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.
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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 km² 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.

Table 1
Invertebrates represented in each resource in the model (Durell et al., 2006).

Name of Resource	Latin names of invertebrate prey species included in the survey (all Latin names correct in March 2014 WoRMS Editorial Board (2014))		
Worms & Little Worms (Marine polychaeta, oligochaeta and Nemertea)	*Hediste diversicolor* *Alitta virens* *Nephtys hombergeii* *Arenicola marina* *Scoloplos armiger* *Harmothoe* spp. *Polycirrus caliendrum* *Ampharete grubei*	*Glycera tridactyla* *Phyllodoce mucosa* *Eteone longa* *Malacoceros fuliginosus* *Scolelepis squamata* *Scolelepis foliosa* *Pygospio elegans* *Spio* spp.	*Cirriformia tentaculata* *Aphelochaeta filiformis* *Capitella capitata* *Heteromastus filiformis* *Tubificoides* spp. Nemertea spp.
Worm size classes (mm)	0–4.99, 5–14.99, 15–29.99, 30–44.99, 45–59.99, 60–74.99, 75–89.99, 90–104.99, 105+		
Crustacea including *Cyathura*	*Gammarus locusta* *Microdeutopus gryllotalpa* *Corophium volutator*	*Corophium arenarium* *Urothoe poseidonis* *Cyathura carinata*	
Bivalves	Cerastoderma edule	Venerupis philippinarum	Abra spp.
Bivalve size classes (mm)	5–9.99, 10–14.99, 15–19.99, 20–24.99, 25–29.99, 30–34.99, 35–39.99, 40–44.99, 45–49.99, 50–54.99		
Peringia	*Peringia ulvae*		
Earthworms	Terrestrial oligochaeta		
Earthworm size classes (mm)	5–14.99, 15–29.99, 30–44.99, 45–59.99, 60–74.99, 75–89.99, 90–104.99, 105+		

Table 2
Modified parameter files and changes to invertebrate size classes.

Modification	Invertebrate size classes available to waders (x = changed value)
No worms	All bivalves
No bivalves	All worms
Reducing maximum worm size available	$0 - x$ mm in length available
Reducing maximum bivalve size available	$0 - x$ mm in length available
Increasing minimum worm size available	$x - 105 +$ mm in length available
Increasing minimum bivalve size available	$x - 54.99$ mm in length available
Convergent worm biomass size	Losing largest and smallest classes sequentially
Convergent bivalve biomass size	
Divergent worm biomass size	Losing middle classes outwards
Divergent bivalve biomass size	

Table 3
Explanations of the regime shifts simulated in the parameter files.

Modification to invertebrate size classes	Regime shift simulated
No worms or bivalves	A shift that removes all one phylum from an ecosystem and the other phylum survives. (Extinction)
Reducing maximum size available	This represents the effect of overfishing, over predation or the after effects of a population recovery after a total crash. (Negative directional shift)
Increasing minimum size available	After a recruitment failure smaller size classes would be lost and increasing it shows the effects over multiple years. (Positive directional shift)
Convergent biomass size	When two of the above scenarios occur together i.e. both overfishing and recruitment failure
Divergent biomass size	As above, the combined effect of recovering populations after a failure to reproduce or overfishing/predation of certain sizes

2.3. Parameterisation

To simulate regime shifts the model's invertebrate populations were changed to represent different distributions of size classes of worms and bivalves. Within the model there are six different types of resource – Worms, *Cyathura* (crustacea: isopoda), Crustacea (other than *Cyathura*), Bivalves, *Peringia* (mollusca: gastropoda) and terrestrial Earthworms (see Table 1). Of these resources Worms, Bivalves and Earthworms are divided further into size classes (9, 10 and 8 classes respectively) and this provided the means to simulate a regime shift within invertebrate populations. We only manipulated Worms and Bivalves to simulate regime shifts as these are the main elements of the five wader's diets. The smaller phylum Nemertea was combined with the larger phylum Annelida as they were uncommon in our invertebrate survey and individually made little difference to the final output.

