

# Predicting shorebird mortality and population size under different regimes of shellfishery management

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## Summary

1. Human interests often conflict with those of wildlife. In the coastal zone humans often exploit shellfish populations that would otherwise provide food for populations of shorebirds (Charadrii). There has been considerable debate on the consequences of shellfishing for the survival of shorebirds, and conversely the effects of shorebird predation on the shellfish stocks remaining for human exploitation. Until now, it has been difficult to determine the impact of current shellfishery practices on birds or to investigate how possible alternative policies would affect their survival and numbers.

2. One long-running contentious issue has been how to manage mussel *Mytilus edulis* and cockle *Cerastoderma edule* shellfisheries in a way that has least effect on a co-dependent shorebird, the oystercatcher *Haematopus ostralegus*, which also consumes these shellfish. This study used a behaviour-based model to explore the effects that the present-day management regimes of a mussel (Exe estuary, UK) and a cockle (Burry inlet, UK) fishery have on the survival and numbers of overwintering oystercatchers. It also explored how alternative regimes might affect the birds.

3. The model includes depletion and disturbance as two possibly detrimental effects of shellfishing and some of the longer-term effects on shellfish stocks. Importantly, model birds respond to shellfishing in the same ways as real birds. They increase the time spent feeding at low tide and feed in fields and upshore areas at other times. When shellfishing removes the larger prey, birds eat more smaller prey.

4. The results suggest that, currently, neither shellfishery causes oystercatcher mortality to be higher than it would otherwise be in the absence of shellfishing; at present intensities, shellfishing does not significantly affect the birds. However, they also show that changes in management practices, such as increasing fishing effort, reducing the minimum size of shellfish collected or increasing the daily quota, can greatly affect oystercatcher mortality and population size, and that the detrimental effect of shellfishing can be greatly increased by periods of cold weather or when prey are unusually scarce. By providing quantitative predictions of bird survival and numbers of a range of alternative shellfishery management regimes, the model can guide management policy in these and other estuaries.

**Key-words:** bivalve harvesting, coastal policy, human disturbance, risk assessment.

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## Introduction

How to manage shellfishing for cockles *Cerastoderma edule* L. and mussels *Mytilus edulis* L. with least effect on the survival of overwintering oystercatchers

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*Haematopus ostralegus* L., which also feed on shellfish, has been a contentious issue for at least four decades (Goss-Custard, McGrorty & Durell 1996c). Shellfishing removes the large-sized shellfish that are most profitable to oystercatchers (Zwarts *et al.* 1996). Shellfishers may also disturb the birds. The removal of shellfish from the most productive beds, along with any disturbance it causes over low water, drives birds from their preferred feeding areas to poorer quality areas where, additionally, increased bird densities intensify interference and exploitation competition for food (Goss-Custard & Verboven 1993). This reduces intake rate and increases the probability that oystercatchers die of starvation (Clark 1993) in winter, when they may already have difficulty in obtaining their energy requirements (Goss-Custard *et al.* 1996b).

Despite intensive research, the effects on oystercatchers of current and potential shellfishery management policies are usually unknown. To help resolve this, we built and field-tested a behaviour-based model (Stillman *et al.* 2000a). This can evaluate both current and alternative shellfishery regimes because it incorporates the main bird responses to shellfishing, which are behavioural (Goss-Custard *et al.* 2000). By coupling the behaviour-based model for oystercatchers with a conventional demographic shellfish population model, the cumulative effects of policy over many years can also be explored for both birds and shellfish.

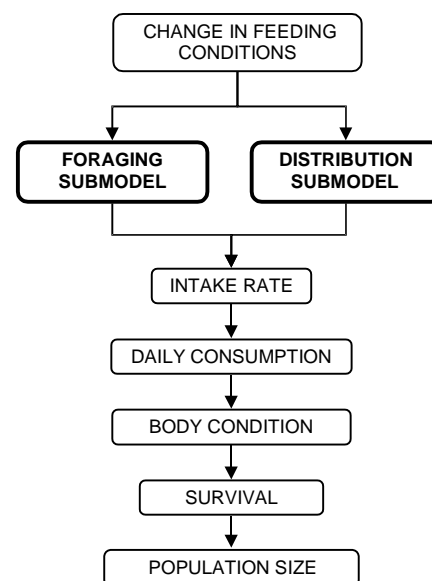
The behaviour-based model predicts the changed intake rates of oystercatchers forced by shellfishing to alter their diet and/or to redistribute themselves over resource patches of varying quality (Goss-Custard *et al.* 2000). It does this using foraging theory and game theory, which are thought to provide a reliable basis for prediction (Goss-Custard 1996; Goss-Custard & Sutherland 1997). The behavioural responses of model birds to shellfishing are based on decision principles, such as intake rate maximization, which are unlikely to be affected by shellfishing, even if the particular choices made by individuals, and thus their chances of surviving, do change. Model birds are therefore believed likely to respond to current and alternative shellfishing regimes in the same way as real birds.

This study explored the impacts of the present-day management regime of the mussel fishery on the Exe estuary, south-west England (50°38'N, 3°26'W), and of the cockle fishery on the Burry inlet, south Wales (51°39'N, 4°10'W), on the survival and numbers of overwintering oystercatchers. It also explored the effect on birds of some possible alternative ways of managing these shellfisheries, and how the impact was affected by periods of cold weather, low prey abundance and the availability of supplementary feeding opportunities.

## The model

### BASIC MODEL: EXE ESTUARY OYSTERCATCHER–MUSSEL SYSTEM

Stillman *et al.* (2000a) describes the basic model and lists parameter values; Fig. 1 shows a flow chart of its



**Fig. 1.** Flow chart of the behaviour-based model for predicting the effect of shellfishing on the body condition of individual oystercatchers, their survival rates and population size. The two behaviour submodels are outlined with heavy lines.

general structure. The model includes the main intertidal and terrestrial foods of oystercatchers, and their accessibility to oystercatchers at each stage of the tidal cycle. It follows the day-time and night-time prey choice and feeding location of each oystercatcher from 1 September to 15 March. It uses the rate maximizing foraging submodel to calculate the sizes of shellfish eaten on each shellfish bed and the interference-free intake rate of birds of average efficiency. A game theoretic approach in the distribution submodel then determines where each individual feeds at each tidal stage. The model tracks the body reserve and survival consequences of these decisions for all individuals in the population.

