Improvement Programme for England’s Natura 2000 Sites (IPENS) – Planning for the Future IPENS025

Predicting the mussel food requirements of oystercatchers in the Exe Estuary

Exe Estuary Special Protection Area (SPA)

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Foreword

The **Improvement Programme for England's Natura 2000 sites (IPENS)**, supported by European Union LIFE+ funding, is a new strategic approach to managing England's Natura 2000 sites. It is enabling Natural England, the Environment Agency, and other key partners to plan what, how, where and when they will target their efforts on Natura 2000 sites and areas surrounding them.

As part of the IPENS programme, we are identifying gaps in our knowledge, and where possible, we are addressing these through a range of evidence projects. Results from these projects will feed into Theme Plans and Site Improvement Plans. This project forms one of these studies.

The purpose of this project was to assess the mussel (*Mytilus edulis*) food requirements of oystercatcher (*Haematopus ostralegus*) in the Exe Estuary, which has been designated a Special Protection Area (SPA) for overwintering waterbirds, including oystercatcher. The overwintering oystercatcher population of the Exe Estuary has been well-studied, and the birds are known to feed predominantly upon mussels in intertidal areas. There have been recent declines in the population size of oystercatcher in the Exe Estuary, the reasons for which are unknown.

The project developed an individual-based model to predict the food requirements of oystercatchers; and whether there is / could be any effect on oystercatcher survival of the current / potential future ways of managing the mussel fishery on the Exe Estuary. The current mussel fishery on the Exe provides a feeding resource for oystercatcher on intertidal lays that are exposed on spring tides. Two potential management options that could be effective at improving the feeding conditions of oystercatcher would be to increase the number and area of intertidal mussel lays, and / or to place mussel discards at a relatively high shore level close to the oystercatcher roost.

The key audience for this work is the staff within Natural England and the Devon and Severn Inshore Fisheries and Conservation Authorities (D&S IFCA). The purpose of commissioning this was to provide evidence in support of good fishery management practice that could be used to manage the fishery in a sustainable way.

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1 SUMMARY

The purpose of this project was to assess the mussel (*Mytilus edulis*) food requirements of oystercatcher (*Haematopus ostralegus*) in the Exe Estuary, which has been designated a Special Protection Area for overwintering waterbirds, including oystercatcher. The overwintering oystercatcher population of the Exe Estuary has been well-studied, and the birds are known to feed predominantly upon mussels in intertidal areas. There have been recent declines in the population size of oystercatcher in the Exe Estuary, mirroring wider declines throughout Europe, the reasons for which are unknown.

The study comprised:

- The collection of new data on the area of mussel beds, the density and size distribution of mussels on these beds, and the numbers and behaviour of oystercatcher on these beds;
- The collation of existing data on the food supply of oystercatchers in the Exe Estuary;
- The development of models to predict the food requirements of oystercatcher;
- Running simulations of the models to predict whether there is / could be any effect on oystercatcher survival of the current / potential future ways of managing the mussel fishery on the Exe Estuary.

The current mussel fishery on the Exe provides a feeding resource for oystercatcher on intertidal lays that are exposed on spring tides. Two potential management options that could be effective at improving the feeding conditions of oystercatcher would be to increase the number and area of intertidal mussel lays, and / or to place mussel discards at a relatively high shore level close to the oystercatcher roost.

This project documented a number of changes that have occurred to the Exe Estuary mussel and oystercatcher populations including:

- The number and size of mussel beds have decreased since traditional methods of maintaining mussel beds in the estuary have ceased.

- The density of mussels within the size range consumed by the birds has generally decreased, but the density of the larger mussels within this size range, which are more profitable to oystercatcher, has generally increased.
- Oystercatcher lose a higher proportion of mussels to attacks by carrion crows and herring gulls than they have in the past.
- The number of oystercatcher wintering in the estuary has declined, but the number of birds feeding on the mussel beds has been relatively stable.

The models developed in the project predict that the present day mussel population is sufficient to support the number of oystercatcher that were observed to feed on mussels.

The presence of mussel lays provides extra food for oystercatcher when these lays are exposed on spring tides. The present area, or increases in the area of mussel lays could increase the survival rate of oystercatcher if the number of birds feeding on mussels was over 2000. Below this threshold, starvation was predicted to affect 0 % of the population and so additional food resources cannot further reduce the starvation. The effect over 2000 birds is relatively small because the lays are only exposed for a short time, and so oystercatcher will obtain the majority of their food from mussel beds that are higher on the shore, and hence exposed for longer. Simulations were not run in which lays were positioned higher on the shore because this would not be commercially viable from a fishery perspective; the growth rate of mussels declines as they are positioned further up the shore because they are inundated with water for less time and so have less time to feed.

Factors that would affect the beneficial effect of discards include the size of the discards, the size of the discard bed and the date from which discards are replenished. Our simulations predicted that larger discards spread at lower density over a larger bed increased oystercatcher survival by the greatest amount. This happened because interference competition excluded some birds from smaller patches, and oystercatcher can maintain high intake rate down to low mussel densities. It is unlikely that the size of discards could be increased, but the simulations suggest that the greatest benefit to oystercatchers could be achieved by spreading discards over a larger area. Our simulations predicted that making discards available from January increased oystercatcher survival by the same amount as making them available from September. This was because the feeding conditions of birds deteriorate through winter as, for example, the ash-free dry mass of prey declines, interference competition intensifies and day length shortens. The intake rate of birds feeding on discards was not measured during the study, but we recommend that this is done to between understand the potential benefit of discards. We recommend that the best place for the discard bed would be along the top of the shore on an area of gravel (and hence of relatively low food value to the birds), to the south of Cockwood. This is south of an area where discards have been laid and exploited by oystercatcher in the past, but would experience lower levels of disturbance from human activity.

2 INTRODUCTION

Temperate estuaries across northern and western Europe are important sites for populations of shellfish, which support commercial shellfisheries. Commercial shellfish harvesting is estimated to be worth £250 million per annum to the UK economy, providing both food and employment (DEFRA, 2013). These shellfish are also the principal overwintering food resource for a range of species of migratory wading birds, hereafter referred to as ‘shorebirds’. Shorebird species are key components of UK coastal biodiversity and are protected under the European Union Wild Birds Directive (2009/147/EEC), which legally obligates the UK government to maintain healthy shorebird populations. The shared shellfish resources within estuarine areas have led to conflicts between economic and conservation interests across estuaries in northwest Europe (Tinker, 1974; Ens, 2006; Laursen *et al*., 2010). Enough shellfish must be left unharvested to allow the birds to meet their food requirements. The responses of shorebird species to insufficient food supplies during the overwinter period, which include reduced individual body condition, increased mortality and reduced population sizes, have been well-documented in the scientific literature (Camphuysen *et al*., 1996; Verhulst *et al*., 2004; Atkinson *et al*., 2003; Atkinson *et al*., 2005; Atkinson *et al*., 2010). Therefore, a central question facing statutory authorities of estuaries is: how much food should be reserved for the bird population?

The purpose of this project was to assess the mussel (*Mytilus edulis*) food requirements of oystercatcher (*Haematopus ostralegus*) in the Exe Estuary (**Figure 1**), which has been designated a Special Protection Area (SPA) for overwintering waterbirds, including oystercatcher (European Union Directive 79/409/EEC). The overwintering oystercatcher population of the Exe Estuary has been well-studied, and the birds are known to feed predominantly upon mussels in intertidal areas (Goss-Custard & Durell, 1983; Ens & Goss-Custard, 1984). There have been recent declines in the population size of oystercatcher in the Exe Estuary (**Figure 2**), the reasons for which are unknown. There have been associated declines in the area of mussel beds. The study comprised: (i) the collection of new data on the area of mussel beds, the density and size distribution of mussels on these beds, and the numbers and behaviour of oystercatcher on these beds; (ii) the collation of existing data on the food supply of oystercatchers in the Exe Estuary; (iii) the development of an individual-based models and a more simple model (see below for details of the models) to predict the food requirements of oystercatcher; and (iv) running simulations of the models to predict whether there is / could be any effect on oystercatcher survival of the current / potential future ways of managing the mussel fishery on the Exe Estuary.

2.1 History of mussels in the Exe Estuary

In large intertidal areas, such as Morecambe Bay and the Wadden Sea, large amounts of spat mussels settle onto ‘clean’, mussel-free stony ‘skears’ or sand to form new mussel beds. In small estuaries like the Exe (**Figure 1**), however, spat rarely settle elsewhere than on established mussel beds. If they do settle elsewhere, the spat seldom last long, mainly because they are rapidly consumed by crabs. In experiments on the Exe estuary, McGrorty *et al*. (1990) found that 96-100% of spat mussels 2-16mm long were taken by crabs over a single high water period whereas only 30-53% disappeared when the spat were placed amongst older mussels. Spat mussels on the Exe Estuary only seem able to protect themselves from crab predation by settling deep within the clean byssal threads of the already established adults.

This finding has important implications for understanding why there used to be so many mussel beds on the Exe whereas now there are much fewer (**Figure 3**), although still more than would have been the case without intervention by man. In September 1976, McGrorty *et al*. (1990) identified 31 separate mussel beds occupying a combined area of approximately 80ha. Of these, the 12 largest - the ‘main’ beds - contained 82% of the entire intertidal mussel population of the estuary; the remaining 19 mussel beds were small in comparison and contained only the remaining 18% of the total mussels. Of the 12 main beds, four – two on Bull Hill and two at Cockwood – had a shingle base and may have been natural beds. Many of the remaining beds in 1976, however, were situated in muddy areas where spat mussels do not settle unless adults are present. In addition, spat mussels tend to avoid muddy places even if adults are present; this is probably because the adult byssus threads are covered in mud and are thus inaccessible to spat, and because some of the spat that do settle are subsequently smothered by further deposits of mud (McGrorty & Goss-Custard, 1991). Had the beds in the muddy areas of the estuary not been laid and maintained in the first place by fishermen, there would be far fewer mussel beds and mussels in the Exe Estuary today than there are, even 50 years after shellfishing began to decline. It is likely that the only mussel beds would have been those on Bull Hill and at Cockwood.

Up until the 1950s/60s, the fishermen and their families spent the summer maintaining their mussel beds. Unless this was done, the mussels would be gradually washed away and/or smothered by mud. This degradation of the mussel beds was prevented by importing spat mussels from elsewhere, mainly from the sub-littoral parts of the estuary and nearby inshore waters. The low-lying area at the west side of Bull Hill, called '17 buoy Cut' because it is near buoy 17, frequently provided large quantities of spat for this purpose. The mussels that had previously been harvested or washed away from the fishing grounds were thereby replaced and the 'health' of the mussel bed maintained.

This restocking of the mussel beds was vital for the persistence of these small family grounds. This was illustrated by the research of McGrorty *et al*. (1990). In 1976, 19 small mussel beds contained 18 % of all the intertidal mussels but storms and smothering had so reduced their size that they contained only 2 % by March 1980. This decline occurred despite the natural immigration – by 'drifting' - of mussels from naturally exporting mussel beds further down river (McGrorty & Goss-Custard, 1991). The numbers of mussels on the 12 main mussel beds had remained more-or-less constant because the huge dead-weight of these sheets of mutually-attached mussels prevented their gradual erosion, except at their leading edges that faced the prevailing storms. Recent observations (John Goss-Custard, pers. obs.) have shown that this erosion of mussels from the exposed, south-western edges of the large mussel beds on the east side of the estuary is continuing.

Since farming the mussel beds stopped in the 1950s/60s, the intertidal area occupied by mussels has shrunk considerably. Recent field trips (John Goss-Custard, pers. obs.) confirmed that almost all of the smaller beds have now completely disappeared.

The majority of the existing mussel beds in the Exe Estuary fall within areas closed to mobile fishing gear by the Devon and Severn Inshore Fisheries Conservation Authority (IFCA). The exceptions are the mussel beds on the western shore near Cockwood and Dawlish Warren (**Figure 4**).

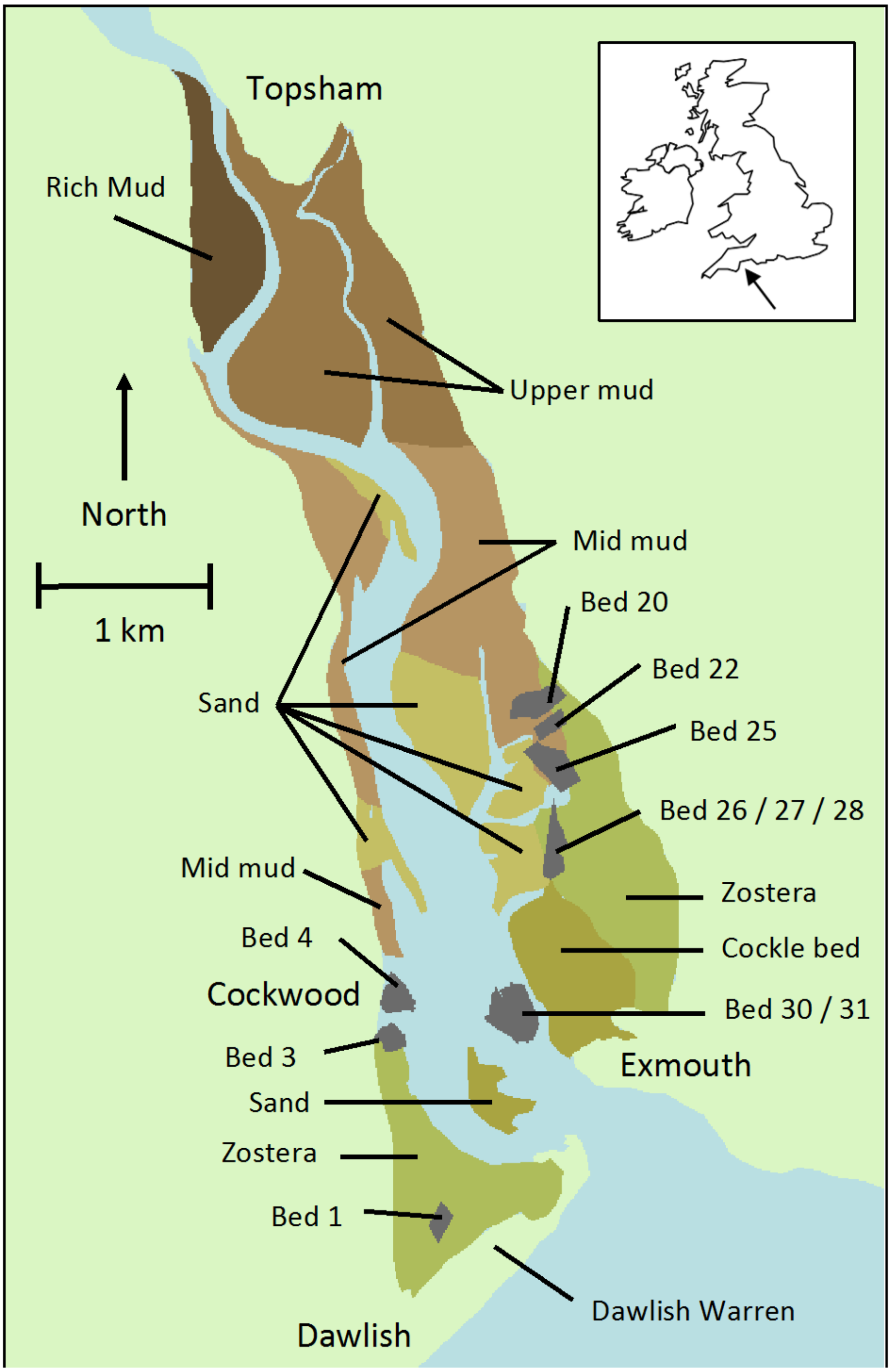

Figure 1: *Map of the Exe estuary showing the distribution of the mussel beds surveyed during the study (Beds 1 - 31). The colours of other intertidal habitat show the patches derived from an intertidal invertebrate survey of the Exe (Durell et al. 2007). See* ***Table 1*** *for more details of the mussel beds and other patches.*

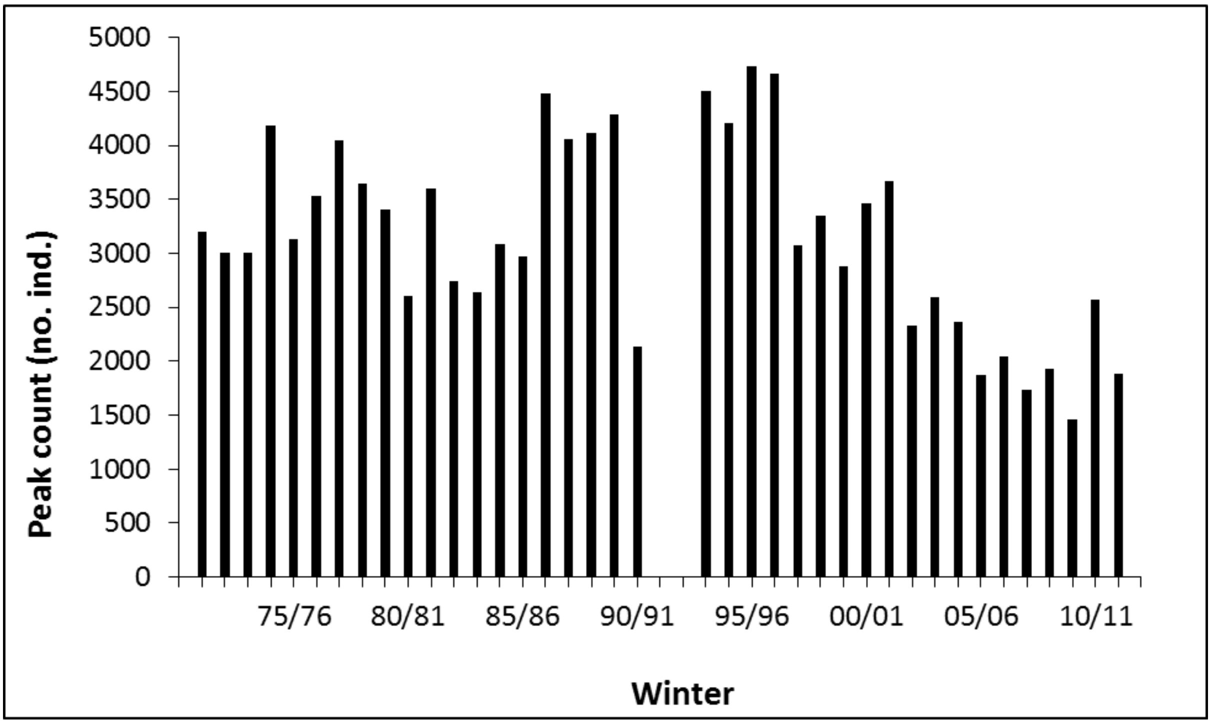

Figure 2: *The peak overwinter counts of oystercatchers in the Exe estuary over the period 1971/72 to 2011/12 (Austin* et al*., 2014). No data are available for the 1991/92 and 1992/93 winters.*

