m^2 for smaller cockles (ca. 1 gram wet flesh weight per cockle); such low values were rarely reached when De Vlas (1982) conducted his studies.

If fishing is completely systematic, it takes A/a_s hours to clear away the entire bank, assuming all fishable cockles are retained by the dredge. During this time the rate at which cockles would be collected equals

$a_s.d_f$=v.w.d_f. Only banks with a cockle density above d_{min} will be fished, but no fishable cockles will be left on these banks.

Although technically feasible, systematic fishing is not practised (J. Holstein pers. comm.). The alternative extreme assumption is that fishing resembles a random process in which fished areas are very quickly refished so that the cockle collection rate will drop as time goes on. Under the assumption of a random process, we can calculate that after t hours a fraction exp(-a_d(t)) of the area has not been fished. If we assume that no fishable cockles are left after the first pass of the dredge, the average cockle density that remains at time t can then be calculated as d_f.exp(-a_d(t)). By definition, fishing will stop when the average density of fishable cockles has dropped to the giving up density d_{min}. We can now calculate how long this will by solving the following equation for t:

$$d_{min} = d_f.\exp(-a_d(t)) = d_f.\exp(-a_s.t/A). \qquad 5.1.2$$

From this it follows that:

$$\ln(d_{min}) = \ln(d_f)-a_s.t/A. \qquad 5.1.3$$

Hence, the time t_d to deplete the bed to the average density that can still be exploited amounts to:

$$t_d = A.\ln(d_f/d_{min})/a_s. \qquad 5.1.4$$

Finally, knowing that after time t the average cockle density remaining on the bed amounts to d_f.exp(-a_d(t)), we can calculate that after time t the rate of cockle collection will have dropped to $a_s.d_f$.exp(-a_d(t)) = v.w.d_f.exp(-a_d(t)). We can also calculate that A.d_f.(1-exp(-a_d(t))) cockles will have been fished during this time.

Suction dredging not only depletes profitable cockles. Apart from unintentional damage to undersized cockles, long-lasting effects may occur because of the damage to other benthic animals and the reworking of the sediment (De Vlas 1982). A change in the sediment might affect growth and recruitment of the cockles. Franklin & Pickett (1978) provide evidence that cockle settlement was reduced in commercially dredged areas, which may have been due to fishing being continued during the time of spat settlement. When dredging took place several months before the time of spat settlement, no difference between dredged and control areas emerged. One may expect this to depend on the type of area. An extremely pessimistic scenario involves the destruction of a shallow solid layer of clay or shells, for instance, which prevents the area from being colonized by *Arenicola.* Once the area is colonized, the excessive bioturbation of this worm may prevent future recruitment of cockles (or mussels) in the area. According to Piersma *et al.* (1993), knot have declined around the island of Griend in the Dutch Wadden Sea because cockle and mussel fishing affected the sediment in such a way that the baltic tellin (*Macoma balthica*), the preferred prey of the knot, no longer recruits in sufficient numbers.

5.1.3.4 "Blowing out"

This technique requires an anchored boat; by steering the boat around in ever decreasing circles, the propeller of the boat is used to stir up cockles into a large pile for subsequent collection. "Blowing out" necessarily occurs when the mudflats are still covered with water, so no disturbance of the birds will occur. In contrast, collection of the cockles occurs during low tide, so the birds will be disturbed. Per collected cockle, the amount of disturbance is expected to be less than with hand gathering or tractor dredging, since collection of the cockles that are piled up can be very efficient. Possible damage to the undersized cockles and other benthic fauna has not been assessed. The efficiency of extraction of the cockles is probably comparable to suction dredging. Effects on the sediment are quite dramatic, especially when the sediment is muddy (Franklin & Pickett 1978).

5.1.4 Regulations imposed on the fishery

In Denmark, cockle fishing may only be carried out in three well-defined areas, of which only one can be fished in any one year. Mussel culture is banned from the Danish Wadden Sea and three large areas, together constituting 46% of the estuarine Danish Wadden Sea, have been closed for mussel fishery. In the open area, only fishery for consumption sized mussels is allowed, but there are quotas that operate on a daily and weekly basis. There is an annual quota per vessel and an annual total allowable catch (TAC). Marketable mussels exceed 50 mm in size, but 10% may be smaller.

In Germany, the cockle fishery has been stopped in the entire German part of the Wadden Sea. Furthermore, nearly the entire German Wadden Sea has been included in a protection area consisting of three national parks. In the core zone of these parks (about 50%), culture of shellfish is being phased out. Outside the core zones, mussel culture and fishery is still allowed. Seed fishery on intertidal flats in Schleswig-Holstein has been voluntarily stopped completely since 1987 and since 1996 it has been forbidden. In Niedersachsen, fishery authorities have closed certain beds for fisheries. Marketable sizes of mussels are 50 mm and 40 mm respectively for Niedersachsen and Schleswig-Holstein. In both cases, 10% of the catch may be below this size.

In The Netherlands mussel and cockle fisheries have been placed under new regulations since 1993. Since that year, 26% of the tidal zone in the Dutch Wadden Sea has been closed permanently for all shellfish fishery. For the open areas, it has been agreed that the fishery sector and the government co-operate in the management of fisheries. The cockle and mussel fishery are to a large extent regulated by means of self-imposed fishing plans. These self-imposed fishing plans include limits to the total number of hours each vessel is allowed to fish. In years of limited food supply for shorebirds, part of the mussel and cockle stocks will be reserved for them. At present, this part is set at 60% of the cockles and mussels needed by the birds. Similar restrictions apply to the Dutch Delta area. The minimum size of marketable cockles is 15 mm. No size restrictions apply to mussels fished to seed culture plots.

The UK cockle fishery is managed in different ways in different estuaries. For each estuary sea fisheries committees make byelaws to control cockle fishing (Huggett 1993). A common byelaw is that raked and tractor dredged cockles must not pass through a 20-22mm mesh, whilst bars in riddles on suction dredges should not be closer than 14 mm (Huggett 1993). A good contrast can be found between Burry inlet and the Wash. In the Burry inlet there is a low intensity traditional fishery which is very strictly controlled, and in the Wash a high intensity fishery which, before 1992, had very little regulation. Since then, strong regulation has been in operation.

In the Baie de Somme in France, part of the area is open for fishery and Oystercatchers may be hunted there. Another part of the bay is designated as a Nature Reserve where hunting is forbidden. In part of the reserve, cockle fishery is allowed, and another part is closed for fishing.

5.2 DISTURBANCE PARAMETERS

R A Stillman & J D Goss-Custard

Shellfishing has two direct effects on shorebirds. First, shellfishing can result in the depletion of shorebirds' food stocks and hence a potential reduction in intake rates (see functional responses in chapter 3). Second, when shellfishing occurs at low tide in areas used by shorebirds for feeding, the human presence can result in disturbance of the feeding birds. This section presents the results of field experiments carried out under the present contract to measure the spatial and temporal scales over which human disturbance affects foraging oystercatchers. The results of this experiments are used to parameterise the model.

5.2.1 Experimental methods

Experiments were conducted on the Exe estuary between October 1994 and September 1996. The experiments involved the controlled disturbance of oystercatchers feeding on mussels at low tide. The experimental procedure relied on the controlled disturbance being the only major source of disturbance during the low tide period. Thus the choice of study area within the estuary was limited to a mussel bed on which disturbance due to factors such as shellfishing and recreational activities was sufficiently infrequent to allow experiments to be carried out. However, it was also considered important that some human activities should normally occur on the bed so that birds feeding on the bed had had some previous experience of disturbance. Given these constraints, bed 20 (see Figure 3.2) was chosen as the study area as it was subject to an intermediate level of human disturbance. This mussel bed is located close to the upper shoreline (from which bird counts could be made), has a maximum exposed area of 9.4ha and is fully exposed at low tide for approximately 2 hours.

Two different experiments were performed, one designed to measure the impact of disturbance on the birds immediately surrounding a static source (local disturbance), and the other to measure the impact of disturbance on the population of birds on the entire bed (bed-wide disturbance). Seasonal changes in the impact of disturbance were studied by repeating experiments throughout the winter periods. In order to reduce the likelihood that birds became habituated to the controlled disturbance, experiments were conducted infrequently, with only one experiment occurring on each spring tide series. Experimental days were therefore separated by approximately 14 days. Experimental results for the different years were similar and so are combined for analysis.

5.2.1.1 Local disturbance

A 25x150m transect divided into six 25x25m cells was marked out on the mussel bed at a distance of approximately 250m from the shore, and running directly away from the shore. The transect was located on a relatively level part of the bed (30 minutes separated the exposure of the highest and lowest level cells), and in an area used continuously by birds throughout the low tide period. Experiments started when the bed was fully exposed by the receding tide and finished when the advancing tide first started to cover the bed. At the start of an experiment, an observer located on the shore, with a view directly along the length of the transect, counted the numbers of feeding and non-feeding birds in each of the six cells prior to disturbance. These counts were repeated at 5 minute intervals for approximately 15 minutes, after which the observer walked on to the mussel bed until they reached the nearest edge of the transect. The number of feeding and non-feeding birds in each of the cells was then counted again to find the initial impact of disturbance. Changes in the impact of disturbance through time were recorded by the observer remaining at the same location, and continuing to count the number of birds in each cell every 5 minutes. During the first winter of the study, the observer remained in place (for up to 2 hours) until the advancing tide started to cover the bed. In subsequent experiments the observer remained on the bed for approximately 30 minutes and then returned to their initial location on the shoreline. Once on the shore, the return of birds to the disturbed area was measured by counting the number of birds in each cell until the advancing tide started to cover the bed. Experiments were conducted on spring tides, with one experiment being performed during each spring-neap cycle. Control counts of the number of birds in each cell of the transect throughout the low water period in the absence of disturbance were carried out on two days in the first winter; one in autumn and one in late winter.

5.2.1.2 Bed-wide disturbance

An observer located in an elevated position on the shoreline counted the number of feeding and non-feeding birds on the whole of the bed and on an adjacent sand ridge (on which birds were known to congregate after disturbances (Goss-Custard *et al.* 1994)) at 10 to 20 minute intervals from first exposure of the bed. These counts continued (for approximately 2 hours) until the bed was fully exposed at low tide to determine the behaviour and density of birds on the bed prior to disturbance. At low tide a second person walked across the bed following a standard route such that all parts of the bed were approached to within approximately 75m and all birds took flight. In most experiments the majority of birds left the bed and settled on or near the sand ridge, but in late winter many birds returned immediately to the bed, landing on areas previously covered by the disturbance. In these cases the person did not alter their route to redisturb areas of the bed, but adhered to the standard route, thus ensuring a constant source of disturbance throughout winter. As soon as the second person left the bed the observer restarted counting the birds on the bed and the sand ridge at 10 to 20 minute intervals to monitor the return of birds after disturbance. Counts continued until the bed was completely covered by the advancing tide, approximately 4 hours later. Experiments were conducted on spring tides, with one experiment being performed during each spring-neap cycle. Two control counts, one in autumn and one in late winter, were made on undisturbed days to record changes in the numbers of birds on the bed in the absence of disturbance.

5.2.2 Results

5.2.2.1 Local disturbance experiment

The control counts showed that in the absence of disturbance all cells along the transect were used by feeding birds throughout the low tide period in both autumn and winter. The mean density of birds in the transect at low tide was 74 birds ha^{-1} (sd=33), with a mean of 88% (sd=20) of birds feeding. Thus the mean density of feeding birds was 64 birds ha^{-1} (sd=30). Similarly, all cells in the transect were occupied by birds immediately prior to the start of each experiment. As all cells were occupied on undisturbed days and at the start of experiments, any absences during experiments can be attributed solely to the impact of human disturbance.

As the observer walked onto the mussel bed towards the transect, birds took flight or walked away so that no birds were found within a certain distance of the observer by the time they reached the start of the transect. This initial *exclusion distance* was measured as the distance between the observer and the centre of the nearest cell occupied by birds. Initial exclusion distance ranged from 62.5 to 137.5m with a mean of 81m (sd=21; n=24). This approach only provided a measure in the direction of the transect, but estimates of the distances to the nearest birds in other directions suggested that this measure was comparable to the exclusion distance surrounding the observer. Birds continued to move away from the observer as time progressed so that, after 15 minutes, the exclusion distance had increased to 96m (sd=21; n=23) and was significantly greater than the initial distance (paired t-test=4.1, $p<0.01$). Further increases in the exclusion distance were slight; after 30 minutes the exclusion distance was 103m (sd=21; n=24) but this was not significantly different to that after 15 minutes (paired t-test=1.3; $p>0.2$). Exclusion distance thus increased most rapidly during the first few minutes of the disturbance and showed no tendency to increase or to decrease thereafter even if the observer remained on the bed for up to 2 hours (Figure 5.2.1). The exclusion distance after 30 minutes of disturbance is referred to as the final exclusion distance.

Seasonal changes in the initial and final (after 30 min) exclusion distances are shown in Figure 5.2.2. During the first half of the season (up to 100 days since 1st August), all initial exclusion distances except two were greater than 75m, whereas later in the season initial distances of less than 75m were frequent. But despite this, initial exclusion distance was not significantly related to stage of the season (y=95.3[se=8.7]-0.105[se=0.065]x; n=27; p>0.1). Early in the season, most exclusion distances had increased to over 125m after 30 minutes, whereas later in the season exclusion distances of around 100m were most frequent. In contrast to the initial exclusion distance, the exclusion distance after 30 minutes decreased significantly through the season (y=131.1[se=9.0]-0.211[se=0.067]x; p<0.01). Therefore, at all stages of the season the exclusion distance increased with time since the start of disturbance, but the magnitude of this increase was greater in autumn than in winter.

The impact of disturbance on shorebirds depends not only on the size of the area from which birds are totally excluded but also on any changes in the behaviour or density of birds in the surrounding occupied area. Figure 5.2.3 shows changes in the density of birds in transect cells located at increasing distances beyond the exclusion distance. The effect of disturbance changed with increasing distance from the exclusion zone. At the start of disturbance and in the first occupied cell along the transect (termed the boundary zone), the total number of birds and of feeding birds, and the proportion of birds that were feeding, were all reduced. There was a net movement of birds away from this zone and most of those that remained stopped feeding. As time progressed and the exclusion distance increased (Figure 5.2.1), the density of birds in the boundary zone remained relatively low but a higher proportion of those present began to feed. After 30 minutes, bird behaviour in the boundary zone was similar to that in more distant cells. The low density of birds in this area has two potential explanations. First, bird density was measured in 25x25m cells and on average birds would be absent from one half of the nearest occupied cell. A lower density would therefore be expected in the boundary zone simply due to the method used to measure density. Second, it is likely that individual birds differed in their reaction to the disturbance; some tending to approach closer to the disturbance source than others. This variation would cause bird density to be lower in the boundary zone than in cells further away from the disturbance source. In the more distant cells 25-75m beyond the exclusion zone, the initial impact of disturbance was an increase in total bird density, no change in the density of feeding birds and a decrease in the proportion of birds feeding. There was a net movement of birds into this area, but newly arrived birds did not start to feed immediately. But as time passed, the proportion of birds feeding in this area increased, and so the density of feeding birds increased.

After the observer returned to the shoreline, birds started to reoccupy the exclusion area. This reoccupation was the result of birds on the edge of the exclusion area walking towards the previous disturbance source, and of birds flying into the exclusion zone from other areas. Newly arrived birds tended to land close to those already present and so the size of the exclusion zone was decreased from its perimeter inwards. Birds therefore reoccupied the transect initially by moving into the most distant cells and then by moving towards the source of previous disturbance so that the cell nearest the source was usually the last to be reoccupied. The recovery time after disturbance was measured as the time taken for the density of birds in the nearest cell to the disturbance source to reach that before disturbance. During the early part of the season (less than 75 days after 1st August), recovery time exceeded 40 minutes, whereas later in the season it was reduced to approximately 15 minutes (Figure 5.2.4a). Thus recovery time decreased significantly through the season (y=57.6[se=6.5]-0.202[se=0.050]x; n=14; p<0.01). The long recovery time early in the season was simply due to the greater exclusion distances found at this time of the year as the rate at which the exclusion area was reduced in size was not seasonally related (Figure 5.2.4b).

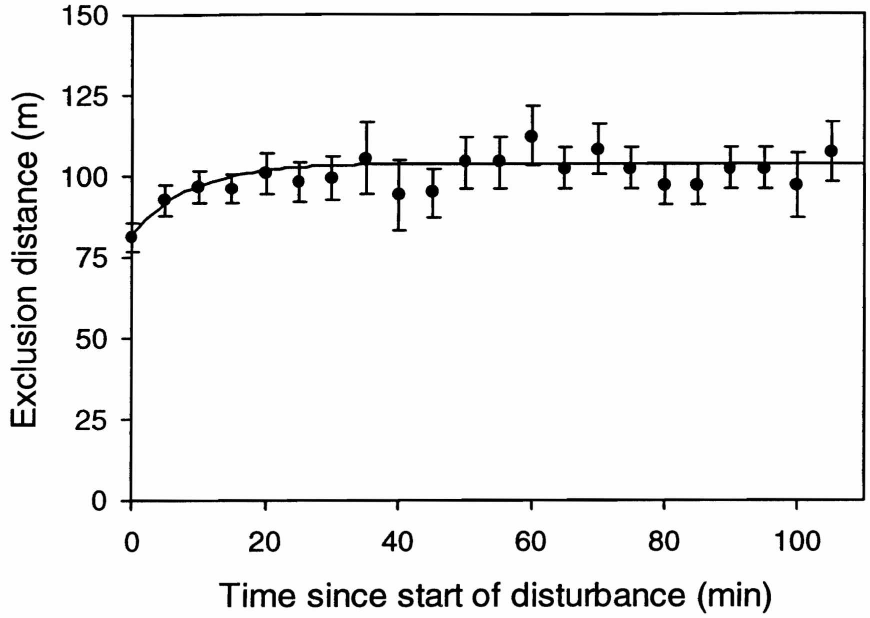


Figure 5.2.1 Oystercatcher exclusion distance from a person standing on a mussel bed in relation to the duration of the disturbance. The symbols show mean values for all experiments with associated standard errors, and the line depicts a relationship fitted using non-linear regression ($y=82+22(1-e^{-0.115x})$; $p<0.01$ for all parameters).

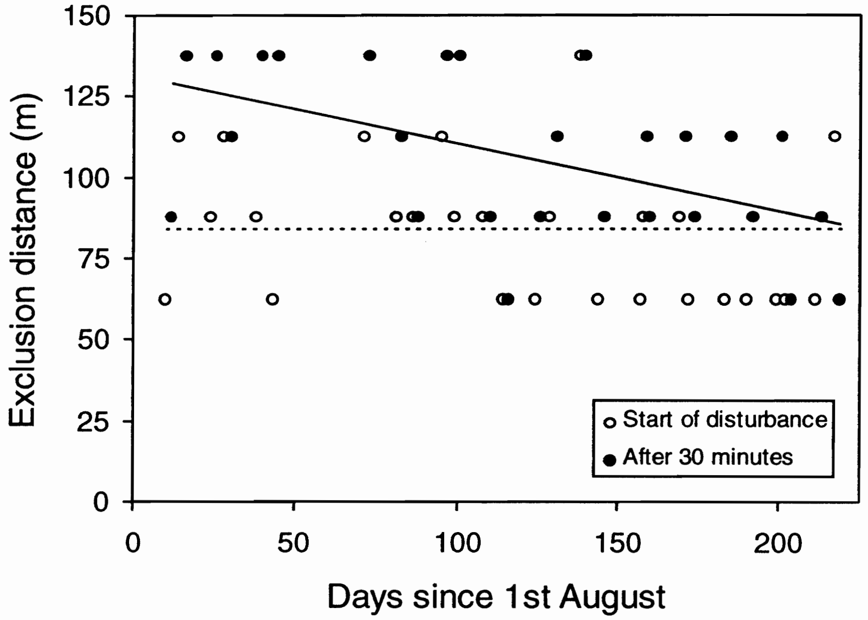
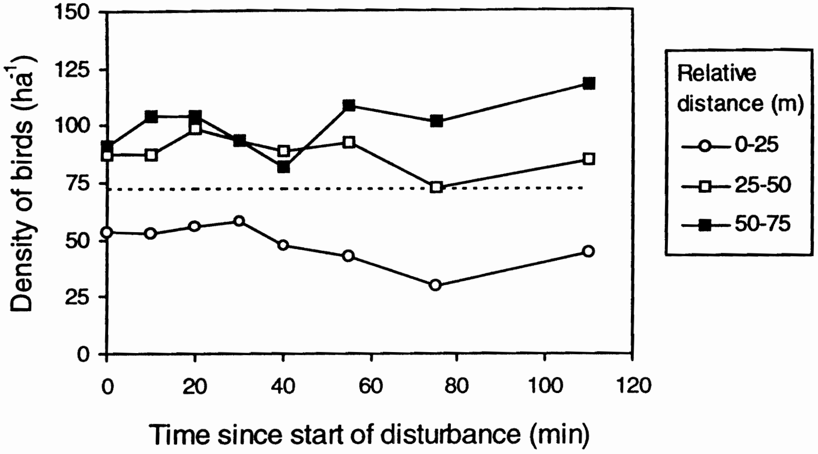
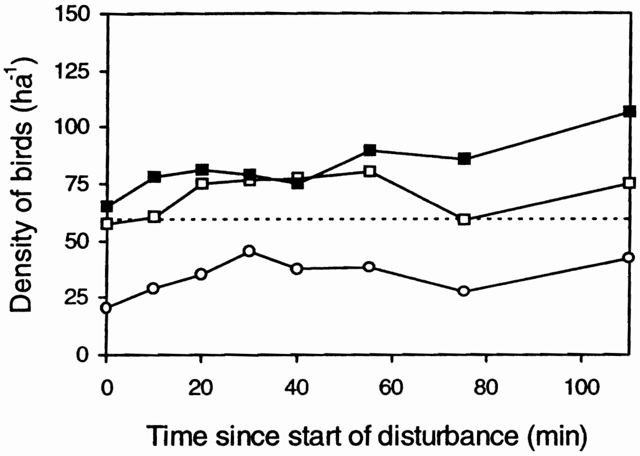


Figure 5.2.2 Seasonal changes in the oystercatcher exclusion distance from a person standing on a mussel bed when the person first walks on to the bed, and after the person has been present for 30 minutes. Each symbol shows the results of one experiment. The broken line shows the mean exclusion distance at the start of disturbance, and the solid line, the relationship after 30 minutes.

(a) All birds



(b) Feeding birds



(c) Proportion of birds feeding

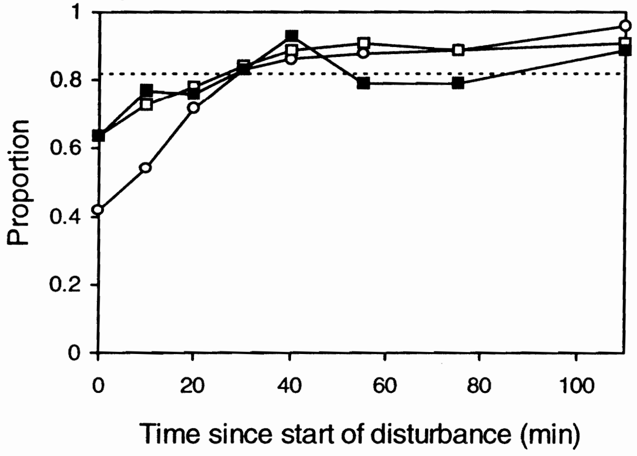
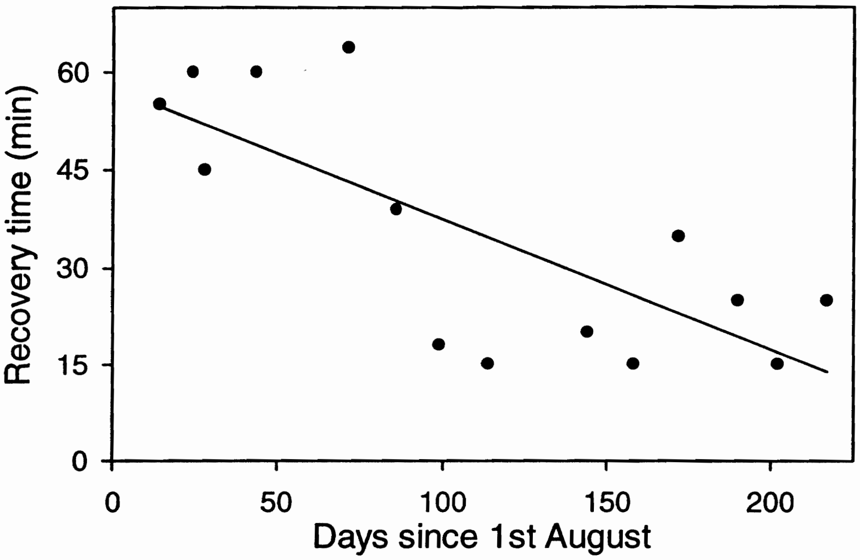
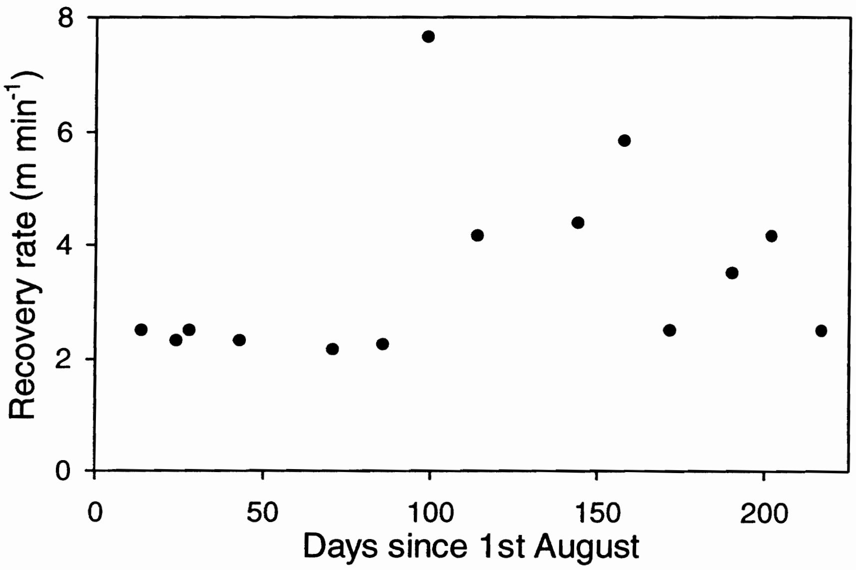


Figure 5.2.3 Changes in the density of feeding and non-feeding oystercatchers at increasing distances from an exclusion zone caused by human disturbance in relation to time since the start of disturbance. The cell located 0-25m from the exclusion distance is the first occupied cell along the transect, that located 25-50m is the second occupied and that at 50-75m is the third. The horizontal lines show expected values over the low tide period calculated in the absence of disturbance on control days.



(a) Recovery time after disturbance



(b) Recovery rate after disturbance

Figure 5.2.4 Seasonal changes in the reoccupation of a mussel bed by foraging oystercatchers following human disturbance: (a) time taken for the density of birds in the nearest cell to disturbance source to recover to that before disturbance; (b) rate at which exclusion distance is reduced in size.

5.2.2.2 Bed-wide disturbance experiment

The changes in the total number of birds on the mussel bed and the adjacent sand ridge on the two control days and two typical experimental days are shown in Figure 5.2.5. On control days the changes in oystercatcher numbers on the bed and sand ridge could be divided into three periods. During the first two hours of the exposure period, the number of birds on the bed increased rapidly and virtually no birds occupied the sand. Throughout this period the area of the bed exposed increased as the tide receded. For the next two hours, over low water, the bed was completely exposed by the tide and the number of birds on the bed remained relatively constant and whereas few birds were found on the sand. From about four hours after first exposure, the number of birds on the bed decreased as it was once again covered by the advancing tide. Initially, the number of birds on the sand increased during this period, as birds left the bed, but then decreased rapidly as the sand bar was also covered by the tide. The major difference between autumn and late winter was the relative numbers of feeding and non-feeding birds on the bed. At low tide in autumn a much lower proportion of birds were feeding than at the equivalent stage of the tide in mid winter.

On disturbed days, the pattern of build up of birds during the first two hours of the exposure period and at low tide before disturbance was similar to that on control days. After the disturbance, the number of birds on the bed decreased substantially and the number on the sand ridge increased as birds flew from the bed to the sand. In the first hour or so after disturbance, the number of birds on the bed increased, and the number on the sand decreased, as birds flew back from the sand to the bed. Although the total number of birds feeding on the bed after disturbance was similar to the number before, very few non-feeding birds were recorded on the bed after disturbance. This pattern was particularly clear in the autumn example shown in Figure 5.2.5 and was repeated on other disturbance days. Bird numbers on the bed reached a plateau after the disturbance, and then decreased as on control days as the bed was covered by the advancing tide.

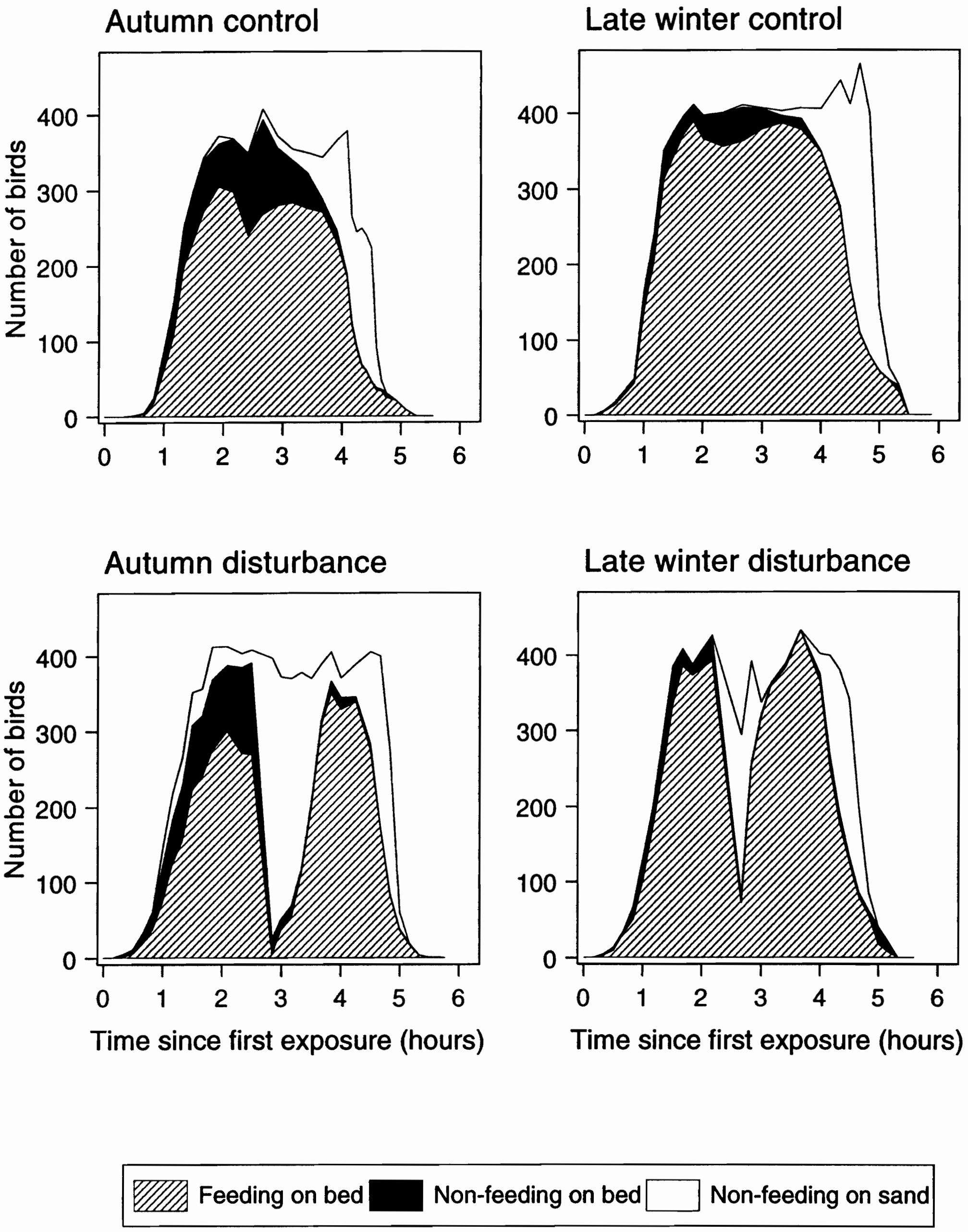


Figure 5.2.5 The number of oystercatchers on bed 20 and on a neighbouring sand ridge through the exposure period. The top figures show results obtained in autumn and late winter on control days in which no disturbance occurred. The bottom figures shows results obtained on days during which a controlled disturbance occurred at low water.

The impact of the controlled disturbance on oystercatchers was quantified by calculating the amount of lost feeding time per bird. Since after one hour the number of birds on the bed had always recovered to a maximum level (although sometimes lower than that before disturbance), we consider the majority of the lost feeding opportunity to have occurred during the first hour after disturbance. Results from the control days showed that the number of feeding birds on the bed remained relatively constant during the low tide period. Thus it was assumed that, had disturbance not occurred on the experimental days, the numbers present prior to disturbance would have remained. The expected number of birds on the bed was calculated using the following equation:

$$N = N_{\max}\left(\frac{T}{T_{\max}}\right)^{r} \qquad \text{if } T \leq T_{\max} \qquad 5.2.1$$

$$N = N_{\max} \qquad \text{if } T > T_{\max}$$

where N = Number of birds on bed, T = Time since first exposure (min), N_{max} = Maximum number of birds on bed at low water, T_{max} = Time at which bird numbers reach a maximum and r = Rate at which bird numbers increase. This equation describes the number of birds on the bed during the initial build up phase and during low tide when numbers are constant. Bird numbers are assumed to increase at a rate r, up to a maximum of N_{max} when the bed has been exposed for T_{max} minutes, after which bird numbers remain constant. Non-linear regression was used to estimate parameter values for each of the experimental days. This equation was able to describe accurately the shape of the build up and plateau of oystercatcher numbers. The predicted value of N occurring immediately prior to the disturbance was taken to be the number of birds that would have occupied the bed throughout the low tide period if disturbance had not occurred. The total oystercatcher feeding time lost due to disturbance was calculated, during the first hour after disturbance, from the area between the observed and predicted number of birds on the bed. This total was divided by the expected number of birds to give the lost feeding time per bird. This value estimates the average amount of time taken for a bird to return to the bed after disturbance and is referred to as return time.

The return time after disturbance decreased significantly through the season (Figure 5.2.6). In autumn the mean return time was approximately 45 minutes per bird, but this decreased to 15 minutes per bird by late winter. Return time at the bed-wide scale showed similar seasonal changes to that measured at the local scale ($y=57.6[se=6.5]-0.202[se=0.050]x$; $n=14$; $p<0.01$; Figure 5.2.6). This suggests that the processes governing the rate at which birds return after disturbance are similar at the two spatial scales.

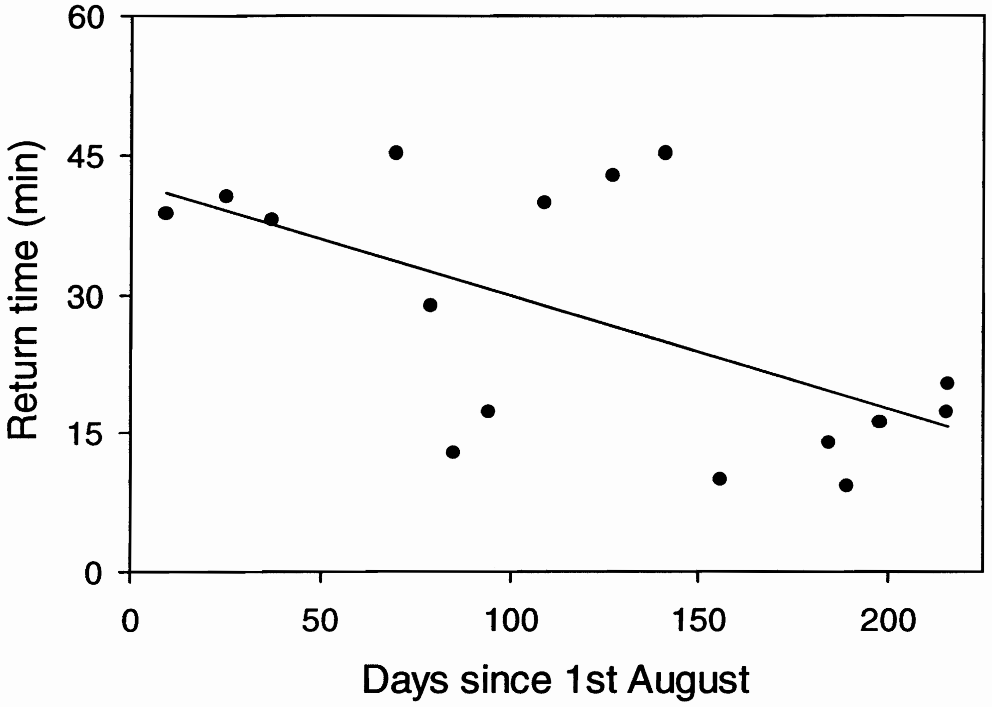


Figure 5.2.6 Seasonal changes in the mean time taken for displaced oystercatchers to return to a mussel bed after human disturbance.

