Deriving simple predictions from complex models to support environmental decision-making

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ABSTRACT

Recent decades have seen great advances in ecological modelling and computing power, enabling ecologists to build increasingly detailed models to more accurately represent ecological systems. To better inform environmental decision-making, it is important that the predictions of these models are expressed in simple ways that are straightforward for stakeholders to comprehend and use. One way to achieve this is to predict threshold values for environmental perturbations (e.g. climate change, habitat modification, food loss, sea level rise) associated with negative impacts on individuals, populations, communities or ecosystems. These thresholds can be used by stakeholders to inform management and policy. In this paper we demonstrate how this approach can use individual-based models of birds, their prey and habitats, to provide the evidence-base for coastal bird conservation and shellfishery management. In particular, we show how such models can be used to identify threshold values for perturbations of food abundance that can impact negatively on bird populations. We highlight how environmental thresholds could be used more widely to inform management of species and habitats under environmental change.

1. Introduction

Environmental change, through processes such as habitat loss, fragmentation, species invasion, climate change and intensification, is applying increasing pressure to ecological systems worldwide (Millennium Ecosystem Assessment, 2005). To understand the consequences of such change, and to make informed decisions, environmental managers and policy makers need to know how ecological systems will be affected. Despite the need, predicting the consequences of environmental change, especially when change is novel, has remained a challenge for ecologists. Yet such predictions are increasingly needed (Evans, 2012).

There is growing realisation that a potential solution, and the route to making ecology a more predictive science, will be to develop a mechanistic approach in which individual-based models are used to predict how population-level processes emerge from the interactions, individual differences and decision making of the individuals which comprise these populations (Starfield, 1997; Sutherland, 2006; Stillman and Goss-Custard, 2010; Evans, 2012; Addison et al., 2013; Stillman et al., 2015). Mechanistic models include more of the underlying mechanisms within ecological systems than more traditional models based on statistical

relationships or population parameters (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). Increases in computing power and software development have allowed more complex models to be developed and run, and new techniques for describing and testing these models have allowed them to be described in a more transparent and repeatable way (e.g. Grimm et al., 2006).

Simple communication of predictions, understandable by a range of stakeholders and non-modelling specialists, is also vital if these models are to be used to support environmental decision-making. This can be achieved by predicting threshold values for environmental perturbations (e.g. climate change, habitat or food loss, sea level rise) associated with negative impacts on ecosystems. These thresholds can then be used by stakeholders to inform decision-making. In this paper we show how such an approach can be used to support the conservation of birds and shellfishery management by predicting thresholds of food abundance that are required to maintain high survival rates of the birds. We emphasise how the approach could be used more widely to inform management of species and habitats under a range of environmental changes.

2. Individual-based models of shorebirds and wildfowl

Shorebirds and wildfowl occur in vast numbers in coastal habitats, and both the birds and their habitats have international protection. For example, within the European Union shorebirds

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are protected under the EU Wild Birds Directive (2009/147/EEC), which legally obligates member states to safeguard the birds and their habitats in order to maintain healthy populations. A range of potential threats to coastal bird populations have been identified, including coastal development, eutrophication, sea level rise, anthropogenic disturbance, and shellfishing (Sutherland et al., 2012; Maclean, 2014). To advise conservation in the face of such threats, ecologists need to predict how changes to the environment will affect either population size or the demographic processes, such as survival rate, that determine population size (Sutherland and Norris, 2002). Despite this need, it has been difficult to use traditional techniques, such as population models or habitat selection models, to accurately predict how changes to the environment influence either population size or survival rate of these birds (Goss-Custard and Stillman, 2008; Stillman and Goss-Custard, 2010). Difficulties include: (i) the fact that environmental changes to sites are often novel phenomena without precedent and consequently there are rarely historical data to inform how population size within a site will be influenced by such changes; and (ii) measuring survival in such mobile, long-lived species is complex and time consuming, meaning that survival rates have been measured at relatively few sites (Green and Hirons, 1991).

Individual-based models (IBMs) have proven to be an appropriate solution because population-level processes in shorebirds and wildfowl can be understood as emerging from individual physiological and behavioural mechanisms that can themselves be accurately measured or predicted (Goss-Custard and Stillman, 2008; Stillman and Goss-Custard, 2010; Stillman et al., 2015). Furthermore, there is a good understanding of the fitness-related factors on which these species can base their decisions. Starvation and body condition depend on the adaptive behaviour of individuals (e.g. choice of diet and feeding location), the number of birds present within a site, variation in foraging efficiency and dominance hierarchies of individuals, local competitive interactions among individuals, the area, quality and spatial arrangement of feeding habitat, the time for which feeding habitat is exposed by the tide, and the effects of food and competitor density on the rate at which birds consume food (Stillman and Goss-Custard, 2010).