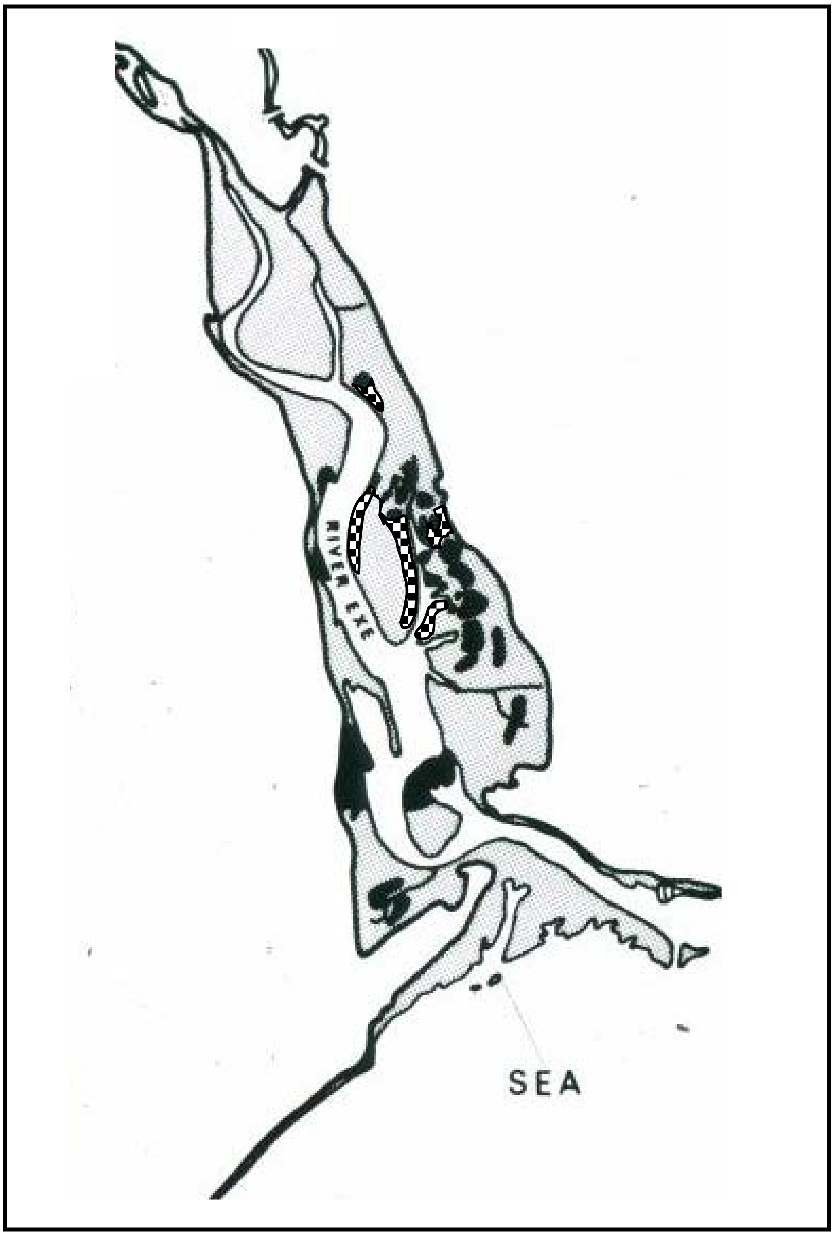

Figure 3: *The approximate areas occupied by mussels in the 1960s and 1976. The black and white areas show the approximate locations of places where mussel beds were laid and maintained by local fishermen in the 1960s, but which had disappeared by 1976: the black areas show those that remained in 1976.*

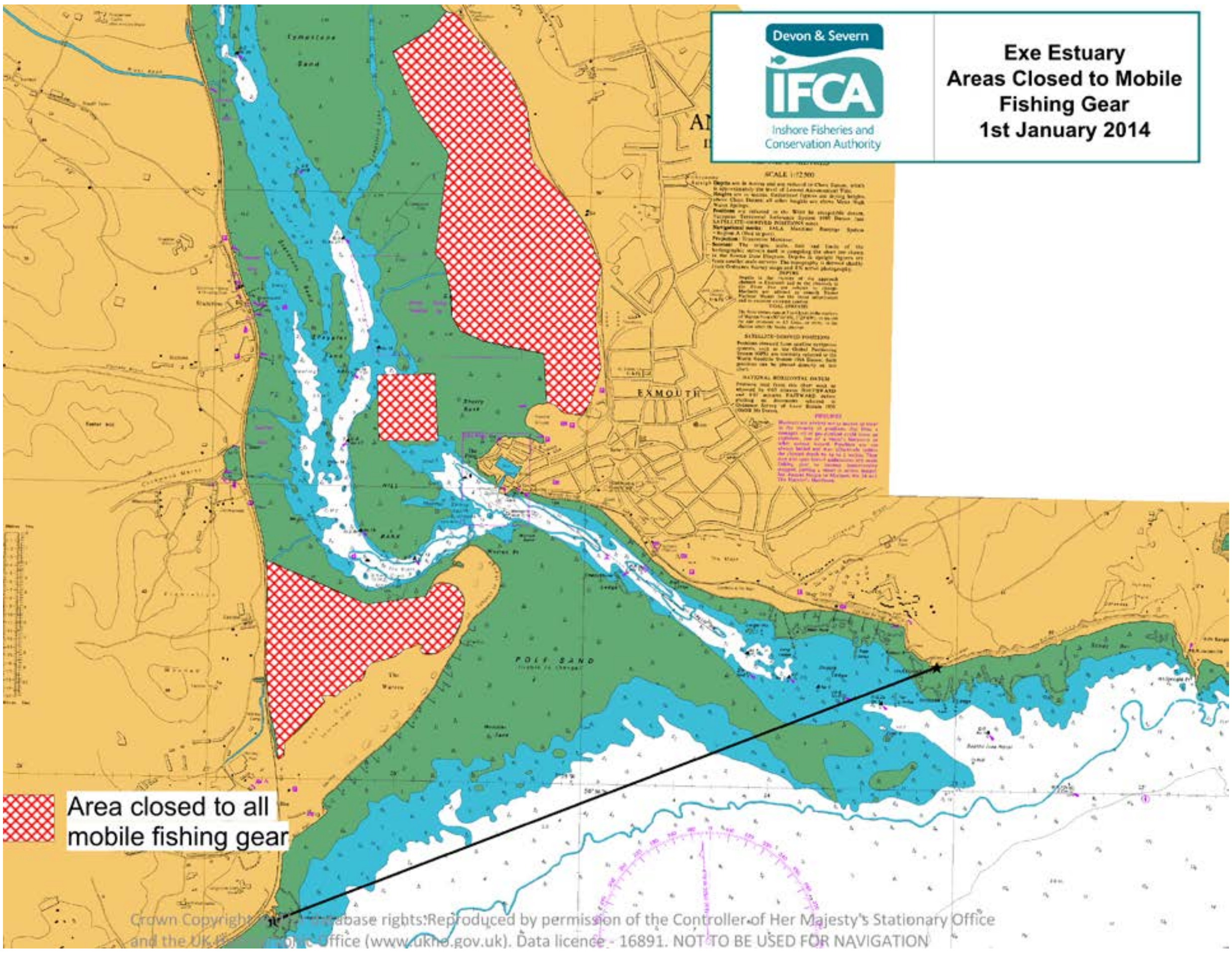

Figure 4: *Areas of the Exe Estuary closed to mobile fishing gear. Map produced by Devon and Severn IFCA.*

2.2 Present management regime of the Exe Estuary mussel fishery

The following two sections give an overview of the present mussel management regime on the Exe Estuary and ways in which this could potentially be adapted for the potential benefit of the birds. Our understanding was derived through discussion with Myles Blood-Smyth of The Exmouth Mussel Company (www.exmouthmussels.com).

Mussels in their first year of life are harvested from the seabed with a suspended elevator and transported by boat to a number of areas just off Cockwood and Starcross (**Figure 1**). These young mussels are then laid very low down the shore where their growth rates will be high. Here they stay until they have grown to marketable size, which they reach in their second or third year. They are then harvested – again using a suspended elevator over high water – processed and sold.

In previous years, many of the young mussels were laid at a level of the shore where they would be exposed at low water on spring tides but not on neap tides. When the mussels had grown to a length of 35 mm or more, they provided oystercatchers with a profitable source of food that was additional to that provided by the main mussel beds within the estuary. However, the mussels that were exposed at low water on spring tides did not grow as well as those that were permanently submerged in the sub-littoral. This is because mussels can only feed when they are covered by water and can feed for longer when they are permanently underwater than when they are not. Accordingly, the decision was taken to lay all the young mussels below extreme low water springs so that they would be permanently inundated and grow on to marketable size at the fastest possible rate. However, some mussels have been laid somewhat further upshore where they are exposed at extreme low water springs. This is not done as a condition for obtaining the licence but provides an additional source of food that can be used by oystercatchers.

Sometimes, after harvesting, mussels that have been collected from the main sub-littoral lays that are not yet of marketable size. These under-sized mussels are re-laid in the estuary in a lay just downshore of the mussel bed at Cockwood. Being exposed at low water spring tides, where they remain until they too reach a marketable size. These mussels are consumed by oystercatchers.

After marketable mussels have been harvested and processed, there remains a collection of shells that are termed ‘discards’. These consist of some mussels that have been broken during process but also many slipper limpets, *Crepidula fornicata*, a non-native species, that does not survive for long out of water. The mussel fishery returns the discards to the Bull Hill mussel bed, part of which has been eroding over the last decades. The intention is that the shells of the dried-out and dead slipper limpets and mussels will form a substrate upon which spat mussels can settle. As they grow, these mussels will help to stabilise the sediment and contribute towards the long-term maintenance of Bull Hill. Were Bull Hill to erode away, the entire hydrology, sedimentology and ecology of the estuary would be changed.

2.3 Options for managing the fishery for oystercatcher

There are two management options that could be effective at improving the feeding conditions of oystercatcher, but would not make uneconomic demands on the fishery (derived from discussions with Myles Blood-Smyth of The Exmouth Mussel Company).

2.3.1 Discards

Oystercatchers can be hard-pressed during spells of cold winter weather when their two main supplementary sources of feeding – the upshore mudflats and fields - are unavailable because they are frozen over. During such spells, putting broken mollusc shells containing some flesh at the upper level of the shore could help the birds. The best place to do this would be high up the shore in the Bite, between Dawlish Warren and Cockwood, where many oystercatchers already accumulate at the beginning and end of the exposure period. This would enable the birds them to feed for longer. This practice used to be carried out at Cockwood and oystercatchers, along with some other shorebird species, made much use of the easy pickings thereby made available to them (John Goss-Custard, Pers. Obs.). In addition, the discards might attract carrion crows and herring gulls away from the main mussel beds where currently they steal many of the mussels that have been found and opened by oystercatchers.

2.3.2 Intertidal lays

If the mussel fishery was enabled to collect young mussels in quantities that exceeded the area that they could seed in the commercial sub-littoral lays, the surplus could be laid over the disappearing former lays at the bottom of the shore near to the wreck off Cockwood. As the mussels grew into the size classes taken by oystercatchers, they would provide an additional source of food for the birds that they could use over low tide on spring tides. Such a sponsored lay would also be rather inaccessible to people as there is a depression that runs between the main shore. This lay could provide a disturbance-free feeding site for any birds displaced from the main mussel beds at Cockwood where bait-diggers and casual cockle pickers often occur over dead low water, particularly on spring tides. An area of up to 2 ha with 100 tonnes is the amount that could possibly be considered for this sponsored lay.

In this project, we use computer model simulations (see below for details of the model) to predict whether or not such discards and / or an additional lay could help oystercatcher to survive the non-breeding season in good condition.

2.4 Using individual-based models to assist shorebird conservation

In migratory shorebirds such as oystercatcher, population size is a function of the interaction between (i) mortality and reproductive rates in the breeding ranges and (ii) mortality rate in the non-breeding range, including migratory routes (Stillman & Goss-Custard 2010). Therefore, the best measure of the impact of change (e.g. changes in mussel abundance) on population size is one which, directly or indirectly, determines these demographic rates (Goss-Custard *et al*., 2002). For migratory shorebirds during the non-breeding season, this means that the impact should be measured in terms of its effect on two factors: (i) the storage of fat reserves needed to fuel migration in spring and to breed successfully after the birds have reached the breeding grounds and (ii) the number of birds that die during the non-breeding season (Goss-Custard et al., 2002).

Individual-based models, comprised of fitness-maximising individuals, are a means of predicting fat storage and mortality rates and hence can be used to determine the population consequences of environmental change (e.g. Stillman & Goss-Custard

2010). Such individual-based models have been used to predict the effect of habitat loss, sea level rise and disturbance on coastal bird populations at several European sites (e.g. Caldow *et al*., 2004; Durell *et al*., 2005, 2006, 2007; Stillman *et al*., 2000, 2001, 2003, 2010). These models track the behavioural decisions and locations of all animals within a population, and predict population parameters, such as mortality rate, from the fates of all individuals. Model individuals are designed to always behave in order to maximise their own chances of survival and reproduction, no matter how much the environment changes. Therefore, model animals are expected to respond to environmental change in the same ways as real ones would. In this report we used the MORPH individual-based model (Stillman, 2008) to predict the effect of mussel abundance and potential fishery management on the survival rates of oystercatcher. MORPH has been applied to several systems, including the interaction between oystercatcher and shellfish in the Burry Inlet (Stillman *et al*., 2010), the Wash (Stillman *et al*., 2003), Morecambe Bay (West & Stillman, 2010) and Solway Firth (Stillman & Goss-Custard, 2010).

2.4.1 Overview of MORPH

MORPH predicts how environmental change (e.g. changes in shellfishing, habitat loss, changes in human disturbance, climate change and changes in population size) affects foraging animal populations. MORPH's key assumptions are that individuals behave in order to maximise their perceived fitness (i.e. their expected survival and reproduction associated with alternative behaviours). MORPH contains a basic framework to describe animal physiology and foraging behaviour, and the distribution and abundance of resources.

MORPH tracks the foraging location, body condition and ultimate fate of each individual within an animal population. During each day, each animal in the population must consume enough food to meet its energy demands. It attempts to do this by feeding in those locations and at those times of the day where its intake rate is maximised. Although all individuals decide on the same principle, intake rate maximisation, the actual decisions made by each differ. Their individual choices depend on their particular competitive ability which depends on two characteristics. Interference-free intake rate is the rate at which an individual feeds in the absence of competition and measures its basic foraging efficiency. Susceptibility to interference measures how much interference from competitors reduces its intake rate as competitor density rises. Survival is determined by the balance between an individual's daily rates of energy expenditure and consumption. Energy expenditure depends on metabolic costs. Energy consumption depends on the time available for feeding, intake rate while feeding and the energy content of the food being consumed. When daily energy consumption exceeds daily expenditure, individuals accumulate energy reserves or maintain them if a maximum level has already been reached. When daily requirements exceed daily consumption, individuals draw on their reserves. If reserves fall to zero, an individual dies of starvation.

2.4.2 Testing the accuracy of predictions

If IBMs such as MORPH are to be of applied value they need to produce accurate predictions. MORPH has been tested as thoroughly as possible using all data available for each study system. Two questions can be asked about whether an IBM predicts real events reasonably well. One question asks whether the model captures with good precision the behaviour of real birds in the system being modelled. Because the predictions for survival are derived from the behaviour of the birds in the model, and because decision making by fitness-maximizing individuals is the fundamental feature of the model, it is vital that the model adequately represents the behaviour of real birds. The other question is whether the model accurately predicts the fitness measures (e.g. survival) that are derived from this underlying behaviour. Although the tests have varied between sites, data have been typically available to test the predicted distribution of birds throughout a site and the major prey species consumed by birds. Typically, patch selection and prey choice were accurately predicted for the majority of species (e.g. Stillman & Goss-Custard 2010). In some sites, data were available on the proportion of the time spent feeding each day (an important indicator of the difficulty birds are having in surviving winter) and overwinter mortality rates. Both the proportion of the time spent feeding and overwinter mortality were accurately predicted in all cases (e.g. Stillman & Goss-Custard 2010). These accurate predictions increase confidence that the model provides a realistic description of the real world, and therefore that predictions for novel scenarios, which cannot be tested, are also likely to be accurate.

2.4.3 Parameters required to apply MORPH to a new system

To be applied to a new system, the key parameters that need to be measured or obtained from previous studies or the literature are: (i) the distribution of the food supply and how food quality and abundance changes through the season; (ii) the tidal availability of feeding areas; (iii) the rate at which foragers are able to consume food given the abundance of food and competitors; (iv) the amount of food a forager needs to consume each day in order to avoid starvation; (v) the distribution and seasonal changes in other factors which influence the foraging behaviour and survival of foragers. In practice the only new parameters that have been measured for new shorebird systems have been the distribution and abundance of invertebrate prey and the availability of this prey through the tidal cycle. Typically, other parameters have been either obtained from the literature or from previous studies of the site. As a result models have typically been parameterised and applied to conservation issues using one autumn survey of prey populations (sometimes supplemented with a second in the spring), and estimates of the tidal exposure of patches either derived from local knowledge, patch heights on the shore, or existing tidal models. Once data are available, models have typically been parameterised and simulations run to address conservation issues within two months. Once a model is parameterised for a system, simulations can be run to address new issues within a matter of hours. The experience has therefore been that it has been possible to apply MORPH within a time scale that is compatible with the time constraints of coastal conservation issues.

2.5 A simplified model to assist shorebird conservation

Detailed individual-based models, such as MORPH, can predict the amount of food required by populations of shellfish-feeding birds to survive through winter (e.g. Stillman, 2008; Stillman & Goss-Custard, 2010). However, specialist knowledge is required to run these models, and they have typically been applied on a site by site basis. Despite recent attempts to make individual-based models more user-friendly (e.g. West *et al*., 2011), model complexity can still be perceived as a barrier to the successful use of individual-based models. A complementary, approach would be to use a simplified method to assess bird food requirements that could be used in a consistent way across a range of sites. The simplified approach could synthesise the predictions of the more detailed models. An ideal would be a piece of software into which data on the number of birds and abundance and species of shellfish are entered, which then predicts using simple steps, the amount of food required by the birds. The predictions should be accompanied by appropriate caveats, the assumptions used to calculated them, and confidence limits. The simplified approach could potentially be used in combination with individual-based models, highlighting priority systems in which more detailed modelling and data collection could occur.

