Predicting the effect of environmental change on wading birds: insights from individual-based models

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This thesis has been submitted in partial fulfilment of the
requirements of the degree of Doctor of Philosophy

Bournemouth University in collaboration with HR Wallingford

September 2016

“All models are wrong but some are useful” **–George. E. P. Box**

Abstract

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With the pressures that today's ecosystems are being placed under, from both environmental change and anthropogenic developments, the speed at which management decisions need to be made has increased. Coastal development means that estuaries are particularly affected and their characteristic species, like wading birds (Charadrii), are now experiencing worldwide declines. In such situations there is a need for predictive ecology to understand in advance how species might react to future changes.

This thesis looks into how we can use individual-based models (IBM) to make accurate predictions of how wading birds are affected by environmental change. Starting with previously validated models I show the importance of measuring size of invertebrates though an IBM investigation into regime shifts and wading birds responses. The models show that by altering their diet preferences, birds adapt to regime shifts in their prey but that this maintenance of population size masks the true changes in the system and limits the use of waders as direct bio-indicators of ecosystem health. Using the current literature, an analysis on empirical responses of wader populations to environmental change revealed the lack of comparability between studies and the scarcity of studies on small scale events.

Data from literature and fieldwork was used to develop a comparable suite of individual-based models for five UK estuaries with up to eleven wading bird species. These models were validated using current BTO Wetland Bird Surveys data to increase confidence in final results. Using these new models, investigations of population thresholds and environmental change were carried out. Increases to current populations revealed that several estuaries are no longer able to support the number of birds around the time of Special Protection Area designation. This, alongside higher populations currently seen since the years of designation, indicates the need for re-assessment of

SPA species numbers. When looking at the impacts of two types of environmental change, habitat loss and sea-level rise, certain species declined predictably across sites whilst the individual make up of each estuary had particular impacts on some waders more than others.

The work of this thesis further indicates the great potential of using individual-based models to predict the effects of a wide range of environmental changes. With the new models and a quicker and systematic way of developing IBMs for additional areas, we can aid the conservation and management of estuarine systems for wading birds.

Acknowledgements

I would like to sincerely thank my primary supervisors Richard Stillman and Roger Herbert for all their knowledge, support and guidance through the course of this PhD. Both of them have involved me in fascinating ecological discussions while Richard patiently taught me the intricacies of individual-based models and Roger made sure I know the importance and place of marine invertebrates! Thank you both for your time and encouragement.

I was generously match-funded by HR Wallingford and would like to thank my secondary supervisor John Baugh for his expertise and support with the hydrodynamic modelling. John and his colleagues Diane Jones, Kerry Marten, Tom Benson and Kate Rossington have all taken the time and effort to help make that section of my PhD a lot easier – thank you very much.

Outside of my supervisors I have also been fortunate to have met other researchers who have provided a friendly ear for discussion and advice who I need to thank. In particular John Goss-Custard has given me a lot of ‘food-for-thought’ during our chats both when on fieldwork and via email which helped immensely with several modelling aspects. Greg Murray and Sui Chian Phang both provided me with advice and tips on developing IBMs that helped throughout the PhD process. Mike Pienkowski provided me with some wonderful papers I would not have been able to access whilst Duncan Golicher, Shaun Bendall, Harry Manley and Elena Cantarello all provided technical support for all the new programs, packages and hardware that I needed. Without which this PhD might have taken a lot longer….

For keeping me sane during long days in the office and modelling sessions I would like to thank the IBM club (‘invertebrates, birds and mud’) who have helped talk through issues, suggested new methods and provided laughter when needed – Alice Hall, Ann Thornton, Catherine Collop, Clare Davies, Kathryn Ross, Kevin Wood and Leo Clarke – thank you all! Outside of this bunch lots of other PhDs have made living and working in Bournemouth enjoyable, so thank you all who’ve passed through C232 and in particular the winning quiz team of Hannah Haydock, Emily Norton and Arjan Gosal!

I wouldn’t have made it to this point without the support of many people during my days as a field/research assistant. My first thanks go to Michael Griesser who gave me my first job, and who along with Simone Webber helped set me on this path; they always encouraged me to keep going and provided a good ear to discuss all manner of things. In addition to these two, many other employers have cheered me on and helped develop all manner of field skills – thank you Beryl, Christina, Lucie, Janeene, Tim and Steve as well as their numerous other field assistants. Also to the family and friends who’ve known me for years, thank you all for keeping me cheerful, motivated and active outdoors!

My final thanks go to my parents for always being there to listen to me no matter whether you understood the various technical terms I was using! You've always encouraged me in my goals and chosen career and never let it get to me. As you always said about life 'things happen for a reason'…..

Author's declaration

I confirm that the work presented in this thesis is my own work, with the following exceptions:

Chapter 2 is published in collaboration with Richard A. Stillman and Roger J. H. Herbert as:

Bowgen, K.M., Stillman, R.A. & Herbert, R.J.H. (2015) Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK. *Biological Conservation*, 186, 60-68.

The Exe estuary invertebrate surveys for Chapter 4's suite of individual-based models were obtained via data licence 748 from CEH.

The individual-based models of chapters 2, 4, 5 and 6 used the MORPH individual-based modelling platform created by Stillman (2008).

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Definitions and abbreviations

ABM	Agent-based model (alternative name for IBM)
AFDM	Ash-free dry mass
BTO	British Trust for Ornithology
CD	Chart datum
CEH	Centre for Ecology and Hydrology
IBM	Individual-based model
JNCC	Joint Nature Conservation Committee
LCT	Lower Critical Temperature
OD	Ordnance Datum (at Newlyn, UK)
RPSB	Royal Society for the Protection of Birds
SPA	Special Protection Areas
SSSI	Sites of Special Scientific Interest
Waders	Wading birds (Charadrii)
WeBS	Wetland Birds Survey

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1. An introduction to wading birds, their current status and how individual-based models can answer questions about their ecology.

This chapter introduces the ecology of the study organisms - Charadrii wading birds - and briefly covers the current status of their populations and threats from environmental change. The history and potential of individual-based modelling (IBM) is detailed and its use in wading bird conservation is made clear.

1.1 A changing world

Our world is under pressure. With increasing human populations and decreasing natural resources, people are becoming more aware of their impact on the environment, but finding simple solutions whilst allowing progress has proven difficult (Elliott et al. 2007). To find solutions, or mitigation measures that will preserve and hopefully improve ecosystems, researchers often turn to empirical studies and fieldwork. Whilst these can be used to relate previous events to current issues or to experimentally investigate potential problems, the timescales needed and the high-variability of each environment promotes a need for new, quicker methods.

Estuaries are found along most coastlines and, although of relatively low species diversity, provide highly productive ecosystems (McLusky and Elliott 2004) that are vital for many organisms from algae and invertebrates to larger birds and mammals (Kennish 2002; Dürr et al. 2011). Their importance for wading bird populations cannot be underestimated, as millions of individuals use estuarine sites and other intertidal areas to support themselves during the non-breeding season, if not year-round (van de Kam et al. 2004). Many intertidal sites are protected to preserve the flora and fauna (Davidson et al. 1991; Davidson 2014; JNCC 2016) but still face pressure from anthropogenic and climatic sources. The popularity of the coastal zone for development and trade adds to anthropogenic pressures, as does the growing proportion of the world's population now living in these areas (Kennish 2002; Dürr et al. 2011).

These estuarine systems are therefore likely to be facing future impacts from 'environmental changes'. Various scenarios come under the term environmental change, and with regards to estuarine systems, the impacts of sea-level rise, habitat loss and pollution are the most often considered to affect coastal birds (Robinson et al. 2009; Sutherland et al. 2012; Davidson 2014). These changes have knock-on effects for the species living in these estuaries and the impacts on a single species may affect many more in the local food web (Móréh et al. 2009). There is only a certain amount of environmental change that any system or species can tolerate, and often the impacts of larger shifts are only seen once a limit has been passed (Weijerman et al. 2005; Wethey et al. 2011; Bowgen et al. 2015). Understanding more about the impacts of environmental change will allow for better focused management and conservation measures.

1.2 Wading birds and their threats from environmental change

1.2.1 Current status of Charadrii

Wading birds, also known as 'waders', are a member of the order Charadriiformes along with gulls and auks (del Hoyo et al. 1998). They form their own sub-order, Charadrii, containing species from across the globe that inhabit a range of habitats including the coastal zone (van de Kam et al. 2004). Coastal waders utilise estuaries either year-round or seasonally, taking advantage of the high productivity (Fujii 2012) to maintain their energy levels (Martins et al. 2013). Many species travel vast distances between breeding grounds (Battley et al. 2012) and their non-breeding sites, and face multiple risks to their survival along the way; risks that are potentially being increased by environmental change (Robinson et al. 2009).

Whilst 11.7% of the worldwide Charadrii sub-order fall within the threatened categories in the IUCN Red List (Critically endangered, Endangered or Vulnerable); within Europe only one, the Slender-billed Curlew *Numenius tenuirostris*, is threatened (Birdlife International 2015). That eight other European wading birds are 'near threatened' is a concern, but it is still positive that they have not, as yet, declined enough to be classified as threatened. Within Europe many birds take advantage of the East Atlantic Flyway (Ens et al. 1994; van de Kam et al. 2004), and as such many estuarine sites are linked by the birds' preference for using multiple sites on migration routes (Niles et al. 2008; Hooijmeijer et al. 2013; Martins et al. 2013). More species are present during the non-breeding season (either as residents or during stopovers), and thus this PhD will focus on this period to understand the effects of environmental change.

For waders living on estuarine sites, intertidal invertebrates tend to be their preferred prey (Cramp and Simmons 1983; van de Kam et al. 2004), and they spend the majority of their time foraging during the non-breeding seasons to maintain energy levels before moving on to breed (Pienkowski et al. 1979). The need to understand the impact of environmental change effects on waders is partially driven by their potential status as a bioindicator in estuarine ecosystems

(Furness 1993; Rehfisch et al. 2004) as well as a ‘sentinel of environmental change’ (Piersma and Lindström 2004).

Table 1.1. A summary table of environmental changes that affect wading birds and their environments. For references see sections 1.2.2 and 1.2.3.

Environmental change	**subtype**	**Impacts on wading birds**
Habitat loss	Barrages/dams Port expansions Increasing *Spartina* Loss of fields/meadows Draining of wetlands/marshes	Loss of feeding areas, reduced time for feeding, increased densities of birds (risk of interference)
Shellfisheries	Overfishing Dredging	Loss of invertebrates, disturbance to mudflats for prey development
Sea-level change	Sea-level rise	Reduced foraging area and time to forage
		Shifts in prey communities
Temperature	Warming climate	Reduced metabolic costs
	Colder climate	Increase metabolic costs
	Frozen mudflats	Inaccessible areas
	Reduced tidal amplitude	Prey inaccessible or have reduced energy content
	Prey move away or deeper	
	Prey are less active	
	Prey energy reduces	
Weather	Eroding sediment	Shifts in prey distribution
	Rainfall	Increased invertebrate activity and reduced visibility from rain
	Strong winds	Drying substrates = reduced prey numbers
		Increased handling time from wind
		Increased energy demands from windchill
Pollution	Metals/Toxins	Reduced prey numbers and energy
		Build up of metals and toxins in birds
	Effluent	Increases in prey numbers
	Artificial light	Better visibility for prey, more time to forage
		Increased predation risk
Disturbance	Human origin disturbance	Reduced time for feeding, increased energy costs

The literature is well populated with papers detailing the effects of environmental change on wading birds and their estuaries. Of these, the most prominent studies have looked into environmental change on the loss of time and space to forage, and the shifts in energetic needs to support an individual through the non-breeding season (Table 1.1). Greater detail is provided in a later chapter (Chapter 3) but the initial concepts and research will be briefly presented below.

1.2.2 Threats to wading birds that impact their foraging space and time

A visible impact on estuaries is the loss of habitat, particularly foraging areas through increasing industrial and residential developments. In several areas around the world, coastal intertidal areas and their nearby terrestrial habitats (e.g. fields and meadows) are being lost for new ports and land (for agriculture, industry and housing), flooded from dams/storm-surge barriers or being overrun by plants such as *Spartina sp.* (Goss-Custard and Moser 1988; Lambeck 1990; Morrison 2004; Burton 2006; Yang et al. 2011; Moores et al. 2016). Additional losses may also occur from intensive or unmanaged shellfisheries (Stillman et al. 2003; Goss-Custard et al. 2004; Ens 2006). The impact of overfishing or dredging removes invertebrates and damages the sediment enough to hinder populations of wading birds, in a similar manner to pure habitat loss (Goss-Custard et al. 2004; Atkinson et al. 2010). Some increases in habitat are seen to mitigate environmental conditions (Yozzo et al. 2004; Scarton et al. 2013), but these are not quickly colonised by invertebrates (Mander et al. 2007; French and Burningham 2009). Habitat creation may also provide suitable roosting locations, if sheltered and above the tideline, allowing for more birds to rest safely between foraging bouts, and if closer than previous roost sites allow more efficient energy usage moving between roost and foraging areas (Atkinson et al. 2001).

Sea-level rise from melting ice-caps (Bindoff et al. 2007) also has the potential to reduce foraging habitat. With predictions of increasing temperatures over the next 100 years (Murphy et al. 2009), many areas of the world will find their coastlines shifting. For wading birds, intertidal mudflats and surrounding areas for roosting and breeding are likely to be either lost or be inaccessible for longer periods due to changing tidal cycles (Austin and Rehfisch 2003; Fujii 2012; Clausen et al. 2013). Depending on the timescale of predicted sea-level rise, the rate at which intertidal areas are created naturally from higher shorelines will be variable (Fujii and Raffaelli 2008), and will be heavily influenced by the plasticity of a system in response to such changes. Additionally, prey species inhabit specific areas of the shore and may have to move to find new suitable areas (Mendez Aragón 2012).

In general, a reduction in area will result in increased densities of birds already using a site, increasing the potential for interference competition (Goss-Custard et al. 2004; Santos et al. 2005), and altering the availability of prey items due to depletion by the birds. Current research suggests that the ‘carrying capacity’ of wading birds’ forging areas can be reduced by habitat loss (Schekkerman et al. 1994; Goss-Custard and West 1997). Whether estuaries are thought to be near their ‘carrying capacity’ is a complicated measurement (Goss-Custard and West 1997; Goss-Custard et al. 2002), but any loss of foraging area is likely to impact upon a site and must be investigated. Birds may have to change to alternative habitats, move further away or find themselves competing with conspecifics (and non-conspecifics) for resources (Gill et al. 2001; Gunnarsson et al. 2005).

1.2.3 Threats to wading birds that have energetic implications

Considering the more energetic impacts from environmental change, predicted increases in temperature will also affect waders and their prey. Increasing ambient temperatures may reduce metabolic costs of foraging for waders (Tulp et al. 2009), but may also reduce the abundance and availability of their prey species (Pörtner 2012) as well as remove hospitable areas of habitat (Beukema 1990; Beukema et al. 2009; Schückel and Kröncke 2013). Extreme cold events are known to occur even in this time of 'global warming' and pose their own risks to waders (Osborn 2011; Prior and Kendon 2011). Increasing energetic costs for waders during lower ambient temperatures are known (Kersten and Piersma 1987; Zwarts et al. 1996), as are reductions in detecting prey that are less active, and that might have lower energy content (Pienkowski 1981; Lambert et al. 1992; Zwarts and Wanink 1993).

More extreme weather conditions can potentially impact on foraging time as well, with ice locking up mudflats (Strasser et al. 2001), or heavy rain and wind hindering prey detection and handling times (Goss-Custard 1969; Pienkowski 1981, 1983). It may be in these cases that birds move to wintering areas in more suitable climes (Austin and Rehfisch 2005), and thus reduce the current biodiversity present in the estuaries.

With ever increasing industrialisation and human populations in coastal areas, the risk of pollution affecting marine and estuarine environments must be carefully managed. Many effects of heavy metals are unknown for waders (Bryan and Langston 1992), but their impacts on invertebrate species are better studied. Declines in prey numbers through mortality events at both juvenile stages and in adults of reproductive age have been observed (Evans et al. 1995; Langston et al. 2003; Durou et al. 2005; Hagger et al. 2006), whilst reduced energy content may also be affected (Heard et al. 1986; Wright et al. 2013, 2015). Effluent and agricultural run-off are known to promote invertebrate numbers (Beukema 1991; Alves et al. 2012) and potentially aid wader populations, meaning that recent 'clean up' schemes have reduced this benefit (Evans et al. 1994). The less well known pollution from artificial light is currently being promoted as having both positive effects, by increasing foraging time and visibility (Dwyer et al. 2012; Davies et al. 2014), and negative effects, through increased predation risk (Dwyer et al. 2012).

Finally, disturbance of human origin is a widely researched topic that is known to hinder the daily life cycles of wading birds. Residential and infrastructural development, recreation and commercial activities all have the potential to disturb the time and area a bird has to forage, as well as increasing their energy expenditure through being flushed (Cayford 1993; Goss-Custard et al. 2006b; Weston et al. 2012). In combination with any of the other environmental changes this will increase the pressures that wading birds are experiencing and will need to be monitored and regulated for conservation purposes.

1.3 Predictive ecology: its role and use in conservation science.

There is a growing need for predictions and predictive ecology in the modern world of conservation management (Evans et al. 2012; Wood et al. 2015). With the increasing amount of administration and other requirements put on academics, let alone conservationists, the amount of time available to understand how organisms might respond to environmental change is falling. From studies that have looked into the working habits of conservationists (and researchers), we know that more time is being spent during evenings and weekends submitting papers let alone answering important conservation questions (Campos-Arceiz et al. 2013).