The shorebird and wildfowl IBMs (see Stillman and Goss-Custard, 2010; Stillman et al., 2015 for overviews) run on an hourly time step, and divide space into a number of discrete patches of fixed area. The hourly availability of patches is determined by their exposure through the tidal cycle. Patches contain the food supply of the birds; for shorebirds patches typically comprise discrete size classes of intertidal invertebrates including bivalve molluscs, polychaete worms and crustaceans, whilst for wildfowl, patches comprise the biomass of plant species including intertidal eelgrass (*Zostera* spp.) and terrestrial grasses. The birds are represented as individuals, varying in their dominance and foraging efficiency, with species-specific daily energy requirements. Resource competition is incorporated through the depletion of shared resources and behavioural interactions such as prey stealing and competitor avoidance. Birds attempt to meet their daily energy requirements by feeding in the patches and on the prey that maximise their rate of energy assimilation. Birds that are not able to meet their daily energy requirement draw on their energy reserves, and die of starvation if these reserves fall to zero. The overall population mortality rate is the proportion of individuals which starved, even though each, by maximising its rate of energy assimilation, was attempting to minimise the chance of this happening. Other predictions include the distribution of individuals among patches, the range of prey species included in the diets of birds, the amount to which food resources are depleted by the birds, the proportion of time each bird spends feeding, and the body condition of each bird (i.e. proportion of energy reserves remaining).

The important advantages of these IBMs over alternative models are: (i) that predictions are derived from fitness-based decision-making (i.e. birds feed on the patch and prey that maximise their rate of energy assimilation), which is more likely to persist when the birds encounter novel environments than the empirical relationships within habitat association models; and (ii) that IBMs directly predict survival and body condition, which are closely linked to factors determining population size (Grimm and Railsback, 2005). These IBMs have been applied to over 35 coastal systems, for species including dunlin (*Calidris alpina*), redshank (*Tringa totanus*), black-tailed godwit (*Limosa limosa*), oystercatcher (*Haematopus ostralegus*), curlew (*Numenius arquata*), brent goose (*Branta bernicla*) and pink-footed goose (*Anser brachyrhynchus*), and used to advise conservationists on the potential impact of environmental change caused by sea level rise (e.g. Durell et al., 2006), food loss (e.g. West et al., 2007), habitat loss (e.g. Durell et al., 2006), shellfishing (e.g. Stillman et al., 2003), disturbance from humans, tidal barrages, wind farms, nuclear power stations, and changes in agriculture and hunting (see Stillman and Goss-Custard, 2010; Stillman et al., 2015 for an overview).

However, a limitation has been the relative complexity of these models (Stillman and Wood, 2013). While they have been kept as simple as possible, technical modelling experience is still required to develop, run and interpret them (West et al., 2011). Given that they are designed to make accurate predictions to inform environmental decision making, there are limits to the number of parameters and processes that can be removed. A range of stakeholders use the predictions of these models, including shellfishing organisations, conservation bodies, government departments, charities and industry, but the models themselves have typically been developed, run and interpreted by modelling specialists (Stillman et al., 2010, 2015; Stillman and Wood, 2015). The ideal would be a model that could produce accurate predictions using a minima of parameters and steps that could be used by a range of coastal interests groups.

3. Deriving simple predictions for complex systems

Although relatively complicated compared to many types of model traditionally used in ecology, the shorebird and wildfowl IBMs have typically been used to answer relatively simple questions of the type:

"Will an environmental change at a site reduce the number of birds that can survive the non-breeding season on the site?"

The question may be simple, but answering it is complicated, which is why IBMs have been used in preference to more traditional methods. IBM simulations have typically included the presence or absence of an environmental change (e.g. tidal barrage presence or absence), or successively increased the amount of an environmental change (e.g. percentage habitat loss or reduction in food supply). Simulations have typically predicted that as the amount of potentially detrimental environmental change increases (i.e. a change that is expected to have a neutral or negative effect on biodiversity, such as a reduction in habitat area), a point is reached at which the survival of the birds begins to decrease (Stillman and Goss-Custard, 2010). Survival does not always decrease with relatively small changes because model birds, as real birds, can compensate for changes, for example, by feeding for longer, feeding in alternative places or drawing on their energy reserves.