A recent contract between Bournemouth University and the Welsh Government started to develop such a model (Stillman & Wood, 2013a), termed the *Ecological Requirement Model* henceforth. The purpose of the model is to calculate the food requirements of a shorebird population consuming shellfish within a site. Data on the number of birds of each species feeding on shellfish, the time for which the populations must be supported and the initial stocks of each shellfish species are entered into the model. The model then calculates the amount of food required in the environment to maintain high survival within the bird population. This is calculated using the results of empirical and individual-based modelling studies of shorebirds in shellfisheries throughout the UK. Importantly, the model calculates the amount of food required in the environment to maintain high bird survival rate (the *ecological requirement*), rather than the amount actually eaten by the birds (the *physiological requirement*). The ecological requirement exceeds the physiological requirement because the birds cannot locate all of the food, not all of the food is available all of the time, interference competition may exclude birds from the food supply, and the food supply may be depleted due to factors other than the birds. This model has been applied to the Burry Inlet (Stillman & Wood, 2013a), Dee Estuary (Stillman & Wood, 2013b) and Solway Firth (Stillman & Wood, 2013c).

In this report we use the Ecological Requirement Model to assess the food requirements of the oystercatcher population, and compare its predictions with those of the more complicated individual-based model.

3 BIRD AND MUSSEL SURVEYS

3.1 Bird surveys

Each month between October 2013 and March 2014 inclusive, each of the nine mussel beds (Beds 1, 3, 4, 20, 22, 25, 26/27/28, 30 and 31; McGrorty *et al*. 1990) were surveyed for oystercatchers, carrion crows and herring gulls over a complete tidal cycle. We recorded whether each oystercatcher was foraging or resting. Surveys were conducted over spring tides. During each survey, every 10 - 30 minutes the number of oystercatchers present on the mussel bed was recorded. Furthermore, we recorded whether each individual was foraging or resting. Observations were made using tripod-mounted telescopes. Between counts we scanned the mussel bed looking for an oystercatcher in the process of seizing a mussel. We then followed that individual until the outcome of the foraging attempt was observed. We recorded whether the mussel was successfully opened and swallowed, or whether the individual lost the mussel due to a kleptoparasitic attack by a carrion crow or herring gull. If the individual abandoned the mussel without opening it, or was lost from view, then the observation was terminated and no record was made.

3.2 IFCA mussel surveys

The Devon and Severn IFCA sampled the abundance and size distribution of mussels on the six main mussel beds (3, 4, 20, 25, 26/27/28, 30, 31; McGrorty *et al*. 1990) during 2013 and 2014, following the methods described by Gray (2012). **Figure 1** shows the distribution of mussel beds recorded in the mussel surveys.

The area of each bed was recorded by walking its perimeter and marking points with a handheld GPS, which were then plotted onto MapInfo GIS software.

To determine coverage and patch density transects were walked in a zig-zag across the bed, right up to the perimeter, to provide optimum coverage through the bed. A 4’ bamboo cane with an 11 cm ring attached to the end, so that the ring sits flat on the ground when held out to one side, was used to determine the mussel coverage for each transect. Every three paces along each transect the cane was flicked out to one side and it was recorded whether it is a “hit” if the ring contained live mussel, or a “miss” if the ring did not contain live mussel. On every fifth hit the contents of the ring were taken as a sample, using an 11 cm diameter corer. All mussel samples from the same transect were collected together in a tub, but kept separate from those of other transects.

Once all transects were complete the mussel samples were sieved and cleaned. For each transect the number of samples taken was recorded, all mussels measured and then divided into 5 mm size groups. The total number and mass of each group was recorded. The data collected were used to calculate the coverage, density and area of the mussel bed, which were then used to estimate the mussel tonnage on each bed. Size distribution was obtained from the length measurements of mussels in the retained samples. The hit/miss data were also pooled, to calculate the average coverage and patch density for the whole bed, compensating for the possibility of some transects being longer than others.

3.3 Bournemouth University mussel surveys

Two relatively low density mussel beds (1, 22; McGrorty *et al*. 1990) were not included in the IFCA survey, but are used by some oystercatchers (**Figure 1**). Therefore, a reduced survey was conducted on these beds to obtain an estimate of mussel size class density. A transect was walked across each bed. During each pace the surveyor checked whether there were any live mussels within a virtual 20x20 cm quadrat to the front of their leading foot. On every third occurrence of live mussels, all mussels within the quadrat were collected and pooled. The maximum length of each mussel was measured to the nearest mm. The percentage cover of mussels was obtained from the proportion of paces in which live mussel(s) were present. Mussel size class density was derived from the total number of mussels within a 5 mm class, the number and area of samples and the percentage cover of mussels. The area of these beds was not measured. Instead it was assumed that their area was 70 % of the area estimated by McGrorty *et al*. (1990). This is because the areas of beds measured in the IFCA survey were on average 70 % of the areas estimated by McGrorty *et al*. (1990).

4 INDIVIDUAL-BASED MODEL

We parameterised the individual-based model MORPH (Stillman, 2008) for the Exe estuary and its overwintering oystercatcher population. Many parameter values were available from earlier models of the Exe oystercatcher population (Stillman *et al*., 2000; Durell *et al*., 2007). **Figure 5** shows a screenshot of the model. **Tables 1, 2 and 3** show the parameter values used in the model.

4.1 Overview of MORPH

MORPH is an individual-based model (IBM) and tracks the foraging location, body condition and ultimate fate of each individual within an animal population. During each day, each animal in the population must consume enough food to meet its energy demands. It attempts to do this by feeding in those locations and at those times of the day where its intake rate is maximised. Although all individuals decide on the same principle, intake rate maximisation, the actual decisions made by each differ. Their individual choices depend on their particular competitive ability which depends on two characteristics. Interference-free intake rate is the rate at which an individual feeds in the absence of competition and measures its basic foraging efficiency. Susceptibility to interference measures how much interference from competitors reduces its intake rate as competitor density rises. Survival is determined by the balance between an individual's daily rates of energy expenditure and consumption. Energy expenditure depends on metabolic costs. Energy consumption depends on the time available for feeding, intake rate while feeding and the energy content of the food being consumed. When daily energy consumption exceeds daily expenditure, individuals accumulate energy reserves or maintain them if a maximum level has already been reached. When daily requirements exceed daily consumption, individuals draw on their reserves. If reserves fall to zero, an individual dies of starvation.

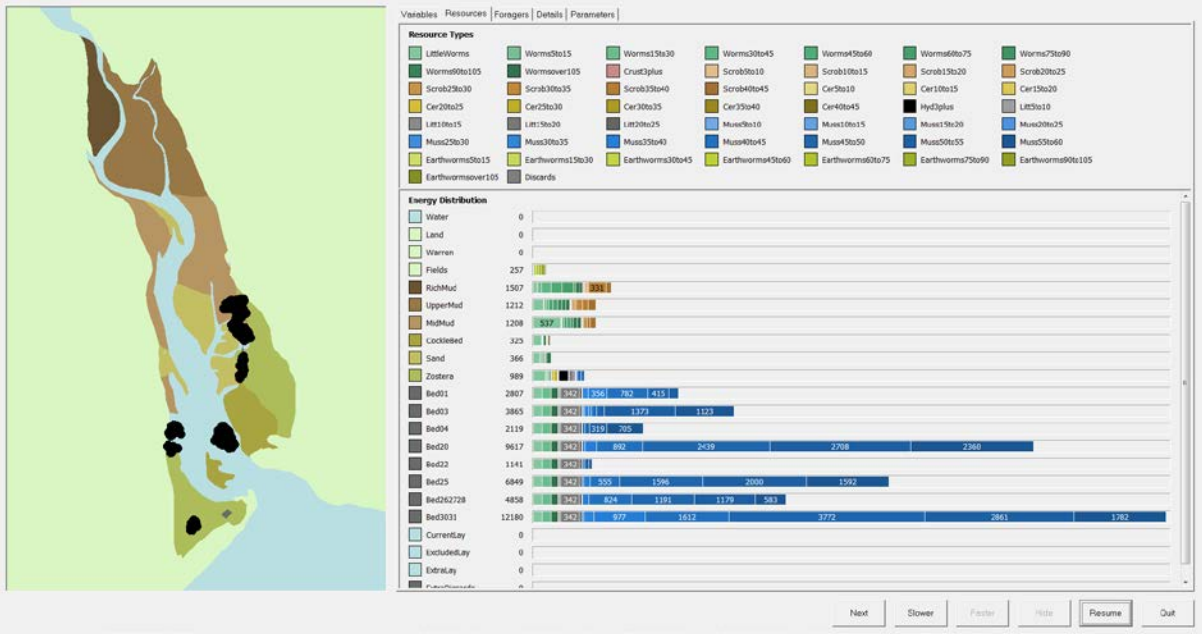

Figure 5: *Screenshot of MORPH parameterised for oystercatcher in the Exe Estuary. The map to the left shows the distribution of patches available to birds, and the location of birds (black circles) on the mussel beds during this time step. The bars to the right show the amount of prey energy (kJ m*$^{-2}$*) on each patch. Tabs to the top right allow different views of model outputs. Buttons to the bottom right allow the simulation to be run at different speeds, paused or quit.*

4.2 Time, space and environmental conditions

Simulations ran from 1st September to 31st March, encompassing the major overwintering period of oystercatcher on the Exe Estuary. Simulations proceeded in one hour time steps, during each of which environmental conditions were assumed to remain constant. Birds were assumed to occupy a single patch, and consume a single diet during each time step, but could change patches and diets between time steps. The time of day of each model time step was that for the mid-point of the time step measured in Greenwich Mean Time. The model incorporated the diurnal cycle, with daylight assumed to occur between the times of sunrise and sunset.

The model comprised the intertidal and terrestrial feeding habitat of oystercatcher in the Exe Estuary. The model divided this space into a number of patches representing mussel beds and lays, other intertidal habitats, terrestrial fields and the roost on Dawlish Warren. Intertidal habitats were available to the birds while they were exposed by the tide, the roost was always available, and the fields were available during the hours of daylight. **Table 1** shows the area and shore elevation of patches used in the model.

The tidal exposure of patches was predicted from the shore elevation of the patch and the height of the tide near Starcross on the West shore of the Exe Estuary. It was assumed that there was no tidal lag across the estuary – i.e. high and low water occurred at the same time in all intertidal patches. A patch was assumed to be exposed by the tide if the tidal height was less than the shore elevation of the patch. The shore elevation of mussel beds and lays were derived by observing the times of exposure and covering of these patches in the field. The model incorporated the tidal height each hour as predicted between 1st September 2001 and 31st March 2002 (Durell *et al*., 2007), and so incorporated the spring-neap, and changes in the magnitude of spring and neap tides during the year. We have no reason to believe that the tidal range or timing of tides have changed between 2001/02 and the present day.

Table 1. *Area and shore elevation of patches used in the model.*

Name	Type	Maximum area exposed (ha)	Shore elevation (m)
Dawlish Warren	Roost	n/a	Always exposed
Fields	Terrestrial patch	75	Always exposed
Rich Mud	Intertidal patch	66	2.70
Upper Mud	Intertidal patch	225	2.65
Mid Mud	Intertidal patch	206	1.80
Cockle Bed	Intertidal patch	66	2.18
Sand	Intertidal patch	133	1.66
Zostera	Intertidal patch	242	2.36
Bed 1	Mussel bed	3.9	1.96
Bed 3	Mussel bed	3.0	1.51
Bed 4	Mussel bed	4.4	1.13
Bed 20	Mussel bed	5.9	2.00
Bed 22	Mussel bed	2.9	1.64
Bed 25	Mussel bed	7.1	1.92
Beds 26, 27 and 28	Mussel bed	5.4	2.00
Beds 30 and 31	Mussel bed	10.9	1.71
Current Lay	Current mussel lay	3.9	0.69
Extra Lay	Potential additional lay	2.0	0.69
Extra Discards	Potential mussel discards	Varies between scenarios	2.25

4.3 Food supply for the birds

The following prey types were included in the model: marine worms (e.g. Ragworm *Hediste diversicolor*), *Scrobicularia plana*, Cockles (*Cerastoderma edule*), Winkles (*Littorina* sp.), Mussels (*Mytilus edulis*) and earthworms (*Lumbricus* sp.) (Durell *et al*., 2007). The food supply of the birds at the start of winter was derived from the following sources. (i) Non-mussel intertidal and terrestrial prey were from surveys conducted during 2001/02 (Durell *et al*., 2007), the only suitable surveys of these food resources throughout and around the Exe Estuary. These surveys were suitable because they covered the full extent of the estuary and surrounding fields, and also measured the size distribution, as well as the numerical density of invertebrates. (ii) Mussel abundance and size distribution were from surveys conducted by the Devon and Severn IFCA during 2013/14 (see Section 3.3). (iii) Mussel flesh content was derived from surveys conducted during the 1970s – 90s (Stillman *et al*., 2000), as no other suitable data were available. These data were suitable because they measured the flesh content of different sized mussels across all beds on the Exe Estuary and so accounted for the effects of mussel size and bed shore level and location on the flesh content of mussels. The model incorporated changes in the abundance and flesh content of prey during the winter. Changes in mussel prey were obtained from Stillman *et al*. (2000) and changes in other prey were obtained from Durell *et al*. (2007). The energy content for each prey type was given by Zwarts & Wanink (1993). **Table 2** shows the mussel size class abundance used in the model.

Table 2. *Abundance of mussels on the Exe Estuary derived from surveys conducted by the Devon and Severn IFCA and Bournemouth University (BU). The IFCA surveys were conducted as part of their routine monitoring and so were spread over a number of months. The Bournemouth University surveys were conducted on beds that were not included in the IFCA survey. As mussel density does not vary greatly through the season, the surveyed mussel densities were used as the starting mussel density in the model. Only mussels in the size range 30- 59 mm are shown as these comprise the diet of oystercatcher. The mussel densities for the lay are a representative "maximum" density recorded from an unharvested part of the lay.*

Bed	**Date of survey**	**Survey team**	**Size class (mm)**					
			30-34	**35-39**	**40-44**	**45-49**	**50-54**	**55-59**
1	28/2/14	BU	19.7	44.0	72.3	30.7	11.0	0.8
3	4/11/13	IFCA	13.8	4.6	7.1	8.0	61.9	43.2
4	4/11/13	IFCA	1.3	0.0	3.7	5.4	14.7	26.3
20	22/8/13	IFCA	7.1	22.7	63.9	127.6	109.5	77.0
22	27/2/14	BU	0.0	0.3	1.3	1.8	3.1	1.9
25	22/8/13	IFCA	4.9	14.3	42.6	92.4	92.3	61.2
26, 27 and 28	30/1/14	IFCA	2.5	13.8	68.5	77.0	62.0	25.8
30 and 31	24/7/13 21/8/13	IFCA	30.6	99.8	116.5	208.8	128.3	67.7
Current Lay	28/2/14	BU	19.7	44.0	72.3	30.7	11.0	0.8

4.4 Oystercatcher population size, body mass and energetics

The oystercatcher population size in the model was the maximum observed during our counts conducted during the present study (**Table 3**), but in test simulations the number of birds present in March was reduced to match the observed decline in numbers during this month (see **Figure 6**). All birds were assumed to arrive on the first day of simulations and remained until the final day of the simulation unless they died of starvation during the course of winter.

Model birds had a target body mass that they attempted to maintain throughout the course of winter. Target body mass was based on observed body of oystercatcher on UK estuaries (**Table 3**).

Energy density is the amount of energy (kJ) contained in a gram of fat reserves and was assumed to be 33.4 kJ g^{-1} (Kersten & Piersma, 1987) (**Table 3**). Bird energy density and prey energy content influenced how birds gained weight. For example, if 1 g of bivalve flesh was assimilated, only 22/33.4 g of extra fat would be stored because fat can store the energy more efficiently than the bivalve flesh.

The daily energy requirements of the birds were calculated from body mass (**Table 3**). If birds were able to consume enough food to meet their energy requirements, they maintained or increased their body mass up to the target mass. Birds that could not meet their energy requirements had to draw on their energy reserves and so lost mass. Model birds also had a starvation body mass, derived from the observed mass of starved birds (**Table 3**). If the mass of a model bird decreased to the starvation body mass, the bird died of starvation. Starvation was the only source of bird mortality included in the model.

Assimilation efficiency is the proportion of the energy within the prey consumed by a bird that is assimilated into the bird's body. It was 0.75 for worms and 0.85 for mollusc prey (Goss-Custard *et al*., 2006) (**Table 3**).

For simplicity it was assumed that no time and energy costs were associated with moving between patches.

4.5 Oystercatcher foraging behaviour

Birds were assumed to vary in their foraging efficiency (normal distribution), which influenced the rate at which birds consumed food in the absence of competitors, and dominance (uniform distribution), which influenced a bird's susceptibility to interference from competitors. The standard deviation of foraging efficiency 0.125 (mean=1) was the average observed in oystercatchers on the Exe estuary (Stillman *et al*., 2000) (**Table 3**).

The relative rates at which oystercatcher can feed during the day and night were derived from Sitters (2000), who measured the night and day feeding rates of Oystercatchers consuming mussels. Night time efficiency was 100 % of daytime for individuals opening prey using the stabbing feeding method and 62 % of daytime for individuals opening prey using the hammering feeding method, giving a mean of 81 % (**Table 3**). We assumed that the same night time efficiency applied to all oystercatcher diets.

The influence of the food supply on a bird's intake rate was calculated using the following functional response:

$$IFIR = f\frac{IFIR_{\max}B}{B_{50}+B}, \qquad \text{Equation 1}$$

where *IFIR* is the interference-free intake rate (mg s-1), *f* is the foraging efficiency the of focal individual, *B* is the patch biomass density of prey within the size range consumed (mg m^{-2}), $IFIR_{max}$ is the maximum intake rate when prey are superabundant and B_{50} is the prey biomass density at which intake rate is 50% of its maximum.