Although all individuals decide on the same principle, intake rate maximization, the actual decisions made by each differ. Their individual choices depend on their particular competitive ability, which depends on two characteristics related to bird age and feeding method. Interference-free intake rate is the rate 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 is determined by the balance between an individual's daily rates of energy expenditure and acquisition. Energy expenditure depends on metabolic costs plus any cost of thermoregulation at low temperatures. Energy acquisition depends both on the time available for feeding and intake rate while feeding. When daily energy acquisition exceeds daily expenditure, individuals accumulate energy reserves or maintain them if a maximum level has already been reached. When daily requirements exceed daily acquisition, individuals draw on their reserves. If reserves fall to zero, an individual starves, the only source of mortality in the model and the main

source of overwinter oystercatcher mortality in the wild (Goss-Custard *et al.* 1996b). The model includes seasonal changes in the flesh content of shellfish and in the weather and the neap–spring and diurnal cycles. It includes the three main food supplies of oystercatchers: a number of shellfish beds (e.g. 10 mussel beds on the Exe), which are exposed for approximately 6 h; upshore feeding areas, which are exposed for 8 h; and terrestrial fields, which are available throughout the tidal cycle. The tidal exposure patterns are the same as in the real system. The basic model predicts the mortality of first-year, second-year and adult mussel-feeding oystercatchers during a single winter and does not incorporate shellfishing. The observed overwinter mortality was relatively low during the years for which the model was parameterized (1976–80), being 13.9% in first-years, 10.4% in second-years and 2.0% in adults (Stillman *et al.* 2000a).

#### ADDITIONS TO THE BASIC MODEL

##### *Modelling oystercatcher breeding*

To predict the consequences of shellfishing on oystercatcher population size, the model needed to incorporate the recruitment of young during summer. This was done using the approach of Durell, Goss-Custard & Clarke (1997), with parameter values based on a literature review (Goss-Custard *et al.* 1996a). At winter's end, we assume that all adults migrate to a single breeding site of area  $A$  (= 525 ha), whereas all immatures and juveniles stay on the winter site. The area of the breeding site was not measured in the field but was set to a value such that the number of oystercatchers returning to the Exe each year in long-term simulations without shellfishing, remained constant and close to the observed value. We assume that 5% of adults die during migration to the breeding site (i.e. the average summer mortality of adults wintering on the Exe; Durell *et al.* 2000) but that no juveniles or immatures die during summer (Durell *et al.* 2000). Having reached the breeding site, all the  $N$  surviving adults form  $P$  potential breeding pairs (where  $P = N/2$ ), of which the  $B$  number breeding, by obtaining a territory, is calculated from the rearranged equation 1 in Durell, Goss-Custard & Clarke (1997):

$$B = \frac{P}{10^{b(P/A)-a}} \quad \text{eqn 1}$$

where  $a$  (= 0.891) and  $b$  (= 0.5) are density-dependent territory acquisition parameters. The model limits the number of breeding pairs calculated by this equation so that it does not exceed the number of potential breeding pairs.

At this stage all individuals are aged by changing the previous year's juveniles to immatures and the previous year's immatures to adults. The number of juveniles ( $R$ ) reaching the Exe in autumn is calculated by assuming a constant output per breeding pair (Goss-Custard *et al.* 1996a):

$$R = rB$$

eqn 2

where  $r$  = number of young per breeding pair surviving until the start of winter (= 0.495). We assume that no adults die during their return to the Exe.

##### *Modelling Exe mussel population dynamics*

Mussel population dynamics on the Exe were incorporated using a demographic model (Stillman *et al.* 2000b) that allowed the interaction between birds and mussels to be modelled for successive years. The model is spatially structured (10 beds) and age-structured (nine age classes). Empirically determined, density-dependent and density-independent mortality rates operate on each age class of mussels on each bed in winter (September–March) and in summer (March–September); full details and parameter values for the simplest version used here are in Stillman *et al.* (2000b). The only change was that the mortality rate of third-winter and older mussels was 6% (measured in the absence of oystercatcher predation; S. McGrorty unpublished data) rather than the values used in Stillman *et al.* (2000b), which included mortality caused by oystercatcher predation.

A key feature is that spat mussels only recruit where adults are present; without protection amongst adult byssus threads, they are quickly predated (McGrorty *et al.* 1990). Hence the rate of spat recruitment increases as adult density increases, in contrast to cockles where, if anything, spat recruitment decreases as adult density increases, although this is speculative (Goss-Custard, McGrorty & Durell 1996c). Methods of shellfishing that strip a shellfish bed therefore reduce the area occupied by mussels in the long term, but not of cockles.

##### *Modelling the Burry inlet oystercatcher–cockle system*

In the absence of long-term data on the dynamics of cockles on the Burry inlet, the effect of shellfishing was modelled over a single winter only (1 September–15 March).

The tidal cycle was divided into high (5.9 h) and low (6.5 h), as in the real system (I. G. Johnstone, personal observation). Weather patterns were assumed to be the same as on the Exe, due to south-western location of the two estuaries within the UK. Ten cockle beds were exposed over low tide only, and one field was always available. No feeding was done by oystercatchers in upshore areas (I. G. Johnstone, personal observation). Within each cockle bed, cockles were divided into five size ranges (0–7; 7–15; 15–22; 22–29; 29+ mm) to match those used by the oystercatcher–cockle functional response model (see below). The September size distribution on the 10 beds was set to that recorded in a random sample of 10 of the 25 × 25-m plots used to develop the functional response model, each patch having the size distribution recorded in one study plot (I. G. Johnstone, unpublished data). Each of these beds was assumed to occupy one-tenth (0.5 km<sup>2</sup>) of the total

area (5 km<sup>2</sup>) of the Burry inlet cockle population. Cockle beds on the Burry inlet are fully exposed during low tide throughout the spring–neap cycle, and so all cockle beds in the model had the same exposure pattern.

