



BTO Research Report No 354

Assessing the impacts of shell-fishing
and mussel farming on Oystercatcher populations
in the Wash, England.

Phase 1: Identification of model parameters to be refined.

Authors

R.A. Stillman, N.A. Clark, P.W. Atkinson, A.D. West, S. McGrorty,
S.E.A. Le V. dit Durell and M.G. Yates.

This is a joint report from the British Trust for Ornithology (BTO) and CEH to English Nature

March 2004

© **British Trust for Ornithology**

The British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU
Registered Charity No. 216652

CONTENTS

	Page No.
Chapter 1 Overview	3
Chapter 2 CEH behaviour-based model	5
2.1 Overview of the model	5
2.2 Testing the model	7
2.3 Parameterising the model	7
2.4 Predicting the consequences of environmental change	7
Chapter 3 Existing Wash Oystercatcher-shellfish model	9
3.1 Description of the existing model	9
3.2 Predictions of the existing model	12
3.3 Using the existing model to advise shellfishery management	
15	
Chapter 4 How to improve the model's predictions	17
4.1 Surveying mussel and cockle abundance	17
4.2 Measuring quality of mussels and cockles	17
4.3 Measuring the tidal exposure of shellfish beds	17
4.4 Surveying alternative food supplies	17
4.5 Surveying Oystercatcher distribution	18
4.6 Observing Oystercatcher foraging behaviour	18
Chapter 5 Summary	19
Chapter 6 References	21
Chapter 7 Acknowledgements	23

Chapter 1. Overview

Behaviour-based models predict the responses of animal population to environmental change from the combined behavioural responses of the individual animals within these populations. These models predict how individual animals will alter their behaviour in order to respond to environmental change. Their central assumption is that, no matter how much the environment changes, each individual will behave in a manner that maximises its own fitness. Because of this, model animals are expected to respond to environmental change in the same way as real animals. By following the behaviour and ultimate fate of each individual, a behaviour-based model is able to predict the population consequences of the optimal decisions of individuals. These models should therefore provide a reliable means of predicting how animal populations will be influenced by environmental change. Sutherland & Norris (2002) give an overview of behaviour-based models and their application to conservation problems.

The Centre for Ecology and Hydrology (CEH) has applied behaviour-based models to a range of environmental problems affecting coastal birds (*e.g.* West *et al.* 2002, 2003; Stillman *et al.* 2003). The purpose of this report is to describe how a behaviour-based model could be developed to predict the effect of shellfish abundance and distribution, and shellfishery management on the survival rates of oystercatchers overwintering on the Wash. The report describes an existing model based on provisional data (Stillman *et al.* 2003), and the data that are required to increase the accuracy of the models predictions.

The report is divided into the following sections.

- (i) A general description of the CEH behaviour-based model, to explain how the model functions, what it is able to predict and how it can be used to assess the effects of environmental change.
- (ii) A summary of the results of the existing model.
- (iii) A summary of the new data required to improve the accuracy of the model's predictions.

Chapter 2. CEH behaviour-based model

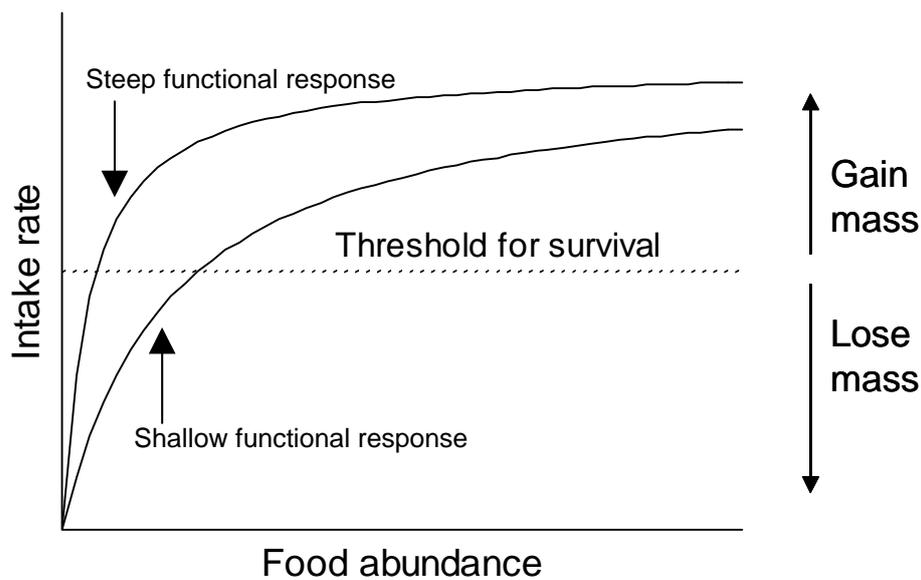
This section provides a brief overview of the CEH behaviour-based model, what it is able to predict and how it is used to predict the effect of environmental change on animal populations.

2.1 Overview of the model

The model predicts how food competition influences the proportion of birds which survive a season, the body condition of the survivors and the rates of mass gain during the season. It incorporates two forms of food competition, depletion and interference (Figure 2.1). Depletion occurs as the abundance of prey within a patch decreases as prey are consumed by birds. To understand how depletion competition influences animal populations it is important to know the shape of the functional response, the relationship between the rate at which animals feed and the abundance of their food. Interference occurs when animals fight over individual prey items or patches of prey. At high competitor densities, more dominant animals may steal food from less dominant animals, reducing their feeding rate.

