

# The Burry shellfishery and oystercatchers: using a behaviour-based model to advise on shellfishery management policy

Andrew D. West<sup>1,\*</sup>, John D. Goss-Custard<sup>2</sup>, Selwyn McGroarty<sup>1</sup>, Richard A. Stillman<sup>1</sup>, Sarah E. A. le V. dit Durell<sup>1</sup>, Barry Stewart<sup>3</sup>, Peter Walker<sup>4</sup>, David W. Palmer<sup>4</sup>, Philip J. Coates<sup>5</sup>

<sup>1</sup>Centre for Ecology and Hydrology Dorset, Winfrith Technology Centre, Winfrith Newburgh, Dorchester 8ZD, United Kingdom

<sup>2</sup>30 The Strand, Topsham, Exeter EX3 0AY, United Kingdom

<sup>3</sup>36 Pencaecrown Road, Penyrheol, Gorseinon, Swansea SA4 4FU, United Kingdom

<sup>4</sup>The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft NR33 0HT, United Kingdom

<sup>5</sup>South Wales Sea Fisheries Committee, Queens Buildings, Cambrian Place, Swansea SA1 1TW, United Kingdom

**ABSTRACT:** The Burry inlet, South Wales, supports a licensed cockle *Cerastoderma edule* fishery and occasional mussel *Mytilus edulis* fishery. It is also an important overwintering ground for oystercatchers *Haematopus ostralegus*. In recent years mussels have settled over parts of some cockle beds, preventing cockle fishery there and leading to a request by shellfishers to remove this 'mussel crumble'. Conservation managers, however, were concerned that the mussel crumble might be providing a high-quality food source for the oystercatchers, making its removal detrimental to the birds. A behaviour-based model of oystercatcher feeding on cockles and mussels was parameterised for the inlet and its predictions tested against the distribution of birds across the shellfish beds and the amount of time they spent feeding. The model was then used to explore whether the birds were currently food-limited and what would be the effects on their mortality rate and body condition if the mussel crumble were to be removed, thereby re-exposing underlying cockle beds. The model predicted successfully the proportion of birds feeding on the different types of food and the number of hours birds spent feeding on neap tides. It was predicted that, at current bird population sizes, there would have to be a 50% reduction in shellfish stocks and the areas of shellfish beds from 2000–01 levels to cause noticeable extra emigration or mortality. A given area of mussel bed was predicted to be able to support more birds than the same area of cockle bed, but the greater area of the cockle beds meant that they were more important than mussels in determining the number of birds supported by the inlet. The simulated removal of mussel crumble to expose underlying cockles had no effect on predicted bird mortality and body condition at 2000–01 shellfish stock levels. However, there were circumstances under which the mussel crumble was predicted to increase the inlet's capacity to support birds, particularly when the area of existing cockle and mussel beds was substantially reduced.

**KEY WORDS:** Shellfishery management · Behaviour-based model · Oystercatcher · Cockle · Mussel

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Intertidal shellfish populations provide a source of food for both shorebirds (Charadrii) and humans. This

leads to potential conflicts between the interests of commercial shellfishers and those of conservationists. For example, shellfishers are often concerned about the effects of shorebird predation on shellfish stocks,

while on the other hand conservationists are concerned with the effect of shellfishing on the ability of those same stocks to support bird populations. In this paper we use a behaviour-based modelling approach to make quantitative predictions in one particular case where such conflicts arise. We predict the effects of different shellfish management options on a population of oystercatchers *Haematopus ostralegus* in the Burry inlet, South Wales.

The Burry inlet is an internationally important wintering site for oystercatchers. The birds that overwinter there feed mainly on intertidal cockle *Cerastoderma edule* and mussel *Mytilus edulis* beds. The main fishery in the inlet is the licensed hand-gathering of cockles, which takes place throughout the year. There is also occasional mussel fishing by hand and dredging of mussels for re-laying in commercial fisheries elsewhere in the country. In the past, concern over the impact of oystercatcher predation on cockle stocks in the Burry inlet (Davidson 1967) led to the shooting of thousands of oystercatchers during the winter of 1973–74 (Prater 1974). Over the last few years a new source of potential conflict has arisen — there has been extensive settlement of young mussels over areas of the cockle beds on Llanrhidian Sands and elsewhere in the inlet (Fig. 1). The Burry inlet cockle industry, suspecting that this 'mussel crumble' would smother the cockles lying in the sand beneath and thus remove some of the resources upon which their industry depends, requested permission to remove the crumble

overlying Llanrhidian Sands. In addition, these mussels would provide seed for laying elsewhere once removed, and thus in themselves be a valuable source of new income. Conservation managers were concerned, however, that there might be circumstances in which the mussel crumble would be of great benefit to the oystercatchers that overwinter in the inlet. For example, for the ca. 85% of oystercatchers in the inlet that mainly eat cockles, it was thought possible that the mussel crumble could provide a supplementary food source in years when cockle stocks are low and at times during the tidal cycle when most of the cockle beds are submerged.

The likely effect of any proposal to change the shellfishing regime within the inlet depends on how near the oystercatchers are to being food-limited under present conditions. Being 'food-limited' is defined here as some birds having difficulty in meeting their energy requirements so that they either fail to accumulate the energy reserves needed to migrate back to their breeding grounds, leave the area, or starve to death. First, therefore, we explore how close oystercatchers in the inlet are to being food-limited at present. We then explore the consequences of changing the stocks of cockles and mussels in the inlet in general for a range of oystercatcher population sizes in terms of 4 indicators of food limitation (mortality/emigration, fat storage, feeding time and percent of shellfish stocks eaten). Finally, we explore in a similar way the consequences for a range of oystercatcher population sizes of the removal of the mussel crumble over a range of cockle and mussel stock scenarios.

For 2 reasons, a modelling approach was required to assess the impact of removing the mussel crumble. Firstly, there was no information about past mortality rates on the inlet, and in any case the crumble is a recent phenomenon, so past experience could not provide any indication of the likely effects. Secondly, interference competition has been shown to occur between oystercatchers feeding on mussels (Zwarts & Drent 1981, Ens & Goss-Custard 1984, Goss-Custard & Durell 1987) and on cockles (Triplet et al. 1999) at the ranges of bird and shellfish densities that occur in the Burry inlet, so approaches based solely on the quantity of food available under different scenarios would be inappropriate (Pettifor et al. 2000) and risk greatly underestimating mortality (Goss-Custard et al. 2001). The model used in this paper is an individual-based model, which is also behaviour-based. It was developed to explore the relationship between oystercatchers and

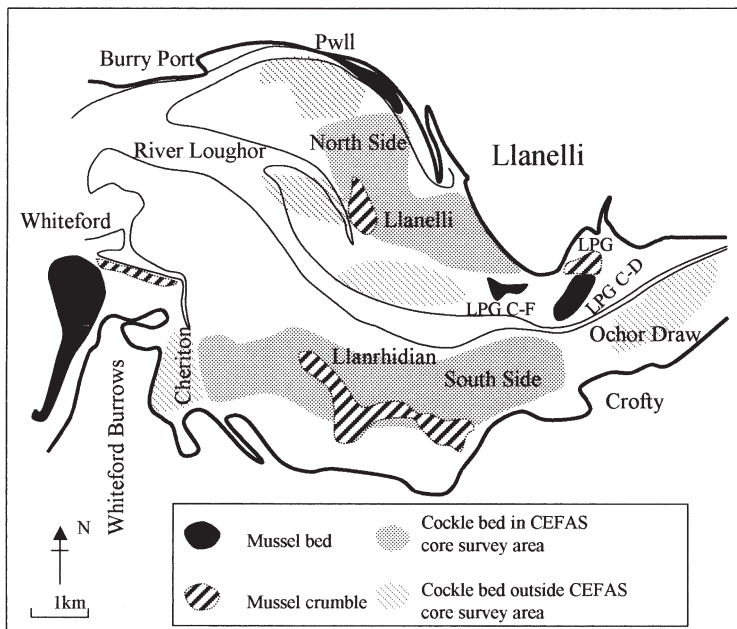


Fig. 1. Sketch map of the Burry inlet, showing the location of cockle *Cerastoderma edule* beds and mussel *Mytilus edulis* crumble in winter 2000–01

shellfish populations in order to inform policy-makers of the consequences for oystercatchers and the shellfish industry of alternative ways of managing shellfisheries (Goss-Custard et al. 2000). The model is described in detail in Stillman et al. (2000), where the successful testing of its most important predictions, particularly winter mortality, is also described and a comprehensive sensitivity analysis performed. Its application to 2 particular systems (birds eating mussels on the Exe Estuary and birds eating cockles on the Burry inlet) is described in Stillman et al. (2001). In this paper, the model is applied to both cockle and mussel-feeding oystercatchers in the Burry inlet and is used to make predictions about the potential consequences of a real-world practical shellfish management issue.