The modified parameter files contained changes to the invertebrate numbers per m^2 (Table 2) each simulating a type of regime shift (detailed in Table 3). The total invertebrate biomass, measured in ash-free dry mass (AFDM), was either retained or not retained in each model. When retained, the biomass of excluded size classes was redistributed across the remaining size classes in proportion to their biomass. This prevented any reduction in supported bird numbers being due to reduced biomass rather than the distribution of biomass between invertebrate species and size classes.

The simulated regime shifts in Worms and Bivalves (see Table 3.) represented either *phylum extinction* or changes in size distribution. Four changes in size distribution were simulated: *positive regimes shift* – loss of shortest individuals leading to increased mean size; *negative regime shift* – loss of largest individuals leading to decreased mean size; convergent regime

Table 4
Dietary preferences of the five wader species modelled in this investigation. Adapted and simplified from Durell et al. (2006) (developed from Goss-Custard et al. (2006b)). The values are in mm size classes where '<' indicates prey are taken from the smallest available item to a set value (minimum), and '+' indicates that the birds take sizes up to the maximum length present in the sediment.

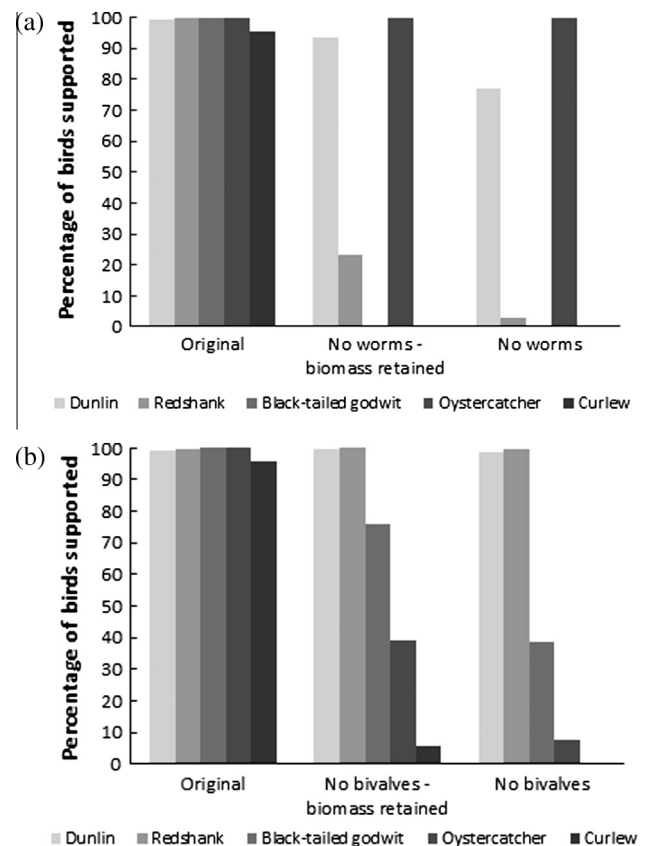| Diets eaten	Dunlin	Redshank	Black-tailed Godwit	Oystercatcher	Curlew
Small worms <30mm	✓				
Medium worms 30-59.99mm	✓	✓	✓	✓	
Large worms 45+mm		✓	✓	✓	✓
Crustacea 3+mm	✓	✓			
Small bivalves 5-9.99mm	✓	✓			
Medium bivalves 10-19.99mm			✓		✓
Large bivalves 20+mm				✓	
Peringia 3+mm	✓	✓			
Small earthworms 15-29.99mm	✓	✓			
Medium earthworms 30-59.99mm		✓	✓	✓	
Large earthworms 45+mm			✓	✓	✓

shift – removal of shortest and largest individuals leading to reduced size distribution; divergent regime shift – loss of intermediate sized prey leading to a population of smaller and larger individuals.

Each scenario was run five times from which average predictions were calculated. The key prediction was the mean number of birds supported at the end of the non-breeding period (Table A1). The mean number of foragers consuming each diet was also compared to the original values to understand how bird's diets changed between scenarios. Our confidence in the predictions of these models is supported by the validation of the Poole Harbour model in this study, and the accurate predictions produced by similar models of other coastal wader populations (Stillman and Goss-Custard, 2010). Sensitivity analyses of these models shows that predictions are most sensitive to variation in parameters measuring the gross flow of energy, such as prey intake rate, prey assimilation efficiency and bird energy requirements.