The predicted responses of shorebirds and wildfowl to environmental change represent a wider phenomenon in ecological systems. Different systems will have varying amounts of resilience to potentially detrimental environmental change, for example, due to the amount of previous change or the size of ecological populations
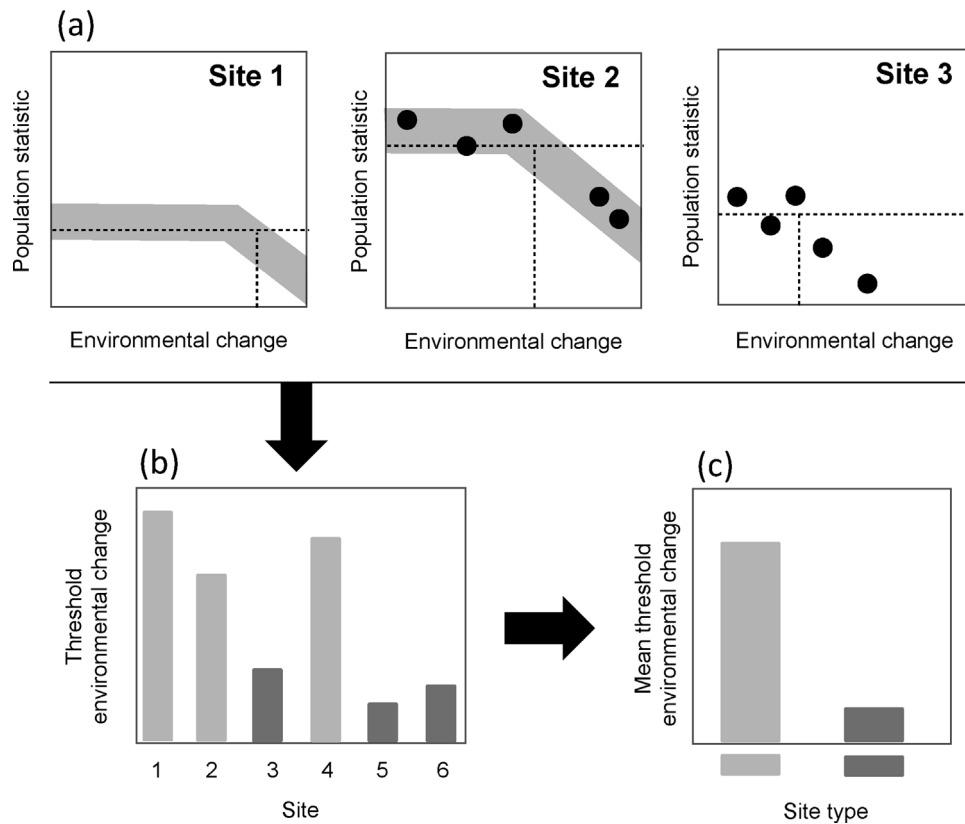
Fig. 1. How simple predictions can be derived for complex systems and used to inform environmental decision making. (a) Complex models are used to predict the relationship between a population statistic (e.g. population size or survival rate) and the amount of environmental change at different sites. Empirical data may also be available for some sites. Three examples are shown: Site 1 – only model predictions available (grey shading, showing variation in predictions); Site 2 – both model predictions and empirical data (black circles) available; Site 3 – only empirical data available. The horizontal broken lines indicate a value of the population statistic at which environmental change would be deemed to have had an adverse effect (e.g. 10% decline in population size or survival rate). The vertical broken lines indicate the amount of environmental change leading to an adverse effect (termed threshold environmental change). (b) The threshold environmental change is likely to vary between sites (values for example sites 4, 5 and 6 are also shown), and may be associated with characteristics of the sites (termed site type and indicated by shading of vertical bars in this example). (c) Analysis of among-site variation in the threshold environmental change may allow the threshold to be understood in terms of site characteristics (in this example, site type, as defined by shading). Stakeholders can use this result to determine whether an anticipated amount of environmental change is likely to have an adverse effect given the characteristics of a site.

relative to the resources available. The question posed above could be expressed more generally as:

> "Will an environmental change have a negative effect on the ecosystem?"

Answering this question depends on the amount of environmental change, and determining what a negative effect would entail and how this could be measured or predicted. The answer to such a question, although potentially derived from complex models, can be expressed in simple terms understandable to stakeholders and decision makers (Fig. 1).