5.2.3 Discussion and conclusions

Previous studies of human disturbance in the Wadden Sea (summarized in Smit & Visser 1993) and Exe estuary (Goss-Custard *et al.* 1994) have shown that the impact of disturbance differs greatly between species and between different locations and depends on factors such as the intensity and predictability of disturbance. Most of these studies measured the impact of disturbance as the distance at which birds took flight (flushing distance). This equates to the initial exclusion distance recorded in the present study. In the Wadden Sea, oystercatcher flushing distances ranged from approximately 80m in relatively disturbed areas and on mussel beds, to 110m in less disturbed areas. The lower values are very close to the initial exclusion distance measured in the present study.

The experiments showed that the impact of disturbance, measured as either the exclusion area around a source of disturbance or the recovery time after disturbance, decreased during the course of the winter. Since all controlled disturbances were of similar intensity this result must be due to changes in the bird's responses. Birds left the exclusion area because they perceived the person as a threat, but in doing so were forced either to feed in areas of higher competitor density or to feed in less preferred areas or to stop feeding altogether. Thus, the net effect of moving on the displaced birds is likely to have been decreased intake rates. The response of birds to the disturbance can be viewed as a trade-off between (1) not moving and risking the perceived threat, and (2) avoiding the theat by moving but suffering reduced intake rate. Changes in the birds response could be due either to changes in the perceived threat or to changes in the costs of reduced intake rate. The perceived threat could have been reduced through winter as birds became habituated to the presence of the observer during experiments or to other human activities occurring throughout other periods. Since the experiments were conducted infrequently, the chance that birds became habituated to the controlled disturbance was minimal. However, habituation to other human activities (to which birds would have been constantly exposed) cannot be discounted. Increased costs to moving from the disturbed area could also explain the seasonal changes. Throughout winter the energetic demands of birds increase due to deteriorating weather conditions, and there is an associated decline in the food supply. The net result is that individuals have more difficulty in meeting their energy demands later in the season and so the potential risk of reduced intake rate when displaced by disturbance is likely to increase during the season. Unfortunately, the experiments do not allow the separation of the two possible causes of the seasonal changes in the response of birds to disturbance as the potential of habituation and the likely costs associated with displacement both increase in parallel through the season.

In accord with the experimental results, the shorebird-shellfish model incorporates shellfishing disturbance by reducing the area and time for which birds are able to feed on a patch during a tidal stage. As the results of the experiments at the two spatial scales were similar, all parameters used in the model were derived from the local disturbance experiment. In the model, each fishing unit (fisherman or dredge) present on a patch during low tide is surrounded by a circular zone from which all birds are excluded. Fishing is assumed to last longer than 30 minutes, and so the radius of the exclusion zone for a given day of winter is found from (Figure 5.2.2):

$$\text{Exclusion zone radius (m)} = 131.1 - 0.211 \text{ Days since 1st September} \qquad 5.2.2$$

This equation generates exclusion areas that decrease from approximately 5ha in autumn to 2ha in late winter. The area of bed 20 was 9.4ha and so in autumn over 50% of the mussel bed could be disturbed by a single person, whereas in late winter only 20% would be affected. After fishing units leave a patch, birds return to occupy the exclusion zone after a set period of time. This recovery time on a given day of winter is found from (Figure 5.2.4a):

$$\text{Recovery time (hours)} = 57.6 - 0.202 \text{ Days since 1st September} \qquad 5.2.3$$

In the model, these equations are used to find the area of a patch disturbed by a single fishing unit. The combined effect of several units is found using the procedure described in section 5.3. It is assumed that disturbance has the same effect on all individuals in the model regardless of their dominance or internal state (i.e. their level of energy reserves). Although captive oystercatchers have been shown to increase their intake rates after a period of food deprivation (Swennen, Leopold & Bruijn 1989), the only field study of the effect of lost feeding time caused by disturbance (Urfi, Goss-Custard & Durell 1996) showed that the intake rates of oystercatchers did not increase after disturbance. Therefore, the model assumes that birds are not able to increase their intake rates being disturbed.

5.3 SHELLFISHING MODELS

R A Stillman

The primary aim of the shellfishing simulations was to demonstrate the value of the model for answering management questions on the conflict between shellfisheries and shorebirds. The secondary aim was to gain some preliminary insights into the different effects of various shellfishing practices (both methods and regulations) on shorebirds. The basic modelling approach was to simulate the interactions between shellfishing, shellfish and shorebirds on the well-studied Exe estuary and the Burry Inlet. Various fishing scenarios were simulated in these estuaries. Each scenario included a combination of a shellfishing method and a management policy.

This section describes the models used to simulate mussel fishing on the Exe estuary and cockle fishing on the Burry Inlet. Although a range of models are used to simulate different types of shellfishing, all have two functions:

(1) to calculate the rate at which shellfish patches are depleted by fishing;

(2) to calculate the extent to which shellfishing disturbs shorebirds.

Table 5.3.1 provides a summary of the parameters used in the shellfishing models.

Table 5.3.1 Parameters used to model mussel fishing on the Exe estuary and cockle fishing on the Burry Inlet.

Parameter	Description	Units
NumFishUnit	Number of hand gatherers or dredges active on an estuary during a single year.	
MinFishSize	Minimum size of mussel or cockle that can be legally landed. Size classes greater than this length are termed *fishable size* classes. Default value is 45mm for mussels and 22mm for cockles.	mm
CaptureRate	Rate at which fishing removes each fishable size class from a patch. This parameter is calculated in different ways for different fishing techniques.	hr^{-1}
TidalQuota	Maximum fresh mass of shellfish that can be legally removed by each fishing unit during a single tidal cycle.	g
ExclusionArea	Area around each fishing unit from which shorebirds are excluded. Only applies to fishing at low tide.	m^2
RecoveryTime	Time taken for shorebirds to recolonise areas previously disturbed by shellfishing. Only applies to fishing at low tide.	hr

5.3.1 Shellfishing effort

In the model, fishing activities are performed by *fishing units*, which represent either hand gatherers or dredges depending on the fishing technique being simulated. The level of fishing effort is measured by the number of fishing units (*NumFishUnit*) present on an estuary. For convenience, it is assumed that within a single year only one fishing technique is employed on an estuary and that fishing effort remains constant throughout the year.

During each day of simulations, the model finds the number of fishing units exploiting each intertidal shellfish patch using the following procedure. Initially the maximum density of fishable shellfish (i.e. those that can be legally landed) available on any patch is calculated. Fishing effort is then allocated equally to all patches with fishable shellfish densities greater than 75% of the maximum density. For example, if the maximum density on any patch is 500 shellfish m^{-2}, fishing effort will be equally divided between all patches with densities greater than 375 shellfish m^{-2}. If four such patches exist, and in total there are 40 fishing units, 10 units will exploit each patch. The arbitrary value of 75% was chosen simply to ensure that fishing effort was not always concentrated on a single patch, and may be considered to represent the errors real fishermen make in locating the best fishing areas.

Although the overall level of fishing effort remains constant on an estuary throughout winter, the distribution of fishing effort between different patches may change in response to changes in the density of shellfish on different patches. These density changes are caused by shellfishing itself, but may also result from shorebird predation and other sources of shellfish mortality. The precise way in which fishing depletes stocks, and hence influences the redistribution of fishing effort, depends on the fishing technique being modelled.

5.3.2 Shellfishing techniques

The following sections describe the different methods used to model the exploitation of mussels and cockles. The modelling of mussel fishing is based on current and potential future methods used on the Exe estuary, and that for cockle fishing based on current practices on the Burry Inlet and Wadden Sea. The models differ in detail, but all have a number of common features. The models take as input the abundance of each shellfish size class on a patch, and the minimum shellfish length which may be legally landed (*MinFishSize*). They then calculate the rate at which size classes larger than *MinFishSize* (termed fishable mussels or cockles) are removed by a single fishing unit (*CaptureRate*).

5.3.2.1 Mussel thinning

This model assumes that only fishable mussels are removed from mussel beds, and hence that all smaller mussels are unaffected by fishing. The rate of fishing is expressed as the area of mussel bed covered by each fishing unit per hour. Within this area, all fishable mussels are removed; hence the rate at which mussels are collected is proportional to the density of fishable mussels. No estimates of the fishing rate of real fishermen were available and so a range of values are considered in simulations.

Fishing causes a reduction in the density of fishable mussels on exploited beds, and hence a reduction in the rate with which mussels can subsequently be captured. The reduction in density on exploited beds causes fishing units to spread out and exploit a wider range of beds as simulations progress.

Mussel thinning on the Exe estuary occurs during the hours of daylight, at low tide and is restricted to spring tides, as mussel beds are not fully exposed on neap tides. Therefore, in the model, mussel thinning is restricted to low tide periods, which occur predominately during the daylight hours, on days during the spring extreme of the spring-neap cycle (*SpringProp* >= 0.5; see chapter 2 for the definition of this parameter). As fishing occurs at low tide it causes disturbance to shorebirds.

On the Exe estuary, no limits are currently imposed on the number of mussels removed during a single fishing bout. In the model, fishing units therefore exploit mussel beds throughout each low tide period.

5.3.2.2 Mussel stripping

The mussel stripping model assumes that all mussels within an exploited area are removed. Although all mussels are removed during fishing, mussel capture rate is still measured by the rate at which fishable mussels are removed. As with mussel thinning, the rate of fishing is expressed as the area of mussel bed covered by each fishing unit per hour, and so capture rate is proportional to the density of fishable mussels. No field estimates of the fishing rate of real fishermen were available and so a range of values were considered in simulations.

Stripping differs from thinning in the way in which mussel stocks are depleted. Stripping depletes mussels by reducing the total area of mussel beds rather than reducing the density of fishable mussels. As a consequence, fishing does not alter the density of mussels remaining on mussel beds as they decrease in size. Fishing units continue to exploit the best beds until they are removed completely, or reduced to a minimum area, before moving on to other beds. It is assumed that stripping at low tide is able completely to remove patches, whereas stripping from boats at high tide can only reduce the area of a patch to 25% of its initial value.

On the Exe estuary, mussel stripping occurs by hand during the hours of daylight, at low water on spring tides. Although it does not occur currently on the Exe estuary, stripping could also occur from boats at high tide. Both methods of fishing are modelled. In the model, stripping occurs either during low or high tide periods, which occur predominately during the daylight hours, on days during the spring extreme of the spring-neap cycle. In reality, stripping at high tide would not be restricted to any particular stage of the spring-neap cycle, as it does not rely on beds being fully exposed, but this constraint is imposed in the model for comparison with the low tide mussel fishing methods. Only low tide stripping causes any disturbance to shorebirds.

As no limits are imposed on the quantity of mussels removed from the Exe estuary (see above), the model assumes that fishing units strip mussel beds throughout each low or high tide period.

5.3.2.3 Hand gathering of cockles

The cockle hand gathering model assumes that only cockles within the fishable size range are removed. The rate at which cockles are removed is based on observations of fishermen on the Burry Inlet (Equation 5.1). Using this relationship the model calculates the number of 25kg sacks filled by each fishing unit during a low tide period based on the density of cockles in the substrate. Each sack contains approximately 25kg of cockles, and so the model calculates the depletion of each cockle size class from the size distribution of cockles in the substrate and their fresh mass. The calculation assumes that cockles of a given size class are captured in proportion to their abundance in the substrate. For example, if two fishable size classes are available with densities of 100 and 200 m^{-2}, the latter will be captured with twice the frequency of the first, and so be twice as numerous in sacks.

As with mussel thinning, hand gathering reduces the density of fishable cockles and so reduces the rate at which cockles can subsequently be captured. The reduction in density on exploited beds causes fishing units to spread out and exploit a wider range of beds as simulations progress.

Cockle fishing on the Burry Inlet occurs at low tide, during the hours of daylight. The cockle beds are fully exposed at all stages of the spring-neap cycle (as they occur at a relatively high shore level), and so fishing occurs throughout this cycle. In the model, cockle beds are therefore exploited throughout the spring-neap cycle, but only during low tide periods occurring predominantly during the hours of daylight.

At the present on the Burry Inlet, an upper limit is imposed on the total fresh mass of cockles removed by each fisherman during a single low tide period. In the model, fishing units therefore remain on cockle beds until they have reached their tidal quota of cockles (*TidalQuota*). On the Burry Inlet this quota is currently 100kg, but different values have been set in the past. Simulations therefore tested the effect of different quota values.

5.3.2.4 Cockle fishing using the Wonderklauw

In the model, fishing units using the Wonderklauw operate during the hours of daylight throughout the spring-neap cycle. Fishing bouts occur at high tide and last for 3 hours. During this time a single fishing unit removes all fishable cockles (those 15mm or more in length) from an area of $100m^2$. No cockles below the fishable size range are removed. Although in the model fishing occurs during high tide, it may be considered to occur during that part of the high tide period in which cockle beds are covered only by a shallow layer of water. As fishing occurs at high tide, it does not disturb shorebirds.

As with hand gathering, the Wonderklauw reduces the density of fishable cockles. The model assumes that both the area fished by the Wonderklauw and the duration of fishing are uninfluenced by the density of cockles, and so as cockle density is reduced the number of cockles captured within a fishing bout decreases. The reduction in density on exploited beds causes fishing units to spread out and exploit a wider range of beds as simulations progress.

In reality, fishing using the Wonderklauw is only profitable at very high cockle densities. Therefore, in the model, the Wonderklauw is only used on patches in which the density of fishable cockles exceed $500m^{-2}$. If all patches are depleted to below this limit, fishing ceases.

5.3.2.5 Suction dredging of cockles

In the model, suction dredging occurs during the hours of daylight throughout the spring-neap cycle. Fishing bouts occur at high tide and last for 4 hours. The area fished during this time is calculated using the approach in section 5.1.3.3 and by assuming that suction dredges follow random paths across patches. Cockle beds in the model are $0.5km^2$ in area, and so based on the equations in section 5.1.3.3, a single dredge covers an area of $7750m^2$ in 4 hours. All fishable cockles (those 15mm or more in length) are removed from the area fished. Smaller cockles are not affected by fishing. As fishing occurs at high tide, it does not disturb shorebirds.

Suction dredging reduces the density of fishable cockles. The area fished and the duration of fishing are uninfluenced by the density of cockles, and so as cockle density is reduced the number of cockles captured within a fishing bout decreases. The reduction in density on exploited beds causes fishing units to spread out and exploit a wider range of beds as simulations progress.

Suction dredges are able to work profitably at lower cockle densities than the Wonderklauw. Therefore, in the model, suction dredges operate until the density of fishable cockles falls to below $50m^{-2}$. In the Netherlands, suction dredges only operate during the first four days of each week. This method of regulation was incorporated into the model by only allowing suction dredges to operate on 4 out of every seven days.

5.3.3 Disturbance to shorebirds

Each fishing model calculates the number of fishing units present on each patch during each low tide or high tide period. As the model simulates shorebirds feeding on exposed patches, no disturbance occurs when fishing occurs at high tide. At low tide, the extent of disturbance is based on the results presented in section 5.2. Each fishing unit on a patch is surrounded by a circular exclusion zone, in which no birds are found (*ExclusionArea*; section 5.2). If more than one unit is present on a patch, it is assumed that the total exclusion area is found from the sum of individual zones. This procedure therefore assumes that fishing units are dispersed widely across the patch. The impact of the exclusion zone is to increase the density of birds feeding on undisturbed parts of patches, or to exclude all birds from a patch if the exclusion area is greater than the patch area. In the case of cockle fishing, where fishing units may only be present for part of the low tide period, exclusion areas persist for a set amount of time after fishing units depart (*RecoveryTime*; section 5.2).

5.3.4 Summary and conclusions

Fishing effort is directed towards patches containing a high density of fishable shellfish. Therefore, as shellfish densities change during the course of simulations, the distribution of fishing effort may also change. The shellfishing techniques incorporated into the model either deplete shellfish stocks by reducing the density of fishable size classes (low tide mussel thinning, cockle hand gathering, Wonderklauw and suction dredging) or by removing all size classes and thereby reducing the area of patches (low and high tide mussel stripping). These differences influence the redistribution of fishing effort. As simulations progress, fishing techniques that reduce the density of fishable size classes tend to exploit a wider range of patches as densities are reduced on the best patches. In contrast, fishing techniques that reduce the area of patches, exploit patches until they are reduced to a minimum area, and then move to other patches. Disturbance to shorebirds only occurs in those fishing techniques occurring at low tide.

Chapter 6 MODEL TESTS

R A Stillman, J D Goss-Custard, A D West & S E A le V dit Durell

6.1 INTRODUCTION

The major objective of this contract is to produce general predictions on the interaction between shellfishing, shellfish and shorebirds. Many of these predictions are beyond current observations and so cannot be tested. Therefore, the model must first be tested directly against field data so that the accuracy of its predictions can be measured. If the model is able to accurately predict patterns previously observed in real systems, more confidence may be placed in its predictions which lie beyond empirical range.

The present version 3 of the shorebird-shellfish model, although based on version 2 of the Exe estuary oystercatcher-mussel model (Clarke & Goss-Custard 1996), was developed in a different programing language and incorporated many additional features. The possibility existed that programing errors were made during development of version 3. Therefore, before being directly tested against field data, tests were performed to locate any programming errors made during model development. The new model can still be run in a simplified form which mimics version 2, and so tests were used to determine whether the two models produced similar predictions. These tests confirmed that when run in a simplified form, and using parameter values used in the previous model, version 3 of the shorebird-shellfish model produced identical predictions to the earlier model. These results showed that the basic elements of the shorebird-shellfish model, which were shared with or were similar to the previous model, were correctly programmed.

Version 3 of the model was tested separately against field data for each of the oystercatcher-prey systems covered by the contract: oystercatchers and mussels; and oystercatchers and cockles. For these systems the model was parameterized and tested on single estuaries in which oystercatchers have been studied intensively. Mussel feeding predictions are tested for the Exe estuary, and cockle feeding predictions for the Burry Inlet. These model tests involved direct comparison of the models predictions with observed patterns, and sensitivity analyses to determine which of the model parameters most strongly influenced its predictions. The knot-cockle model was parameterized for the Burry Inlet, but not tested directly against field data. This was because knot foraging behaviour was simulated using a previously published and tested model (Piersma *et al.* 1995), and because the cockle population dynamics model was the same as that used and tested for oystercatchers.

6.2 OYSTERCATCHERS AND MUSSELS

6.2.1 The oystercatcher-mussel model

The model was tested for oystercatchers and mussels by using simulations based on the Exe estuary. Simulations ran over one winter period from 1st September to 15th March. The tidal cycle was divided into four stages; high tide lasting approximately four hours; receding tide lasting one hour; low tide last approximately six hours; and advancing tide lasting one hour. Three types of feeding patch, mussel beds, upshore areas and fields, were available each with a different exposure pattern during the tidal cycle. These comprised 10 intertidal mussel beds only exposed at low tide, one upshore area exposed at low tide and on the advancing and receding tides, and one field which was always available. Although only one upshore area and field were included in the model, these represent a number of such areas in the real system. Within each mussel bed, mussel populations were aged-structured with age classes ranging from 0 (i.e. spat) to 9+ years. Standard growth curves were used to convert the age distribution on a mussel bed to the size distribution (0 to 70mm) required to calculate oystercatcher intake rates. See section 4.4 for full details of the mussel population dynamics model. The intake rate of an individual oystercatcher foraging on mussel beds was calculated from the abundance, size distribution and flesh content of the mussels (section 3.2.1), the individuals feeding efficiency and local dominance, and the density of its competitors (section 3.2.2). No details of the prey population in the upshore areas and fields were included. Intake rate in these areas was simply set by an individuals feeding efficiency, and was not affected by interference or depletion (section 3.4). Full details of the model are given in chapter 2. The model was parameterised using data collected between 1976 and 1982 and so all tests were made with data also collected during this period.

6.2.2 Distribution between mussel beds

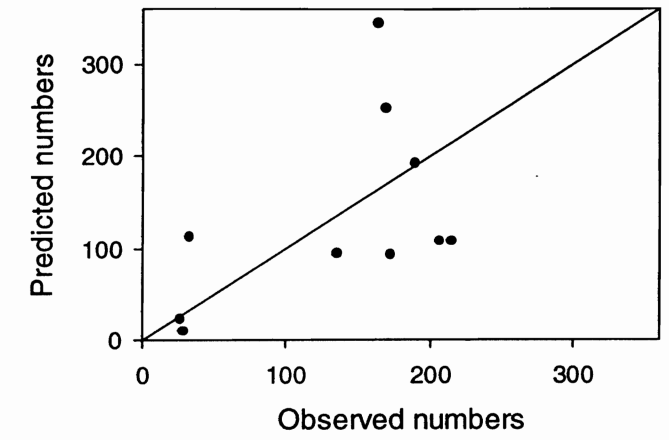
Field data on the distribution of oystercatchers between the 10 mussel beds used in the model were obtained at low water, on spring tides. These data were compared to those predicted for the period October to January when the total number of birds observed on the Exe remained relatively constant. Both the observed and predicted distribution of oystercatchers were measured as the mean number and density of birds on each of the mussel beds.

The predicted number of birds on each mussel bed was not significantly different from that observed (Figure 6.2.1a). Linear regression of predicted against observed numbers produced an intercept which was not significantly different from zero ($a=42.1$; $se=63.1$; $p>0.1$), and a gradient not significantly different from one ($b=0.686$; $se=0.415$; $p>0.1$). In contrast, the predicted density of birds on each bed did not show such a close agreement with reality (Figure 6.2.1b). A regression of predicted against observed again produced an intercept which was not significantly different from zero ($a=20.0$; $se=9.1$; $p>0.05$) but a gradient significantly less than one ($b=-0.007$; $se=0.391$; $p<0.05$). This contrast occurred because the two tests of distribution measured different components of the system. The number of birds on a bed depends both on bed quality and its area (i.e. for a given bed quality, more birds will feed on a large bed than on a small bed). Bird density simply depends on the quality of a bed.

The discrepancy between observed and predicted densities implies that the model does not include some important aspect of the real world. One factor which has previously been strongly associated with oystercatcher distribution on the Exe estuary is the substrate softness of mussel beds (Goss-Custard, Caldow & Clarke 1992). Softer beds tend to have a lower density of birds than would be expected from the food supply available. Bed softness was not incorporated into the model as the exact method in which it influences bird density is not clear; birds may have higher energy expenditure foraging on a soft substrate, but other factors such as increased parasite loads and ingestion of the substrate may also be important (Goss-Custard, Caldow & Clarke 1992). The difference between observed and predicted densities occurred largely because three beds with low observed densities were predicted by the model to have very high densities (Figure 6.2.1b). These beds (20, 22 and 25) all have soft substrates. To test whether substrate softness could account for errors in the prediction, the difference between observed and predicted densities were regressed against rank bed softness (Figure 6.2.2). There was a significant positive relationship between prediction error and substrate softness ($y=5.8$ ($se=0.8$) $+ 0.15$ ($se=0.06$) x; $p<0.05$), indicating that the model was over predicting densities on soft beds and under predicting densities on firm beds. Bed substrate softness therefore accounts for the difference between predicted and observed densities.

In summary, the model correctly predicted the observed numbers of birds on each bed at low tide. The error in predicted density on each bed occurred because bed softness was not incorporated into the model.

(a) Oystercatcher numbers



(b) Oystercatcher density

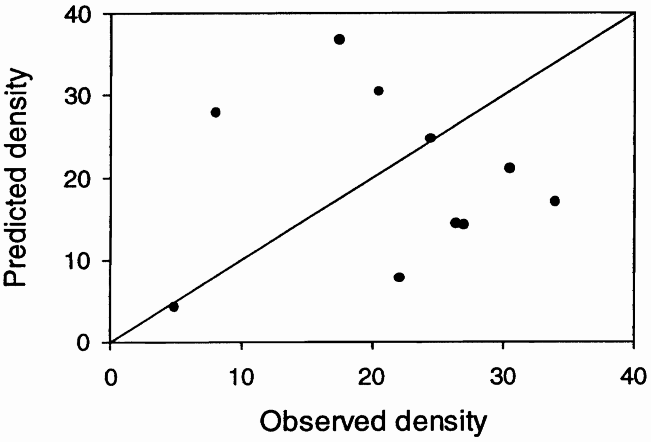


Figure 6.2.1 Test of the predicted distribution of oystercatchers across 10 mussel beds in the Exe estuary. Distribution is measured as either the number (a) or density of birds (b) on each bed predicted by the model and observed. In each figure the line shows the expected relationship if the observed and predicted values were identical. The comparison is limited to spring tides between October and January.

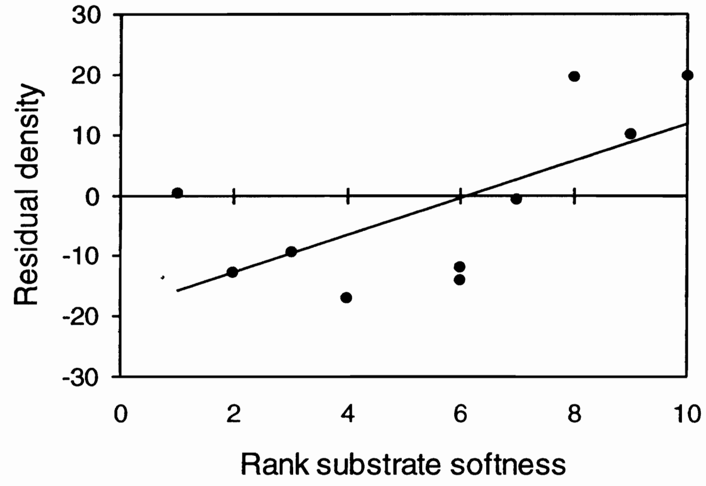


Figure 6.2.2 Effect of the bed substrate softness on the accuracy of the models predictions. Residual density is the difference between the predicted and observed density of oystercatchers on a mussel bed. Beds of higher rank have a softer substrate.

6.2.3 Use of supplementary feeding areas

Field estimates of the number of birds feeding in fields at high tide have previously been obtained from monthly counts between September and February. In reality, field feeding birds are composed of those using the mussel beds at low tide, and those feeding on other food sources, particularly *Nereis diversicolor* in autumn and *Scrobicularia plana* in winter (Goss-Custard & Durell 1983). The model population is composed only of mussel feeders and so a direct comparison between the number predicted to use the fields by the model and the number observed cannot be made. Two alternative estimates of the number of birds using the fields were therefore obtained from the field data. The first was the total number of birds observed, which should always exceed that predicted by the model as it includes types of birds that are not in the model. The second was the number of birds minus the total number of *Nereis* and *Scrobicularia* feeders which are frequently observed in the fields but are not included in the model. This second estimate should provide a closer estimate of the actual number of mussel feeders in the fields, but will be too high if many birds taking other prey (e.g. cockles) occur frequently in the fields and too low if some *Nereis* and *Scrobicularia* feeders do not use the fields at high tide.

The model predicted that mussel feeders would make increasing use of fields at high water during the course of winter (Figure 6.2.3). Early in the season, both the predicted and observed number of birds in the fields were very low. From about day 50, the predicted number of birds using the fields on both neap and spring tides started to increase, reaching a maximum on neaps on day 125 and on springs day 175. As occurs in reality (Goss-Custard & Durell 1983), more birds used the fields on neap tides than on springs, implying that birds had more difficultly in meeting their energy demands on neap tides. The numbers observed in the fields at high water differed according to the method used to estimate them. The total number, including all bird types, was always greater than that predicted after day 50. The numbers, excluding *Nereis* and *Scrobicularia* feeders was less than that on neaps after day 75 and less than that on springs after day 100. The predicted numbers tended to fall between the two extreme field estimates, and therefore within the expected range.

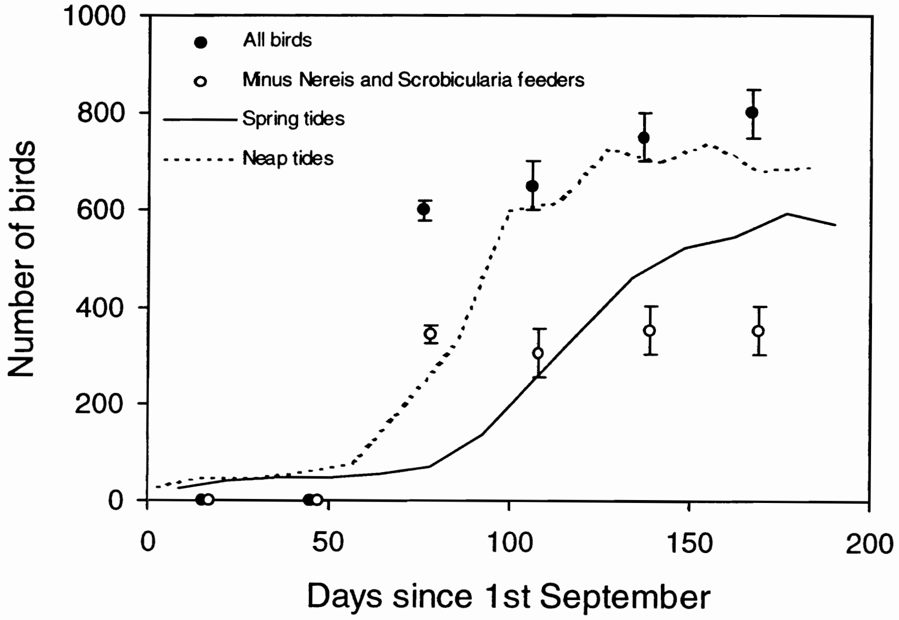
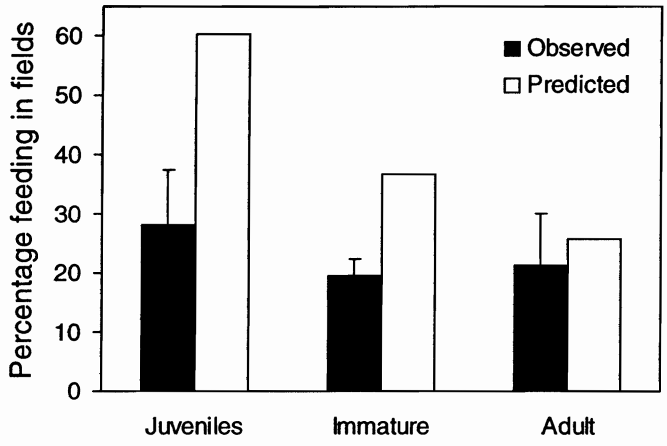


Figure 6.2.3 The predicted and observed numbers of oystercatchers in fields at high water. The lines show model predictions on spring and neap tides. The symbols show two field estimates of the use of fields by mussel feeders obtained throughout the spring-neap cycle. The higher field estimates refer to the total count of birds in the fields and the lower to the total count minus the number of *Nereis diversicolor* and *Scrobicularia plana* feeders on the estuary.

Data on the use of fields by different types of birds have previously been obtained by searching fields between November and February for mussel-feeding colour-ringed birds of known feeding method. These birds could be grouped according to their age and feeding method to give estimates of the proportion of individuals of each bird type that used fields at some stage during winter. The mean proportion of birds in each bird type that used fields at least once in winter was calculated and compared with that predicted by the model (Figure 6.2.4). In both the predicted and observed data, the use of fields for supplementary feeding was not equally divided between the different age classes of birds and feeding methods (Figure 6.2.4). In both cases, a higher proportion of stabbers used the fields than hammerers, and the use of fields decreased with age. The qualitative predictions of the model were therefore correct. However, the quantitative predictions were not so accurate; in general, a higher proportion of juvenile and immature stabbers were predicted to use fields than were actually observed to do so.

In summary, the predicted general pattern of the use of the fields throughout the year is similar to that actually observed. The disproportionate use of fields by stabbers and by juveniles and immatures in the model is also in accordance with reality, but the frequency of use by juvenile and immature stabbers in the model is higher than was observed. The results suggest that stabbers have more difficultly than hammerers, and juveniles more difficultly than adults in meeting their energy requirements.

(a) Stabbers



(b) Hammerers

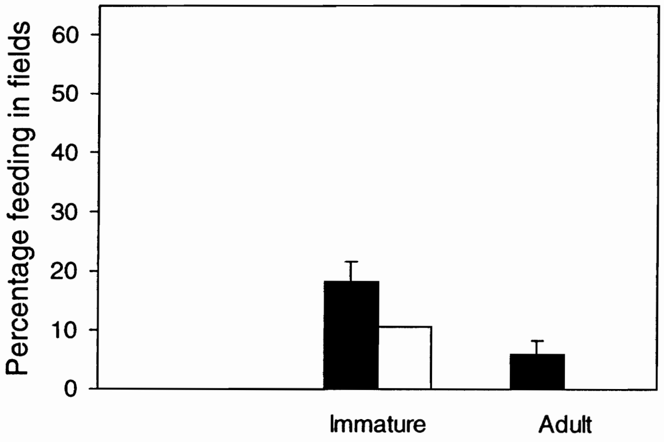


Figure 6.2.4 Observed and predicted use of supplementary feeding in fields at high tide by different classes of birds. Both observed and predicted refer to the mean number of birds of each type feeding in fields between November and February. No colour-ringed juvenile hammerers were present and so no comparison for this bird type is possible.

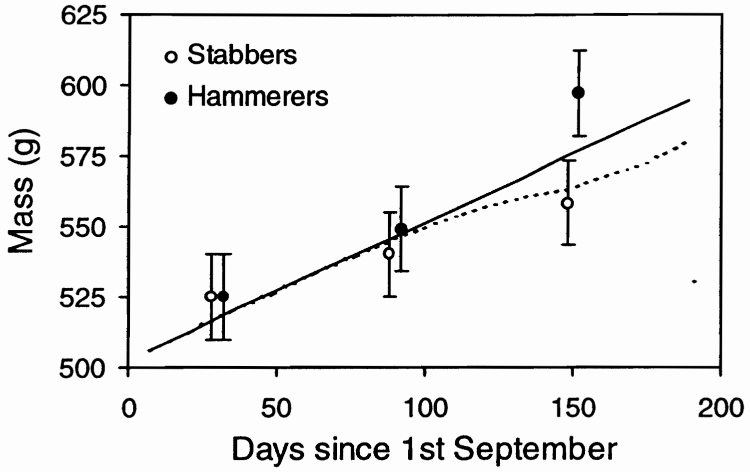
6.2.4 Body mass of survivors

The predicted body mass of oystercatchers was compared to that observed throughout the course of winter (Figure 6.2.5). Field estimates of mass were made at monthly intervals from birds caught on the high tide roost but, to increase sample sizes, were combined into bi-monthly estimates. The field data used to test the model were also used to calculate the target body masses that birds in the model attempt to achieve. For this reason, the overall patterns of mass change observed in the model would be expected to follow those observed. The test of the model is whether the ability of different feeding methods within each age class to achieve their target mass is similar to that observed.

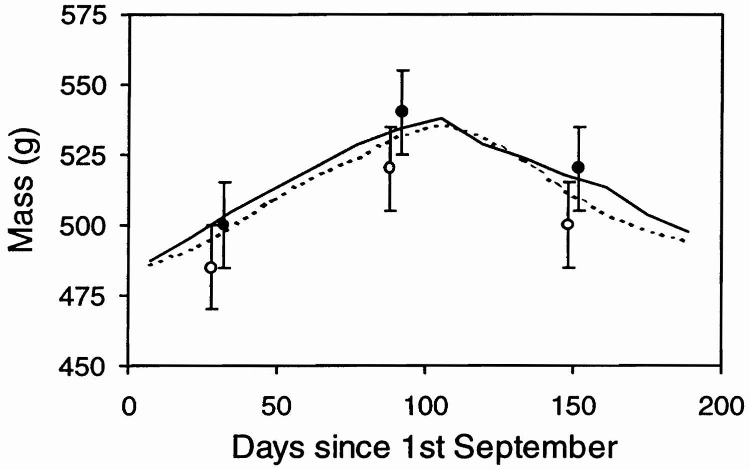
Adults of both feeding methods increased in mass during the course of winter both in the model and in reality. Although being given the same target mass in the model, however, the mass achieved differed between the two feeding methods. Hammerers increased in mass at a constant rate, exactly matching their target mass throughout winter. Stabbers matched their target mass up to about day 100, after which their mass fell below that of hammerers and their target. This pattern was also observed in reality, although the magnitude of the difference in mass was greater. In the model, all hammerers could have reached the mass observed in reality, but their target mass, which was derived as the mean mass of all birds of unknown feeding method, prevented them from doing so. Both the predicted and observed masses of immatures in both feeding methods increased and then decreased during winter. However, throughout this period, the predicted and observed masses of stabbers were slightly below those of hammerers. Again the magnitude of the difference was greater in the observed data. The model predicted that juvenile stabbers had a lower mass than hammerers. No field data were collected on juvenile hammerers with which to test this prediction, but the masses of stabbers were similar to that observed and below their target mass.