Foraging efficiency was normally distributed, with unit mean and a standard deviation of 0.125. A literature review was used to estimate the values of $IFIR_{max}$ and B_{50} (Goss-Custard *et al*., 2006). *IFIRmax* was predicted from:

$$\log(IFIR_{\max}) = -2.802 + 0.245\log_e(M_{oystercatcher}) + 0.365\log_e(rM_{prey}) - 0.227P_{mussel}, \qquad \text{Equation 2}$$

where $M_{oystercatcher}$ is the average body mass (g) of oystercatcher in September (=500g; Goss-Custard et al, 2006), M_{prey} is the mean ash-free dry mass (mg) of prey within the size range consumed, *r* is the ratio of size of prey consumed to size in patch, and P_{mussel} equals 1 if the prey is a mussel and 0 if not. A literature review showed that birds select the larger sized prey within the size range consumed, giving a value of *r* of 1.05 (Goss-Custard *et al*., 2006). B_{50} was unrelated to either bird or prey mass, with a mean value of 0.761 g ash-free dry mass m^{-2}. The influence of oystercatcher competitors on a bird's intake rate was incorporated using the following interference function (Stillman *et al*., 1996):

$$IR = IFIR\left(\frac{gD+1}{D_0+1}\right)^{-\left(m_{\max}-\left(m_{\max}-m_{\min}\right)d+st_{Sep1}\right)}, \qquad \text{Equation 3}$$

where IR = intake rate (mg s^{-1}), D = oystercatcher competitor density in patch (ha^{-1}), D_0 = oystercatcher competitor density above which interference reduces intake rate, g = aggregation of birds within a patch, d = dominance of focal individual (0–1), m_{max} = susceptibility to interference of least dominant individual (d = 0), m_{min} = susceptibility to interference of most dominant individual (d = 1), t_{Sep1} = number of days from 1st September and s = coefficient measuring the effect of season of the strength of interference in mussel-feeding oystercatchers. D_0 was set to 100 birds ha^{-1} for non-mussel feeding birds (Stillman *et al*., 1996; Triplet *et al*., 1999; Yates *et al*., 2000) and 58.3 birds ha^{-1} for mussel-feeding birds (Stillman *et al*., 2000). The aggregation factor (g) was set to 10 for all bird and prey combinations, except for mussel feeding oystercatchers where it was 6 (Stillman *et al*., 2000). Interference for oystercatcher consuming worms, which are mobile prey and can often rapidly escape into the sediment as birds approach, was assumed to occur through prey depression (m_{max} = 0.48; m_{min} = 0.48) with the same strength as that observed between *Corophium*-feeding redshank (Yates *et al*., 2000). For other prey, interference was assumed to occur through prey stealing. For winkles, which are relatively small prey, the strength of interference was assumed to be that for prey with short handling time (<10 s) (m_{max} = 0; m_{min} = 0.08) (Stillman *et al*., 2002). For *Scrobicularia*- and cockle-feeding oystercatchers, which are larger prey, the strength of interference was assumed to be that for prey with longer handling times (m_{max} = 0; m_{min} = 0.5) (Stillman *et al*., 2002; Triplet *et al*., 1999). For mussel-feeding oystercatchers, the strength of interference depended both on a bird's dominance and the number of days since 1st September (m_{max} = 0; m_{min} = 0.1595; s = 0.0018) (average values for birds using the stabbing and hammering methods to open mussels; Stillman *et al*., 2000).

The intake rate of each bird, as predicted by Equations 2 and 3, was adjusted by the proportion of mussels observed to be stolen by carrion crows and herring gulls on the bed on which the bird was feeding (**Figure 11**). For example, if the proportion of mussels stolen on a bed was observed to be 0.2, a model oystercatcher would have a consumption rate 0.8 times the predicted intake rate (i.e. intake rate = (1 – proportion of mussels stolen) x predicted intake rate).

Maximum intake rate was based on the maximum daily energy assimilation calculated from body mass using standard equations (Kirkwood, 1983) (**Table 3**). This assumed that birds could achieve this maximum value by feeding for just 50 % of the day to allow them, if possible, to consume their daily requirements from intertidal prey alone. This maximum limited the maximum amount of food a bird could consume within a time step.

4.6 Oystercatcher decision rules

Birds either consumed the diet and occupied the patch which maximised their energy assimilation rate (i.e. energy assimilated during a time step) or roosted. Birds fed if their energy store was less than 95% of its target value (i.e. they had been losing mass), or if any of the available diets yielded an energy assimilation rate greater than the average achieved over the last 24 hours (i.e. relatively high quality prey were available). Birds roosted if their energy store was greater than 95% of its target value (i.e. they had not been losing mass), and if none of the available diets yielded an energy assimilation rate greater than the average over the last 24 hours (i.e. only relatively low quality prey were available). In effect, this rule meant that birds tended to roost over high water unless they were losing mass, in which case they would supplement their intertidal feeding by feeding in terrestrial fields.

Table 3. *The value and derivation of parameters included in the model.*

(a) Global parameters

Parameter	**Value**	**Units**	**Reference**
Time step length	1	Hours	Stillman (2008)
Duration of simulation	212	Days	Total number of days in the overwinter period: 1st September to 31st March
Daylight	0 or 1 during a time step	Hours	Range of hours of daylight (sunrise to sunset) over the September 2013 to March 2014 period, calculated using the United States Naval Observatory Astronomical Applications Department calculator (www.usno.nav.mil/data/docs/RS_OneDay.php)
Tidal height	0.3 – 2.2	m	Predictions for Starcross on the western shore of the Exe Estuary (Durell et al. 2007).

(b) Patch parameters

Parameter	**Value**	**Units**	**Reference**
Number of patches	22	-	Stillman *et al*. (2000)
Patch size	2.9 – 242	ha	See **Table 1** (Stillman *et al*. (2000)
Initial numerical density			
Marine worm	varies	m^{-2}	Durell et al. (2007)
Cockle	varies	m^{-2}	Durell et al. (2007)
Winkle	varies	m^{-2}	Durell et al. (2007)
Scrobicularia	varies	m^{-2}	Durell et al. (2007)
Earthworm	varies	m^{-2}	Durell et al. (2007)
Mussel	varies	m^{-2}	This study (see **Table 2**)
Overwinter mortality excluding depletion by oystercatcher (ranges for size classes)			
Marine worm	20 -85	%	Durell et al. (2007)
Cockle	0 -94	%	Durell et al. (2007)
Winkle	45 - 75	%	Durell et al. (2007)
Scrobicularia	65	%	Durell et al. (2007)
Earthworm	0	%	Durell et al. (2007)
Mussel	6	%	Durell et al. (2007)
Overwinter decline in ash-free dry mass (ranges for size classes)	0	%	Durell et al. (2007)
Marine worm	15 - 43	%	Durell et al. (2007)
Cockle	15	%	Durell et al. (2007)
Winkle	0 - 20	%	Durell et al. (2007)
Scrobicularia	0	%	Durell et al. (2007)
Earthworm	26 - 33	%	Durell et al. (2007)
Mussel			
Energy content of prey	22.0	kJ g^{-1} AFDM	Zwarts & Wanink (1993)

(c) Oystercatcher parameters

Parameter	**Value**	**Units**	**Reference**
Population size	1500	Individuals	This study
Body mass	540	g	Zwarts *et al*. (1996b)
Starvation mass	350	g	Stillman *et al*. (2000)
Energy density of body tissue	33.4	KJ g^{-1}	Kersten & Piersma (1987)
Initial energy store size	6346	KJ	Stillman *et al*. (2000); Kersten & Piersma (1987)
Target energy store	6346	KJ	Stillman *et al*. (2000); Kersten & Piersma (1987)
Energy expenditure	762	KJ day^{-1}	Nagy *et al*. (1999)
Maximum energy assimilation	1099	KJ day^{-1}	Kirkwood (1983)
Prey sizes consumed			
Marine worm	15 +	mm	Durell *et al*. (2007)
Cockle	15 +	mm	Durell *et al*. (2007)
Winkle	10 +	mm	Durell *et al*. (2007)
Scrobicularia	20 +	mm	Durell *et al*. (2007)
Earthworm	15 +	mm	Durell *et al*. (2007)
Mussel	30-59	mm	Durell *et al*. (2007)
Assimilation efficiency			
Marine worm	75	%	Durell *et al*. (2007)
Cockle	85	%	Durell *et al*. (2007)
Winkle	85	%	Durell *et al*. (2007)
Scrobicularia	85	%	Durell *et al*. (2007)
Earthworm	75	%	Durell *et al*. (2007)
Mussel	85	%	Durell *et al*. (2007)
Functional response and interference	-	-	See text
Proportion of mussels lost to carrion crow and herring gull	Varies between mussel beds		See text

5 ECOLOGICAL REQUIREMENT MODEL

In order to estimate the oystercatcher food requirements in the Exe Estuary, we used the Ecological Requirement Model developed by Stillman & Wood (2013a). This model has recently begun to be used to predict shorebird food requirements in UK estuarine sites (e.g. Stillman & Wood, 2013b, c). The purpose of the model is to calculate the ecological requirement of a shorebird population consuming shellfish within a site. Data on the number of oystercatcher feeding on shellfish, the time for which the population must be supported and the initial stocks of shellfish are entered into the model. The ecological food requirements of the birds (the amount of food required in the environment to maintain high survival) is calculated from the physiological requirements of the oystercatcher population (the amount actually eaten) and an ecological multiplier (measuring how much greater the ecological requirements are than the physiological requirements). More food needs to be reserved in the environment than the amount actually eaten because birds cannot find all of the food, some birds can be excluded from the food through competition and food is lost due to factors other than the birds (Goss-Custard *et al*., 2004).

5.1 Site-specific data

In order to parameterise the model, we required data on the number of oystercatcher supported by shellfish in the site (N_{Bird}) and the time period over which birds are supported (T). The number of birds supported by shellfish can either be assumed to be the entire population, as these shellfish form the main prey of oystercatcher, or can be estimated from counts of the number of oystercatcher feeding on these prey. For example, birds feeding on other prey within the site, or feeding on prey outside of the site could potentially be excluded from calculations. The number of birds used in the model should either be the mean number counted within the site or the mean number counted feeding on shellfish. The time for which the bird population needs to be supported should be the time for which the majority of the bird population occupies the site – for example, a typical wintering period would be from 1st September until 31st March. The proportion of the oystercatcher feeding on mussels (p_{Mussel}), as opposed to cockles should also be estimated. This is used to calculate the amount of cockle and mussel biomass that needs to be reserved for the birds, and also to calculate the size of the ecological multiplier.

The model can account for uncertainty in the minimum size of cockles and mussels consumed by oystercatcher. For example, calculations can either based on the typical minimum size of cockles and mussels consumed, 15 mm and 30 mm respectively, or lower minimum sizes that may be consumed when larger prey are absent, 10 mm and 20 mm respectively. It is assumed that there is no maximum size of cockle that can be consumed by oystercatcher but that mussels greater than 60 mm in length cannot be consumed (Stillman & Wood, 2013a). To calculate oystercatcher food requirements, the model requires the fresh mass of cockles and mussels within the following size ranges to be calculated: cockles – 10 mm to maximum ($B_{C10\text{-}max}$) and 15 mm to maximum ($B_{C15\text{-}max}$); mussels – 20 mm to 60 mm ($B_{M20\text{-}60}$) and 30 mm to 60 mm ($B_{M30\text{-}60}$).

5.2 Default parameters

A number of default parameters are used in calculations which are assumed to be the same in all sites. The average body mass (B_{Bird}; g) of oystercatcher is set to 540g (www.bto.org/about-birds/birdfacts). The energy content of mussels and cockles (E_{CM}) is set to 22 KJg^{-1}, the average value for bivalves (Zwarts *et al*., 1996a). The efficiency with which mussels and cockles are assimilated (p_{assim}) is set to 0.85 for oystercatcher (Kersten & Visser, 1996). The ratio of AFDM to fresh mass ($p_{DryFresh}$) is set to 0.041, the average for mussels and cockles (Ricciardi & Bourget, 1998). The ecological multiplier is set to 3.3 for oystercatcher populations consuming cockles or a mixture of cockles and mussels (M_{CM}), and to 7.1 for oystercatcher populations just consuming mussels (M_M) (Stillman & Wood, 2013a).

5.3 The model

The model has two alternative ways of calculating the daily energy requirements of each bird in the population. If no data are available on overwinter temperature the model calculates daily energy requirements from body mass using the all bird equation of Nagy (1999).

$$E_{Bird} = 10.5\left(B_{Bird}\right)^{0.681} \qquad \text{Equation 4}$$

where E_{Bird} = daily energy requirements of each bird (KJ) and B_{Bird} = body mass (g). For oystercatcher, if suitable overwinter temperature data are available the model calculates daily energy requirements from energy expenditure in the absence of thermoregulation and the additional costs due to thermoregulation following Stillman *et al*. (2000) and Zwarts *et al* (1996c).

$$E_{Bird} = \left(1 - p_{therm}\right)673.2 + p_{therm}\left(673.2 + 31.8\left(10 - t_{therm}\right)\right) \qquad \text{Equation 5}$$

where p_{therm} = proportion of time for which temperature is below that at which oystercatcher need to thermoregulate (i.e. 10 ^{o}c) and t_{therm} = mean temperature during this time. In this equation the daily energy demands of each oystercatcher is 673.2 kJ in the absence of thermoregulation. For every degree below 10 ^{o}c (Zwarts *et al*. 1996c) the daily energy requirements of each bird are increased by 31.8 kJ (Zwarts *et al*. 1996c).

The total ash-free dry mass (AFDM) (g) consumed by each bird is then calculated from the duration of the time period for which the birds need to be supported, the daily energy requirements of the bird, the energy content of cockles and mussels and the efficiency with which cockles and mussels are assimilated.

$$C_{Bird} = \frac{T \cdot E_{Bird}}{p_{Assim} \cdot E_{CM}} \qquad \text{Equation 6}$$

Where C_{Bird} = total AFDM consumed by each bird (g AFDM), T = time period for which birds need to be supported (days), p_{Assim} = efficiency of assimilating energy from cockles and mussels and E_{CM} = energy content of cockles and mussels (kJ g^{-1}).

The total AFDM (g) consumed by the bird population is calculated from the mean number of birds present.

$$C_{BirdPop} = N_{Bird}C_{Bird} \qquad \text{Equation 7}$$

where $C_{BirdPop}$ = total AFDM consumed by the bird population (g AFDM) and N_{Bird} = mean number of birds present. The physiological food requirement of the population is found by converting AFDM to fresh mass and converting g to tonnes.

$$R_{Phys} = \frac{C_{BirdPop}}{1000000 \cdot p_{DryFresh}} \qquad \text{Equation 8}$$

where R_{Phys} = Physiological food requirement of the bird population (tonnes fresh mass including shell) and $P_{DryFresh}$ = ratio of AFDM to fresh mass including shell in cockles and mussels. The combined ecological multiplier (M), which accounts for the proportion of cockles-and mussel-feeding birds, is calculated from the proportion of birds feeding on mussels and cockles.

$$M = \begin{cases} M_{CM} & \text{if}\, p_{Mussel} < 1 \\ M_M & \text{if}\, p_{Mussel} = 1 \end{cases} \qquad \text{Equation 9}$$

where M_{CM} = ecological multiplier for birds feeding on cockles alone or a mixture of cockles and mussels, M_M = ecological multiplier for birds feeding on mussels alone and p_{Mussel} = proportion of birds feeding on mussels. Stillman & Wood (2013a), based on a review of modelling and empirical studies, estimated M_{CM} as 3.3 and M_M as 7.1 for oystercatcher. The ecological requirement is then found by multiplying the physiological requirement by the combined ecological multiplier.

$$R_{Ecol} = M \cdot R_{Phys} \qquad \text{Equation 10}$$

where R_{Ecol} = ecological requirement (tonnes fresh mass including shell). The ecological requirement obtained from cockles (R_{EcolC}) and mussels (R_{EcolM}) is then calculated from the proportion of birds feeding on mussels.

$$R_{EcolC} = \left(1 - p_{Mussel}\right) \cdot R_{Ecol} \qquad \text{Equation 11}$$

$$R_{EcolM} = p_{Mussel} \cdot R_{Ecol} \qquad \text{Equation 12}$$

The final step is to calculate the biomass of cockles and mussels that are not required by the bird population. For oystercatcher, calculations are either based on the typical minimum size of cockles and mussels consumed, 15 mm ($X_{C10\text{-}max}$) and 30 mm ($X_{C15\text{-}max}$) respectively, or lower minimum sizes that may be consumed when larger prey are absent, 10 mm ($X_{M20\text{-}60}$) and 20 mm ($X_{M30\text{-}60}$) respectively. The biomass not required by the birds is found by subtracting their requirements from the initial biomass of cockles and mussels within these size ranges.

$$X_{C10-\max} = B_{C10-\max} - R_{EcolC} \qquad \text{Equation 13}$$

$$X_{C15-\max} = B_{C15-\max} - R_{EcolC} \qquad \text{Equation 14}$$

$$X_{M20-60} = B_{M20-60} - R_{EcolM} \qquad \text{Equation 15}$$

$$X_{M30-60} = B_{M30-60} - R_{EcolM} \qquad \text{Equation 16}$$

Stillman & Wood (2013a) explains the graphical output of the spreadsheet model and describes some example results.

6 RESULTS

6.1 Mussel surveys

A comparison of current and past (Stillman *et al*. 2000) bed areas and mussel densities is shown in **Table 4**. Comparison of mussel densities is restricted to the size range consumed by oystercatcher (i.e. 30-59 mm). The area of all mussel beds has reduced by an average of approximately 30%. Current bed area was not measured for beds 1 and 22 and so in the models it was assumed that the current bed area was 30% lower than that presented by Stillman *et al*. (2000). There are no consistent patterns in the changes in the total density of 30-59 mm mussels; total mussel density has increased on beds 20 and 30/31, and decreased on other beds. Despite the general trend for a decrease in the density of 30-59 mm mussels, the density of 50-59 mm mussels has increased on all beds expect 4 and 22. So on all beds except 4 and 22, the current mussel populations comprise a higher proportion of larger mussels than they did historically.

Table 4. *Current and past mussel bed areas and mussel densities in the Exe Estuary. Current values are derived from the present study. Past values are those present by Stillman et al. (2000) for the period 1976 to 1990. Mussel bed area was not recorded for beds 1 and 22 during the current study. For comparison, mussels are divided into 10mm size classes. See Table 2 for the 5mm size classes used in the individual-based model.*

	Mussel bed area (ha)		**Mussel size class (mm) density (m^{-2})**							
			30-39		**40-49**		**50-59**		**All**	
Bed	**Current**	**Past**	**Current**	**Past**	**Current**	**Past**	**Current**	**Past**	**Current**	**Past**
1	-	5.49	63.7	179.0	103.0	60.5	11.8	6.6	178.4	246.1
3	3.0	4.45	18.4	102.3	15.1	116.2	105.1	48.7	138.6	267.2
4	4.4	6.31	1.3	124.2	9.1	157.1	41.0	58.5	51.4	339.8
20	5.9	9.41	29.8	68.9	191.5	98.3	186.6	54.6	407.8	221.8
22	-	4.06	0.3	15.9	3.1	31.5	5.0	42.5	8.3	89.9
25	7.1	8.3	19.2	118.6	135.0	155.6	153.5	56.5	307.8	330.7
26	5.4	7.79	16.3	311.5	145.5	160.7	87.8	24.2	249.6	496.4
30/31	10.9	15.43	130.4	245.7	325.3	172.7	196.0	51.4	651.7	469.7

6.2 Bird surveys

In each month, the numbers of oystercatchers – including both foraging and non-foraging individuals - present on all mussel beds tended towards a unimodal distribution, with numbers rising and falling as the mussel beds were exposed and covered, respectively, by the tide (**Figure 6**). Peak numbers were observed approximately 90 minutes before and after low water, with a slight decline in numbers at low water, possibly due to some birds being missed due to the topography of beds 30 & 31. The greatest number of oystercatchers observed at any time was 1489 individuals in October. The greatest number of oystercatchers observed at low water across all mussel beds was 1330 in November. In contrast, the lowest count across all mussel beds at peak low water occurred in March (378 individuals).