As the amount of potentially detrimental environmental change increases, a point will be reached at which populations are adversely affected, for example, as measured by a specified change in a population statistic (e.g. 2% reduction in survival rate) used to assess the conservation status of a species (Fig. 1a). For shorebirds and wildfowl, such relationships have usually been derived from IBM predictions, but empirical data have been available on some sites, sometimes in combination with model predictions (Stillman and Goss-Custard, 2010). The threshold amount of environmental change leading to a change in a population statistic is likely to vary between sites (Fig. 1b). Reasons for this may include among-site differences in the density of individuals, quality or type of food available, differences in site shape or location. If the underlying reasons for such differences can be understood, it will be possible to relate threshold amounts of environmental change leading to adverse effects to site characteristics (Fig. 1c). Stakeholders can

then use these final relationships to inform their decision-making, either in the sites for which models have been developed, or potentially for other sites with similar characteristics. Although simple, the relationships are derived from the predictions of complex models, but stakeholders do not need to use these models directly in order to make informed decisions from their predictions.

4. Simple predictions to support shellfishery management and shorebird conservation

We now demonstrate how the approach detailed in Fig. 1 can be used to support environmental decision making. Our example concerns the long-running conflict between the conservation of shellfish-feeding shorebirds and the management of intertidal shellfisheries.

Shallow coastal habitats are important sites for populations of shellfish, such as cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*), many of which support commercial shellfisheries that provide food and employment. These shellfish are also the principal overwintering food resource for shorebirds species such as oystercatcher, which has led to disputes between economic and conservation interests (Stillman and Wood, 2015). The key challenge facing managers and decision-makers at such sites is how to ensure that enough shellfish are left unharvested to allow the birds to meet their food requirements, whilst enabling a viable shellfishery to exist.
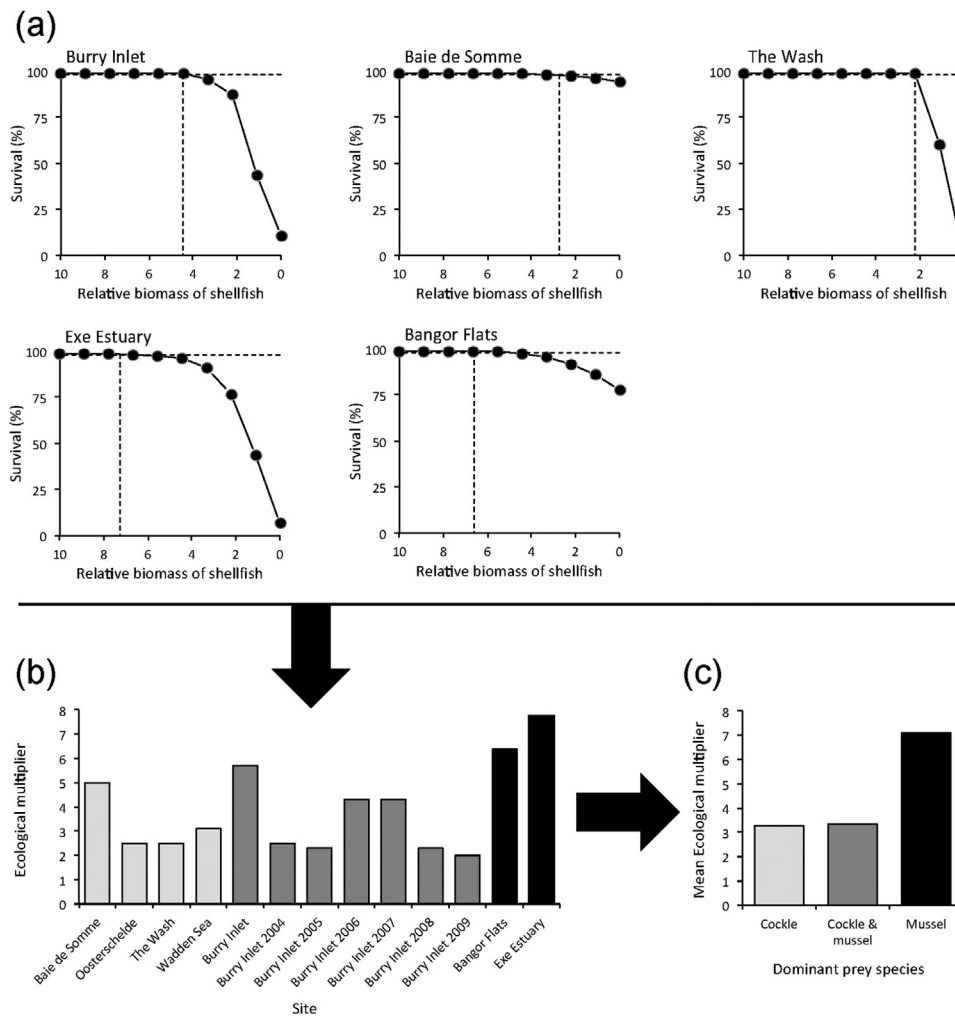
Fig. 2. Deriving simple predictions from shorebird IBMs. (a) Effect of changes in shellfish biomass on the predicted non-breeding season survival rate of oystercatcher in five sites (data from Goss-Custard et al., 2004). Shellfish biomass is expressed per bird and is relative to the amount actually consumed by the birds (e.g. a relative biomass per bird of 2 means that twice as much food is present at the start of simulations than will be consumed by the birds. The horizontal broken lines show a survival rate of 98% and the vertical broken lines show the relative biomass at which predicted survival falls below 98%. This is termed the ecological multiplier and measures the amount of food that needs to be reserved for the birds relative to the amount they actually eat. (b) Predicted and observed values of the ecological multiplier on different sites (data from Table 1). The shading of bars indicates the predominant shellfish species on the site: black – mussels; dark grey – cockles and mussels; light grey – cockles. (c) Mean value of the ecological multiplier in relation to the predominant prey species. These values can be used to advise the management of shellfisheries taking into account the dominant shellfish species.