## MATERIALS AND METHODS

**Model structure.** The model is fully described in Stillman et al. (2000). Fig. 2 shows the outline structure of the model, as applied to shellfishing. Two modules predict the main effects of shellfishing on oystercatchers. The shellfishing module predicts any effects of shellfishing on the abundance, size distribution and species composition of the birds' food supply. It also predicts the effects of any disturbance to birds caused by shellfishing. Disturbance prevents birds from feeding within a certain distance of shellfishers and may also force them to feed in other places, often of poorer quality, where interference and exploitation competi-

tion may intensify because of increased bird density. The disturbance also costs the birds lost feeding time and the energy involved in moving. All these effects are included in the model (West et al. 2002). The shorebird module predicts how these changes and disturbances will affect the distribution of birds across shellfish beds and, consequently, their intake rates. The responses to shellfishing made by model birds are based on game theory, using intake-rate maximisation as their decision principle. This basic principle is unlikely to change in the new scenarios even if the specific decisions made by individual animals, and thus their chances of surviving, do change. The birds in the model are therefore thought to respond to shellfishing as real birds would.

The model follows the daytime and night-time prey choice and location of each oystercatcher in the model throughout 'winter', which for oystercatchers is considered to run from September (when birds arrive from the breeding grounds) to March (when they return). At low tide, each individual in the model chooses to feed on the size classes of shellfish and on the shellfish bed where it will maximise its intake rate. Each individual therefore takes into account the food supply and the number and competitive abilities of other oystercatchers on each bed. The model includes seasonal changes in prey quality, the weather and the neap-spring and diurnal cycles. Whether an individual survives the winter is determined by the balance between its daily rates of energy acquisition and temperature-dependent energy expenditure. Energy acquisition depends

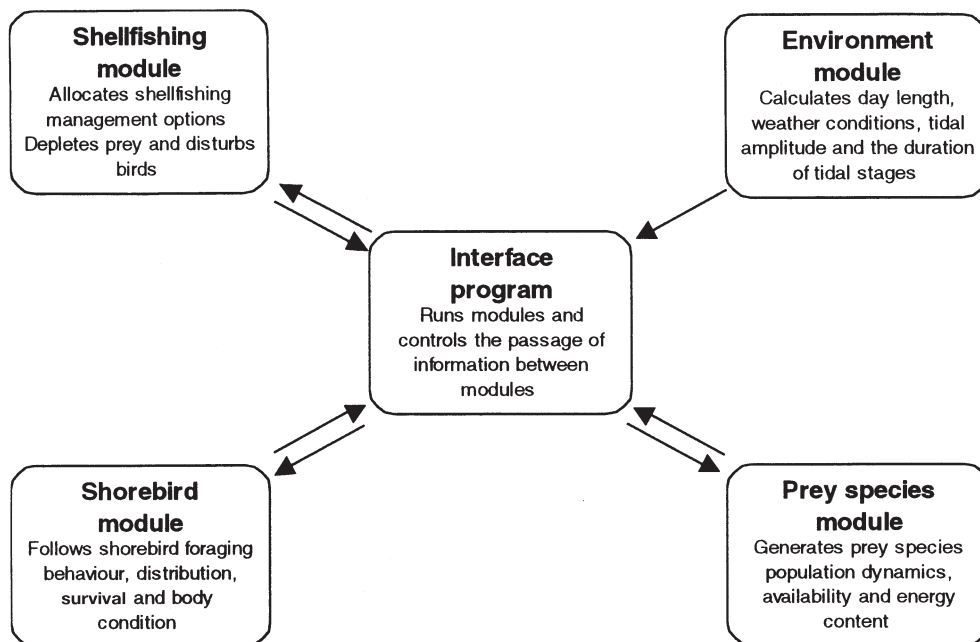


Fig. 2. General structure of the behaviour-based individuals model of oystercatchers feeding on shellfish

both on the time available for feeding and the intake rate while feeding. When daily energy acquisition exceeds daily expenditure, individuals accumulate fat reserves, up to a specified and seasonally varying maximum level. When daily requirements exceed daily acquisition, individuals draw on their reserves. If reserves fall to zero, the individual starves to death, the only source of mortality in the model and the main cause of winter deaths in nature.

**Parameterising the model. Defining the food resources:** The model included all the main food supplies available to oystercatchers in the Burry inlet. These were: (1) 5 patches of cockles *Cerastoderma edule*, which are exposed and available to birds for periods of between 6 and 12 h over low water, depending on their level on the shore and the stage of the spring-neap cycle; (2) 9 mussel *Mytilus edulis* beds, 4 of which represented the mussel crumble under investigation in this study, which were exposed for between 4 and 8 h over low tide; (3) earthworms and insect larvae in fields, which are continuously available.

**Cockle survey:** The distribution of cockles throughout the estuary was determined using methods described in Palmer (2001). Cockle distribution was surveyed both within the 'core' survey area, which is surveyed annually by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS), and outside this in the 'extra' survey area (Fig. 1). Samples were collected at 50 m intervals along a series of transects through all the main cockle beds in the inlet. At each sampling station a single sample was collected using a 0.1 m<sup>2</sup> quadrat, driven into the sand to a depth of 6 cm. Sand was removed using a rake and fingers and sieved through a 4 mm mesh sieve. All cockles were counted and aged immediately. On each transect, 2 or 3 samples were retained for more detailed age determination, weighing and measuring which was carried out within 12 h of collection. Cockle lengths were measured using a simple caliper gauge. From the retained samples on each bed, up to 10 cockles of each 1 mm length group were dried on a paper towel and weighed individually, to the nearest 0.1 g below, on a Sartorius QT1600 electronic balance. The wet weights thus obtained were used to convert monthly landing tonnages into numbers of cockles removed by shellfishers.

**Mussel survey:** Mussel patches were surveyed using the methods described in McGroarty et al. (1990). A baseline was established alongside the mussel bed or patch of crumble using bamboo canes or existing marker posts. The distance across the mussel bed was measured using a 1 m pacing stick along a series of regularly spaced transects at right-angles to the baseline. The distances at which the boundaries of the bed were crossed were noted. At each 1 m pace across the

bed, the presence or absence of one or more mussels (>20 mm) within a 20 × 20 cm quadrat was noted. These data were used to draw an outline map of the mussel bed, to calculate its area and the percentage cover of mussels within it and hence the actual area of mussels.

To estimate mussel density, between 10 and 55 samples (20 × 20 cm quadrat) of mussels were taken at random from each bed or patch of crumble. The number was determined on site according to the area and the variability of the mussel cover/density within it. In total 200 samples were collected. A separate sample of 40 to 50 mussels covering a wide range of sizes (20 to 70 mm) was also taken at random from each of the main areas to determine the ash-free dry mass of the mussels. This was determined by drying the flesh of 40 to 50 mussels individually at 90°C and burning in a muffle furnace at 550°C, both to constant mass.