To account for the possibility of some missing birds at low water, we ran simulations with a population size of 1500 oystercatchers, which is the approximate number expected in October (the month in which the greatest numbers of birds were recorded) without the observed decline around low water (**Figure 6**).

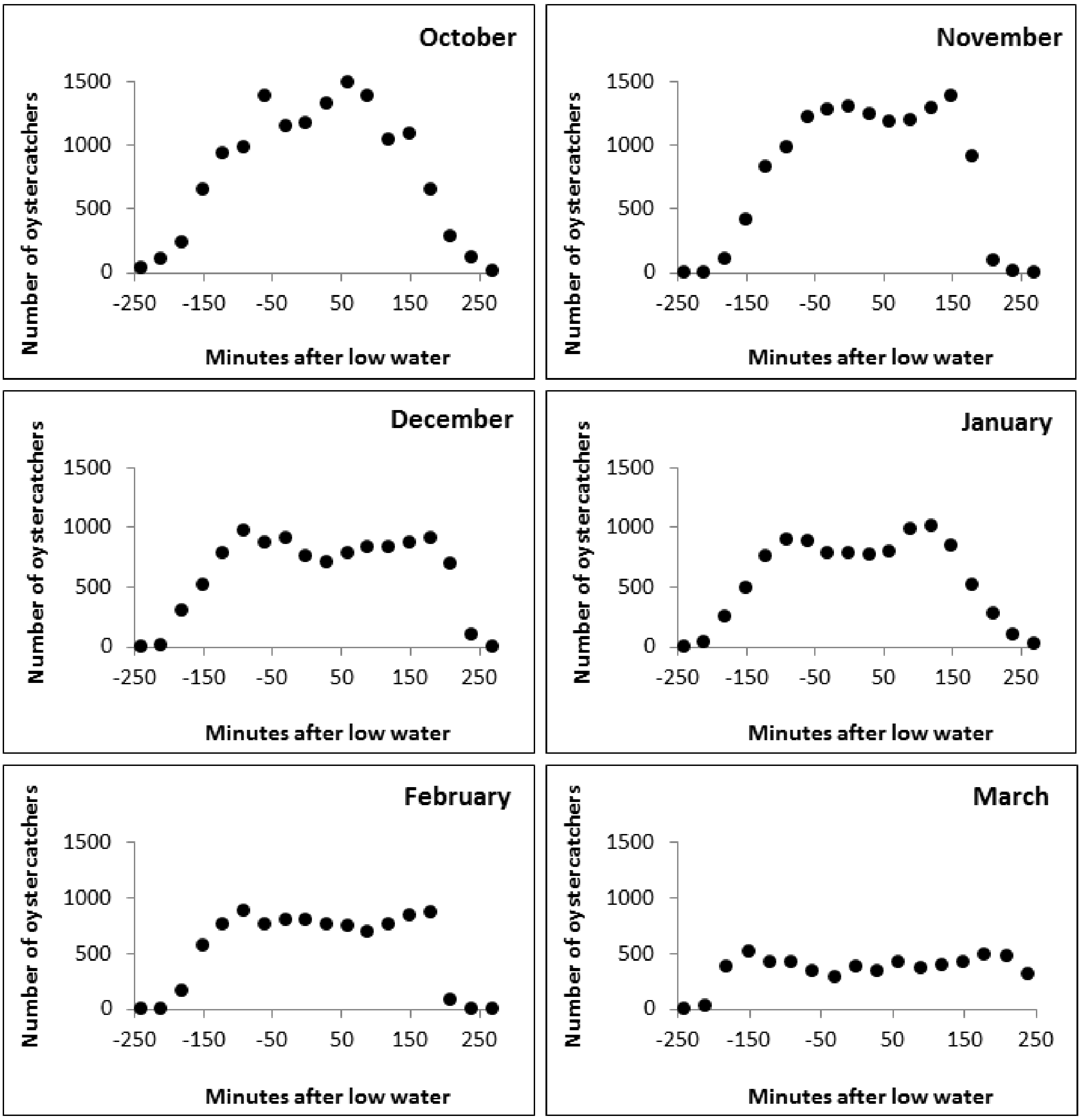

__Figure 6:__ The total numbers of oystercatchers present on all mussel beds across the tidal cycle.

In each month the numbers of carrion crows (**Figure 7**) and herring gulls (**Figure 8**) observed across all mussel beds increased towards the point of low water, decreasing thereafter, similar to the pattern observed for oystercatchers. Between October and December, crows were the most numerous kleptoparasite species present on the mussel beds, with peak counts of over 200 individuals. However, from January onwards far fewer crows were observed, with peak counts never above 81 individuals (**Figure 7**). Herring gull numbers showed no such decrease, and thus between January and March gulls were the most numerous kleptoparasite species present on the mussel beds, with peak counts of over 100 individuals (**Figure 8**). The lowest monthly peak count of carrion crows (45 individuals) was recorded in February, whilst fewest herring gulls (113 individuals) were observed in October.

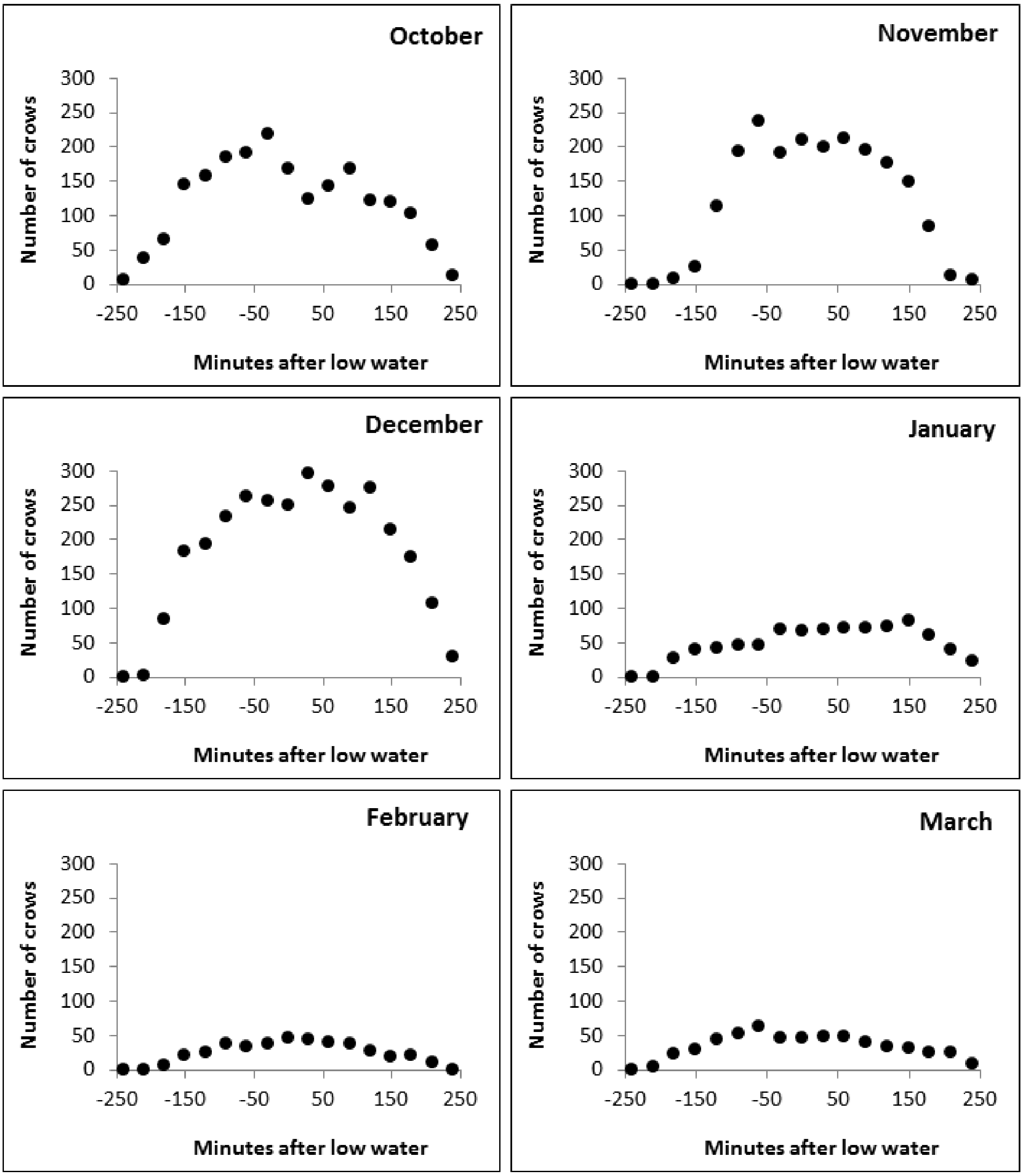

Figure 7: *The total numbers of carrion crows present on all mussel beds across the tidal cycle.*

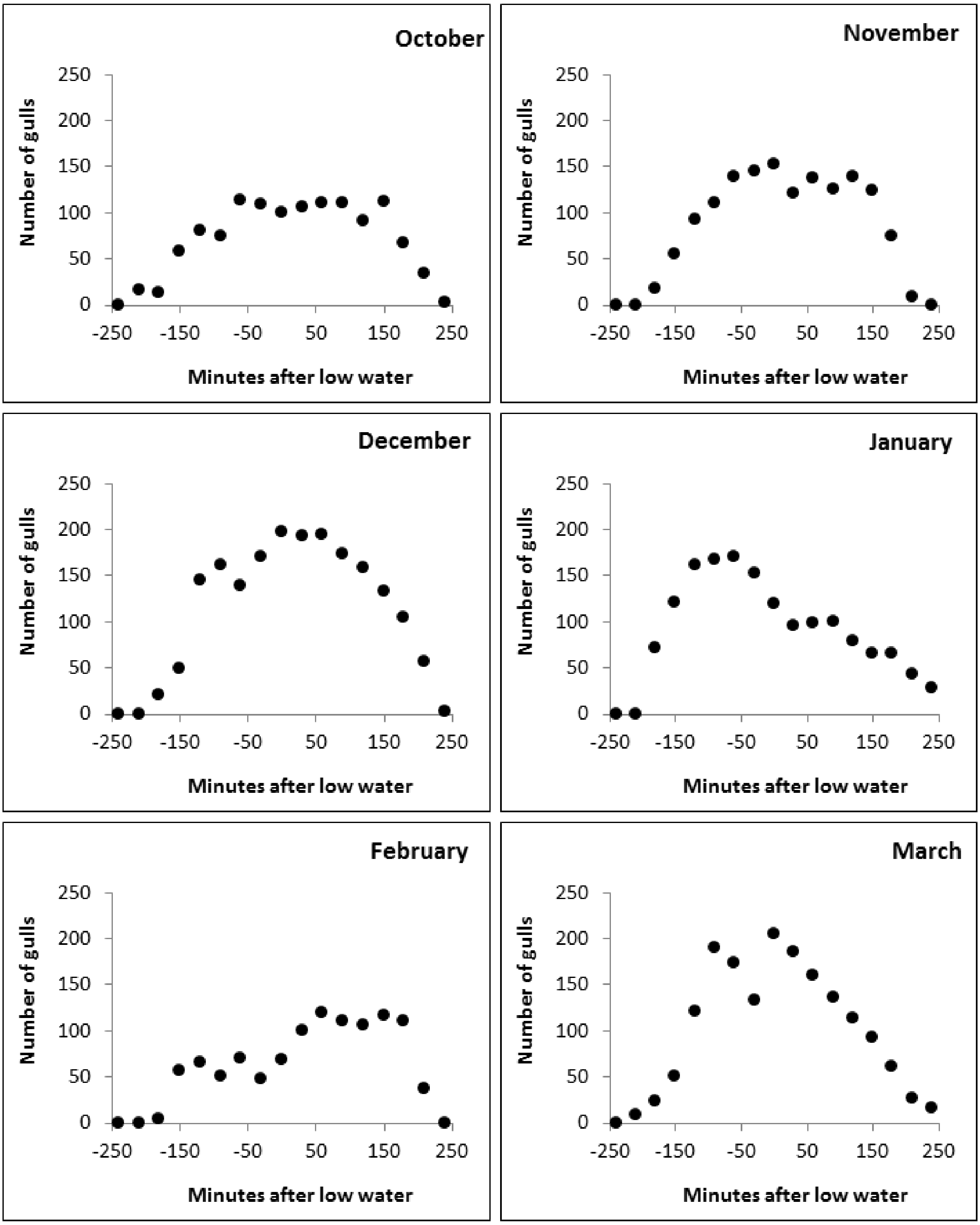

Figure 8: *The total numbers of herring gulls present on all mussel beds across the tidal cycle.*

The mean percentage of observed oystercatchers foraging at a given point in time across all mussel beds ranged between 41.8 % and 100 % (**Figure 9**). However, these values do not account for birds not present on mussel beds, for example those resting at a roosting site, such as a nearby sandbank. Thus we calculated the percentage of the total available time during the intertidal exposure periods that the total mussel-feeding Exe oystercatcher population spent foraging each month (F) as follows:

$$F = \left(\sum \left(\left(n_t \cdot Prop_t \right) \cdot l \right) / \left(O_{max} \cdot \left(w \cdot l \right) \right) \right), \qquad \text{Equation 17}$$

where n_t was the number of birds present on the mussel beds at time t; $Prop_t$ was the proportion of all the birds present which were feeding at time t; O_{max} was the maximum number of mussel-feeding oystercatchers observed in that month's survey; w was the number of 30 minute observation windows over the tidal cycle; and l was the length of those observation windows (i.e. 30 minutes). We also calculated the time spent foraging over a single exposure period by a typical oystercatcher in each month; an oystercatcher spent between 224 and 273 minutes of the exposure period foraging (**Table 5**).

Table 5. *Calculations of the amount of time spent foraging by an oystercatcher over a single exposure period.*

Month	Time spent foraging (minutes)	Total time available (minutes)	Time spent foraging (%)
October	224	510	44.0
November	235	450	52.2
December	273	480	57.0
January	237	510	46.4
February	246	420	58.6
March	253	510	49.5

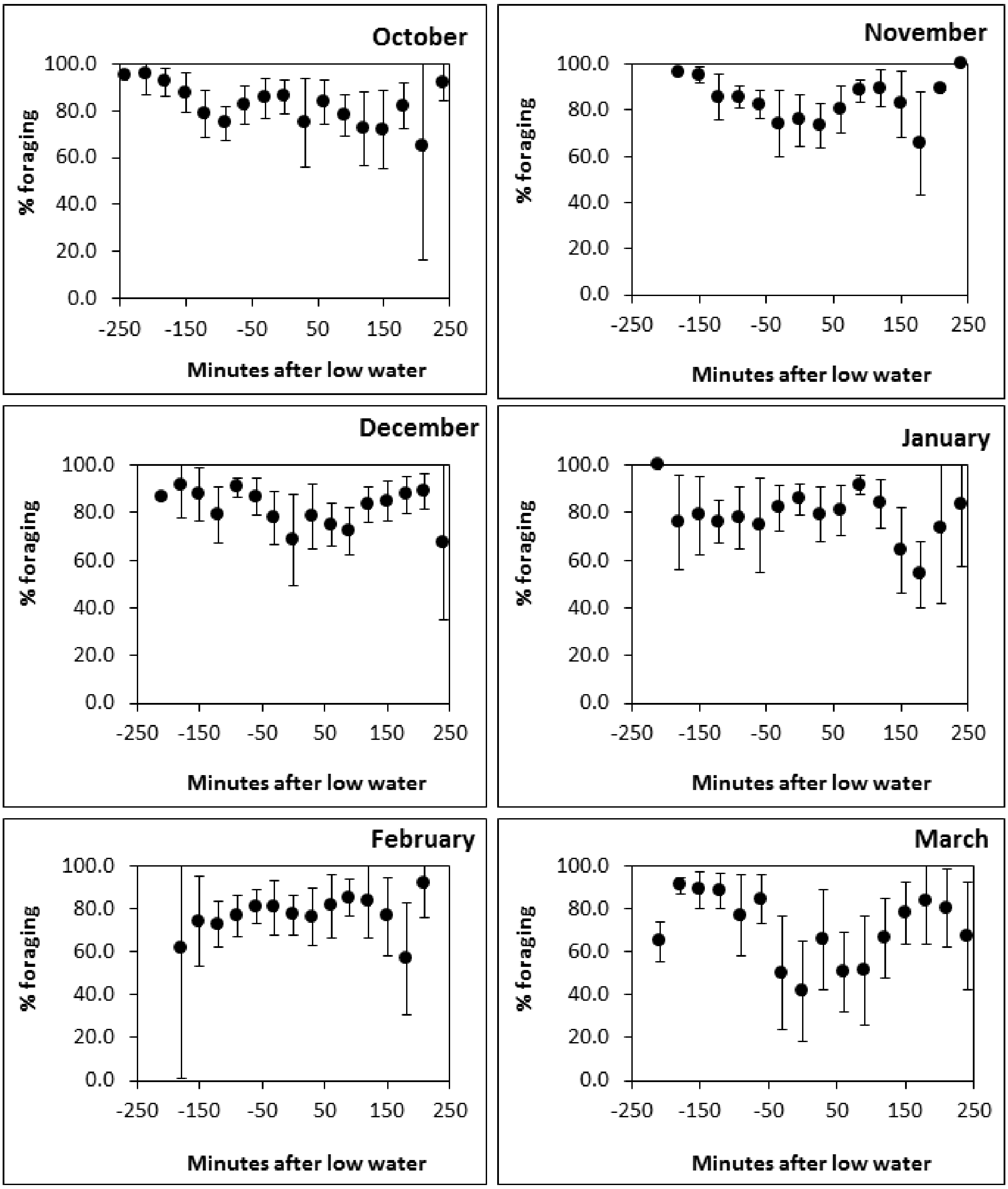

Figure 9: *The variation in the mean (± 95 % CI) percentage of all oystercatchers present on all mussel beds observed to be foraging, across the tidal cycle.*

Across all mussel beds we recorded 997 observations of oystercatcher feeding attempts between November and March (**Table 6**). No data on food stealing behaviours were collected during October 2013. Kleptoparasitism by carrion crows and herring gulls on mussel-feeding oystercatchers was observed in all months between November and March. We also observed that jackdaws (*Corvus monedula*

Linnaeus, 1758) and common gulls (*Larus canus* Linnaeus, 1758) made unsuccessful attempts to steal mussels from oystercatchers, but these occurrences were rare. Intra-specific and inter-specific food stealing behaviour was also observed between the carrion crows and herring gulls themselves.