Shellfishing has a range of effects on coastal birds, some negative and some positive (Goss-Custard et al., 2000; Caldow et al., 2004). Mussel and cockle fishing removes the large-sized shellfish which are also eaten by oystercatcher, and hence reduces the amount of food available to them (Smit et al., 1998). Shellfish harvesting may also reduce the densities of non-target invertebrate species consumed by the birds (e.g. Masero et al., 2008). If shellfishing occurs at low tide when shorebirds are feeding, it can also disturb them and force them to spend energy flying away or to move to poorer quality habitat (Stillman and Goss-Custard, 2002; Goss-Custard et al., 2006). By contrast, when artificial shellfish beds are created in the intertidal zone by dredging mussels from deep waters, the amount of food available to birds is increased (Atkinson et al., 2005). Damaged shellfish left in intertidal areas after harvest can also provide good feeding for birds. The effects of shellfishing can be simulated by changing the abundance of the food supply (to account for depletion or the creation of new beds), or by excluding birds from all or part of some patches (to account for disturbance).

IBMs were originally designed to address this issue for oystercatchers feeding on mussels on the Exe Estuary, UK, and have since been applied to many sites (Stillman and Goss-Custard, 2010;

Stillman and Wood, 2015). Accurate predictions of bird survival, foraging effort and distribution have been derived from these models and they have been used widely to support shellfishery management in several shellfisheries within the UK, including the Solway Firth, Morecambe Bay, Dee Estuary, Menai Straights, Burry Inlet, Three Rivers, Exe Estuary and the Wash (Stillman and Goss-Custard, 2010; Stillman and Wood, 2015; Stillman et al., 2015). However, as with other IBMs, these models have been limited to use by modelling specialists, and so a simpler option available to non-specialists is needed.

A primary aim of shellfishery management is to reserve sufficient food for the birds such that they can survive the non-breeding season in good condition (Smit et al., 1998; Stillman and Wood, 2015). Environmental change in this sense is being caused by the amount of food harvested by shellfishing. The amount of shellfish required to support shorebird populations has been predicted by running simulations with varying amounts of shellfish food, which simulates environmental change caused by differing amounts of shellfish harvesting (Fig. 2a). The number of birds varies between sites, and hence so does the total amount of food required by the birds. To account for this, shellfish biomass can be expressed per

Table 1
A comparison of the physiological and ecological food requirements reported in the literature (Stillman and Wood, 2013). Following the method of Ens (2006) the kg AFDM estimates of Goss-Custard et al. (2004) and Stillman et al. (2010) were transformed to kg wet flesh, assuming that 1 kg wet flesh corresponded to 0.041 g AFDM (Ricciardi and Bourget, 1998).