3. Results

3.1. Phylum regime shift: removing a whole phylum

Removing worms from the model entirely and redistributing biomass across bivalves resulted in curlew and black-tailed godwits not being supported (<1% of the starting population survived to the end of the non-breeding season), and redshank being reduced to 23% of their original population (Fig. 1a). Dunlin and oystercatchers were supported with only minimal population reductions compared to the original model values. Without redistribution of biomass, i.e. when the biomass was completely removed from the system; a similar pattern was predicted where dunlin were reduced to 77% of their starting population and oyster-catcher not affected at all. The other species were reduced to less than 5% of their original supported values (Table A1).

Fig. 1. Percentage of birds supported when (a) worms are completely removed and (b) when bivalves are completely removed; both where biomass was retained or not.

Removing bivalves with biomass replacement reduced curlew to 6% of the original numbers, oystercatchers to 39% and black-tailed godwits to 76%. When the biomass was not redistributed, curlew were removed entirely, oystercatchers dropped to 8% and black-tailed godwits to 38% (Fig. 1b). Dunlin and redshank were not affected in either of the scenarios.

3.2. Negative directional regime shift: reducing maximum worm size available

The results of sequentially decreasing the uppermost worm sizes available to wading birds are shown in Fig. 2a. As the maximum invertebrate size range decreased, the survival of bird species reduced in a stepwise fashion. Curlew had a survival threshold (the point at which their survival dropped dramatically) at 0–74.99 mm when they dropped to <5% of their original population (Table A1). Black-tailed godwit were affected at the same point with a slightly slower decline between models ending at <10% supported at 0–54.99 mm. Redshank had an even more pronounced curve starting at 0–59.99 when they dropped below 90% supported and reached <5% population at 0–29.99 mm. Dunlin were also affected but only towards the latter stages of the model sequence, 0–29.99 mm downwards, when they then sat around the 80% supported mark until the end of the model run. Oystercatchers were not affected during this set of models.

Looking at the shifts in percentage of time spent foraging on each diet during the models we can see that, curlew had to increase their intake of earthworms during the reduction in worm biomass sizes (Fig. 2b). Black-tailed godwit follow a comparable pattern as similarly, this bird cannot compensate with other marine invertebrates (Fig. A1a). Redshank become dependent on crustaceans towards the end of the sequence and whilst dunlin also followed the same pattern (Figs. 2b and 1Ac), they were able to forage upon the smallest worms right up until the end which may explain their higher supported values. Oystercatchers foraged
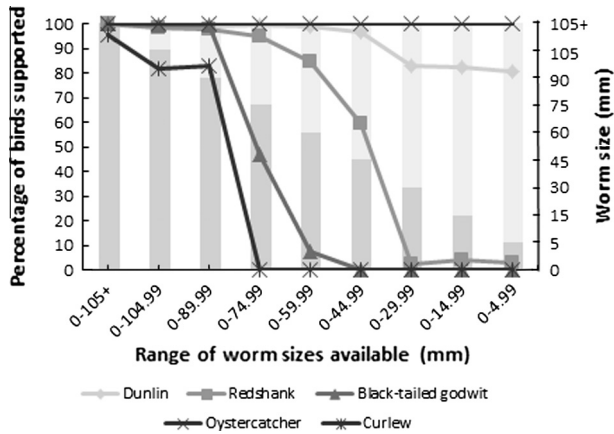

Fig. 2a. Percentage of birds supported with decreasing worm biomass size plotted against a right hand axis showing the biomass of worms present by size and length in each model run (dark grey for present and light grey for removed).

(b)

(c)

Fig. 2b and c. Percentage of diets consumed with decreasing worm biomass size for (b) curlew and (c) redshank.

upon large bivalves at a similar proportion right through the model sequence (Fig. A1e).