In summary, the model successfully predicted the relative body masses of hammerers and stabbers in different age classes. Stabbers are lighter than hammerers indicating that some of the surviving birds are unable to meet their energy demands and reach their target mass.

(a) Adults



(b) Immatures



(c) Juveniles

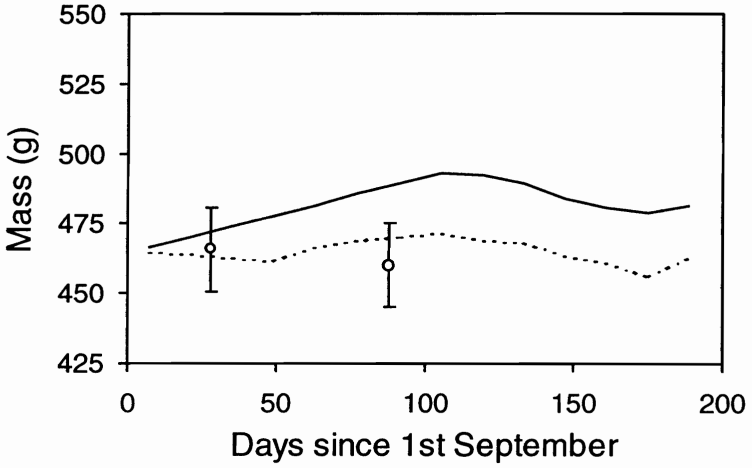


Figure 6.2.5 Observed and predicted changes in oystercatcher body mass during the course of winter. Model predictions for hammerers are shown with a solid line, and those for stabbers with a broken line. The symbols show observed bi-monthly means and standard errors.

6.2.5 Overwinter mortality

The model predicted 5% mortality of birds during the course of winter. Mortality rate was initially low, increasing to a maximum between days 125 and 175, and then decreasing towards the end of winter (Figure 6.2.6). Mortality rate initially increased as feeding conditions deteriorated, temperature decreased and day length shortened. These changes caused the energy demands of birds to increase and reduced the rate at which they are able to feed (at night, feeding efficiency was lower on upshore areas for both feeding methods and on mussel beds for stabbers and birds were unable to feed in fields at high water). Towards the end of winter, both temperature and day length increased, and so energy demands were reduced and more feeding occurred during the hours of daylight. The low mortality rate at the end of winter meant that the model predictions of overall mortality were insensitive to the precise date chosen to terminate winter simulations.

Mortality was not evenly divided between feeding methods with 9.6% mortality in stabbers and 0.4% in hammerers. Similarly, mortality differed between age classes with 25.9% mortality in juveniles, 31.2% in 2nd years, 1.9% in 3rd and 4th years, and 0.2% in adults. These values compare to 12%, 9.4%, 2% and 1.5% respectively observed on the Exe between 1976 and 1981 (Goss-Custard *et al.* 1982). The model therefore over predicted mortality in young birds and under predicted that in adults. The decrease in mortality with age is in accordance with observations.

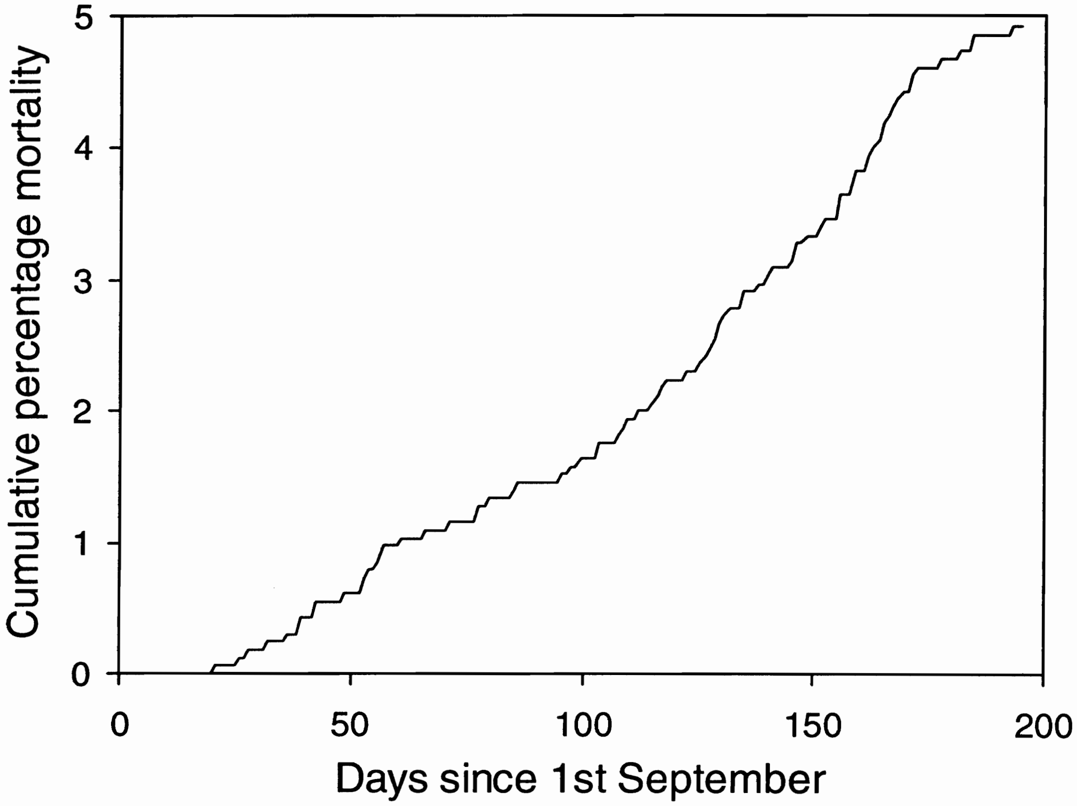


Figure 6.2.6 Predicted cumulative percentage mortality of oystercatchers on the Exe estuary.

6.2.6 Sensitivity analysis

The tests showed that the model could predict with reasonable accuracy the observed patterns in the Exe estuary. These predictions were based on a set of default parameter values. The next stage in testing the model is to determine how sensitive its predictions are to variation in these parameter values.

The model contains many parameters and can produce many predictions so it was not feasible to test the influence of all parameters on all predictions. Instead, sensitivity analyses were applied to a limited set of parameters which were either thought likely to influence the model predictions or for which values were uncertain. The most important model output in the present context is the shorebird overwinter mortality and so the sensitivity analysis was restricted to this prediction. Due to the large number of parameters in the model, it was not possible to investigate interactions between parameters and so only one parameter was varied at a time with all others set to their standard values. The sensitivity analysis involved either increasing or decreasing each parameter by 25% and recording the predicted overwinter mortality. The results of the sensitivity analysis are shown in Table 6.2.1. The parameters included in the sensitivity analysis apply to three different components of the model: (i) the food supply available on mussel beds (mussel bed area, mussel density and flesh content); (ii) oystercatcher foraging behaviour (interference on mussel beds, night feeding efficiency and supplementary intake rate); and (iii) oystercatcher energy expenditure (metabolic rate and thermoregulatory costs).

Of the parameters associated with mussels, only changes in flesh content had a large influence on mortality. The reason for this is that, in the model, oystercatcher intake rate was not influenced to any extent by mussel density over the range of densities found in the Exe estuary (section 3.2.1). The low impact of mussel density would therefore be expected. Mussel flesh content, on the other hand, has a direct impact on intake rate through the value of each mussel captured. Changes in flesh content caused large changes in intake rate, and therefore survival. For the same reason, the feeding efficiency of individuals would have a large impact on survival, as has already been shown in simulations with version 2 of the model (Goss-Custard *et al.* 1996). Changes in mussel bed area change the total supply of mussels and influence the density of birds and hence interference. The low sensitivity of the model to bed area implies that the oystercatcher population was not limited by the total mussel food supply and that interference did not have a large impact on mortality. Further evidence of the low impact of interference was the low sensitivity of mortality to changes in the strength of interference.

Night feeding efficiency is one of the most difficult model parameters to estimate. Fortunately, the model was not very sensitive to this parameter and so a small error in its estimation should not have a large influence on its predictions. The model predicted extensive use of supplementary feeding areas (Figure 6.2.3) and it is therefore not surprising that mortality was highly sensitive to changes in supplementary feeding rates.

Aspects of oystercatcher energy expenditure were included in the sensitivity analysis as they are difficult to measure under field conditions. Mortality was highly sensitive to changes in both metabolic rate and the rate of increase of thermoregulatory costs at low temperatures, indicating that accurate estimates for these parameters must be obtained.

In summary, the sensitivity analysis showed that the main model output, the rate of oystercatcher mortality, was most strongly influenced by changes in mussel flesh content, intake rate on supplementary prey, and oystercatcher energy demands. The accuracy of the model predictions therefore depend most on the accurate estimation of these parameters.

Table 6.2.1 Sensitivity of the model prediction of overwinter mortality to changes in selected parameter values. The table shows percentage mortality occurring when each parameter is either increased or decreased by 25%, and the difference in mortality between these two extremes. With the standard set of parameter values, the model predicts 4.9% overwinter mortality.

Parameter	Parameter decreased	Parameter increased	Difference
Mussel bed area	4.8	4.8	0.0
Mussel density	5.4	4.2	1.2
Mussel flesh content	28.1	2.3	25.8
Interference coefficient (m) on mussel beds	3.0	6.1	3.1
Feeding efficiency at night	11.8	4.1	7.7
Supplementary intake rate	25.6	0.1	25.5
Oystercatcher mean metabolic rate	0.0	28.0	-28.0
Thermoregulatory costs	2.7	22.8	-20.1

6.2.7 Simulated period of cold weather

In many parts of Europe, winter mortality rates are higher than those recorded on the Exe during the mild winters of 1976-77 to 1980-81 (Goss-Custard *et al.* 1995). The main reason for this is that, on the continent, severely cold winters occur every 9 years or so and, directly and indirectly, kill many oystercatchers (Hulscher, Exo & Clark 1996). Periods of cold weather affect shorebirds in two ways (Goss-Custard *et al.* 1996). Increased costs of thermoregulation mean that birds need to consume more food per day in order to survive. Yet, the availability of prey often decreases due to freezing of the substrate. Food availability therefore decreases as the food requirements increase, so many shorebirds are vulnerable to prolonged periods of cold weather.

The impact of such a cold weather period was simulated in the model by reducing the temperature to 0°c for a two week period in mid January; this compares with the standard simulations in which temperature was approximately 5°c throughout this period. As there is no evidence that intake rate in mussel feeding oystercatchers (Goss-Custard *et al.* 1996) or in cockle feeding oystercatchers (Goss-Custard *et al.* 1977) is affected by temperature above 0°c, only the intake rate in fields was reduced at low temperatures in the model. All other model parameters were unchanged. As soon as the cold weather period started, more birds needed to use supplementary feeding areas due to increased thermoregulatory costs. Accordingly, the average proportion of time spent feeding on mussels at low water and on supplementary upshore prey increased (Figure 6.2.7a). However, as birds were unable to feed in the fields at low temperatures, increased feeding was not sufficient to maintain the body mass of many birds and so mean body mass decreased (Figure 6.2.7b). Birds started to lose mass as soon as temperature decreased, but the mortality rate did not reach a peak until about 10 days after the start of the cold period, after which it remained high until the end of the cold period (Figure 6.2.7c). When the temperature returned to its standard value, mortality ceased, the proportion of time spent feeding decreased and body mass increased. The mean mass of all birds increased at a low rate after the cold weather period, implying that many birds had been below their target mass and so would have been very susceptible to a second cold period. The model clearly predicts that cold spells at this time of the year could have a major impact on survival. High mortality rates in periods of severe weather have frequently been observed in oystercatchers (Goss-Custard *et al.* 1996) supporting this prediction of the model.

6.2.8 Loss of supplementary feeding areas

The model successfully predicted the considerable use made of the supplementary feeding areas from mid to late winter, especially during periods of cold weather. This occurred because many birds did not meet their energy requirements by feeding on the mussel beds alone over low water, particularly when cold stressed. The sensitivity analysis also showed that mortality was strongly influenced by changes in intake rate on supplementary feeding areas. To further test the importance of supplementary feeding for the survival of birds, the model was run with only mussel beds available as feeding areas. The removal of both upper shore level and high tide supplementary feeding areas, had a large impact on overwinter survival. Of the initial 1650 birds, 794 (48.1%) died during the course of winter, compared to 4.8% when supplementary food was available. This additional mortality indicates that 43.3% of birds that usually survive only do so because of the presence of supplementary food. Mortality was not evenly divided between the two feeding methods, the rate being 93.2% in stabbers but only 4.4% in hammerers. Apart from stressing the importance of supplementary feeding in this population, these simulations confirm the suspicion that version 2 of the model over predicted mortality because it contained no provision for the birds to supplement their intake when mussel beds were covered by the tide (Goss-Custard *et al.* 1996). As the predicted use of supplementary feeding was very close to that observed it is not unreasonable to assume that they are of similar importance to real birds, and hence that in reality the loss of supplementary food supplies could cause large-scale mortality.

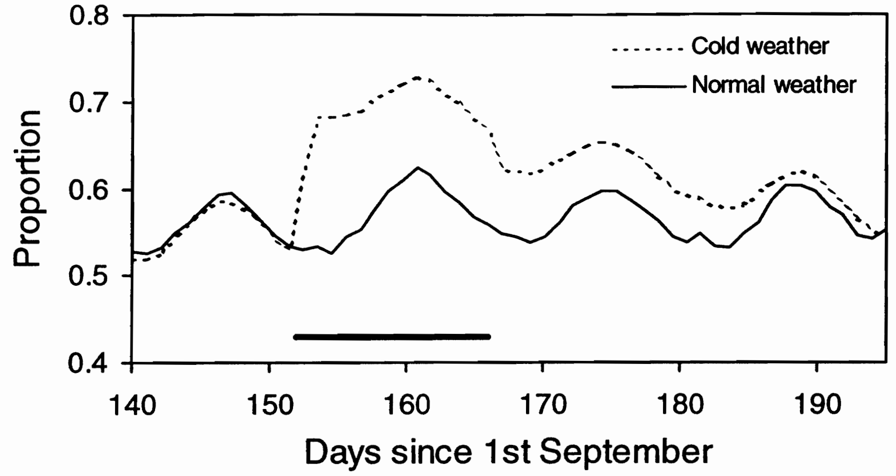
6.2.9 Summary and conclusions

Overall the model successfully predicted qualitative patterns observed in the Exe estuary. Stabbers tended to have lower mass, require more supplementary feeding and have a higher mortality rate than hammerers. Supplementary feeding and mortality tended to decrease with increasing bird age. All of these patterns were also observed in the real system. Some quantitative predictions of the model were also very close to reality. Particularly accurate predictions were made for the number of birds using fields at high tide throughout winter, and changes in body mass of different bird classes during winter.

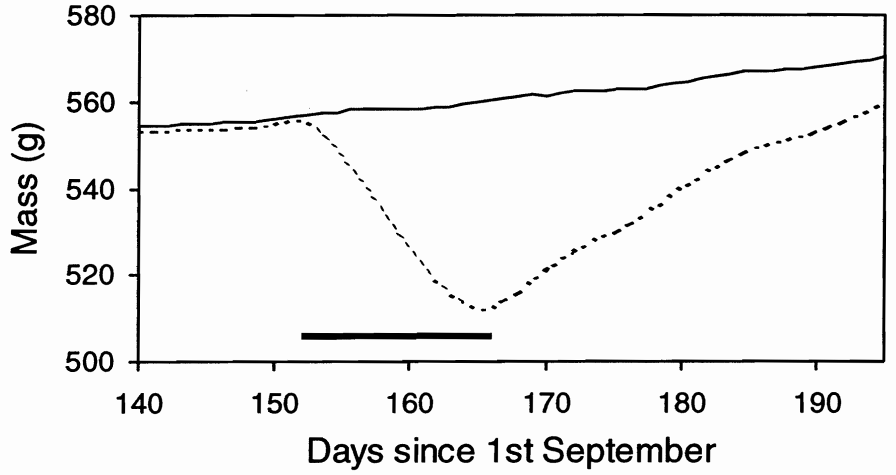
The predicted distribution of birds between mussel beds was less satisfactory. Although the predicted and observed numbers were similar, the predicted density of birds was not as expected. This discrepancy occurred because bird density on the Exe mussel beds is influenced by substrate softness, and this factor is not incorporated in the model. More birds than expected were predicted on soft beds and less on firm beds. Bed substrate was not incorporated in the model as the mechanism by which it effects density is unclear.

The model highlights the importance of upshore areas and fields for supplementary feeding, and the vulnerability of birds to prolonged periods of cold weather. The general simulations of shellfishing practices need therefore to address the interaction between shellfishing intensity, the availability of supplementary feeding and weather conditions.

(a) Proportion of time spent feeding



(b) Body mass



(c) Mortality

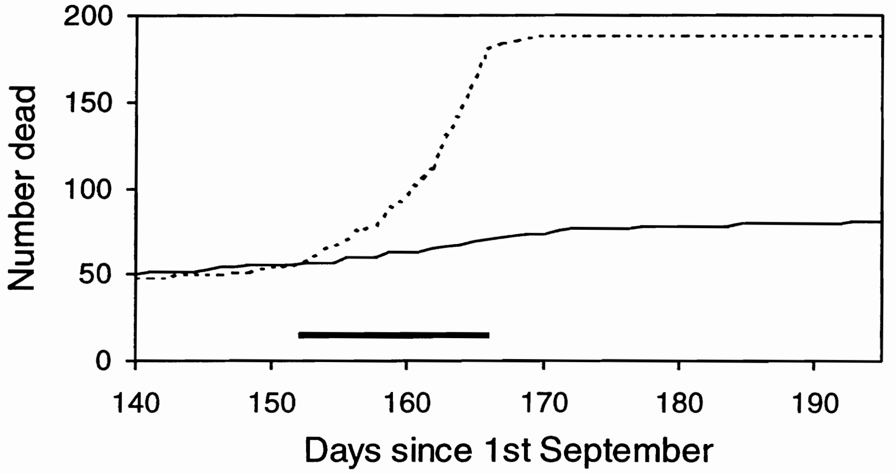


Figure 6.2.7 Predicted influence of a 14 day period of cold weather on the proportion of time spent feeding, body mass and mortality of oystercatchers on the Exe estuary. The horizontal bars show the duration of the cold weather period.

6.3 OYSTERCATCHERS AND COCKLES

R A Stillman, K Norris & A D West

The oystercatcher-cockle version of the model was parameterised and tested using data collected on the Burry Inlet. This section provides an overview of the structure of this model and describes the test results. Full details of the structure and function of general aspects of the model are given in chapter 2.

6.3.1 The oystercatcher-cockle model

The oystercatcher-cockle model was tested using simulations which ran over one winter period from 1st September to 15th March. The tidal cycle was divided into two stages; high tide lasted for approximately 6 hours and low tide for 6.5 hours. The duration of these tidal stages was estimated on the Burry Inlet during the field study. It was assumed that weather patterns on the Burry Inlet were the same as those on the Exe estuary.

Eleven patches, of two types, were available as feeding areas; 10 cockle beds were exposed during low tide only, and one field was always available. Although only one field was available in the model, it can be considered to represent a number of fields in the real system. No upshore areas were included in the model as such areas on the Burry Inlet appear to have very low densities of suitable prey species.

Within each cockle bed, cockle populations were divided into five size ranges (0-7; 7-15; 15-22; 22-29; and 29mm+) to match those used by the oystercatcher-cockle foraging model (see section 3.2). The September size distribution of cockles on the 10 beds was set to that recorded in a random sample of ten of the 25x25m plots used to collect the foraging data, each patch having the size distribution recorded in one study plot. Each of these beds was assumed to occupy one tenth of the total area of the Burry Inlet cockle population. The total area of cockle beds in the Burry Inlet is 5km^2, and so each bed had an area of 0.5km^2. Cockle beds on the Burry Inlet are fully exposed during low tide throughout the spring-neap cycle, and so all cockle patches in the model had a similar pattern of exposure.

Shellfishing was incorporated into the test simulations at the rate currently observed on the Burry Inlet. Fifty fisherman gathered cockles by hand during the hours of daylight throughout the course of winter at all stages of the spring-neap cycle. During each fishing bout, each fisherman collected cockles over 22mm in length up to a maximum fresh mass of 100kg (the daily quota). Full details of the cockle fishing model are given in section 5.3. Fishermen remained on cockle beds until they had collected their daily quota, and then left. While on the cockle beds, fishermen disturbed birds as described for oystercatchers on the Exe estuary (Section 5.2).

The intake rate of an individual oystercatcher feeding on cockles was calculated from the abundance, size distribution and flesh content of cockles (see section 3.3 for full details). The model incorporated depletion of cockle stocks due to oystercatcher predation and shellfishing, and changes in the flesh content of cockles during the course of winter (see section 4.2). While feeding in the field, oystercatchers were assumed to obtain an intake rate that was independent of the food supply available, but related to temperature (see section 3.3 for full details). Individuals were assumed to vary in their feeding efficiency on both cockle beds and the field; feeding efficiency was normally distributed with a particular mean and standard deviation. In mussel feeding oystercatchers, the standard deviation of feeding efficiency is approximately 10% of its mean. The variation of feeding efficiency in cockle feeders in unknown and so was assumed to be the same as that in mussel feeders (i.e. standard deviation = 10% of mean). No interference occurred either on cockle beds or in the field.

Approximately 15,000 oystercatchers were present on the Burry Inlet during the two study years. However, the model only simulates individuals feeding exclusively on cockle beds at low tide, and it is uncertain how many individuals in the real system adopted such a feeding strategy. Therefore, initial simulations were based on different oystercatcher populations which covered the full range of possibilities: 1000, 5000, 10000 and 15000 individuals. In reality, the number of birds present on the Burry Inlet varies during the course of winter, but for simplicity in the model a constant number was assumed to remain throughout winter.

6.3.2 Distribution between cockle beds

In the model, ten cockle beds were available as feeding areas during each low tide period, but only three of these beds were used throughout winter, regardless of the size of the oystercatcher population (1000-15000 birds). The model predicted that beds used by oystercatchers had higher densities of cockles greater than 22mm in length, than those that were not used, which enabled oystercatchers to achieve higher intake rates on these beds. Although the densities of cockles on these favoured beds were depleted during the course of winter, depletion did not reduce intake rates sufficiently to cause birds to spread out to a wider range of feeding locations.

The predicted distribution of oystercatchers does not appear to be supported by field observations. All of the study plots from which the range of cockle densities used in the model were obtained were used by oystercatchers throughout winter. The model therefore predicts a far higher aggregation of birds into areas of high cockle densities than was observed. Two factors could have caused this discrepancy.

(1) Interference was not incorporated into the model as it was not observed in the field study (section 3.2). The general effect of interference is to prevent all individuals occupying patches containing the highest densities of prey. Adding interference to the model would have produced an oystercatcher distribution closer to that observed. Although not observed in the Burry Inlet, interference has been recorded between cockle feeding oystercatchers on the Baie de Somme, France (P. Triplet, unpublished data). The possibility exists that interference does occur between oystercatchers in the Burry Inlet, but could not be detected.

(2) The model assumes that birds move to feeding locations in which their intake rates are maximized. However, the field study showed that in early winter oystercatchers were not maximizing their intake rates (section 3.2); within a patch, intake rates were lower than those theoretically possible given the food supply available. Therefore, it is possible that the choice of feeding locations by oystercatchers was not based on intake rate maximization. For example, birds may have been content simply to feed in areas where their intake rates exceeded a threshold value, rather than those maximizing intake rate. If so they would occupy a wider range of feeding locations than birds that rate maximised. The difference between the predicted and observed distribution may therefore have occurred because, in reality, oystercatchers on the Burry Inlet do not always maximise their intake rates.

6.3.3 Overwinter survival, body mass and supplementary feeding

No birds died during the course of winter simulations, regardless of the number of birds using the cockle beds. Furthermore, all were able to maintain their target body mass throughout winter by feeding on the cockle beds alone. No birds needed to use the fields for supplementary feeding. The model clearly predicts that, at the current level of fishing effort and with the present number of birds feeding on the cockle beds, all individuals are able to meet their energy demands. These predictions appear to be supported by observations on the Burry Inlet. No birds were observed feeding in the fields during the study, even though, in the 1970's, many oystercatchers used fields around the Inlet in years when cockle stocks were very low (I. Johnson pers. comm.). Furthermore, most only fed for a small proportion of the exposure period. If birds were having difficulty in surviving, the observed amount of time spent feeding on cockle beds would be expected to have been higher, and more birds would have been observed in the fields. In comparison to the Exe estuary, where about 5% of birds die and many rely on supplementary feeding for survival (section 6.2), conditions on the Burry Inlet appear to be far more favourable.

6.3.4 Proportion of low tide period spent feeding

The model predicted that the amount of time spent feeding on cockle beds each day increased during the course of winter (Figure 6.3.1). In September, birds were able to meet their energy requirements by feeding for just over 2 hours each day, but by March they needed to feed for over 4.5 hours. The predicted increase in time spent feeding was due to a combination of four factors:

(1) the birds' energy requirements increased during the course of winter as temperature decreased;

(2) day length decreased during winter, and so the proportion of time spent feeding at night (when feeding efficiency was lower than during daylight) increased;

(3) during winter the density of cockles decreased due to oystercatcher predation, shellfishing and other mortality sources;

(4) the flesh content of cockles decreased during winter.

Therefore, the energy demands of birds increased during winter (1) as their intake rate fell (2-4).

The proportion of time spent feeding also varied throughout the spring-neap cycle. For a fixed stage of the season, birds needed to feed for a longer time during neap tides than during spring tides. This pattern was due to the relative timing of low tide on neap and spring tides. On spring tides in the Burry Inlet simulations, one low tide period occurred during daylight and one at night. In contrast, on neap tides both daily low tide periods were divided between the hours of light and dark. In winter, when nights were long, the majority of neap low tides occurred during darkness, whereas at least one spring low tide period occurred during daylight. As feeding efficiency was lower at night, birds needed to spend longer feeding on neap tides because a greater proportion of the two daily low tide periods fell during the night.

In the model, cockle beds were exposed for approximately 13 hours each day. Therefore, at the end of winter birds were feeding for less than 40% of the time during which cockle beds were exposed. This result suggests that birds' energy demands would need to increase greatly, or the feeding conditions to deteriorate substantially, before birds would need to use fields for supplementary feeding.

Unfortunately, no quantitative data exist with which to test the predicted duration of feeding. However, the general model prediction that birds only need to feed for a small proportion of the low tide period does appear to be supported by observation. During low tide periods throughout winter the majority of birds were observed to roost at low water (observations from field study). Birds only fed in any numbers on the receding and advancing tides. It seems unlikely that birds ceased feeding because cockles could not be captured during this period, implying that birds did not need to feed for part of the exposure period.

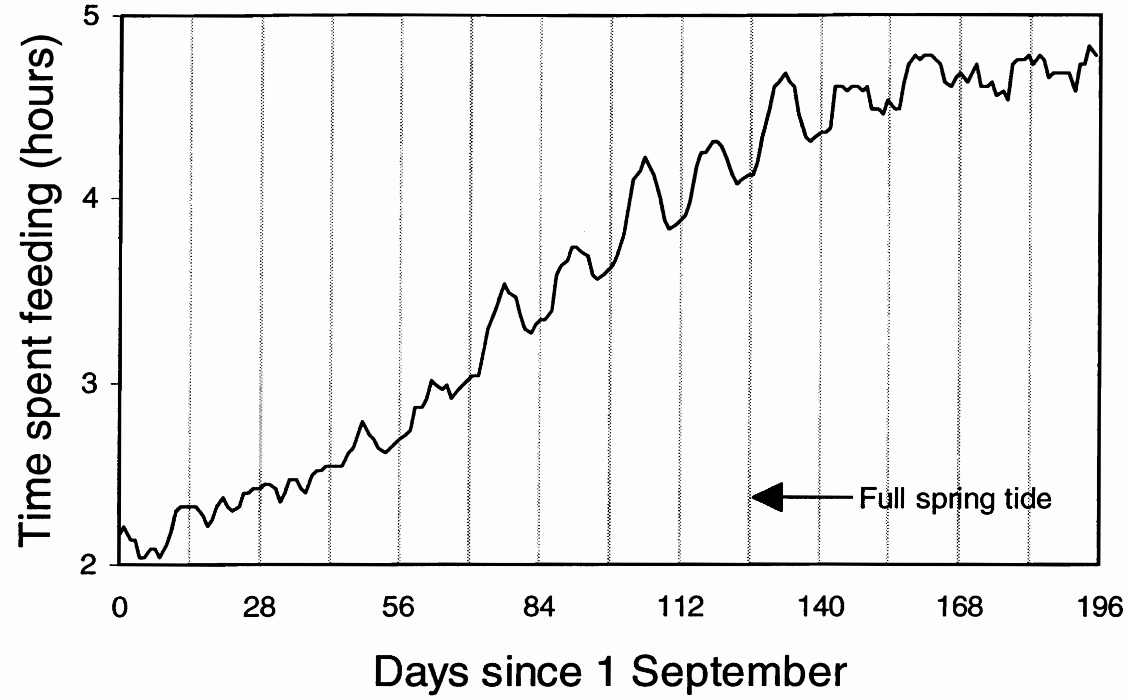


Figure 6.3.1 Predicted amount of time oystercatchers spend feeding on cockles each day on the Burry Inlet in relation to stage of the season. Values show the mean time spent feeding on each day of winter.

6.3.5 Influence of cold weather

In section 6.1, the model predicted that mussel-feeding oystercatchers were very susceptible to prolonged periods of cold weather, and high oystercatcher mortality has indeed frequently been observed in Europe during particularly cold spells (Goss-Custard *et al.* 1996). Cold weather increases the energy demands of birds, and freezes fields on which supplementary feeding occurs. The impact of cold weather on cockle-feeding birds was tested by repeating the simulation applied to mussel feeders. In these simulations, temperature was reduced to 0°c for a two week period in mid January. In standard simulations temperature remained at approximately 5°c during this period. No other model parameters were changed.

The only impact of the cold weather period was to increase the amount of time spent feeding on cockle beds at low tide (Figure 6.3.2). Under normal weather conditions, birds in mid January spent approximately 37% of each low tide period feeding. Cold weather conditions caused birds to feed for approximately 46% of low tide periods. During the cold weather period, the energetic demands of birds increased, but could be matched through an increases in the time spent feeding on cockles. In comparison, increased feeding effort in mussel feeders was not sufficient to meet increased energy demands, leading to decreased mass and high mortality (Figure 6.2.7). The results of these simulations show that oystercatchers feeding on the Burry Inlet are less susceptible to prolonged cold weather than those on the Exe estuary.

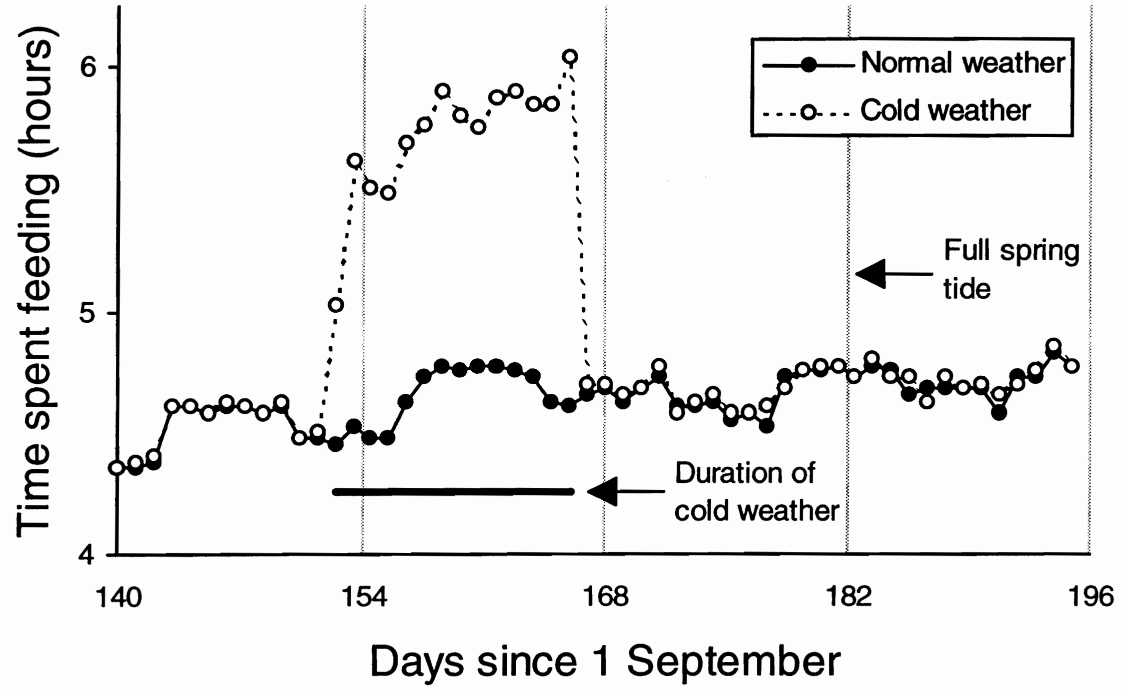


Figure 6.3.2 Predicted influence of a two week spell of cold weather (0°c) in mid January on the time spent feeding each day by oystercatchers in the Burry Inlet.

6.3.6 Sensitivity analysis

The predictions of the oystercatcher-mussel model were shown to be highly sensitive to variation in a number of parameter values (Table 6.2.1). A similar analysis was applied therefore to the oystercatcher-cockle model (Table 6.3.1). None of the combinations of parameter values used in the sensitivity analysis caused any oystercatchers to die, lose mass or use fields for supplementary feeding. The only model prediction to vary was the time spent feeding on cockle beds at low tide, and so the results of the sensitivity analysis are presented for this output alone. It is important to note, however, that the analysis was based on the current, high abundance of cockles on the Burry Inlet. If the sensitivity analysis had been run for a lower cockle abundance, it is likely that the oystercatcher mortality rate would have been sensitive to variation in the models parameters.

Three of the parameters tested in the sensitivity analysis, cockle bed area, cockle density and cockle flesh content, refer to the oystercatcher food supply. The model was insensitive to variation in either cockle bed area or cockle density; 25% changes in either parameter caused less than 5% changes in the amount of time oystercatchers spent feeding. These two results can be explained by the high cockle densities found in the Burry Inlet in the study years. Under such conditions, oystercatchers encountered cockles at a very high rate and intake rates were limited more by handling time than by encounter rate. Changes in encounter rate caused by variation in cockle density did not therefore cause large changes in intake rate; hence the time spent feeding was relatively constant. The main influence of changed bed area was to influence the rate at which cockle stocks were depleted. The changes in cockle density caused through changes in the rate of depletion had a low impact for the same reasons as given above. Changes in the flesh content of cockles had a large influence on the model's predictions. This result is not surprising as intake rate in the model is directly proportional to cockle flesh content; a 25% increase in flesh content results in a 25% increase in intake rate.

The remaining three parameters considered in the sensitivity analysis refer to the oystercatchers themselves. Night time feeding efficiency and thermoregulatory costs both had a moderate impact on the amount of time spent feeding. In contrast, changes in general energetic costs (i.e. the cost of activity, digestion and other body functions but excluding thermoregulatory costs) had a larger effect than any other parameter; 25% changes caused 25% changes in time spent feeding. The difference between the two categories of energetic costs occurred because simulations were run with mild weather (minimum winter temperature of 5°c). Thermoregulatory costs were therefore relatively low compared to other energetic costs and a25% change therefore had a lower impact on daily energy expenditure than a 25% change in general energetic costs. The sensitivity of the model to changes in thermoregulatory costs would have been greater if simulations had been run for colder winters.