Location of study	Type of study	Dominant prey species	Physiological requirement (kg bird^{-1} winter^{-1})	Ecological requirement (kg bird^{-1} winter^{-1})	Ecological multiplier	References
Baie de Somme (France)	Modelling	Cockle	85	424	5.0	Goss-Custard et al. (2004)
Oosterschelde (Netherlands)	Empirical	Cockle	146	366	2.5	Rappoldt et al. (2003a)
The Wash (England)	Empirical and modelling	Cockle	102	256	2.5	Goss-Custard et al. (2004), Stillman et al. (2003)
Wadden Sea (Netherlands)	Empirical	Cockle	159	488	3.1	Rappoldt et al. (2003b)
Burry Inlet (Wales)	Modelling	Cockle & mussel	100	566	5.7	Goss-Custard et al. (2004)
Burry Inlet 2004 (Wales)	Modelling	Cockle & Mussel	54	134	2.5	Stillman et al. (2010)
Burry Inlet 2005 (Wales)	Modelling	Cockle & Mussel	54	122	2.3	Stillman et al. (2010)
Burry Inlet 2006 (Wales)	Modelling	Cockle & Mussel	54	232	4.3	Stillman et al. (2010)
Burry Inlet 2007 (Wales)	Modelling	Cockle & Mussel	54	232	4.3	Stillman et al. (2010)
Burry Inlet 2008 (Wales)	Modelling	Cockle & Mussel	54	122	2.3	Stillman et al. (2010)
Burry Inlet 2009 (Wales)	Modelling	Cockle & Mussel	54	110	2.0	Stillman et al. (2010)
Bangor Flats (Wales)	Modelling	Mussel	100	641	6.4	Goss-Custard et al. (2004)
Exe Estuary (England)	Empirical and modelling	Mussel	100	783	7.8	Goss-Custard et al. (2004)

bird and relative to the amount of food actually consumed by the birds (Fig. 2a). In each site the predicted survival rate decreases after a threshold food biomass has been reached. This threshold is termed the *ecological multiplier*, and measures the amount of food that needs to be reserved for the birds (termed the *ecological requirement*) relative to the amount they actually eat (termed the *physiological requirement*).

Table 1 and Fig. 2b show values of the ecological multiplier derived from a combination of modelling and empirical studies. Importantly, all of the ecological multiplier values exceed one, reaching 7.8, indicating that in order to maintain high survival rates, more food needs to be reserved for the birds than the amount they actually eat. This is because birds are not able to find all the food, some birds can exclude others from part of the food supply through interference competition, and some food is lost due to factors other than the birds themselves (e.g. predation by crabs; McGrorty et al., 1990). The value of the ecological multiplier depends at least partially on the predominant shellfish species within a site (Fig. 2c). In sites dominated by cockles, or with an approximately equal amount of cockles and mussels, the mean value of the ecological multiplier is 3.3, whereas in sites dominated by mussels the mean value is 7.1. Thus, relatively more food needs to be reserved in mussel-dominated sites. This is because more birds can be excluded through interference competition from highly aggregated mussel beds than from more dispersed cockle beds (Goss-Custard et al., 2004).

The ecological multiplier varies between sites, even if they have a similar composition of cockles and mussels (Table 1). Although the values are given above (i.e. 3.3 and 7.1) are based on the mean value of the ecological multiplier in cockle- and mussel-dominated sites, and alternative would be to use the highest values (i.e. 5.7 and 7.8). This would lead to a precautionary prediction of the amount of food required by the bird population.

The ecological multiplier allows the biomass required to maintain high oystercatcher survival rates (the ecological requirement) to be calculated across a range of sites from the amount consumed by the birds (the physiological requirement).

Ecological requirement

= Ecological multiplier × Physiological requirement

The ecological multiplier can be calculated from the predominant prey species in a site. The physiological requirement can be calculated from the size of the oystercatcher population on a site, the length of the non-breeding season, and daily food consumption of the birds (which in turn can be calculated from standard equations relating daily energy expenditure to body mass, and the energy value of the food).

Physiological requirement

= Number of birds × Number of days × Daily food consumption

These equations can be used by stakeholders without specialist modelling experience and using the type of data typically available from shellfisheries. They are based on a range of biological parameters, including bird population sizes, the energy requirements of the birds, and the energy content of shellfish. Many of these parameters are routinely collected as part of the management of shellfisheries and conservation of shorebird populations, and so do not need to be measured for each new site. Crucially though the ecological multiplier is derived from the predictions of IBMs, supported by empirical data, across a range of sites. The stakeholders do not need to run these IBMs, but can still use their predictions when calculating the food requirements of the birds.