Oystercatcher intake rate was calculated from the abundance, size distribution and flesh content of cockles using the rate maximizing functional response model of Norris & Johnstone (1998a). Interference seems insignificant on the Burry inlet (Norris & Johnstone 1998b), probably because prey are so abundant (Triplet, Stillman & Goss-Custard 1999a), so interference was assumed to be absent. As for the Exe, the model incorporated depletion due to oystercatchers and shellfishing, the 50% overwinter decline in the flesh content of cockles (Norris & Johnstone 1998a) and the overwinter mortality not attributable to oystercatchers or shellfishing [60% in 0–7 mm (first-winter) cockles (Hancock 1971) and 10% in larger ones (Horwood & Goss-Custard 1977)]. Intake rates in the field were assumed to be the same as in the Exe model. Individuals were assumed to vary in feeding efficiency on both cockle beds and the field; feeding efficiency was normally distributed with the same 12.5% coefficient of variation as in mussel-feeding Exe oystercatchers (Stillman *et al.* 2000a). Based on extensive field studies (Prys-Jones, Howells & Kirby 1989), the model was seeded with 13 000 individuals to represent the present-day oystercatcher population.

#### *Modelling shellfishing*

Shellfishing was incorporated by following the location and activities of a number of fishing units (people or boats depending on the method). Shellfishing effort was varied by changing the number of fishing units. A certain number of fishing units occupied beds with the highest densities of mussels or cockles within their target size range, on which they could therefore harvest mussels at the highest rate. As they depleted the shellfish stocks in the initially most preferred beds, fishing units spread out to occupy a wider range of beds. In order to prevent all fishing units unrealistically occupying the same bed, they were assumed to occupy any beds with target mussel or cockle densities greater than 75% of that on the bed with the highest density.

For fishing performed during low tide, disturbance was incorporated by assuming that birds were displaced from a circular zone around each fishing unit. If more than one unit was present on a bed, the total exclusion area was the sum of individual zones, realistically assuming that units dispersed widely across the patch. When enough were present to disturb the complete bed, no birds could feed on it over low tide. Disturbance was assumed to persist throughout low tide, even if the time spent actively fishing was shorter than the duration of low water, thus realistically including time spent by shellfishers arriving, departing and resting on the bed. Birds displaced from one shellfish bed by shellfishers went to another which, under current conditions, maximized their intake rate. Although the energy and time

costs of moving between beds could be included in the model, this was not done here because the distances involved in these estuaries were small.

The model can simulate any type of shellfishing, but here we consider only those that are either currently used on the Exe estuary or Burry inlet, or could be employed were the shellfishery regime to change. Hand-picking mussels: individual mussels are selected by hand during low tide. Hand-raking mussels: areas are raked by hand at low tide. Dredging mussels: mussels are dredged from a boat at high tide. Hand-picking and -raking are currently the main ways of fishing for intertidal mussels on the Exe, but dredging is frequently used elsewhere. Hand-raking cockles: areas are raked by hand at low tide. Suction-dredging cockles: cockles are dredged from a boat at high tide. Currently, only hand-picking occurs on the Burry inlet, but suction-dredging is widely employed elsewhere.

These fishing methods influence the shellfish and oystercatcher populations in different ways (Table 1). Hand-picking mussels and hand-raking and suction-dredging cockles only select shellfish within a target size range and do not reduce the density of smaller ones or reduce bed area. In contrast, both hand-raking and dredging mussels remove all mussel sizes and so also reduce bed area. Although usually happening at a slower rate, hand-raking mussels can reduce bed area more than dredging. Continued dredging fragments a bed, making submerged mussels increasingly difficult to locate. In contrast, hand-raking can remove complete beds as mussels are visible. Both the rate of shellfish depletion and the area of disturbance (in low tide methods) increase as the number of fishing units increases. Based on current evidence, we assume that hand-picking mussels and hand-raking and suction-dredging cockles have no adverse effects on the survival of shellfish outside the target size range (Goss-Custard *et al.* 2000).

## **Results**

Simulations for the current and possible alternative shellfishery management regimes were examined together to facilitate comparison between them. On the Exe, the current daily fishing effort amounts to no more than two fishing units (hand-pickers or -rakers) and on most days is considerably less than this. But to be cautious, simulations for the current shellfishery regime were run with two fishing units. On the Burry inlet, 50 shellfishing licences (for hand-raking) are issued annually, although not every fisherman fishes every day. However, there is some casual and illegal fishing and, to allow for this and again to be cautious, we used 50 fishing units to represent the current regime.

### BEHAVIOURAL RESPONSES OF OYSTERCATCHERS TO SHELLFISHING WITHIN A SINGLE WINTER

The model predicted that current fishing methods and effort has no significant effect on the proportion of time