Within avian ecology, many approaches have been used in the past to predict wader behaviours and physiology (Hostetler et al. 2015), from simple linear equations (Kingsford and Thomas 1995; Maclean et al. 2008; Aarif et al. 2014) through matrix models (Klok et al. 2009; Dinsmore et al. 2010) to simulation models (Ens et al. 2004; Durell et al. 2007; Garcia et al. 2011). All of these models have their advantages but whilst traditional methods in predictive ecology (linear models, matrixes) tend to have a specific set of parameters, simulation models have more flexibility (DeAngelis and Mooij 2005; Grimm and Railsback 2005). With the development of greater computing power, simulation modelling has been able to develop rapidly (Judson 1994; Lomnicki 2011), and has allowed more complex scenarios to be implemented. In replicating an environment, even with increased computing power, there are always simplifications that must be applied that might result in researchers mistrusting the results, but validation and sensitivity analysis can alleviate these fears (Aber 1997). The famous quote by Box (1979) that "*all models are wrong but some are useful*" depicts this situation well, and emphasises the importance of creating models with simplifications, compared to not modelling at all. In this thesis the type of simulation-based models called "individual-based models" will be used to investigate environmental change effects on wading birds following previous ecological studies (DeAngelis and Grimm 2014).

1.3.1 The developmental history of IBMs and their current use within avian ecology

Individual-based modelling is a type of simulation that has become popular over the past few decades particularly within ecology (Grimm 1999; DeAngelis and Grimm 2014). Early papers used ‘simulation modelling’ to describe their models before IBM was used as standard (Newnham 1964; Kaiser 1974; Thompson et al. 1974; Myers 1976). Since the first use of the term “individual-based model” in a paper abstract in 1989 the numbers of articles using the term has exponentially increased (Figure 1.1) to a current standing of 3,102 (Scopus, www.scopus.com, 28.08.16). When considering papers solely from the fields of ‘agriculture, biological and environmental sciences’ (Scopus search category) the number of papers found is 2,377, which is a considerable proportion of the total discovereable papers (Scopus, www.scopus.com, 28.08.16). Also known as ‘agent-based modelling’ (most commonly within social science (MacPherson and Gras 2016)), these models treat individuals as discrete entities that interact on a local scale and have their own properties that make them different from each other (Grimm and Railsback 2012).

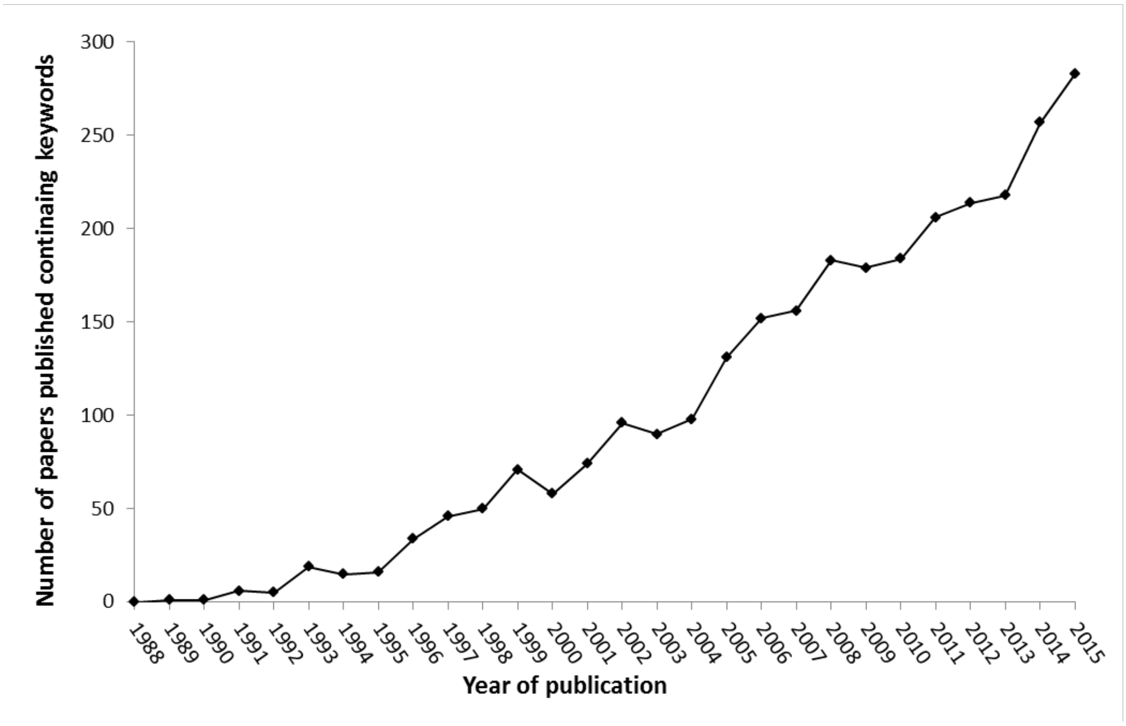

Figure 1.1: A chart showing number of papers published per year containing the phrase “individual-based model” in the article title, abstract or keywords using Scopus (correct as of 28/08/16).*

Working from the principle that individuals are the ‘building blocks’ that ecosystems are built upon (Grimm and Railsback 2005), ecological IBMs simulate an environment with resources that individual organisms can interact with based on their own properties – a ‘bottom up’ approach (DeAngelis and Mooij 2005). For example, within simulations of bird behaviour, all individual foragers of a species are modelled from the same principles but the levels of certain state-variables and behaviours range over expected statistical distributions (Hogeweg and Hesper 1990; DeAngelis and Grimm 2014). With this individuality of physiology and behaviour, organisms will have slightly different goals to reach during the model and adapt their behaviours to meet these. Understanding that the difference between individual animals aids predictions is an important point that was first emphasised by Łomnicki (1978) and has been frequently stressed. The emergent properties that arrive from these behaviours, as individuals seek to maintain their fitness levels, are then compared with observations to validate the models against the real world (McLane et al. 2011).

Many approaches to develop IBMs exist and software is continuously being updated to make the applications of such ideas possible. From the earliest IBM-style models that were directly programmed to answer specific ecological questions (Newnham 1964; Botkin et al. 1972; Deangelis et al. 1980), the development of models has relied upon good programming; but often the expansion of the field was hindered by researchers having the necessary skills (Lorek and Sonnenschein 1999; Grimm and Railsback 2005). More recently the advent of modelling platforms such as NetLogo (Wilensky 1999) and simpler programming languages like Python (Macal and North 2014) has led to greater numbers of researchers utilising IBMs. Modelling platforms allow easy manipulation of environmental variables to speed up the time needed to develop and investigate ecosystems and environmental changes.

Within wading bird ecology, the work of Goss-Custard, Stillman, Caldow, Clarke and colleagues has investigated the behaviours of many species in estuarine environments that have been invaluable to conservation and management decisions (Durell et al. 2005, 2006, 2007, 2008, Stillman et al. 2005, 2010; Caldow et al. 2007; Stillman 2010). Earlier work on 'behaviour-based models' (another synonym for IBMs) has led to the development of the modelling platform MORPH (Stillman 2008) that allows IBMs to be developed rapidly within a standardised framework. MORPH develops IBMs that use fitness-maximising decisions to determine the behaviours and decisions of individual foragers, and allows a high degree of flexibility in updating or adjusting habitats and scenarios (for example prey switching, habitat preference and taking account of conspecific density, see Stillman 2008 for full details).

With these, and other avian IBMs, several environmental change scenarios have been investigated (Durell et al. 2004, 2006, 2007; Goss-Custard et al. 2006a; Caldow et al. 2007). The results of these investigations have been relied upon for management and conservation decisions, thus showing their acceptability for mangers and stakeholders. It is gratifying that the recent history and use of IBMs has been able to prove wrong older concerns that science would not be able to adequately predict ecosystems' responses to environmental change (Stillman and Goss-Custard 2010).

An important attraction of using IBMs is the reduction in time between (i) the initial proposal to investigate a potential environmental change on species survival and (ii) the final results that might allow, halt or moderate future works. However, the use of IBMs will never supersede fieldwork, as empirical observations and measurements will always drive the parameterisations and validation. The future of predictive ecology for wading birds and related ecosystems is promising. With more interest being shown in its applications both within and outside of academia, the development and use of a suite of IBMs for wading birds that this PhD will investigate will be highly relevant.

1.4 Project aims and objectives

The overall aim of this thesis is to develop a suite of models that will aid understanding of how wading birds (Charadrii) are affected by environmental change. The use of individual-based models will allow researchers to fully understand how populations respond to a wide range of changes – including habitat loss and sea-level rise through to temperature changes and pollution – and to make predictions that can be used by conservationists. By modelling a range of environmental changes, critical thresholds of change will be found, and underlying impacts on species' diets and habitat usage revealed. The objectives to attain these aims are:

O1. Investigate the importance of invertebrate populations on wading birds using individual-based models (Chapter 2).

O2. Determine how environmental changes have, are, and will impact on wading birds, and investigate the predictive potential of the current literature (Chapter 3).

O3. Develop a suite of standardised models, that have comparable predictions, to investigate the effects of environmental change on wading birds (Chapter 4) though:

  a. Investigating carrying capacity and how this impacts on current conservation targets and protection (Chapter 5).
  b. Investigating the impacts of the most important environmental changes found in Objective 2 (Chapter 6).
  c. Making general predictions of how these environmental change effects could impact species on other estuaries (Chapters 5 & 6).

1.5 Thesis structure

The thesis reviews understanding of the current environmental changes impacting on wading birds, and uses established models and a new suite of standardised IBMs to provide comprehensive explanations of the effects of change on wading birds. The chapters are listed below:

Chapter 1 - An introduction to wading birds, their current status and how individual-based models can answer questions about their ecology.

Chapter 2 - Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK.

Chapter 3 - The effects of environmental change on wading birds and their habitats: a review and analysis.

Chapter 4 - Development of a suite of individual-based models to predict environmental change effects on wading birds.

Chapter 5 - Can estuaries support increased populations of waders? An investigation of population change using individual-based models.

Chapter 6 - Using individual-based models to predict how wading birds will be affected by environmental change.

Chapter 7 - Overall discussion and conclusions.

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

This chapter investigates the how stepwise regime shifts in invertebrate prey impacts wading birds. It uses a previously developed and validated individual-based model to investigate the effect of invertebrate regime shifts on wader populations and the underlying behaviour of individual birds. The text of this chapter is presented as seen in its published version in Biological Conservation (Bowgen et al. 2015).

2.1 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; Bhaud et al. 1995; Beukema et al. 2009) 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 2.1 and Goss-Custard et al. 2006). 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 (van Roomen et al. 2005, 2012; Weijerman et al. 2005; Piersma 2007). The Wash in 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 1980’s reduced invertebrate stocks in the Wadden Sea (Beukema 1990, 1992) and during the 1990’s 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).

Table 2.1. 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			✓	✓	✓

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 (Strasser et al. 2001; Atkinson et al. 2010) 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 (Olive and Cadnam 1990; Alves et al. 2012). 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 (Grimm et al. 1999; Grimm and Railsback 2005; Goss-Custard et al. 2006a; Stillman et al. 2007; Stillman and Goss-Custard 2010). 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.

2.2 Methods

2.2.1 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.

2.2.2 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 (Thomas et al. 2004; Caldow et al. 2005) 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 2.2 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 to 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 2.2. 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*	*Glycera tridactyla*	*Cirriformia tentaculata*
	Alitta virens	*Phyllodoce mucosa*	*Aphelochaeta filiformis*
	Nephtys hombergeii	*Eteone longa*	*Capitella capitata*
	Arenicola marina	*Malacoceros fuliginosus*	*Heteromastus filiformis*
	Scoloplos armiger	*Scolelepis squamata*	*Tubificoides* spp.
	Harmothoe spp.	*Scolelepis foliosa*	Nemertea spp.
	Polycirrus caliendrum	*Pygospio elegans*	
	Ampharete grubei	*Spio* 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 (incl. *Cyathura*)	*Gammarus locusta*	*Corophium arenarium*	
	Microdeutopus gryllotalpa	*Urothoe poseidonis*	
	Corophium volutator	*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+		

2.2.3 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 (Table 2.2).

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 2.3) each simulating a type of regime shift (detailed in Table 2.4). 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.

Table 2.3. 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	

The simulated regime shifts in Worms and Bivalves (Table 2.4.) 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 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.

Table 2.4. 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.

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 A1.1). 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.

2.3 Results

2.3.1 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 (Figure 2.1a). 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 oystercatcher not affected at all. The other species were reduced to less than 5% of their original supported values (Table A1.1).

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% (Figure 2.1b). Dunlin and redshank were not affected in either of the scenarios.

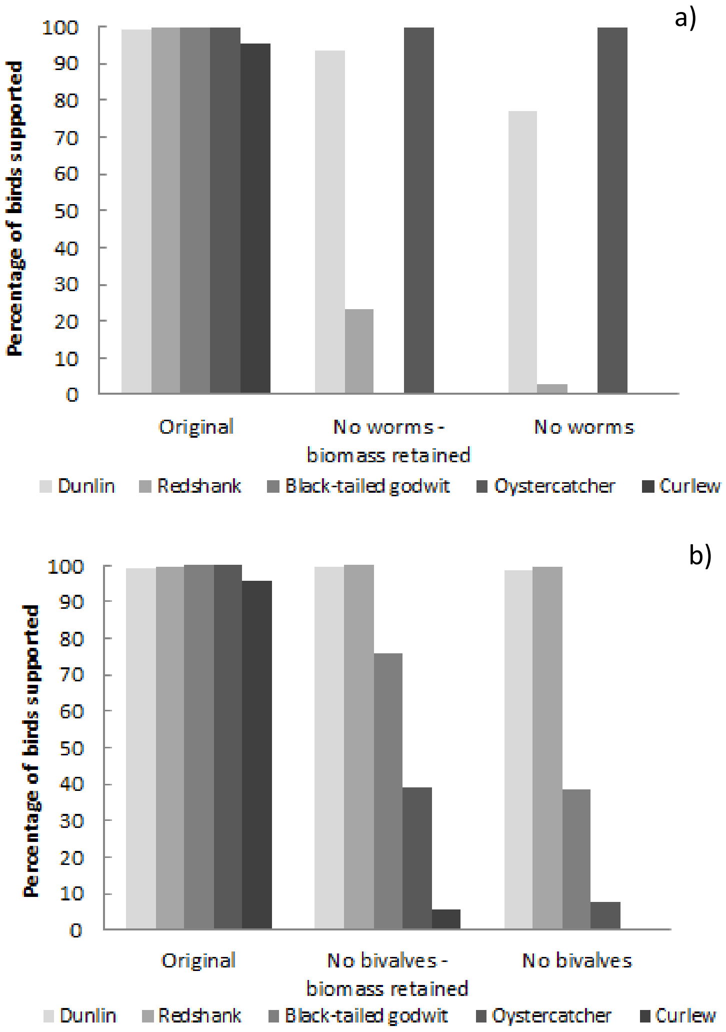


Figure 2.1. Percentage of birds supported when a) worms are completely removed and b) when bivalves are completely removed; both where biomass was retained or not.

2.3.2 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 Figure 2.2a. 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 A1.1). 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.

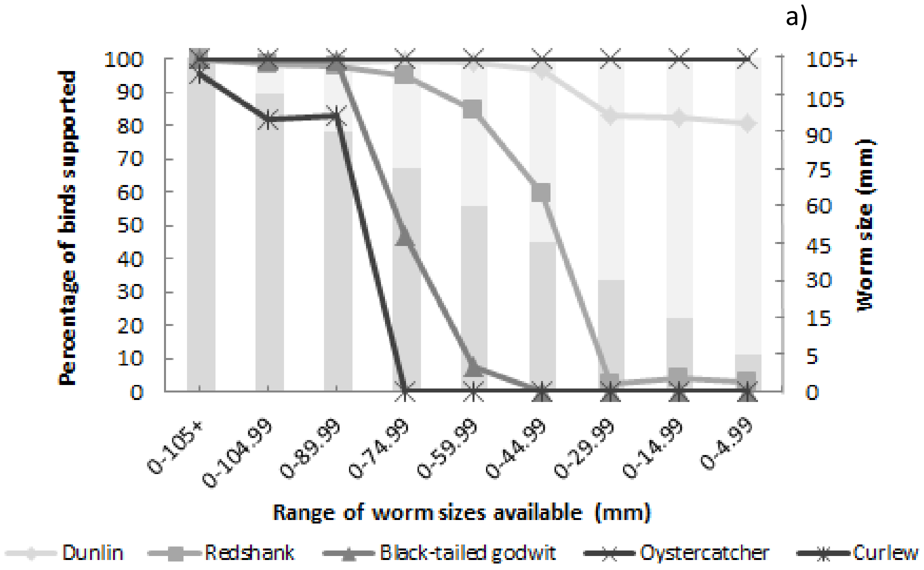
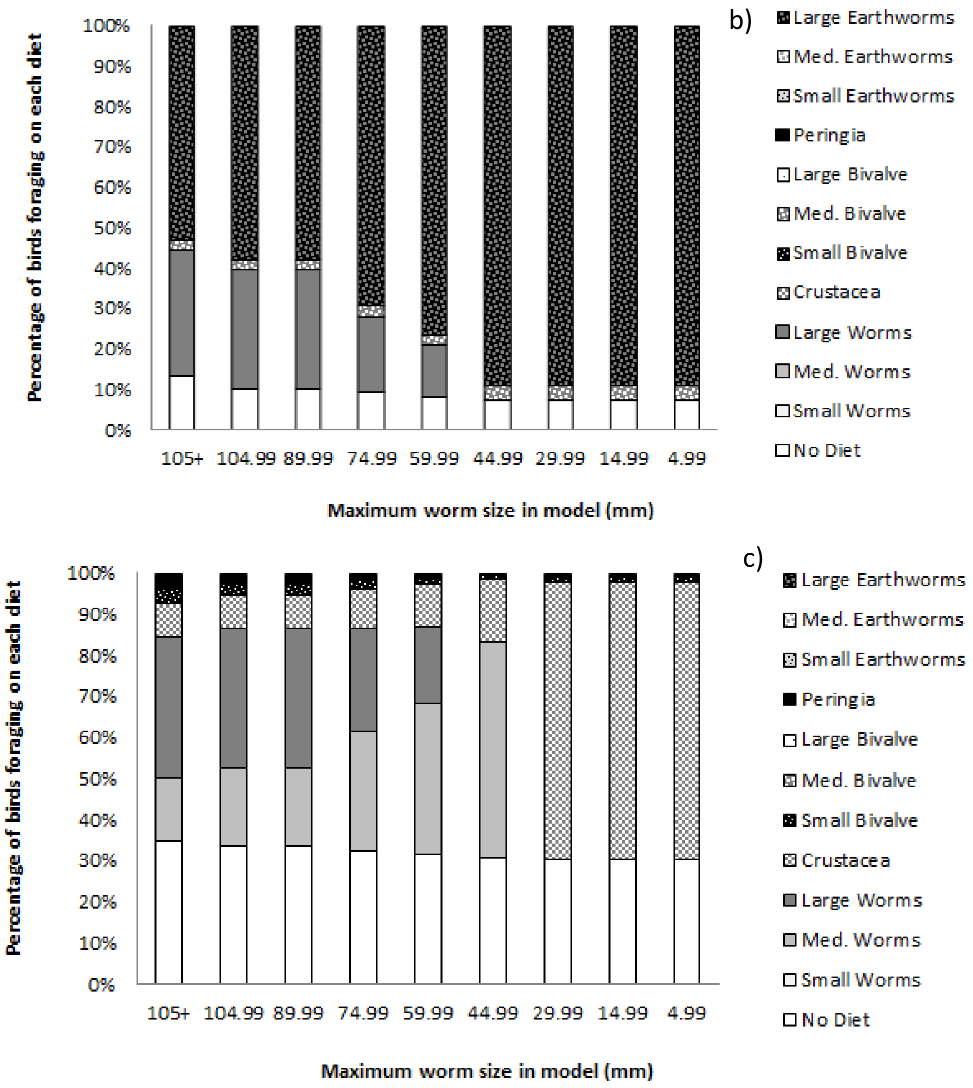


Figure 2.2a. Percentage of birds supported with decreasing worm biomass size plotted against a right hand axis showing the biomass of worms present by size and length in each model run (dark grey for present and light grey for removed).