**Shellfishing activities:** The South Wales Sea Fisheries Committee (SWSFC) provided data on the monthly tonnage of cockles landed and the number of licensed cockle fishers. In the model, each fisher disturbed a circular area around him or her, preventing birds from feeding there. The number of shellfishers therefore determined the amount of disturbance that the birds experienced. A fixed daily quota and a variable number of shellfishers was used to vary the level of the fishing activity carried out on the cockle beds at each stage of the winter.

Shellfishers were assumed to take cockles of all size-classes above the current permitted minimum and to do so in proportion to the density at which each size-class was present. Model shellfishers raked cockles at a rate derived from Norris & Johnstone (1996). This rate determined how long it took a shellfisher to obtain the permitted take for a given day, and thus also determined for how long that shellfisher disturbed the birds. Unlicensed cockle fishing is known to take place on the inlet. Local fisheries staff estimate that this amounts to 10% of the legal take, so the total amount of cockles taken by shellfishers in the model was increased by 10% above recorded landing figures. Appendix 1 gives a full list of model parameters and their values.

**Validating the model.** Several predictions were tested to assess how closely the model system matched the real world. These were: (1) the proportion of oystercatchers using each type of food (cockles, mussels, and mussel crumble); (2) the numbers of birds using each patch of food within each of these prey types, and (3) the amount of time birds spent feeding through the tidal cycle. These measures were chosen because they test whether model birds are feeding on the correct prey and fulfilling their daily energy requirements in the same amount of time as real birds. They are also more sensitive to changes in conditions and easier to

measure in the field than bird mortality and weight distribution. Oystercatcher mortality and weight data are not currently available for the Burry inlet. The chosen indicators were measured as follows.

**Distribution between prey types and patches:** The numbers of oystercatchers feeding on each cockle and mussel patch in the inlet was counted over low tide on 7 occasions during January and February 2001 (Stewart 2001). These figures were used to determine the average proportion of birds feeding on cockles and mussels and the average number feeding on each patch.

**Time spent feeding:** Stewart (2001) performed a series of half-hourly counts in specific areas over the period for which shellfish beds were exposed, on 8 occasions between January and March 2001. It was thought likely that many birds were not visible at low tide on spring tides, because they were feeding either in areas low down the shore within the inlet or on feeding areas exposed on the low-level sand flats just outside. For this reason, only neap tide counts were used to calculate time spent feeding. On each of the 4 occasions, the highest counts in a specified area were assumed to represent the numbers of birds that obtained most or all of their food in that area — the 'resident population'. Then, for each half-hour period, the numbers that were actually visible and recorded as feeding were expressed as a proportion of the resident population. Thus birds that could not be seen were assumed not to be feeding but to be roosting out of sight. The proportion of birds feeding during each half hour was then used to calculate the average amount of time spent feeding for each half hour, and the results combined to give the total amount of time spent feeding during the day, on average, on each of the 4 occasions. Oystercatchers are known to feed at night (McNeil et al. 1992, Sitters 2000) and were able to do so in the model, but it was not possible to measure time spent feeding at night during this study.

**The simulations. Model validation:** To test the model as described above, simulations were run with bird numbers, prey densities and patch areas as measured during winter 2000–01. This included cockle beds outside the normal CEFAS survey area (Fig. 1), which were surveyed in order to parameterise these simulations (Walker 2001). These simulations were used to test whether the model predicted the 3 readily observed aspects of bird behaviour on the estuary correctly.

**Food limitation:** To explore how close to food limitation the model predicted the birds to be in the inlet, simulations were run at 3 different bird population sizes of 10 000, 15 000 and 20 000 (the population in winter 2000–01 varied between approximately 10 000 and 16 000). On the basis that little is known about stocks outside the CEFAS core survey area, cockle

stocks in these simulations were based on this core area only (Fig. 1). The cockle beds found outside these areas were thought to be due to an exceptionally high spatfall in 1999, so may not be present every year.

In these simulations, the abundance of mussel crumble was kept the same as measured during the survey whilst cockle and mussel stocks were varied by changing the area of the shellfish beds. This way of varying the stocks, as opposed to varying densities, was chosen because it matches the kind of applied problems that have to be resolved (e.g. the wholesale removal of parts of mussel beds by dredging) and because it is the more precautionary approach in a system where interference competition is present and will increase if shellfish beds become smaller. The annual cockle harvest in the Burry inlet is based on the fishable biomass determined by the CEFAS survey. Thus, shellfishing was varied in line with the changes in shellfish stocks, for example, when cockle beds were reduced to half of their 2000–01 sizes, the amount of cockle fishing was also halved.

**Removing mussel crumble:** In these simulations, all areas of mussel crumble in the model were removed and replaced by equal areas of cockles occurring at a density and with a size distribution the same as those on the cockle patch nearest to the removed crumble. Simulations of the most precautionary scenario, in which cockle and mussel stocks varied together, were then repeated.

## RESULTS

### Model validation

#### Percent feeding on different types of prey

Over the winter as a whole, the model accurately predicted the percentages of birds feeding on cockles, mussels and mussel crumble over the low tide period to within the 95% confidence intervals (Fig. 3). The model also predicted well the number of oystercatchers feeding in fields at high water. In the winter of 2000–01, less than 3% of the birds were predicted to feed over high water in fields around the inlet. This accords well with the observations that only very small numbers of oystercatchers were actually recorded feeding around the inlet that winter (Stewart 2001).

#### Numbers using each patch

The comparison between the predicted and observed distribution is made for January and early February, an important time for the birds because the low



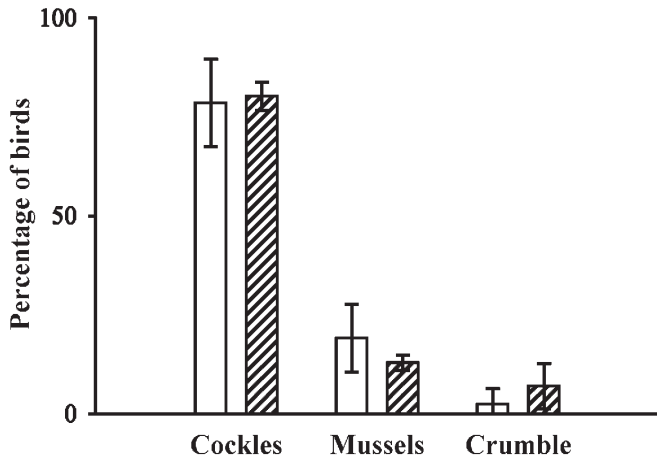


Fig. 3. *Haematopus ostralegus*. Observed (open bars) and predicted (hatched bars) proportion of birds feeding on each patch type, with 95% confidence intervals

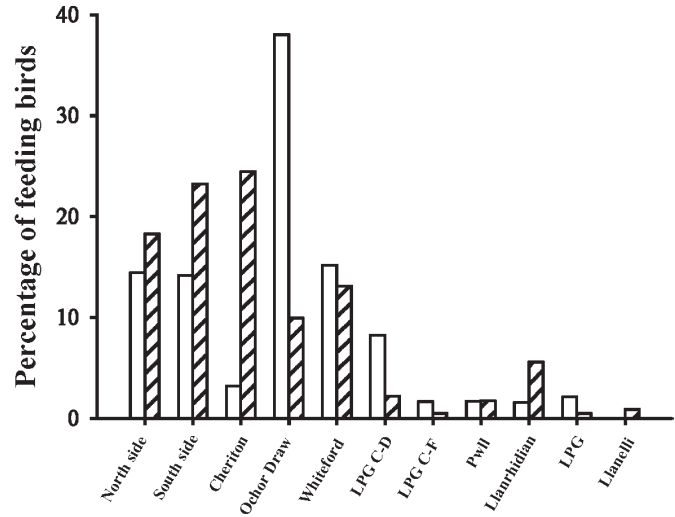


Fig. 4. *Haematopus ostralegus*. Observed (open bars) and predicted (hatched bars) numbers of birds feeding on different parts of the Burry inlet