Table 6.3.1 Sensitivity of the mean number of hours spent feeding each day during the last spring-neap cycle of winter to 25% changes in selected parameter values. The table shows the amount of time spent feeding expressed as an absolute value and as a percentage change from that with the standard set of parameter values. The model predicts that birds feed for 4.72 hours per day over the equivalent period with the standard set of parameter values.

	Absolute value		Percentage change	
Parameter	Parameter decreased	Parameter increased	Parameter decreased	Parameter increased
Cockle bed area	4.78	4.64	+1.3	-1.7
Cockle density	4.86	4.60	+3.0	-2.5
Cockle flesh content	5.75	3.95	+21.8	-16.3
Feeding efficiency at night	5.25	4.29	+11.2	-9.1
Daily non- thermoregulatory energy expenditure	3.42	5.97	-27.5	+26.5
Daily thermoregulatory energy expenditure	4.47	4.89	-5.3	+3.6

6.3.7 Summary and conclusions

The simulations clearly predicted that oystercatchers feeding on the Burry Inlet have less difficultly in surviving the winter than those feeding on the Exe estuary. In the Burry Inlet, birds could meet their energy demands in late winter by feeding for only 4 hours. No birds died, lost mass or needed to use fields for supplementary feeding. In comparison, 5% of birds died during the course of winter on the Exe estuary, and many needed to use supplementary feeding areas in order to survive. Simulations of both estuaries were run with identical weather patterns, and so these differences can be attributed to the more abundant food supply on the Burry Inlet.

Although the model's predictions for the Burry Inlet could not be tested as thoroughly as those for the Exe estuary (due to lack of suitable data), the ease with which birds were predicted to survive the winter does appear to be supported by observations. Throughout winter many birds were observed to spend a high proportion of low tide periods resting when cockle beds were still exposed. Additionally, no birds were observed feeding in fields surrounding the estuary, even though apparently suitable fields were present. Such observations would not be expected if a high proportion of birds were struggling to meet their energy requirements.

6.4 KNOTS AND COCKLES

R A Stillman & A D West

This section describes the knot-cockle model and the results of some trial simulations. The model is developed solely from previous studies and so is not tested as fully as the oystercatcher-mussel and oystercatcher-cockle models which were largely developed under the present contract. The main aim of this section is therefore to demonstrate the general properties of the knot-cockle model.

6.4.1 The knot-cockle model

The knot-cockle version of the shorebird-shellfish model was based on the Burry Inlet. Simulations ran over winter periods from 1st September to 15th March. The tidal cycle was divided into two stages; high tide lasted for approximately 6 hours and low tide for 6.5 hours. The duration of these tidal stages was estimated on the Burry Inlet during the field study (K. Norris & I. Johnson pers. obs.).

Ten cockle beds were available as feeding areas at low tide. It was assumed that no fields or upshore areas were available for supplementary feeding and so birds roosted when cockle beds were covered by the tide. Each cockle bed was 0.5km^2 in area and was fully exposed during low tide throughout the spring-neap cycle. All aspects of the cockle population were identical to those in the oystercatcher-cockle model (section 6.3).

Shellfishing was incorporated into the test simulations at the rate currently observed on the Burry Inlet. Fifty fisherman gathered cockles by hand during the hours of daylight throughout the course of winter at all stages of the spring-neap cycle. During each fishing bout, each fisherman collected cockles over 22mm in length up to a maximum fresh mass of 100kg (the daily quota). Full details of the cockle fishing model are given in section 5.3. Fishermen remained on cockle beds until they had collected their daily quota, and then left. While on the cockle beds, fishermen disturbed birds as described for oystercatchers on the Exe estuary (Section 5.2).

The intake rate of an individual knot feeding on cockles was calculated from the abundance, size distribution and flesh content of cockles (see section 3.5 for full details). The model incorporated depletion of cockle stocks due to knot predation and shellfishing, and changes in the flesh content of cockles during the course of winter (see section 3.3). Individuals were assumed to vary in their feeding efficiency on cockle beds; feeding efficiency was normally distributed with a given mean and standard deviation. In mussel feeding oystercatchers, the standard deviation of feeding efficiency is approximately 10% of its mean. A similar variation in feeding efficiency was assumed for knot. No interference occurred between foraging knots.

For simplicity, the model assumed that the energy expenditure of knots was constant throughout the course of winter (i.e. that thermoregulatory costs were constant). The rate of energy expenditure was an average overwinter value estimated for knots wintering in the Wadden Sea (Poot & Piersma 1994; see chapter 2 for further details).

6.4.2 Knot mortality within a single winter

The test simulations of the model were used to predict the effect of the size of the knot population in September on the subsequent survival of cockles within the size class consumed by knots and the survival of knots themselves (Figure 6.4.1).

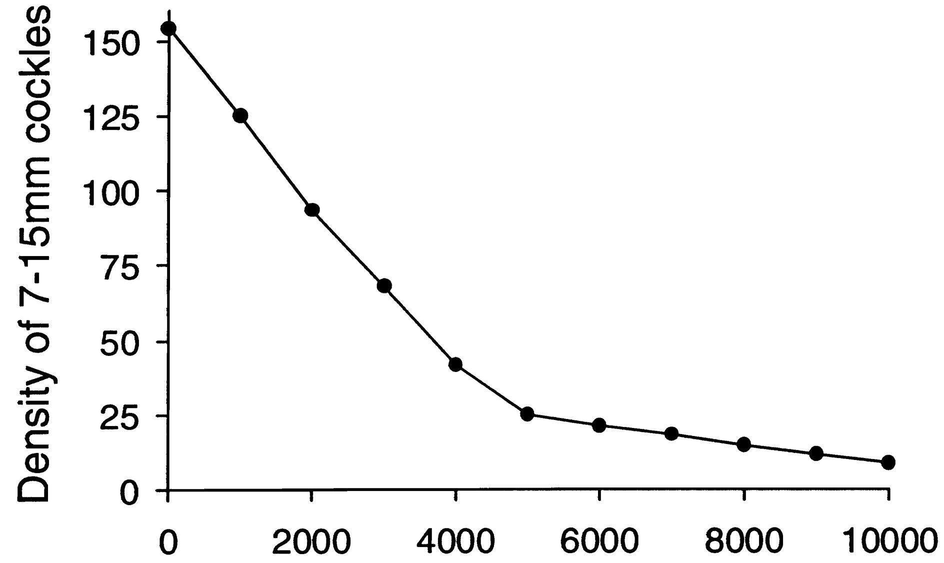
In simulations with knot populations of less than 4,000, the density of 7-15mm cockles surviving at the end of winter was directly proportional to the initial knot population; the cockle density at the end of winter was decreased by 14 cockles m^{-2} for every additional 1,000 knots present at the start of winter. Despite this depletion, cockle stocks remained high enough to allow all knots to meet their energy demands and so none died. However, this situation changed dramatically when knot populations larger than 4,000 were simulated. These large populations depleted the cockle stocks to such an extent that the individuals comprising the population were unable to meet their energy demands and hence died. The model therefore predicted a threshold knot population size, below which all individuals survived winter and above which all died.

In the simulations, knot were killed by the continued depletion of cockle stocks during the winter. Figure 6.4.2 shows how cockle stocks were depleted during a single winter, and how this depletion affected the feeding, body mass and survival of knots. The example shown refers to an initial knot population of 5,000 individuals (i.e. just above the population size at which all knot die). The density of 7-15mm cockles was steadily depleted by knot predation and other mortality sources during the course of winter, falling from about 400 m^{-2} in September to about 25 m^{-2} in March. As a consequence of the reduced food supply, knots needed to feed for longer in order to meet their energy demands. This increased feeding time was solely due to the decreased food supply because the simulations assumed that the energy expenditure of knots was constant throughout winter. When the cockle density reached 25m^{-2}, knot needed to feed throughout the low tide period. Feeding effort could not be increased any further because no high tide supplementary food supplies were available. As a result, knot were unable to meet their energy demands and so started to lose mass. With a two week period, the mean mass of surviving knot fell from its target value to just above the starvation mass. Within a similar period of time virtually all birds died. The model therefore predicted large scale mortality of knot over a very short time scale.

The general patterns of depletion and knot feeding effort shown in the previous example were repeated for all other knot population sizes. The only differences between simulations were the rate at which cockle stocks were depleted (being higher for larger populations) and the actual percentage of time spent feeding by knots (at a given stage of winter, a higher percentage of time was spent feeding when the knot population was larger). In simulations of knot populations less than 4,000 birds, depletion was never great enough to cause birds to feed constantly and so all maintained their body mass and none died. Above this population size, at some stage of the winter all birds had to feed constantly. At this point, birds lost mass and died within a very short period of time. The only difference between these simulations was the stage of the season at which birds died, this being earlier in the season in simulations with larger initial knot populations.

The predicted mortality rate in knots switched, over a very narrow range of the initial population sizes or over a short period of time, from being very low to being extremely high. The model predicted such a "step-function" type of response in knot mortality because the individuals comprising the population each had very similar characteristics. Individuals only differed with respect to the efficiency with which they consumed cockles, and this parameter did not vary widely between individuals (the standard deviation of feeding efficiency was 10% of its mean). Therefore, as the feeding conditions deteriorated, either as the population size was increased or through time, all individuals had a similar ability to cope. As all individuals had a similar response, changes in the overall mortality rate were sudden. Such a sudden population response would not have been predicted if the individuals in the population were more variable. A further discussion of the importance of variation between the individuals of a population is given for cockle and mussel-feeding oystercatchers in section 7.3.

(a) Cockles



(b) Knots

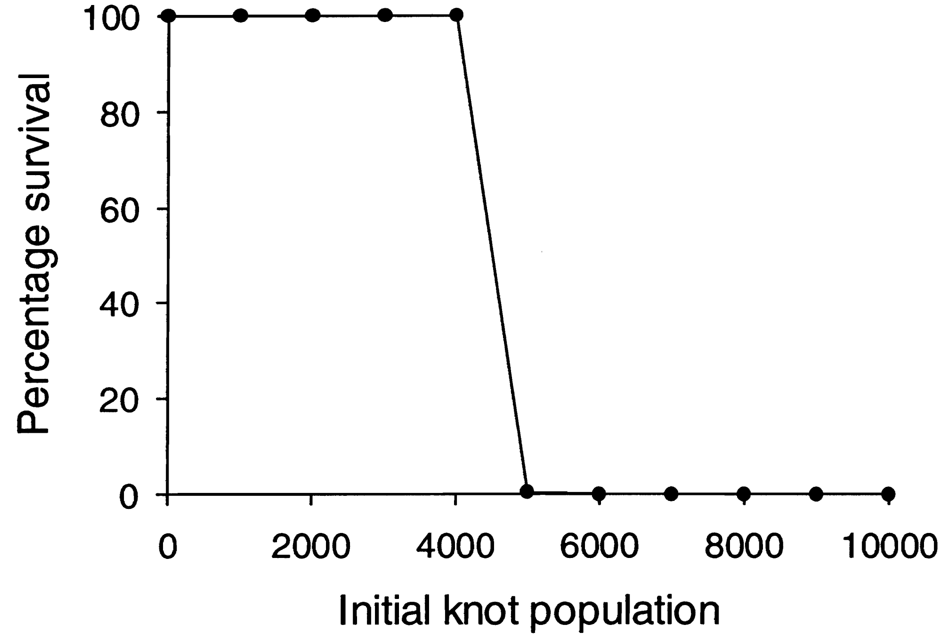


Figure 6.4.1 The predicted effect of the size of the initial Burry Inlet knot population on (a) the density of 7-15mm cockles (i.e. those consumed by knots) at the end of winter and (b) the percentage overwinter survival of knots.

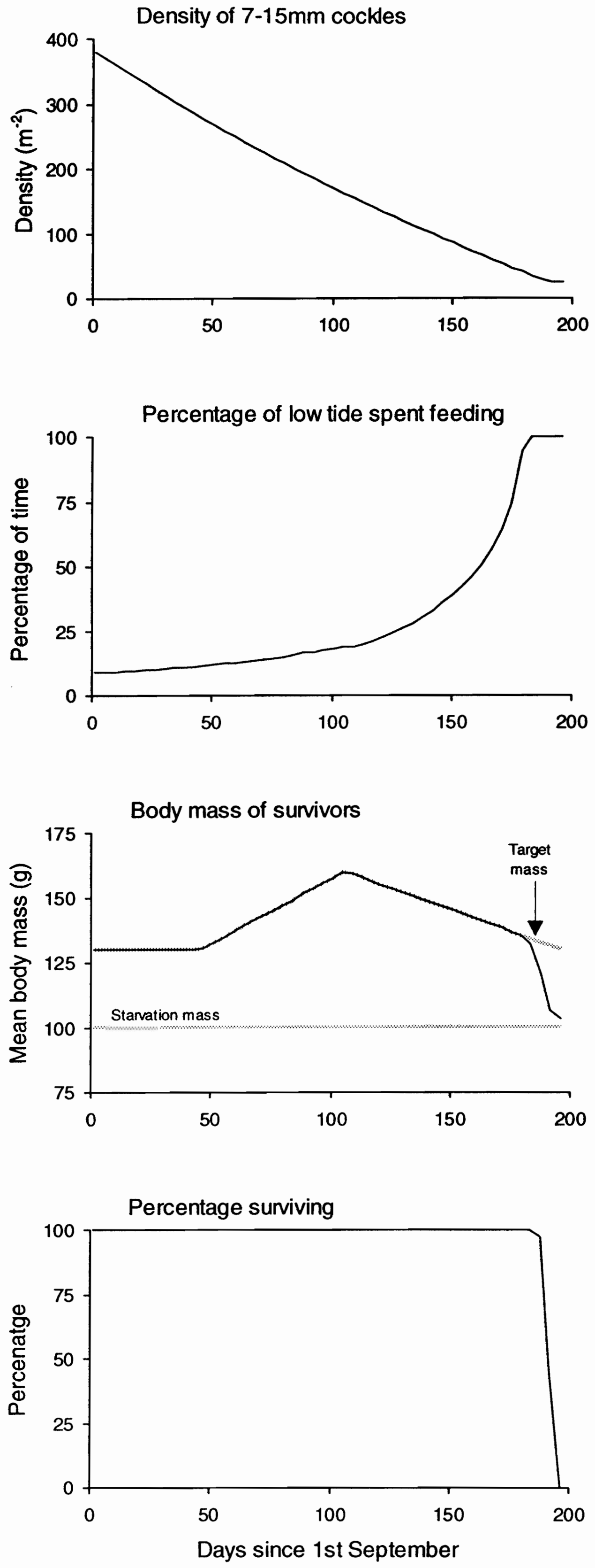


Figure 6.4.2 Predicted overwinter changes in cockle abundance and knot feeding effort, body mass and survival on the Burry Inlet. The initial knot population was 5,000 individuals.

6.4.3 Knot mortality in successive winters

The model predicted that the current cockle population in the Burry Inlet could support at most 4,000 knot over a single winter. The size of the knot population supported by the estuary depends on the density of the 7-15mm cockles that knot consume. These cockles are all in their 1st winter, and so their density depends on the level of recruitment. Recruitment will vary between winters and so the model was run over a ten year period to determine how the maximum knot population changed through time. In the first year of these simulations the density of recruits was the same as in the previous set of simulations. In subsequent years, the density of recruits was calculated from the density of adults using the stock-recruitment curve given in section 4.6. For simplicity, these simulations assumed that a constant number of knot settled on the estuary each September regardless of the level of mortality experienced the previous year.

Figure 6.4.3 shows yearly changes in the mortality of cockles and knots predicted when 3,000 knots settled on the estuary each September. The cockle population fluctuated widely between years, and as a consequence the mortality of knots also varied greatly. However, these fluctuations did appear to have some pattern; years of low cockle abundance and high knot mortality were generally followed by years of high cockle abundance and low knot mortality. This result was due to the stock-recruitment curve used in the model. When recruitment was high and 1st winter cockles were abundant, all knot survived. However, this high level of recruitment increased the adult population in the following year. When adults were abundant, the stock-recruitment curve generated few new recruits (see section 4.6). As a result, the density of 1st winter cockles dropped in the subsequent year and knot mortality was high. This low recruitment lead to low adult densities. Low adult densities resulted in high recruitment (see section 4.6) and so the cycle started once again.

The cockle population showed similar cyclic patterns when lower knot populations were present. However, smaller knot populations could be supported by lower cockle populations and so high knot mortality occurred in fewer years (Figure 6.4.4). The model could not therefore be used to generate a single knot population that could be supported over a long period of time. Instead, it predicted the proportion of years in which a given population could be supported.

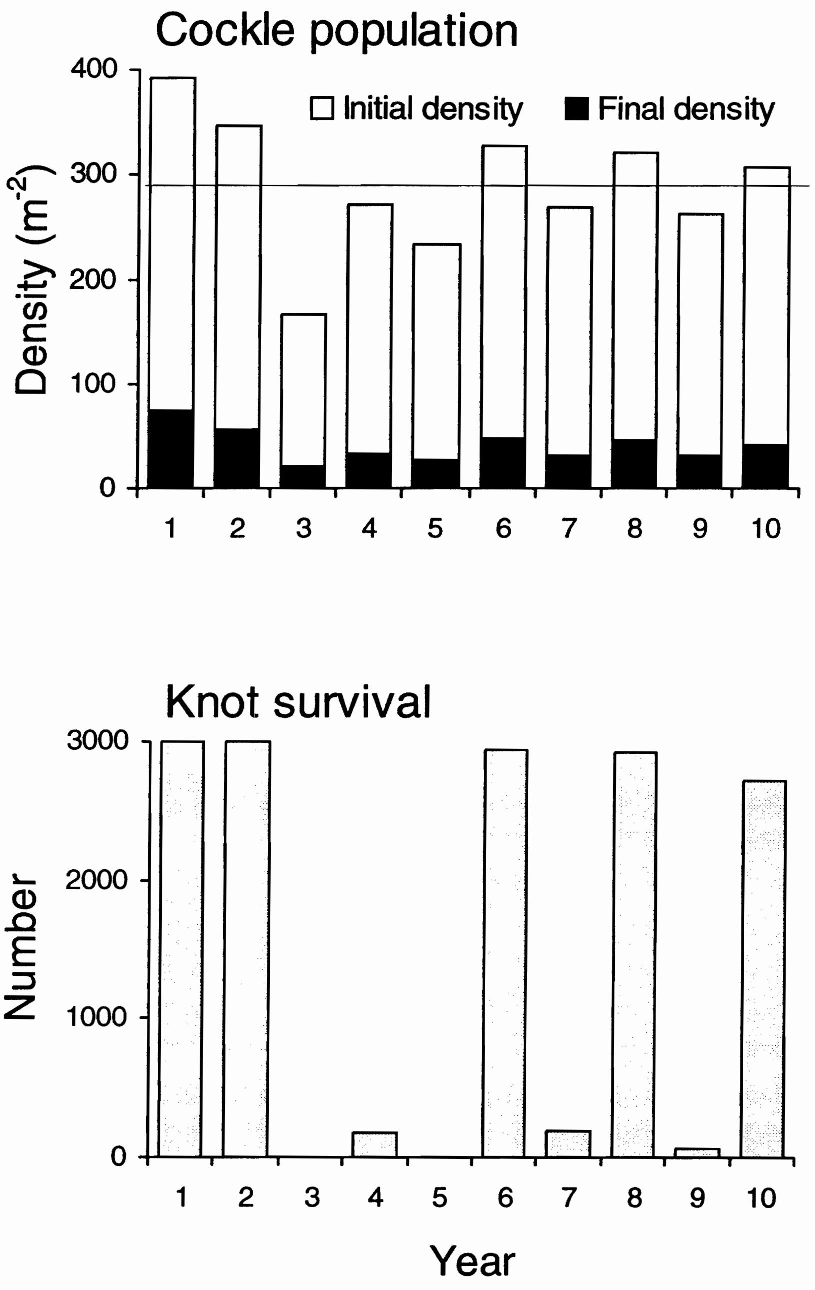


Figure 6.4.3 Predicted yearly changes in the density of 7-15mm cockles and survival of knot in the Burry Inlet. The cockle population is shown in September (Initial) and March (Final) each year. The horizontal line across the top figure indicates the initial cockle population above which most knot survive and below which most die. 3,000 knot settled in the estuary each year.

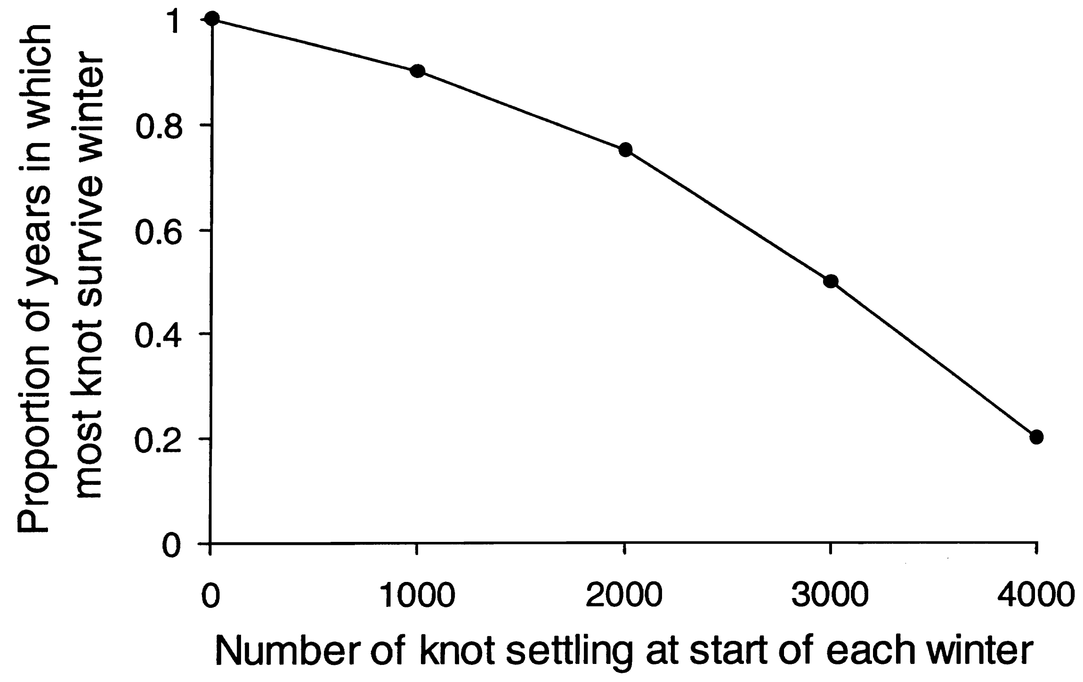


Figure 6.4.4 The relationship between the number of knot settling on the Burry Inlet each year and the proportion of years in which most knot will survive.

6.4.4 Summary and conclusions

The simulations of the knot-cockle model predicted that the present day Burry Inlet cockle population could support up to 4,000 knot over a single winter. This carrying capacity was reached when sufficient knots were present to deplete the density of 7-15mm cockles (i.e. the size range consumed by knots) to less than 25m^{-2}. Below this density very few individual knots were able to achieve a high enough intake rate to meet their energy requirements and so virtually all died. In the model, all 7-15mmcockles were in their first winter and subject to 50% overwinter mortality due to factors other than knot predations. Any changes in the rate of mortality due to these other causes or the density of new recruits to the population will change the carrying capacity predicted by the model.

The maximum knot population that could be supported by the estuary varied between years. This was because the density of recruits generated by the stock-recruitment curve used in the model alternated between successive years. Years of high recruit density were generally followed by years of low density. As a result the mortality of knots also fluctuated between years. However, smaller knot populations could be supported in more years than could larger populations.

It should be re-emphasised that the model predictions only apply to the carrying capacity of the cockle population, whereas in reality knot will exploit a range of other prey species. These species were not incorporated into the model as no suitable knot foraging models were available. However, it would seem most likely that incorporating other prey species would increase the carrying capacity predicted by the model.

The model predicted an "all or nothing" response of knot mortality. For a certain knot population size, either all birds survived winter or virtually all died. A similar, but less marked, response was predicted for cockle-feeding oystercatchers (section 7.3). These responses differ from the gradual changes in mortality predicted by the oystercatcher-mussel model (section 6.2). As discussed for oystercatchers in section 7.3, the reason for the type of response predicted in knots is that all individuals have very similar characteristics. In the model, individual knot only differed with respect to the efficiency with which they fed on cockles (i.e. their intake rates at a set cockle density). Feeding efficiency was assumed to be normally distributed with a standard deviation of 10% of the mean. Given these parameters, the feeding efficiency of 95% of individuals will be within 20% of the mean. The response of mortality in knot was stronger than that in cockle feeding oystercatchers because knot were assumed to be less variable. While knot only differed in their feeding efficiencies on cockles, oystercatchers differed in their feeding efficiencies on both cockles and terrestrial prey in fields.

Seasonal changes in the body mass and survival of knots were also relatively rapid. The reason for these rapid changes is, one again, the high degree of similarity between individual knots. Once the density of 7-15mm cockles had been depleted, all individuals started to loss mass at a similar stage of the season, and likewise all died within a period of a few days. This results suggests that slight changes in the food supply available may cause large changes in the response of birds.

Although the knot-cockle model was simplistic in comparison for those developed for oystercatchers, it emphasised the fact that large scale mortality may occur when individuals comprising a population are very similar.

Chapter 7 SHELLFISHING SIMULATIONS

R A Stillman, J D Goss-Custard, A D West & S E A le V dit Durell

7.1 INTRODUCTION

This chapter presents the shellfishing simulations performed under the current contract. These simulations show the effect of shellfishing on three shorebird-prey systems: the oystercatcher-mussel system on the Exe estuary, and the oystercatcher-cockle and knot-cockle systems on the Burry Inlet. The simulations are designed to predict the impact of shellfishing on oystercatchers in these estuaries, to indicate conditions under which the birds are particularly vulnerable, and to compare the effects of different shellfishing methods. Although the simulations are restricted to specific estuaries, we highlight predictions which are also likely to apply to other systems.

7.2 OYSTERCATCHERS AND MUSSELS

7.2.1 Overview of simulations

Mussel fishing on the Exe estuary currently occurs by hand, at low tide, on spring tides during the hours of daylight, and can be divided into two methods: (1) stripping, in which all mussels are removed from the substrate and later sorted into saleable (40mm or greater in length) and non-saleable size ranges; and (2) thinning, in which only mussels within the saleable size range are removed. The two methods differ in the way in which they deplete the mussel stock. Stripping removes sections of mussel beds and so reduces their area, the mussel density in the remaining bed area being unchanged. Thinning reduces the density of mussels over 40mm in length, but not those below this range, and doesn't reduce the total area of the bed. As both methods occur at low tide, they both influence birds through disturbance.

An alternative method, which does not occur currently on the Exe estuary, is dredging mussels from submerged intertidal beds at high water. This method, which we term high tide stripping, will deplete mussels through a reduction in bed area, as does low tide stripping, but will not disturb birds. High tide stripping also differs from that at low tide as it is not possible to remove completely mussel beds using dredges. Continued dredging will cause a mussel bed to become fragmented. The fragments will become increasingly difficult to relocate (as they are submerged), and eventually dredging will become unprofitable. In contrast, low tide stripping can potentially remove complete beds as they are exposed and hence visible.

Three methods of fishing were used therefore in the simulations; low tide thinning, low tide stripping and high tide stripping (Table 7.2.1). In order to compare the methods, it was assumed that fishing only occurred on spring tides, during the hours of daylight, at either low tide (low tide thinning and stripping) or high tide (high tide stripping).

Table 7.2.1 Fishing methods modelled for the Exe estuary oystercatcher-mussel system.

	Low tide thinning	Low tide stripping	High tide stripping
Reduces mussel density	Yes	No	No
Reduces mussel bed area	No	Yes, and potentially removes whole bed	Yes, but only to 25% of original area
Minimum saleable mussel length	40mm	40mm	40mm
Removes mussels from below saleable range	No	Yes, as bed area is decreased	Yes, as bed area is decreased
Disturbs birds	Yes	Yes	No

The shellfishing simulations were based on the standard set of parameter values used to test the Exe model in chapter 6. At present, shellfishing occurs at a very low intensity on the Exe, and so rather than use current fishing levels, a range of potential values was simulated. The overall level of fishing effort was varied by changes in (1) the number of fishing units (fishermen or dredges) and (2) the area of mussel bed fished by each unit per hour. It is assumed that thinning removes all mussels over 40mm from the area fished, and that stripping removes all mussels within this area. The following range of values was used for each parameter: number of fishing units = 5, 10, 20, 50, 100 or 200; fishing rate = 2.5, 5, 10, 25, 50 and 100 $m^2 hr^{-1}$. The range of values chosen was sufficient to cover all likely levels of fishing. In each set of simulations, one variable was altered while the other was held at a constant value of either 10 fishing units or 5 $m^2 hr^{-1}$. For a particular simulation, the total fishing effort is found by multiplying the number of fishing units by the rate at which each fishes. Fishing effort therefore had a value of either 25, 50, 100, 250, 500 or $1000m^2 hr^{-1}$.

7.2.2 Total mussel catch

As would be expected, increased fishing effort increased the total yield of mussels regardless of the fishing method adopted (Figure 7.2.1). The predicted yield ranged from less then 5% to over 70% of the initial mussel stock. Therefore, the range of fishing efforts used in the simulations is likely to cover all potential levels of fishing effort on the Exe estuary.

The method by which fishing effort was varied (i.e. changing the number of fishing units or the rate at which they fished) had no influence on the total yield, as for a given effort, both methods removed mussels from the same area per unit time. However, there were differences in yield between the different fishing methods, with low tide stripping producing the highest yield for a given fishing effort. The highest effort of low tide stripping removed approximately 75% of the stock, in comparison to 55% removal with either of the other methods (Figure 7.2.1). This result occurred because of the different ways in which the different methods depleted the mussel stock. Low tide stripping was able to completely remove the highest density mussel beds and so had a high yield per unit area of mussel bed fished. The other two methods did not exploit the highest density beds as thoroughly and so had lower yields. High tide thinning only removed 75% of these beds before less profitable beds were fished. Low tide thinning reduced the density of fishable mussels on the highest density beds and therefore reduced the rate at which mussels were subsequently collected.

Although a simple measure of yield has been presented, the model holds much more information on the pattern in which mussel beds are depleted. For example, the following statistics could also be obtained.

- Total yield per fishing unit
- Yield obtained from each mussel bed
- Changes in the distribution of fishing units as mussel beds become depleted

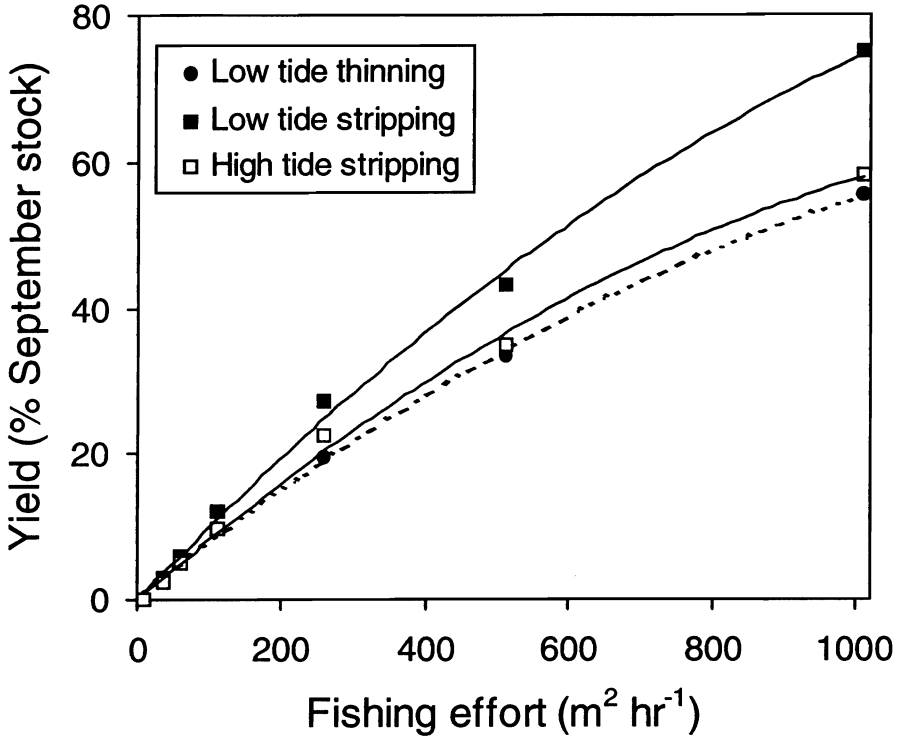


Figure 7.2.1 Total yield of mussels greater than or equal to 40mm in length (percentage of September stock) obtained between 1st September and 15th March through different fishing methods and levels of effort. Yield was identical when fishing effort was varied through either fishing rate or the number of fishing units, and so the mean yield for the two methods is shown.

7.2.3 Oystercatcher survival

7.2.3.1 *Survival within a single winter*

In the absence of fishing, and using the standard set of Exe estuary parameters, the model predicts an overwinter survival of 95.5%. For all fishing methods, increased effort reduced survival, but the impact was most pronounced for low tide stripping (Figure 7.2.2). This fishing method reduced survival to 90% at the highest level of fishing effort, in comparison with 93% for high tide stripping and 95% for low tide thinning. Although different fishing methods differed in their impact on survival, no differences were apparent between the two methods used to vary fishing effort.

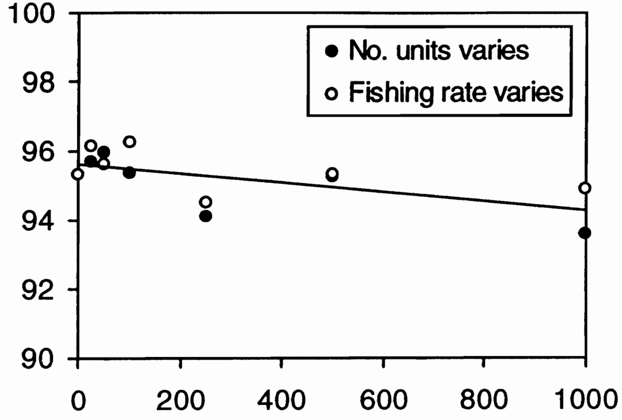
The impact of fishing differed between the two oystercatcher feeding methods. The survival of stabbers was decreased by increased fishing, whereas all hammerers survived regardless of the level of fishing. Similarly, the changes in survival caused by fishing were not equally divided between the different age classes of birds. In the absence of fishing approximately 0.2% of adults and 25% of juveniles die. At the highest fishing effort, low tide stripping increased the mortality of adults to 3.5% and that of juveniles to 50% (Figure 7.2.3). Although the mortality of juveniles was still greater than that of adults, the proportional increase in mortality was greater in adults. Similar patterns were observed for the other fishing methods, although the increases in mortality were less pronounced (Figure 7.2.3).

Both in terms of overall survival, and of the survival of individual age classes, the influence of low tide stripping was greatest, followed by high tide stripping and then low tide thinning. These differences are due to the different ways in which the three fishing methods influence oystercatchers. Fishing at low tide causes disturbance and so reduces the area available for feeding. Bird density is therefore increased in non-disturbed areas, increasing interference and decreasing intake rates. However, fishing disturbance is only temporary, as fishing only occurs on spring tides during daylight. Low tide thinning also reduces the density of mussels and so could potentially reduce intake rates. However, mussel density needs to be reduced to very low levels before intake rates are reduced (see the functional response of mussel feeders in chapter 3) and these levels were not reached over the levels of fishing simulated. Stripping decreases the area of mussel beds and so permanently increases the density of birds. This method therefore causes the intensity of interference to be permanently increased. Over the range of fishing efforts used in the simulations, the severity of these factors can be ranked from reduction of mussel bed area (permanently increasing interference), through disturbance (temporarily increasing interference) to reduced mussel density.

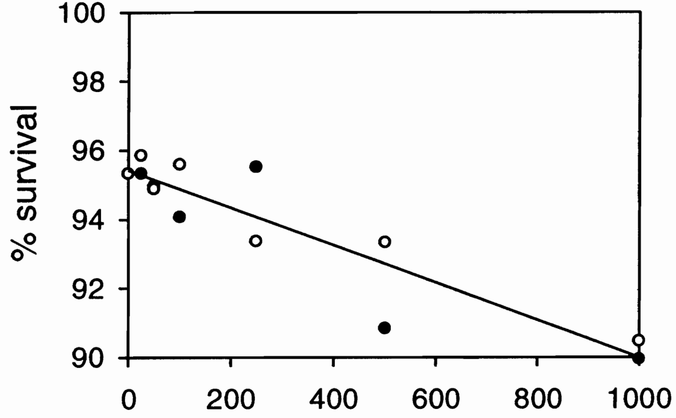
Low tide thinning reduces mussel density, and causes disturbance, but does not decrease the area of mussel beds. In contrast, stripping does reduce mussel bed area and when performed at low tide also causes disturbance. Low tide stripping has the greatest effect on mortality because it permanently reduces the area of mussel beds, and additionally causes disturbance. High tide stripping has a lower effect because it only causes a reduction in area. Although low tide thinning causes both disturbance and a reduction in density, it has a relatively low impact because disturbance is temporary and the density reduction does not reduce intake rate (at least over the range of fishing efforts used).