The CEH model is individuals-based and tracks the foraging location, body condition and ultimate fate of each individual within the population. During each day, each bird in the population must consume enough food to meet its energy demands. These energy demands include any energy required to gain mass. Each bird attempts to meet its demands by feeding in those locations and at those times of the day where and when its intake rate is maximised. Although all individuals decide on the same principle, intake rate maximization, the actual decisions made by each may differ. Their individual choices depend on their particular competitive ability, which depends on two characteristics. Interference-free intake rate is the rate at which an individual feeds in the absence of competition and measures its basic foraging efficiency. Susceptibility to interference measures how much interference from competitors reduces its intake rate as bird density rises. Survival and mass gain rate are determined by the balance between an individual's daily rates of energy expenditure and consumption. Energy expenditure depends on metabolic costs plus any cost of thermoregulation at low temperatures. Energy consumption depends both on the time available for feeding and intake rate while feeding. When daily energy consumption exceeds daily expenditure, individuals accumulate energy reserves or maintain them if a maximum level has already been reached. When daily requirements exceed daily consumption, individuals draw on their reserves. If reserves fall to zero, an individual starves, the only source of mortality in the model. Stillman *et al.* (2000, 2001) describe the model in detail and Stillman *et al.* (2000) perform a sensitivity analysis of the model.

(a) Depletion competition – functional response



(b) Interference competition – interference function

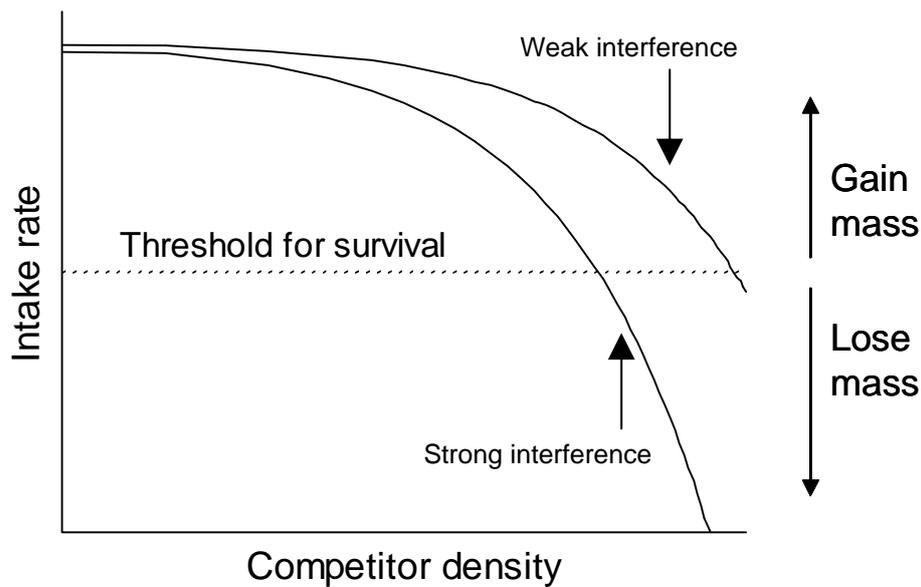


Figure 2.1 How food competition through (a) depletion and (b) interference is incorporated into the model. Birds need to maintain a threshold intake to survive; if their intake exceeds this threshold they can gain mass, but if their intake is below the threshold they lose mass and will ultimately die of starvation. Depletion occurs when prey density is reduced by birds feeding. The shape of the functional response determines how depletion affects intake rate and hence rates of mass gain and survival (a steep functional response means that birds can survive at lower prey densities). Interference occurs through either direct or indirect competitive interactions. The shape of the interference function determines how competitor density affects intake rate and hence rates of mass gain and survival (weak interference means that birds can survive at higher competitor densities). The shapes of the functional response and interference function may vary between different species, or between individuals of the same species.

2.2 Testing the model

The model was originally developed for oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis* in the Exe estuary, UK, and has been most thoroughly tested for this system (Stillman *et al.* 2000, 2001). The model was developed by comparing its predicted mortality rate with the observed rate on the Exe estuary during 1976–81. As a test of the model, its predicted mortality rate was compared with the observed rates during 1981–91, a period when the oystercatcher population increased and there was a density-dependent increase in the mortality rate. The model successfully predicted this increase, even though it was only developed to predict the mortality rate when the population size was considerably lower (Stillman *et al.* 2000). Furthermore, the underlying behaviour of the birds, such as the amount of time spent feeding on mussels and their impact on them, the distribution of birds throughout the estuary and the changes in body mass through the season (Stillman *et al.* 2000). These tests demonstrate the potential of this model in particular, and behaviour-based models in general, to predict with to new circumstances outside the range of conditions for which they were parameterised.