temperatures at this time of year increase their energy demands, and the shellfish are in much poorer condition than in autumn. The predicted and observed mean numbers of oystercatchers, from a total population of ca. 12 000, actively feeding over the low water period during January and early February were very similar: observed = 6268 (SE 1071); predicted = 6571 (SE 185). The predicted and observed distributions of birds were compared by expressing the numbers feeding in each patch over low water as a percentage of all of the birds in the inlet that were actively feeding over the low water period (Fig. 4). In cases where bird count areas encompassed more than 1 cockle patch, predicted numbers for those cockle patches were combined. The model predicted the percentage of the feeding birds that were foraging on the mussel beds at Whiteford and Pwll well but slightly over-predicted the percentage using mussel crumble, especially on Llanrhidian Sands. The predictions for the percentage of birds feeding on cockles on the north side of the inlet matched observed values reasonably well. The model also predicted the overall percentage of birds feeding on the south side of the inlet quite well. However, the predicted distribution between beds on the south side of the inlet was not as good. The model under-predicted the number of birds feeding on the Ochoor Draw cockle bed and over-predicted the numbers feeding on the other south-side beds.

Time spent feeding

The model predicted the number of hours spent feeding by an average oystercatcher during a daytime

tidal cycle with encouraging precision (Table 1). Across all 4 comparisons, the model over-predicted the time spent feeding by only 11% (40 min).

Food limitation

Given the abundance of cockles present in the CEFAS core survey area in 2000–01 and current oystercatcher population levels of 10 000 to 16 000, the model predicted that very few birds (<1%) would either have to leave the inlet or starve to death during the winter. The model predicts that density-dependent mortality starts to occur within the range of oystercatcher numbers observed on the inlet that year. As the population increased to 20 000 an increasing percentage of birds were predicted to leave the inlet or die from starvation (Fig. 5a). The percentage of birds failing to reach their target weight for migration at the end of winter followed a similar trend, although the numbers were higher and the density-dependence stronger (Fig. 5b). As population size increased from

Table 1. *Haematopus ostralegus*. The predicted and observed number of hours spent feeding by the average oystercatcher over a daytime tidal cycle on 4 neap tides in winter 2000–01

Prey	Date (dd/mm/yy)	Predicted	Observed
Cockles	22/01/01	6.00	5.08
Cockles	18/02/01	6.29	7.15
Mussels	19/01/01	6.75	6.55
Mussels	03/03/01	7.09	4.67
Mean		6.53	5.86

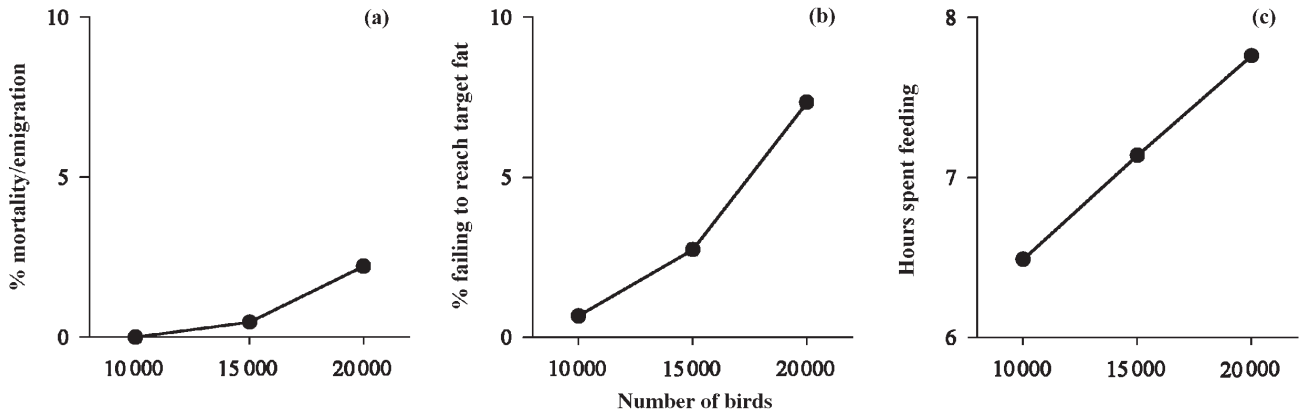


Fig. 5. *Haematopus ostralegus*. Predicted (a) emigration/mortality, (b) percentage of birds failing to reach target-fat accumulation at the end of winter and (c) number of hours spent feeding per 12.4 h tidal cycle vs bird population size. Shellfish stocks based on 2000–01 CEFAS core survey area

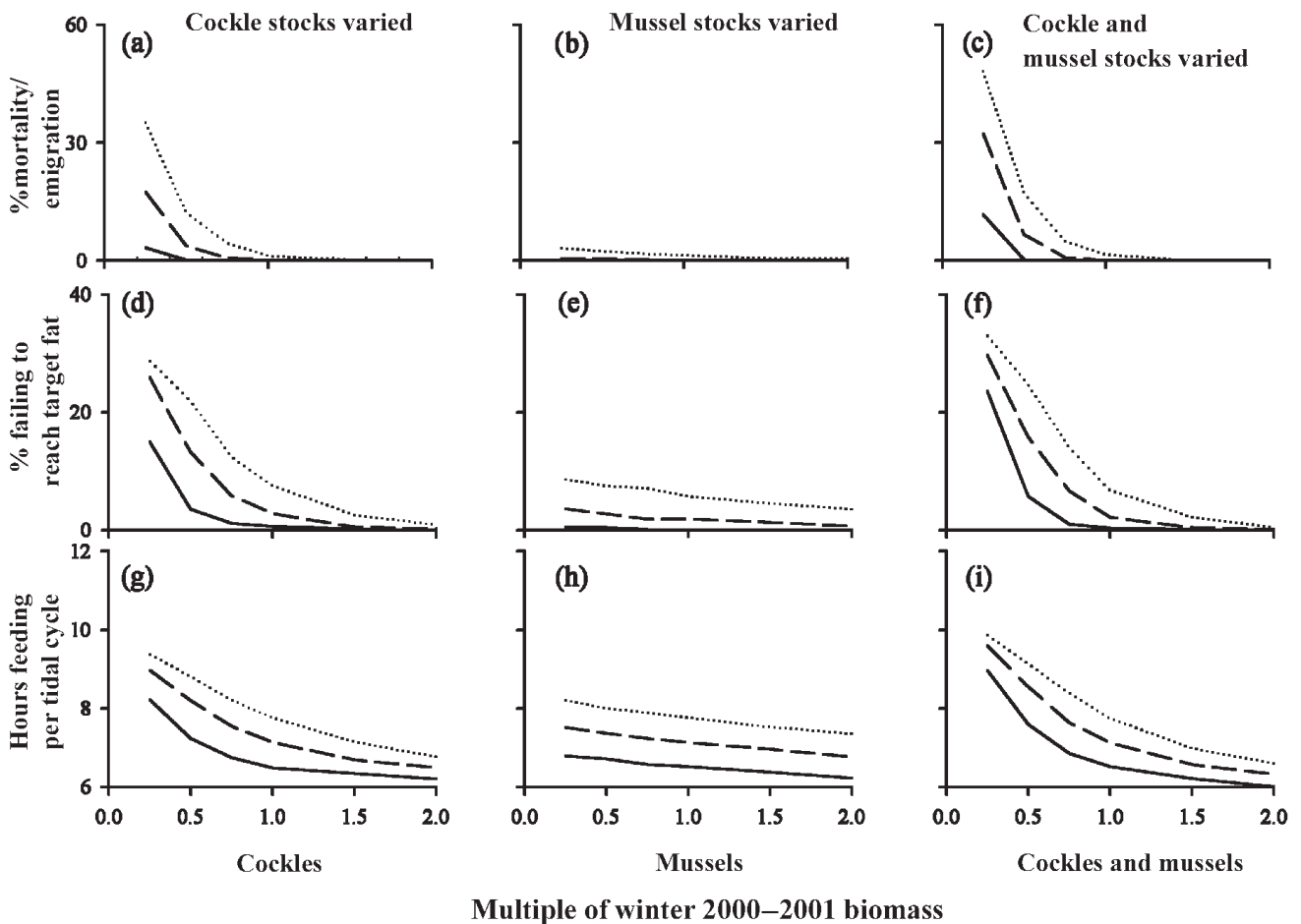


Fig. 6. *Haematopus ostralegus*. Predicted (a–c) emigration/mortality, (d–f) percentage of birds failing to reach target fat accumulation at the end of winter and (g–i) number of hours spent feeding per 12.4 h tidal cycle at 3 different bird population sizes (10 000 solid lines, 15 000 dashed lines, 20 000 dotted lines) when shellfish stocks are varied in relation to their 2000–01 levels. (a,d,g) cockle stocks varied; (b,e,h) mussel stocks varied; (c,f,i) cockle and mussel stocks varied simultaneously