Fig. 3. Percentage of birds supported with increasing worm size plotted against a right hand axis showing the biomass of worms present by size and length in each model run (dark grey for present and light grey for removed).
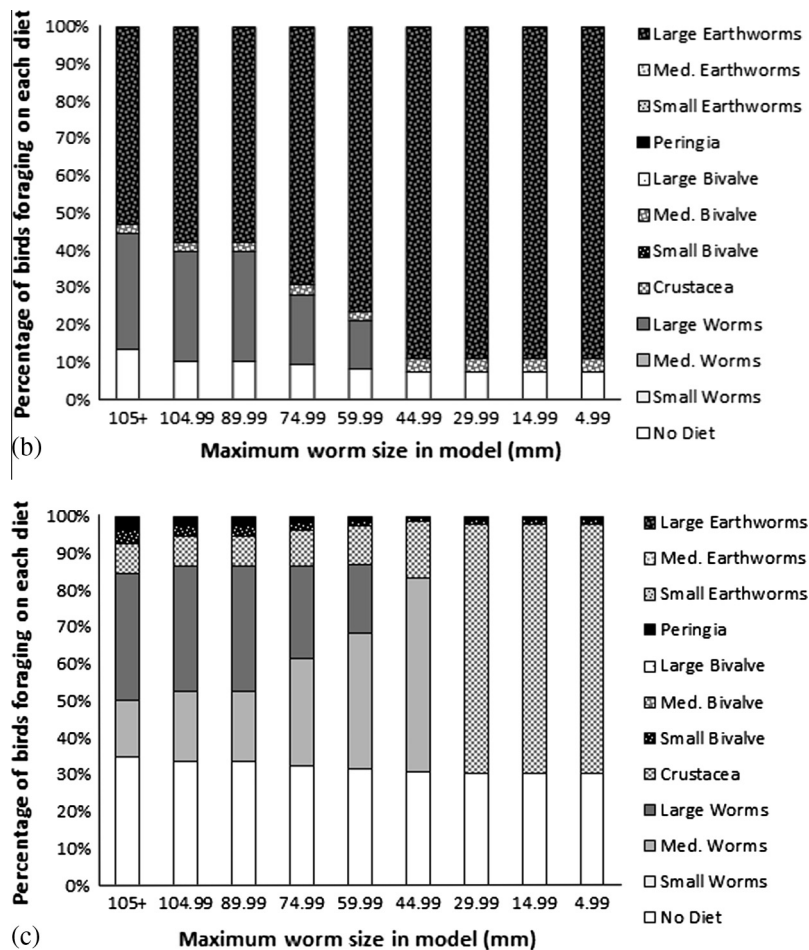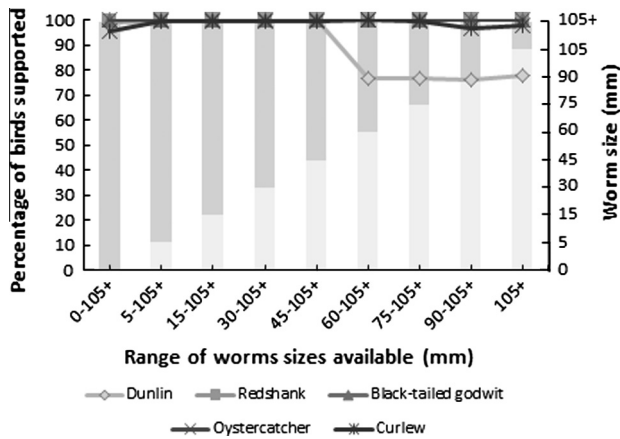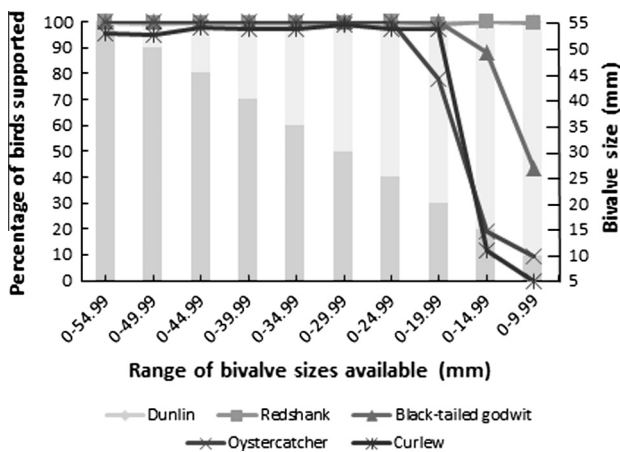

Fig. 4a. Percentage of birds supported with decreasing bivalve biomass size plotted against a right hand axis showing the biomass of bivalves present by size and length in each model run (dark grey for present and light grey for removed).