**Table 1.** Details of the shellfishing methods modelled

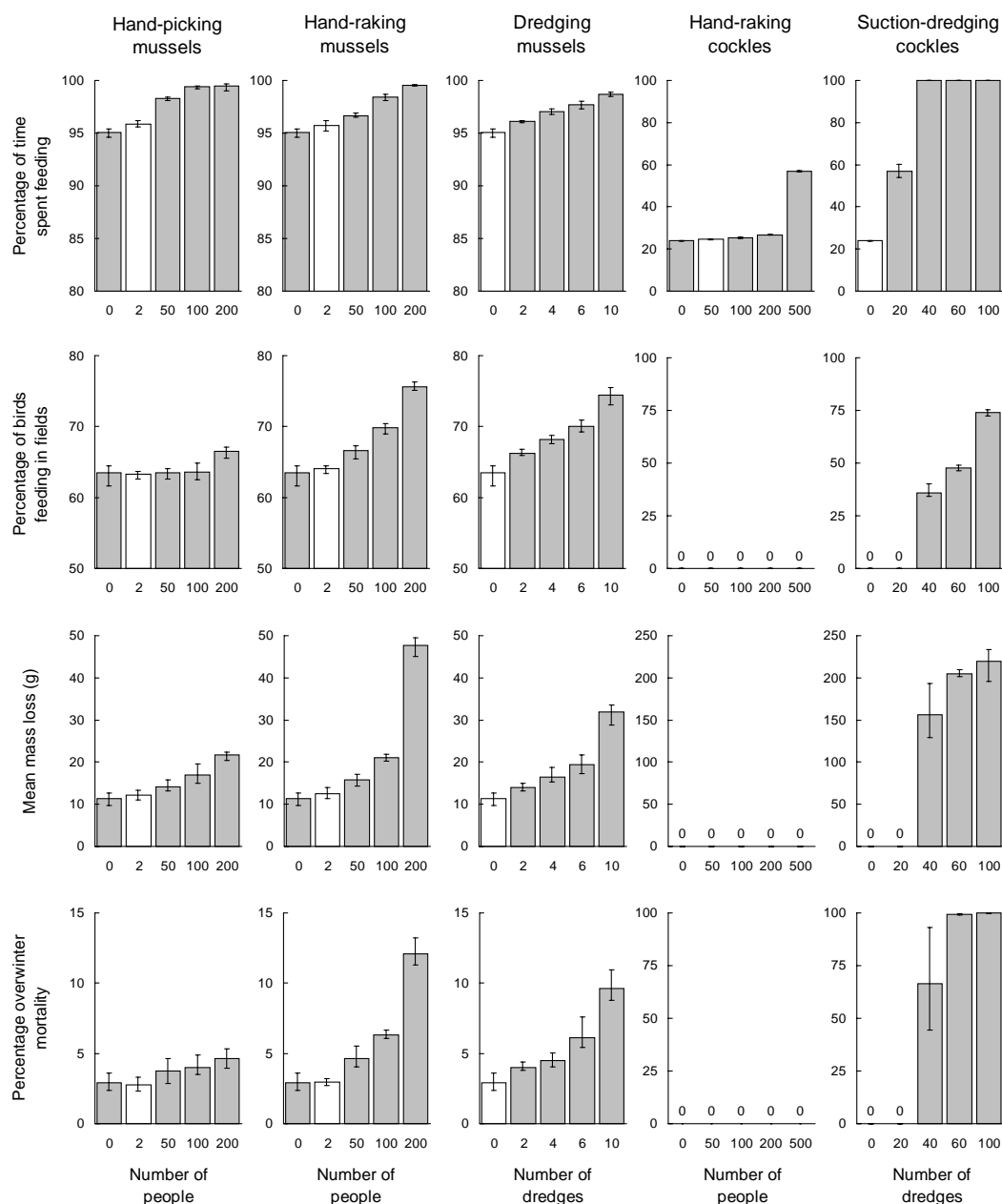
Method and target species	Fishing unit in the model represents	Days and tides fished	Duration of fishing and amount of time beds occupied	Method by which shellfish are removed by fishing	Rate at which shellfish are removed by fishing	Target size range	Maximum daily quota	Minimum density fished	Disturbance to birds
Hand-picking mussels	A person	Low water on spring tides, during daylight	4 h fishing during low tide but shellfishers on bed throughout low tide	Only removes target size classes and does not reduce bed area	All 40+ mm mussels removed from 5 m <sup>2</sup> per hour fishing	40+ mm*	None	0 m <sup>-2</sup>	Disturbed throughout low tide. Area disturbed (m <sup>2</sup> ) = $\pi(125 - 0.211x)^2$ where $x$ = days after 1 Sept (R. A. Stillman, unpubl.)
Hand-raking mussels	A person	Low water on spring tides, during daylight	4 h fishing during low tide but shellfishers on bed throughout low tide	Removes all size classes and reduces bed area	5 m <sup>2</sup> of bed removed per hour fishing	40+ mm* but also removes shorter prey	None	0 m <sup>-2</sup>	Disturbed throughout low tide. Area disturbed (m <sup>2</sup> ) = $\pi(125 - 0.211x)^2$ where $x$ = days after 1 Sept (R. A. Stillman, unpubl.)
Dredging mussels	A boat	High water on spring tides, during daylight	4 h fishing during high tide	Removes all size classes and reduces bed area	100 m <sup>2</sup> of bed removed per hour fishing	40+ mm but also removes shorter prey	None	0 m <sup>-2</sup>	No disturbance
Hand-raking cockles	A person	Low water on any tide, during daylight	Fishing throughout low tide or until quota reached but shellfishers on bed throughout low tide	Only removes target size classes and does not reduce bed area	Fresh mass (kg) of 22 mm+ cockles removed per hour = $x/(14.03 + 0.22x)$ $x$ = 22 mm+ cockle density (m <sup>-2</sup> ) (I. G. Johnstone, unpubl.)	22+ mm†	100 kg fresh mass of 22 mm+ cockles†	0 m <sup>-2</sup>	Disturbed throughout low tide. Area disturbed (m <sup>2</sup> ) = $\pi(125 - 0.211x)^2$ where $x$ = days after 1 Sept (R. A. Stillman, unpubl.)
Suction-dredging cockles	A boat	High water on 4 days each week,‡ during daylight	4 h fishing during high tide‡	Only removes target size classes and does not reduce bed area	Cockles removed from 780 m <sup>2</sup> per hour fishing (Stillman <i>et al.</i> 1996)	15+ mm‡	None	50 m <sup>-2</sup> §	No disturbance

\*Limit imposed on Exe estuary.

†Limit imposed on Burry Inlet.

‡Limit imposed in Wadden Sea.

§Minimum profitable density in Wadden Sea.