Table 6. *Monthly observations of successful oystercatcher foraging and successful kleptoparasitism by carrion crows and herring gulls.*

Month	**Total observations**	**Oystercatcher successes**		**Thefts by Carrion Crows**		**Thefts by Herring gulls**	
		n	**%**	***n***	**%**	***n***	**%**
November	214	171	79.9	30	14.0	13	6.1
December	102	65	63.7	25	24.5	12	11.8
January	163	140	85.9	13	8.0	10	6.1
February	233	208	89.3	13	5.6	12	5.2
March	285	249	87.4	23	8.1	13	4.6
All winter	712	584	82.0	81	11.4	47	6.6

Overall, across all mussel beds oystercatchers successfully swallowed mussels on 83.6 % of occasions, whilst kleptoparasitism by crows and gulls accounted for 10.4 and 6.0 % of foraging attempts respectively (**Figure 10**). Oystercatcher foraging success was lowest in December (63.7 %; *n* = 102) and greatest in February (89.3 %; *n* = 233). Crows were responsible for a greater percentage of mussel thefts compared with gulls in each month between November and March (**Figure 10**).

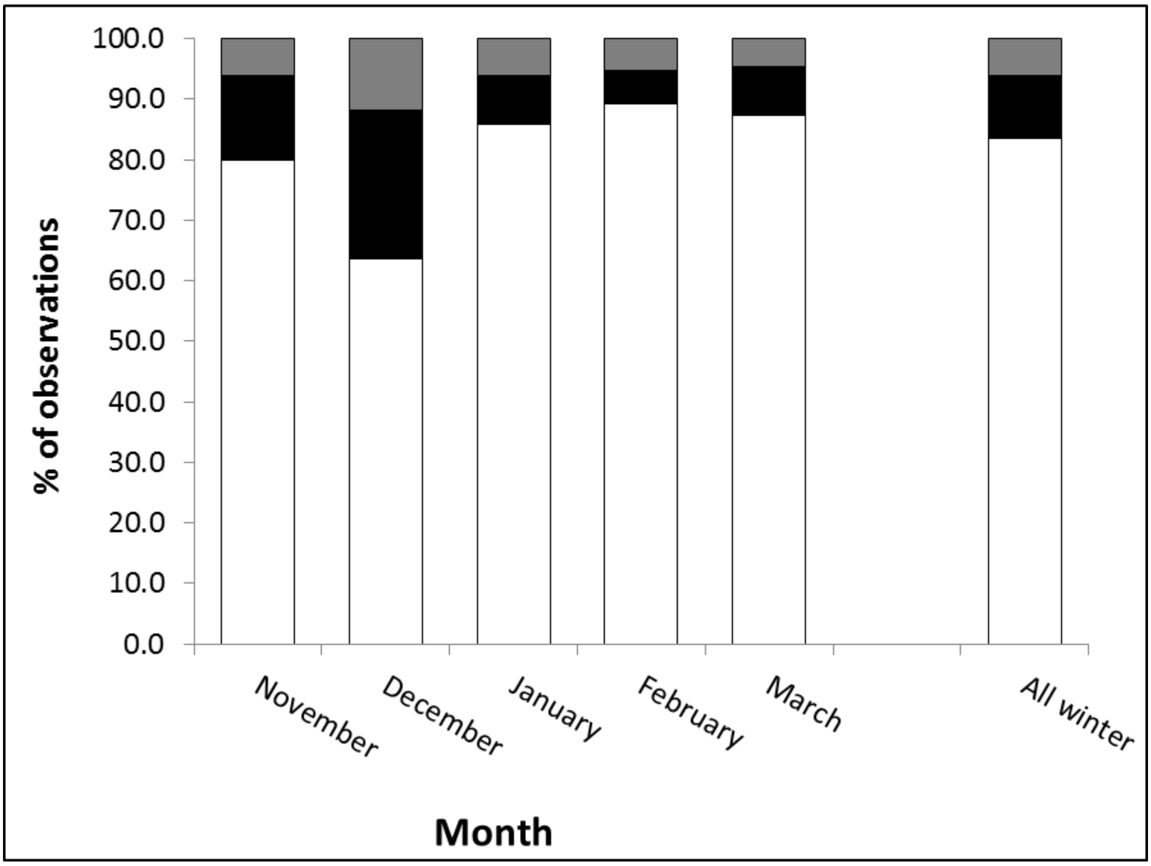

Figure 10: *The percentage of oystercatcher foraging attempts on mussels that resulted in (i) successful swallow (white bar), (ii) kleptoparasitism by carrion crows (black bar), and (iii) kleptoparasitism by herring gulls (grey bar).*

We examined oystercatcher foraging success and kleptoparasitism on each group of mussel beds, by grouping data from all months in which observations were made (November to March). Oystercatcher foraging success was greatest (and thus risk of kleptoparasitism lowest) on beds 20&22 and 30&31, where 86.8 % of mussels were swallowed successfully (**Figure 11**). Oystercatcher foraging success was lowest (and thus risk of kleptoparasitism greatest) on beds 3&4, where only 78.8 % of mussels were swallowed successfully. Crows were responsible for a greater percentage of thefts on all beds except on beds 30&31, on which gulls stole 6.8 % of mussels compared with the 6.4 % of mussels stolen by crows (**Figure 11**).

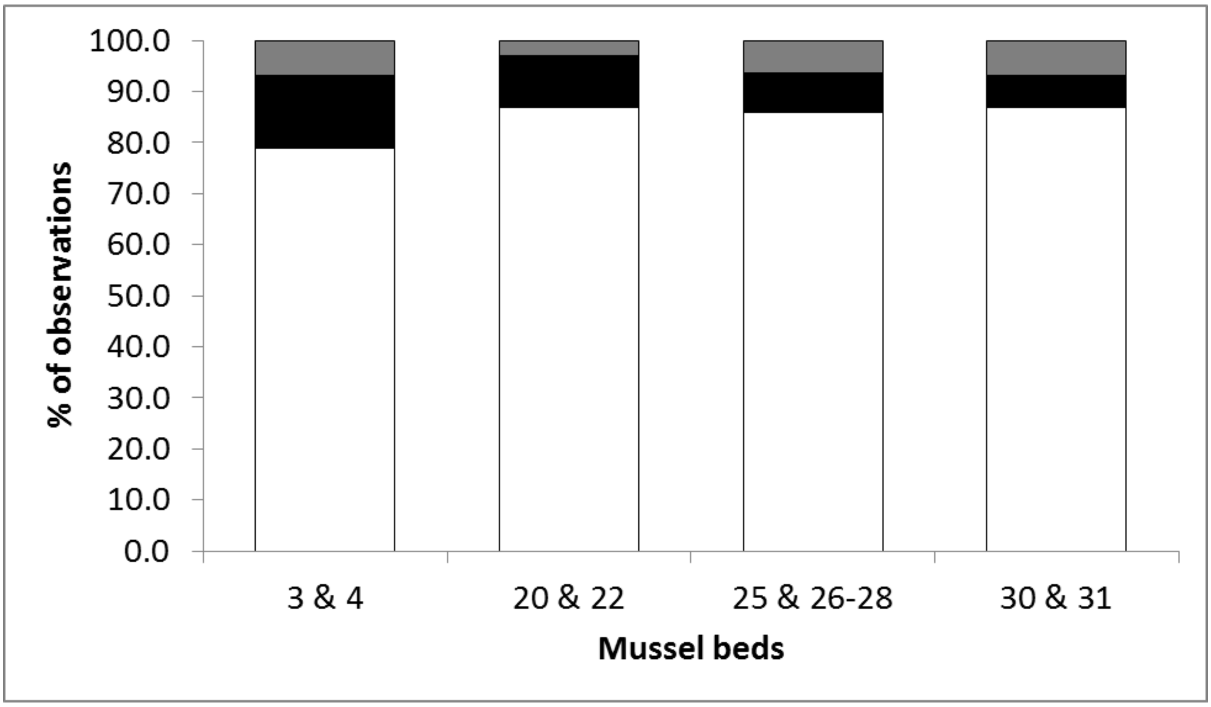

Figure 11: *The percentage of oystercatcher foraging attempts on mussels on each group of mussel beds that resulted in (i) successful swallow (white bar), (ii) kleptoparasitism by carrion crows (black bar), and (iii) kleptoparasitism by herring gulls (grey bar).*

6.3 Tests of the individual-based model

We assessed the accuracy of our model predictions by comparing predictions of (i) oystercatcher foraging effort in each month and (ii) oystercatcher distributions across the mussel bed, with observed field data on each of these properties (**Table 7**). Given that only the mussel prey were resurveyed during this current study, there is some uncertainty as to the validity of the non-mussel prey densities within the intertidal and field patches. Thus we ran three scenarios in which (i) all food patches were available, (ii) only mussel beds and fields were available, and (iii) only mussel beds were available. For each of these three scenarios we ran the model 5 times to assess the degree of between-simulation variation in model predictions. In these simulations, the number of birds in March was reduced to 500 to match the observed decline in bird numbers during this month (**Figure 6**). For the overwinter period the mean (± SD) percentage of time devoted to foraging was predicted to be 33.8 ± 0.3 where all food was available, 53.8 ± 0.3 where only mussel beds and fields were available, and 53.5 ± 0.2 where only mussel beds were available. Hence the greatest difference existed between the model where birds could access all patches, and the models where they were excluded from certain types of patch. For the simulations in which the birds were allowed access to non-mussel intertidal patches as well as mussel patches, model predictions of foraging effort were consistently lower than those observed during the bird surveys (**Table 7**). The model birds obtained more of their food from non-mussel intertidal prey than the real birds, and hence spent a lower proportion of time feeding on mussels. An explanation for this is that in reality there is a trade-off between feeding on mussels (which tends to blunt bill tips) and feeding on other intertidal prey which requires a thinner bill tip to probe within sediment. This trade-off was not incorporated into the model, which could explain why the model birds spent a relatively higher amount of time feeding on non-mussel prey. Models in which birds were excluded from non-mussel intertidal prey typically gave predictions of foraging effort that were close to observed values, although foraging effort for March was consistently overestimated by the model. The mean (± SD) number of oystercatchers present on all mussel beds at low water was predicted to be 618.0 ± 0.7 where all food was available, 1042.1 ± 6.3 where only mussel beds and fields were available, and 1041.3 ± 4.4 where only mussel beds were available, compared with 864 observed (**Table 7**). The percentage of the oystercatcher population predicted to starve was predicted to be 100.0 % for all simulations.

Of the three scenarios, greater accuracy of predictions was achieved for the scenarios in which oystercatchers had access to the mussel beds and / or fields, but not to other intertidal feeding areas (**Table 5**). Furthermore, neither the food supply nor behaviour of oystercatcher was measured in the fields during the present study, and terrestrial food can become unavailable when fields are frozen. It was therefore decided that in all subsequent simulations oystercatchers were allowed to feed on the mussel beds but not on non-mussel intertidal prey or in fields. These simulations can be considered precautionary because in reality birds will have access to these food resources.

Table 7. *A comparison of the model predicted values and observed values for a suite of properties of the study system. The values for mean time spent foraging were calculated from Equation 17. Accuracy was calculated as (Predicted / Observed) * 100. For each comparison the most accurate prediction is indicated in bold.*

Test		**Observed**	**Predicted (all food patches)**	**Accuracy (%)**	**Predicted (mussels beds and fields only)**	**Accuracy (%)**	**Predicted (mussels beds only)**	**Accuracy (%)**
Mean time spent foraging over tidal cycle (%)	October	44.0	31.7	72.0	49.0	111.4	**48.7**	**110.7**
	November	52.2	34.2	65.5	53.9	103.3	**53.6**	**102.7**
	December	57.0	35.5	62.3	**55.9**	**98.1**	55.6	97.5
	January	46.4	37.5	80.8	58.6	126.3	**58.3**	**125.6**
	February	58.6	37.7	64.3	62.4	106.5	**62.0**	**105.8**
	March	49.5	35.8	72.3	57.6	116.4	**57.2**	**115.6**
Proportion of total population present on bed at low water	Bed 1	0.8	**10.3**	**1268.7**	10.3	1272.5	10.3	1269.7
	Bed 3	3.9	5.2	132.0	4.6	116.6	**4.6**	**116.4**
	Bed 4	9.0	**4.1**	**45.1**	3.4	38.1	3.4	38.1
	Bed 20	20.9	**21.6**	**102.9**	23.0	109.7	23.1	110.4
	Bed 22	2.8	3.6	131.3	3.3	119.2	**3.3**	**119.1**
	Bed 25	14.4	**19.7**	**137.5**	20.3	141.6	20.3	141.4
	Beds 26-28	10.4	**14.0**	**134.1**	14.9	143.3	14.8	142.5
	Beds 30&31	37.7	**21.6**	**57.1**	20.1	53.3	20.1	53.3
Mean number present on bed at low water	Bed 1	7	**64**	**907.4**	107	1534.8	107	1530.2
	Bed 3	34	**32**	**94.4**	48	140.4	48	140.6
	Bed 4	78	25	32.3	36	45.9	**36**	**46.0**
	Bed 20	181	133	73.6	241	133.1	**239**	**132.3**
	Bed 22	24	**23**	**93.9**	35	143.8	34	143.5
	Bed 25	124	**122**	**98.3**	212	170.8	211	170.4
	Beds 26-28	90	**86**	**95.9**	156	172.8	155	171.8
	Beds 30&31	326	133	40.9	209	64.2	**210**	**64.3**
% starved	All winter	**0.0**	**0.0**	**100.0**	**0.0**	**100.0**	**0.0**	**100.0**

Based on our initial 5 model runs for the mussel-bed only scenarios, we estimated the number of model runs (n) that would be required to detect a given magnitude of change in (i) foraging effort and (ii) oystercatcher numbers at low tide with a power of 80 % (Crawley, 2005), using the equation:

$n = 8 \cdot e / c^2$, Equation 18

where e is the error (standard deviation) associated with the estimate, and c was the size of the difference that needed to be detected (i.e. for a 10 % change in a value of 19, $c = 1.9$).

As expected due to the relatively deterministic nature of the model, the number of model runs required to predict a given magnitude of change in (i) oystercatcher foraging effort (**Figure 12**) and (ii) oystercatcher numbers at low water (**Figure 13**), was low and declined rapidly as the size of the change increased. We found that 3 model runs were sufficient to detect a 5 % change in oystercatcher foraging effort and numbers at low water. Therefore, 3 model runs were carried out for all subsequent simulations.

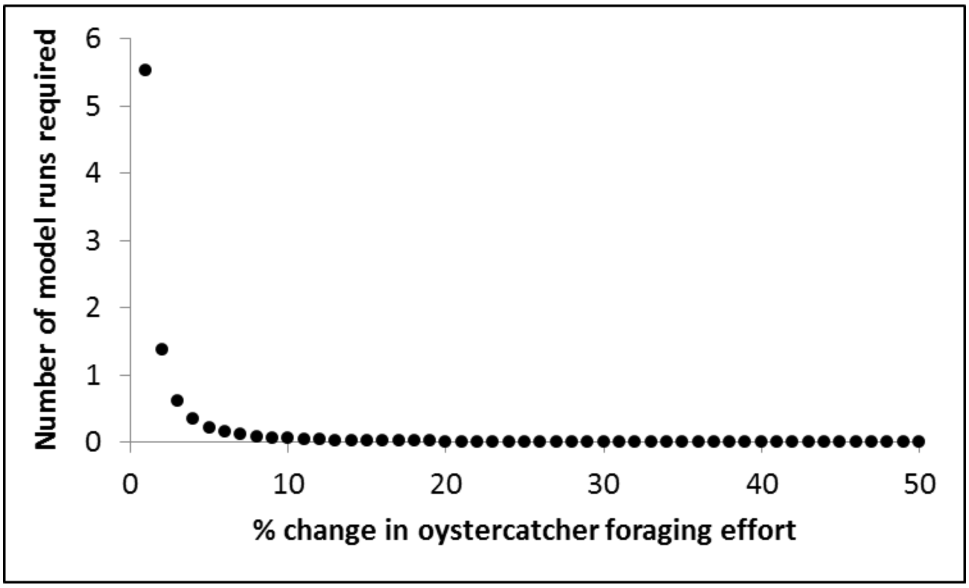

Figure 12: *The number of model runs required in order to detect a given size of change in the percentage of time that oystercatchers spend foraging.*

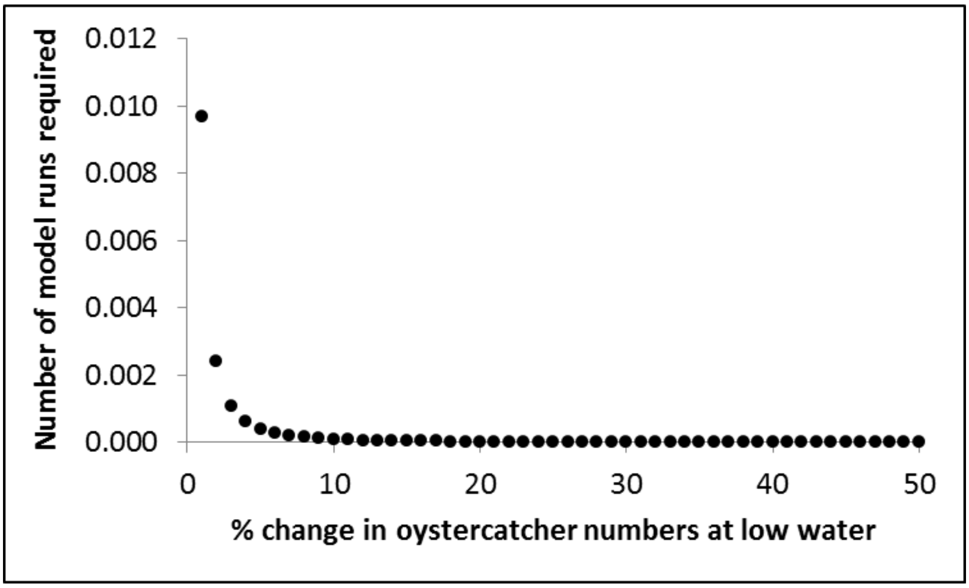

Figure 13: *The number of model runs required in order to detect a given size of change in the total number of oystercatchers observed at low water.*

6.4 Sensitivity analysis of the individual-based model

We assessed the sensitivity of the model predictions of oystercatcher (i) starvation and (ii) foraging effort, to changes in the mean value of each parameter using the one-at-a-time method of local sensitivity analysis (Hamby, 1994). The one-at-a-time method of sensitivity analysis has been frequently used to assess the sensitivity of the predictions of ecological models to changes in parameter values (e.g. Wood *et al*., 2012; Wood *et al*., 2013a; Wood *et al*., 2013b). To examine which parameters had the greatest relative effect on model projections, we subjected key parameters in turn to (a) an increase of 10 % and (b) a decrease of 10 %.

The sensitivity analyses indicated that ±10 % changes in the values of selected parameter had little effect on model predictions of mortality due to starvation. Starvation was predicted to affect 0 % of the population in all simulations, except for simulations with +10 % oystercatcher numbers (0.4 % starvation) and metabolic rate (1.1 % starvation) (**Figure 14**). Changes of ±10 % in the values of selected parameter were found to have a slightly greater effect on the predicted foraging effort of oystercatchers (**Figure 15**). In particular either decreasing or increasing metabolic rate by 10 % was found to change the percentage of time spent feeding by – 10.0 % and + 10.1 % respectively; these changes correspond to the oystercatchers devoting 48.6 % and 59.5 % of the total tidal exposure period to foraging, respectively.