Other potential outputs: The results presented have been limited to overwinter survival of different classes of birds. However, as the model follows the fates of individuals, a range of other outputs can be generated, such as:

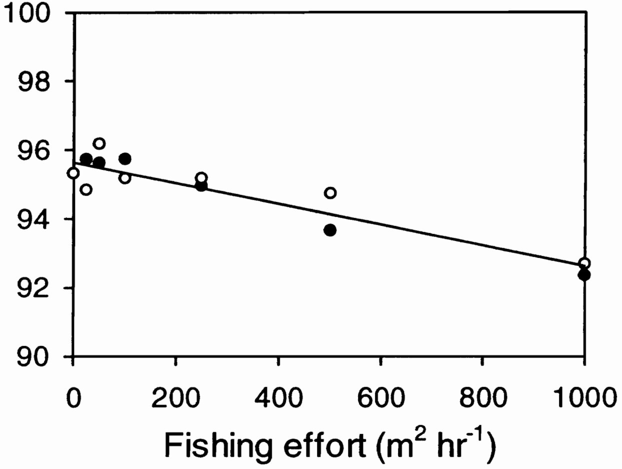
- The time of year at which individuals die
- The stage of the spring-neap cycle at which individuals die
- The feeding efficiency of individuals that die
- The dominance of individuals that die



(a) Low tide thinning



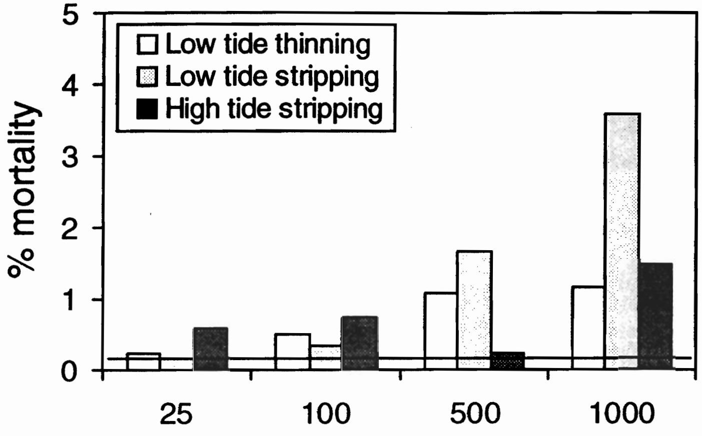
(b) Low tide stripping



(c) High tide stripping

Figure 7.2.2 Overwinter percentage survival of oystercatchers in relation to fishing method and effort. Fishing effort is varied either by changing the number of fishing units or the rate at which each unit fishes, while holding the other parameter constant (see text for parameter values).

(a) Adults



(b) Juveniles

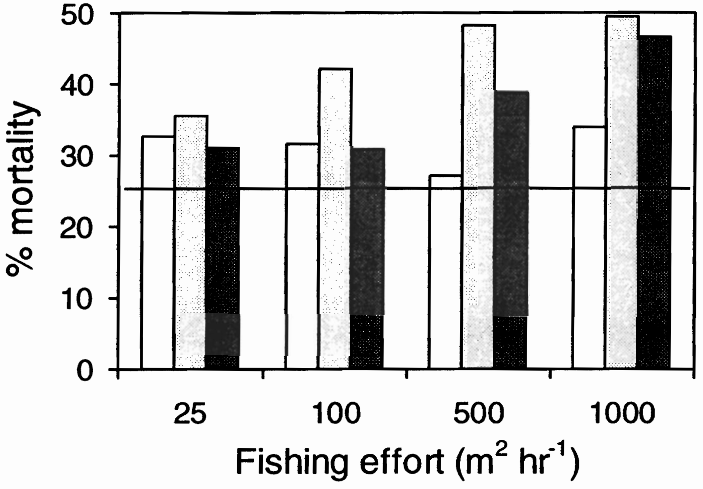


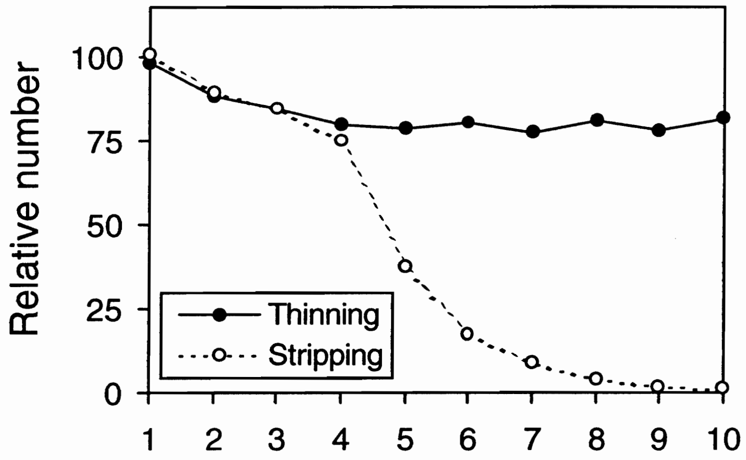
Figure 7.2.3 Influence of shellfishing on the mortality of (a) adult and (b) juvenile oystercatchers. The horizontal lines show the level of mortality in the absence of shellfishing. Note that the two graphs are plotted on different scales.

7.2.3.2 *Sustained fishing over a number of years*

Although the impact of fishing may be small within a single year, subsequent fishing is likely to have a greater effect if the population of either oystercatchers or mussels does not recover by the following year. For example, the stripping methods of fishing reduce the area of mussel beds. If this loss of area is not replaced, either by natural increases in area, or by restocking of mussel beds, the impact of fishing will increase from year to year. To demonstrate this effect, multiple year simulations were run with intermediate levels of fishing effort using low tide stripping and thinning (Figure 7.2.4). In these simulations, the recruitment of young was modelled using the procedure described in chapter 2.

Low tide thinning over 10 years reduced the oystercatcher population to 75% of that predicted in the absence of fishing. Although thinning depleted the mussel stocks, recruitment and the growth of smaller mussels were sufficient to maintain the population of mussels over a number of years. Thus the oystercatcher food supply was sustained. In contrast, low tide stripping reduced the total area of mussel beds, and so constantly reduced the mussel population. Despite the reduced mussel population, the oystercatcher population over the first four years did not differ from that caused by thinning. It was not until the mussel population reached a very low level that the oystercatcher population started to decreased rapidly. The oystercatcher population persisted for a few years after the mussel beds were removed because birds still fed in fields and upshore areas. However, these areas cannot support the population permanently and so its size finally fell to zero. The simulations show that the consequences of shellfishing over a number of years may be much more severe than those over a single winter.

(a) Oystercatcher population



(b) Mussel population

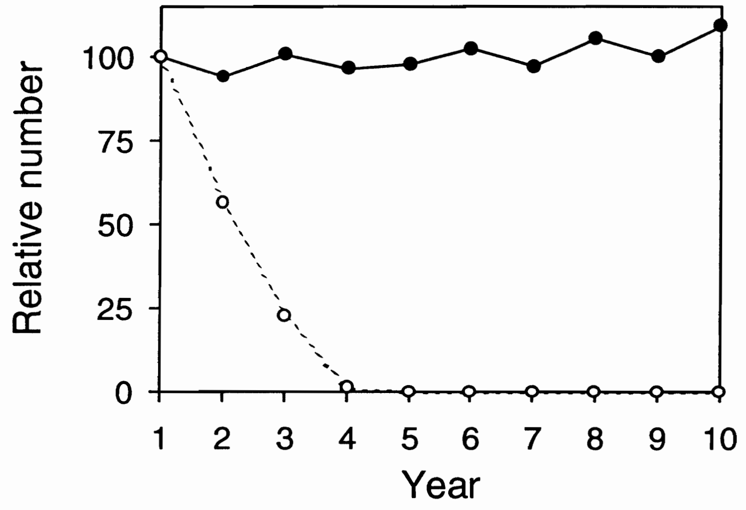


Figure 7.2.4 Predicted changes in the Exe estuary oystercatcher and mussel populations at the start of winter caused by an intermediate level of low tide thinning and stripping (100 fishing units, each fishing $5m^2$ of mussel bed per hour). Populations are shown as a percentage of those predicted in the absence of shellfishing.

7.2.3.3 *Stable population size*

Although all levels of fishing effort reduced survival, the magnitude of this reduction was often very small. For example, low tide thinning only reduced overall survival by 2% even when fishing effort was at a maximum. Oystercatchers are long lived birds and have a relatively low reproductive rate. Small changes in mortality in such species can cause large changes in population size if the recruitment of young is not sufficient to replace those individuals dying.

The impact of changes in winter survival caused by fishing on overall population size was tested using the population dynamics model developed by Goss-Custard *et al.* (1995). This model is age-structured and incorporates density-dependent mortality on wintering grounds, and density-dependent reproduction. It simulates the north-west European oystercatcher population and predicts the stable size of this population given the values of mortality and recruitment. Full details of the model may be found in Goss-Custard *et al.* (1995). The model was adapted to simulate a population of oystercatchers wintering on the Exe estuary and migrating to another site to breed. The influence of shellfishing was incorporated into the model by varying the overwinter mortality of each age class in proportion to that caused by fishing. The model predicted the stable number of birds returning to winter on the Exe.

The simulations showed that small changes in mortality could indeed have a large impact on the overall population size at equilibrium (Figure 7.2.5). Intermediate levels of low tide thinning only reduced overwinter mortality by 1% but reduced population size by over half. Similar levels of low tide stripping caused the population to go extinct. Small changes in mortality caused by fishing should not therefore be assumed to be of low importance to long-term population size. Their aggregate effect over many winters, especially when juvenile mortality is elevated (Goss-Custard & Durell 1984) can have a disproportionate effect on equilibrium population size.

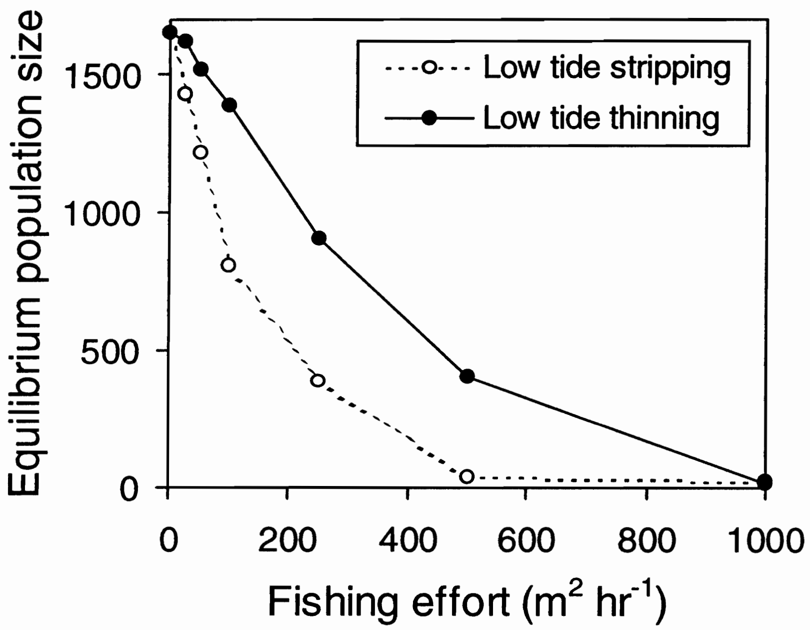
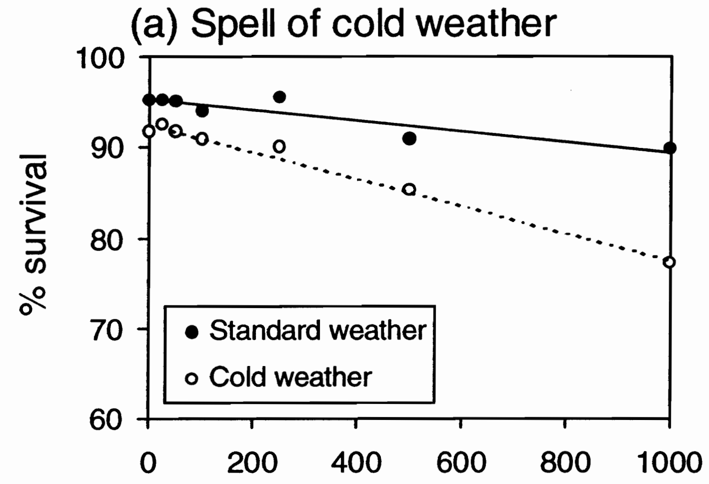


Figure 7.2.5 Stable population size of oystercatchers wintering on the Exe estuary in relation to the effort of low tide thinning and stripping. It is assumed that during each year of simulations low tide stripping reduces the area of mussel bed, but that areas recover between years.

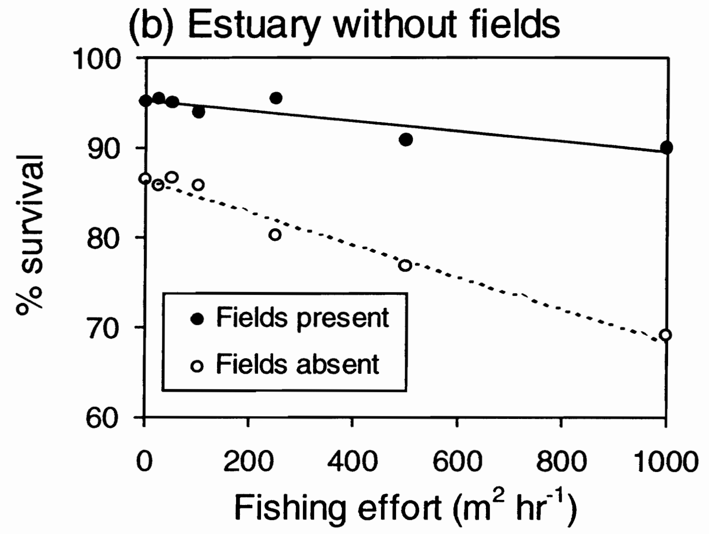
7.2.3.4 *Cold weather and the absence of fields*

Simulations in chapter 6 showed that oystercatchers were particularly vulnerable during periods of cold weather and on estuaries that are not surrounded by fields. Cold weather increases the birds' energy demands and freezes fields (so preventing feeding). In the absence of fields, birds are unable to supplement their intake at high tide. Simulations were run, therefore, to determine the interaction between these factors and effect of shellfishing on oystercatcher survival. In the cold weather simulations, the environmental temperature was reduced to 0°c for a two week period starting in mid January. In the standard weather simulations, the temperature was approximately 5°c throughout this period.

The impact of fishing on survival was accentuated both by cold weather and by the absence of fields (Figure 7.2.6). When either cold weather occurred or fields were absent, survival decreased more rapidly with increased fishing effort than in the standard simulations. These simulations clearly show that oystercatchers will be particularly vulnerable to shellfishing if winters contain any periods of cold weather, and on estuaries without, or with a limited supply, of fields for supplementary feeding.



(a) Spell of cold weather



(b) Estuary without fields

Figure 7.2.6 The influence of fishing effort on the overwinter mortality of oystercatchers assuming (a) that a two week spell of cold weather (0°c) occurs at the end of January and (b) that no fields are present for supplementary feeding.

7.2.3.5 *Conclusions*

The following conclusions can be drawn from the simulations with regard to the impact of shellfishing on oystercatcher survival.

- All fishing methods potentially reduce survival
- Low tide stripping has the greatest impact on survival
- Small changes in annual overwinter survival due to fishing may cause large changes in long-term population size
- Birds are particularly vulnerable to the effects of shellfishing during periods of cold weather
- The impact of fishing will be greater on estuaries not surrounded by fields where oystercatchers can supplement their intake

7.2.4 Oystercatcher body mass

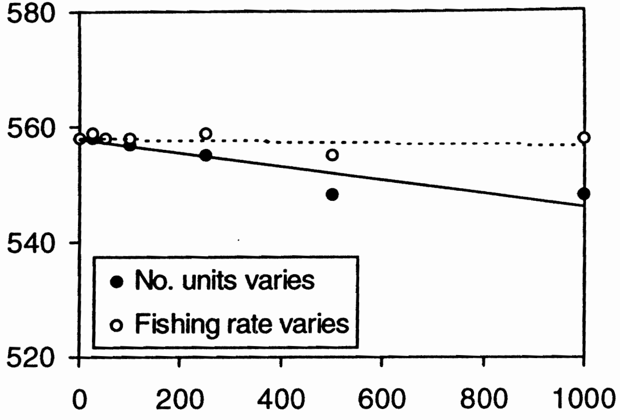
Increased fishing effort not only decreased oystercatcher survival, but also decreased the mean mass of the stabbers surviving the winter (Figure 7.2.7). In contrast, all hammerers were able to maintain their target body mass throughout winter. Low tide stripping had the largest impact on the mass of stabbers, reducing the mean value to approximately 530g. The overall reduction in mass resulting from fishing was not great however, the maximum reduction of 30g being only a 5% reduction from mass in the absence of fishing. There are two explanations for the low change in mass. Firstly, only the mass of surviving birds is considered, and so excludes any that lost sufficient mass to starve. Secondly, the values represent means, and as there is considerable variation in the foraging ability and dominance of birds, many will be able to maintain their target mass.

The method by which fishing effort was varied influenced the impact of low tide thinning. Increases in the number of fishing units reduced mass to a greater extent than did increases in fishing rate. This occurred because larger numbers of fishing units disturb a larger area of mussel beds. Interference is therefore increased during bouts of fishing, so reducing intake rates and decreasing the mass of birds that cannot meet their energy demands. This effect was not apparent for survival because body mass provides a more sensitive measure to changes in intake rate.

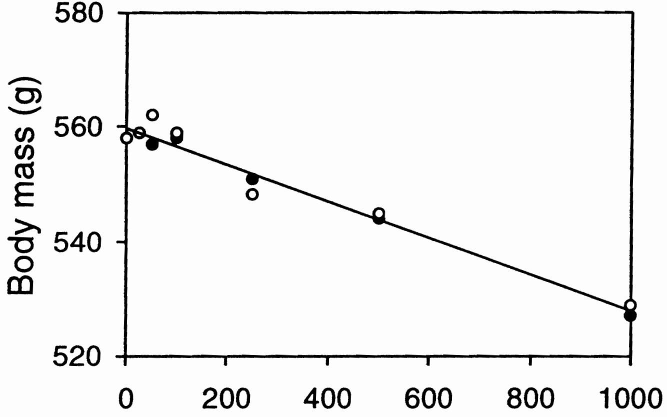
7.2.5 Use of supplementary feeding areas

Increased fishing effort increased both the use of fields at high tide (Figure 7.2.8) and upshore areas on the advancing and receding tide (Figure 7.2.9). Fishing decreases intake rate on mussel beds (either through disturbance or decreases in mussel bed area) and so increases the proportion of birds that are unable to meet their energy demands through feeding on the mussel beds alone. These birds must use the supplementary feeding areas if they are to survive. Although the number of birds using supplementary feeding areas increased with increased fishing effort, the time of year at which birds started to move into these areas was not influenced by the intensity of fishing. Numbers started to increase around the end of October as is predicted in the absence of fishing (see chapter 5). Experience throughout Europe shows that this is how real oystercatcher populations respond to reduction in low tide prey availability (Goss-Custard *et al.* 1996).

(a) Low tide thinning



(b) Low tide stripping



(c) High tide stripping

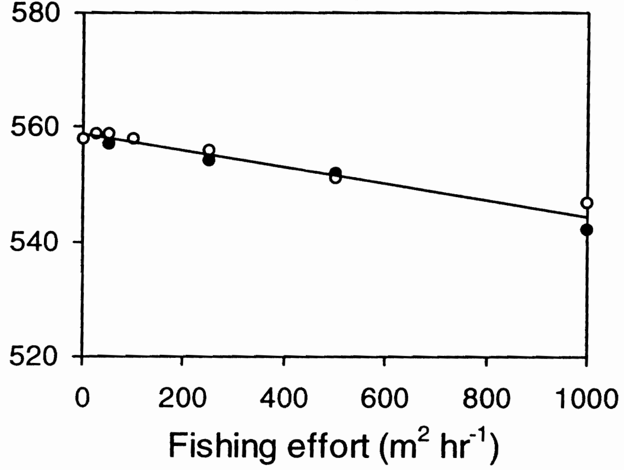
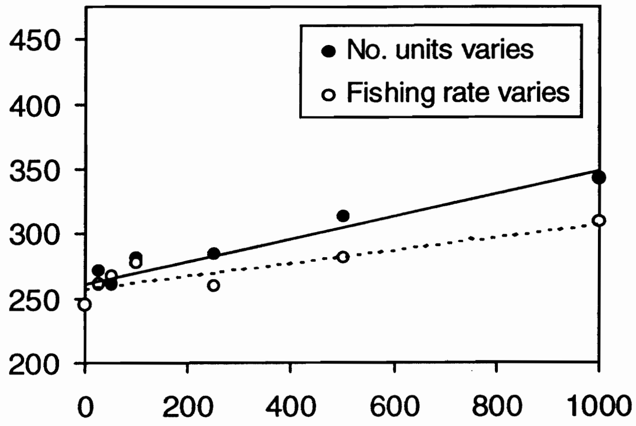
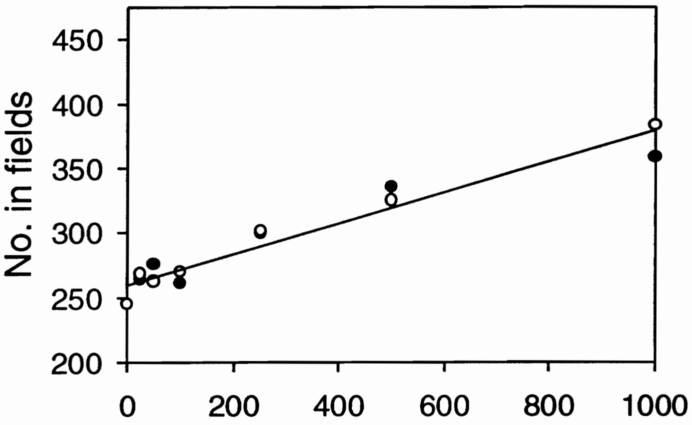


Figure 7.2.7 Mean body mass of oystercatchers using the stabbing feeding method surviving at the end of winter in relation to fishing method and effort. The body mass of hammering oystercatchers was unaffected by the level of fishing effort.

(a) Low tide thinning



(b) Low tide stripping



(c) High tide stripping

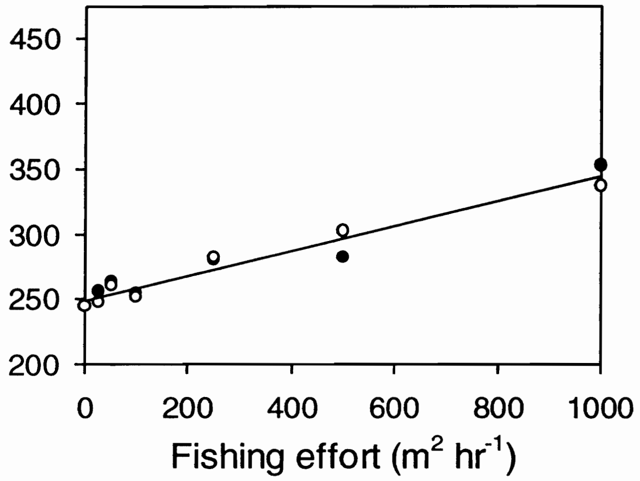
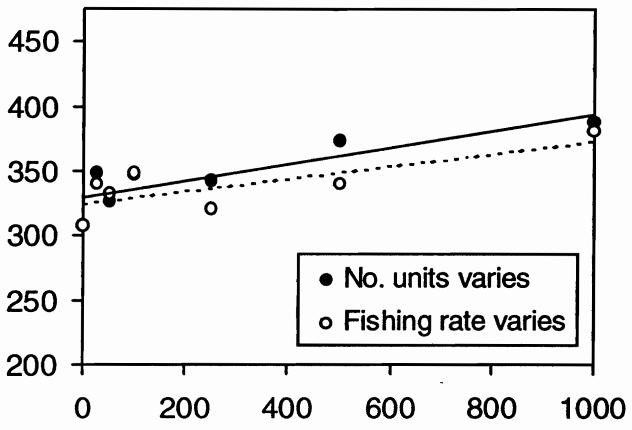
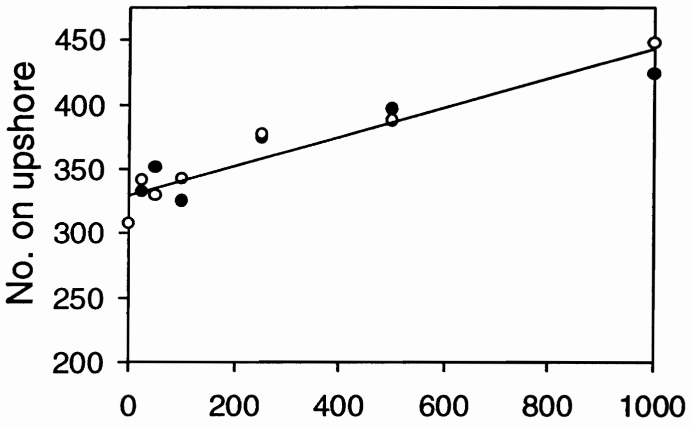


Figure 7.2.8 Mean number of birds feeding in fields at high tide between November and March in relation to fishing method and effort. Simulations were run with an oystercatcher population of 1,650 individuals.

(a) Low tide thinning



(b) Low tide stripping



(c) High tide stripping

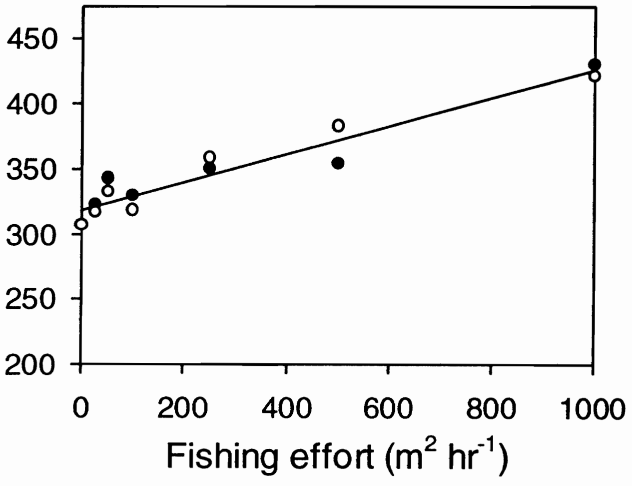


Figure 7.2.9 Mean number of birds feeding on upshore areas on advancing and receding tides between November and March in relation to fishing method and effort.

7.2.6 Detecting the impact of shellfishing in the field

The simulations clearly showed changes in mortality, body mass and use of supplementary feeding areas due to different levels of fishing effort. Each of these measures could therefore be monitored in the real system in order to detect the influence of current levels of fishing or any changes in these levels. The relative merits of each measure depend on the relative ease with which it can be measured accurately and the sensitivity of the measure to changes in the stress of birds.

In terms of ease of measurement, counting the number of birds using supplementary feeding areas is most straightforward. Each of the other factors can only be estimated through more intensive study. Measuring body mass involves capturing and weighing birds, and estimates of survival are most reliably obtained from the return rate of individually marked birds (Goss-Custard *et al.* 1982).

The sensitivity of each factor to changes in fishing effort also vary markedly (Figure 7.2.10). The number of birds using supplementary areas (both fields and upshore areas) is clearly much more sensitive to changes in fishing effort than are changes in mortality or body mass. At the highest fishing effort, these parameters increase by 50% of their values in the absence of fishing, in comparison to only 5% increases in survival and mass. In view of the relative simplicity of counting the numbers of birds using supplementary feeding areas, and the high sensitivity of these numbers to changes in fishing effort, counting the numbers of birds using these areas (upshore and/or fields) is most useful for monitoring the stress of the oystercatcher population.

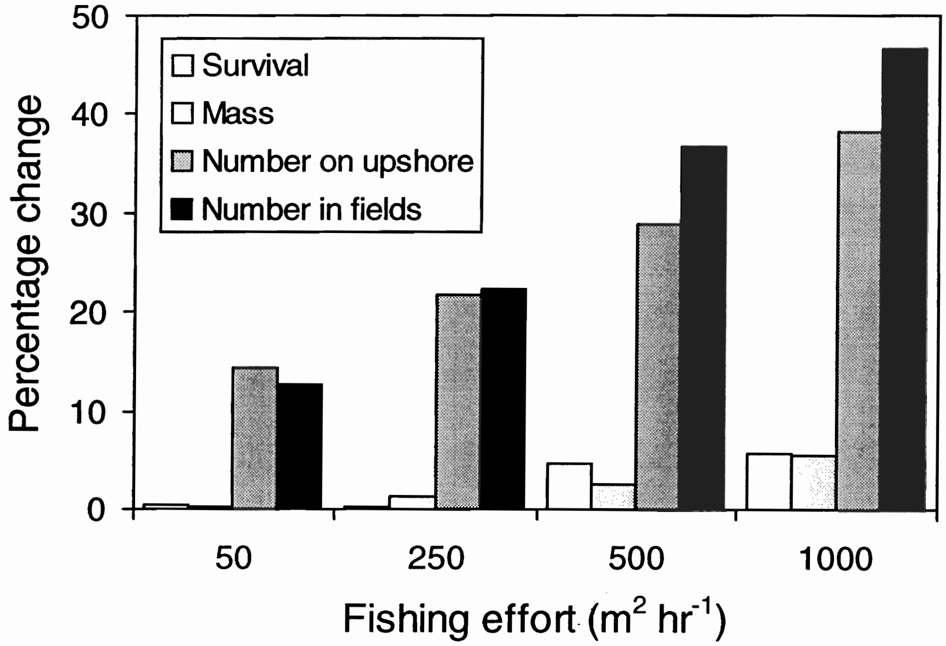


Figure 7.2.10 Percentage change in different measures of oystercatcher behaviour, body condition and survival in relation to increased fishing effort (varied by increasing the number of fishing units using low tide stripping; fishing rate = 5m^2 hr^{-1}).

7.2.7 Summary and conclusions

The simulations showed that increased fishing effort reduces oystercatcher survival, decreases the average mass of surviving individuals and increases the number relying on supplementary feeding areas in order to maintain their body mass. The impact of fishing differed between the different fishing methods. Low tide stripping has the greatest impact, followed by high tide stripping and lastly low tide thinning. Low tide stripping has the greatest impact on survival as it causes disturbance to the birds and permanent reduction in mussel bed areas.

Oystercatchers are more vulnerable to the effects of shellfishing during periods of cold weather and in the absence of fields in which they can feed at high tide. Empirical observations of high oystercatcher mortality during periods of severe weather (e.g. Goss-Custard *et al.* 1996) also highlight their vulnerability to such conditions.

Although within year effects of shellfishing on oystercatcher survival were sometimes small, their influence could be magnified if fishing persisted over a number of years. Firstly, although a large reduction in mussel abundance caused by low tide stripping had a relatively low impact on oystercatcher survival within a single year, continued fishing over a number of years caused extremely high mortality because mussel populations were unable to recover between years. Secondly, apparently small changes in survival caused large changes in the long-term population size because oystercatchers have a relatively low reproductive rate. It is likely that this prediction will hold for any other shorebird with similar characteristics.

Over the range of fishing efforts simulated, the number of birds using upshore and high tide supplementary feeding areas was the most sensitive to changes in fishing effort. These parameters are relatively simple to estimate, and so regular counts on an estuary could provide a useful means of monitoring the impact of changes in shellfishing intensity on shorebirds.

7.3 OYSTERCATCHERS AND COCKLES

R A Stillman & A D West

7.3.1 Overview of simulations

The cockle fishing simulations were based on the Burry Inlet version of the shorebird-shellfish model (see section 6.2 for full details and tests of this version of the model). Cockle fishing on the Burry Inlet currently occurs by hand, at low tide, throughout the spring-neap cycle during the hours of daylight. This fishing method was therefore included in the simulations. Two alternative methods of fishing for cockles, which although not currently employed on the Burry Inlet are used in the Wadden Sea, are Wonderklauw and suction dredging. Both of these methods occur during the hours of daylight throughout the spring-neap cycle. Suction dredging occurs at high tide, and wonderklauw occurs on the advancing and receding tides when cockle beds are covered by shallow water. These Dutch fishing methods were also included in the simulations. Full details of each fishing method is given in section 5.1 and the shellfishing model is described in section 5.3. Table 7.3.1 compares the parameters used to model each fishing method.

Table 7.3.1 Fishing methods modelled for the oystercatcher-cockle system.

Parameter	Hand gathering	Wonderklauw	Suction dredging
Reduces cockle density	Yes	Yes	Yes
Reduces cockle bed area	No	No	No
Minimum fishable cockle length	22mm	15mm	15mm
Kills cockles below fishable length	No	No	No
Fishing rate	Low but see section 5.1 for full details	$100m^2$ $3hours^{-1}$	High but see section 5.1 for full details
Daily quota	100kg fresh mass	3 hours fishing	4 hours fishing on 4 days each week
Minimum density of fishable cockles	$0m^{-2}$	$500m^{-2}$	$50m^{-2}$
Disturbs birds	Yes	No	No

A number of comparisons can be made between the three fishing methods.

- Fishing rate: Hand gathering and Wonderklauw both remove cockles at a relatively low rate, whereas suction dredging, being highly mechanised, depletes cockle stocks at a very high rate.
- Daily quota: On the Burry Inlet, each fishermen is limited to a daily catch of 100kg of cockles. In The Netherlands, the cockle catch is limited by the time available for fishing. Wonderklauw occurs for a maximum of 3 hours during each tide. Suction dredging occurs for 4 hours on 4 days each week.
- Minimum cockle density: Both suction dredging and hand gathering are profitable at low cockle densities, whereas Wonderklauw is only profitable at very high densities.
- Disturbance: Wonderklauw and suction dredging occur while cockle beds are submerged, and hence do not cause disturbance to foraging shorebirds. Hand gathering occurs at low tide, and when it also occurs in areas used by shorebirds for feeding, does cause disturbance.

7.3.2 Hand gathering

The test simulations of the oystercatcher-cockle model (section 6.1) suggested that the current level of fishing effort on the Burry Inlet (50 fishing licences) did not reduce oystercatcher overwinter survival. In these simulations, birds only needed to feed for a short period each day even in late winter when cockle stocks and flesh content were at a minimum and the birds energy requirements were at a maximum. No birds needed to feed in fields surrounding the estuary. At the present on the Burry Inlet, both the number of fishing licences and the daily quota are lower than they have been in the past. Therefore, the initial shellfishing simulations were designed to show how increases in the number of fishing licences (i.e. the number of fishing units exploiting the estuary) and the daily quota influenced oystercatchers. Additionally, the simulations investigated the effect of reducing the minimum fishable cockle size from 22mm to 15mm. All simulations were run with the seasonal temperature changes used in the Exe estuary model.

Increases in both the number of fishing units and the daily quota increased the total number of cockles collected during simulations. As a result, the percentage survival of fishable cockles was decreased (Figure 7.3.1). Indeed, the highest levels of fishing effort removed all fishable cockles from the estuary (zero values of overwinter survival).

Cockle-feeding oystercatchers select larger cockles (section 3.3), and so the effect of increased fishing effort was to reduce the abundance of their preferred food. However, if fishing was restricted to cockles larger than 22mm (as occurs in reality), the effect of increased fishing effort was minimal (Figure 7.3.1). Even when the number of fishing units was increased to 500 (10 times its current value) and the daily quota was increased to 500kg, no birds died. The only effect of this level of fishing was to cause a very small percentage (less than 1%) of birds to use the fields for supplementary feeding at high tide. Fishing had such a minor effect because birds were able to survive by feeding on cockles less than 22mm in length, and these size classes were not exploited by fishermen.