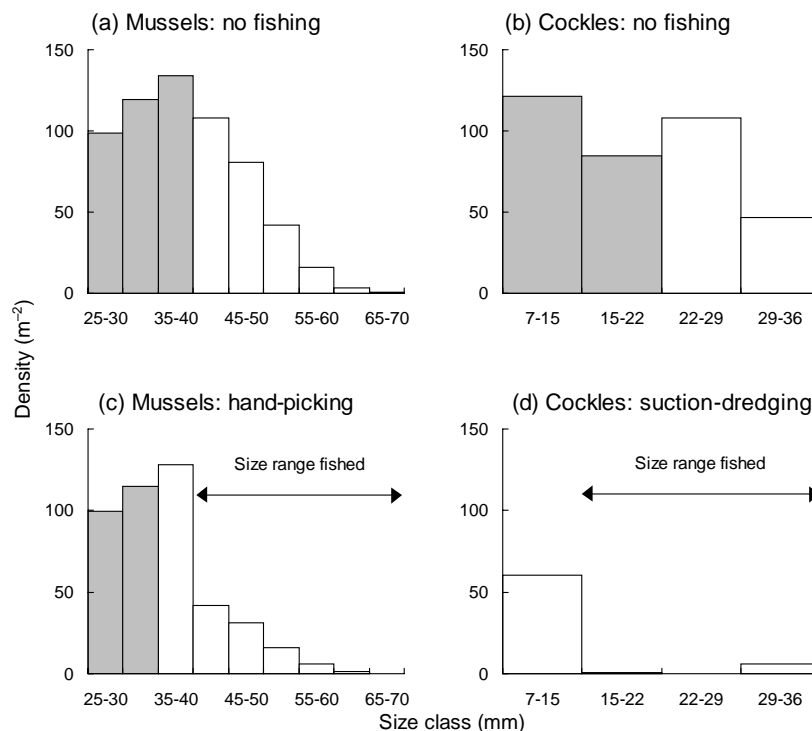
**Fig. 2.** Predicted effect of shellfishing during one winter on oystercatcher behaviour, body condition and mortality rate. Columns show predictions for five fishing methods; predictions for mussel fishing are for the Exe estuary and those for cockle fishing are for the Burry inlet. Rows show four predictions: (1) the average percentage of time bird's spent feeding during the last spring low tide of winter; (2) the average percentage of birds feeding in fields on neap high tides during daylight throughout winter; (3) the average difference between actual and target body mass in surviving birds at the end of winter; and (4) the percentage overwinter mortality of birds. Bars show the mean and range of values produced by six replicate model runs (means of zero are indicated with a value). White bars show predictions for the current fishing effort on each estuary. Note that the vertical axis range differs for mussels and cockles.

oystercatchers spend feeding at the end of winter (Fig. 2) or the use made of fields above high tide (Fig. 2). However, increasing shellfishing above current levels, and the use of dredges on either estuary, raised the time spent feeding (Fig. 2), and, with the exception of hand-raking cockles, more birds used supplementary feeding areas (Fig. 2). Hand-raking cockles had little effect because it only removed cockles > 22 mm. The model calculates intake rates on shellfish from an optimal diet model, so model birds took more small shellfish as

the larger and more profitable ones were fished by shellfishing carried out at well above current rates (Fig. 3).

#### EFFECT OF SHELLFISHING ON OYSTERCATCHER BODY CONDITION WITHIN A SINGLE WINTER

Present-day methods and fishing effort did not affect the body condition of model oystercatchers on either the Exe or Burry (Fig. 2). But with increased shellfishing,



**Fig. 3.** Predicted effect of shellfishing on the range of mussel and cockle size classes included in the diet of oystercatchers on the Exe estuary and Burry inlet. Predictions for mussel-feeders are for 200 hand-pickers and those for cockle-feeders for 60 suction dredges. Graphs show the range of sizes surviving at the end of winter on one mussel and one cockle bed, and the range of size classes either excluded from (grey bars) or included in the diet of oystercatchers (open bars) feeding on these beds. The arrows show the range of size classes removed by fishing.

and the use of dredging, a point came when many oystercatchers could not compensate by feeding for longer or eating more smaller prey. Unsuccessful birds then drew on their energy reserves and so lost mass. The model predicted that increasing fishing effort substantially above current levels would reduce the average mass of surviving birds for all methods, except hand-raking cockles (Fig. 2).

#### EFFECT OF SHELLFISHING ON OYSTERCATCHER MORTALITY WITHIN A SINGLE WINTER

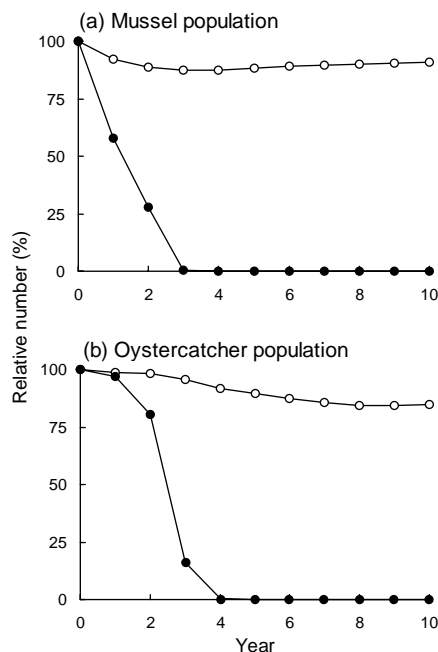
Current methods and fishing effort did not affect mortality rate on either the Exe or Burry (Fig. 2). But increased fishing effort in each fishing method, except hand-raking cockles, and the use of dredging increased oystercatcher mortality rate, but by different amounts (Fig. 2). The differences were due to the different rates of depletion and disturbance caused by each method. Mussel dredges and suction dredges removed mussels or cockles at a much higher rate than hand-raking or hand-picking: 60 suction dredges could kill all the Burry oystercatchers whereas 500 hand-rakers had no effect. With mussel fishing, hand-raking increased mortality by the greatest amount per unit area fished, followed by dredging and lastly hand-picking. Hand-raking had the greatest effect because it both reduced the area of beds, permanently increasing interference, and disturbed

birds, temporarily increasing interference. In contrast, dredging only decreased bed area. Although hand-picking caused disturbance, it did not reduce the area of beds available.