Fig. 3 shows how these steps can be used to provide the evidence-base for the management of shellfisheries. First, the ecological multiplier, in combination with the physiological requirement, can be used to determine the amount of shellfish biomass that needs to be left unharvested to maintain high survival rates of the birds (i.e. the ecological requirement; Fig. 3a). This amount can then be compared with the amount actually available to determine the maximum amount that could be harvested by shellfishing without adversely affecting the birds (Fig. 3b). Three possibilities exist: (i) if stocks are low relative to the requirements of the birds (horizontal lines on left of Fig. 3b), shellfishing should not proceed as any reduction in shellfish biomass is likely to adversely affect the birds; (ii) if stocks are high relative to the requirements of the birds (diagonal lines to right of Fig. 3b), an appropriate total allowable catch can be set without adversely
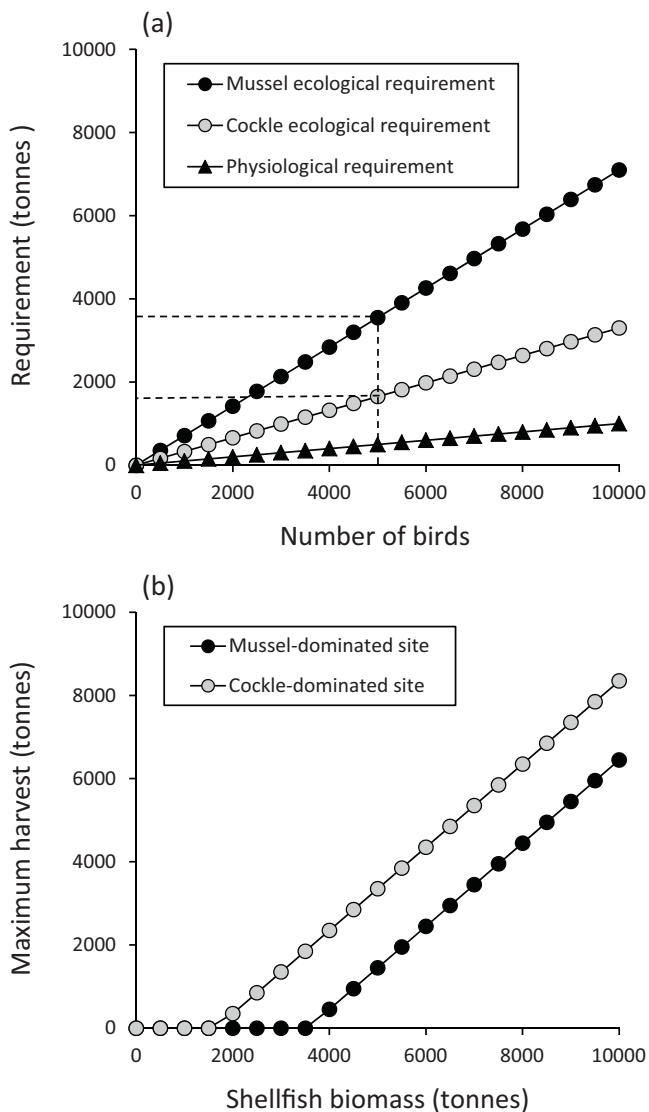
Fig. 3. How simple predictions can be used to support shellfishery decision making. (a) The ecological multiplier can be used to assess the amount of food that needs to be reserved for birds to maintain high survival rates. In this case each bird is assumed to consume 100 kg wet mass of shellfish during the non-breeding season (i.e. the physiological requirement). The horizontal broken lines show the ecological requirement for a population size of 5000 birds on cockle- and mussel-dominated sites. (b) The maximum harvestable biomass (vertical axis) is calculated from the total biomass available (horizontal axis) minus the ecological requirement (in this case that for a population size of 5000 birds).

affecting the birds; (iii) with total allowable catches close to the maximum, more detailed and site-specific modelling is required to determine more precisely whether or not shellfishing can proceed without adversely affecting the birds.

To date this approach has been used to inform shellfishery management at sites within the UK, including The Wash, Morecambe Bay, Burry Inlet, Solway Firth, and Exe Estuary (Stillman and Wood, 2015). This simplified approach provides a straightforward way of quantifying the amount of food required by a bird population and hence offers shellfishery managers an evidence-based means of managing shellfisheries.

5. Discussion

Complex models can be needed to address complex problems, but non-modelling specialists can have difficulty interpreting the results of such models. This limits the extent to which these models can be used to support environmental decision-making (Addison et al., 2013). The approach highlighted in this paper uses complex models to produce simple predictions that can be understood and interpreted by stakeholders without any modelling experience.