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 (Figure 2.2b). Black-tailed godwit follow a comparable pattern as similarly, this bird cannot compensate with other marine invertebrates (Figure A2.1a). Redshank become dependent on crustaceans towards the end of the sequence and whilst dunlin also followed the same pattern (Figs 2.2c and A2.1c), they were able to forage upon the smallest worms right up until the end which may explain their higher supported values. Oystercatchers foraged upon large bivalves at a similar proportion right through the model sequence (Figure A2.1e).



Figures 2.2b & c. Percentage of diets consumed with decreasing worm biomass size for a) curlew and b) redshank.

2.3.3 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 Figure 2.3). In these scenarios curlew did marginally better than the original model, with 1-4% larger final populations (Table A1.1).

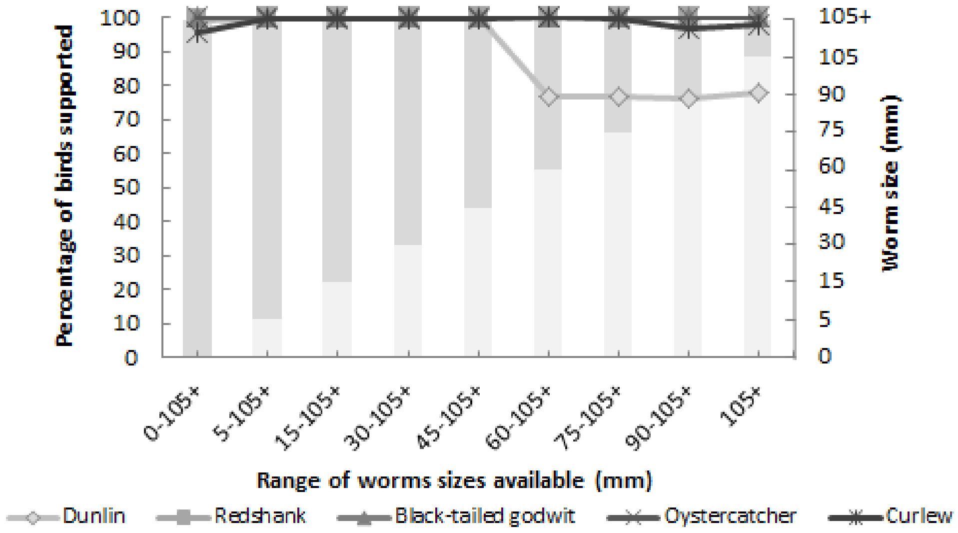


Figure 2.3.Percentage of birds supported with increasing worm size plotted against a right hand axis showing the biomass of worms present by size and length in each model run (dark grey for present and light grey for removed).

2.3.4 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 (Figure 2.4a). In contrast to being unchanged during reducing worm size (Fig 2.2a), 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 (Table A1.1).

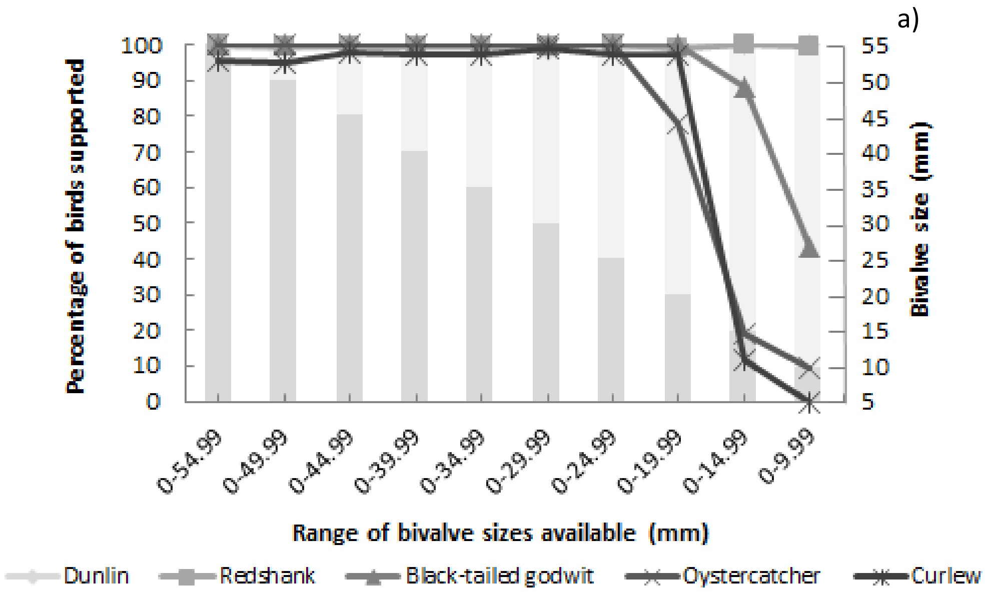


Figure 2.4a. Percentage of birds supported with decreasing bivalve biomass size plotted against a right hand axis showing the biomass of bivalves present by size and length in each model run (dark grey for present and light grey for removed).

From the percentage of time spent foraging on each diet (Figure 2.4b) 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 (Figs A2.2a and A2.2b).

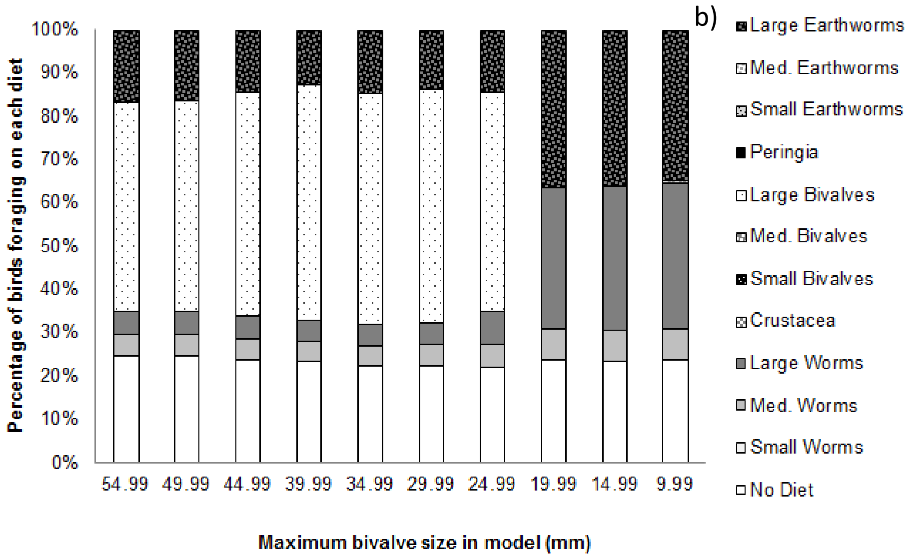


Figure 2.4b. Percentage of diets consumed with decreasing bivalve biomass size for oystercatcher.

2.3.5 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 (Figure 2.5). No other species are affected by any more than a 0.6% population drop compared to the original results (Table A1.1.).

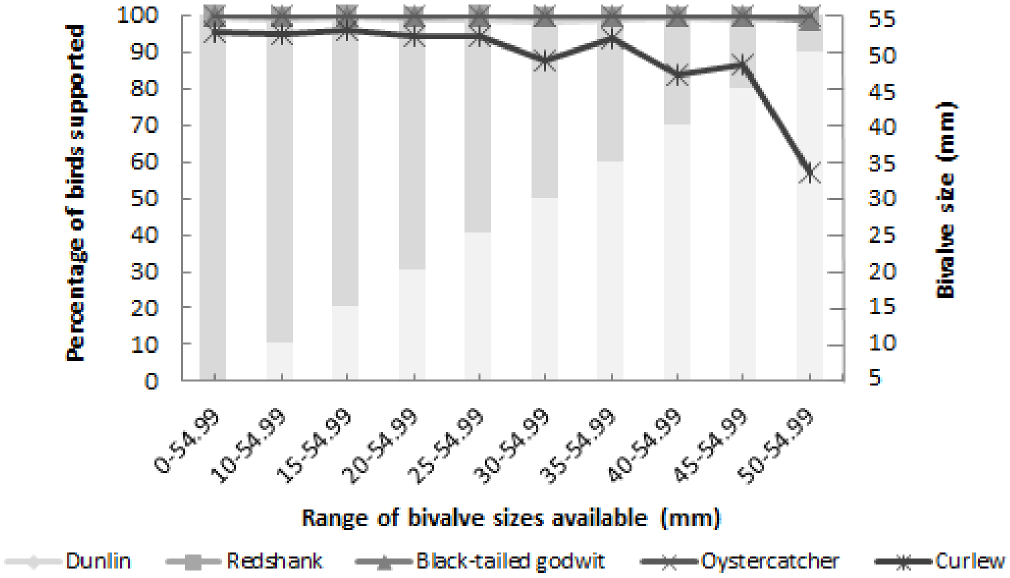


Figure 2.5.Percentage of birds supported with increasing bivalve biomass size plotted against a right hand axis showing the biomass of bivalves present by size and length in each model run (dark grey for present and light grey for removed).

2.3.6 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 (Figs A2.3a and A2.3b). Curlews, who have responded the strongest in these experiments, only drop to 92% and 95% respectively in the worm and bivalve based models.

2.3.7 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 A2.3a and A2.3b). Here you can see in Figure A2.4b 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 15-89.99mm) 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 (Figure A2.4a).

2.4 Discussion

Though it is known that regime shifts occur in estuarine invertebrate populations (Beukema 1990; Weijerman et al. 2005; Alves et al. 2012) 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 (Olive and Cadnam 1990; Olive 1993; Strasser et al. 2001; Alves et al. 2012), 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 (Olive 1993; Goss-Custard et al. 2004).

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 on 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 (Ruiz et al. 1989; Morrison 2004).

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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3. The effects of environmental change on wading birds and their habitats: a review and analysis

This chapter reviews the current research into the impacts of environmental change on non-breeding wading birds, analyses of current trends in the academic literature of this topic and derives a literature-based relationship between percentage habitat loss and bird population size.

3.1 Introduction

People want predictions. People want them now. One potential method for producing rapid predictions is individual-based modelling in which fitness-maximising rules are used in conjunction with a computer realised environment to predict how individuals will react to changes in their environment (Davies et al. 2001; Grimm and Railsback 2005; Durell et al. 2006; Stillman 2008; Phang et al. 2016). However, these models can be complex, with high data requirements leading some researchers to favour field studies.

Wading birds are often viewed as bioindicators for estuaries, as changes in their supported numbers can indicate the health of an environment (Furness 1993; Rehfisch et al. 2004). To understand how environmental change can affect such species we can look to several sources – species responses to past events, experimental manipulation and fieldwork, and predictive modelling. Of these options fieldwork is not always possible as there is often limited time available. The risk of causing damage to the environment with experimental work means that predictive modelling becomes appealing.

Before developing models to investigate the effects of environmental change on wading birds we first have to understand what has already been researched. On a very basic scale, the survival of non-breeding waders is determined through each individual having enough foraging time and space to survive through the season. As such, many of the impacts of environmental change can be reduced to their inhibiting a wader’s ability to either find enough foraging area or enough time. With carrying capacity and density dependence often cited in reports and literature when discussing the effects of environmental change (Durell et al. 2000; Goss-Custard et al. 2002, 2003; Ge et al. 2008), finding out how ‘close to the edge’ birds are requires extra information that is not always available. For some years, researchers have been putting together literature reviews and horizon scans that provide a basis of what might affect birds (Robinson et al. 2009;

Sutherland et al. 2012; Cresswell 2014; van de Pol et al. 2014) but there is no specific review for current effects of environmental change on wading birds.

Looking specifically at the non-breeding populations, this chapter i) analyses the current trends in wading bird research publications through two large scientific search engines, ii) reviews the literature to understand how environmental changes have affected wading birds, iii) derives a literature-based relationship between percentage habitat loss and bird population size, and (iv) discusses the potential for individual-based models to fill knowledge gaps.

3.2 Which types of environmental change are most frequently reported in the scientific literature?

To determine the frequency with which the effects different types of environmental change are reported in the literature, a set of search terms was devised (Table 3.1).

Table 3.1. List of environmental change search terms used in Web of Science and Scopus. Specific terminology searched presented including appropriate Boolean operators.

Environmental Change terms	**Search terms used to cover common variations of environmental change**
Environmental change	*AND "environmental change"*
Climate change	*AND "climat* change"*
Global warming	*AND "global warm*"*
Anthropogenic	*AND anthropogen**
Habitat loss	*AND ("habitat loss" OR "habitat dec*")*
Habitat gain	*AND ("habitat incr*" OR "habitat creat*")*
Shellfisheries	*AND (shellfisher* OR shellfishin* OR fisher*)*
Air/ambient temperature	*AND ("air temp*" OR "ambient temp*")*
Weather	*AND "weather*"*
Sea-level	*AND ("sea level*" OR "sea-level*")*
Pollution and toxins	*AND (pollut* OR tox*)*
Eutrophication/sewage/effluent	*AND (eutrophic* OR sewag* OR effluen*)*
Disease/parasites	*AND (diseas* OR parasit*)*
Disturbance	*AND disturb**

Between 24th September and 29th October 2013, I used Thompson Reuter's Web of Science (http://wok.mimas.ac.uk/) and Elsevier's Scopus (www.scopus.com) search engines, as they are two of the most comprehensive and wide-ranging search engines for scientific papers

(Chadegani et al. 2013). Other search engines were considered, such as CAB abstracts, Copac and BIOSIS Previews, but these were not available from Bournemouth University. Google Scholar was initially used for searching the grey literature, but was not considered flexible enough to be used further (Boolean operators are not as widely accepted within this site).

3.2.1 Search term protocol

Fourteen different environmental change categories were searched for using the two websites (Table 3.1) within the title, abstract, keywords (‘Topic’ in WoS) of an article. Following initial trials of various base search terms, each search began by looking for papers on waders or shorebirds (term used - (wader* OR shorebird*)), followed by the specific environmental change terms, and then repeated with terms to specifically select only winter and non-breeding papers (term used - AND (winter* OR "non-breed*"). The addition of this last search term assisted in removing all papers specifically linked to the breeding season as this thesis is only concerned with non-breeding populations. It must be noted that when looking for shellfisheries papers in Web of Science an additional term was added to remove papers that had been tagged by WoS with “Water research and fishery biology” as these papers were not relevant (full search used – ((wader* OR shorebird*) AND (shellfisher* OR shellfishin* OR fisher*) AND (winter* OR "non-breed*") NOT "Water research and fishery biology"). Please note that the common Boolean operators ‘AND’, ‘OR’, ‘NOT’ were used as well as the wildcard ‘*’ which allow for variations in word endings to capture a greater range of papers. These terms did not work in the same way with Google Scholar where brackets and ‘*’ were ignored or overlooked, hence why this search engine was not used.

Although I used the initial terms of wader* OR shorebird*, as these returned the best set of initial results, I found that the relevant papers I discovered through other searches were not always found by these searches. This is due to the abstracts and titles not containing either of these terms; rather they contain only the species name e.g. redshank (*Tringa totanus)*. It would not have been practical to carry out all searches on every wader species currently extant. I carried out a repeat of my searches in both Scopus and Web of Science but with wader* OR shorebird* OR charadrii* but found that these both returned too many results for ease of sorting and more notably returned papers containing gulls and auks due to the order Charadriiformes being found. With the search term charadrii, I had hoped to collect any additional papers that might have used Charadriiformes or Charadrii itself. As such I decided to continue with my original format of wader* OR shorebird* as the data in the papers that were missed was often published elsewhere under different terminology.