#### LONG-TERM EFFECTS OF MUSSEL FISHING: RECOVERY OF MUSSEL STOCK

Although the impact of fishing may often be small within a single year, subsequent fishing may have a greater effect if the oystercatchers or shellfish, or both, do not recover by the following year. For example, hand-raking reduces the area of mussel beds and, unless replaced by natural increase or restocking, the impact of fishing will increase annually. The data required to run multiple-year simulations of cockle fishing were not available so long-term effects were explored for the Exe alone.

Because the current fishing effort has no long-term effect on either the mussel stocks or birds, multiple-year simulations were run with 50 times the current fishing effort using hand-picking or hand-raking (Fig. 4). Hand-picking over 10 years reduced the oystercatcher population by 15%. Although picking depleted mussel stocks each winter, recruitment maintained them at 90% of those without fishing. In contrast, hand-raking reduced the area of mussels and so reduced the space available to recruiting spat mussels, causing the mussel population, and thus bird numbers, to decrease greatly



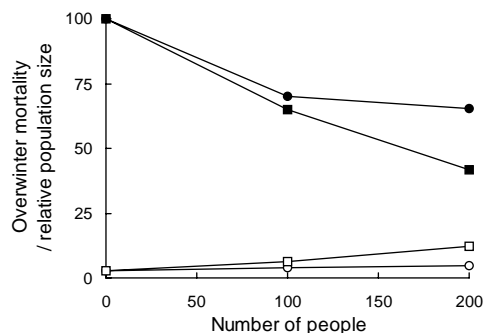
**Fig. 4.** Predicted effect on hand-picking (open circles) and hand-raking mussels (closed circles) over 10 years on the numbers of (a) mussels and (b) oystercatchers at the start of each winter. Note that mussel and oystercatcher numbers are plotted as a percentage of the equivalent value predicted in the absence of fishing. In simulations, 100 hand-pickers and hand-rakers fished throughout each winter, representing 50 times the present-day fishing effort.

over the years. The consequences of shellfishing can be greatly increased over a number of years when shellfish do not recover between years.

#### LONG-TERM EFFECTS OF MUSSEL FISHING: EQUILIBRIUM OYSTERCATCHER POPULATION SIZE

In species having low annual mortality rates, a small absolute increase in mortality can cause large reductions in equilibrium population size, unless there is a compensatory increase in recruitment (Goss-Custard 1980; Danchin, González-Dávila & Lebreton 1995). In oystercatchers, an increase in annual mortality rate from 1% to 2% can reduce equilibrium population size by up to 50%, depending on the strength of the compensatory density-dependence in recruitment (Goss-Custard *et al.* 1996a). Although the 1% increase is in absolute terms very small, it represents a doubling in the annual mortality rate, with a consequent large cumulative effect on the position of the equilibrium at which birth and death rates are equal.

The simulations with the oystercatcher demographic population model showed that relatively small increases in mortality due to intensive shellfishing could indeed greatly reduce population size (Fig. 5). For example, overwinter mortality within a single winter was increased from 2.9% to 4.6% by 200 hand-pickers and to 12.1% by 200 hand-rakers. These increases in mortality resulted



**Fig. 5.** Predicted effect of hand-picking (circles) and hand-raking mussels (squares) on the overwinter mortality of oystercatchers in a single winter (initial number of birds = 1550) (open symbols) and the equilibrium population size of oystercatchers returning to the Exe estuary each winter (closed symbols). Population size is expressed as a percentage of the equivalent value in the absence of fishing (equilibrium population size = 2140). Predictions for equilibrium population size were derived from the model described by Durell, Goss-Custard & Clarke (1997).

in a reduction in population size of 35% for hand-picking and 58% for hand-raking. Therefore, small increases in mortality caused by fishing should not be assumed to be of little importance.

#### INTERACTION BETWEEN SHELLFISHING, WEATHER AND PREY ABUNDANCE

Cold weather increases the birds' energy demands and freezes fields, which prevents birds feeding during high tide. With low shellfish stocks in autumn, fishing a fixed amount should have a greater impact on birds than when stocks are abundant. Although unlikely to arise on the Exe at current fishing effort, it could be instructive for guiding policy elsewhere to explore the impact of shellfishing on oystercatcher survival under alternative scenarios of stock size, supplementary prey and winter climate.

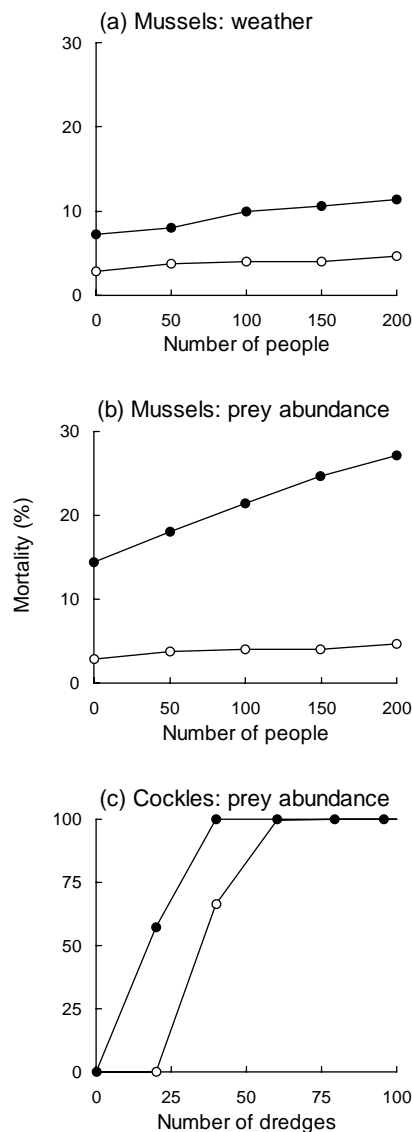
To simulate cold weather on the Exe, ambient temperature was reduced from approximately 5 °C to 0 °C for a 2-week period in late January. Low prey abundance was modelled by removing fields from around the Exe and halving initial cockle density on the Burry.