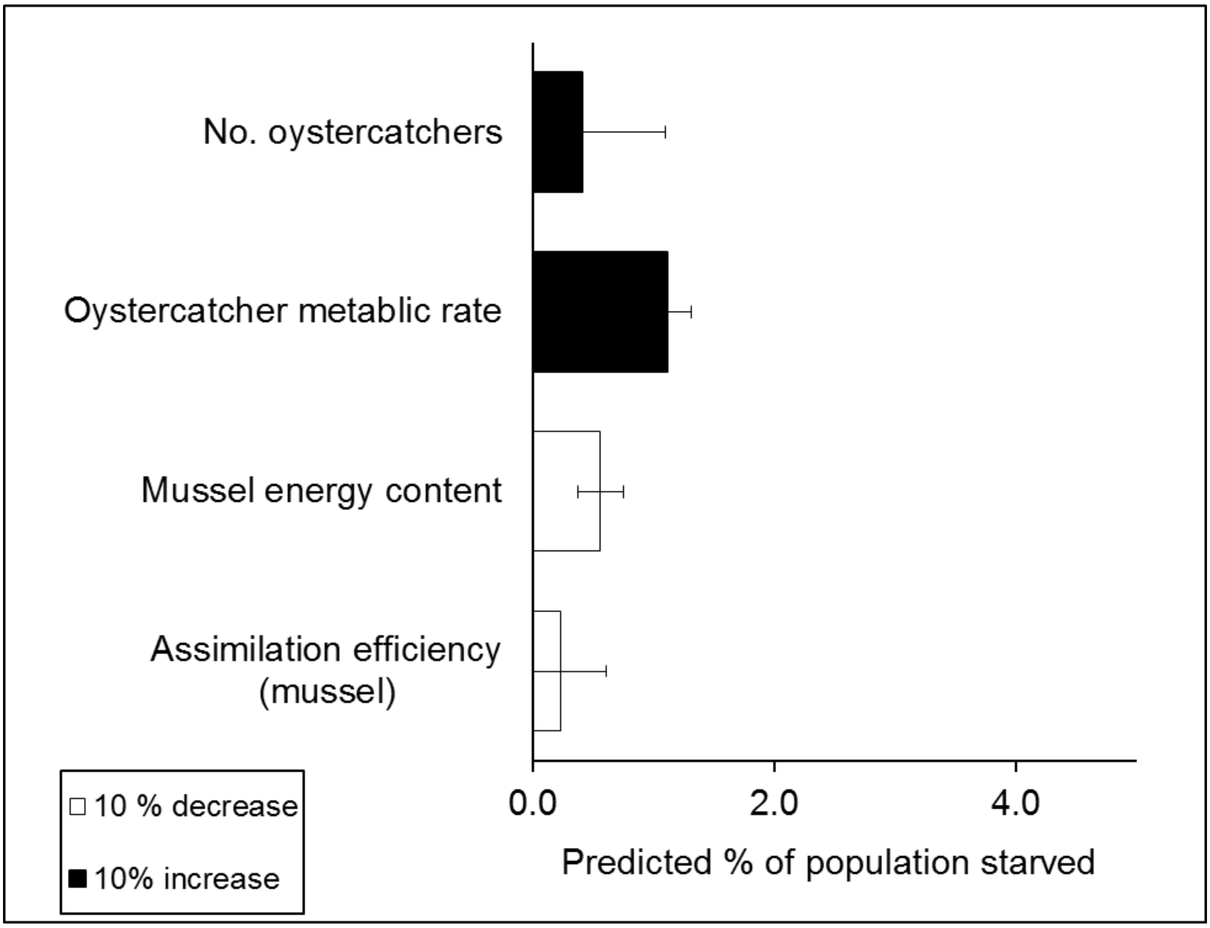

Figure 14: *The sensitivity of model predictions (mean ± SD) of the percentage of the total population that starved overwinter to ±10 % changes in the mean value of key parameters.*

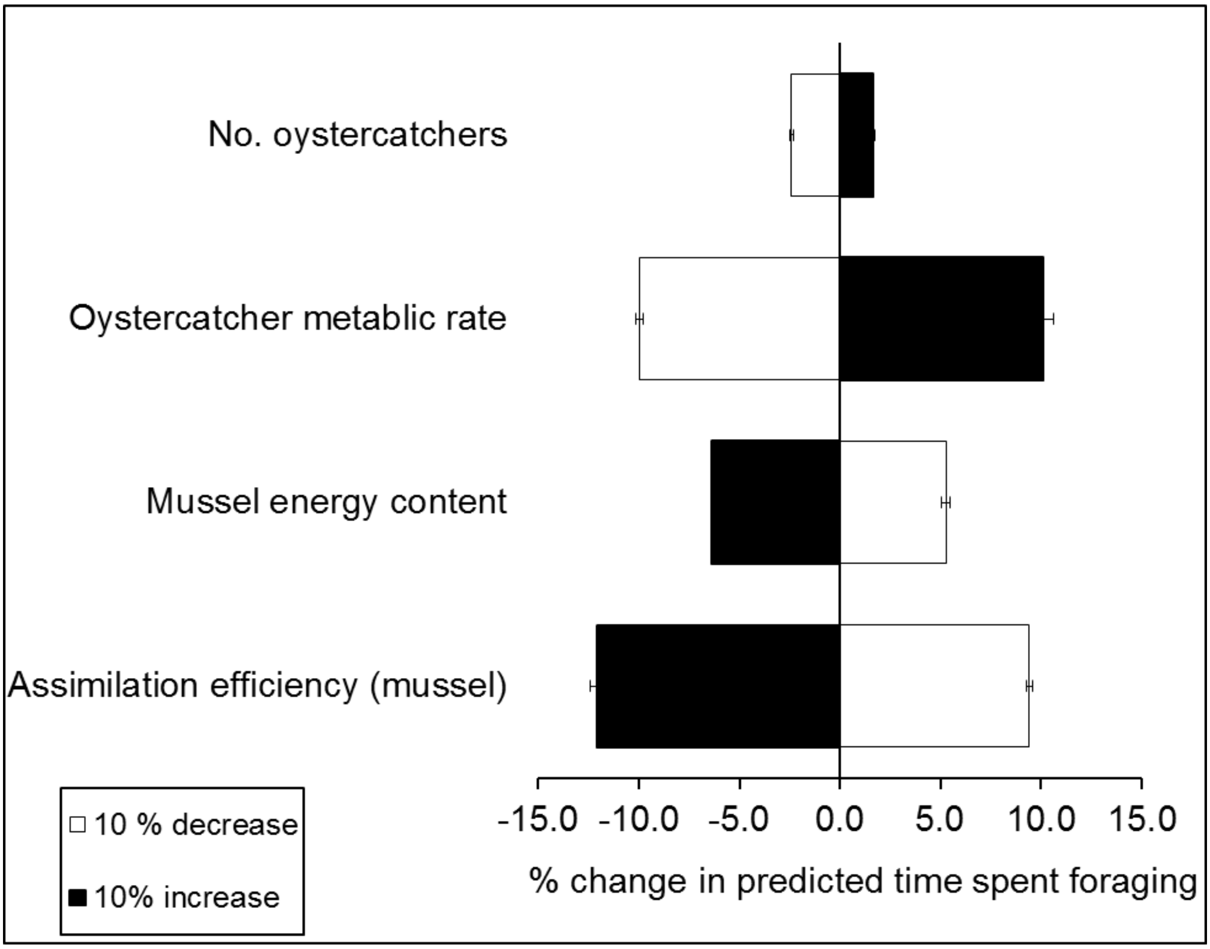

Figure 15: *The sensitivity of model predictions (mean ± SD) of oystercatcher foraging effort to ±10 % changes in the mean value of key parameters. A 5 % increase in predicted time spent foraging indicates an increase from 54.0 % to 56.7 % of the total exposure period spent foraging.*

6.5 Predictions of the Ecological Requirement Model

Table 8 shows the parameter values are predictions of the Ecological Requirement Model. The biomass of mussels was derived from mussel bed area (**Table 1**), the numerical density of 30 – 59 mm mussels (**Table 2**) and the ash-free dry mass of mussels within this size range (Stillman *et al*., 2000). The model assumed that mussels were the only food supply of oystercatchers, and so is precautionary as other food supplies will be available from intertidal and terrestrial patches. The model also excludes mussels on lays. The model predicted that the ecological requirement of the oystercatcher population (1500 birds) was 2244 tonnes fresh mass. This was 7.1 times the physiological requirement of 316 tonnes (i.e. the amount actually consumed). The total biomass of mussels was 2869 tonnes, and so a higher biomass of mussels were available than the amount required to support the population.

Table 8. *Parameters and predictions of the Ecological Requirement Model.*

(a) Parameters

Parameter	**Value**	**Units**	**Reference**
Population size	1500	Individuals	This study
Number of days for which population is supported	212	days	1st September until 31st March
Body mass	540	g	Zwarts *et al*. (1996b)
Energy expenditure	762	kJ day^{-1}	Nagy *et al*. (1999)
Ecological multiplier	7.1	-	Stillman & Wood (2013a)
Mussel prey sizes consumed	30-59	mm	Durell *et al*. (2007)
Energy content of mussels	22.0	kJ g^{-1}	Zwarts *et al* (1996a)
Mussel assimilation efficiency	85.0	%	Durell *et al*. (2007)
Total biomass of 30-59 mm mussels on all mussel beds excluding lays(fresh mass)	2869	tonnes	Area (**Table 1**). Mussel density (**Table 2**). Mussel ash-free dry mass (Stillman *et al.*, 2000). Conversion from ash-free dry mass to fresh mass (Ricciardi & Bourget, 1998)

(b) Predictions

Parameter	**Value**	**Units**
Physiological requirement of oystercatcher population	316	Tonnes fresh mass
Ecological requirement of oystercatcher population	2244	Tonnes fresh mass
Biomass not required by oystercatcher population	625	Tonnes fresh mass

6.6 Effect of fishery management on oystercatcher survival

6.6.1 Mussel lays

We used our IBM to predict the relationship between oystercatcher population size and the percentage of the overwintering oystercatcher population predicted to starve in the (i) absence of mussel lays, (ii) presence of currently existing mussel lays only, and (iii) presence of current and proposed new mussel lays.

Where no mussel lays were available our model predicted 0 % starvation among overwintering oystercatcher populations of ≤ 1500 individuals (**Figure 16**). For population sizes of ≥ 2000 individuals, the percentage of the population starving during the overwinter period increased with population size. For the maximum population size tested in our model (6000 individuals), overwinter starvation was predicted to cause the deaths of 35.9 ± 0.2 % (mean ± SD) of the total population. For the current food supply within the Exe estuary, where the existing mussel lays were available, our model predicted 0 % starvation among overwintering oystercatcher populations of ≤ 1500 individuals (**Figure 16**). For the maximum population size tested in our model (6000 individuals), overwinter starvation was predicted to cause the deaths of 35.3 ± 0.2 % (mean ± SD) of the total population, which corresponds to only a 0.6 % reduction in mean starvation values compared with the scenario in which no lays were available. Similarly, where additional new mussel lays were also available, our model predicted 0 % starvation among overwintering oystercatcher populations of ≤ 1500 individuals (**Figure 16**). For the maximum population size tested in our model (6000 individuals), overwinter starvation was predicted to cause the deaths of 34.9 ± 0.6 % (mean ± SD) of the total population, which corresponds to only a 1.0 % reduction in mean starvation values compared with the scenario in which no lays were available.

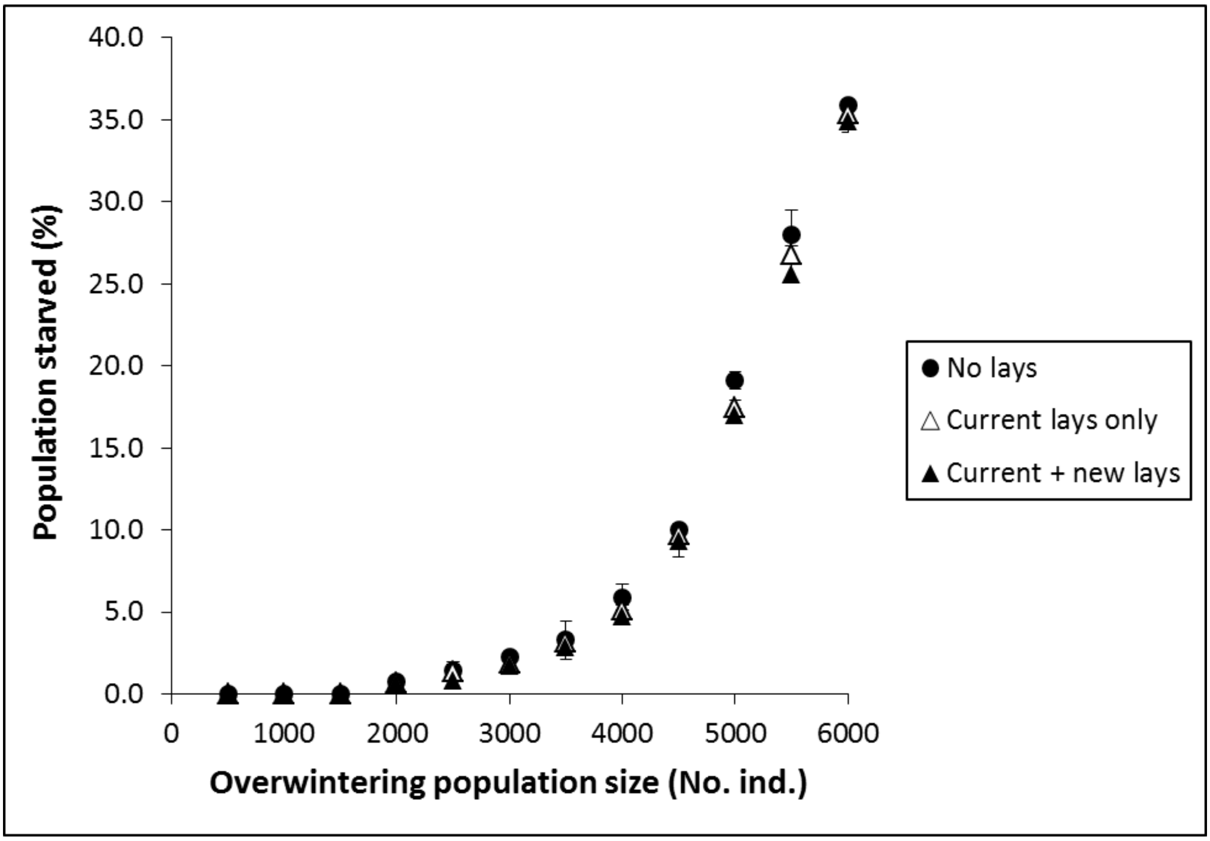

Figure 16: *The relationship between oystercatcher population size and the mean (± SD) percentage of the overwintering oystercatcher population predicted to starve in the (i) absence of mussel lays, (ii) presence of currently existing lays only, and (iii) presence of current and proposed new lays.*

6.6.2 Discards

Simulations were run assuming that 1200 kg fresh mass of discards were available per week, based on the values provided by Myles Blood Smith. It was assumed that 1200 kg fresh mass of discards were placed on the discard bed starting from a specific month. This allowed us to explore whether the time at which discards started to be placed on the discard bed influenced the affect of discards on oystercatcher survival. We also explored the effect of the area over which the discards were spread (i.e. the size of the discard bed), given that the same mass of discards could either be positioned at a higher density over a smaller area, or a lower density over a larger areas. We ran simulations in which discard flesh content ranged from 100 % of the ash-free dry mass of lay mussels, through to 25 % of this value, to assess the effect of discard size on model predictions. The intake rate of oystercatcher feeding on discards was assumed to be the same as oystercatcher feeding on mussels with the equivalent ash-free dry mass. Interference competition between oystercatcher feeding on discards was assumed to be of the same strength as interference competition between oystercatcher feeding on mussels. It was assumed that the proportion of discards lost to gulls and crows was the same as the proportion of mussels lost to on Beds 3 and 4 (i.e. the highest lost rates observed).

Simulations were initially run assuming that the discard bed was 2 ha in area (**Figure 17**). For a population size of 3000 oystercatchers our model predicted that the higher the AFDM of discards the fewer birds that starved (**Figure 17**). However, for the lower population size of 1500 birds no effect of discard mussel AFDM was found, as the percentage of the population predicted to starve was 0 % even without the provision of discards. Thus whilst the provision of discards was not predicted to benefit a population of 1500 birds, providing discards for a population of 3000 birds was predicted to decrease the percentage of oystercatchers starving overwinter. The previous simulations, in which no extra food sources (e.g. lays) were available (see **Figure 16**) predicted that, for a population of 3000 birds, the mean (± SD) percentage that starved overwinter would be 2.2 ± 0.3 %. However, for the simulations in which discards were provided the mean (± SD) percentage that starved overwinter was predicted to be 0.8 ± 0.3 % across all AFDM simulations (**Figure 17**). Where discard mussel AFDM was only 25 % of the AFDM of lay mussels, the mean (± SD) percentage that starved overwinter was predicted to be 0.9 ± 0.3 %. In contrast, where discard mussel AFDM was assumed to be 100 % of the AFDM of lay mussels, the mean (± SD) percentage that starved overwinter was predicted to be 0.6 ± 0.1 % (**Figure 17**).

