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Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK

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ABSTRACT

Regime shifts in benthic invertebrates within coastal ecosystems threaten the survival of wading birds (Charadrii). Predicting how invertebrate regime shifts will affect wading birds allows conservation management and mitigation measures to be implemented, including protection of terrestrial feeding areas. An individual-based model was used to investigate the impact of regime shifts on wading birds through their prey (marine worms and bivalves) in the estuarine system Poole Harbour, (UK). The model predicted the number of curlew (*Numenius arquata*), oystercatcher (*Haematopus ostralegus*), black-tailed godwit (*Limosa limosa*), redshank (*Tringa totanus*) and dunlin (*Calidris alpina*) supported in the Harbour during the non-breeding season (autumn and winter months). The most dramatic declines in bird numbers were for regime shifts that reduced the abundance of the largest invertebrates, particularly marine worms. The least adaptable bird species (those with the most restrictive diets) were unable to compensate by consuming other prey. Generally, as birds adapt to changes by switching to alternative prey species and size classes, changes in invertebrate size and species distribution do not necessarily affect the number of birds that the Harbour can support. Our predictions reveal a weakness in using birds as indicators of site health and invertebrate regime shifts. Differences in bird populations would not necessarily be detected by standard survey methods until extreme changes in invertebrate communities had occurred, potentially beyond the point at which these changes could be reversed. Therefore, population size of wading birds should not be used in isolation when assessing the conservation status of coastal sites.

1. Introduction

With an increasing risk of rapidly changing environmental conditions and extreme weather events, there is a high probability of the size of individuals and the magnitude and diversity of ecological populations shifting dramatically. These 'regime shifts' mark the rapid change between different system states and can impact higher trophic levels within an ecosystem (Kraberg et al., 2011). Within marine and intertidal ecosystems, invertebrates experience both incidences of population loss or range expansion to the potential detriment of other species (Weijerman et al., 2005) and can sometimes benefit from alterations in the habitats allowing species to colonise new areas (Herbert, 2001; Hewitt et al., 2003). Changes in temperature (Beukema, 1990; Beukema et al., 2009; Bhaud et al., 1995) and the impact of sewage outflows (Alves et al., 2012) are examples of events that impair and benefit invertebrate populations respectively. Such regime shifts are likely to impact upon wading birds (Charadrii) due to the different types and size of invertebrates that each species forages upon (see Table 4 and Goss-Custard et al., 2006b). Waders are dependent on specific size categories of invertebrates, with some more generalist than others (greater numbers of species and sizes eaten), and any shift in prey species abundance or size range could cause a loss of available food (Cayford, 1993). At the top of the food chain birds are used as indicators of the health of an ecosystem and as a consequence many feeding areas are protected (Fernández et al., 2005). In particular, wading birds are often used as sentinels of environmental change and indicators of pollutants, as increases and decreases in their populations have been linked to changes in the prey biomass (Furness, 1993).

Regime shifts affecting coastal birds have been described in addition to moderate population changes associated with the availability of their preferred prey. In the Wadden Sea (Netherlands), the loss of mussel beds has been linked with declines in molluscivorous birds and subsequent increases in worm-eating birds from growth in polychaete numbers (Piersma, 2007; van Roomen et al., 2012; van Roomen et al., 2005; Weijerman et al., 2005). The Wash in

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the UK has also seen a shift to more worm-eating waders alongside declines in bivalve eating waders after losses in bivalve populations (Atkinson et al., 2010). In addition to anthropogenic causes, cold winters in the late 1980s reduced invertebrate stocks in the Wadden Sea (Beukema, 1990, 1992) and during the 1990s increases in salinity led to reduction in benthic vegetation in a costal lagoon in western Denmark that decreased bird numbers (Petersen et al., 2008). A regime shift was seen in Alaska where piscivorous birds reduced after an upwards temperature shift changed fish composition and the Exxon Valez oil spill put extra pressures on the system (Agler et al., 1999). In the mid-2000s large polychaetes increased near sewage outlets in the Tejo estuary, Portugal increasing the numbers of birds that could be supported on these areas (Alves et al., 2012).

In general the specific types of shifts that may affect wading birds include the loss of individuals at the lower and upper ends of prey size range (Kraberg et al., 2011), removal of entire prey species or family (Atkinson et al., 2010; Strasser et al., 2001) and increases in new or formerly under represented prey (Caldow et al., 2007). Increases in fishing for molluscs and bait-collecting for marine worms will also remove the larger sizes of invertebrates and older breeding stock and thus potentially reduce the overall population numbers (Olive, 1993). In other cases, pollution, toxicity and temperature fluctuations in an environment can impinge on recruitment and cause a loss in the smaller sizes of invertebrates; though in the short term it can add nutrients to a system and increase invertebrate numbers (Alves et al., 2012; Olive and Cadnam, 1990). This investigation becomes important when considering the resilience of a system to such changes, as it has been proposed that to reduce the risk of regime shifts we should investigate gradual changes that could potentially lead to catastrophic shifts (Folke et al., 2004).