The impact of fishing on survival was accentuated by all three changes. With cold weather, no fields or scarce cockles, survival decreased more rapidly with increasing fishing effort than in the standard simulations (Fig. 6). These simulations show by how much more oystercatchers can be affected by shellfishing in hard winters, on estuaries without suitable surrounding fields or when their primary shellfish prey are unusually rare.

#### CHANGES IN MANAGEMENT PRACTICES

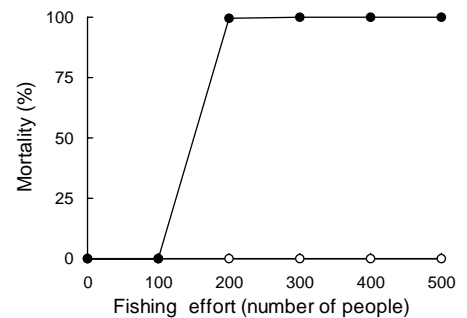
With present-day practices (daily quota per shellfisher of 100 kg fresh mass of cockles > 22 mm long) no birds





**Fig. 6.** Predicted interaction between shellfishing effort and the weather and prey abundance. (a) Cold weather was simulated by reducing the temperature in mid-January from approximately 5° to 0° (open circles = normal weather; closed circles = cold weather). Low prey abundance was simulated (b) on the Exe by removing fields (open circles = fields present; closed circles = fields absent) and (c) on the Burry inlet by halving the initial density of cockles (open circles = normal prey abundance; closed circles = half normal prey abundance). Simulations of the Exe estuary were based on hand-picking and those of the Burry inlet on suction-dredging. Note that the range of the vertical axis is different for mussels and cockles. Six replicate simulations were run for each combination of parameters and the results averaged.

were killed by hand-raking cockles on the Burry inlet. To guide policy there and elsewhere, the effect of changing these limits was simulated. The minimum size of cockles collected was reduced to 15 mm and the daily quota was increased to 500 kg. Hand-raking cockles could then kill all birds if fishing effort was high enough (Fig. 7), showing that management practices may have a very large impact on oystercatcher survival.



**Fig. 7.** Predicted effect on the percentage mortality of oystercatchers of changes in the minimum size and maximum daily catch of cockles collected by hand-raking on the Burry inlet. Open circles show the present limits (minimum size = 22 mm; maximum daily quota = 100 kg fresh mass). Closed circles show the effects of reducing the minimum size (= 15 mm) and increasing the daily quota (= 500 kg). Six replicate simulations were run for each combination of parameters and the results averaged.

## Discussion

### PREDICTED EFFECTS OF SHELLFISHING WITH CURRENT FISHING EFFORT

The main fishing methods on the Exe are hand-picking and hand-raking, while on the Burry it is hand-raking. The model predicted that the current fishing methods and efforts do not increase oystercatcher mortality or affect their body condition at either site. Both are low-intensity fisheries and the shellfish stocks are high relative to oystercatcher numbers. There is no reason to believe that intensifying restrictions on either of these fisheries would increase oystercatcher numbers.

### PREDICTED EFFECTS OF SHELLFISHING AT HIGHER LEVELS OF FISHING EFFORT

The simulations above the current fishing effort and using more intensive techniques, such as suction-dredging, showed that shellfishing can affect oystercatcher survival and numbers, but to different degrees, depending on the circumstances. The varying impacts of the different fishing methods reflect differences in the way in which they deplete shellfish stocks and whether they also disturb birds. Mussel-fishing techniques that reduced bed area (hand-raking and dredging) both reduced the food available and forced birds to feed at higher densities, thus increasing both exploitation and interference competition. In contrast, the other techniques did not reduce bed area but instead reduced the density of the most profitable sizes of shellfish. Techniques used at low tide also disturbed birds. The oystercatcher populations of the Exe and Burry contrasted in their predicted response to increasing shellfishing. The mortality rate on the Burry was a step-function response to increasing fishing effort; either no oystercatchers died or most did. Within the region of the threshold, very small changes in fishing effort produced large changes in oystercatcher

mortality but, further away, mortality rate was unrelated to fishing effort. This contrasted with the predicted response of the Exe population, in which mortality changed gradually and across a wide range of simulated fishing efforts. These differences arose from the degree of difficulty model birds had in meeting their energy demands in the absence of fishing (more difficulty on the Exe) and the amount of between-individual variation in intake rate (more on the Exe); low variation introduces scramble competition and thus a step-response in mortality. In the absence of fishing, or when fishing effort was very low, Burry model birds were able to meet their energy demands by feeding for only a fraction of the time cockle beds were exposed. In contrast, many Exe model birds needed to feed for nearly all the available time. Small increases in fishing effort therefore caused some birds to die on the Exe (because these were only just surviving in the absence of fishing) whereas equivalent increases on the Burry inlet did not increase mortality (because all birds had enough time available to compensate).

Although within-year effects of shellfishing on oystercatcher mortality were sometimes small, their cumulative influence over a number of years could be much larger. In the case of hand-raking mussels, for example, continued fishing caused extremely high bird mortality because mussel populations were unable to recover between years. Second, small, changes in oystercatcher mortality caused larger changes in the long-term population size because the oystercatcher population did not recover from the effects of shellfishing between winters.

The model predicted that the impact of shellfishing on oystercatchers depends not only on fishing effort but also on environmental factors such as the weather and overall food abundance. Again, this happened because the effect of fishing depended on the degree of difficulty birds were already having in the absence of fishing. If the majority met their demands by feeding for only a small proportion of the available time, conditions would have to deteriorate greatly for the mortality rate to be increased by shellfishing. If, instead, most birds were only just meeting their requirements, even a small deterioration in conditions could increase mortality. Either a short spell of cold weather or scarce prey increased the difficulty most birds had in surviving, and so increased the impact of shellfishing. In order to reduce oystercatcher mortality, fishing effort should perhaps be reduced during periods or winters in which birds are already having difficulty surviving.