3.3. Positive directional regime shift: increasing minimum worm size available

Increasing biomass size through raising the lower end of the classes available did not have the same impact as found with decreasing it. Here only dunlin were affected once the range reached 60 mm at its lower end (dunlin dropped to 76–78%, see Fig. 3). In these scenarios curlew did marginally better than the original model, with 1–4% larger final populations (see Table A1).
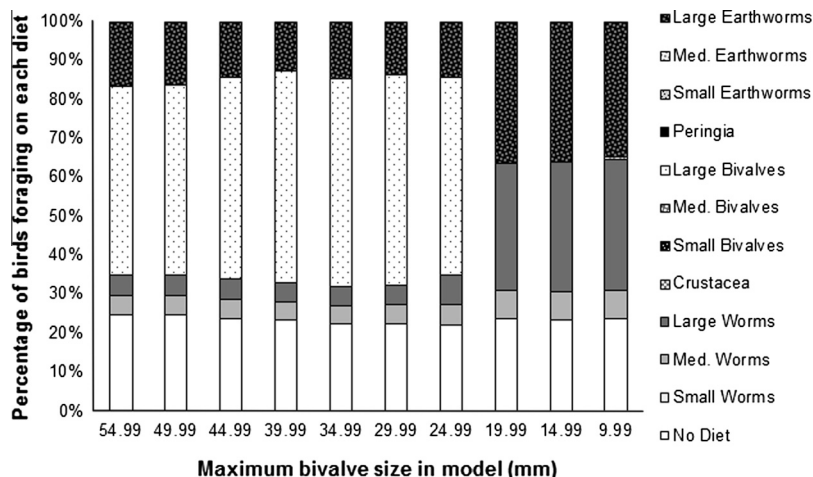
3.4. Negative directional regime shift: reducing maximum bivalve size available

Reducing the upper end of the bivalve size range did not affect species until only the very smallest bivalves were left (Fig. 4a). In contrast to being unchanged during reducing worm size (Fig. 2a), oystercatcher populations were the first affected at 0–19.99 mm when they dropped to 78% supported then quickly down to 19% and 9% at 0–14.99 and 0–9.99 mm respectively. Curlew dropped at 0–14.99 mm to 12% supported before reaching 0 at 0–9.99 mm and black-tailed godwits follow at 0–14.99 mm when they drop to 88% then 43% at the end. Both dunlin and redshank were not affected by more than 0.7% during this set of models (see Table A1).

From the percentage of time spent foraging on each diet (Fig. 4b) we can see that oystercatcher lose all dependence on large bivalves at the 0–19.99 mm size class model and from then on are competing with black-tailed godwit, curlew and redshank for the same resource (large worms). Interestingly, both black-tailed godwit and curlew have almost identical patterns of diet preference throughout the sequence of models tested (see Figs. A2a and A2b).

3.5. Positive directional regime shift: increasing minimum bivalve size available

Curlew are the only species that reduced in supported numbers over the non-breeding season, starting to waver around the 30–54.99 mm model and dropping to 57% when only 50–54.99 mm bivalves are available (Fig. 5). No other species are affected by any more than a 0.6% population drop compared to the original results (see Table A1).

Fig. 4b. Percentage of diets consumed with decreasing bivalve biomass size for oystercatcher.
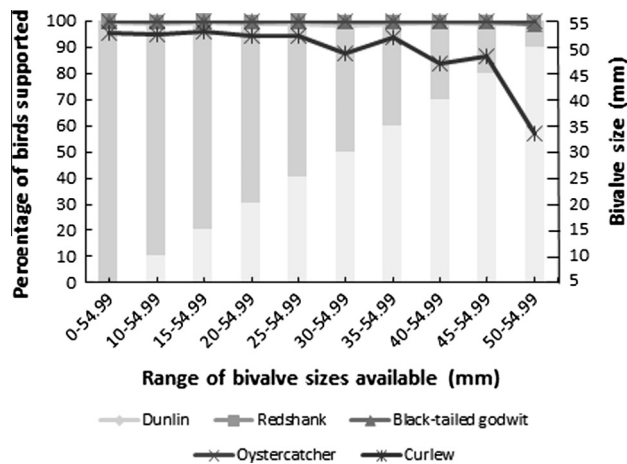
Fig. 5. Percentage of birds supported with increasing bivalve biomass size plotted against a right hand axis showing the biomass of bivalves present by size and length in each model run (dark grey for present and light grey for removed).