10 000 to 20 000 the predicted number of hours spent feeding by the average bird increased by approximately 20% (Fig. 5c). The effects of varying shellfish stocks depended on the initial bird population size and on which stocks were varied. When mussel stocks alone were varied, there was relatively little change in mortality (Fig. 6b), the percentage achieving their target weight (Fig. 6e) or the time spent feeding (Fig. 6h). When cockle stocks were reduced, alone or in combination with mussel stocks, mortality increased gradually at first, then more steeply as stocks became lower (Fig. 6a,c). At the lowest bird population size of 10 000, mortality from starvation did not begin to occur until shellfish stocks were less than 50% of the values recorded in 2000–01. At higher initial population sizes mortality began to occur at higher shellfish stock levels, and increased more steeply as stocks declined further. The percentage of birds failing to reach their

target weight at the end of winter followed similar trends.

The average number of hours spent feeding was greater at higher population sizes across the whole range of shellfish stocks used in the simulations. Again, varying mussel stocks on their own had relatively little effect, whereas varying cockle stocks alone or in combination with mussel stocks led to marked increases in the time spent feeding at low stock levels.

Unsurprisingly, reducing the initial level of a particular shellfish stock resulted in a greater percentage of that stock being eaten (Fig. 7a,e,g,h). However, reducing cockle stocks had little effect on the percentage of mussel stocks eaten (Fig. 7b), and vice versa (Fig. 7d). The percentage of the mussel crumble eaten was also largely unaffected by reducing cockle and mussel stocks separately (Fig. 7c,f), although reducing both

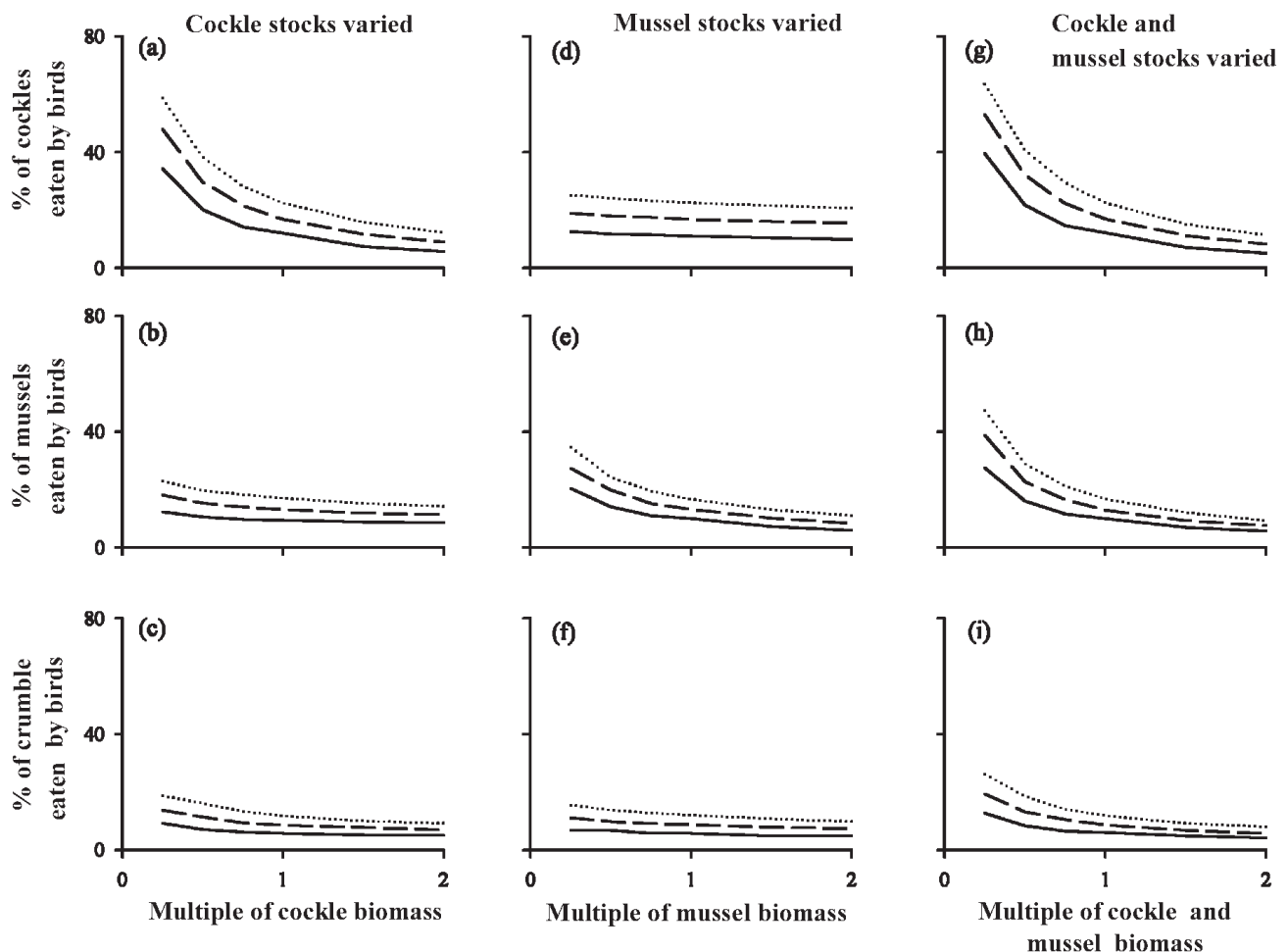


Fig. 7. Predicted percentage of cockle *Cerastoderma edule*, mussel *Mytilus edulis* and mussel-crumble standing crop eaten by oystercatchers *Haematopus ostralegus* at 3 different population sizes (10 000 solid lines, 15 000 dashed lines, 20 000 dotted lines) when shellfish stocks are varied in relation to their 2000–01 levels. (a–c) cockle stocks varied, (d–f) mussel stocks varied, (g–i) cockle and mussel stocks varied simultaneously



stocks together caused more mussel crumble to be eaten (Fig. 7i).

### Removing mussel crumble

At current population sizes and shellfish stocks, removal of mussel crumble to uncover an equivalent area of cockles was predicted to increase mortality/emigration by 0.5% or less (Fig. 8a). There were also small increases in the percentage of birds failing to reach their target weight (<2.5% increase) and the average number of hours spent feeding on intertidal food supplies (<10 min increase) (Fig. 8b,c).

However, when the stocks of cockles and mussels in the inlet were reduced, there were circumstances in which removing mussel crumble made it more difficult for the birds to keep their fitness at present-day levels. The main indicator of this is increased mortality rate at low shellfish stocks (Fig. 8a). This increase was especially apparent when shellfish stocks were reduced below half of the 2000–01 levels. When the shellfish stocks were reduced by only 25%, the increase in mortality rate at present-day population sizes was quite small (<2%).