Although oystercatchers were not affected by the exploitation of 22mm+ cockles within a single winter, they could potentially be affected in the long term if successive fishing over a number of years reduced the cockle population. To test this possibility, simulations were run over a 15 year period assuming that the highest level of fishing effort (500 fishing units removing 500kg of cockles greater than 22mm per day) occurred in all years. During each winter all cockles greater than 22mm were completely removed by fishing. Despite the continued exploitation, a high level of recruitment was maintained and the growth of cockles into the size range consumed by oystercatchers ensured that no birds died. This result occurred because the stock-recruitment curve used in the model (see section 4.3) assumed that spat settlement was greater in areas of low adult cockle density over the range of cockle densities generated in the simulations. The reduced density of adult cockles caused by intensive fishing did not, therefore, reduce recruitment. This situation contrasts with that in estuarine mussels, where recruitment is higher in areas of high adult density (section 4.2).

The effect of increased fishing effort was much more severe when cockles as small as 15mm were exploited (Figure 7.3.1). At low levels of fishing effort (less than 100 units removing a daily quota of 500kg, or any number of units removing a quota of 100kg) no birds died and none needed to feed in the fields, as was found for the exploitation of 22mm+ cockles. However, as fishing effort increased the situation changed dramatically. When fishing effort was high enough to remove virtually all cockles greater than 15mm in length, all birds needed to use the fields for supplementary feeding. This supplementary feeding was insufficient to maintain their body mass and so all died. The transition from all birds surviving winter to all birds dying occurred over a relatively narrow range of fishing effort. No birds died when 100 fishing units removed a daily quota of 500kg, but all died when 200 units were present. Fishing had such a large effect in these simulations because birds were not able to maintain their body mass by feeding on cockles less than 15mm in length.

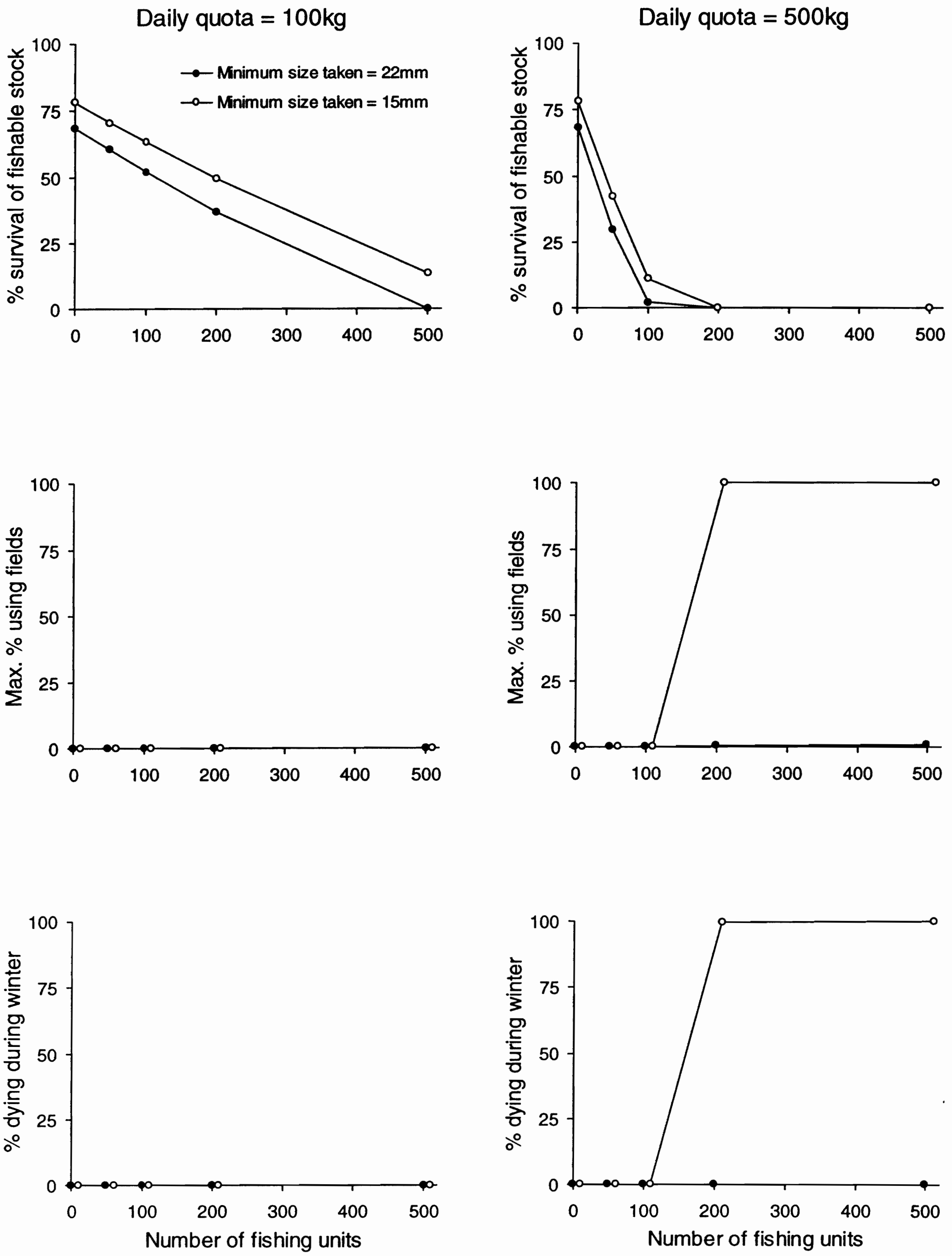


Figure 7.3.1 The simulated effect of changes in the intensity of hand gathering in the Burry Inlet on its cockle and oystercatcher populations. A daily quota of 100kg of cockles per fishing unit is used in the left hand figures and a daily quota of 500kg used in the right hand figures. The solid circles show the effects of fishing when cockles larger than 22mm are fished, and the open circles the effects when cockles larger than 15mm are fished. All simulations used an oystercatcher population of 10,000 individuals and ran over one winter period.

7.3.3 Wonderklauw and suction dredging

The previous simulations of the Burry Inlet showed that hand gathering of cockles over 22mm in length, as is currently practised, did not cause any oystercatcher mortality. A further set of simulations were run in order to compare the effect of the two Dutch fishing methods, Wonderklauw and suction dredging, on the cockle and oystercatcher populations (see Table 7.3.1 for the parameter values used to model these fishing methods). Figure 7.3.2 shows that these fishing methods contrast markedly in their impact on both the cockle and oystercatcher population.

Wonderklauw fishing had a relatively minor impact on the cockle population, and increases in effort above 150 units did not cause a subsequent reduction in cockle survival. This result occurred because Wonderklauw fishing is only profitable at very high cockle densities (over 500 m^{-2}). Once cockle beds had been reduced to this level in the model, no further fishing occurred. The oystercatcher population could be sustained by this density of cockles, and so not even the highest levels of Wonderklauw fishing caused any oystercatcher mortality. The effect of the minimum fishable cockle density on oystercatcher survival was tested by running a set of simulations which assumed that fishing could continue until cockle density reached 50 m^{-2}. Such a situation could only arise in reality if cockle fishing was very systematic. In these simulations, Wonderklauw fishing depleted cockle stocks to a greater extent and lead to high oystercatcher mortality (Figure 7.3.3).

In contrast to Wonderklauw fishing, suction dredging had a major impact on the cockle population. The presence of just a few suction dredges throughout winter caused a substantial reduction of the cockle population. Three or more suction dredges removed virtually all cockles over 15mm in length. Given the large depletion of cockle stocks, it is not surprising that when more than three suction dredges were present, all oystercatchers died in the simulations.

The different effects on oystercatchers of hand gathering, Wonderklauw and suction dredging were due to differences in the minimum size and density of cockles fished. Suction dredging had the largest effect because it harvested cockles as small as 15mm in length and continued until cockles were at a low density ($<50m^{-2}$). Once the density of cockles longer than 15mm had been reduced, oystercatchers could not survive by feeding on smaller cockles and in the fields. Hand gathering had little effect because cockles in the 15-22mm size range were not exploited. Oystercatchers were able to survive by feeding on this size range, even if all larger cockles were removed by fishing. Wonderklauw had no effect on oystercatchers because this method only exploited very high cockle densities. Cockle densities were never depleted to such an extent that oystercatchers starved.

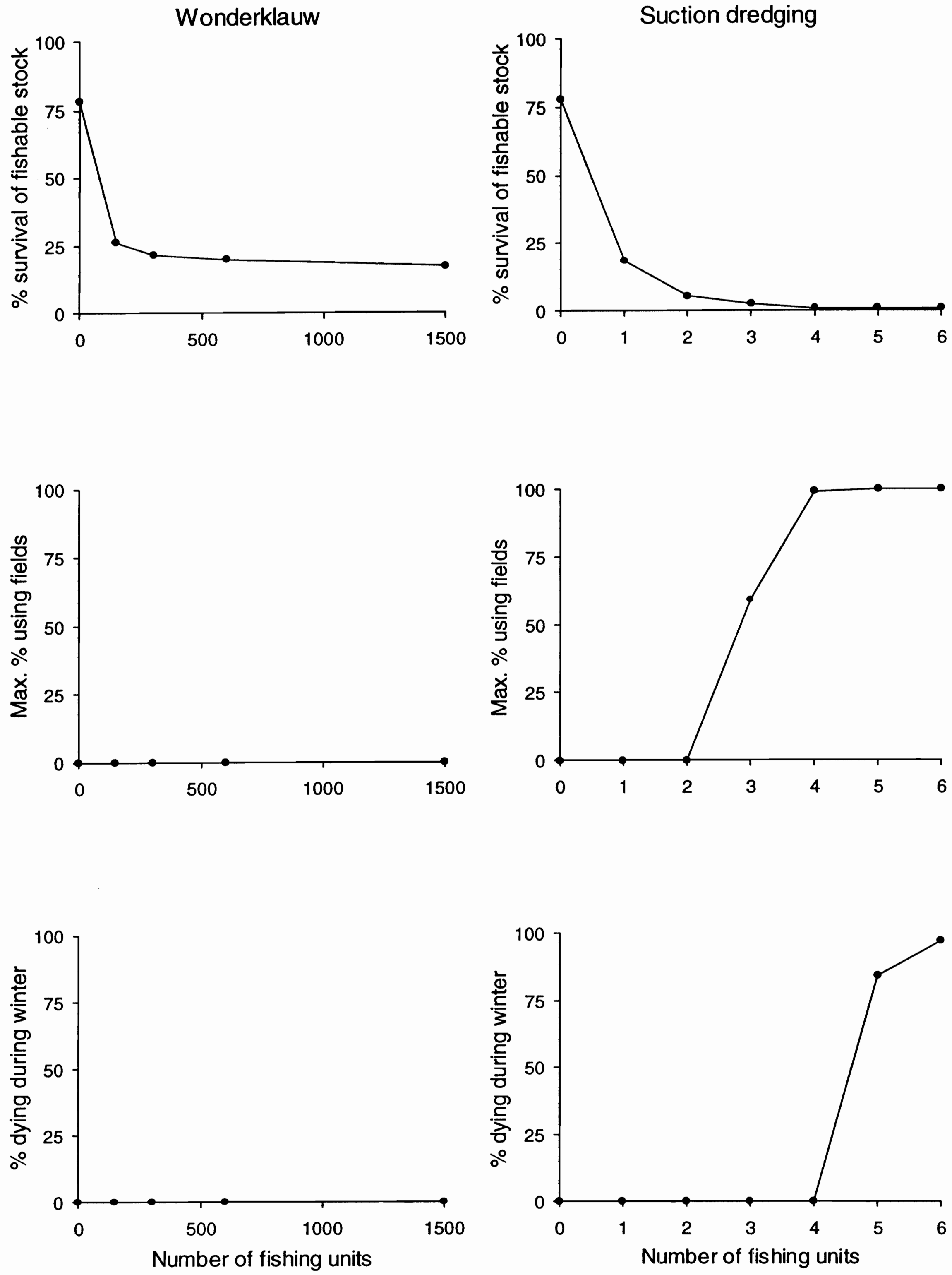


Figure 7.3.2 The simulated effect of changes in the level of Wonderklauw fishing (left hand figures) and suction dredging (right hand figures) in the Burry Inlet on its cockle and oystercatcher populations. All simulations assumed an oystercatcher population of 13,000 individuals and ran over one winter period.

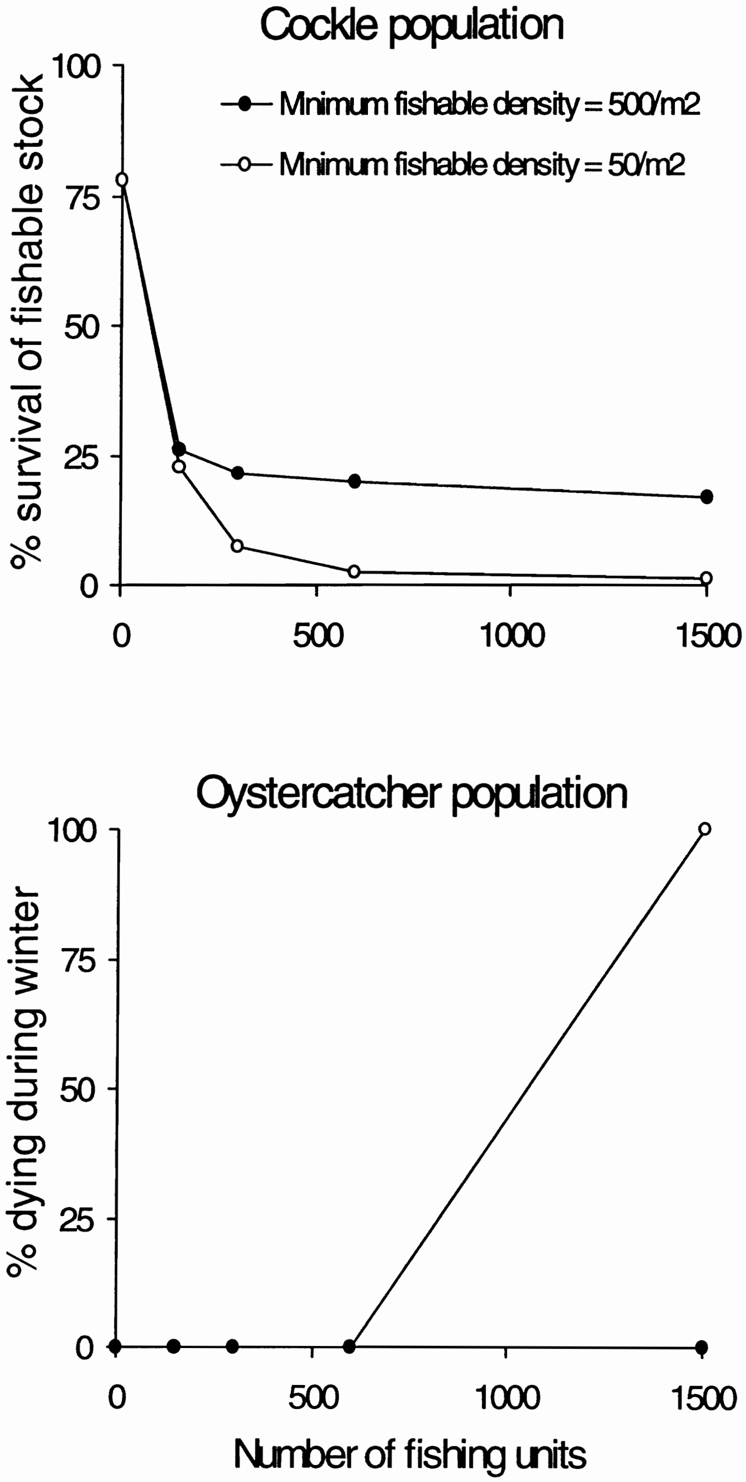


Figure 7.3.3 The effect of the minimum density of cockles exploited by Wonderklauw fishing on the survival of cockles and oystercatchers. All simulations ran over one winter period.

7.3.4 Low cockle abundance and cold weather

The previous sets of simulations assumed relatively mild weather conditions and relatively high cockle abundance. These values applied to the Burry Inlet in recent years. Although estuaries in the south-west of Britain, such as the Burry Inlet, typically have mild climates, those further east and north usually experience much lower winter temperatures. In recent years, the Burry Inlet cockle population has been at a high level, but has been at much lower levels in the past. A range of simulations were performed, therefore, to show the effects of fishing in situations where winter temperatures and cockle abundance are lower. "Cold weather" simulations were run by reducing the daily temperature 5°c below that in standard simulations. Temperature in these simulations decreased to approximately 0°c in January. "Low biomass" simulations were run by assuming that the density of all cockle size classes was half of that in the standard conditions. No other parameters in these simulations were changed from their default values. Although the simulations were largely based on the Burry Inlet, the cold weather simulations may be considered to represent an estuary on the east coast of Britain or the Wadden Sea, and the low biomass simulations to represent the Burry Inlet in years of low cockle abundance or estuaries that do not support such dense cockle populations.

The effects of changes in climate and cockle abundance were the same for all fishing methods. Therefore, results are simply presented for one method, suction dredging. Figure 7.3.4 shows the effect of suction dredging on the oystercatcher population for the four possible combinations of cockle abundance and climate. In the absence of fishing, no birds died with any combination of these parameters, and only a small percentage used the fields. Any mortality or use of the fields in simulations that included fishing was, therefore, due to fishing itself rather than due to the climate or initial cockle abundance. Both decreased winter temperature and cockle abundance increased the impact of a fixed level of fishing effort. For example, in the standard simulations (high biomass and mild climate), the presence of three suction dredges caused just over 50% of the birds to use fields. This supplementary feeding was sufficient to allow the birds to meet their energy requirements and so none died during the course of winter. When cockle biomass was halved (low biomass and mild climate), an equivalent fishing effort caused all birds to use the fields and 40% of birds died. Reduced winter temperature (high biomass and cold climate) increased the birds' energy requirements and lowered their feeding efficiency in the fields. This also caused all birds to use the fields, but also killed nearly all birds. Not surprisingly, the combination of both cold weather and low food abundance (low biomass and cold climate) was even more severe; all birds were killed by three suction dredges. In these sets of simulations, the precise magnitude of the changes made to winter temperature and cockle abundance meant that decreased temperature had a greater effect than decreased biomass. However, this is purely a consequence of the relative magnitude of the changes made to the two parameters; a greater reduction in cockle abundance, and a lesser reduction in temperature could have reversed this result. The general result of the simulations is that the effect of fishing will be magnified in regions with a cold climate, and in years or places in which cockles are rare.

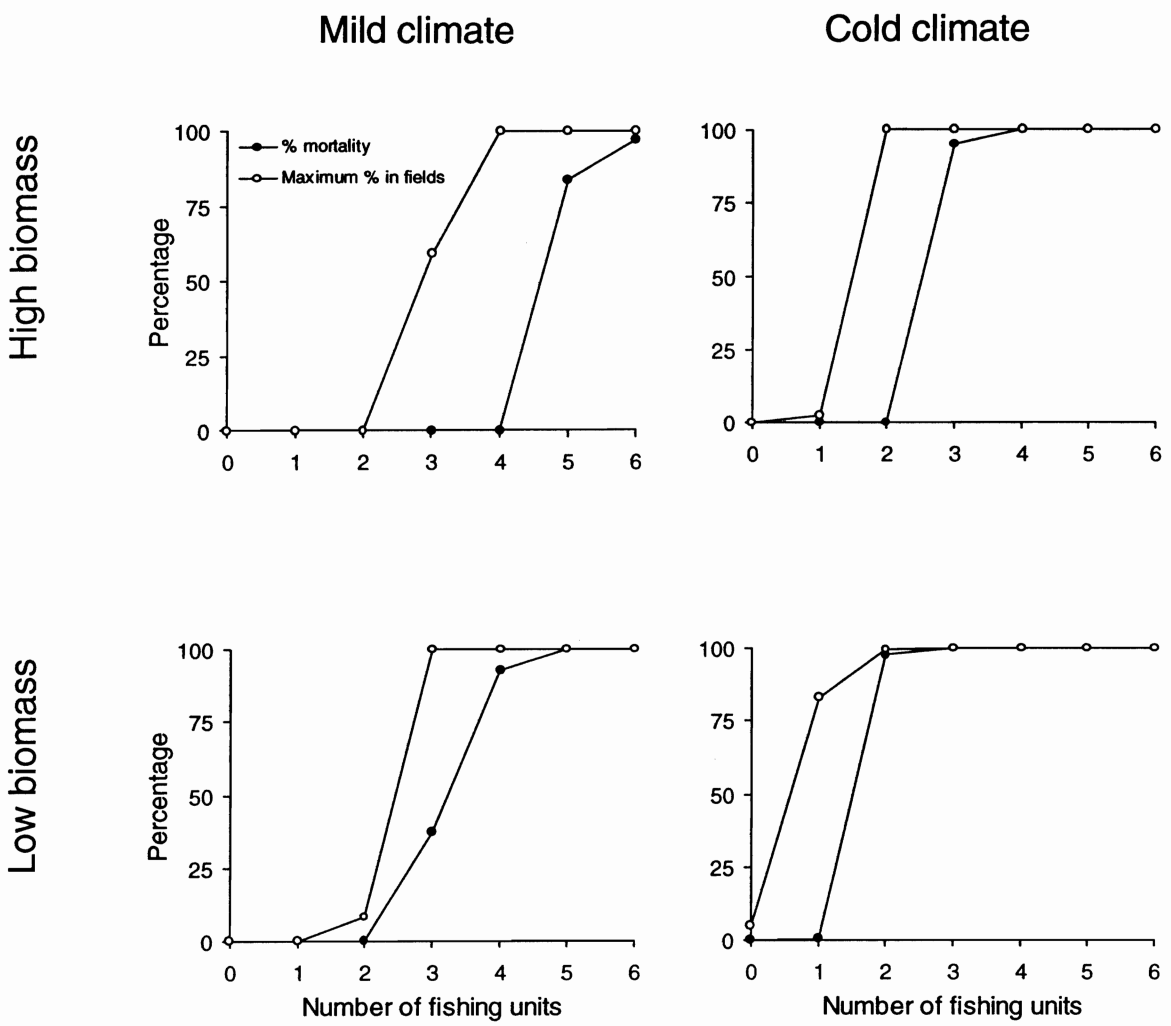


Figure 7.3.4 The effects of winter temperature and cockle abundance on the vulnerability of oystercatchers to suction dredging. "Mild climate" and "high biomass" simulations assumed the seasonal temperature changes recorded on the Exe estuary and the cockle densities measured on the Burry Inlet during the study period. In "low biomass" simulations, the abundance of cockles of all size classes on all beds was halved. In "cold climate" simulations, the environmental temperature was decreased by 5°c throughout winter. All simulations ran over one winter period.

7.3.5 Vulnerability of the oystercatcher population

The oystercatcher-cockle model predicts that the Burry Inlet oystercatcher population will show a non-linear response to changes in fishing effort (see previous figures and Figure 7.3.5 for a further example). Typically, for each population parameter (e.g. mortality rate or the number of birds feeding in fields at high tide), a threshold fishing effort exists, above and below which the parameter does not respond to changes in fishing effort (Figure 7.3.5). In the region of the threshold, however, very small changes in fishing effort cause a large change in the population parameter. For example, a 20% increase in the level of fishing using the Wonderklauw from 500 to 600 units, caused a 900% increase in the percentage of birds using fields for supplementary feeding (Figure 7.3.5). The percentage overwinter mortality showed a similar rate of change between a fishing effort of 750 and 1000 units.

The model predicts a "step-function" type of response in the oystercatcher population parameters because the individuals comprising the population each have very similar characteristics. Individuals only differ with respect to the efficiencies with which they consume cockles and supplementary prey in fields, and each of these parameters does not vary widely between individuals (the standard deviation of either feeding efficiency is 10% of its mean). Therefore, as fishing effort is increased and the feeding conditions deteriorate, all individuals have a similar ability to cope. As all individuals have a similar response to a certain level of fishing effort, changes in population level parameters to changes in fishing effort are sudden.

The oystercatcher-mussel model predicted more gradual responses in population parameters. This difference occurred because individuals in the oystercatcher-mussel model differ more widely than those in the oystercatcher-cockle model. They differed not only with respect to their feeding efficiencies on their main prey (i.e. mussels) and supplementary prey in fields, but also in their dominance, feeding efficiency in upshore areas, age-related susceptibility to interference and feeding method. Different individuals, therefore, showed widely different responses to a particular set of conditions, and so population level parameters changed more gradually.

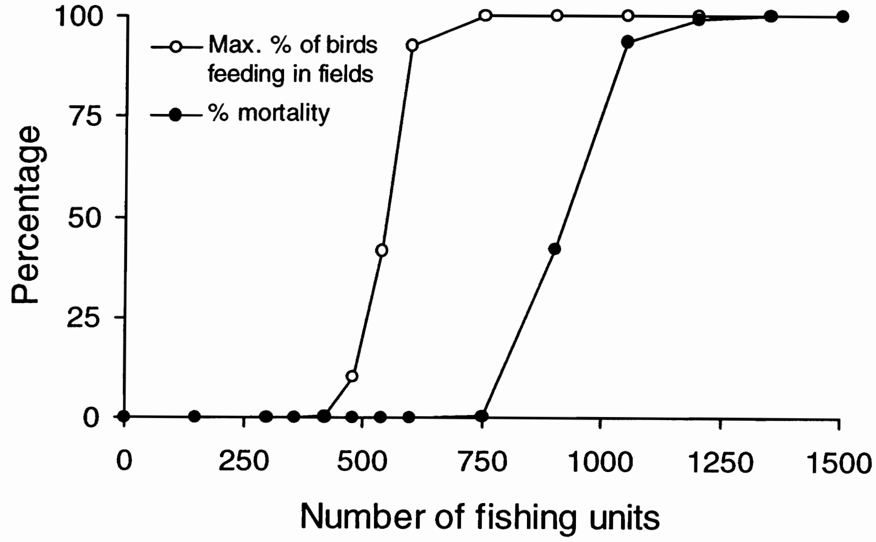


Figure 7.3.5 The effect of increased fishing effort on the maximum percentage of oystercatchers needing to use fields for supplementary feeding and overwinter percentage mortality. Simulations were based on the Wonderklauw fishing method and assumed that densities as low as 50 fishable cockles m^{-2} could be exploited (fishable cockles were longer than 15mm in length). The simulations ran over one winter period.

The model predicts that the Burry Inlet oystercatcher population will be very vulnerable to increases in fishing effort in the region of the threshold fishing effort. This vulnerability is not restricted to increases in fishing effort, but applies to any factor that reduces the birds' rate of food consumption or increases their energy requirements. Such factors include decreased cockle abundance, unusually cold weather, habitat loss and an increased oystercatcher population. For example, cold weather will increase birds' energy demands whilst freezing fields and so eliminating the possibility of supplementary feeding at high tide. Figure 7.3.6 shows the effect of a two week spell at 0°c in mid January on overwinter mortality across a range of fishing efforts. At very low levels of fishing effort, no birds died either in simulations that assumed standard weather or in those that assumed a cold spell (Figure 7.3.6a). In these simulations, the cold spell increased birds' energy demands but, as fishing had not depleted the cockle stocks greatly, they were able to compensate by feeding on cockles for longer. Very high levels of fishing effort depleted cockle stocks to such an extent that all birds died regardless of the type of weather assumed (Figure 7.3.6a). However, in the region of the threshold the cold weather spell increased mortality dramatically. Over 40% of the oystercatcher population, which did not die during standard weather, were killed by the two week cold spell (Figure 7.3.6b). This occurred because in the region of the threshold many individuals were only just able to survive winter. The small deterioration in conditions caused by the cold spell was sufficient to kill these individuals.

The simulations predict that the current level of fishing on the Burry Inlet has no adverse effects on oystercatcher survival, and that moderate increases in effort would likewise have little effect. However, continued increases in fishing effort could change this situation dramatically. These results suggest that the oystercatcher population should be accurately monitored, particularly if fishing effort is increased but also during any periods of low cockle abundance, high oystercatcher abundance or cold weather. As was the case for oystercatchers in the Exe estuary (section 7.1.6), counting the number of birds using fields for supplementary feeding at high tide appears to be a useful parameter to monitor. The number of birds using fields is relatively simple to measure, and responds strongly to increased fishing effort before the mortality rate starts to increase (Figure 7.3.5).

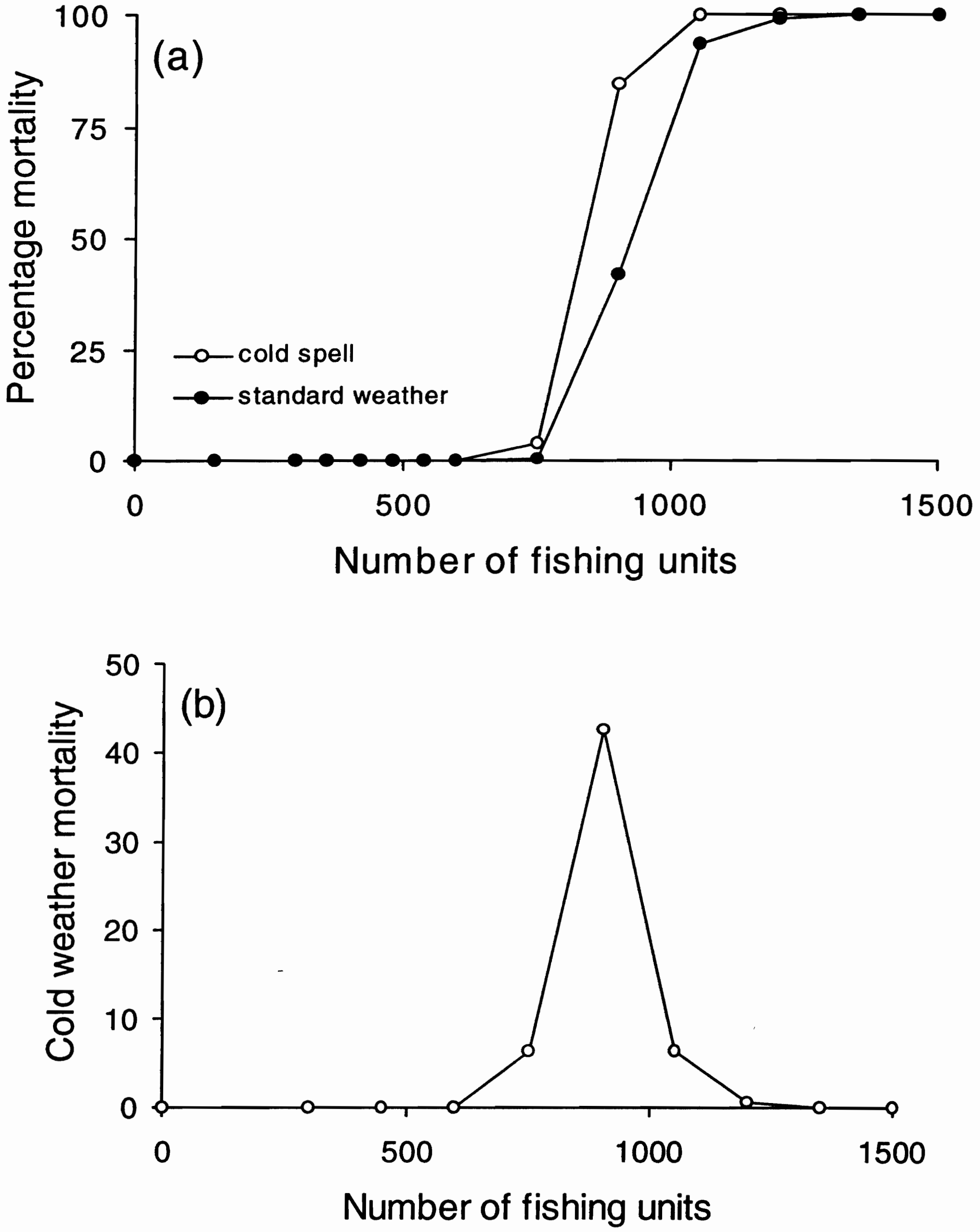


Figure 7.3.6 The simulated effect of fishing effort and cold weather on oystercatcher mortality in the Burry Inlet: (a) percentage overwinter mortality assuming either standard weather throughout winter or standard weather with a two week spell of cold weather (0°c) in mid January; (b) percentage of the mortality that occurred during the cold weather period. Simulations were based on the Wonderklauw fishing method and assumed that densities as low as 50 fishable cockles m^{-2} could be exploited (fishable cockles were longer than 15mm in length). In standard simulations, the environmental temperature remains at approximately 5°c during mid January). The simulations ran over one winter period.

7.3.6 Summary and conclusions

The cockle fishing simulations showed that, of the three fishing methods considered, suction dredging could cause a far greater reduction in both cockle and oystercatcher survival than could either the hand gathering or Wonderklauw methods. Perhaps the most obvious difference between the fishing methods is that suction dredging depletes cockles at a far higher rate per fishing unit than either of the other methods. However, it is not this difference that caused the contrasting effects of the different methods. Even though depletion rates *per unit* were higher with suction dredging, equivalent overall rates (i.e. rates summed over all fishing units) could be achieved by the other methods if many fishing units operated simultaneously. The key differences between the methods were the minimum size of cockle fished and the minimum cockle density below which fishing was not profitable. The lower that either of these values is, the higher the proportion of the cockle stock that may be exploited. If a fishing method can exploit a higher proportion of the cockle stock, it has a higher potential to reduce the cockle population and therefore to reduce oystercatcher survival. Suction dredging exploited cockles as small as 15mm and densities as low as 50 cockles m^{-2}. The other methods did not exploit such a large proportion of the cockle stock, hand gathering exploited larger cockles (>22mm) and Wonderklauw operated at higher cockle densities (>500 m^{-2}), and so did not have such large impacts on either the cockle or oystercatcher population.

The initial shellfishing simulations were based on the present situation on the Burry Inlet and so assumed a relatively mild climate and high cockle abundance. However, lower winter temperatures are experienced in eastern Britain and the Wadden Sea, and periods of lower cockle abundance have occurred previously on the Burry Inlet and not all estuaries support such dense cockle populations. Further simulations predicted that oystercatchers were more vulnerable to the effects of fishing when the cockle biomass was lower and when winters were colder.

In the oystercatcher-cockle model, oystercatcher population parameters (e.g. mortality rate) showed "step-function" type responses to increasing fishing effort. Each population parameter had a threshold fishing effort, around which its value changed very rapidly with changes in fishing effort. Away from the threshold, population parameter values were not related to changes in fishing effort. This form of response contrasts to that predicted by the oystercatcher-mussel model based on the Exe estuary, in which population parameters changed gradually and across the full range of fishing efforts simulated. This difference is due to the different degree of variation between the individuals in the two models. Individuals in the oystercatcher-mussel model differ in terms of their age, feeding method, feeding efficiencies on mussels, upshore prey and prey in fields, and dominance. Those in the oystercatcher-cockle model only differ in terms of their feeding efficiency on cockles and prey in fields.

The model predicted that increased stress of the oystercatcher population due to increased fishing effort caused large numbers of birds to use fields for supplementary feeding at high tide. This prediction was also made by the oystercatcher-mussel model. Therefore, monitoring the number of birds using fields around the Burry Inlet should provide a sensitive measure any changes in the stress of the oystercatcher population caused by changes in fishing effort.

7.4 KNOTS AND COCKLES

R A Stillman & A D West

7.4.1 Overview of simulations

The knot-cockle model was parameterized for the Burry Inlet (section 6.4). All aspects of the environment and cockle population in this model were therefore shared with the oystercatcher-cockle model. The shellfishing simulations of the oystercatcher-cockle model contrasted the effects on oystercatchers of hand gathering as currently practised in the Burry Inlet and two Dutch fishing methods, Wonderklauw and suction dredging. Suction dredging had the greatest impact on oystercatcher survival because it could exploit a higher proportion of the cockle stock. In contrast, the current form of hand gathering used on the Burry Inlet and Wonderklauw did not cause any oystercatcher mortality.

The interaction between knots and shellfishing differs from that between oystercatchers and shellfishing in one key respect: knots consume small cockles that are not exploited by fishing, whereas oystercatchers consume larger cockles that are within the size range fished. Therefore, in the absence of any disturbance caused by fishing and assuming cockle size classes below the fishable size are not killed by shellfishing, within a single winter shellfishing will not affect knots. Conversely, knots will not affect the density of fishable cockles within a single year. Knots and shellfishing can only interact over a number of years. Knots deplete the stocks of young cockles, which reduces the numbers growing on to be exploited by fishing in later years. The combined effect of knots and shellfishing will reduce cockle abundance which may in turn affect recruitment in subsequent years so changing the food supply available for knots.

The model was used to determine whether this difference between knots and oystercatchers changed the models predictions. The simulations were restricted to hand gathering and suction dredging as the oystercatcher-cockle model showed that both Wonderklauw and hand gathering had similar effects on oystercatchers. Full details of these fishing methods are given in chapter 5 and Table 7.3.1. As knots and shellfishing do not interact within a single winter, all simulations were run over a number of years.