After completing the searches, all abstracts were read to check for any papers that were not relevant to the subject searched for. This included papers that were not principally about wading birds, or were about other species related to them (e.g. ibis, spoonbills and grebes). I also removed papers that were not about the environmental change searched for, e.g. not about habitat loss that had occurred, but had suggested that habitat loss could occur in the future.

3.3.2 Results of searches

Both search engines returned a large number of papers with the base term of '(wader* OR shorebird*)' (6,099 WoS and 4,591 Scopus). However, these were greatly reduced when the search was focused to wintering and non-breeding populations (1,197 WoS and 1,050 Scopus).

The returned papers showed some interesting publication patterns (Tables 3.2 and 3.3). Table 3.2 shows that without the non-breeding season search term, papers including disturbance were the most prevalent, followed by disease/parasites, pollutions and toxins, and weather. Once the search terms 'winter' and 'non-breeding' were included I found that there was a change in the types and prominence of papers (Table 3.3). Disturbance still tops the list of papers published, but 'weather' follows in second place with 'habitat loss', 'climate change', and pollution and toxins trailing although the combination varied between search engines. Scopus also has disturbance most frequent, followed by weather then 'climate change', anthropogenic and 'habitat loss'.

Table 3.2. Numbers of wading bird papers found for different environmental changes in Web of Science and Scopus (bold figures are the five highest values)

Environmental Change *(search terms in Table 3.1)*	**Number of papers (all seasons)**		**Number of papers (winter/non-breeding)**	
Search Engine	**WoS**	**Scopus**	**WoS**	**Scopus**
Environmental change	25	35	9	17
Climate change	**127**	**95**	**54**	**44**
Global warming	11	14	5	7
Anthropogenic	59	**100**	24	**41**
Habitat loss	92	77	**53**	**40**
Habitat gain	15	27	3	7
Shellfisheries	53	42	21	14
Air/Ambient temperature	48	32	14	12
Weather	**124**	88	83	47
Sea-level	45	50	23	19
Pollution and toxins	**98**	**95**	**40**	33
Eutrophication/sewage/effluent	68	40	22	17
Disease/parasites	**130**	**90**	24	16
Disturbance	**216**	**181**	**97**	**60**

Between the two search engines, similar results were seen for all papers (Figure 3.1) but Web of Science found more “winter/non-breeding” papers for most categories than Scopus (Figure 3.2). It is known that WoS covers a wider range of years (1900+ vs. 1966+) than Scopus (Burnham 2006; Sullo 2007) and thus finds more papers.

The literature searches support focusing my future IBM questions on the main environmental changes – disease/parasites, pollutions/toxins, weather and habitat loss. I have discounted disturbance due to a fellow PhD student, Catherine H. Collop, focusing on this topic.

Table 3.3. Numbers of papers found for each environmental change as a percentage of the total wading bird papers found in each search engine (bold figures are the five highest values)

Environmental Change ***(search terms in Table 3.1)***	**Percentage of papers (all seasons)**		**Percentage of papers (winter/non-breeding)**	
Search engine	**WoS**	**Scopus**	**Wos**	**Scopus**
Environmental change	0.41	0.76	0.75	1.62
Climate change	**2.08**	**2.07**	**4.51**	**4.19**
Global warming	0.18	0.3	0.42	0.67
Anthropogenic	0.97	**2.18**	2.01	**3.90**
Habitat loss	1.51	1.63	**4.43**	**3.81**
Habitat gain	0.25	0.59	0.25	0.67
Shellfisheries	0.87	0.91	1.75	1.33
Air/Ambient Temperature	0.79	0.7	1.17	1.14
Weather	**2.03**	1.92	**6.93**	**4.48**
Sea-level	0.74	1.09	1.92	1.81
Pollution/Toxins	**1.61**	**2.03**	**3.34**	3.14
Eutrophication/sewage/effluent	1.11	0.87	1.84	1.62
Disease/parasites	**2.13**	**1.96**	2.01	1.52
Disturbance	**3.54**	**3.94**	**8.1**	**5.71**

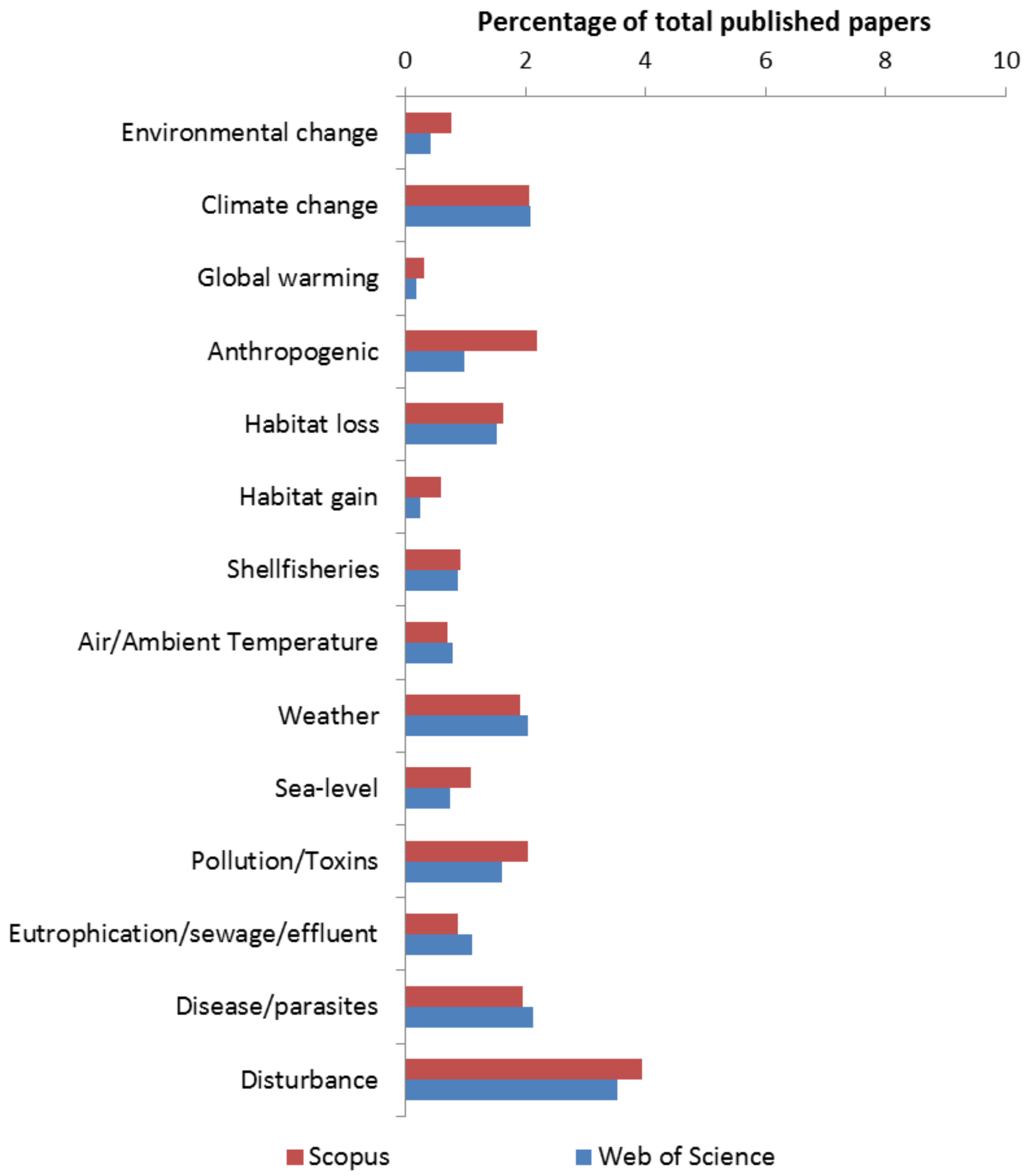

Figure 3.1. Percentage of total published papers for each environmental change effect on wading birds in Web of Science and Scopus. Total papers for Web of Science was 6,099 and for Scopus 4,591.

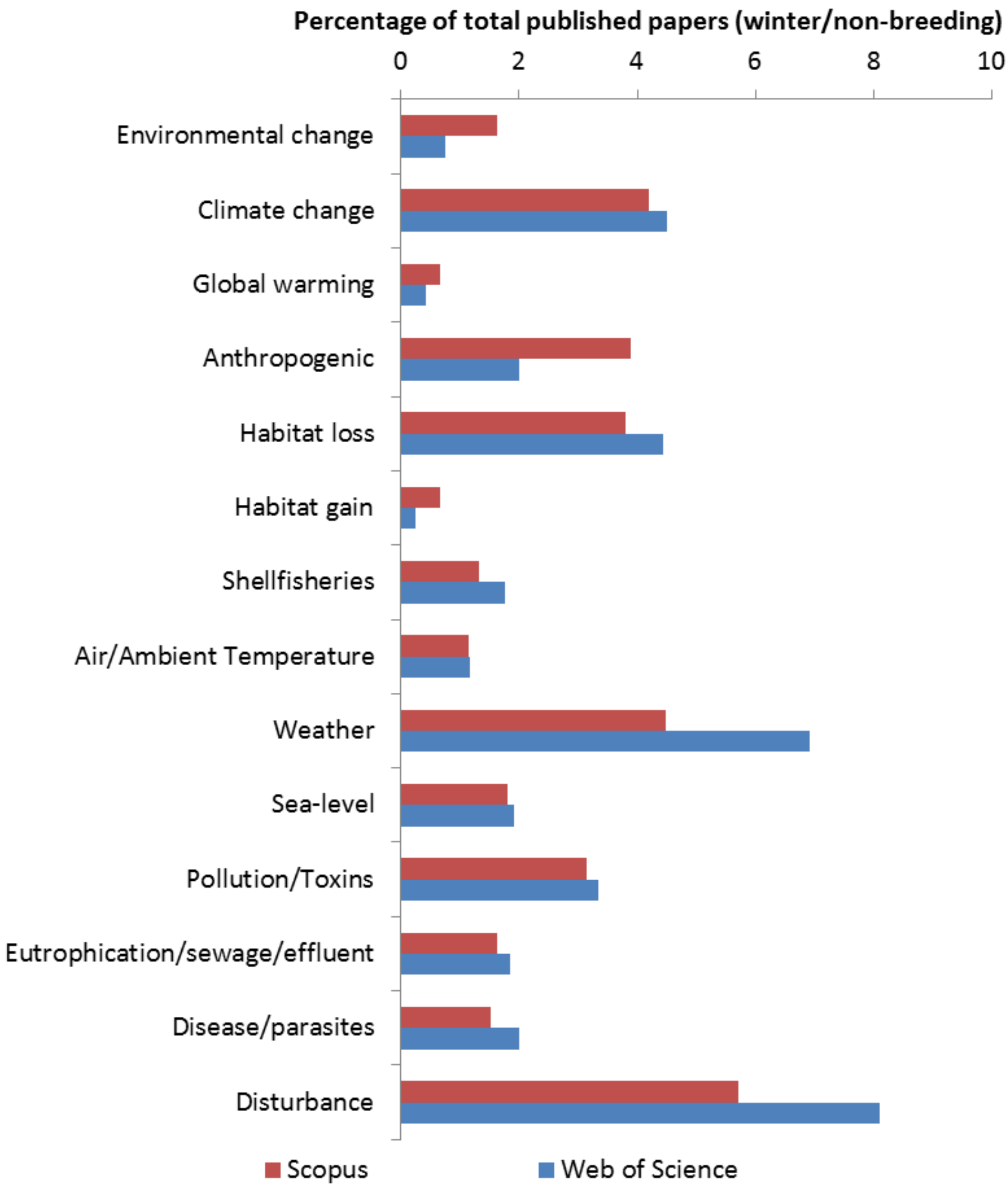

Figure 3.2. Percentage of total published papers for each environmental change effect on winter and non-breeding wading birds in Web of Science and Scopus. Total winter and non-breeding papers for Web of Science was 1,197 and for Scopus 1,050.

3.3 What environmental changes affect wading birds?

This section overviews the current literature to understand the effect of environmental change on wading birds. Figure 3.3 shows a conceptual model, derived from the review, of the range of ways in which environmental change can affect these birds.

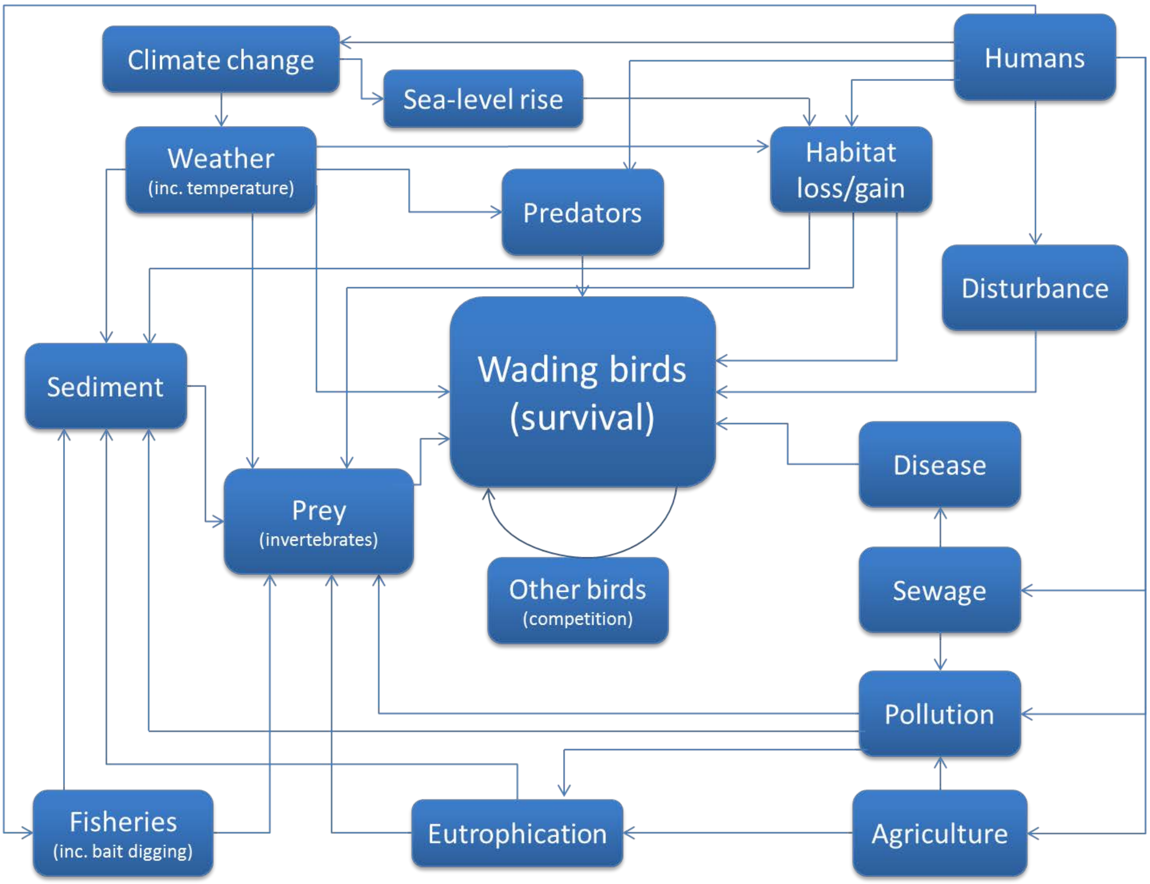

Figure 3.3. A conceptual model detailing the effects of environmental changes on wading birds.

3.3.1 Habitat loss

The impact of reduction in habitat size on wading birds is well represented in the literature with many examples, particularly in Europe. Loss of prime habitat causes birds to change their foraging behaviours to maintain the same levels of energy they need to survive and can incur additional costs through flight to new areas (Weston et al. 2012). Reduction in habitat can also cause higher densities of birds to occur around foraging sites and thus increase the chance of interference competition from both conspecifics and other species (Goss-Custard 1977; Rappoldt et al. 2010).

One of these well studied locations is the Dutch coastline which contains important habitats for wading birds throughout the year, but particularly during passage and non-breeding periods (van de Kam et al. 2004; van Roomen et al. 2012). A widely researched area is the Oosterschelde ecosystem in the south-west of the Netherlands which has been under increased pressure since its tidal area was reduced by a third during the late 1980s (Meire 1991; Duriez et al. 2009). Survival rates of oystercatchers (*Haematopus ostralegus*) declined during severe winters after the partial closure of the Oosterschelde (Schekkerman et al. 1994), although studies have shown that during mild winters there was no noticeable difference in survival (Duriez et al. 2009). In general the foraging densities rose, particularly affecting the oystercatcher populations (Meire 1991). In the Dutch Wadden Sea, red knots (*Calidris canutus islandica*) lost 55% of their foraging habitat and this was paralleled by a 42% decrease in population size (Kraan et al. 2009).

Britain has a history of estuarine habitat decline with over 85% of estuaries affected by reclamation and it is thought that many have lost 25% of their area since Roman times (Evans et al. 1979; Davidson et al. 1991). A major loss of habitat that has been well documented in its effect on wading birds is the reduction in feeding areas at Teesmouth, England, where during 100 years over 2,400ha of intertidal area was reduced to 140ha by 1974 (Pienkowski 1973; Pienkowski et al. 1979). Several species were highly affected, with flocks of curlew (*Numenius arquata)* reduced in size and knot (*Caldris canutus*) also present in smaller groups (Pienkowski 1973). The loss of habitat was not only a reduction in physical size of foraging area, but also a reduction in the time for which the habitat was available, as upper-shore habitat was mainly lost; a reduction from 12 to 8 hours (Evans 1978/79). The various studies on this system show that some species are able to use alternative foraging areas to compensate for the loss of preferential sites in the estuary (Evans 1978/79). During 1973/74, a 60% loss in feeding habitat and 30% loss in feeding time quoted by the latter paper (Evans and Pienkowski 1984) coincided with reductions in wading bird populations in the Seal Sands area of Teesmouth. As mentioned, the specific part of mudflat removed can also have a large effect on the amount to which birds are affected. Goss-Custard and Moser (1988) suggest that removal of the top levels of the shore have a greater impact.