Mussel and cockle fishing differed in the ways in which they affected shellfish stocks. On the Exe, mussel spat only recruit where adults are present, so the recruitment rate increases as adult density increase (McGrorty *et al.* 1990). In cockles, in contrast, spat recruitment is either unrelated to adult density or decreases as adult density increases (Dempster 1975; Beukema 1992; van der Meer 1997; Bannister 1999). This difference in spat recruitment means that shellfishing methods that strip

the mussel bed clean reduce the area occupied by mussels in the long term. In cockles, however, shellfishing may even enhance subsequent spat settlement, if settlement is indeed inversely dependent on adult density, and the sediment is not rendered unsuitable by the method employed.

#### APPLICATION OF THE MODEL TO OTHER SHELLFISHERIES

The model was not built to demonstrate simply that increasing fishing effort will eventually decrease oystercatcher survival. Instead, it was developed to predict: (i) whether the current intensity of shellfishing increases the difficulty oystercatchers have in surviving winter; and (ii) by how much oystercatcher survival and population size would be changed by alternative ways of managing shellfisheries. Only in extreme circumstances, when most shellfish have disappeared, may the effect of current shellfishing on shorebirds become clear from monitoring bird mortality rates and population size (Clark 1993). The effects of alternative shellfishery management cannot be determined empirically from past experience because the effects of all possible alternatives on oystercatcher mortality, and particularly on its density dependence, are largely unknown. Accordingly, a model was required to make quantitative 'what-if' predictions.

The behaviour-based approach is thought appropriate because it incorporates the ways in which real birds are most likely to respond to the changes in their feeding conditions caused by shellfishing (Goss-Custard *et al.* 2000). The present model has many parameters, but this proved to be necessary in sensitivity tests with the Exe model to predict mortality accurately (Stillman *et al.* 2000a). On the other hand, many parameter values are in the literature and likely to apply to other systems, a minimal list including: (i) the optimality foraging sub-models; (ii) individual variations in foraging efficiency and susceptibility to interference; (iii) oystercatcher energy expenditure, energy assimilation and fat storage efficiency; (iv) the mass and energy density of shellfish. The main new information needed to apply the model elsewhere is either readily available (weather), easily obtained with minimal fieldwork (shellfish bed exposure times), routinely surveyed anyway (shellfish abundance) or becoming much better known (mortality rate). Some additional information, for example on intake rates in fields in daylight or on shellfish at night, may improve model precision, but absence of data on this is not fatal. The model can be applied very rapidly to other systems to provide predictions for single winters of the effect of a wide range of alternative shellfishery management options, and is currently being used in England, Wales, Northern Ireland and France.

The model can also be applied with some confidence to guide policy because its predictions for the mortality rate of oystercatchers at current levels of fishing effort have been tested successfully on the Exe (Stillman *et al.* 2000a). The multiple-year simulations of the Exe model

illustrate, however, that policy will be most reliably informed by models that couple the population dynamics of the birds and shellfish. We could not do this for the Burry system because of a lack of information on cockle spat recruitment, and especially its possible dependence on adult density. But once this issue has been resolved, it will be possible to explore the long-term intergeneration effects on oystercatchers, shellfish and shellfishery yield of alternative shellfish management regimes on this estuary as well as on the Exe.

#### HOW THE MODEL CAN GUIDE SHELLFISHERY MANAGEMENT POLICY

Currently, there exist some quite simple approaches to managing shellfisheries in Europe. In the Netherlands, for example, a run of poor spat-fall years and overfishing resulted in virtually no intertidal mussels for oystercatchers (Beukema 1993). However, the new policy in the Oosterschelde estuary is to reserve 100% of the total requirements of the bird population in areas above a threshold cockle density of 50 m<sup>-2</sup> over a large enough area such that bird density in the area occupied by cockles does not exceed the highest ever recorded. The shellfishery harvests what is left after the demands of the birds have been taken into account.

Our model provides a complementary management tool to this year-by-year approach. It can be used (i) diagnostically to investigate whether the current shellfishery regime is causing some oystercatchers to starve, and (ii) prescriptively to explore the long-term consequences for oystercatchers of alternative management regimes.

In many areas, monitoring whether shellfishing affects oystercatcher survival is impractical, unless any effects are very large and obvious (Clark 1993). The data required are either not available or there are confounding factors, such as high levels of disturbance, that prevent any impact of shellfishing alone from being established. In addition, oystercatchers switch to alternative prey when shellfish are scarce (Desprez *et al.* 1992; Beukema 1993; Lambeck, Goss-Custard & Triplet 1996; Triplet *et al.* 1999b) and, as the present paper has shown, can thereby significantly improve their chances of survival. In these circumstances, the model can establish whether the current shellfishery policy is likely to be raising winter mortality.

In its prescriptive or predictive 'what-if' role, the model can inform shellfishery policy on several issues. First, oystercatchers have survived in large numbers when shellfish were scarce by eating alternative prey (Beukema 1993; Lambeck, Goss-Custard & Triplet 1996). The model can be used to explore the consequences of a shellfishery policy that depleted stocks to the extent that the oystercatcher population could not obtain all of its requirements from shellfish alone. Secondly, when shellfishing affects oystercatcher survival through disturbance, the model can alert policy-makers to levels of shellfishing that, while leaving enough shellfish for the birds, would none the less reduce survival through

disturbance. Thirdly, the model can be used to predict by how much the relaying of subtidal mussels at different levels of the intertidal zone would reduce oystercatcher mortality, and also how many of the transplanted mussels would be consumed by oystercatchers before reaching a harvestable size. Finally, the model can be used to explore the importance to oystercatchers of either maintaining existing terrestrial feeding habitats or of providing additional such habitats as a further insurance when shellfish stocks are low.

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