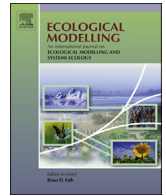




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Deriving simple predictions from complex models to support environmental decision-making

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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.

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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

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