The percentage of birds failing to reach their fat target was not predicted to be very different if crumble was removed and replaced by cockles (Fig. 8b). Similarly, birds spent, on average, very little extra time feeding when crumble was removed (Fig. 8c).

## DISCUSSION

The model used here has previously been parameterised and tested for oystercatchers feeding on mussels on the Exe Estuary (Stillman et al. 2000). In that case, it accurately predicted the distribution of birds across different types of food, although the distribution of birds between individual feeding patches was predicted less well. It also successfully predicted over-winter mortality. In the current case, the model's predictions matched the observed behaviour of the birds quite well. Most importantly, the proportion of the population feeding on cockles as opposed to mussels was predicted well, as was the number of hours for which the birds fed to obtain their energy requirements. This indicates that the main processes and parameter values that determine the birds' foraging success in this system have been captured by the structure and parameterisation of the model. As with the Exe estuary model, the distribution of birds between patches was predicted less well. The Burry inlet model under-predicted the large number of birds that fed on the Ochor Draw cockle bed and over-predicted the num-

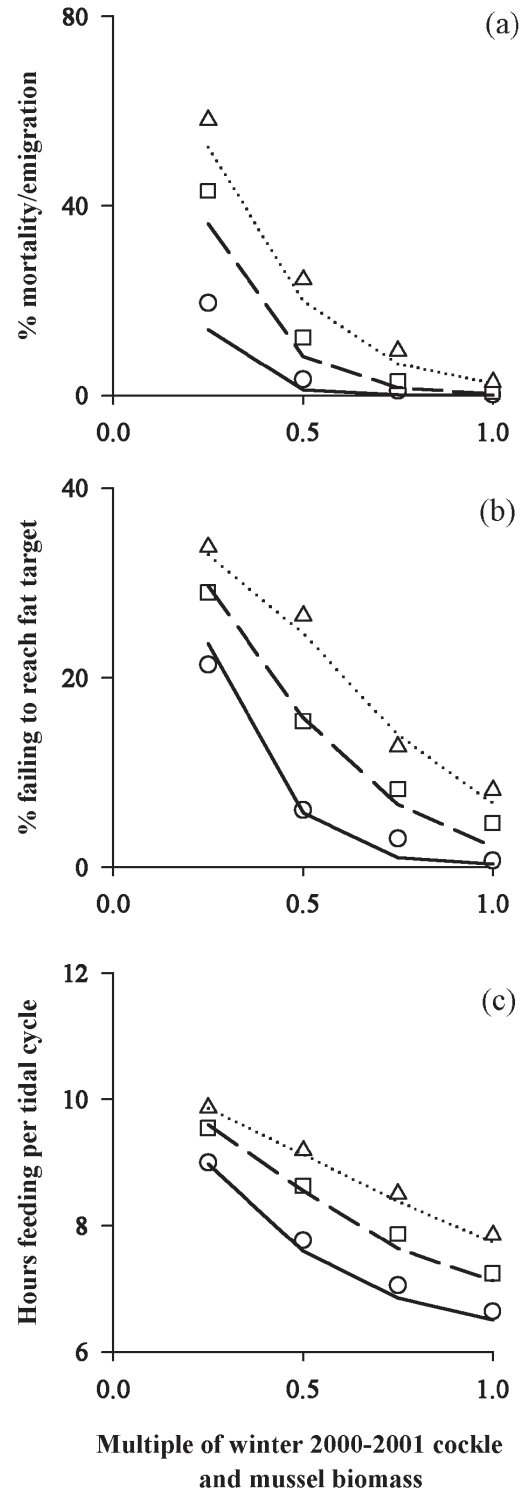


Fig. 8. *Haematopus ostralegus*. Comparison of (a) predicted mortality/emigration, (b) percentage of birds alive at the end of winter which have failed to reach their target-fat accumulation, (c) hours spent feeding per 12.4 h tidal cycle with mussel crumble present (lines) or replaced by cockles (symbols) with varying cockle and mussel biomass at 3 different bird population sizes (10 000 solid lines, circles; 15 000 dashed lines, squares; 20 000 dotted lines, triangles)

ber on Cheriton (Fig. 4). The survey data showed no reason for this discrepancy, so other factors which influence oystercatcher distribution, for example the muddiness of the sediment (Johnstone & Norris 2000), may explain the difference between predicted and observed distributions at the patch scale.

The simulations showed that, at the current shellfish stocks and bird population sizes, birds on the Burry inlet are not food-limited. This supports the preliminary conclusion for the inlet that was reached earlier with a less-comprehensive version of the model, which included only cockle stocks (Stillman et al. 2001). The percentage of birds starving or failing to reach their target weight in spring was calculated by the model as being zero, or very close to it, under current conditions. This was the case even when cockle stocks only included the core CEFAS survey areas; in reality, cockles may also occur outside these areas in some, perhaps many, winters. However, the results suggested that oystercatchers would be much closer to being food-limited in winters in which most or all of the cockle stocks only occur within the core area surveyed by CEFAS. It was predicted that reducing the cockle stocks to 25–50% of current values, especially in combination with mussel stocks, would result in a significant increase in the percentage of the initial population emigrating or dying, and hence fewer birds being supported on the Burry inlet. The main cause of increased mortality and failure to reach target weight when stocks were reduced in the simulations was not the loss of shellfish biomass per se—even under the harshest conditions simulated, when ca. 50% of an initial population of 20 000 birds died, some 40% of the cockle stock, 50% of the mussel stock and 70% of mussel crumble remained uneaten. The key driver is the fact that the shellfish patches were reduced in area.

The fact that so much of the shellfish stocks remained uneaten by the birds, even when mortality was as high as 50%, underlines the importance of interference competition as a limiting factor in this system. Interference competition between oystercatchers feeding on mussels is usually stronger than on cockles (Goss-Custard & Durell 1987, Triplet et al. 1999). This, combined with the disparity between the total areas of cockle and mussel beds on the inlet, leads to large differences in the consequences of varying cockle and mussel stocks. As mussel beds shrink, birds must either face increased interference competition there or switch to feeding on cockles. The relatively large area of the cockle beds, and the weaker interference competition there, mean that many birds are able to make this switch and maintain an intake rate sufficient to satisfy their energy requirements. Thus, reducing mussel stocks has a relatively small impact on the

birds. Conversely, when cockle stocks decline, only a small number of birds can switch to feeding on mussels before the intensifying interference competition makes this strategy less profitable than continuing to feed on the cockle beds. A reduction in cockle stocks is therefore predicted to have greater impact on the birds. Fishing methods, such as hand raking, that reduce shellfish density but do not substantially affect the area of shellfish patches, would be likely to have much less impact on the birds than has been predicted here.

Under the worst-case scenario of 75% of cockle and mussel biomass removed together, birds were predicted to spend an average of nearly 10 h feeding during each tidal cycle. This means that the majority of birds would be reliant on areas of prey becoming available just over an hour after high tide. In circumstances like these, areas of prey at high shore-levels that were available for a large proportion of the tidal cycle would be very important in determining the survival and body condition of Burry inlet oystercatchers. Thus, the loss of such high shore-level food supplies would be more detrimental to the birds than an equivalent loss of food lower down the shore.

Removing mussel crumble had little effect on the number of birds supported by the inlet at 2000–01 shellfish stock levels, regardless of the initial population size of oystercatchers. This was true even though only the core cockle survey area was included in these simulations. With moderate reductions in the stocks of cockles and mussels, the effect of crumble removal was also small and would be further reduced in years when there is settlement of cockles outside the core survey area. With the exception of Walker's (2001) survey, there is no available information about the occurrence and extent of cockle stocks outside the regular survey area. If cockle and mussel bed areas were to be very substantially reduced, to 25% of 2000–01 core area levels, the crumble would become more important—between 5 and 7% more of the oystercatcher population was predicted to die or be forced to leave the inlet if the crumble was removed, leaving only underlying cockles.