7.4.2 Influence of knots on the cockle population

The long-term effects of knots of the cockle stock were investigated by running the knot-cockle model over a period of ten years. Two simulations were run; one assumed that no knot were present and the other assumed that 4,000 knots settled on the estuary in September each year. This size of knot population could not be supported during every year of simulations (see section 6.4). However, the simulations were only designed to predict the effect of a constant, high level of knot predation on cockles. In the first year of these simulations, the model was seeded with the cockle population measured on the Burry Inlet during the present contract. In subsequent years, the population structure was determined by the pattern of cockle mortality due to knot predation, shellfishing and other factors, and the density of new recruits (see section 4.6 for full details of these aspects of the model). In both simulations, shellfishing was conducted by hand gathering at the rate currently existing on the Burry Inlet (i.e. 50 licences). This fishing rate is relatively low and so will not have a large impact of the cockle population.

Yearly changes in the cockle population predicted at the beginning and end of winter are shown in Figure 7.4.1. Neither in the present or absence of the knot population did the cockle population become extinct or increase greatly in size. Overall, knots had little effect on the cockle population dynamics. The density of 7-15mm cockles was increased slightly at the start of each winter and decreased at the end. However, these changes were slight and had very little effect on the abundance of larger size classes.

The overall effect of knots on the cockle population can be understood in terms of the heavy depletion of first winter cockles caused by knot and the stock-recruitment curve used in the model (section 4.6). The heavy knot predation in the model decreased the density of cockles in their first winter and therefore the number surviving to become adults. The direct effect of knots was therefore to reduce the density of adult cockles. However, the density of recruits generated by the stock-recruitment curve is negatively related to the density of adults when adult density exceeds 150m^{-2} and the level of predation was never sufficient to cause the density of adults to fall below 150m^{-2}. Therefore, the secondary effect of knots was to increase the level of recruitment.

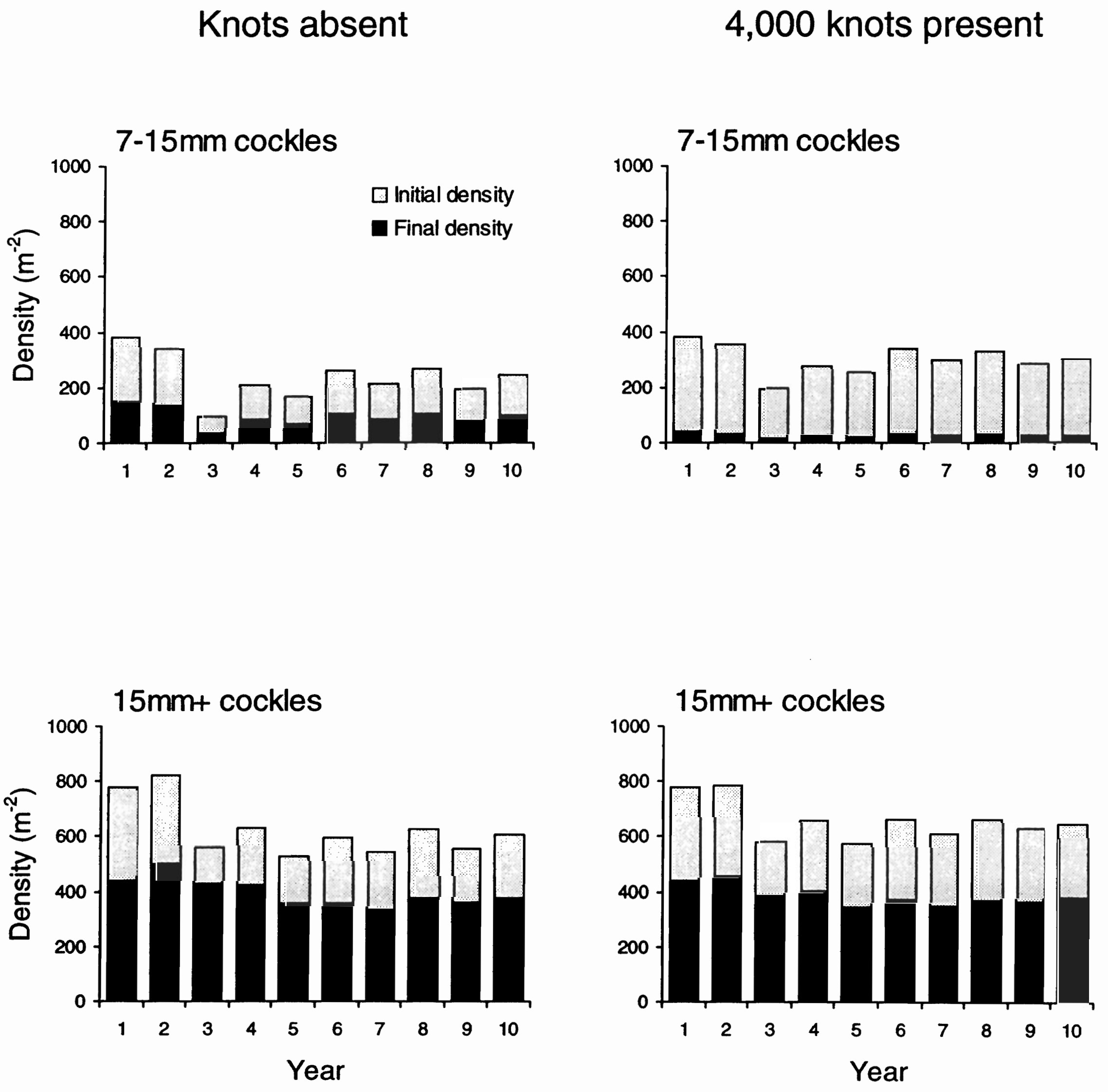


Figure 7.4.1 The predicted effect of knot predation on the abundance of 7-15mm cockles (i.e. the size range consumed by knots) and larger cockles in the Burry Inlet. At the start of each year 4,000 knot settled on the estuary and remained until they exhausted the food supply or until the end of winter. The initial cockle density is that in September and the final density is that in March.

7.4.3 Influence of fishing effort on the cockle and knot populations

The previous simulations incorporated hand gathering at the relatively low rate currently practised on the Burry Inlet. Fishing effort on this estuary has been much greater in the past and so a further set of simulations were run to find the effect of increased numbers of hand gatherers on the cockle and knot populations. Two sets of simulations were run; one assumed that 50 hand gatherers operated throughout winter as currently occurs in reality (low intensity simulation) and the other that 500 hand gatherers operated (high intensity simulation). Both simulations ran over a period of ten years and assumed that 4,000 knot settled on the estuary in September each year.

The immediate effect of increased fishing effort was to reduce the density of cockles over 22mm in length (i.e. the minimum fishable size) that survived to the end of winter (Figure 7.4.2). The secondary effect of increased fishing effort was to increase the level of recruitment, since the density of recruits generated by the model was negatively related to adult density. The combination of these two factors greatly increased the density of the 7-15mm cockle size class exploited by knots (Figure 7.4.3). As a result the cockle population was able to support the knot population in more years (Figure 7.4.3). Increased fishing effort therefore increased the capacity of the estuary to support knot.

In terms of the yield of cockles to the fishery, increased fishing effort had a detrimental effect as it eliminated the largest cockle size class (29mm+). This occurred because virtually all cockles were removed once they reached 22mm in length, and so none grew into the 29mm+ size class.

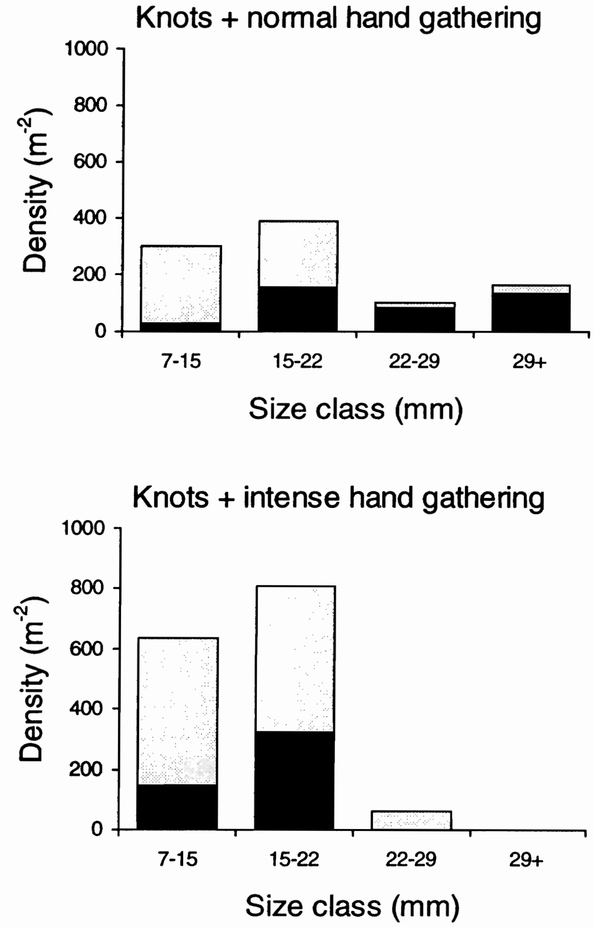


Figure 7.4.2 The effect of the intensity of hand gathering of the size distribution of cockles on the Burry Inlet in September (grey bars) and March (black bars). The results are for the 10th winter of simulations. Normal hand gathering is 50 fishing units and high intensity hand gathering is 500 units.

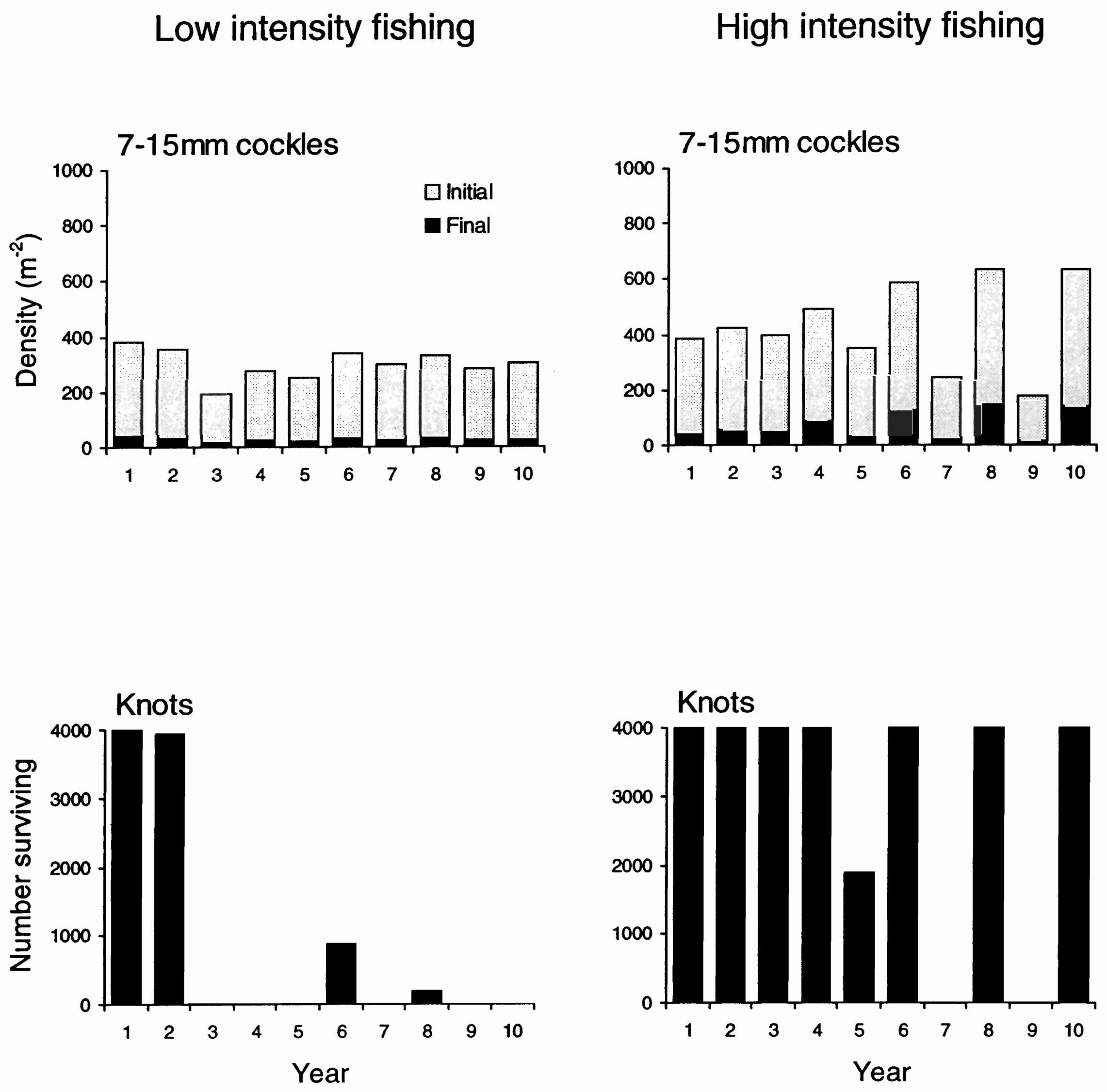


Figure 7.4.3 The predicted influence of the intensity of hand gathering on the Burry Inlet on cockle and knot populations. Low intensity refers to 50 fishing units and high intensity to 500 units. Initial refers to the situation in September and final to the situation in March.

7.4.4 Comparison of hand gathering and suction dredging

Suction dredging removes cockles at a higher rate than hand gathering and in the Netherlands exploits cockles as small as 15mm, whereas hand gathering in the Burry Inlet is restricted to cockles over 22mm in length. The effects of these differences on the cockle and knot populations were investigated by running a ten year simulation in which 4 suction dredges operated throughout winter. This number of dredges reduced the density of 15mm+ cockles to below 50m^{-2} within a single winter (section 7.3).

The effect of suction dredging on the cockle and knot populations was similar to that of intense levels of hand gathering, but more dramatic. Initially, suction dredging greatly reduced the density of cockles over 15mm in length (Figure 7.4.4). This reduction lead to high levels of recruitment, which were maintained over the ten year period of the simulation (Figure 7.4.4). As recruitment was constantly high, the knot population was supported in all years (Figure 7.4.4). The high mortality of 15-22mm cockles caused by suction dredging meant that virtually none survived to grow into larger size classes (Figure 7.4.5).

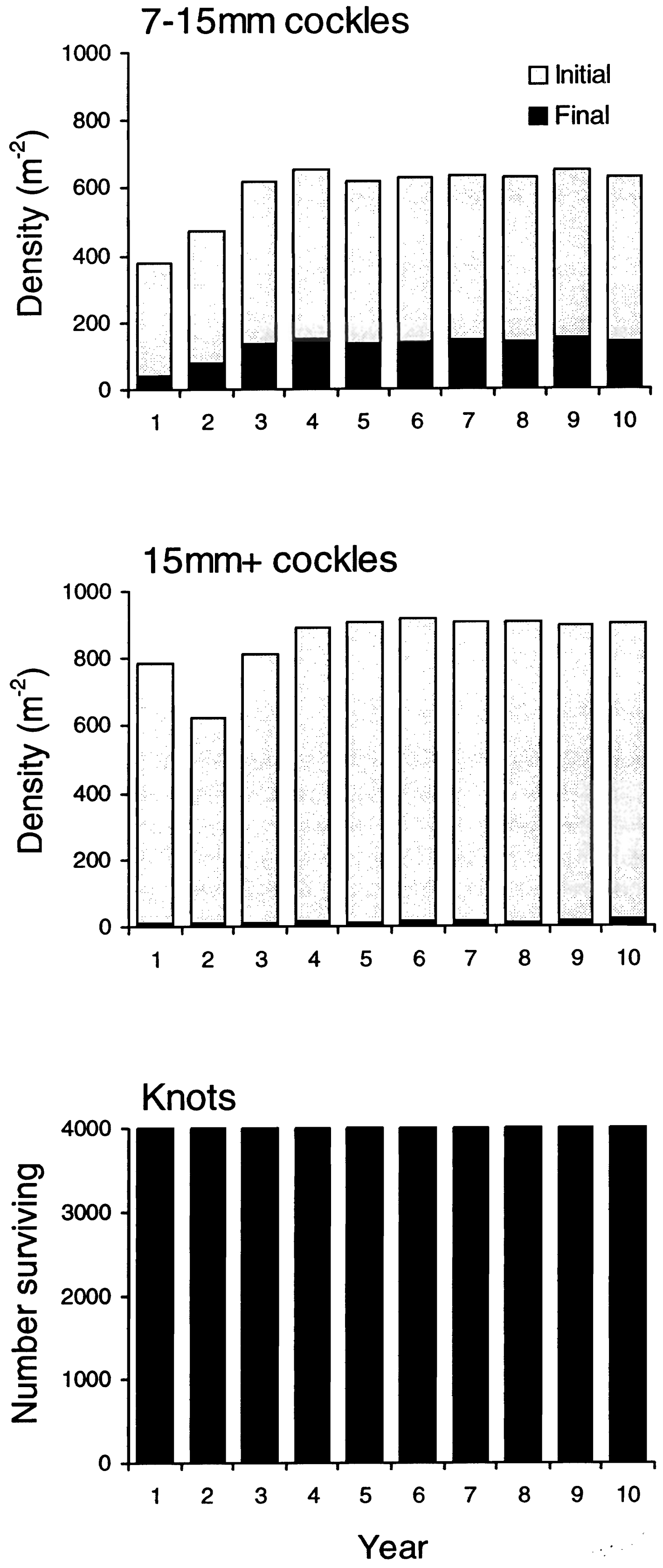


Figure 7.4.4 The predicted effect of suction dredging on the survival of cockles and knots in the Burry Inlet. During each year 4 suction dredges were in operation and 4,000 knot settled on the estuary in September. The initial densities of cockles are those in September and the final densities those in March.

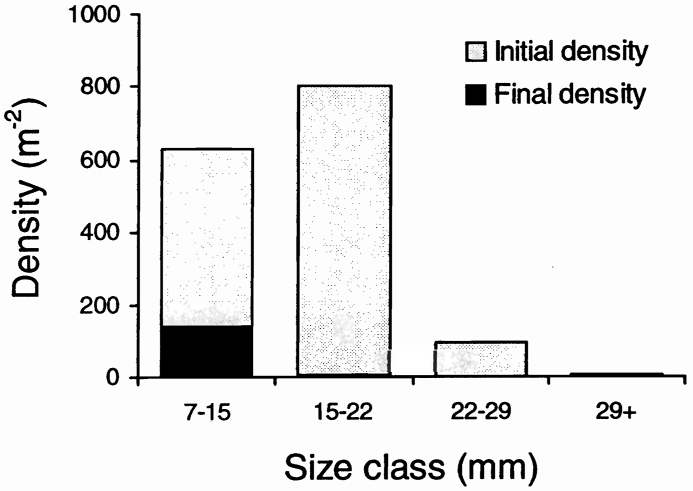


Figure 7.4.5 The size distribution of cockles in the Burry Inlet after ten years of intensive suction dredging (4 units) of cockles greater than 15mm in length.

7.4.5 Summary and conclusions

The simulations predicted that increased fishing effort on the Burry Inlet increased the number of knot that the estuary could support. This prediction opposes all those made for the interaction between oystercatchers and shellfishing. In both the oystercatcher-mussel and oystercatcher-cockle models, increased fishing effort either had no effect on mortality or increased mortality. This difference is due to two factors: (1) the relative size of prey consumed by knots and oystercatchers; and (2) the stock-recruitment curve used for cockles.

(1) Knots and shellfishermen exploit different size ranges of cockles and so within a year the reduced density of large cockles could not affect knots. In contrast, cockle and mussel feeding oystercatchers exploit size classes also exploited by fishermen. As a result, shellfish depletion due to fishing can adversely effect oystercatchers within a single year.

(2) Knots can only be affected by the reduced densities of large prey if this subsequently reduces the density of the 1st winter recruits which they exploit. The stock-recruitment curve used in the model predicted increased recruitment at lower adult cockle densities and so fishing had a positive effect on knots rather than a negative one. This result would not occur if recruitment was positively related to adult density or showed no relationship to adult density. In estuarine mussels, spat settlement is greater where adult densities are higher (section 4.2). In this system, increased depletion of large mussels by fishing can only have a negative effect on the level of recruitment, and hence any predator exploiting new recruits.

Although the model predicted a positive effect of fishing on knots it is important to note that this may not occur in reality. Firstly, the model assumed that fishing had no adverse effects on the small cockle size classes. This may not be the case if the act of fishing damages these size classes, removes them from the substrate or damages the structure of the substrate. None of these factors were included in the model although they may occur in reality (see section 5.1). Furthermore, the models predictions are dependent on the stock-recruitment curve used in the model which predicts a negative relationship between recruit density and adult density. Although this curve may apply to the Burry Inlet on which it was derived, in the Wadden Sea, intensive studies have not found any relationship between cockle spat and adult densities (section 4.5). The predictions of the model may, therefore, not be of general applicability.

Chapter 8 CONCLUSIONS

8.1 PREAMBLE

The need at the beginning of this project was to develop a predictive model which allowed us to explore the consequences of changes in fishing activities and bird numbers on commercial shellfish stocks and on the birds themselves.

Fishing affects the birds in two ways. Those methods of harvesting that require people to be present on the intertidal flats over the low water period, such as hand gathering, disturb birds by driving them away from areas that they would otherwise have used for feeding. The disturbance itself costs the birds lost time, because they temporarily stop feeding, and increases their energy requirements if they fly to another place. Disturbance may also increase any competition that occurs between foraging birds because they have been squeezed by disturbance into a smaller foraging space so that the density of the birds increases. Disturbance may thus both directly and indirectly reduce the intake rates of the birds and increase any difficult they may have in obtaining their energy requirements. The second way in which shellfishing affects the birds applies to all fishing techniques. In the winter in which the fishing takes place and in successive winters, fishing may reduce the abundance of the shellfish stocks to the point at which it makes it more difficult for the birds to obtain their energy requirements. Shellfishing may thus have both short-term and long-term effects on the oystercatchers and knots that also depend on shellfish stocks (Goss-Custard, McGrorty & Durell 1996).

The model developed in this report includes all of these effects on the birds. The model is empirical and based on many years of field data collection in several European countries. By being based on game theory, the model is also founded on a conceptual framework that has been very successfully applied in a number of areas of behavioural ecology. The key feature of such an approach in the present context is that the model incorporates the realistic responses of birds to the various impacts of shellfishing. For example, birds in the model move from an area that is occupied by shellfishers and attempt to feed in another part of the intertidal flats, with a success that depends on the food abundance and level of competition that they experience there. How well the displaced birds fare in the new area depends, therefore, on the responses of other birds to the disturbance as much as on their own responses. The models also allow individuals some measure of compensation for the impact of shellfishing upon their foraging. Thus the birds are able to extend their foraging by feeding upshore on poor quality shellfish stocks as the tide ebbs and flows and also to feed in fields over high tide. In this way, the model tracks the fortunes of individual birds and thus incorporates the vital biological reality of variation between animals in their responses to environmental change. After all, it is individual animals that respond to environmental change and not populations *per se*.

The model itself was developed in the first instance by expanding an existing ITE model on the interaction between oystercatchers and mussels on the Exe estuary in south-west England. The main tests of our whole approach were also carried out in this study system. The tests showed that model predictions were generally in line with the results of field observations. Of greatest importance in the present context was the success with which the model predicted the levels of oystercatcher winter mortality that have been recorded on the Exe. The effect of shellfishing on bird mortality is the fundamental issue that arises when its effect on shorebirds is discussed; to be of any practical use, the model had to be able to predict mortality and to predict it with some accuracy. Almost as important, the model predicted well the numbers of birds that compensated for failing to achieve an adequate rate of food intake on the estuary at low tide by feeding in the fields over the high water period. The model would be of little predictive value if it had been unable to allow birds to compensate in realistic ways for any ill-effects of shellfishing on their ability to feed on mussels and cockles. Furthermore, it would give little guidance as to what might be the first detectable signs in the field that birds were beginning to be disadvantaged by a change in fisheries policy. The model shows that monitoring the numbers of birds using the fields at high water is a sensitive method for detecting the first signs of difficulty.

The one disadvantage of the model is that it is a simulation model rather than an analytical model and is thus rather slow to run. But extensive sensitivity tests revealed that the key output - mortality - is sensitive to the values given to a number of parameter values. Were we to have reduced their numbers in an analytic model, the predictive power of the model for the most important output measure of the effect of shellfishery policy would have been substantially reduced. Nonetheless this contract has shown that, even with such a model, it is possible to measure parameter values for a new system (the Burry Inlet) after only two years of new field work.

8.2 MAIN PREDICTIONS OF THE MODEL

The range of shellfish policy options that has been explored in this contract has been narrow compared with the range that is possible in principle. For example, the model is capable of exploring the effects on shorebirds of such options as (i) varying the particular shellfishing technique used and the total fishing effort expended; (ii) fishing only at certain times of day, or on particular days of the week, or at certain stages in the neap-spring cycle or times of year; (iii) fishing on some beds but not others; and (iv) regulating the total catch taken in different ways. The report details the predictions of a limited set of example fishing scenarios to illustrate the uses to which the model could be put. But it has also made some predictions that have important implications for shellfishery management and that are likely to apply across a wide range of estuaries and fisheries. Some of the predictions had been realised before this contract was completed but the important point is that the model enables the quantitative effect on shorebird mortality of a wide range of different shellfish policy options to be estimated.

Some key predictions are as follows:

- It is possible to exploit shellfish stocks without increasing the winter mortality of shorebirds. A number of conditions must apply if this is to be true. These conditions include a high abundance of shellfish and the presence of alternative food sources to which the shorebirds can turn when shellfish become scarce. Cockle fishing in the Burry Inlet, for example, at its present intensity and with the current levels of both shellfish and oystercatcher abundance would seem most unlikely to affect the survival chances of the birds. In contrast, increased fishing for mussels on the Exe is predicted to increase oystercatcher mortality by an amount which depends on the fishing method and effort deployed and on the severity of the winter.
- The effects of a given intensity of shellfishing depend crucially on local conditions of the climate and the general abundance of food. Shorebirds are most vulnerable during severe winter weather when their energy demands are elevated and, in the case of oystercatchers, their supplementary food sources on the upshore flats and in fields are made inaccessible through freezing.
- For a given amount of shellfish removal by a fishery, methods that disturb the birds over the low water period, such as hand gathering, can be significantly more damaging to the birds' chances of survival than those that are not disturbing, such as the Dutch 'wonderklauw'. Clearly, though, this depends on the fishing effort and therefore on the number of person-days of disturbance. It also depends crucially on the intensity of any interference that occurs in the areas to which the shorebirds are displaced; if no interference occurs, their intake rates in these areas would be unaffected by the increased density of competitors and would depend solely on food abundance.
- As has already been mentioned, the number of birds using alternative food sources provides an early warning that a change in shellfishery practice is beginning to have an effect on the birds. Potentially this is a very important management tool because the numbers of birds using these food sources is usually very easy to monitor, especially as large numbers of amateur ornithologists can be mobilised to help with the counts.
- It is not just the efficiency of the shellfishing technique that has an influence on the extent to which the shellfish and hence the birds are affected. A key consideration is the proportion of the shellfish stock that is affected. The key parameters determining this are: (i) the density of shellfish down to which the stocks can be reduced before fishing ceases to be economic - the fishery 'giving-up' density; (ii) the

minimum size of shellfish allowed to be fished, and (iii) how many of the shellfish that are below the legally-taken size range are killed.

- The long-term interaction between shellfishing and shorebirds may reveal patterns that are not apparent in the short-term. This will occur particularly when the shellfish or shorebird populations cannot recover from the effects of fishing within a single year. In such cases, the deleterious effects of fishing will be cumulative, and although these may be minor in the short-term, they may become much more serious after a number of years have passed.
- The cumulative effects of small increases in shorebird mortality in winter can over a period of years greatly affect stable population size. One reason for this is that the effects of shellfishing fall disproportionately on the inexperienced and often subdominant young birds that, although not contributing large numbers in any one year to the total population size, are the seed corn of the future generations. It is therefore vital to predict not just how many birds will die if a shellfishery option is implemented but also which birds die and how a reduction in their numbers will affect long-term equilibrium population size.
- The final and very important point is that, as fishing effort increases, shorebird mortality may be hardly affected initially but then may suddenly increase dramatically once a threshold level of fishing effort has been reached. This happens when the individuals comprising the population vary only a little in their ability to compensate for increased levels of fishing. This in turn reflects the assumptions made about the range of ways in which birds can differ from one another; ie. individual variation in feeding efficiency on preferred and supplementary prey and in their susceptibility to interference.

8.3 FUTURE RESEARCH REQUIREMENTS

The contract has exposed a number of research areas by which our ability to predict the effect of shellfishing on shorebirds could be significantly enhanced.

- The intensity of interference affects the quantitative predictions of the model in a number of crucial respects. There is currently uncertainty about the effect of the general abundance of shellfish on the intensity of interference amongst foraging birds, and this needs to be better understood and modelled. Thus, there was little evidence of interference occurring amongst cockle-feeding oystercatchers in the Burry Inlet where food is currently very abundant. But this does not mean that interference would not become as intense as it already is on the mussel beds of the Exe were cockles to be much scarcer.
- The finding that Burry Inlet cockle-feeders only appeared to be rate-maximising at certain stages in the winter is a timely reminder that the introduction of state-dependency into predictive models is a priority. When birds are actually faced with starvation, their decisions will change; for example, they would be expected to take more risks by feeding closer to people and to forage in areas that they would normally avoid because of a high risk of being attacked by raptors. The model developed in this contract predicts the numbers of birds that will die. It is thus of crucial importance that the decisions that birds make in the model are as close as possible to the decisions that real birds would make when faced with imminent starvation.
- The population response to an increase in fishing effort depends a great deal on the variation between individual birds in the efficiency with which they exploit their food sources. In general in biology, little is known about the magnitude of the variation in efficiency between individuals, its causes and how present levels are maintained by evolution. In contrast, much research effort has been devoted to the causes of variation in social dominance and its effect on susceptibility to interference. The uncertainty about the biology of individual variations in foraging efficiency is a handicap for predicting the effect of shellfishing on shorebirds and needs to be addressed by further research.
- The weather patterns included in the simulations for this contract are very simple. However, the model is constructed in such a way that it can use real values of daily variation in wind speed, temperature and solar insolation, the three climate variables that are believed most to affect shorebird energy

demands. It would be very constructive to run shellfishery scenarios with more realistic weather patterns. This is because the birds in the model, as in the real World, can accumulate fat between periods of harsh weather that enable them to survive the next difficult period. The temporal sequencing of the climate is therefore important for determining the impact of a given fishing effort and technique on shorebird survival.

- The model was used to generate population predictions at the global level but only in a very preliminary fashion. In the real world, if an estuary is over-fished, shorebirds would be expected to move to another wintering area, and this possibility was not included in the present report. This could be modelled by extending the present model to include the energetic costs of moving from one estuary to another and the decision rules used by individuals in deciding whether to stay or leave their present estuary, given the risks of failing to find a suitable alternative. There is, therefore, a need for a model that includes game theory and life history strategy theory as applied to processes that occur at this greater spatial scale.

REFERENCES

Ambrose, W.G. 1986. Experimental analysis of density-dependent emigration of the amphipod *Rhepoxynius abronius. Marine Behaviour and Physiology.* **12,** 209-216.

Andre, C. & Rosenberg, R. 1983. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria. Marine Ecology Progress Series,* **71,** 227-234.

Armonies, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Marine Ecology Progress Series,* **83,** 197-206.

Atkinson, R.J.A. & Parsons, A.J. 1973. Seasonal patterns of migration and locomotor rhythmicity in populations of *Carcinus. Netherlands Journal of Sea Research,* **7,** 81-93.

Bailey, N., Howell,T., Chapman, C.J. & Thain, S. 1991. *Solway Cockle Surveys 1990.* Scottisch Fisheries Working Paper No. 27/91, November 1991, Aberdeen.

Barnett, P.R.O. & Watson, J. 1986. Long-term changes in some benthic species in the Firth of Clyde, with particular reference to *Tellina tenuis* da Costa. *Proceedings of the Royal Society of Edinburgh.* **90B,** 287-302.

Bayne, B.L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology,* **33,** 513-523.

Bayne, B.L. & Widdows, J. 1978. The physiological ecology of two populations of *Mytilus edulis* L.*Oecologia (Berl.).***37,** 137-162.

Beaumont, A.R., Abdul-Matin, A.K.M. & Seed, R. 1993. Early development, survival and growth in pure and hybrid larvae of *Mytilus edulis* and *M. galloprovincialis. Journal of Molluscan Studies.* **59,** 120-123.

Beddington, J.R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology,* **44,** 331-340.

Bernstein, C., Krebs, J.R. & Kacelnik, A. 1991. Distribution of birds amongst habitats: theory and relevance to conservation. *Bird population studies - relevance to conservation and management,* (eds C.M. Perrins, J-D. Lebreton & G.J.M. Hirons), pp 317-345. Oxford University Press, Oxford.

Beukema, J.J. 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. *Neth. J. Sea Res.* **8,** 94-107.

Beukema, J.J. 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Netherlands Journal of Sea Research,* **13,** 203-223.

Beukema, J.J. 1982. Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. *Netherlands Journal of Sea Research,* **16,** 37-45.

Beukema, J.J. 1985. Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea. In: *Marine biology of polar regions and effects of stress on marine organisms* (Ed. J.S. Gray & M.E. Christiansen), pp. 351-361. John Wiley & Sons, London.

Beukema, J.J. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. *Helgoland Meeres,* **43,** 405-415.

Beukema, J.J. 1991. The abundance of shore crabs, *Carcinus maenas (L.),* on a tidal flat in the Wadden Sea after cold and mild winters. *Journal of Experimental Marine Biology and Ecology.* **153,** 97-113.

Beukema, J.J. 1992. Expected changes in the Wadden Sea benthos in a warmer World: lessons from a period with mild winters. *Netherlands Journal of Sea Research.* **30,** 73-79.

Beukema, J.J. & Essink, K. 1986. Common patterns in the fluctuations of macrozoobenthic species living at different places on the tidal flats in the Wadden Sea. *Hydrobiologia*, **142**, 199-207.

Bierbaum, R.M. & Ferson, S. 1986. Do symbiotic pea crabs decrease growth rate in mussels? *Biological Bulletin*, **170**, 51-61.

Boates, J.S. & Goss-Custard, J.D. 1989. Foraging behaviour of oystercatchers *Haematopus ostralegus* during a diet switch from worms *Nereis diversicolor* to clams *Scrobicularia plana*. *Can. J. Zool.* **67**, 2225-2231.

Bowman, R.S. 1985. The biology of the limpet *Patella vulgata L.* in the British Isles: spawning time as a facror determining recruitment success. In: *The ecology of rocky coasts: essays presented to J.R.Lewis, D.Sc.*, edited by P.G. Moore & R. Seed, 178-193. London, Hodder & Stoughton.

Camphuysen, C.J., Ens, B.J. & van der Meer, J. in press. Oystercatcher winter mortality in the Netherlands: the effect of severe weather and food supply. Ardea.

Cayford, J.T. 1988. The foraging behaviour of Oystercatchers (Haematopus ostralegus) feeding on mussels (Mytilus edulis). *Unpublished Ph.D. thesis, University of Exeter.*

Cayford, J.T. & Goss-Custard, J.D. 1990. Seasonal changes in the size selection of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus:* an optimality approach. *Animal Behaviour*,**40**, 609-624.

Charnov, E.L. 1976. Optimal foraging: attack strategy of a mantid. *American Naturalist*, **110**, 141-151.

Clarke, N. 1993. Wash oystercatchers starving. *BTO News no. 185*: 1 and 24.

Clarke, R.T. & Goss-Custard, J.D. 1996. The Exe estuary oystercatcher-mussel model. In: *The oystercatcher: from individuals to populations*, edited by J.D. Goss-Custard, 390-393. Oxford: Oxford University Press.

Cook, W. 1988. *Mechanical cockle dredge observations, Southport, 16th Feb 1988.* Internal report of NW & N Wales Sea Fishery Committe.

Craeymeersch, J.A. , Herman, P.M. & Meire, P.M. 1986. Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S.W. Netherlands). *Hydrobiologia*, **133**, 107-115.

Crowley, P.H., Nisbet, R.M., Gurney, W.S.C. & Lawton, J.H. 1987. Population regulation in animals with complex life-histories: formulation and analysis of a damselfly model. *Advances in ecological Research.* **17**, 1-59.