3.6. Convergent regime shift: loss of intermediate worm and bivalve biomass sizes

When we removed the outer most size classes, little change was seen with either bivalve or worm scenarios (see Figs. A3a and A3b). Curlews, who have responded the strongest in these experiments, only drop to 92% and 95% respectively in the worm and bivalve based models.

3.7. Divergent regime shift: loss of largest and smallest worm and bivalve biomass sizes

When the innermost size classes were removed slightly more of an effect than the above models is seen (Figs. A3a and A3b). Here you can see in Fig. A4a that curlews drop to 38% and 49% in the final two worm models whilst dunlin maintain around 14–17% drop between the final three to support 83–85% of the starting population. Other species dropped a little in their supported numbers, like black-tailed godwit to 88% in the third model (without 15–89.99 mm) but the others fall less than 10%.

When the same is applied to bivalves only curlew drop in numbers to 86% then 52% between the final three models (see Fig. A4b).

4. Discussion

Though it is known that regime shifts occur in estuarine invertebrate populations (Alves et al., 2012; Beukema, 1990; Weijerman et al., 2005) the potential impact of such events on wading birds has yet to be fully understood. In our study we found that larger birds with more specific feeding strategies such as the curlew will be affected first due to their inability to compensate (in terms of prey) on a mudflat alone and having to resort to terrestrial resources which are less profitable (Durell et al., 2006). Other species that are more generalist in their feeding strategies, such as the oystercatcher, survived in almost all simulated scenarios unless there was competition for other resources. In total we predicted how changes to invertebrate species presence and size distribution affected how many birds could be supported during a non-breeding season. The scenarios mimicked regime shifts that may occur in response to environmental change (Alves et al., 2012; Olive, 1993; Olive and Cadnam, 1990; Strasser et al., 2001), and provide insight into the effects that environmental change can have on wading bird populations.

From simulations of complete phylum loss we found that some birds were unable to compensate with other available resources regardless of whether biomass was redistributed or not. It is well known that certain invertebrate species can be susceptible to variations in water chemistry or temperature and thus an incidence of critical change to an environment can occur and remove species quickly in ecological time (De Bettencourt et al., 1999; Strasser et al., 2001). In our extreme scenarios only dunlin and oystercatcher were able to survive when all worms were lost, and redshank and dunlin were supported when bivalves were removed. Though the chance of such dramatic changes are low in a real system, lag effects before a new species expands into an empty niche do occur and may mimic small scale phylum loss (Allendorf and Lundquist, 2003).

The largest prey in wader's diets were found to be the most important, as the regime shifts that had the largest effect on supported numbers were those where the largest invertebrates were lost. These types of shift can occur from losing the oldest worms and bivalves (which are usually the largest), for example from overfishing for recreational angling bait (Goss-Custard et al., 2004; Olive, 1993).

The dietary shifts explained how each species compensated with the loss of preferred prey items. When birds such as curlew and black-tailed godwit were unable to find marine worms to forage upon they both shifted to foraging for earthworms eon fields and this must be considered in any mitigation planning. For example, if it is predicted that there will be a loss of estuarine habitat, and thus marine worms will be reduced, provisions should be taken to make sure that nearby terrestrial habitats, such as agricultural fields, are maintained to support birds that may change their foraging habitat preferences. Redshanks gradually switched to a more crustacean-based diet which would explain their slower reduction in numbers. Along with dunlin, these species would be harder to accommodate for; as unlike the species that require greater access to terrestrial habitats and fields, mitigation would need to be considered in development proposals. In previous observations redshank only forage on fields at high water in winter (Goss-Custard, 1969) as have dunlin (Morrison, 2004; Ruiz et al., 1989).