Understanding how animals might respond to prey regime shifts can be achieved through field experiments and observations but this can be time consuming and often takes several seasons of field work before useful management conclusions can be made concerning their impacts on both waders and their habitats (Deyoung et al., 2008; Goss-Custard and Stillman, 2008). Modelling provides an attractive alternative and, in particular, individual-based models (IBMs) have been shown to produce accurate predictions that can advise conservation decision making (Goss-Custard et al., 2006a; Grimm and Railsback, 2005; Grimm et al., 1999; Stillman and Goss-Custard, 2010; Stillman et al., 2007). IBMs follow fitness-maximising procedures to allow individual model birds to act independently over the course of a season and provide an ecosystem view that is closer to reality than analytical models such as differential-equation or matrix models (Stillman, 2008). They can also be manipulated quickly to provide answers to a range of conservation questions from only a single season of invertebrate data collection.

In this paper we will explore how regime shifts in invertebrate populations can affect the survival of five species of wading birds in Poole Harbour, UK using a validated IBM of the site. We investigated the following types of regime shift:

(i) complete loss of a prey species,
(ii) directional (loss from either smaller or larger ends of prey size classes),
(iii) divergent and convergent (bi-directional loss of prey size classes).

We predict that birds will respond to invertebrate regime shifts through alterations to the range of prey species and sizes included in their diets. We also discuss the consequences of regime shifts for the numbers of birds supported by the site. From our hypothesised outcomes we expect to find that when prey size ranges are reduced, birds will switch to less preferred species which will (a) decrease the number of birds that can be supported in the area and (b) change the composition of the bird feeding assemblage.

2. Materials and methods

2.1. Study area

In the south of the UK, Poole Harbour hosts large numbers of coastal birds during the non-breeding season and at 36 km^2 it is one of the largest estuarine systems in Europe (JNCC, 2008). Designated a Special Protection Area (SPA) in 1999, it also contains several Sites of Special Scientific Interest (SSSIs), is a Ramsar site and is recognised as supporting important numbers of coastal birds during the non-breeding season. Furthermore, the Harbour contains much activity with shipping, fishing and recreational activities occurring throughout the year which have increased since its industrialisation in the early 20th century (Humphreys and May, 2005).

Non-breeding bird populations are protected by national and international conservation legislation, notably the EU Birds Directive (European Community, 2009). The species that provide the internationally important bird numbers during winter and that have given Poole Harbour its SPA status include black-tailed godwit (*Limosa limosa islandica*), avocet (*Recurvirostra avosetta*) and common shelduck (*Tadorna tadorna*). In addition, dunlin (*Calidris alpina*), redshank (*Tringa totanus*) and curlew (*Numenius arquata*) are also present in nationally important numbers (English Nature, 2000). Oystercatchers (*Haematopus ostralegus*) are considered in this study due to being present in large, though not internationally important numbers (Holt et al., 2012) and taking into account their regional importance.

2.2. The model

We used a pre-existing model of Poole Harbour (Durell et al., 2006) designed in MORPH (Stillman, 2008) which predicts the numbers of birds supported at the end of the non-breeding season due to the closed nature of the model compared with the real world where birds can move to different regions when faced with starvation. This model was validated against field observations from the British Trust for Ornithology's Wetland Bird Surveys (Durell et al., 2006).

The model incorporated invertebrate survey data collected in 2002 (Caldow et al., 2005; Thomas et al., 2004) from a grid of 80 sample sites across the intertidal mudflats. In addition, forager parameters were added for the five species that are characteristic of the Harbour's wading birds; the parameters for both the invertebrates and birds were drawn from both the literature and field studies and are referenced in Durell et al. (2006). Table 1 shows the parameter values used in the model.

All parameter values (except the modified invertebrate populations) were unchanged from those in the original paper and run for the same length of time – hourly for 212 days between 00:00 1st September and 23:59 31st March. The five types of foragers were similarly kept the same for continuity with the original model. A parameter file was checked and re-parameterised (to conform to the parameters listed in Durell et al., 2006) with the values listed in the original paper and then run several times to confirm that the predictions in the original paper were reproduced.

Many IBMs are developed for a single purpose, such as to understand one environmental change event. In this paper, we show that these pre-existing models and new models can be used to understand additional scenarios such as the impacts of invertebrate regime shifts on wading birds.