The introduction of man-made structures such as barrages or dams, to help with regulating tidal flows and maintaining water sources, pose challenges for developers and conservationists. Whilst they prove useful to the surrounding human populations they often reduce large areas of bird foraging habitat and affect tidal amplitude (Lambeck et al. 1996). In the case of the loss of intertidal habitat in Cardiff Bay (Burton et al. 2006), redshank populations were seen to respond with almost complete abandonment of any residual areas in the bay and moved to areas further along the coast. After three years, most redshanks were found 4 km from the bay, confirming the bird's attachment to their wintering sites over several years (Burton and Armitage 2008). In terms of survival, this study indicated that annual survival of adult redshank from this area declined by 8% as a result of displacement and individuals had difficulty maintaining their body mass soon after the closure of Cardiff Bay (Burton et al. 2006). From this we learn that, although the birds were able to compensate to some extent in the wider area (the ecosystem being apparently not at carrying capacity), similar developments may need to establish additional foraging areas. In the Netherlands where similar displacement was seen following habitat loss, questions have been raised about where birds can move to if high densities are already present nearby (Lambeck et al. 1996).

Several studies have considered that increased competition from loss of foraging habitats makes it harder for species to survive during the non-breeding season. Papers on this subject point out resident species that are present year-round will be more severely impacted by potentially adverse climates (Goss-Custard 1977; Goss-Custard and Moser 1988).

Habitat loss can come from other sources asides from anthropogenic causes. In the north-east of England an expansion of the invasive cord-grass (*Spartina anglica*) covered previously suitable foraging habitats and is a probable cause of dunlin (*Calidris alpina*) declines during the 1970s (Goss-Custard and Moser 1988), as removal of *S.anglica* at Lindisfarne saw increases in waders in the previously covered areas (Evans 1986). Yet the loss of *S.anglica* has been noted to affect the roosting areas of populations (Morrison 2004). *S.anglica* has also been known to expand onto mudflats near the top of the shore and thus reduced the fitness of wading birds (Goss-Custard and Stillman 2008).

Away from estuarine mudflats, agricultural land, fields and pastures are also very important in supporting birds during times when they cannot access mudflats (Goss-Custard 1969; Heppleston 1971; Navedo et al. 2013; Furnell and Hull 2014), though these have their own drawbacks, including increased risk of predation and disturbance (Morrison 2004). Many species are observed to feed on fields for earthworms and invertebrates (Goss-Custard 1969; Heppleston 1971; Goss-Custard and Dit Durell 1983; Quinn and Kirby 1993; Vickery et al. 1997; Hayhow 2009; Furnell and Hull 2014) and agricultural pastures are used as alternative roosting sites. As the majority of British estuaries and their immediate surrounds (88%) have been modified by the construction of sea defences and claim for agriculture of former intertidal habitat (Davidson and Evans 1986), the further loss of these areas could hinder foraging of birds already facing additional pressures.

With the rapid expansion of coastal industry in east Asia more provinces are reclaiming land for city expansions and port building (Yang et al. 2011; Ryu et al. 2014; Wang et al. 2014). Over 13,380km^2 of Chinese mudflat was reclaimed between 1950 and 2008 and has been occurring at an increasing rate since 1990, when only 8,241km^2 had been reclaimed (Fu et al. 2010). Bohai Bay has been heavily developed in the past decades, with 218km^2 of intertidal flats lost between 1994 and 2010 (Yang et al. 2011). Surveys of waders passing through this area have recorded wintering Eurasian curlew numbers increasing in the remaining areas as well as spring-staging migrants (Yang et al. 2011).

On the Korean side of the Yellow Sea, the construction of the Saemangeum dam has reclaimed 232km^2 of intertidal land (Ryu et al. 2014) and is thought to be responsible for declines in wading birds such as the great knot (*Calidris tenuirostris*), the population of which has reduced by about 25% since 2000 (Moores et al. 2008). Another species thought to be heavily affected by this dam is the Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*) which was reduced from over 34 seen in 2006 to only 3 in 2008 once the dam was complete (Moores et al. 2008). In all, the diversity of birds present after the construction of the dam had changed significantly compared to before (Ryu et al. 2014), with ten species of birds (not just waders) showing declines of over 30% (Moores et al. 2008). It is often hoped that such affected species will be supported by habitats nearby, but in the case of Saemangeum there has not been much increase in populations of the affected species outside the region, and in Australia a decline in total great knot has been observed returning from migration (Moores et al. 2008).

A need for more information on previous bird numbers has come to light with the loss of the Mesopotamian (Iraq) marshes. During the period 1991 to 2000 15,000 km^2 of wetlands were lost following a systematic regime to drain the marshes by Saddam Hussein, leaving only 10% by 2000 (Richardson and Hussain 2006). The loss impacted on multiple wetland bird species, including waders, but the hostility of the area meant that accurate surveys of the populations were not possible until the mid-2000s (Gretton 1996; Salim et al. 2009). By then the area had been re-flooded following the destruction of various dams etc. in 2003 and the area was recovering rapidly with almost 50% of the habitat returned by 2006. However, this has come under renewed threat from drought and water flow restrictions, both in Iraq and in neighbouring countries (Richardson 2010). The wildlife does seem to have thrived in the recovery period, despite the new threats, with recent surveys of the marshes showing high numbers of bird species, including 27 Charadriiformes, though many bird species are of conservation concern (Salim et al. 2009), and the total species number is lower than expected based on historical records (Richardson 2010).

3.3.2 Habitat gain (creation)

Whilst the loss of habitat is more often mentioned in the literature, habitat creation is also occurring in estuarine systems. This addition of space can be of benefit to species inhabiting an area, and is often a mitigation measure when other areas of habitat are lost, although it needs to be of a similar quality to the area removed (Goss-Custard and Stillman 2008).

In estuaries and harbours used for shipping, dredging (maintenance and capital) is carried out on a semi-regular basis and authorities in the UK are now encouraged to find ‘beneficial uses’ for the removed sediment such as to increase the size of existing areas or to create new ones (MMO 2014). This can provide space for new species to colonise, thus increasing the foraging capabilities of the site, but it may take time for invertebrate species to establish, and so this additional stage needs to be factored in to mitigation (Evans et al. 1998; Yozzo et al. 2004; French and Burningham 2009; Scarton et al. 2013). The timescale for populating a newly created intertidal area with invertebrates may be on the scale of decades rather than years as indicated by French and Burningham (2009) in some areas, but less than five years in others (Mander et al. 2007). Breeding areas from dredging material have been successfully created in the Venice lagoon (Scarton et al. 2013), but more work is needed regarding the improvement of non-breeding habitats. It should also be noted that this material does not always result in positive habitat for invertebrates on areas covered by sediment (as opposed to newly created areas). In one in depth study on the west coast of America, polychaete populations declined immediately after replenishment (Wooldridge et al. 2016).

Relating these newly created areas to wading bird populations is less well documented outside of the breeding season. There have been studies showing that there is a positive correlation between sediment types (i.e. proportion of silt and clay) and the densities of dunlin, emphasising the previous point that creating new habitat will not immediately provide suitable habitat for the birds (Clark 2006; Vanermen et al. 2006). The investigation into the new intertidal habitat at Paull Holme Strays (UK) showed that waterbirds were supported at low water within three years, making this type of mitigation promising, but this is only one study (Mander et al. 2007). It should be noted that the clay content of sediment can affect the growth of prey, with slower rates reported for bivalves in higher clay contents (Wanink and Zwarts 1993).

The physical preservation of mudflat features is also important. For example, it has been noticed that in the Tagus estuary (Portugal) that waders are particularly drawn to the networks of drainage channels on mudflats (Lourenco et al. 2005), and the same paper warns that changes or losses of these features may affect the carrying capacity of the area.

Finally, additional foraging areas can arise for waders with changes other than the physical creation of habitat. In the Tejo estuary in Portugal, greater numbers of birds have been observed feeding on the mudflats near sewage outflows where polychaete worms are present at a much greater density than elsewhere (Alves et al. 2012).

3.3.3 Shellfisheries

Shellfishing for molluscs and bait-digging for annelid worms often occur in habitats preferred by wading birds. Unlike habitat loss, the impact of shellfisheries on wading birds is not as directly reported in the literature. Instead, most of the potential effects appear to be mentioned as an aside when discussing other changes to the invertebrates from shellfishing.

One of the more direct impacts from fisheries on the intertidal zone is dredging for clams and cockles (*Cerastoderma edule*). Although regulated, it can disturb the sediment and affects other invertebrates such as marine worms (Saiz-Salinas and González-Oreja 2000; van Gils et al. 2006; Durell et al. 2008a). Trawling for invertebrates and benthic fish causes direct mortality of benthic invertebrates through sediment disturbance, as found in the Netherlands during the late twentieth century (Collie et al. 2000; Piersma et al. 2001; Ens et al. 2004). These changes to invertebrates are then likely to have an impact on wading birds through reduction in the number and quality of prey (van Gils et al. 2006). Outside of mechanical methods, there is less evidence of effects on birds of smaller-scale practices such as hand picking (Goss-Custard et al. 2004; Atkinson et al. 2005).

In the Wash in Eastern England, mussel (*Mytlius edulis*) and cockle stocks underwent a decline in numbers resulting in a shift in wader species from those that predominantly eat bivalves to those preferring marine worms (Atkinson et al. 2010). This occurred over a number of winters and was associated with high mortality in oystercatchers. Another related study points out that specialist bivalve-feeders are affected most acutely after overfishing of shellfish stocks, with species such as oystercatchers and knots experiencing higher mortality events (Atkinson et al. 2003), from which the numbers of oystercatchers were still low ten years later (Clark 2006). Oystercatchers also experience higher levels of competition when shellfish stocks are reduced in early winter (Goss-Custard et al. 2004). In the Netherlands, overfishing of shellfish following a period of reduced productivity, caused mass mortality in oystercatchers and common eiders (*Somateria mollissima*) as the fisherman attempted to maintain their landings (Ens 2006). The same paper links a decline of an estimated 90,000 oystercatchers to this loss of mussel beds in the Wadden Sea.

Apart from bivalves, marine worms are vital to many species of wading birds and are also affected by fisheries industries. Marine worms are harvested as bait (*Arenicola marina, Alitta virens* and *Nephtys hombergii*) and the impacts of bait digging are being investigated in areas such as Poole Harbour (UK), where anecdotal evidence shows that birds may be using the dug trenches as new foraging areas after the diggers have left (*pers. comm.* S.Birchnough, *Southern IFCA*). Studies have noticed declines in the larger-sized worms, presumably breeding individuals, when bait digging is more prevalent (Olive 1993).

In Poole Harbour, a method particular to the area called 'bait-dragging' is thought to have potential effects on the marine worm populations (Birchenough 2013; Fearnley et al. 2013). A report by the Southern Inshore Fisheries and Conservation Authority (SIFCA) into the potential effect of bait dragging mentioned that there is no overlap with the important bird areas (Birchenough 2013), but further study is needed on the potential effects of this method. Its current limited use to a single estuary means that there is no immediate wider need for future research, but I have been informed that studies are still being carried out by SIFCA. In the Netherlands, mechanical dredging for lugworms (*Arenicola marina*) has been carried out since the 1980s and caused a decline of 50% worm densities in just four years (Piersma et al. 2007) and other benthic invertebrates declined as well. The disturbance of the sediment is the cause of these declines, as invertebrates, particularly cockles, find it more difficult to resettle after the disturbance (Dare et al. 2004). The effect on wading birds was noticed through increased gizzard mass, as the birds attempted to compensate for the losses with other, less energy rich prey (Piersma et al. 2007).

3.3.4 Ambient air temperature

Shifts in ambient air temperature directly affect individual birds by altering their energetic needs, and in colder weather they require greater quantities of prey to maintain their energy levels due to increased thermoregulatory costs (Kersten and Piersma 1987; Zwarts et al. 1996b). For oystercatchers, 10°C is the critical air temperature beneath which energetic costs increase (Zwarts et al. 1996a), whilst turnstone's (*Arenaria interpres*) lower critical temperature is 22-23°C and grey plover's (*Pluvialis squatarola*) is 15-20°C (Kersten and Piersma 1987). The same study in 1987 found that oystercatchers needed 40-50% more energy during periods of cold temperatures (10-0°C) and high winds (Kersten and Piersma 1987). In the Netherlands, during cold spells in 1986 and 1987, wading bird mortality increased, particularly in oystercatcher, and after strong frosts many emigrated (Lambeck 1990). There have been cases when low temperatures themselves have caused mudflats to be completely frozen, thus preventing any birds from foraging (Dobinson and Richards 1964). Studies of ring recoveries in the UK confirmed increases in wader mortality during severely cold periods and are being used to investigate differences between species around the coasts (Clark et al. 2004).

Some cues that birds rely upon when moving to their breeding grounds are temperature-based (Sims et al. 2015). Therefore, alterations to local climates in winter may shift their phenological movements, and thus have a knock-on effect on the subsequent breeding season (Bairlein et al. 2007).

It has been shown that winter temperature has an effect on the desirability of an area for birds, as in the case of the northern Wadden Sea, where more waders stay during milder winters compared to more severe periods (Bairlein et al. 2007). Birds tend to move eastwards during milder climates (Austin et al. 2000; Austin and Rehfisch 2003) suggesting that under harsher conditions, western areas are most appropriate to maintain energy (Austin and Rehfisch 2005). Also, although the effects will be described more in the next section, the temperature of the sediment on the Ythan estuary, UK in 1964/65 was shown to be positively correlated with increasing wading bird numbers on mudflats (Goss-Custard 1969).

Higher temperatures have resulted in waders such as plovers (subfamily Charadriinae) foraging on larger items (Pienkowski 1983). In the same paper, the time birds spent waiting for prey to be detected was also noticed to reduce with increasing temperature (up to ~6°C), and is thought to be due to greater availability of invertebrates. Other papers have noted that western sandpipers (*Calidris mauri*) change their foraging behaviours with temperature of the sediment, with more probing actions seen at higher temperatures as the invertebrates remain closer to the surface (Nebel and Thompson 2005).

3.3.5 Sea and sediment temperatures

Fluctuations or prolonged changes in temperature of an estuarine system can affect the life cycles of wader’s prey in terms of reproduction and survival. Prey may shift further away from traditional bird foraging areas to find more amenable climes (Beukema 1990; Kendall et al. 2004; Beukema et al. 2009; Schückel and Kröncke 2013) and thus indirectly force waders to move foraging locations and increase the flight and searching costs that may ensue (Gill et al. 2014).

In general terms, during hotter periods prey move deeper in the substrate (Pörtner 2012) and become less active during colder periods (Pienkowski 1981; Zwarts and Wanink 1993). *Corophium volutator* has been seen in one study to become less active when temperatures drop lower than 6°C (Goss-Custard 1969). Additionally, *Hediste diversicolor* stopped food searching activity below 8°C and increased this between 13 and 23°C (Lambert et al. 1992), and these movements are often used by waders to aid their prey location (Dias et al. 2009). The discovery that some bivalves open less at lower temperatures proves a problem for birds that search for open bivalves (Zwarts and Wanink 1993). Handling time increases were also noted in Pienkowski (1983), where ringed plovers were seen to be affected indirectly by the rising temperatures when handling large worms – possibly due to changes in the time the worms spent on the sediment surface, when detectable by the birds. The activity of invertebrates changes throughout the year depending on temperature fluctuations, with less activity happening in the cooler times of the year, making it harder for birds to find prey (Esser et al. 2008). Some papers have shown that there is not always a link between seasonal temperature variation and bivalves burrowing depth (Zwarts and Wanink 1993), so we cannot always assume that sediment temperature changes will have effects on the foraging success of the birds.

In some cases invertebrates may die off in severe winters (Beukema 1990), thus reducing the prey numbers in traditional foraging areas of waders. However, one observation that was advantageous to birds returning after a severe winter is that prey populations recovered quickly after cold winter with high recruitment levels via overcompensation. In general though, higher temperatures are more beneficial to invertebrate species richness (Beukema 1990). Beukema (1992) reported that several mild winters in the Wadden Sea resulted in recruitment failures of shellfish, whilst a very cold winter in the early 1960s saw large recruitment of cockles in the Wash (UK) (Dare et al. 2004). Several species of bivalves have poor recruitment following winters with an average temperatures of >4°C, as cold winter results in cold springs, but in general there is no significant influence of winter temperatures (Beukema et al. 2009). Additional evidence for recruitment increases after cold winters comes from Weijerman et al. (2005), where after the cold winter of 1977/78, biomass of invertebrates increased in the west Wadden Sea, and Armonies et al. (2001) who saw a similar increase after the 1995/96 winter in the north German Wadden Sea.

Although recruitment may be favoured by a harsh winter, the effects of several mild winters have been shown to negatively affect the amount of prey stock available for birds. In the Wadden Sea, the mild winters of 1988 to 1990 ended with poor bivalve levels and large numbers of oystercatcher and eiders left the area (high numbers of eiders were reported dead as well) (Beukema 1992). The size of invertebrates in the sediment can also be affected by lower temperatures, as some species do not grow until a certain temperature has been reached (Beukema et al. 2009).

Several seasons of recruitment failures may lead to disproportionate communities of large sizes of invertebrates and thus only favour those bird species that forage on larger invertebrates (Goss-Custard et al. 1977). The reverse, loss of larger invertebrates from other causes such as overfishing (Olive 1993), could also have an impact on wader populations. Larger prey species may contain more nutrition per item, but often have a greater handling time (Zwarts and Blomert 1992; Vanermen et al. 2006), and are prone to being stolen via kleptoparasitism (Leeman et al. 2001; Wood et al. 2015).