2.3 Parameterising the model

Although the model was developed as part of a long-term field study, only a small fraction of the data collected during that study was used to parameterise the model. The model is being applied to a range of wader conflicts, and has been parameterised for a range of sites and species. Usually it can be applied to a new site in less than a year because general relationships can be used to predict the behaviour of birds at the site. What usually needs to be measured at a new site is the abundance of food and its distribution throughout the site and exposure through the tidal cycle. Food abundance and distribution can be measured from a survey of the site at the start of the season. Changes in the abundance of food through that season can be measured by repeated surveys. The exposure of food through the tidal cycle can be derived from local knowledge or new measurements, or predicted through the use of tidal models.

2.4 Predicting the consequences of environmental change

The model is able to predict the consequences of environmental change caused by factors such as changes in prey abundance, habitat loss, disturbance, shellfishing, recreation, climate change and sea level rise. The model represents the feeding habitats of birds as a number of discrete patches, each of which, at any point in time, has a certain area exposed by the tide and a certain abundance and quality of food. To determine the effect of a change in the environment, the model is initially parameterised and run for the current-day environmental conditions. These simulations are used to predict the current mortality rates and body conditions of birds. At this stage, the model's predictions are compared with as much empirical data as possible in order to assess the accuracy of its predictions. If data are available on the mortality rate and body condition of birds, these are compared with the model's outputs. If these data are not available, as is often the case, empirical data on the distribution of birds throughout a site, prey selection or the proportion of time birds spend feeding are compared with predictions. This assesses how well the model describes the underlying behaviour from which mortality and body condition are predicted.

To predict the consequences of environmental change, appropriate alterations are made to the model's parameters and simulations run to predict mortality rate and body conditions under the new environmental conditions. Change caused by habitat loss is simulated by altering the

area of one or more of the habitat patches. Loss of habitat that is above or below average quality may be simulated by changing the quality of remaining patches as well as their area. Habitat loss may be compensated for by habitat creation schemes, and the relative benefits of difference schemes can be simulated by adding to the model new habitat, of varying quality and exposure through the tidal cycle. Human disturbance excludes birds from areas that would otherwise be used for feeding or roosting, increases the energy demands of birds by causing them to take flight and reduces the amount of time they have to feed. The effect of disturbance can be modelled by excluding birds from some patches, by reducing the time they have to feed and by increasing their energy needs. The effects of shellfishing can be simulated by changing the abundance of the food supply for birds (to account for depletion of prey caused by shellfishing) or by excluding birds from all or part of some patches (to account for disturbance caused by shellfishing).

Chapter 3. Existing Wash Oystercatcher-shellfish model

The predictions of the existing Wash model have been published in Stillman *et al.* (2003). The following sections summarise the model's parameters, predictions and limitations. A full description of the model and its predictions can be found in Stillman *et al.* (2003).

3.1 Description of the existing model

The existing Wash model is a version of the model developed and tested for mussel-feeding oystercatchers in the Exe estuary (Stillman *et al.* 2000, 2001). The Wash model was parameterised for the seven winters between 1992/93 and 1998/99, and simulated the period from 1st September to 15th March each winter. The model versions for each winter differed in the size of the oystercatcher population, the abundance of cockle and mussel food supplies (Figure 3.1) and the climate. The total number of oystercatchers present each winter was taken as the average monthly maximum recorded during Wetland Bird Survey (WeBS) counts between September and March (see Musgrove *et al.* (2001) for methods). The target body masses of oystercatchers (the body mass which each individual attempted to maintain) were the average monthly masses of birds captured on the Wash (Johnson 1985). Oystercatcher daily temperature-dependent energy requirements and digestive restriction on intake rate were the same as used in the Exe estuary model (Stillman *et al.* 2000). Daily temperatures (mean of daily minimum and maximum) were from Hunstanton on the north-east coast of the Wash, and were obtained from the British Atmospheric Data Centre (BADC).

The foraging behaviour of oystercatchers was modelled in a more simple way than in the Exe estuary version of the model. General relationships were used to predict the feeding rate of oystercatchers and how this depended on the densities of mussels or cockles, and the densities of other oystercatchers on the mussel or cockle bed on which a bird was feeding. As general relationships were used, no new data needed to be measured on the behaviour of oystercatchers in the Wash.

The abundance of shellfish within 5 mm size classes in September each year was derived from data routinely collected by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) and the Eastern Sea Fisheries Joint Committee (ESFJC). Each September the abundance of cockles (over 15 mm) and mussels (over 20 mm) on natural and laid beds below the 4 m Chart Datum contour was surveyed from a boat. Data were unavailable for some beds in some years. These were estimated using the most likely values based on observations on adjacent beds or on the same bed in previous or subsequent years, using interpolation or mean values where appropriate. Up to ten cockle beds (Breast, Daseley's, Gat, Herring Hill, Holbeach, Inner Westmark Knock, Mare Tail, Roger/Toft, Stubborn Sand and Wainfleet/Wrangle/Friskney), six wild mussel beds (Inner Westmark Knock, Mare Tail, Daseley's, East Gat, West Gat and South Gat) and five mussel lays (Tofts, Thief, Scotsmans, Pandora and Le Strange) were used in the model (Figure 3.1). Each cockle or mussel bed was represented as a single patch in the model.