Dare, P.J. 1976. Settlement, growth, and production of the mussel, *Mytilus edulis* L., in Morecambe Bay, England. *Ministry of Agriculture, Fisheries and Food, Fisheries Investigations,* Series II, Volume **28**, Number **1**, 1-25.

Dare, P.J. & Edwards, D.B. 1981. Underwater television observations on the intertidal movements of shore crabs, *Carcinus maenas,* across a mudflat. *Journal of the Marine Biological Association of the United Kingdom.* **61**, 107-116.

Dare, P.J., Edwards, D.B. & Davies, G. 1983. Experimental collection and handling of spat mussels (*Mytilus edulis L.*) on ropes for intertidal culture. *Fisheries Research Technical report, MAFF Directorate of Fisheries Research, Lowstoft.* **74**, 1-23.

Davidson, N.C. & Evans, P.R. 1982. Mortality of Redshanks and Oystercatchers from starvation during severe weather. *Bird Study*, **29**, 183-188.

Davidson, P.E. 1967. A study of oystercatchers (*Haematopus ostralegus* L.) in relation to the fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Investigations Series II*, Volume XXV, no. 7.

De Vlas, J. 1982. *De effecten van de kokkelvisserij op de bodemfauna van Waddenzee en Oosterschelde.* RIN-rapport 92/19, Rijksinstituut voor Natuurbeheer, Texel.

Dempster, J.P. 1975. *Animal population ecology.* London: Academic Press.

Desprez, M., Ducrotoy, J.P. & Elkaim, B. 1987. Crise de la production des coques (*Cerastoderma edule*) en Baie de Somme. I Synthese des connaissances biologiques. *Revue Travaux Institut Peches Maritime*, **49**, 215-230.

Diaz, J.A. & Asensio, B. 1991. Effects of group size and distance to protective cover on the vigilance behaviour of Black-billed Magpies *Pica pica. Bird Study* **38,** 38-41.

Doherty, P.J. 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology.* **64(1)**, 176-190.

Dolman, P.M. 1995. The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenox nivalis. Oecologia*, **102**, 511-514.

Dorjes, J., Michaelis, H. & Rhode, B. 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). *Hydrobiologia*, **142,** 217-232.

Durell, S.E.A. le V. dit & Goss-Custard, J.D. 1984. Prey selection within a size-class of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus. Animal Behaviour,* 32, 1197-1203.

Ens, B.J. 1982. Size selection in mussel-feeding Oystercatchers. *Wader Study Group Bulletin,* **34**, 16-20.

Ens, B.J. 1992. The Social prisoner: causes of natural variation reproductive success of the Oystercatcher. *Ph.D. thesis, Rijksuniversiteit Groningen.*

Ens, B.J. & Alting, D. 1996. The effect of an experimentally created musselbed on intake rate, diet and feeding density of Oystercatchers Haematopus ostralegus. *Ardea*, **84,** in press.

Ens, B.J. & Cayford, J.T. 1996. Feeding with other Oystercatchers. In: *The Oystercatcher: from individuals to populations*, edited by J.D. Goss-Custard, 77-104. Oxford: Oxford University Press.

Ens, B.J., Dirksen, S., Smit, C.J. & Bunskoeke, E.J. 1996. Seasonal changes in size selection and intake rate of oystercatchers, *Haematopus ostralegus*, feeding on the bivalves, *Mytilus edulis* and *Cerastoderma edule. Ardea* **84A**, in press.

Ens, B.J. & Goss-Custard, J.D. 1984. Interference among Oystercatchers, *Haematopus ostralegus* L., feeding on mussels, *Mytilus edulis* L., on the Exe estuary. *Journal of Animal Ecology*, **53**, 217-232.

Ens, B.J., Piersma, T. & Drent, R.H. 1994. The dependence of waders and waterfowl migrating along the East Atlantic Flyway on their coastal food supplies: what is the most profitable research program? *Ophelia,* **supplement 6**, 127-151.

Ens, B.J., Piersma, T. & Tinbergen, J.M. 1994. Towards predictive models of bird migration: theoretical and empirical bottlenecks. NIOZ report 1994-5.

Ens, B.J., Piersma, T., Wolff, W.J. & Zwarts, L. 1990. Homeward Bound: Problems waders face when migrating from the Banc d'Arguin, Mauritania, to their northern breeding grounds in spring. *Ardea*, **78**, Special Supplement.

Essink, K. & Bos, A.H. 1985. Growth of three bivalve molluscs transplanted along the axis of the Ems estuary. *Netherlands Journal of Sea Research,* **19 (1)**, 45-51.

Faldborg, K., Jensen, K.T. & Maagaard, L. Dynamics, growth, secondary production and elimination by waterfowl of an intertidal population of *Mytilus edulis* L. *Ophelia Supplement* **6,** 187-200.

Franklin, A. 1976. The Burry Inlet cockle fishery. *Problems of a small estuary,* (eds. A. Nelson-Smith & E.M. Bridges). UCW Swansea, Swansea, pp 3:1/1.

Franklin, A. & Pickett, G.D. 1978. *Studies on the indirect effects of fishing on stocks of cockles, Cardium edule, in the Thames estuary and Wash.* Fisheries Research Technical Report No. 42. Ministry of Agriculture, Fisheries and Food, Lowestoft.

Frechette, M., Aitken, A.E. & Page, L. 1992. Interdependence of food and space limitation of a benthic suspension feeder: consequences for self-thinning relationships. *Marine Ecology Progress Series,* **83,** 55-62.

Frechette, M. & Bourget, E. 1985a. Energy flow between pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. *Canadian Journal of Fisheries and Aquatic Sciences.***42,** 1158-1165.

Frechette, M. & Bourget, E. 1985b. Food-limited growth of *Mytilus edulis L.* in relation to the benthic boundary layer. *Canadian Journal of Fisheries and Aquatic Sciences.* **42,** 1166-1170.

Frechette, M. & Grant, J. 1991. An in situ estimation of the effect of wind-driven resuspension on the growth of the mussel *Mytilus edulis* L. *Journal of experimental marine Biology and Ecology,* **148,** 201-213.

Fretwell, S.D. & Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica,* **19,** 16-36.

Frid, C.L.J. & Townsend, C.R. 1989. An appraisal of the patch dynamics concept in stream and marine benthic communities whose members are highly mobile. *Oikos.* **56(1),** 137-141.

Gentili, M.R. & Beaumont, A.R. 1988. Environmental stress, heterozygosity, and growth rate in *Mytilus edulis* L. *Journal of experimental marine Biology and Ecology,* **120,** 145-153.

Gerritsen, A.F.G. 1988. General and specific patterns in foraging acts of sandpipers (*Calidris*). In: *Feeding techniques and the anatomy of the bill in sandpipers* (*Calidris*), Thesis, 91-137. University of Leiden.

Goss-Custard, J.D. 1970. Feeding dispersion in some overwintering wading birds. In: *Social behaviour in birds and mammals,* edited by J.H. Crook, 3-35. London: Academic Press.

Goss-Custard, J.D. 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology,* **14,** 721-739.

Goss-Custard, J.D. 1977. Optimal foraging and the size selection of worms by redshank, *Tringa totanus,* in the field. *Animal Behaviour* **25,** 10-29.

Goss-Custard, J.D. 1980. Competition for food and interference amongst waders. *Ardea,* **68,** 31-52.

Goss-Custard, J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. In: *Behavioural Ecology: ecological consequences of adaptive behaviour.* (Eds. R.M. Sibly & R.H. Smith), pp. 169-188. Blackwells, Oxford.

Goss-Custard, J.D. 1993. The effect of migration and scale on the study of bird populations: 1991 Witherby Lecture. *Bird Study,* **40,** 81-96.

Goss-Custard, J.D., Caldow, R.W.G. & Clarke, R.T. 1992. Correlates of the density of foraging Oystercatchers, *Haematopus ostralegus,* at different population sizes. *Journal of Animal Ecology,* **61,** 159-173.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T. & West, A.D. 1995d. Deriving population parameters from individual variations in foraging behaviour: II. Model tests and population parameters. *Journal of Animal Ecology,* **64,** 277-289.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell S.E.A. le V. dit, Urfi, A.J. & West, A.D. 1995a. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis*, **137**, S56-66.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. le V. dit & Sutherland, W.J. 1995c. Deriving population parameters from individual variations in foraging behaviour: I. Empirical game theory distribution model of oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *Journal of Animal Ecology*, **64**, 265-276.

Goss-Custard, J.D., Cayford, J.T., Boates, J.S. & Durell, S.E.A. le V. dit 1987. Field tests of the accuracy of measuring prey size against bill length in oystercatchers, *Haematopus ostralegus*, eating mussels, *Mytilus edulis*. *Animal Behaviour,* **35**, 1078-1083.

Goss-Custard, J.D., Clarke, R.T., Briggs, K.B., Ens, B.J., Exo, K-M., Smit, C., Beintema, A.J., Caldow, R.W.G., Catt, D.C., Clark, N., Durell, S.E.A. le V. dit, Harris, M.P., Hulscher, J.B., Meininger, P.L., Picozzi, N., Prys-Jones, R., Safriel, U. & West, A.D. 1995b. Population consequences of winter habitat loss in a migratory shorebird: I. Estimating model parameters. *Journal of Applied Ecology*, **32**, 317-333.

Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. le V. dit. 1984. Rates of food intake and aggression of Oystercatchers, *Haematopus ostralegus*, on the most and least preferred mussel, *Mytilus edulis*, beds on the Exe estuary. *Journal of Animal Ecology,* **53**, 233-245.

Goss-Custard, J.D., Clarke, R.T., Durell, S.E.A. le V. dit, Caldow, R.W.G. & Ens, B.J. 1995e. Population consequences of winter habitat loss in a migratory shorebird: II. Model predictions. *Journal of Applied Ecology*, **32**, 334-348.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1983. Individual and age differences in the feeding ecology of oystercatchers, *Haematopus ostralegus*, wintering on the Exe. *Ibis,* **125,** 155-171.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1984. Feeding ecology, winter mortality and the population dynamics of Oystercatchers on the Exe estuary. In: *Coastal waders and wildfowl in winter*, edited by P.R. Evans, J.D. Goss-Custard & W.G. Hale. Cambridge: Cambridge University Press.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1987. Age-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. III. The effect of interference on overall intake rate. *Journal of Animal Ecology,* **56**, 549-558.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1987a. Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. Foraging efficiency and interference. *Journal of Animal Ecology*, **56**, 521-536.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1988. The effect of dominance and feeding method on the intake rates of Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. *Journal of Animal Ecology*, **57**, 827-844.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. *Ibis,* **132**, 273-289.

Goss-Custard, J.D., Durell, S.E.A.le V. dit, Clarke, R.T., Beintema, A.J., Caldow, R.W.G., Meininger, P.L. & Smit, C. 1996e. Population dynamics of the Oystercatcher. In: The *Oystercatcher: from individuals to populations, (J.D. Goss-Custard), pp. 352-383.* Oxford University Press, Oxford.

Goss-Custard, J.D., Durell, S.E.A. le V. dit, Goater, C.P., Hulscher, J.B., Lambeck, R.H.D., Meininger, P.L. & Urfi, J. 1996. How oystercatchers survive the winter. In: J.D. Goss-Custard (ed). The oystercatcher: from individuals to populations. Oxford University Press, Oxford. pp 133-154.

Goss-Custard, J.D., Durell, S.E.A. le V. dit, McGrorty, S. & Reading, C.J. 1982. Use of mussel, *Mytilus edulis*, beds by Oystercatchers, *Haematopus ostralegus*, according to age and population size. *Journal of Animal Ecology,* **51**, 543-554.

Goss-Custard, J.D., Durell, S.E.A. le V dit, Sitters, H.P. & Swinfen, R. 1982. Age-structure and survival of a wintering population of oystercatchers. *Bird Study* **29,** 83-98.

Goss-Custard, J.D., McGrorty, S. & Durell, S.E.A. le V. dit 1996a. The effect of Oystercatchers *Haematopus ostralegus* on shellfish populations. Ardea, **84**, in press.

Goss-Custard, J.D. & Rothery, P. 1976. A method for measuring some components of foraging of certain birds in the field. *Animal Behaviour*, **24,** 545-550.

Goss-Custard, J.D. & Sutherland, W.J. in press. Individual behaviour, populations and conservation. In (Eds. J.R. Krebs & N.B. Davies), *Behavioural ecology: an evolutionary approach. 4th edition.* Blackwell Science, Oxford.

Goss-Custard, J.D., Urfi, A.J., de Bruijn, B., Odoni, N., Durell, S.E.A. le V. dit & West, A.D. 1994. *Birds in estuaries - the ability of shorebirds to compensate for lost feeding time.* Institute of Terrestrial Ecology Report.

Goss-Custard, J.D. & Verboven, N. 1993. Disturbance and feeding shorebirds on the Exe estuary. *Wader Study Group Bulletin*, **68**, 59-66.

Goss-Custard, J.D., West, A.D., Caldow, R.W.G., Clarke, R.T., Durell, S. E.A. le V. dit 1996d. The carrying capacity of coastal habitats for Oystercatchers. In: The *Oystercatcher: from individuals to populations, (Ed. J.D. Goss-Custard), pp. 326-351.* Oxford University Press, Oxford.

Goss-Custard, J.D., West, A., Caldow, R.W.G., Durell, S.E.A. le V. dit & McGrorty, S. 1996f. An empirical optimality model to predict the intake rates of Oystercatchers Haematopus ostralegus feeding on mussels Mytilus edulis. *Ardea*, **84**, in press.

Goss-Custard, J.D., West, A.D. & Durell, S.E.A. le V. dit 1993. The availability and quality of the mussel prey (Mytilus edulis) of Oystercatchers (Haematopus ostralegus). *Netherlands Journal of Sea Research*, **31**, 419-439.

Goss-Custard, J.D., West, A.D. & Sutherland, W.J. 1996b. Where to feed. In: The *Oystercatcher: from individuals to populations, (Ed. J.D. Goss-Custard), pp. 105-132.* Oxford University Press, Oxford.

Hancock, D.A. 1967. Growth and mesh selection in edible cockle (*Cardium edule* L.). *Journal of Applied Ecology,* **4**, 137-157.

Hancock, D.A. 1971. The role of predators and parasites in a fishery for the mollusc *Cardium edule* L. In: P.J. den Boer & G.R. Gradwell (eds.). *Dynamics of populations.* Proceedings of the Advanced Study Institute, Oosterbeck, 1970, Centre for Agricultural Publishing and Documentation, Wageningen. pp. 419-439.

Hancock, D.A. 1973. The relationship between stock and recruitment in exploited invertebrates. *Conseil international pour l'Exploration de la Mer, Rapports et Proces-verbaux,* **164,** 113-131.

Hancock, D.A. & Urquhart, A.E. 1965. The determination of natural mortality and its causes in an exploited population of cockles (*Cardium edule* L.). *Fishery Investigation, London Series II*, **24**, 1-40.

Hancock, D.A. & Urquhart, A.E. 1966. The fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Investigations Series II*, Volume XXV, no. 3.

Hassell, M.P. 1975. Density dependence in single species populations. *Journal of Animal Ecology.* **44,** 283-295.

Hassell, M.P., Latto, J. & May, R.M. 1989. Seeing the wood for the trees: detecting density dependence from existing life-table studies. *Journal of Animal Ecology.* **58,** 883-892.

Hassell, M.P. & Varley, G.C. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature*, **223**, 1133-1136.

Holling, C.S. 1959a. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, **91**, 293-320.

Holling, C.S. 1959b. Some characteristics of simple types of predation and parasitism, *Canadian Entomologist*, **91**, 385-398.

Holm, E.R. 1990. Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Marine Ecology Progress Series.* **60**, 141-146.

Holmgren, N. 1995. The ideal free distribution of unequal competitors: predictions from a behaviour-based functional response. *Journal of Animal Ecology*, **64**, 197-212.

Horwood, J.W. & Goss-Custard, J.D. 1977. Predation by the Oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. *Journal of Applied Ecology,* **14**, 139-158.

Huggett, D.J. 1993. *Cockle fishing in England and Wales.* Unpublished draft report, October 1993, RSPB, Sandy.

Hughes, R.N. & Griffiths, C.L. 1988. Self-thinning in barnacles and mussels: the geometry of packing. *American Naturalist.* **132,** 484-491.

Hughes, T.P. 1990. Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology.***71(1),** 12-20.

Hulscher, J.B. 1976. Localisation of cockles (Cardium edule L.) by the Oystercatcher (Haematopus ostralegus L.) in darkness and daylight. *Ardea*, **64,** 292-310.

Hulscher, J.B. 1982. The oystercatcher as a predator of the bivalve, *Macoma balthica*, in the Dutch Wadden Sea. *Ardea* **70,** 89-152.

Hulscher, J.B. 1989. Sterfte en overleving van Scholeksters *Haematopus ostralegus* bij strenge vorst. *Limosa,* **62**, 177-181.

Hulscher, J.B. 1996. Food and feeding behaviour. In: *The oystercatcher: from individuals to populations, edited by* J.D. Goss-Custard, 7-29. Oxford: Oxford University Press.

Hulscher, J.B., Exo, K.-M. & Clark, N.A. 1996. Why do oystercatchers migrate? In: The *Oystercatcher: from individuals to populations.*(Ed. J.D. Goss-Custard), pp. 155-185. Oxford University Press, Oxford.

Jensen, K.T. & Jensen, J.N. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *Journal experimental marine Biology and Ecology,* **89**, 157-174.

Kersten, M. & Piersma, T. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea,* **75**, 175-187.

Kersten, M. & Visser, W. in press. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. Ardea.

Koene, P. 1978. De Scholekster: aantalseffecten op de voedselopname. *Dissertation Zoology Department, University of Groningen, The Netherlands.*

Kristensen, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Archives Neerl. Zool,* **12**, 351-453.

Lambeck, R.H.D. 1991. Changes in the abundance, distribution and mortality of wintering Oystercatchers after habitat loss in the Delta area, SW Netherlands. *Acta XX Congressus Internationalis Ornithologici,* 2208-2218.

Lambeck, R.H.D., Goss-Custard, J.D. & Triplet, P. 1996. Oystercatchers and man in the coastal zone. In: The *Oystercatcher: from individuals to populations, (Ed. J.D. Goss-Custard), pp. 289-326.* Oxford University Press, Oxford.

Lapota, D., Rosenberger, D.E., Platter-Rieger, M.F. & Seligman, P.F. 1993. Growth and survival of *Mytilus edulis* larvae exposed to low levels of dibutyltin and tributyltin. *Marine Biology,* **115,** 413-419.

Levin, L.A. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology.* **65(4),** 1185-1200.

Lewis, J.R. 1986. Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral mollusca and cirripedes. *Hydrobiologia.* **142,** 1-13.

Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67,** 377-385.

Mallet, A.L., Carver, C.E.A., Coffen, S.S. & Freeman, K.R. 1987. Winter growth of the blue mussel *Mytilus edulis* L.: importance of stock and site. *Journal of experimental marine Biology and Ecology,* **108,** 217-228.

Mayhew, P.W. 1987. Vigilance levels in European Wigeon - sexual differences. *Wildfowl* **38,** 77-81.

Maynard-Smith, J. 1982. *Evolution and the Theory of Games.* Cambridge University Press.

McGrorty, S., Clarke, R.T., Reading, C.J. & Goss-Custard, J.D. 1990. Population dynamics of the mussel *Mytilus edulis*: density changes and regulation of the population in the Exe estuary, Devon. *Marine Ecology Progress Series.* **67,** 157-169.

McGrorty, S. & Goss-Custard, J.D. 1991. Population dynamics of the mussel, *Mytilus edulis*: spatial variations in age-class densities of an intertidal estuarine population along environmental gradients. *Marine Ecology Progress Series,* **73,** 191-202.

McGrorty, S. & Goss-Custard, J.D. 1993. Population dynamics of the mussel *Mytilus edulis* along environmental gradients: spatial variations in density-dependent mortalities. *Journal of Animal Ecology.* **62,** 415-427.

McGrorty, S. & Goss-Custard, J.D. 1995. Population dynamics of *Mytilus edulis* along environmental gradients: density-dependent changes in adult mussel numbers. *Marine Ecology Progress Series.* **129,** 197-213.

McGrorty, S., Goss-Custard, J.D. & Clarke, R.T. 1993. Mussel *Mytilus edulis* (*Mytilacea*) dynamics in relation to environmental gradients and intraspecific interactions. *Netherlands Journal of Aquatic Ecology.* **27(2-4),** 163-171.

McNamara, J.M., Houston, A.I. & Lima, S.L. 1994. Foraging routines of small birds in winter: a theoretical investigation. *J Avian Biol* **25,** 287-302.

Meire, P.M. 1991. Effects of a substantial reduction in intertidal area on numbers and densities of waders. *ACTA XX Internationalis Ornithologici:* 2219-2227.

Meire, P.M. 1996a. Interactions between Oystercatchers (Haematopus ostralegus) and mussels (Mytilus edulis): implications from optimal foraging theory. *Ardea,* **84,** in press.

Meire, P.M. & Erwynck, A. 1986. Are Oystercatchers (Haematopus ostralegus) selecting the most profitable mussels (Mytilus edulis)? *Animal Behaviour,* **34,** 1427-1435.

Meire, P.M. & Kuijken, E. 1984. Relations between the distribution of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. In: *Coastal Waders and Wildfowl in Winter.* (Eds. P.R. Evans, J.D. Goss-Custard & W.G. Hale), pp. 57-68. Cambridge University Press.

Meire, P.M. & Kuijken, E. 1986. Are Oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels? *Animal Behaviour*, **34**, 1427-1435.

Menge, B.A. & Farrell, T.M. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Advances in ecological Research.* **19,** 189-262.

Moller, P. & Rosenberg, R. 1983. Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, western Sweden. *Ophelia,* **22**, 33-55.

Moody, A.L. & Houston, A.I. 1995. Interference and the ideal free distribution. *Animal Behaviour*, **49**, 1065-1072.

Morrisey, D.J. 1987. Effect of population density and presence of a population competitor on the growth rate of the mud snail *Hydrobia ulvae* (Pennant). *Journal of experimental marine Biology and Ecology.* **108,** 275-295.

Muschenheim, D.K. & Newell, C.R. 1992. Utilisation of seston flux over a mussel bed. *Marine Ecology Progress Series,* **85,** 131-136.

Naylor, E. 1962. Seasonal changes in a population of *Carcinus maenas* (L.) in the litoral zone. *Journal of Animal Ecology,* **31**, 601-609.

Nelson-Smith, A. & Bridges, E.M. (eds) 1976. *Problems of a small estuary.* UCW Swansea, Swansea.

Newell, C.R. 1990. The effects of mussel (*Mytilus edulis,* Linnaeus 1758) position in seeded bottom patches on growth at subtidal lease sites in Maine. *Journal of Shellfish Research,* **9,** 113-118.

Newkirk, G.F. 1980. Genetics of shell colour in *Mytilus edulis* L. and the association of growth rate with shell colour. *Journal of experimental marine Biology and Ecology,***47,** 89-94.

O'Connor, R.J. & Brown, R.A. 1977. Prey depletion and foraging strategy in the Oystercatcher, *Haematopus ostralegus. Oecologia,* **27**, 75-92.

Okamura, B. 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis. Oecologia.* **69**,341-347.

Oord 1992. *Enquete Handkokkelvisserij: resultaten, diskussie en konklusies.* Rapport in opdracht vanb de vereniging voor handkokkelaars CARDIUM door Buro voor Faunatechniek Oord, Kampen, februari 1992.

Page, H.M. & Ricard, Y.O. 1990. Food availability as a limiting factor to mussel *Mytilus edulis* growth in California coastal waters. *Fishery Bulletin,* **88,** 677-686.

Paine, R.T. 1984. Ecological determinism in the competition for space. *Ecology.* **65(5),**1339-1348.

Parker, G.A. & Sutherland, W.J. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour*, **34**, 1222-1242.

Piersma, T. & Davidson, N. 1992. The migration of Knots. *Wader Study Group Bulletin*, **64**, Supplement.

Piersma, T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in the Knot. *Ph.D thesis, Rijksuniversiteit Groningen.*

Piersma, T., Dekinga, A. & Koolhaas, A. 1993. Modder, nonnetjes en kanoeten bij Griend. *Waddenbulletin*, **28**, 144-149.

Piersma, T., van Gils, J., de Goeij, P. & van der Meer, J. 1995. Holling s functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *Journal of Animal Ecology*, **64**, 493-504.

Piersma, T., Tulp, I. & Schekkerman, H. 1994. Final countdown of waders during starvation: terminal use of nutrients in relation to structural size and concurrent energy expenditure. In: Close to the edge: energetic bottlenecks and the evolution of migratory pathways in the Knot, by T. Piersma. *Ph.D thesis, Rijksuniversiteit Groningen.* pp 220-227.

Poot, M. & Piersma, T. 1994. Energy expenditure of a widely ranging shorebird, the Knot *Calidris canutus*, measured by stable isotope turnover under simulated field conditions. In: Close to the edge: energetic bottlenecks and the evolution of migratory pathways in the Knot, by T. Piersma. *Ph.D thesis, Rijksuniversiteit Groningen.* pp 158-163.

Prater, A.J. 1972. The ecology of Morecambe bay. III. The food and feeding habits of knot (*Calidris canutus* L.) in Morecambe bay. *Journal of Applied Ecology*, **9**, 179-194.

Rabe, D.L., Prince, H.H. & Goodman, E.D. 1983. The effect of weather on bioenergetics of breeding American Woodcock. *Journal of Wildlife Management,* **47**, 762-771.

Raffaelli, D., Karakassis, I. & Galloway, A. 1991. Zonation schemes on sandy shores: a multivariate approach. *Journal of experimental marine Biology and Ecology.* **148,** 241-253.

Reise, K. 1985. *Tidal Flat Ecology. An experimental approach to species interactions.* Berlin: Springer-Verlag.

Rodhouse, P.G., McDonald, J.H., Newell, R.I.E. & Koehn, R.K.1986. Gamete production, somatic growth and multiple-locus enzyme heterozygosity in *Mytilus edulis. Marine Biology,* **90,** 209-214.

Rodhouse, P.G., Roden, C.M., Burnell, G.M., Hensey, M.P., McMahon, T., Ottway, B. & Ryan, T.H. 1984. Food resource, gametogenesis and growth of *Mytilus edulis* on the shore and in suspended culture: Killarney Harbour, Ireland. *Journal of the biological Association, U.K.,* **64,** 513-529.

Rogers, D.J. & Hassell, M.P. 1974. General models for insect parasite and predator searching behaviour: interference. *Journal of Animal Ecology*, **43**, 239-253.

Roughgarden, J. & Iwasa, Y. 1986. Dynamics of a metapopulation with space limited subpopulations. *Theoretical Population Biology.* **29,** 235-261.

Ruxton, G.D., Gurney, W.S.C. & de Roos, A.M. 1992. Interference and generation cycles. *Theoretical Population Biology*, **42**, 235-253.

Sanchez-Salazar, M.E., Griffiths, C.L. & Seed, R. 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule. Estuarine, Coastal and Shelf Science.* **25,** 245-260.

Seed, R. 1976. Ecology. In: *Marine Mussels,* edited by B.L. Bayne.. International Biological Programme, **10**, 13-65. Cambridge: Cambridge University Press.

Smaal, A.C. & van Stralen, M.R. 1990. Average annual growth and condition of mussels as a function of food source. *Hydrobiologia,* **195,** 179-188.

Smit, C.J & Piersma, T. 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In:. *Flyways and reserve networks for water birds.* (Eds. H. Boyd & J.-Y. Pirot). *International Wildfowl Research Bureau Special Publication No. 9.* Slimbridge, England.

Smit, J.C. & Visser, G.J.M. 1993. Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. In *Disturbance to waterfowl on estuaries*, edited by N.C. Davidson & P.I. Rothwell, 6-19. Wader Study Group Bulletin **68**, Special Issue.

Smith, R.H. 1973. The analysis of intrageneration change in animal populations. *Journal of Animal Ecology.* **42,** 611-622.

Sousa, W.P. 1985. disturbance and patch dynamics on rocky intertidal shores. In: *The ecology of natural disturbance and patch dynamics,* edited by S.T.A. Pickett & P.S.White, 101-124. London: Academic Press.

Spencer, B.E. 1991. Predators and methods of control in molluscan shellfish cultivation in north European waters. Aquaculture and the Environment. In: N. De Pauw & J. Joyce (Eds.). *European Aquaculture Society Special Publication No. 16.* Gent, Belgium.

Sprung, M. 1984. Physiological energetics of mussel larvae (*Mytilus edulis).* I. Shell growth and biomass. *Marine Ecology Progress Series,* **17,** 283-293.

Stephens, D.W. & Krebs, J.R. 1986. *Foraging theory.* Princeton University Press, Princeton.

Stiling, P. 1988. Density-dependent processes and key factors in insect populations. *Journal of Animal Ecology.* **57,**581-593.

Stillman, R.A., Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. le V. dit 1996. Shape of the interference function in a foraging vertebrate. *Journal of Animal Ecology,* **65,** in press.

Sueur, F. 1987. Interactions proies-predateurs en milieu estuarien: le cas de la coque, *Cerastoderma edule* (L.), et de la Macome Baltique, *Macoma balthica* (L.), dans le regime de trois Charadriiformes. *Unpublished Ph.D. thesis, University of Paris XI.*

Sukhotin, A.A. & Kulakowski, E.E. 1992. Growth and population dynamics in mussels (*Mytilus edulis* L.) cultured in the White Sea. *Aquaculture,* **101,** 59-73.

Sutherland, W.J. 1982a. Spatial variation in the predation of cockles by Oystercatchers at Traeth Melynog, Anglesey. I. The cockle population. *Journal of Animal Ecology,* **51,** 481-489.

Sutherland, W.J. 1982b. Spatial variation in the predation of cockles by Oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. *Journal of Animal Ecology,* **51,** 491-500.

Sutherland, W.J. 1982c. Do Oystercatchers select the most profitable cockles? *Animal Behaviour,* **30,** 857-861.

Sutherland, W.J. 1983. Aggregation and the ideal free distribution. *Journal of Animal Ecology,* **52,** 821-828.

Sutherland, W.J. & Dolman, P.M. 1994. Combining behaviour and population dynamics with applications for predicting the consequences of habitat loss. *Phil. Trans. R. Soc.* **255,** 133-138.

Sutherland, W.J. & Ens, B.J. 1987. Criteria determining selection of mussels by oystercatchers. *Behaviour* **103,** 187-202.

Sutherland, W.J. & Goss-Custard, J.D. 1992. Predicting the consequences of habitat loss on shorebird populations. *Proc. Int. Orn. Congr.* **XX,** 2199-2207.

Sutherland, W.J. & Koene, P. 1982. Field estimates of the strength of interference between Oystercatchers, *Haematopus ostralegus. Oecologia,* **55,** 108-109.

Sutherland, W.J. & Parker, G.A. 1985. Distribution of unequal competitors. In: *Behavioural Ecology* (Eds. R.M. Sibly & R.H. Smith), pp. 255-273. Blackwell Scientific Publications, Oxford.

Svane, I. & Ompi, M. 1993. Patch dynamics in beds of the blue mussel *Mytilus edulis* L.: effects of site, patch size, and position within a patch. *Ophelia,* **37 (3),** 187-202.

Swennen, C., de Bruijn, L.L.M., Duiven, P., Leopold, M.F. & Marteijn, E.C.L. 1983. Difference in bill form of the oystercatcher *Haematopus ostralegus*: a dynamic adaptation to specific foraging techniques. *Neth. J. Sea Res.* **17,** 57-83.

Swennen, C. & Duiven, P. 1983. Characteristics of Oystercatchers killed by cold-stress in the Dutch Wadden Sea area. *Ardea*, **71**, 155-159.

Swennen, C., Leopold, M.F. & Bruijn, L.L.M. 1989. Time-stressed oystercatchers, *Haematopus ostralegus*, can increase their intake rate. *Animal Behaviour*, **38**, 8-22.

Theisen, B.F. 1973. The growth of *Mytilus edulis* L. (Bivalvia) from Disko and Thule district, Greenland. *Ophelia,* **12,** 59-77.

Thompson, D.B.A. 1983. Prey assessment by plovers (Charadriidae): net rate of energy intake and vulnerability to kleptoparasitism. *Anim. Behav.* **31,** 1226-1236.

Triplet, P. 1989. Comparaison entre deux strategies de recherche alimentaire de l'Huitrier-Pie, *Haematopus ostralegus,* en Baie de Somme, influence des facteurs de l'environment. *Unpublished Memoire D.E.A, University of Paris VI.*

Triplet, P. 1994. Strategie alimentaire dl l'Huitrier-pie, *Haematopus ostralegus*, en baie de Somme. *Gibier Faune Sauvage*, **11**, 235-248.

Triplet, P. & Etienne, P. 1991. L'Huitrier-pie, *Haematopus ostralegus*, face a une diminution de sa principale resource alimentaire, la Coque (*Cerastoderma edule*) en baie de Somme. *B.M. ONC*, **153**, 21-28.

Urfi, A.J., Goss-Custard, J.D. & Durell, S.E.A. le V. dit in press. The ability of oystercatchers *Haematopus ostralegus* to compensate for lost feeding time: field studies on individually marked birds. *Journal of Applied Ecology.*

Vahl, O. 1982. Long-term variations in recruitment of the Iceland scallop, *Chlamys islandica,* from northern Norway. *Netherlands Journal of Sea Research.* **16,** 80-87.

Varley, G.C. & Gradwell, G.R. 1960. Key factors in population studies. *Journal of Animal Ecology.* **29,** 399-401.

Varley, G.C. & Gradwell, G.R. 1968. Population models for the Winter Moth. In: *Insect Abundance,* edited by T.R.E. Southwood, 132-142. Oxford: Blackwell Scientific Publications.

Verhagen, J.H.G. 1982. A distribution and population model of the mussel *Mytilus edulis* in Lake Grevelingen. Paper presented at the Third International Conference on State-of-the-Art in Ecological Modelling, Colorado State University.

Wanink, J.H. & Zwarts, L. 1985. Does an optimally foraging Oystercatcher obey the functional response? *Oecologia*, **67**, 98-106.

Wanink, J.H. & Zwarts, L. 1993. Environmental effects on the growth rate of intertidal invertebrates and some implications for foraging waders. *Netherlands Journal of Sea Research,* **31 (4),** 407-418.

Ward, D. 1993. African black oystercatchers (*Haematopus moquini*) feeding on wedge clams (*Donax sera*): the effects of non-random prey availability in the intertidal on the predictions of an optimal diet model. *Ethology, Ecology & Evolution* **5,** 457-466.

Widdows, J. & Johnson, D. 1988. Physiological energetics of *Mytilus edulis*: scope for growth. *Marine Ecology Progress Series,* **46,** 113-121.

Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. *The Condor*, **96**, 257-279.

Witter, M.S. & Cuthill, I.C. 1993. The ecological costs of avian fat storage. *Phil. Trans. R. Soc. (London)* **340,** 73-92.

Worrall, C.M. & Widdows, J. 1984. Investigation of factors influencing mortality in *Mytilus edulis* L. *Marine Biology Letters,* **5,** 85-97.

Zouros, E. & Mallet, A.L. 1989. Genetic explanations of growth / heterozygosity correlation in marine molluscs. In: *Reproduction, Genetics and Distributions of Marine Organisms,* edited by J.S.Ryland & P.A.Tyler, 317-324.Fredensborg, Denmark: Olsen & Olsen.

Zwarts, L. 1991. Seasonal variation in body weight of the bivalves *Macoma balthica, Scobicularia plana, Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden sea. *Netherlands Journal of Sea Research*, **28**, 231-245.

Zwarts, L. & Blomert, A-M. 1992. Why Knot *Calidris canutus* take medium sized *Macoma balthica* when six prey species are available. *Marine Ecology Progress Series*, **83**, 113-128.

Zwarts, L., Blomert, A-M, & Wanink, J.H. 1992. Annual and seasonal variation in the food supply harvestable by Knot *Calidris canutus* staging in the Wadden Sea in late summer. *Marine Ecology Progress Series*, **83**, 129-139.

Zwarts, L., Cayford, J.T., Hulscher, J.B., Kersten, M., Meire, P.M. & Triplet, P. 1996. Prey size selection and intake rate. In: The *Oystercatcher: from individuals to populations, (Ed. J.D. Goss-Custard), pp. 326-351.* Oxford University Press, Oxford.

Zwarts, L. & Drent, R.H. 1981. Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). *Feeding and survival strategies of estuarine organisms,* (eds. N.V. Jones & W.J. Wolff). Plenum Press, New York, pp 193-216.

Zwarts, L. & Wanink, J. 1989. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Marine Biology*, **100**, 227-240.