With changing temperature it is possible to find that some species start to shift their geographic ranges. For example, the bivalve *Macoma balthica* has moved its southern range limit several hundred km further north, and at the same time the Wadden Sea population has been declining (Beukema et al. 2009).

Changes in temperature might also causes regime shifts in the community structure of the invertebrate biomass in an estuary, thus changing the prey availability for wading birds (Bowgen et al. 2015). A regime shift was observed in 1979 in the west Wadden Sea, through a shift in the numbers in worms, which resulted in the abundance of waders changing (Weijerman et al. 2005).

Invertebrate energy levels change depending on time of year and location (Zwarts 1991). They attain their peak body mass during the summer and decrease in mass during winter. At low temperatures, overwinter body mass is less affected, which is probably due to inactivity. This change in mass means that birds have to compensate for poor nutritional status of prey they consume. As less prey are available over winter, birds need to eat more in harsher conditions (Zwarts 1991). In general, waders need to consume up to 1.5-2 times as many prey items winter, due to the poorer condition of prey items (Zwarts 1991).

3.3.6 Weather patterns

A collation of population trends from Bird Life International reports (Saino et al. 2010) shows that birds have difficultly tracking climate changes such as a “thermal delay” (when birds have not compensated for increasing temperatures). Future predictions, such as a climatic induced regime shift in the English Channel (Wethey et al. 2011), are increasing our awareness of the potential effects on species such as waders that are generally linked to the coastal zone.

Severely cold winters seem to be well represented in the literature (Crisp 1964; Dobinson and Richards 1964; Davidson and Evans 1982; Meininger et al. 1991; Yalden and Pearce-Higgins 1997; Schwemmer et al. 2014; Senner et al. 2015). Davidson (1981) categorises two main effects of these periods on waders. Firstly, they are affected by the changes to the invertebrate diversity and behaviours, and secondly, by the increasing energetic costs of regulating their body temperatures. Waders increase their subcutaneous fat contents over the autumn until December/January when it is at its peak (Davidson and Evans 1982); fat levels then decline, leaving them vulnerable. The age of birds also determines how likely they are to be affected by abnormal weather systems, with younger or first year birds being of a smaller size than their adult contemporaries and less experienced in their feeding strategies (Davidson and Evans 1982). Wading birds are known to lose mass over the course of the winter (lean mass) and in some extremely poor winters this can lead to starvation, either during the winter or on the breeding grounds, if they migrated in poor condition (Davidson 1981).

Disturbance and erosion of sediment following storms can affect the benthic communities that support the waders diets (Schückel and Kröncke 2013). Heavy build-up of ice can cause damage to mussel beds as was seen during the 1995/96 winter in the Wadden Sea, when a scouring effect occurred (Strasser et al. 2001).

A detailed article on the effects of different environmental conditions mentions the various issues birds face related to weather (Pienkowski 1981). A benefit of rainfall is higher moisture content of the substrate, which can increase the activity of earthworms (Gerard 2015) and aid waders in their foraging. Rainfall also promotes earthworms to rise to the surface in fields (Goss-Custard 1969; Townshend 1981) and during harsh weather, curlew were observed to use nearby fields to the Tees Estuary, UK (Eriksson et al. 2010). Rainfall is also known to promote changes to the sediment grain structure, promoting fine sand, and potentially improving the invertebrate densities for certain birds (Silva et al. 2006). Yet rainfall can also hinder foraging efforts through reduced visibility (Goss-Custard 1969; Pienkowski 1981, 1983), and a study in India (Aarif et al. 2014) found that higher rainfall was related to lower wading bird counts, potentially due to changes in habitat nutritional content. Strong winds dry out mudflats which results in decreased activity of invertebrates and provokes waders to move away from these areas (Pienkowski 1981). They can also mask invertebrate activities with increased wave action, reducing the visibility of the casts of worms such as *Arenicola*. Dry sand also presents problems for tactile-foraging birds such as knots (Piersma et al. 1998).

Plovers increased their handling time of thin worms with increasing wind force as their directed movements were less accurate (Pienkowski 1983). Yet Zwarts et al. (1996b) found reduced feeding time was only a problem in the short term.

3.3.7 Sea-level rise

One of the major concerns related to climate change is the risk of sea-level rise (Bindoff et al. 2007). Sea-level rise is one of the main changes, alongside mild winters, that may affect wading bird distribution in Britain (Goss-Custard et al. 1990; Austin and Rehfisch 2003; Fujii 2012; Clausen et al. 2013; Hunter et al. 2015). Some predictions from Bairlein et al. (2007) propose that 85cm of sea-level rise (over 100 years) could cause a loss of mudflat height between 4 and 18cm in areas like the Wadden Sea (Netherlands).

One main impact of rising sea-levels will be to reduce the foraging and roosting habitat accessible by wading birds. Few empirical studies show how sea-level rise is affecting waders and instead research is mainly found from predictive papers (Goss-Custard et al. 1990; Austin and Rehfisch 2003; Fujii 2012). Austin and Rehfisch (2003), detailed the risks of changes in estuary morphology and their potential effects on wader numbers (Austin and Rehfisch 2003), mentioning the link of sea-level rise to several changes.

Marine worm species tend to burying deeper in the sediment as it dries out following receding tides (Vanermen et al. 2006), thus making it harder for waders with shorter bills to reach these individuals. Thus for sites with reducing sea-level or changes in tidal-cycles (e.g. following the addition of a barrage (Burton 2006; Clark 2006; Ferns and Reed 2009)), areas of sediment there were previously suitable for tactile foraging would be drier and thus reduce the available foraging area closer to the waterline (Piersma et al. 1998).

As well as simple change in sea-level, the changes to the shorelines and mudflats from habitat loss, gain and anthropogenic influences can alter the depth and fetch of an estuary. These shifts in estuarine profiles have been noted to lead to alterations in the wader community, structures with deeper shores leading to greater similarity between communities and shallower areas becoming more diverse (Mendez Aragón 2012).

3.3.8 Pollution effects

Alongside habitat loss, pollution is the one of the most common environmental changes mentioned in the literature.

Pollution in estuaries tends to indirectly affect bird populations through their food resources. Invertebrates in the sediment take up or are exposed to pollutants (be they inorganic or not) and respond through population declines and increases (Beukema 1991; Saiz-Salinas and González-Oreja 2000; Ait Alla et al. 2006; Smith and Shackley 2006). Reductions in invertebrates have a knock-on effect on species at higher trophic levels like waders. They find fewer invertebrates, spend more time and energy searching and can gain deleterious levels of heavy metals and other pollutants in their bodies, which potentially move higher up the food chain to their own predators (Blomqvist et al. 1987; Bryan and Langston 1992). The inverse, increases in invertebrate populations, will allow for greater numbers and densities of birds to forage in an area (Alves et al. 2012). A review by Bryan and Langston (1992) found that waders were not affected directly by heavy metals in the environment, apart from one case where alkyl-lead pollution was believed to have killed birds in the Mersey.

3.3.8.1 Declines in waders and invertebrates

Excessive use of chemicals by famers (ending up in estuaries through the water catchment), and those working in the marine industries, results in higher concentrations of pollutants in the marine environment (Langston et al. 1990; Ait Alla et al. 2006; MacDonald 2006; Ponsero and Lemao 2011; Newton et al. 2014). During the 1980s, increases in tributyltin (TBT) caused widespread loss of molluscs in areas like Poole Harbour (Langston et al. 2003), and although legislation restricting TBT came into effect in 1987, sediment levels of the pollutant took time to decrease (Evans et al. 1995). As well as being toxic, TBT is known to affect reproduction in molluscs through imposex occlusion (Li and Collin 2009) and sterilisation of females at higher levels, as well as depressed developmental rates (Maguire 2000). New settlement of molluscs is not likely to reach maturity in TBT-polluted areas due to the high proportion of toxin to body-mass ratios that can build up (Langston et al. 1990). Early life stages of marine invertebrates including molluscs and polychaetes have also been shown to be hindered by TBT through impacts on a cellular level (Hagger et al. 2006).

Aside from TBT, other metals exist in the water column and sediment, but their toxicity on wading birds is less well known (Bryan and Langston 1992). Most of those listed in Bryan and Langston (1992) are present in the invertebrates and sediment (and will be passed onto birds), but only TBT, Mercury (Hg) and Selenium (Se) are known to have effects at high enough doses. Zinc (Zn) has been shown to be lethal in worms in the Authie estuary (France), but the same study also indicated that tolerances can build up over time, as in the nearby Seine estuary less individuals were affected (Durou et al. 2005). In Morocco there was a decrease in polychaete numbers following wastewater discharges in one estuary, potentially due to increasing in salinity and declines in organic matter in the water column (Ait Alla et al. 2006). Younger individuals are more likely to be sensitive to chemical pollutants (Durou et al. 2005) and in that case, younger populations or areas of recolonizing invertebrate fauna might be at greater risk from pollution events.

Algal blooms have been associated with invertebrate mortalities, in particular the lugworm (*Arenicola marina*) (Olive and Cadnam 1990; Olive 1993). The increases in algal mats are now being explored to understand their roles following eutrophication of estuaries and their impact on birds (A.Thornton *pers. comm*). Impacts on waders were noted in the Dutch Wadden Sea where cockles over 25 mm died, probably following oxygen restrictions following decomposing algal blooms (*Noctiluca scintillans*), and although waders benefited while foraging on these dying molluscs, the benefit stopped once all were consumed (Poot et al. 2014).

3.3.8.2 Increases in waders and invertebrates

Another visible pollutant effect on the marine environment is the presence of sewage outflows. The pollutants from these, and the chemicals contained in agricultural run-offs, enrich the marine environment (eutrophication) and increase numbers of invertebrates (Beukema 1991; Alves et al. 2012). Studies of wading birds in the Tejo estuary in Portugal have seen increase in numbers black-tailed godwits (*Limosa limosa*) near sewage outflows, as a result of increased polychaete densities (Alves et al. 2012). This and previous reports of increased wader numbers near coastal areas with sewage outflows (van Impe 1985; MacDonald 2006) has resulted in some reductions in wader numbers once ‘clean-up’ actions have been undertaken (Evans et al.

1994). In addition to increased numbers, large sizes of invertebrates were noticed near sewage outfalls in the Tejo estuary, which are more nutritionally preferable for the birds (Alves et al. 2012).

Whilst changes in abundance are the most obvious effects, complete shifts in invertebrate assemblages have also been seen following increased enrichments of marine systems. Between 1931 and 1991 an area of Budle Bay, UK had been replaced with an oligochaete dominated community that is likely to have resulted from increased agriculture in the nearby areas (Evans et al. 1994).

3.3.8.3 Artificial light

It is well known that waders forage at night, but their techniques are normally limited to tactile foraging (Pienkowski 1983; Wood 1984; Goede 1993; Lourenço et al. 2008) rather than using visual cues. The potential of light pollution to aid waders is now becoming observed. Natural illumination occurs during clear nights with a full moon; conditions under which waders have been seen to visually forage. However, birds in the presence of artificial lighting forage for extended periods of time (Dwyer et al. 2012; Davies et al. 2014). A potential negative effect of artificial lighting may be that predators can also take advantage of the increased visibility of wader populations (Santos et al. 2005), though the inverse is suggested in Dwyer et al. (2012) who imply that waders might be able to spot their predators more readily. This means that for areas at risk of construction growth – either housing or industry – an increase in lighting on areas of mudflat might increase the numbers of birds that an area can support.

3.3.9 Introduced species

Introduced invertebrates are frequently found in areas used by shellfisheries where new sources of stock for commercial use are introduced. In the Netherlands, the Pacific oyster (*Crassostrea gigas*) was introduced for cultivation in 1964 and since the early 21st century it has expanded through the Wadden Sea to a point where the oyster might be replacing mussels as prey for birds (mainly oystercatchers) (Scheiffarth et al. 2007). However, they are not a perfect substitute, as the large individuals are not easily accessible, but are now thought to be providing an alternative food source when mussel stocks are low (Scheiffarth et al. 2007). Another introduced bivalve to Europe, the Manila clam (*Tapes philippinarum*) is also being foraged upon by oystercatcher, and following a similar pattern to the Pacific oyster, is becoming more important when stocks of other invertebrates are low (Caldow et al. 2007a). Sometimes introduced species are too large to be efficiently foraged upon, for example Pacific oysters have been found to often be inaccessible to even specialist bivalve eaters like oystercatchers (Scheiffarth et al. 2007; Bray et al. 2015). Species are not always introduced by humans, changing climates provide opportunities for range expansion and subsequent invasions (Caldow et al. 2007a; Humphreys et al. 2015).

Indirect effects on the prey of wading birds have been shown through an experimental study on the effect of introduced green crabs (*Carcinus maenas*) on dunlin foraging. Higher densities of green crabs reduced polychaete availability whilst increasing the availability of small clams. This shifted the diets of the dunlin to include more small clams (Estelle and Grosholz 2012).

3.3.10 Disturbance and predation

The effects of disturbance on the normal behaviours and activities of birds is becoming better understood, and is being taken into consideration in new management plans and conservation areas (Milsom et al. 1998; English Nature 2000). Disturbance entails the birds being affected by the presence of humans or human developments that are not part of their normal environment (Cayford 1993). Affected birds may respond in a similar way as they respond to predators, moving away a ‘safe’ distance (this is relative to each species) before re-starting their previous behaviours (Weston et al. 2012). The ecological cost to these actions comes from loss of energy, due to the high costs of flight, and the loss of foraging time, especially during already short days and tidal cycles (Goss-Custard et al. 2006b). Rising development along coastlines increases the chance of such occurrences happening, and potentially causes disturbance to wading birds on nearby habitats.

Examples of disturbance effects on wading birds exist throughout recent literature. A study of the effects of construction work showed that the birds’ foraging activity and densities were lower in areas near the construction (Burton et al. 2002). In some cases, waders are not affected by potential disturbance events/areas. In Sussex, UK, wading birds using fields for supplementary feeding were found to have no difference in preference for areas close to fields or footpaths (Milsom et al. 1998; Burton 2007).

Wading birds have also been shown to be sensitive to loss of roost sites. In one area of Poole Harbour, UK, an increase in human activity resulted in a decrease in available roost sites, thus adding pressure to other sites around the area (Morrison 2004). Additional information on the loss of roost sites comes from Bairlein et al. (2007) who mention that decreases of salt marsh areas can increase the risk of disturbance.

Predation risk and disturbance have been shown to influence where wading birds reside, as in the case of the Baie de Somme, France, where oystercatchers are only found inside a hunting-free reserve area rather than the hunted surrounding area (Triplet et al. 1999). Although it should be noted that some studies have found that certain species are more prone to predation than others, such as redshank and dunlin, and might be more affected than large birds when considering predation risk increases (Cresswell and Whitfield 1994).

Disturbance effects on waders can change from loss of habitat, as mentioned in the habitat loss section above, through to having to choose new foraging habitats and increases in kleptoparasitism, due to higher densities on smaller areas, both incurring additional energy requirements and stresses (Rappoldt et al. 2010; Weston et al. 2012). Potential competition may cause some individuals to leave an area if the interference competition is too high (Goss-Custard and Moser 1988). Additionally, increased numbers change the vigilance levels of wading birds (Vahl et al. 2005), although the impacts of kleptoparasitism can then reduce the positive effects.

Problems with measuring the impact of disturbance on populations has been mentioned in the literature, as most papers consider the changes to energy reserves and behaviours of individuals, but not overall survival (Stillman et al. 2007).

3.4 How does environmental change affect wader population sizes?

The wide range of studies found in the literature review potentially allows the effect of environmental change on birds to be quantified. To do this, values would be required for both the amount of environmental change and the response of the birds. To include studies in a single analysis, both the amount of change and the response of the birds would need to be measured in a consistent way. However, the literature review showed that there was a lack of consistency in the values and units used to measure environmental change effects. The only comparable environmental changes were habitat loss, caused either by direct removal of habitat, or indirectly through loss of prey through shellfishing. Papers related to other types of change, such as changing energetics or hours lost feeding, did not quantify change in such a consistent way, and so comparisons between studies could not be made.

Table 3.4 shows values of habitat loss and the related changes in local populations using the affected sites. Figure 3.4 shows the relationship between percentage habitat loss and percentage change in bird population size. A linear regression describing this relationship was fitted in R version 3.2.3 (R Development Core Team 2015) using ggplot2 (Wickham 2009). The linear relationship for the effect of habitat loss on wading bird populations (Arcsine transformed) is just non-significant with a p value of 0.067 ($F_{(1,18)}$=3.79, r^2=0.1739). Interestingly, from both Table 3.4 and Figure 3.4, there is a noticeable lack of papers that cover small scale habitat loss.