As no data were available from the Wash, the mortality rates of mussels and cockles due to factors other than oystercatchers, the length vs. ash-free dry mass (AFDM) relationship in mussels and cockles, the decline in flesh quality through winter in mussels and cockles and the energy density of shellfish were derived from previous studies. Mussel and cockle beds were assumed to expose for six hours during each low tide period (M. G. Yates, personal observation). The amount of shellfish removed from each size class by fishing each year was

also estimated by CEFAS and ESFJC. In the model these quantities were removed from the total stock at the start of simulations as most fishing was early in winter. Most mussel and cockle fishing on the Wash occurs from boats at high tide and so the model assumed that shellfishing did not disturb the birds.

The model only included specific details of the mussel and cockle food supplies below the 4m contour as only these were part of the regular shellfishery survey (Figure 3.1). Relatively few birds feed above the 4m contour at low tide, suggesting that this is a less important feeding area than that below 4 m (Goss-Custard, Jones & Newbery 1977). However, upshore feeding areas can be important to bird survival because they are exposed for longer and hence can provide supplementary feeding when downshore areas are covered by the tide. Upshore areas were incorporated into the model as a single patch, exposing 1 hour earlier and covered 1 hour later (8 hour exposure period) than the shellfish beds below the 4m contour. The supplementary patch represented the food potentially obtained from alternative prey species or mussels and cockles above the 4m contour. For simplicity, depletion and interference were assumed to be insignificant on this patch, meaning that birds feeding on the patch had a constant intake rate throughout the course of winter. The actual intake rate achieved from the upshore during each year was unknown and so simulations were run with a range of possible values. The purpose of the upshore patch was to provide a source of supplementary food which could be exploited if birds were unable to meet their requirements by feeding on the shellfish beds. Birds were not able to survive by feeding solely on the upshore patch.

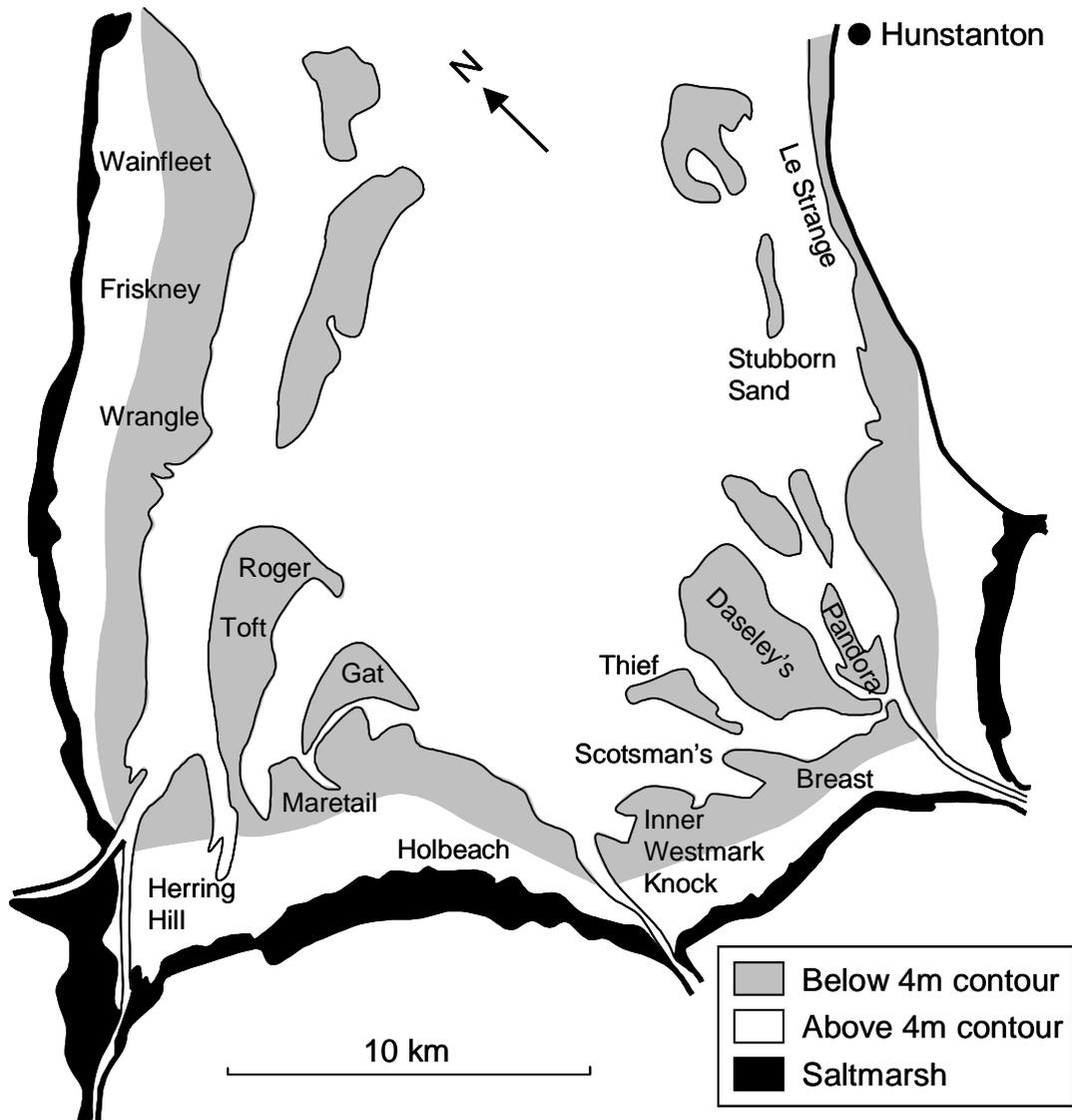


Figure 3.1 Map of the Wash showing the locations of the cockle and mussel beds modelled, and Hunstanton, where weather data were recorded. As the intertidal flats have changed in extent through time, the map is only intended to show the relative locations of the different mussel and cockle beds, rather than their precise location in any one year.