The increased mortality of oystercatchers under some circumstances in which mussel crumble is replaced by cockles demonstrates that, despite stronger interference on mussels, an area of mussels supports a greater number of birds than an equal area of cockles, because both biomass density and mean prey size are greater on the mussel beds. This suggests that the much greater size of the cockle beds in comparison to the mussel beds in the Burry inlet is the major factor contributing to their importance.

The model has allowed us to make predictions about the current situation and the likely effect of the proposal to remove mussel crumble. It predicted that

oystercatchers in the Burry inlet were not food-limited in 2000–01, and would not have been food-limited even in the absence of cockles stocks outside the core survey area. Although the mussel crumble was predicted to increase the inlet's capacity to support oystercatchers in years when shellfish stocks were extremely low, it is not doing so at current stocks and bird population sizes. Cockle stocks over the last 10 yr have remained well above the level at which loss of mussel crumble might significantly affect the birds' ability to meet their energy requirements, accumulate fat and survive on the inlet. Thus, if cockle stocks on the inlet remain stable, and if cockles underlie the crumble, we predict that removal of the mussel crumble is unlikely to affect the oystercatcher population in the inlet.

This is the first application of a behaviour-based bird model to predict the consequences of an actual shellfish-management proposal and thus form the basis of policy advice. The model shows that, particularly for systems in which interference may occur, the conse-

quences of a proposed management action cannot be predicted simply by determining how much food will be available to the birds afterwards. Other factors, such as the method of shellfishing, the level of food supplies on the shore and the relative extents of different food supplies, can be equally important.

In our opinion, behaviour-based models of this type are currently the best method of making quantitative predictions about important aspects of shorebird fitness, such as mortality and the ability to migrate successfully, particularly in sites where previous information is lacking and also for untried management scenarios. We believe their potential as a tool for estuary management should be explored more fully.

*Acknowledgements.* The funding for this work was provided by the Countryside Council for Wales. We are grateful to Sian Whitehead and Mike Bell for their comments on an earlier version of this manuscript.

#### Appendix 1. Parameter values used in the model

Time and environmental conditions		
Parameter		Value
Duration of winter		1 September–15 March
Duration of tidal cycle		12.4444 h
Number of tidal stages		6
Duration of spring-neap cycle		14.5185 d = 28 tidal cycles
Time of first high-water on full spring tides		6.25 h after midnight
Duration of tidal stages (all tides)		0.44444 h, 2 h, 2 h, 4 h, 2 h, 2 h
Duration of longest and shortest days (including the hours of twilight)		18.11 h on 21 June and 9.25 h on 21 December
Prey patches		
Parameter	Prey type	
Number of patches	Cockles	5
	Mussels	5
	Mussel crumble	4
Patch areas (ha)	Cockles	198.2, 128.6, 143.8, 146.9, 231.8
	Mussels	50.97, 2.81, 3.91, 1.45, 4.76
	Mussel crumble	6.13, 36.16, 4.04, 5.36
Proportion of each patch exposed at each tidal stage on full spring tides (high tide first)	Cockles	0.0 0.0 0.4 1.0 0.4 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
	Mussels	0.0 0.0 0.3 1.0 0.3 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 0.5 1.0 0.5 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 0.0 1.0 0.0 0.0
		0.0 0.0 0.0 1.0 0.0 0.0
	Mussel crumble	0.0 0.0 0.0 1.0 0.0 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 1.0 1.0 1.0 0.0
		0.0 0.0 0.0 1.0 0.0 0.0
		0.0 0.0 0.0 1.0 0.0 0.0
		0.0 0.0 0.0 1.0 0.0 0.0

## Appendix 1 (continued)

<b>Prey patches</b>											
Parameter	Prey type										
Proportion of each patch exposed at each tidal stage on full neap tides (high tide first)	Cockles	0.0 0.3 0.5 0.7 0.5 0.3									
		0.0 0.6 1.0 1.0 1.0 0.6									
		0.0 0.9 1.0 1.0 1.0 0.9									
		0.0 0.3 0.8 1.0 0.8 0.3									
		0.0 0.3 0.8 1.0 0.8 0.3									
	Mussels	0.0 0.1 0.4 0.5 0.4 0.1									
		0.0 0.5 1.0 1.0 1.0 0.5									
		0.0 0.7 1.0 1.0 1.0 0.7									
		0.0 0.5 1.0 1.0 1.0 0.5									
		0.0 0.0 0.0 1.0 0.0 0.0									
	Mussel crumble	0.0 0.5 1.0 1.0 1.0 0.5									
		0.0 0.7 1.0 1.0 1.0 0.7									
		0.0 0.8 1.0 1.0 1.0 0.8									
		0.0 0.0 0.0 1.0 0.0 0.0									
	Energy density of prey flesh		22.0 kJ g <sup>-1</sup>								
Number of size classes	Cockles	5									
	Mussels	10									
Width of size-classes (mm)	Cockles	15–19, 20–24, 25–29, 30–34, 35–40									
	Mussels	15–19, 20–24, 25–29, 30–34, 35–39, 40–44, 45–49, 50–54, 55–59, 60–65									
Density (m <sup>-2</sup> ) of prey at the start of winter (columns = age-class, rows = patch)	Cockles	395.2 326.9 120.5 10.6 0.8									
		87.7 129.3 73.5 6.5 0.5									
		349.8 159.2 107.1 15.5 0.5									
		407.1 82.5 55.5 8.0 0.3									
		341.5 344.6 237.8 34.6 1.1									
	Mussels	376.7 268.3 195.8 136.3 114.5 148.3 154.5 75.8 26.3 10.5									
		231.7 180.0 187.5 180.0 112.5 27.5 2.5 5.0 0.0 0.0									
		163.8 136.8 145.0 83.3 58.3 40.0 23.3 1.8 3.3 0.0									
		73.3 104.3 82.5 22.5 8.3 2.5 0.0 0.0 0.0 0.0									
		213.2 111.3 88.8 73.8 102.5 88.8 85.0 53.8 28.8 7.0									
	Mussel crumble	231.7 180.0 187.5 180.0 112.5 27.5 2.5 5.0 0.0 0.0									
		448.8 401.5 491.3 279.3 108.0 45.0 20.5 0.5 0.5 0.0									
		120.0 222.5 115.0 20.0 2.5 0.0 0.0 0.0 0.0 0.0									
		746.7 20.0 71.3 462.5 988.8 620.0 76.3 1.3 0.0 0.0									
	Ash-free dry mass (AFDM) at start of winter (mg) (columns = size-class, rows = patch)	Cockles (all patches)	52.01 117 227.11 399.41 687.57								
Mussels		23.4 58.3 120.9 222.0 373.4 588.7 882.1 1269.2 1766.8 2392.5									
		33.1 71.9 133.4 223.3 347.1 510.5 719.2 979.0 1295.9 1675.6									
		36.5 86.6 172.6 306.5 501.2 770.6 1129.4 1593.1 2177.9 2900.7									
		14.4 66.0 159.8 266.7 352.0 397.2 401.8 376.0 332.3 281.4									
		17.1 46.8 104.8 205.0 364.1 601.8 940.6 1405.7 2025.5 2830.9									
Mussel crumble		33.1 71.9 133.4 223.3 347.1 510.5 719.2 979.0 1295.9 1675.6									
		33.1 71.9 133.4 223.3 347.1 510.5 719.2 979.0 1295.9 1675.6									
		35.1 75.0 137.6 227.9 351.2 512.6 717.2 970.5 1277.4 1643.3									
		16.2 42.8 93.0 177.4 308.4 500.3 769.1 1132.5 1609.8 2222.1									
		0									
Over-winter non-bird mortality of prey			0								
Over-winter decrease in AFDM		Cockles	50%								
		Mussels	40%								
<b>Birds</b>											
Parameter	Values										
Ratio of stabbing to hammering feeding methods in population	1:1										
Proportion of immatures in population	0.138										
Range of feeding efficiencies (coefficient of variation)	Stabber	15%									
	Hammerer	15%									
Daytime feeding efficiency	All types	0.85									
Night-time feeding efficiency	All types	0.85									