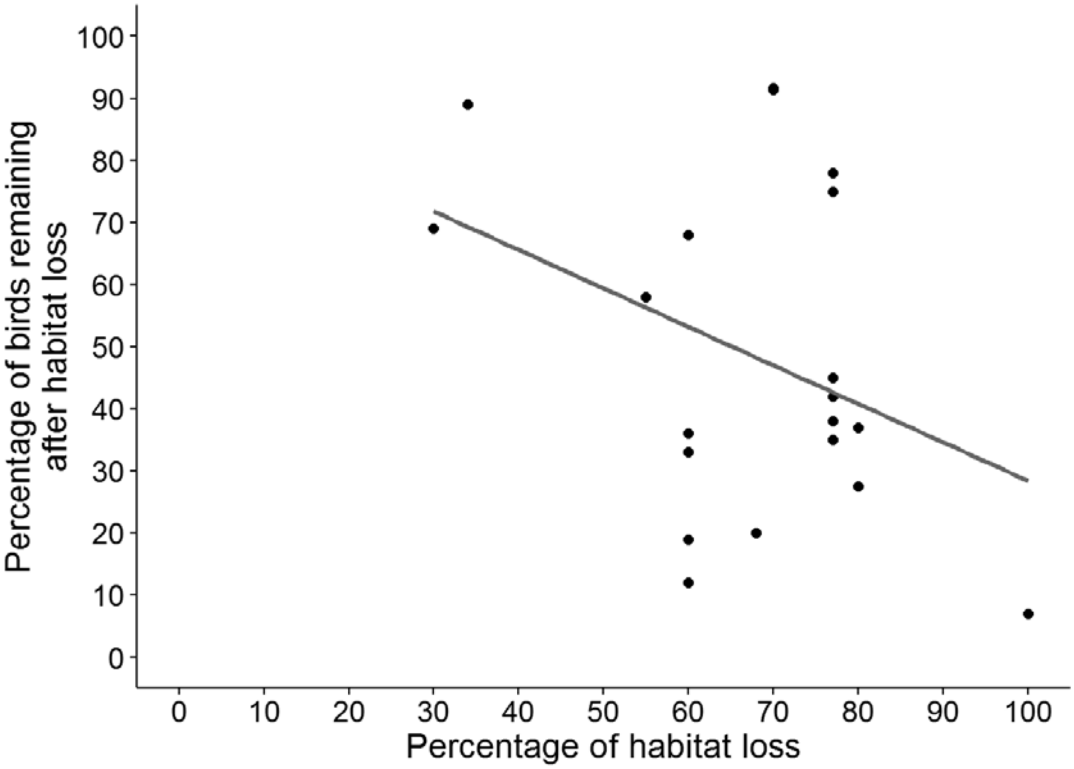

Figure 3.4. Relationship between the percentage loss of habitat and the corresponding percentage of birds remaining following the habitat loss.

Table 3.4. Empirical sources for habitat declines and associated wading bird population declines from the literature. UK=United Kingdom, NL=Netherlands, CN=China.

References - 1)Prater 1981, 2)Evans 1978/79, 3)Atkinson et al. 2010, 4)Schekkerman et al. 1994, 5)Duriez et al. 2009, 6)Atkinson et al. 2003, 7)Dare et al. 2004, 8)Yang et al. 2011, 9)Kraan 2010, 10)Kraan et al. 2009, 11)Piersma et al. 2007, 12)Burton and Armitage 2008, 13)Burton 2006.

Habitat loss type	**Location**	**Species**	**Dates**	**Habitat loss (%)**	**Population remaining (%)**	**Refs.**
Land reclamation	Teesmouth, UK	Dunlin *Calidris alpina*	1970-77	77	75	1
Land reclamation	Teesmouth, UK	Oystercatcher *Haematopus ostralegus*	1970-77	77	78	1
Land reclamation	Teesmouth, UK	Redshank *Tringa totanus*	1970-77	77	45	1
Land reclamation	Teesmouth, UK	Curlew *Numenius arquata*	1970-77	77	42	1
Land reclamation	Teesmouth, UK	Bar-tailed godwit *Limosa lapponica*	1970-77	77	38	1
Land reclamation	Teesmouth, UK	Knot *Calidris canutus*	1970-77	77	35	1
Land reclamation	Teesmouth, UK	Dunlin *Calidris alpina*	1972-74	60	33	2
Land reclamation	Teesmouth, UK	Grey plover *Pluvialis squatarola*	1972-74	60	36	2
Land reclamation	Teesmouth, UK	Bar-tailed godwit *Limosa lapponica*	1972-74	60	12	2
Land reclamation	Teesmouth, UK	Redshank *Tringa totanus*	1972-74	60	19	2
Land reclamation	Teesmouth, UK	Shelduck *Tadorna tadorna*	1972-74	60	68	2
Dredging	The Wash, UK	Oystercatcher *Haematopus ostralegus*	1981-03	70	91.7	3
Dredging	The Wash, UK	Knot *Calidris canutus*	1981-03	70	91.4	3
Dams	Oosterschelde, NL	Waders *unspecified*	1986-87	30	69	4,5
Overfishing	The Wash, UK	Knot *Calidris canutus*	1990-92	80	37	6,7
Overfishing	The Wash, UK	Oystercatcher *Haematopus ostralegus*	1990-99	80	27.5	6,7
Land reclamation	Bohai Bay, CN	Curlew *Numenius arquata*	1994-10	34	89	8
Overfishing	Wadden Sea, NL	Knot *Calidris canutus*	1996-05	55	58	9,10
Dredging	Wadden Sea, NL	Knot *Calidris canutus*	1997-03	68	20	11
Barrage	Cardiff Bay, UK	Redshank *Tringa totanus*	1999-00	100	7	12,13

3.5 Discussion

From the literature review, it appears that the effects of disturbance are the most frequently published. Disturbance research is one that many local councils and governing bodies are becoming more aware of, as seen by updates to current guidance for developers (Scottish Natural Heritage 2016), and increases in contract research to understand the potential impacts for specific developments (Stillman et al. 2012). Looking purely at non-breeding environmental changes, the effects of weather (including temperature), habitat loss (including shellfishery impacts), pollution (including eutrophication etc.) and sea-level rise follow sequentially in terms of frequency of publication. These can all be investigated in individual-based models of wading bird survival, and will be used later in this thesis (see Chapter 6) adding to previous studies of similar scenarios (Goss-Custard et al. 2006c; Caldow et al. 2007b; Durell et al. 2007, 2008b).

As mentioned in the introduction and shown in the review, environmental changes and responses of birds are often not measured in constant enough ways to allow comparisons between studies. With the lack of clearly comparable studies, habitat loss was the only environmental change for which the relationship between environmental change and the response of the birds could be determined. The lack of papers publishing comparable results, and in particular results for habitat loss events of less than 30%, reduces confidence in predicting the effects of small scale losses.

The responses of waders to small habitat losses are therefore currently unknown. Although there may be no effect, for example, if wading birds are not at carrying capacity before habitat loss (Goss-Custard et al. 2003), this is still a major knowledge gap. A lot of future environmental changes have the potential to be relatively small – e.g. loss or introduction of a new pier (Burton et al. 1996), a port berth (ABP 2012) - rather than large scale estuary losses such as that seen in Saemangeum, Korea (Moores et al. 2016).

Several studies have measured the effect of environmental change on waders in closed, caged, environments (Kersten and Piersma 1987; Kersten and Visser 1996; Kvist et al. 2001). These studies provide very valuable insights, but do not directly address how free-living birds may respond to change. Some scenarios, such as increasing temperature or sea-level are still yet to occur at effective levels in the environment to investigate their effects on waders, but overall the lack of information alongside incomparable units does pose a problem to understanding the effects of change from past empirical studies alone.

In the normal daily routine of a non-breeding wading bird, the need to survive is governed by some general criteria – the need for space (foraging, roosting areas), the need for time (time to feed and move between foraging areas) and individual energetics (consumption and assimilation rates). Each of the environmental changes directly impact one or more of these aspects and thus we can categorise the effect on wading birds. In terms of a wader's spatial needs, habitat loss and gain, shellfishing industries and sea-level changes are all likely to affect the amount of area a bird can access. Time is impinged upon by sea-level rise, weather and disturbance through loss of hours that an individual can spend feeding or roosting. A bird's energetics will be affected by weather, temperature, pollutions, diseases and parasites, introduced species and the shellfishing industry; the first four increase energy requirements whilst the last two alter the energy available via prey items.

Overall, while the value of empirical studies cannot be refuted, the missing data for both type and scale of environmental change on waders provides a perfect opportunity for techniques like individual-based modelling to fill the gap. The ability to model any size of environmental change is highly valuable given the increasing need for quick, accurate predictions to aid in conservation and management efforts. Other predictive modelling studies have started to look into the effects of such scenarios (Stillman et al. 2003; Caldow et al. 2004; Durell et al. 2006, 2007; Goss-Custard et al. 2006a; Stillman 2009) and the following chapters of this thesis will add to and update the current knowledge of this subject.

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4. Development of a suite of individual-based models to predict environmental change effects on wading birds

The aim of this chapter is to describe the processes and rationale behind the development of a suite of individual-based models. The completed models are used in the following chapters (Chapters 5 and 6) to answer questions on how environmental change affects wading birds.

Before reading this chapter please note that when parameters are named in the main text they will be capitalised and in italics. Additionally some process and parameters described below are not used in my final models but were developed for related projects and future work.

4.1 Introduction

Modelling animal population dynamics to answer conservation questions is an ever expanding research area. With greater emphasis being placed on effects of anthropogenic impacts both conservationists and developers need new and quick ways to provide understanding for how management and mitigation will work. Wading bird conservation needs to be considered around the UK's many estuarine systems that provide important foraging sites for many European species (Moser 1987; Austin and Rehfisch 2003; Musgrove et al. 2011) and current threats to these habitats come from multiple directions – port and housing expansions (Davidson et al. 1991; van den Bergh et al. 2005; Burton 2006; Yang et al. 2011; Wang et al. 2014), sea level rise (Austin and Rehfisch 2003; Fujii 2012), pollution (Blomqvist et al. 1987; Evans et al. 1995; MacDonald 2006) and human disturbance (Burton et al. 1996, 2002; Fitzpatrick and Bouchez 1998; Stillman and Goss-Custard 2002). With predictive modelling techniques becoming more common we find that many ecological (and avian) systems are having such models developed for them (Pettifor et al. 2000; Aben et al. 2014; Kułakowska et al. 2014; Chudzińska et al. 2016), but with the range of different processes and software used in their development, direct comparisons are not always possible. Researchers and ecological managers are keen to work together to understand future environmental changes (Mouquet et al. 2015; Wood et al. 2015a) and having a range of models that can be easily adapted to new locations and scenarios whilst still be comparable in their outputs is highly desirable.

When considering different types of models to successfully answer ecological questions individual-based models (IBMs) that use the fitness-seeking ideas of individual-based ecology provides a flexible solution (Grimm and Railsback 2005). IBMs are designed to allow an individual organism’s behaviours and interactions to maximise their own fitness within an environment to understand how a population survives over a fixed time period (Grimm and Railsback 2012a). The population level behaviours emerging from modelled individual decisions and interactions provide ‘realism’ to the models that is not seen in other modelling techniques. Compared to traditional models which rely on population level approaches these have shown greater insights into the ability of models to give accurate results (Grimm and Railsback 2005; Stillman et al. 2014b). A great deal of work has been put into improving the understanding of these models and the development of the Overview, Design and Details (ODD) protocol for ease of communication has increased the permeability of this modelling system within ecology (Grimm et al. 2010). The pattern-orientated aspect of IBMs (Grimm and Railsback 2012b) works particularly well for avian systems as thousands of surveys are carried out each year to understand distribution patterns of birds (Wetlands International 2012; Holt et al. 2015) and can be used to validate final model results.

Whilst IBMs (and the equivalent ‘agent-based models’, more commonly found in the social sciences) have been developed for many organisms worldwide (Grimm 1999) including fish (Railsback and Harvey 2002; Kirby et al. 2004; Phang 2013; Murray 2014), mammals (Pitt et al. 2003; Mazaris et al. 2006; López-Alfaro et al. 2012), invertebrates (Butler IV et al. 2005; Choi et al. 2006) and parasites (Lane-deGraaf et al. 2013), they have been particularly used within avian ecology (Goss-Custard and Stillman 2008). The research carried out by Goss-Custard, Stillman, Caldow, Clarke and colleagues culminated in the development of the highly adaptive MORPH individual-based modelling platform, that allows for relatively quick development of IBMs (Stillman 2008). Although primarily designed to understand wading bird ecology it has shown its flexibility by being applied to fish (Phang 2013; Murray 2014), mammals (unpublished –Stillman) and flamingos (Deville 2013).

This chapter of my PhD has taken a previous modelling approach (see Chapter 2 of this thesis) and developed a suite of IBMs for five estuaries that are directly comparable in their outputs. Using these models, the following chapters predict the effects of large scale environmental changes on wading bird populations across the five estuaries and produce general conservation rules and conclusions. The properties of IBMs models make them ideal to use as ‘virtual laboratories’ for testing such scenarios (Grimm and Railsback 2005).

4.2 Methods

4.2.1 Study areas

The five estuaries in this suite of models were chosen due to the pre-existence of high quality invertebrate surveys that most importantly had invertebrate densities separated by size class (see Figure 4.1). As pointed out in the second chapter of this thesis, good quality predictions are not possible in the presence of simplistic invertebrate surveys with no measurements of invertebrates included in them. A result of this selection is that each of the estuaries has previously had IBMs produced, but the suite of models presented in this chapter completely redevelops these. An overview of the estuaries can be found in Table 4.1 with date of designation as a special protection area (SPA), which will be discussed in relation to the models in the following chapters.

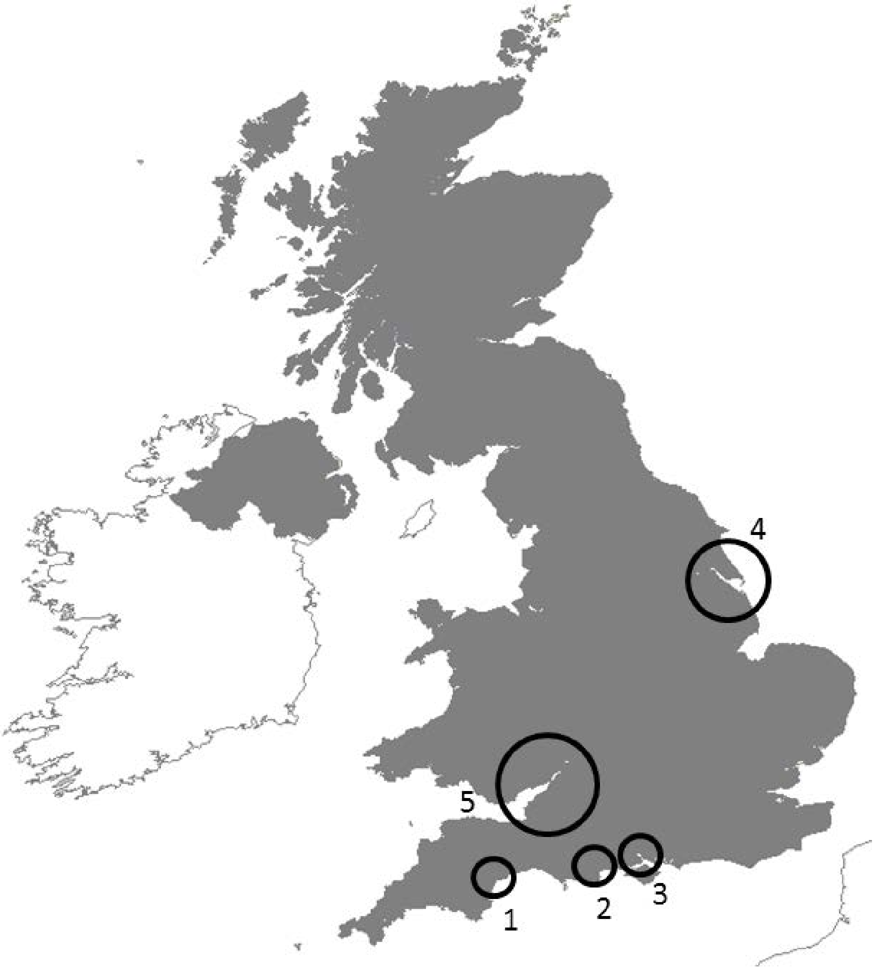


Figure 4.1. Locations of five estuaries used on a map of the UK.

Table 4.1. General information for the five estuaries used in the suite of model

Estuary	Location on map Fig.1	SPA date of designation	SPA area (ha)	Estuary and invertebrate source locations
Exe estuary	1	11/03/1992	2345.71	Durell et al. 2007
Poole Harbour	2	31/03/1999	2271.99	Durell et al. 2006 Herbert et al. 2010
Southampton Water	3	01/10/1998	5505.86	Stillman et al. 2012
Humber estuary	4	28/07/1994	15202.53	Stillman et al. 2005
The Severn estuary	5	13/07/1995	24700.91	Garcia et al. 2011 Stillman 2010

4.2.2 Model description

The IBMs described in this chapter were created using the modelling platform MORPH. This modelling platform and its predecessors has been comprehensively described in Stillman 2008 (Stillman et al. 2005a, 2005b, Durell et al. 2006, 2007; Caldow et al. 2007).

The model simulations run through a series of processes and loops until the allotted time period has been reached (a seven month winter period for these models). Figure 4.2 graphically shows the sequence of events in the model process (scheduling) and more details about the underlying program can be found in Stillman 2008.

The parameter files for the models are created using the assistance of spreadsheet software to produce to final files (signified by a '.par' suffix) to be read into the MORPH.exe program. The parameter files are divided into three entities that define the global environment, the patches (containing resource and components for assimilation) and the foragers. Whilst the global and patches entities are individual to each estuary the forager parameters remain the same (except numbers of birds and calibration adjustments) providing additional comparability between IBMs.

4.2.3 Model parameterisation

The parameter files start with some short code to define the map image coordinates (used by the model to plot the patches and forager visualisations) along with the name of the simulation and any pre-defined images to use on the map. Following this the three entities – Global environment, Patches and Foragers are described.