3.2 Predictions of the existing model

A full description of the predictions of the existing model is given in Stillman *et al.* (2003). This section summarises the main predictions of the model.

The model was tested for each year by comparing the predicted mortality rate of oystercatchers with the observed mortality rate (Atkinson *et al.* 2003). During the 1990s there was considerable variation in the sizes of the mussel and cockle stocks in the Wash. The quantity of mussels and cockles removed by shellfishing also varied considerably between years, although only a small proportion of the available stocks were removed most years and, in effect, the wild mussel beds were closed to fishing during this period due to a large crash in previous years. The shellfish stocks were lowest during 1992/93, 1995/96 and 1996/97 both in terms of the total stock available at the start of winter and the amount remaining after shellfishing. The total population of oystercatchers decreased during the 1990s from around 20,000 in 1992/93 to around 10,000 in 1998/99. There was also considerable variation in the overwinter mortality rates (Atkinson *et al.* 2003). Overwinter mortality rates were considerably higher during 1992/93, 1995/96 and 1996/97, 10-26%, than in the remaining years, *circa* 1%. Higher mortality rates were therefore observed in years when the shellfish stocks available to birds were smaller.

During the four years of low observed overwinter mortality (0.5 – 1.5%), the model predicted less than 10% mortality in each year even if no food was available above the 4 m contour (Figure 3.2a,b). In the years of high observed mortality (10 – 26%), predictions varied widely depending on the intake rate birds achieved from the supplementary upshore patch. The model also predicted that the body condition of birds was lower in the years in which observed mortality was higher. Virtually no mortality was predicted if an intake rate of 1 mg s⁻¹ was assumed on the upshore, but up to 70% was predicted if no supplementary feeding was possible (Figure 3.2a). The model therefore correctly distinguished between the years of low and high observed mortality. The predicted and observed mortalities were related to the size of the shellfish stock at the start of winter relative to the number of birds arriving in September (Figure 3.2b). If more than 40 kg AFDM of shellfish were available per bird at the start of winter, predicted and observed mortalities were low. If less than 30 kg AFDM were available per bird, predicted and observed mortalities were high. Overall, the most accurate predictions were produced with an upshore intake rate of 0.67 mg AFDM s⁻¹; the average predicted mortalities were 17.1% and 0.1% in the years of low and high food abundance respectively, compared with observed values of 16.8% and 1.4% (Figure 3.2b). An upshore intake rate of 0.67 mg AFDM s⁻¹ was also the average value recorded in other sites (Stillman *et al.* 2003), but was not necessarily the average value each year on the Wash.

During the years of low observed mortality, predicted mortality was not sensitive to variation in the abundance of shellfish below the 4 m contour (Figure 3.3a,b). Virtually no mortality was predicted even if the total abundance of shellfish was reduced by 50%. In contrast, during the years of high observed mortality, predicted mortality was influenced by variation in shellfish abundance (Figure 3.3a,b). In each year, the predicted mortality rate was reduced to nearly zero if shellfish abundance was increased by 50%, but increased greatly if shellfish abundance was increased by 50% (Figure 3.3a). Although the model's predictions were sensitive to variation in shellfish abundance, it still distinguished between the years of low and high observed mortality.