## Appendix 1 (continued)

<b>Birds</b>		
Parameter	Values	
Aggregation factor	Cockles	10
	Mussels (stabber)	8
	Mussels (hammerer)	4
Interference coefficients (see Stillman et al. 2000 for meaning of coefficients)	Mussels (stabber)	a = 0.151, b = -0.535, c = 0.0022
	Mussels (hammerer)	a = 0.168, b = -0.081, c = 0.0014
	Cockles (all)	a = 0.5, b = -0.5, c = 0
Temperature-related prey availability	All	Prey fully available at all temperatures
Mass on 1 September (g)	Immatures	483
	Adults	503
Starvation mass (g)	Immatures	340
	Adults	350
Target mass (days since 1 September, target mass in g)	Immatures	0, 483; 106, 550; 196, 510
	Adults	0, 503; 196, 598
Time cost of disturbance (h)	All	0.5
Energy cost of disturbance (kJ)	All	1.0
Gut capacity (g AFDM)	All	11.92
Gut processing rate (g AFDM h <sup>-1</sup> )	All	2.351
Energy expenditure—non-thermoregulatory (kJ d <sup>-1</sup> )	All	673.2
Lower critical temperature (°C)	All	10
Energy expenditure—thermoregulatory (kJ °C <sup>-1</sup> d <sup>-1</sup> )	All	31.8
Prey assimilation efficiency	All	0.854
Energy density of fat reserves (kJ g <sup>-1</sup> )	All	33.4
Fat storage efficiency	All	0.884
Fat usage efficiency	All	1.0
<b>Fishing</b>		
Number of fishing types		4
Patch types fished by each type		Cockles
Number of periods over which each fishing type is banned		0, 1, 0, 2
First and last days of each ban		119 196
		0 61
		155 196
Probability of fishing by each type on each day of week (Monday to Sunday)		1 1 1 1 1 1 0
		1 1 1 1 1 1 0
		1 1 1 1 1 1 0
		1 1 1 1 1 1 0
Probability of fishing during the day by each type at each tidal stage		0 0 0 1 0 0
		0 0 0 1 0 0
		0 0 0 1 0 0
		0 0 0 1 0 0
Probability of fishing at night by each type at each tidal stage		0 0 0 0 0 0
		0 0 0 0 0 0
		0 0 0 0 0 0
		0 0 0 0 0 0
Stage of spring/neap cycle between which fishing by each type is possible		0 1
		0 1
		0 1
		0 1
Patches on which fishing by each type is allowed (column = type, row = patch)		1 1 0 0
		1 1 0 0
		0 0 1 1
		0 0 1 1
Standard survey		0 0 1 1
		0 0 1 1
		0 0 1 1
		0 0 1 1
Number of fishing units of each type		21, 43, 32, 20
Aggregation of fishing effort of each type on each patch type (0–1; 0 = all patches; 1 = one patch)		0.5, 0.5, 0.0, 0.0
Maximum time over which shellfishing occurs (h)		6
Minimum fished size (mm)		19.0
Disturbance radius during fishing (m) and seasonal change (m d <sup>-1</sup> )		124.8, -0.2109
Post-fishing disturbance time (h) and seasonal change (h d <sup>-1</sup> )		0.96, -0.00337
Tidal stage quota (kg fresh mass) per fishing unit of each type		169.56, 169.56, 147.66, 147.66

## LITERATURE CITED

- Davidson PE (1967) A study of the oystercatcher (*Haematopus ostralegus* L.) in relation to the fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. Fish Invest II Vol 24 No 7, HMSO, London
- Ens BJ, Goss-Custard JD (1984) Interference among oystercatchers, *Haematopus ostralegus* L., feeding on mussels, *Mytilus edulis* L., on the Exe estuary. J Anim Ecol 53: 217–232
- Goss-Custard JD, Durell SEA leV dit (1987) Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. 1. Foraging efficiency and interference. J Anim Ecol 56:521–536
- Goss-Custard JD, Stillman RA, West AD, McGrorty S, Durell SEA leV dit, Caldow RWG (2000) The role of behavioural models in predicting the ecological impact of harvesting. In: Gosling LM, Sutherland WJ (eds) Behaviour and conservation. Cambridge University Press, Cambridge, p 65–82
- Goss-Custard JD, West AD, Stillman RA, Durell SEA leV dit, Caldow RWG, McGrorty S, Nagarajan R (2001) Density-dependent starvation in a vertebrate without significant depletion. J Anim Ecol 70:955–965
- Johnstone I, Norris K (2000) The influence of sediment type on the aggregative response of oystercatchers, *Haematopus ostralegus*, searching for cockles, *Cerastoderma edule*. Oikos 89:146–154
- McGrorty S, Clarke RT, Reading CJ, Goss-Custard JD (1990) Population dynamics of the mussel *Mytilus edulis*—density changes and regulation of the population in the Exe Estuary, Devon. Mar Ecol Prog Ser 67:157–169
- McNeil R, Drapeau P, Goss-Custard JD (1992) The occurrence and adaptive significance of nocturnal habits in waterfowl. Biol Rev Camb Phil Soc 67:381–419
- Norris KJ, Johnstone IG (1996) Oystercatchers and cockles. In: Stillman RA, Goss-Custard JD, McGrorty S, West AD and 12 others (eds) Models of shellfish populations and shorebirds: Final Report. Commission of the European Communities, Directorate-General for Fisheries, Brussels, p 255
- Palmer DW (2001) A survey of the cockle stocks in the Burry Inlet, South Wales. November 2000. Shellfish Resource Team Report No. 32. The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft
- Pettifor RA, Norris KJ, Rowcliffe M (2000) Incorporating behaviour in predictive models for conservation. In: Gosling LM, Sutherland WJ (eds) Behaviour and conservation. Cambridge University Press, Cambridge, p 198–220
- Prater A (1974) Oystercatchers v. cockles. BTO News 64:1–2
- Sitters HP (2000) The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding oystercatchers. PhD thesis, University of Oxford
- Stewart B (2001) Relationship between mussel and oystercatcher populations in the Burry Inlet. Part 1B, Section 2. Report No. FC 73–02–188 A. Countryside Council for Wales, Bangor
- Stillman RA, Goss-Custard JD, West AD, Durell SEA leV dit, Caldow RWG, McGrorty S, Clarke RT (2000) Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. J Appl Ecol 37:564–588
- Stillman RA, Goss-Custard JD, West AD, McGrorty S and 7 others (2001) Predicting shorebird mortality and population size under different regimes of shellfishery management. J Appl Ecol 38:857–868
- Triplet P, Stillman RA, Goss-Custard JD (1999) Prey abundance and the strength of interference in a foraging shorebird. J Anim Ecol 68:254–265
- Walker P (2001) The relationship between mussel and oystercatcher populations in the Burry Inlet, Part 1b, Section 3. A report on the cockle stocks in the Burry Inlet, South Wales, outside the standard CEFAS survey area. January 2001. Report No. FC 73–02–188C. Countryside Council for Wales, Bangor
- West AD, Goss-Custard JD, Stillman RA, Caldow RWG, Durell SEA leV dit, McGrorty S (2002) Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. Biol Conserv 106:319–328
- Zwarts L, Drent RH (1981) Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In: Jones NV, Wolff WJ (eds) Feeding and survival strategies of estuarine organisms. Plenum Press, London, p 193–216

Editorial responsibility: Otto Kinne (Editor),  
Oldendorf/Luhe, Germany

Submitted: August 12, 2002; Accepted: November 6, 2002  
Proofs received from author(s): January 28, 2003