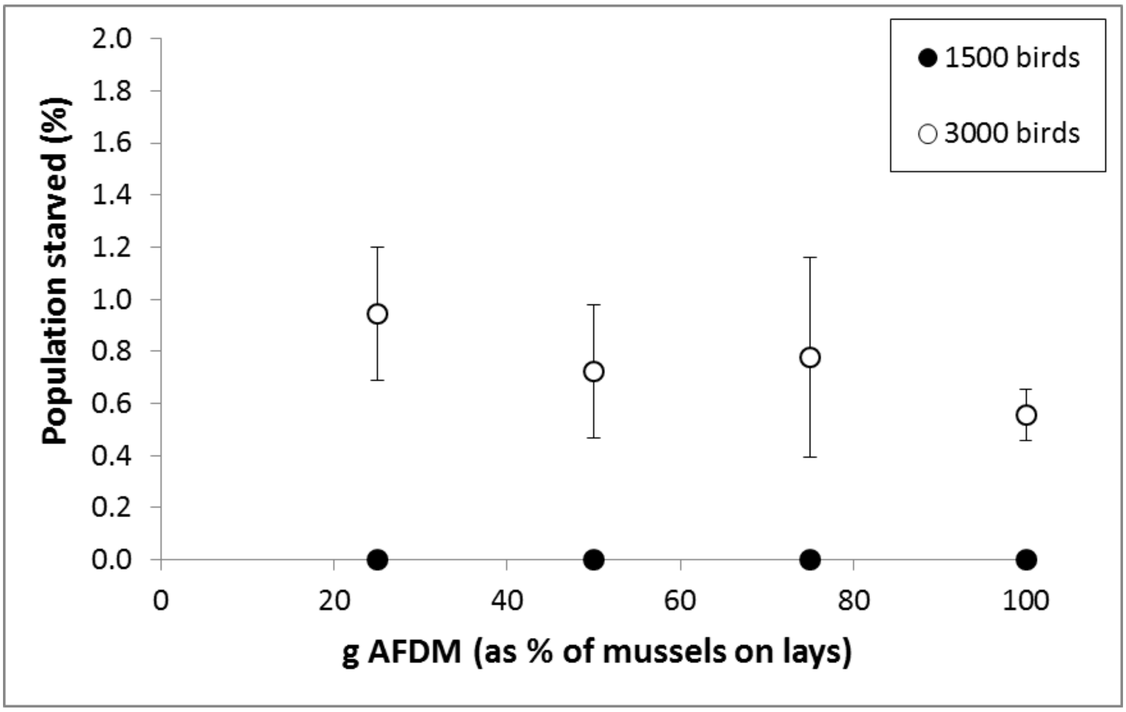

Figure 17: *The effect of the provision of mussel discards of a given AFDM on the overwinter starvation of oystercatcher populations of 1500 (solid circles) and 3000 (open circles) birds. We modelled the AFDM of discard mussels as a fixed percentage of the AFDM of mussels on the lays: 25, 50, 75 and 100 %. These simulations are based on the provision of discards over an area of 2 ha.*

We next ran the IBM to test the effect of the size of the discard area on overwinter oystercatcher starvation. As our previous simulations indicated that no starvation occurred within populations of 1500 oystercatchers (**Figure 17**), we ran simulations using a population size of 3000 birds. Within a given AFDM value (25-100 % of the AFDM of mussels on the lays), greater discard area was typically predicted to lead to lower incidences of starvation among the oystercatcher population (**Figure 18**). For example, where discard AFDM was assumed to be 25 % of lay mussel AFDM, the mean (± SD) percentage of the population predicted to starve was 1.0 ± 0.4 % with a 1.0 ha discard area, 0.9 ± 0.1 % with a 3.0 ha discard bed, and 0.5 ± 0.3 % with a 5.0 ha discard bed (**Figure 18**). However, for simulations in which AFDM was 100 % of lay mussel AFDM, the mean (± SD) percentage of the population predicted to starve was 0.6 ± 0.1 % for 1.0, 3.0 and 5.0 ha discard areas.

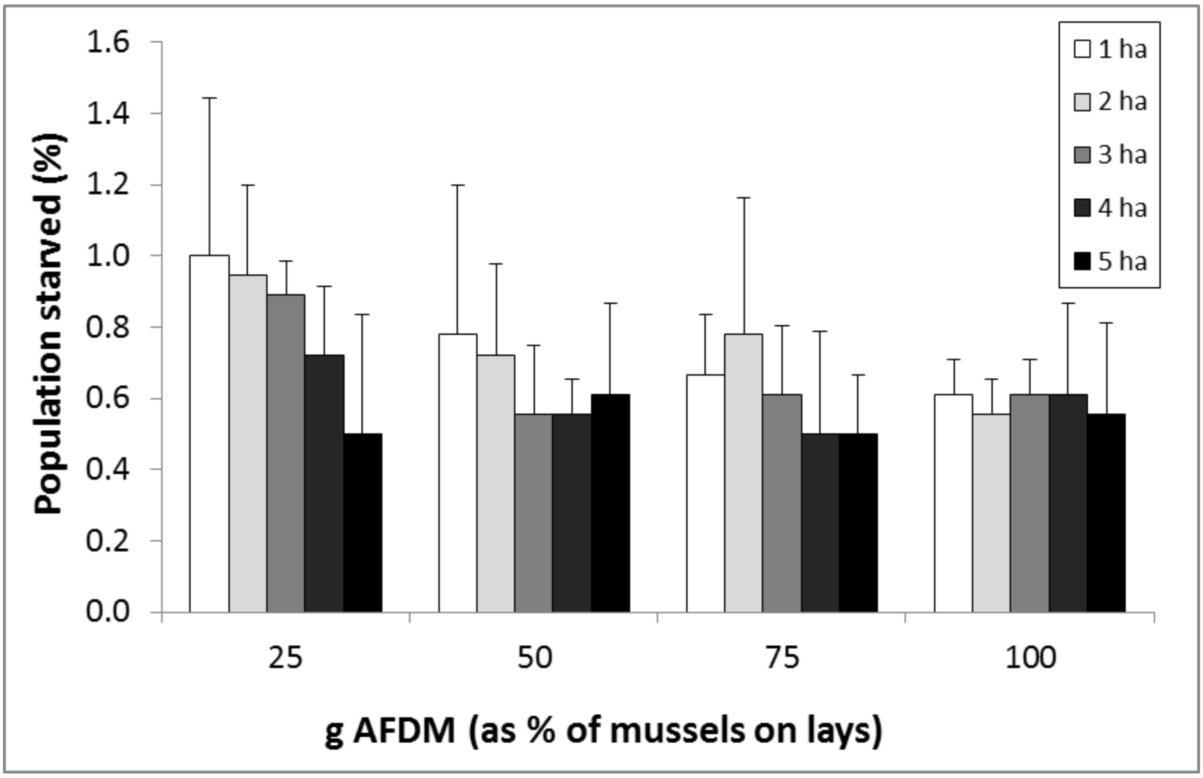

Figure 18: *The effect of the size (ha) of the mussel discards area on the overwinter starvation of oystercatcher populations of 3000 birds. We ran simulations in which discard area was set to 1, 2, 3, 4, or 5 ha. We modelled the AFDM of discard mussels as a fixed percentage of the AFDM of mussels on the lays: 25, 50, 75 and 100 %.*

For a population of 3000 birds with access to discards, fewest birds were predicted to starve where 100 % AFDM mussels were provided over 5 ha (*i.e.* the greatest benefit of discards). To test whether this benefit was depended on the timing of discard provision, we ran subsequent simulations in which these discards were provided from 1st September, 1st October, 1st November, 1st December, 1st January, 1st February and 1st March respectively. Model predictions indicated that greater starvation would occur where discards were only provided late in the winter (**Figure 19**). The mean (± SD) percentage of the population predicted to starve increased from 0.6 ± 0.3 % where discards were provided from September to 1.3 ± 0.4 % where discards were provided from 1st March (**Figure 19**). The greatest increase in starvation occurred between 1st January and 1st February; over this period the mean (± SD) percentage of the population predicted to starve increased from 0.7 ± 0.2 % to 1.2 ± 0.5 % (**Figure 19**).

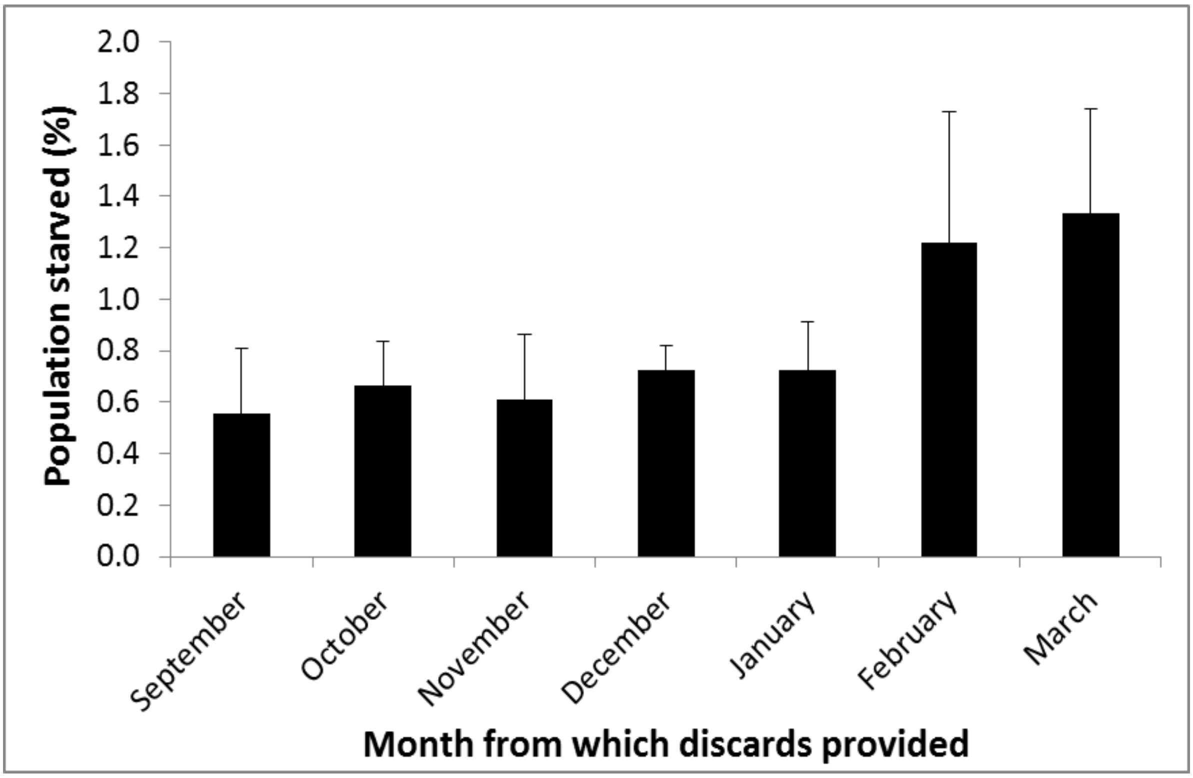

Figure 19: *The effect of the month from which discards were provided on the overwinter starvation of oystercatcher populations of 3000 birds. For each month, discards were provided continuously from the 1st of that month until the end of winter.*

7 DISCUSSION

This project has used a combination of new fieldwork, data collation and modelling to assess the food requirements of oystercatcher on the Exe Estuary, and to predict the effect on oystercatcher survival of current and potential future mussel fishery management. The overwintering oystercatcher population of the Exe Estuary has been well-studied, and the birds are known to feed predominantly upon mussels in intertidal areas (Goss-Custard & Durell, 1983; Ens & Goss-Custard, 1984). There have been recent declines in the population size of oystercatcher in the Exe Estuary, the reasons for which are unknown. There have been associated declines in the area of mussel beds. The current mussel fishery on the Exe provides a feeding resource for oystercatcher on intertidal lays that are exposed on spring tides. Two potential management options that could be effective at improving the feeding conditions of oystercatcher would be to increase the number and area of intertidal mussel lays, and to place mussel discards at a relatively high shore level close to the oystercatcher roost.

Population decline at a given site for migratory species such as oystercatcher must be viewed within the context of the dynamics of the species at a large spatial scale. For example, a decrease in the numbers of a species at one overwintering site may be compensated by increased numbers at other sites, due to a shift in the distribution of a species rather than a population decline. Decreases in the numbers of individuals overwintering at a site may reflect a population decline, a shift in distribution to other sites, or both (Bart *et al.*, 2007; Tománkova *et al.*, 2013). In recent decades many temperate species of birds have exhibited poleward shifts in their wintering ranges in response to climate change (La Sorte & Thompson, 2007). The UK oystercatcher numbers are declining across many overwintering sites, including the Exe estuary, and are not increasing elsewhere, which suggests that the population is declining (Austin *et al*. 2014; **Figure 2**).

On the Exe Estuary, mussel bed area has declined in parallel with decline in oystercatcher numbers, but this does not mean that the decline in oystercatcher population size is being driven by decline in mussel bed area. Other factors may include changes in the flesh content of mussels, changes in the density or size of mussels, changes in the proportion of mussels lost to attacks by carrion crows and herring gulls, changes in the abundance or quality of other prey. Measuring the flesh content of mussels or the abundance of non-mussel prey were not within the scope of this study, but we have shown that the proportion of mussels lost to crows and gulls (now between 14 and 20%) has increased from the value of 3% presented by Stillman et al. (2000). The density of mussels within the size range consumed by oystercatcher has generally declined, but the density of the largest mussels within this range, which are more profitable to the birds, has generally increased. Ecological models, such as individual-based models, which assess bird foraging performance and survival can be useful tools with which to understand the causes of changes in bird numbers at a site.

The Exe estuary currently supports an overwintering oystercatcher population of between 1500 and 2000 individuals (Austin *et al*. 2014; **Figure 2**). Our field surveys together with the predictions of our individual-based model and Ecological Requirements Model suggested that the food resources within the Exe estuary are currently sufficient to support a population of this size. Given that there is currently sufficient food to support the population, any further decline in oystercatcher numbers, unless accompanied by changes in the food supply, should not be attributable to starvation. However, given that the mussel beds were largely the result of discontinued fishing practises and have declined in both area and number in recent decades, further declines in food abundance appear likely (McGrorty *et al*., 1991; McGrorty & Goss-Custard, 1991).

Our individual-based model predicted that the current mussel population Exe estuary is not able to support the total number of birds observed during the 1990s (over 4500), without a proportion of the population starving. However, these simulations assumed that all birds fed on mussels, whereas only a proportion of the Exe oystercatchers do so. For example, Stillman *et al.* (2000) used a population size of 1550 oystercatcher in model simulations for the period 1976 to 1990, as this was the number of birds observed to feed on the mussel beds; the total population size was higher. This figure is very close to the maximum number of birds observed on mussel beds during the present study (1490), suggesting that the number of birds on the mussel beds may not have declined by as large an amount as the total number of birds on the estuary. This is evidence that the decline in oystercatcher population numbers on the Exe may be due to factors other than the changes in mussel population. However, further reductions in the area of mussel beds or mussel density could reduce the number of oystercatcher that can be supported.

If models are to be used to advise conservation and management that must produce accurate predictions. We tested the distribution and feeding effort of oystercatchers predicted by the individual-based model. The predicted proportion of the oystercatchers on each bed was relatively close to the observed; beds with a higher observed proportion of birds tended to have a high predicted proportion of birds. The main exception was for bed 1, which had a much higher predicted than observed proportion of birds. Predictions were based on mussel bed area and mussel abundance. Observation since the 1970s of the mussel size and abundance on this bed, in relation to the number of birds (John Goss-Custard Pers. Obs.), has indicated that fewer birds use the bed than would be expected from the food supply. This indicates that something other than the food supply is affecting the number of birds that use this bed. The predicted feeding effort of the birds was measured as the proportion of the low tide period spent feeding on mussels. This is related to the difficulty birds are having surviving the winter (a higher proportion of time spent feeding indicating more difficulty) and so is an important test. Model predictions were close to observations in all months except March, when the model birds were predicted to spent much more time feeding than the real birds. A possible explanation is that at this time of the year the real birds switch to consuming smaller mussels as the flesh content of the larger mussels declines more rapidly. This process was not included in the model, which could account for the difference. As the model birds were having more difficulty surviving than the real birds, the predictions of the model can be considered precautionary.

Providing additional food resources in the form of current or extra mussel lays, or discards was predicted to have a beneficial effect on the overwinter survival of the oystercatcher population within the Exe estuary, but only for a population of ≥ 2000 birds (**Figures 16 and 17**). Below this threshold, starvation was predicted to affect 0 % of the population and so additional food resources cannot further reduce the starvation. One factor that limited the benefit of the lays to a population of ≥ 2000 birds was the low shore elevation of the lays, which meant that they were exposed for only a short duration and were thus unavailable to the oystercatchers most of the time. Simulations were not run in which lays were positioned higher on the shore because this would not be commercially viable from a fishery perspective; the growth rate of mussels declines as they are positioned further up the shore because they are inundated with water for less time and so have less time to feed.

Factors that would affect the beneficial effect of discards include the size of the discards, the size of the discard bed and the date from which discards are replenished. Larger discards were predicted to increase oystercatcher survival to a greater extent because birds can achieve a higher energy intake rate when feeding on larger prey. The size of the discard bed limited the number of beds that could utilise the bed because interference competition reduced the intake rate that the least dominant birds could obtain; a larger bed would allow more birds to use the bed to supplement their food intake from other sources. Our simulations predicted that larger discards spread at lower density over a larger bed increased oystercatcher survival by the greatest amount. This happened because interference competition excluded some birds from smaller patches, and oystercatcher can maintain high intake rate down to low mussel densities. It is unlikely that the size of discards could be increased, but the simulations suggest that the greatest benefit to oystercatchers could be achieved by spreading discards over a larger area. Our simulations predicted that making discards available from January increased oystercatcher survival by the same amount as making them available from September. This was because the feeding conditions of birds deteriorate through winter as, for example, the mass of prey declines, interference competition intensifies and day length shortens. Hence, the birds only needed to exploit the discards later in the winter. The intake rate of birds feeding on discards was not measured during the study, but we recommend that this is done to better understand the benefit of discards. **Figure 20** indicates our recommended location for the discard bed. This is along the top of the shore on an area of gravel south of Cockwood, but north of a zone from which fishing gear is prohibited (**Figure 4**). The gravel habitat does not provide a large food resource for oystercatcher. However, any other biodiversity or additional importance of the area should be determined and the distribution of the gravel substrate mapped before proceeding. We have consulted Myles Blood-Smyth of The Exmouth Mussel Company to confirm feasibility from a fishery perspective. During different trips, discards would be placed at different locations along the length of the bed, meaning that over time discards would cover the whole bed. **Figure 20** also indicates the location at which discards have been previously placed, and exploited by oystercatcher. The proposed location is on similar habitat, but in an area exposed to less human activity. Therefore, birds would be exposed to less human disturbance and be able to consume discards over a longer period of time at the proposed location.

Figure 20: *Proposed and past locations of shellfishery discard beds. The proposed bed would be along the top of the shore on gravel substrate along line A. Line B indicates the location where shellfishery discards have been laid in the past. Map derived from Google Earth.*

This project has documented a number of changes that have occurred to the Exe Estuary mussel and oystercatcher populations. The number and size of mussel beds have decreased as traditional methods of maintaining mussel beds in the estuary have ceased. The density of mussels within the size range consumed by the birds has generally decreased, but the density of the larger mussels within this size range, which are more profitable to oystercatcher, has generally increased. Oystercatcher lose a higher proportion of mussels to attacks by carrion crows and herring gulls than they have in the past. The number of oystercatcher wintering in the estuary has declined, but the number of birds feeding on the mussel beds has been relatively stable. The models developed in the project predict that the present day mussel population is sufficient to support the number of oystercatcher that were observed to feed on mussels. The presence of mussel lays provides extra food for oystercatcher when these lays are exposed on spring tides. The present area, or increases in the area of mussel lays could increase the survival rate of oystercatcher if the number of birds feeding on mussels was over 2000. This effect is relatively small because the lays are only exposed for a short time, and so oystercatcher will obtain the majority of their food from mussel beds that are higher on the shore, and hence exposed for longer.

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