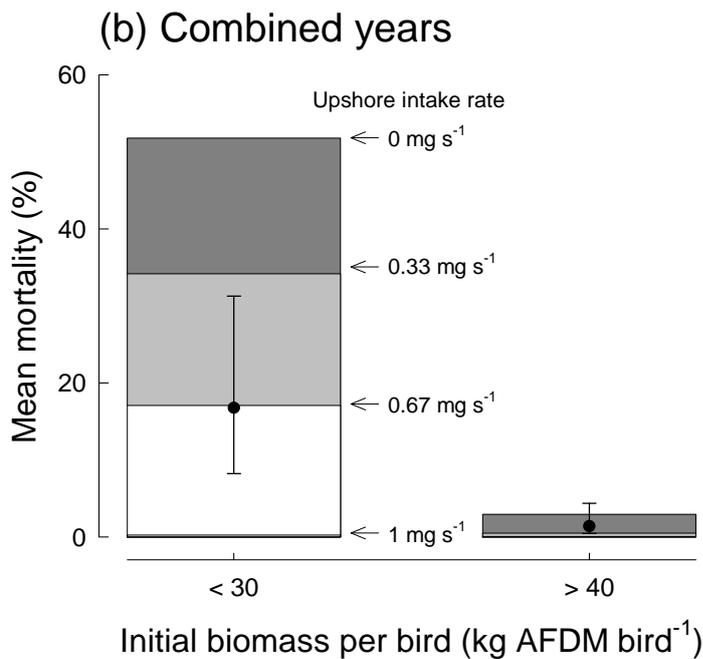
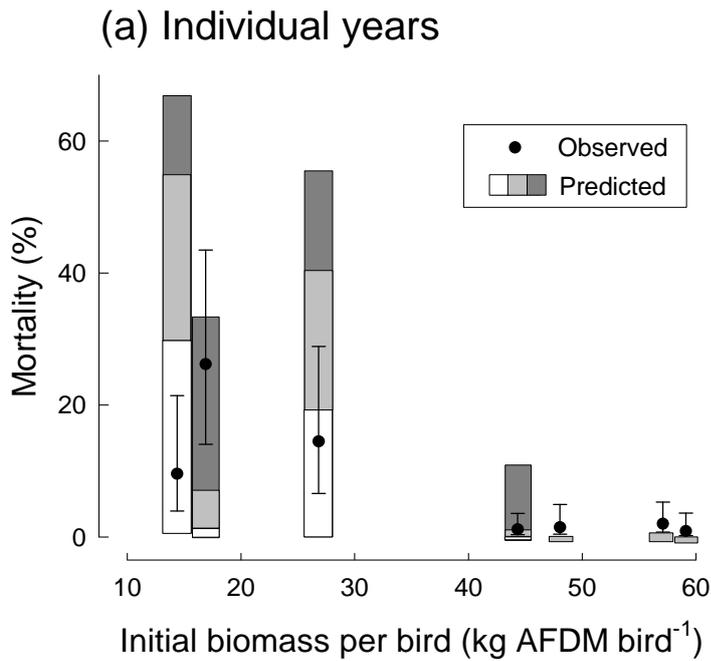


Figure 3.2 Relationship between shellfish stock and oystercatcher overwinter mortality rates on the Wash between 1992/93 and 1998/99: (a) observed and predicted mortality rates during each year; (b) mean observed and predicted mortality rates in years in which the initial biomass of shellfish was either <30 or >40 kg AFDM bird⁻¹. The shellfish stock is measured as the total amount of consumable mussels and cockles per oystercatcher in September each year (excluding the amount removed by shellfishing). The symbols show mean observed mortality and 95% confidence limits. The bars show the sensitivity of predictions to variation in the assumed intake rate achieved by birds from upshore flats. The following upshore intake rates were assumed: 0 mg AFDM s⁻¹ (top of dark grey shading); 0.33 mg AFDM s⁻¹ (boundary between dark and light grey shading); 0.67 mg AFDM s⁻¹ (boundary between light grey and white shading); 1 mg AFDM s⁻¹ (bottom of white shading) (these divisions are highlighted for the left bar in (b)). (Redrawn from Stillman *et al.* 2003)

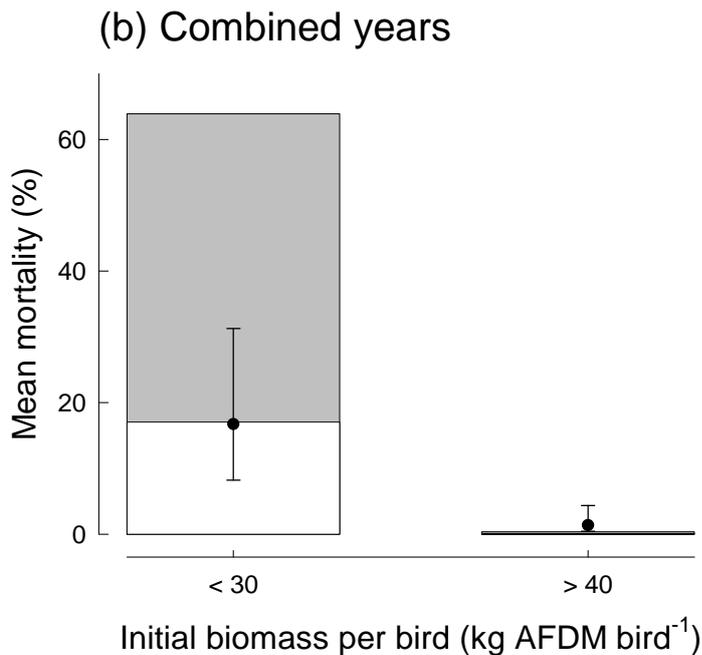
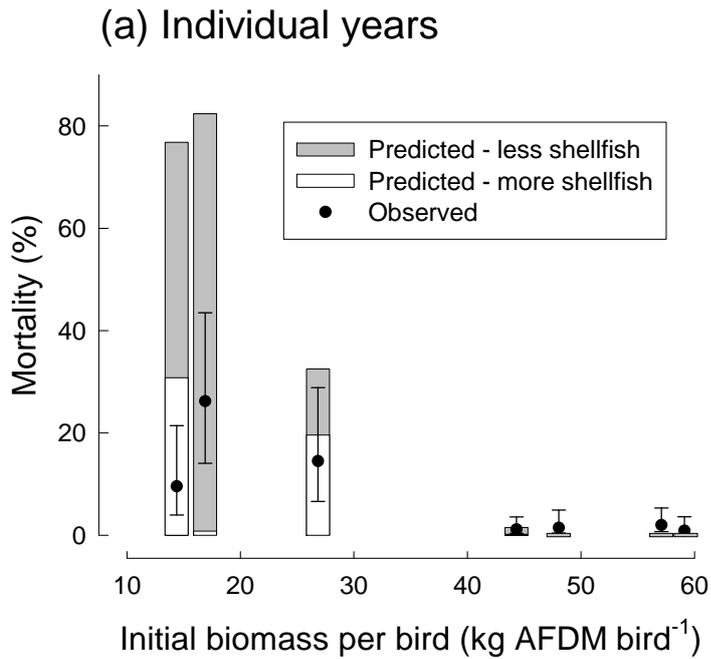