Losing the largest bivalves in a system could occur in similar ways to those explained for marine worms. For example tributyltin (TBT) contamination in Poole Harbour removed some larger bivalve species (e.g. *Scrobicularia*) through endocrine disruption leading to successive recruitment failures (Beaumont et al., 1989; Langston et al., 1990). Shell-fishing measures could reduce the minimum permitted size of harvested bivalves (Stillman et al., 2003) thus removing the largest and most profitable prey and forcing waders to forage for smaller sizes to compensate. From this investigation no detrimental effects were seen until the more extreme modelled scenarios, when only the smallest size ranges were available. At this point, with only small bivalves present, the oystercatcher population was most affected; decreasing to its lowest level in any scenario modelled.

From the dietary changes in the modelled birds we could see that although there was little difference in the proportion of curlew and godwit foraging preferences they did switch to medium sized bivalves at the same point that oystercatchers lost their bivalve diet completely and switched to worms. The competition between these species for the largest worms caused the drop in bird numbers supported. Consequently it can be seen how the loss of certain bivalve sizes can impact indirectly on other birds by causing a more efficient and less specific forager to switch from their preferred food source to that preferred by another species (Caldow et al., 2007).

The loss of the smallest invertebrates produced almost no noteworthy changes suggesting that the birds are able to compensate

with other prey within the ecosystem. Whilst this is important to know, it must be recognised that though they have little impact upon bird population numbers, there will be no warning if an invertebrate population collapses from the bottom upwards, with only the largest prey being available. An estuary containing only the largest invertebrates of a species is vulnerable to the loss of that species if there are successive recruitment failures.

As well as registering the importance of predicting decreases in the number of birds supported, the prey shifts which produce the most extreme declines towards the limits of the size classes need to be monitored closely. Due to these 'masking' effects, indicator species from the avian population will not aid in detecting changes in the invertebrate communities and instead other methods will need to be employed such as sediment surveys. We use the term 'masking' to indicate a situation where no change is seen in the observed bird populations whilst major shifts and losses are occur in invertebrates; the stable bird population masks the change in invertebrates.

The impacts of converging and diverging events were found to have little effect after looking at individual regime shifts. When considering converging biomass, all species were able to adequately compensate during the loss of both the largest and smallest size classes. As a result we would expect that even with a slight reduction in invertebrate size classes, little if any change would be noticeable in the numbers of birds that can be supported. As with converging biomass, most species are able to cope when the middle size classes were lost. Curlew, shown to be the most sensitive of the species studied, do suffer a loss in numbers to nearly half of the originally supported population (for both worm and bivalve models), but whether this is adequate for a full recovery in future years is currently unknown.

In both of these shifts, converging and diverging, we must consider the masking effects of these scenarios as seen with increasing losses of small invertebrates. If the regime shift causes a phylum extinction then bird populations will be seriously affected. Yet these effects would be unpredictable from just recording changes in bird numbers alone as the populations would appear to be well supported until the moment of collapse. It is therefore important to monitor birds and invertebrates simultaneously.

These invertebrate regime shifts may occur in many estuarine systems and therefore we need to have both an understanding of how they will affect wading birds and also how they can provide an indication of the health of an ecosystem by understanding their causes. Our research into the effects of regime shifts on wading birds improves our understanding of the potential changes in the numbers of birds an estuary can support. This can inform appropriate management measures e.g. fisheries, bait digging licences and water quality to prevent any loss of birds and lower taxa.

This paper shows that wader numbers alone may not be as good an indicator of ecosystem health as was previously suggested (Atkinson et al., 2003; Fernández et al., 2005) because they change their behaviours first (foraging on fields or marginal areas) before they die. Whilst those wading birds with more generalist foraging habits will have a greater chance of survival, change in invertebrate size distributions will ultimately affect all species. Models allow us to increase our understanding and have the potential for additional work into other aspects of wader foraging preferences, energy requirements and habitat degradation. They deliver useful proxies for the environment that provide quick and fairly accurate thresholds for environmental planning applications that often require quick results or decisions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.02.032.

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