The shorebird and wildfowl individual-based models incorporate more structural realism than more simplistic regression- or population-based models. This was necessary because environmental change can influence these birds in several ways including changes to the distribution, abundance and tidal availability of their prey, the energy requirements, foraging efficiency and distribution of the birds themselves (Stillman and Goss-Custard, 2010). Shellfishing in particular can influence the birds by reducing the abundance of their prey, and by excluding birds from parts of their intertidal feeding habitat (Smit et al., 1998). Importantly, the models incorporated the fitness maximising behaviour of the birds; model birds chose to feed on the patches and prey that maximised their rate of energy assimilation. This meant that the model birds responded to changes in their environment in ways that are expected to mimic the behaviour of real birds. The model predictions emerge from the physiology and fitness-maximising behaviour of the model birds. These predictions included the distribution of the birds, their survival rates and the amount of shellfish required to maintain high survival rates of the birds.

One extremely important insight arises from the predictions of the shorebird IBMs; the amount of shellfish required to be reserved for high survival (the ecological requirement) was greater than the amount actually consumed by the birds (the physiological requirement). This was because the model birds, as real birds, could not find all of the available food, some birds were excluded from some of the prey by competition, and other factors were reducing food abundance. Although this fact may seem obvious once stated, it has not been recognised in previous management of shellfisheries with serious consequences for the birds. For example, until recently, the policy in The Netherlands for regulating shellfishing within coastal protected areas had been to ensure that 70% of the food requirements of shellfish-eating birds, such as the oystercatcher, remained after harvesting, on the grounds that the remaining consumption would be provided by alternative prey, such as polychaete worms and other bivalves (Camphuysen et al., 1996; Lambeck et al., 1996; Smit et al., 1998). The shorebird IBMs predicted that this provision was inadequate and accounted for the decline in the numbers of these birds in The Netherlands during the last two decades (Goss-Custard et al., 2004), and the observed mass mortality events over this period winters with low shellfish abundance (Camphuysen et al., 1996; Verhulst et al., 2004). The policy has now changed so that much more of the shellfish stocks are reserved for the birds.

Why was it possible to produce simple predictions from the shorebird and wildfowl IBMs? First, the question that these models are designed to answer is itself simple, even if answering it is not. They predict whether a specific amount of environmental change (e.g. due to sea level rise, habitat loss or changes in prey abundance) will reduce the survival rate and body condition of the birds. More broadly, they predict whether environmental change has an adverse effect on ecosystems. Many conservation problems can be expressed in these terms, and so the threshold approach adopted in this paper could potentially be applied much more widely if suitable means of predicting or measuring effects on individuals, populations, communities, or ecosystems could be found. Second, it was possible to understand why the amount of environmental change leading to an adverse effect varied between sites. This depended on the predominant shellfish species within a site and hence, though the aggregation of the prey, the extent to which some birds could be excluded from their prey through interference competition (Goss-Custard et al., 2004). Third, the data required to understand the effect of environmental change on the

birds is routinely collected on many shellfisheries for monitoring and management purposes. These data include: (i) the biomass of shellfish, which is measured as part of shellfishery management; (ii) the population size of the birds, which is monitored in many sites; and (iii) the physiological requirement of the birds, which can be calculated from body size and prey quality.

We believe that using models to identify threshold values for environmental perturbations could be used more widely to inform management of species and habitats subject to environmental change. Whilst we have developed our modelling approach to inform coastal bird population management, there is no reason why such an approach could not be applied more widely to a greater range of environmental issues. Such issues could include the management of populations in the face of anthropogenic disturbance, sea level rise, habitat loss, changes in food abundance, disease outbreaks, and invasive species (Sutherland et al., 2012; Maclean, 2014). A logical next step would be to apply this approach of identifying thresholds of environmental change to other environmental issues for which IBMs are currently being used. For example, IBMs which predict bird responses to habitat loss could be used to identify threshold values of habitat loss associated with population decline (Toral et al., 2012). As a second example, where the ecological impacts of pests or invasive species are a concern to wildlife managers, IBMs could be used to identify threshold densities of individuals associated with such negative impacts (Wood et al., 2014).

In this paper we have shown how simple predictions can be used to inform environmental decision-making for complex ecological systems. Although our examples were restricted to shorebirds and wildfowl, the general framework of predicting thresholds of environmental change leading to negative effects could be applied to any ecosystem.

Acknowledgements

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