Figure 3.3 Sensitivity of predicted oystercatcher mortality rate to variation in the biomass density of cockles and mussels below the 4 m contour: (a) observed and predicted mortality rates during each year; (b) mean observed and predicted mortality rates in years in which the initial biomass of shellfish was either <30 or >40 kg AFDM bird⁻¹. The symbols show mean observed mortality and 95% confidence limits. The bars show the range of predictions when the combined biomass of cockles and mussels is either increased (white shading) or decreased (grey shading) by 50%. Birds were assumed to have achieved an intake rate of 0.67 mg AFDM s⁻¹ from the upshore flats. (Redrawn from Stillman *et al.* 2003)

3.3 Using the existing model to advise shellfishery management

The model was used to determine the amount of shellfish that needs to be reserved in order to maintain low oystercatcher mortality rates. On the Wash each bird consumed 9 kg AFDM of shellfish during winter. However, Figures 3.2 and 3.3 show that oystercatcher mortality rate started to increase when far more food was available for each bird. Up to 26% of birds were observed to die when twice this amount was available at the start of winter. Many birds were dying before all the food supply was used up. The reason for this was the presence of interference and individual variation which caused birds to die before the food was exhausted. Interference excluded less dominant individuals from some of the food supplies, and individuals of lower foraging efficiency starved before the food supply was depleted to the point at which individuals of average efficiency died. This result has important consequences for shellfishery management. It means that more food needs to be reserved for the birds (more than 4 times the amount they actually eat), than might initially be expected.

The model was also used to predict the most efficient way of providing a new food source to reduce oystercatcher mortality rates. One management option is to dredge mussels from deep waters and lay them in the intertidal area to provide an extra feeding area. New beds could be laid either above (upshore) or below (downshore) the 4m contour and a fixed biomass of mussels could either be laid at high density over a small area, or low density over a large area. The model was used to determine how the laying of an extra mussel bed could have reduced the mortality rate of oystercatchers. In the simulations, mussels laid above the 4m contour were exposed for 8 hours instead of 6 hours, but were assumed to contain only 90% of the flesh of mussels below the 4m contour, as mussel flesh content varies with shore level (Goss-Custard, West & Durell 1993). Mussel density in the high density simulations was set to the average density on mussel lays during 1992/1993. Mussel density in the low density simulations was set to the average density on natural mussel beds during 1992/1993, which had lower mussel densities than the mussel lays. The model predicted that the most efficient way of reducing oystercatcher mortality was to create an upshore, low density bed. The advantage of upshore beds was that they were exposed for longer, and so could be occupied by oystercatchers for longer. This outweighed the fact that they contained lower quality mussels than downshore beds. The advantage of low density beds was that, as they were larger in size (for a fixed mussel biomass), oystercatcher density was lower and so interference competition was also lower.

Chapter 4. How to improve the model's predictions

The model was able to distinguish between years of low and high oystercatcher mortality, but does have some limitations. In particular, Figures 3.2 and 3.3 show that the model's predictions are very sensitive to the amount of food on the shellfish beds, and the amount of food above the 4m contour. This section describes the new data required to improve the model's predictions.

4.1 Surveying mussel and cockle abundance

Figure 3.3 showed that the model's predictions were very sensitive to the abundance of mussels and cockles. These parameters were estimated from existing survey data, and were sometimes not available for some beds in some years. The surveys were conducted for the purpose of shellfishery management and so were restricted to parts of the Wash in which shellfishing occurs, and excluded areas which, although unfished, may be important for oystercatchers. As the existing survey data are incomplete and do not cover the full area exploited by oystercatchers, confidence in the model's predictions could be greatly increased by new surveys of the Wash shellfish populations. It would also be an advantage if these surveys tracked changes in the abundance of shellfish through the winter. Ideally, these surveys could be a modification of the existing surveys, covering a larger area of the Wash, than that in which fishing occurs. Ideally, these surveys would be conducted in September and March to measure the food supply at the start and end of winter.

4.2 Measuring quality of mussels and cockles

The food value of mussels and cockles depends on their size, and the amount of flesh within their shells. These parameters were estimated from previous studies, and so the model would be improved if new values were recorded on the Wash. The size distribution of cockles and mussels should be recorded during the surveys described in section 4.1. Flesh content needs to be measured by collecting mussels and cockles of a range of sizes, from a range of beds with different lengths of exposure through the tidal cycle. These data can then be used to derive bed-specific relationships between shell length and the ash-free dry mass of flesh within the shell.

4.3 Measuring the tidal exposure of shellfish beds

The amount of time for which feeding areas are exposed by the tide is also an important factor. In the existing model, tidal exposure was estimated from local knowledge of the site, but was not measured directly. Measuring the tidal exposure times of each cockle or mussel bed is another way of increasing confidence in the models predictions. An alternative to direct measurement would be to predict exposure times, if a suitable tidal model exists.

4.4 Surveying alternative food supplies

Figure 3.2 showed that the model was very sensitive to the amount of food above the 4m contour, even though oystercatchers could not survive by feeding on these alternative areas alone. Ideally, the surveys described in section 4.1 should be extended to alternative food sources, but this will probably be impractical. An alternative is to estimate the likely variation in the abundance of alternative foods from existing surveys. CEH has surveyed the whole or parts of the Wash over recent years, and this data can be used to assess the likely variation in the quality of alternative food supplies.

4.5 Surveying oystercatcher distribution

The model was tested by comparing its predicted oystercatcher mortality rate with the observed rate. This is the key test of the model, because mortality rate is the major model prediction. However, to increase confidence in the model, it is also important to determine whether it is correctly predicting the underlying behaviour from which mortality itself is predicted. An important component of the model is where birds are predicted to feed and what they are predicted to feed on. This could be tested by surveying the distribution of oystercatchers, by counting numbers on different mussel and cockle beds.

4.6 Observing oystercatcher foraging behaviour

The model predicts the foraging behaviour of oystercatchers from relationships derived in other sites. Although not essential, some observations of oystercatcher foraging behaviour on the mussel and cockle beds of the Wash would be preferable. This would determine whether behaviour in this site is typical of that in the sites in which the general relationships have been derived.

Chapter 5. Summary

Behaviour-based models predict the responses of animal population to environmental change from the combined behavioural responses of the individual animals within these populations. The Centre for Ecology and Hydrology (CEH) has applied behaviour-based models to a range of environmental problems affecting coastal birds.

This report describes behaviour-based models, and how an existing model has been used to predict the mortality rate of oystercatchers in the Wash. This model was able to distinguish between years of low and high oystercatcher mortality. Both predicted and observed mortality rates were low when shellfish were abundant, and high when shellfish were more rare. The model was also used to advise how shellfish stocks could be managed to maintain low oystercatcher mortality rates. However, the model does have some limitations and so the report describes the data that could be collected to increase confidence in the model's predictions.

The major requirement is to more accurately measure or gain more information on the abundance of the shellfish food supply and the supply of alternative foods. It is also important to assess the quality of shellfish as food sources by measuring the size distribution of shellfish, and by measuring their flesh content. A further requirement is to improve knowledge of the time for which different cockle and mussel beds are exposed by the tide. Other data could be collected to record the numbers of oystercatchers feeding on different mussel or cockle beds, in order to test the model's predictions. Lastly, some observation of the foraging behaviour of birds could be made, but this is of lesser importance than measurement of the food supply.

Chapter 6. References

- Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A. & Ireland, P.L. (2003) Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biological Conservation*, **114**, 127-141.
- Goss-Custard, J.D., Jones, R.E. & Newbery, P.E. (1977) The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 681-700.
- 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.
- Johnson, C. (1985) Patterns of seasonal weight variation in waders on the Wash. *Ringing & Migration*, **6**, 19-32.
- Musgrove, A.J., Pollitt, M.S., Hall, C., Hearn, R.D., Holloway, S.J., Marshall, P.E., Robinson, J.A. & Cranswick, P.A. (2001) The Wetland Bird Survey 1999-2000: wildfowl and wader counts. BTO/WWT/RSPB/JNCC, Slimbridge.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., Durell, S.E. A. le V. dit, Caldow, R.W.G., McGroarty, S. & Clarke, R.T. (2000) Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology*, **37**, 564-588.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., McGroarty, S., Caldow, R.W.G., Durell, S.E. A. le V. dit, Norris, K.J., Johnstone, I.G., Ens, B.J., van der Meer, J. & Triplet, P. (2001) Predicting oystercatcher mortality and population size under different regimes of shellfishery management. *Journal of Applied Ecology*, **38**, 857-868.
- Stillman, R.A., West, A.D., Goss-Custard, J.D., Caldow, R.W.G., McGroarty, S., Durell, S.E.A. le V. dit, Yates, M.G., Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P. J. & Mander, M. (2003) An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. *Journal of Applied Ecology*, **40**, 1090-1101.
- Sutherland, W.J. & Norris, K. (2002) Behavioural models of population growth rates: implications for conservation and prediction. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **357**, 1273-1284.
- West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W.G., Durell, S.E.A. le V. dit & McGroarty, S. (2002) Predicting the impacts of disturbance on wintering wading birds using a behaviour-based individuals model. *Biological Conservation*, **106**, 319-328.
- West, A.D., Goss-Custard, J.D., McGroarty, S., Stillman, R.A., Durell, S.E.A. le V. dit, Stewart, B., Walker, P., Palmer, D.W., & Coates, P. (2003) The Burry shellfishery and oystercatchers: using a behaviour-based model to advise on shellfishery management policy. *Marine Ecology Progress Series*, **248**, 279-292.

Chapter 7. Acknowledgements

The BTO wishes to acknowledge the financial support of English Nature.