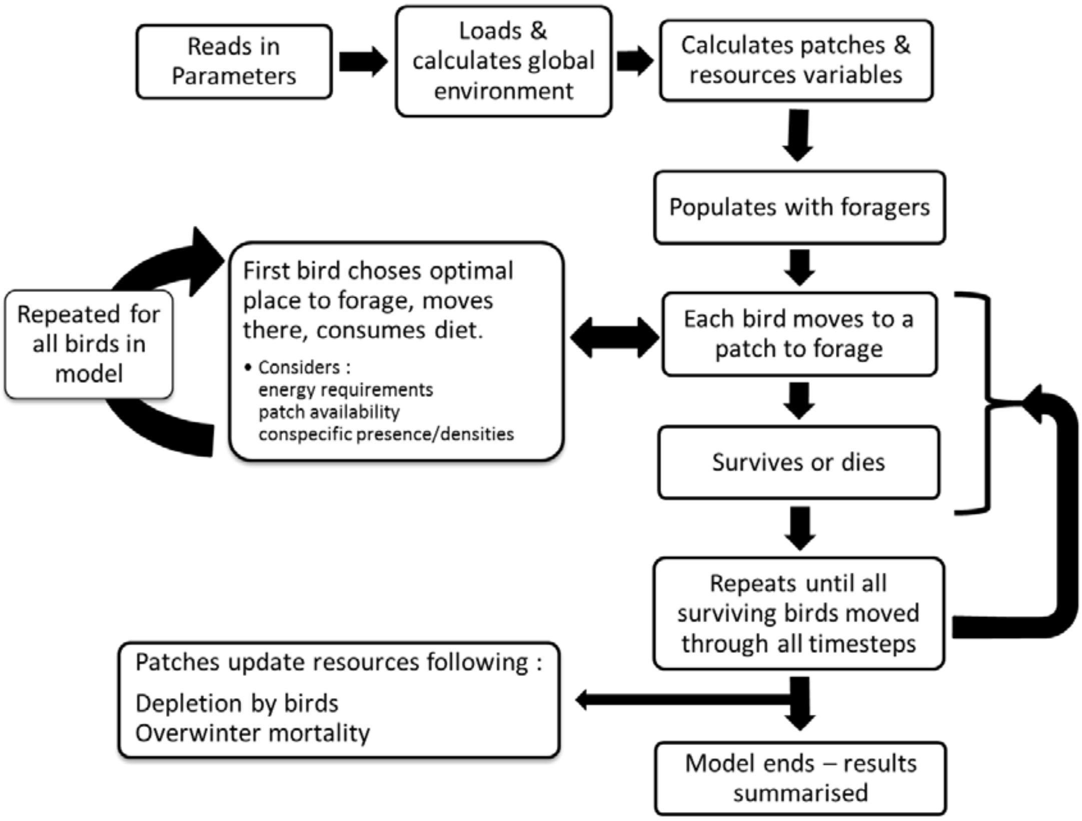


Figure 4.2. Flow chart of scheduling used in MORPH simulations.

4.2.3.1 Global environment

This section defines the state variables that are used throughout the model system. For the overwinter wading bird systems used in my models, a seven month period of 212 days is defined in 5088 hour long time steps of length 1 (indicating 1 hour). As bird numbers (described below in section 5.2.3.3) are averaged over the winters of 2009/10-2013/14, the middle year of this period was used to parameterise the global variables - 1st September 2011 to 31st March 2012.

The global variables are then defined as follows:

i) Day and Weekend

The equation used to define *Day* computes each time step in decimal hours starting from the 1st September through to the 31st March. It is included to allow differentiation between day and night which is used later on in the model to determine the availability of foraging patches.

Weekend is included for future work (not covered in this thesis) that looks at events in the working week versus weekend events that can affect wading birds differently.

Day	*1 + ((TimeStepLength*(TimeStep-1)) div 24)*
Weekend	*If(((Day-1) mod 7 <= 1),1,0)*

ii) Time

An equation is used to convert time steps into hours of the day falling on the half-hour to include effects of a whole hour.

((TimeStepLength(TimeStep-1)) mod 24) + (TimeStepLength/2)*

iii) Daylight

This is a predefined binary list for a central location on each estuary taken from the United States Navy Observatory Astronomical Application Department's website "Sun or Moon Rise/Set Table for One Year" (accessed from http://aa.usno.navy.mil/data/docs/RS_OneYear.php). The data from this website is rearranged to determine presence of daylight (1) or not (0) for the 5088 time steps and is saved as a '.var' file that the MORPH.exe program can read and refer to.

iv) Tide Height

As with daylight these are '.var' files read in from the same location as the parameter file that can be referred to by the model per time step. Using the TideWizard software (Smartcom Software 2009) separate tidal cycles ranging across the estuaries were saved and rearranged into '.var' files for the required years in metres above chart datum.

v) Temperature

Using the UK Daily Temperature Data available from the Met Office Integrated Data Archive System (MIDAS) dataset housed at the British Atmospheric Data Centre, I downloaded daily temperature data (max and min °C) for a central location to each estuary as close to, if not on, the shoreline as possible (Met Office 2006) for around 50 years. A polynomial equation was determined from the mid-point values of the max and min °C of each day and compared with the MORPH day (1-212) related to each calendar date (MORPH day 1 = 1st September). Table 4.2 shows the locations where temperature data was sourced from alongside the years used and the final equation to predict average temperature for each estuary over the last 50 or so years.

Whilst temperature is read in and calculated absolutely for each day, in the model it can be adjusted for investigations into the impacts of climate change. This adjusted temperature, is used by the foragers later on in the model.

Table 4.2. Temperature locations, years covered and final equations for each estuary. Days are counted from the beginning of the model where Day 1 = 1st September through to Day 212 = 31st March.

Estuary	**Location of temperature data**	**Met Office Station Number**	**Dates covered in data**	**Equation**
Exe estuary	Exmouth Starcross	1377 1372	1959-1990 1990-2005	(0.0005034*(Day*Day))-(0.1510*Day)+17.00
Poole Harbour	Poole S Wks	1328	1963-2013	(0.0005790*(Day*Day))-(0.1687*Day)+17.65
Southampton Water	East Park Mayflower Park Southsea	849 848 861	1955-1969 1970-1999 2000-2003	(0.0006050*(Day*Day))-(0.1774*Day)+18.34
Humber estuary	Hull	369	1959-2010	(0.0006540*(Day*Day))-(0.1861*Day)+17.47
The Severn estuary	Filton	676	1957-2015	(0.0006007*(Day*Day))-(0.1739*Day)+17.18

4.2.3.2 Patches

Following work with my third supervisor (John Baugh) and his colleagues (HR Wallingford), I defined the final patches used in each estuary. Initial intertidal areas were found using downloadable Geographical Information System (GIS) shapefiles from the Ordnance Survey's Vector Map District which defines the 'Foreshore' area for all estuaries (Ordnance Survey 2015). This Foreshore is the area of sediment lying between mean high water springs and mean low water springs and using ArcGIS (ESRI 2012) I calculated areas (in m^2) once I had decided on my patches (see Appendix 3 for estuary specific patch names). Additionally, each *Patch Area* has been set up for future simulations of habitat loss; a simple change of a multiplier between 1.0-0.0 (0-100%) will adjust the percentage of habitat available on all accessible patches.

The last two patches of every model (*Roosts* and *Fields*) had their areas defined by slightly different methods. Across all five models *Roosts* were given a large set value of $1,000,000m^2$ (100ha) as this is a 'safe' refuge unlinked to density dependence effects and so the size is arbitrary. *Fields* are important additional foraging sites (Goss-Custard 1969; Townshend 1981a; Hulscher et al. 1993; Smart and Gill 2003; Navedo et al. 2013; Furnell and Hull 2014) and whilst they have been previously studied for their effect on waders in IBMs (Durell et al. 2006) their total area in relation to an estuary has yet to be standardised. There is little published research to help determine the area of fields that a bird population will access from an estuary let alone the distance they will travel to get there. In my calculations I used a maximum distance of 0.5 km from the mean high water of an intertidal area following two studies that indicated this was an appropriate distance birds would travel on average (Hayhow 2009; Furnell and Hull 2014). Using OS maps (Ordnance Survey 2015) and satellite images (Map Data © 2016 Google) I manually drew polygons for all fields and open grassland and calculated the area contained. The resulting area is an overestimate as bird's usage of fields for additional foraging space depends on additional factors such as water table, size and sward height (Hayhow 2009), and so it was decided to reduce the measured size. Using the measured areas of fields exploited by oystercatcher on the Exe estuary (Durell et al. 2007) compared to total field area within a 0.5 km radius of the estuary (measured in ArcGIS using OS maps), a percentage of 23% was arrived upon (areas in study vs. measured areas in GIS) to adjust all field areas.

Using the Mermaid software developed by HR Wallingford (Benson 2016) to interrogate hydrodynamic systems, the shapes of each estuary's patches were applied over the top of a representative tidal cycle model for each of the five estuaries. These patches were then interrogated for differences in lag of periods when the water level was <0.01m or 'dry' (see Appendix 4 for greater detail on this process). Patches with internal lags of greater than 1 hour (the length of a time step in my models) were split into upper and lower shore patches as they expose sequentially over the course of a tidal cycle. These new shapes were then applied back onto the OS Vector Map foreshores to calculate the exact area (in m^2) of each patch.

Coordinates for the image of each estuary that MORPH shows in its view screen were set using a small piece of unpublished software developed by R.A.Stillman to aid in the quick parametrisation of coordinates for MORPH. The final image shows the locations of all patches, and foragers (identified by colour for each type) are shown over the patch they are currently using (Fig.4.3).

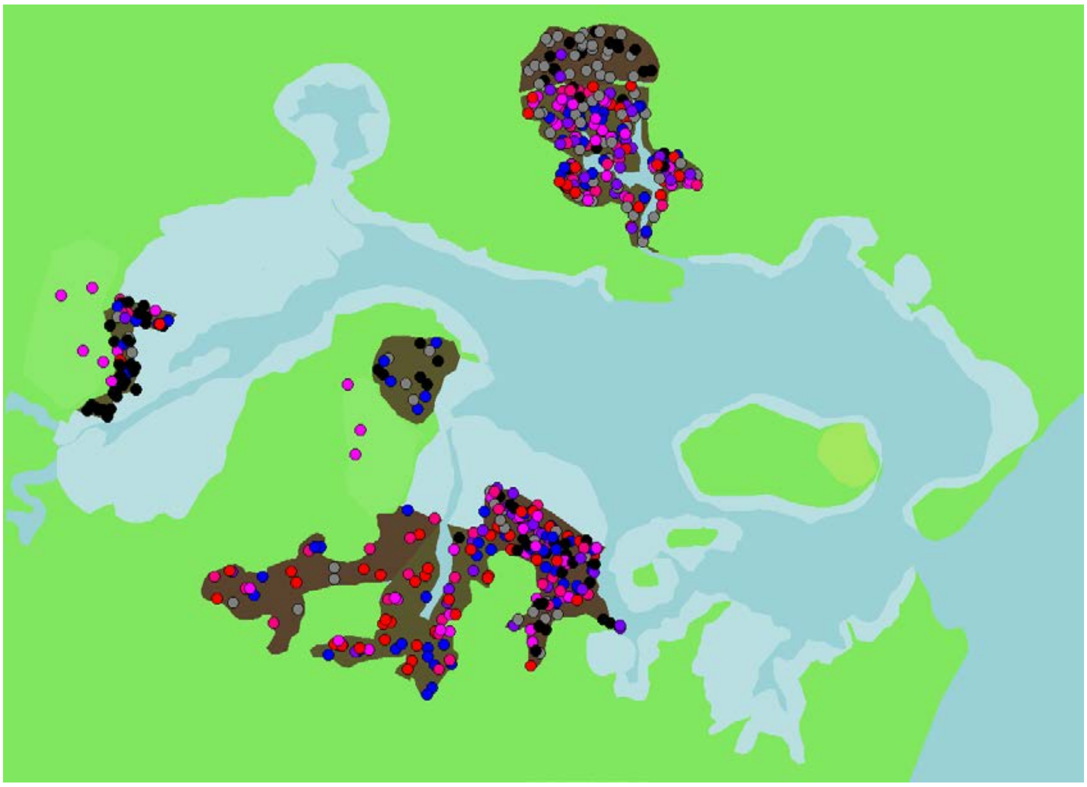


Figure 4.3. A screenshot of the final image (Poole Harbour) shown in the MORPH viewer. Light blue areas indicate currently unavailable foraging habitat whilst lighter green areas are the fields and roost (on the large island). Coloured circles represent the foragers with dunlin = red, grey plover= purple, redshank = blue, black-tailed godwit = pink, oystercatcher = grey and curlew = black.

i) Patch variables

Each patch is available to be used by the foragers depending on a set of three patch variables – *Shoreheight*, *Available* and *Roost*. *Shoreheight* is the median height in metres (chart datum) of a patch's bathymetry and indicates when a patch will be either 50%+ covered with water or 50%+ exposed. MORPH compares the value of each patch's *Shoreheight* to the tidal height (also in chart datum) and if the tide height is less than this value the patch is deemed exposed through the Available variable.

The value of each patch's *Shoreheight* was determined with the help of pre-existing hydrodynamic models for each of the five estuaries (Benson 2016). The 'dry' function mentioned previously determined what percentage of time a patch was exposed during an average spring and neap tidal cycle and then using a comparison table of the appropriate tidal cycle file (see Tide Height section above) used this to determine the *Shoreheight* value in metres that would allow the patch to be exposed to match (see Appendix 4 for further details on this process). It should be noted that *Shoreheights* for the Exe estuary were determined from Admiralty charts (SeaZone Solutions Ltd 2013) as no hydrodynamic model was available.

Unlike the foraging patches, the availability of *Fields* and *Roosts* are not determined by the tidal cycle. *Roosts* are available to the foragers all the time on every estuary whilst fields are only available during daylight hours (Goss-Custard 1969). The final variable *Roost* determines that the patches called *Roosts* are 'safe' areas and can be used by birds when they do not require any energy for a time step or cannot access anywhere else.

ii) Resources

Each patch has the option to contain densities of invertebrates per m^2. The resources are defined initially by prey type and size class (in mm) based on a standard set of invertebrates found on all of the five estuaries and common to the diets of wading birds (see Appendix 5). The importance of size classes has previously been mentioned in chapter 2. As with the *Patch Areas*, these densities per m^2 have been set up with a multiplier (1.0-0.0) that will adjust the percentage of resource available for a patch for future chapters work on the effects of environmental change on wading bird's prey.

Some of the invertebrate surveys are not as comprehensive as others. The majority of surveys took multiple cores but the depths varied between 15cm and 30cm and from 4 to 158 sample sites and as such it is felt by myself and my supervisors that larger prey items may have been missed thus resulting in reduced food supplies for certain (often larger) birds.

It is known that resources densities do not remain the same throughout the winter; for example due to predation by the birds and losses due to other causes (Beaumont et al. 1989; Beukema 1990; Olive and Cadnam 1990; Atkinson et al. 2003). To account for this change, the resource densities are altered by a percentage loss derived from a previously calculated "overwinter mortality". In five previously published MORPH IBMs this overwinter mortality due to non-bird reasons had been calculated by comparing the difference in densities between spring and autumn surveys over a winter (less that taken by the local bird populations) and using this depletion in the models. The overwinter mortality in Poole Harbour (Durell et al. 2006), the Exe estuary (Durell et al. 2007), the Southampton Water (Stillman et al. 2012), the Humber estuary (Stillman et al. 2005b) and the Baie de Somme (Durell et al. 2008) was averaged based on size classes of resources surveyed (see Table A5.1).

iii) Resource component

The final section of the patch parameters concerns the energetic component of the resources consumed by the birds (see Table A5.1). In previous incarnations of wader models this has been stated in grams of Ash Free Dry Mass (AFDM) but in my current model this has been updated to energy in kilojoules (kJ) to match the energy store of foragers (see following Foragers section). As all invertebrate species energy had been measured in AFDM I used a conversion multiplier of 22 kJ g^{-1} (Zwarts and Wanink 1993).

AFDM in grams has been calculated from invertebrate length to AFDM relationships via several sources – principally linear relationships from Thomas et al. (2004) but mussel values have come from surveys on the Exe estuary (Durell et al. 2007; Stillman et al. 2014a). For the smallest size of worms (0-5mm) the AFDM is fixed per item and comes from previous fieldwork work (Herbert et al. 2010). It should be noted that the AFDM equation used for Other Molluscs is for *Scrobicularia plana* as this invertebrate best matches the general profile of mollusc species found in this resource category for my estuaries. Also most crustaceans found in the surveys were on the smaller side of the subphylum and thus the *Gammarus* equation was used to predict AFDM. It is hoped that in future invertebrate surveys larger species will be found either through surface surveys or deeper cores to increase the diversity of resources.

The hard shelled invertebrates of *Cerastoderma*, Mussels, Other Molluscs, *Littorina* and *Peringia* maintain their size throughout the winter due to their external structure but their flesh reduces in size at a constant linear rate (Stillman et al. 2000). As a result, a percentage loss of 28% over the course of the winter is applied to these five resources to reduce their energy store as would be found in nature (Zwarts 1991; Zwarts and Wanink 1993).

With the limited nature of earthworm surveys for the estuaries the densities and AFDM values come from surveys of the Poole Harbour area (Durell et al. 2006) and are used for the other estuaries. Due to earthworms being an additional food source (usually only used when intertidal areas are unavailable) this is not an unreasonable assumption to make (Goss-Custard 1969; Heppleston 1971; Ferns and Siman 1994; Ausden et al. 2001).

4.2.3.3 Foragers

The numbers of individuals in each estuary are based on the latest available five year (2009/10-2013/14) average monthly counts of each species in the Wetland Bird Survey (WeBS) supplied by data request to the BTO (Holt et al. 2015). I chose species that had on average over 100 individuals seen during October to February (to account for the majority of birds outside of immigration and emigration periods). These values were then rounded to the nearest 50 (see Table. 4.3) to allow division into super-individuals that expedite the running time of the models.

Table 4.3. Number of foragers on each estuary based on BTO WeBS count data.

Model name	**BTO code**	**Exe estuary**	**Humber estuary**	**Poole Harbour**	**Severn estuary**	**Southampton Water**
Dunlin	DN	2,450	10,850	1,400	17,550	1,150
Sanderling	SS	0	300	0	0	0
Ringed Plover	RP	0	0	0	100	0
Turnstone	TT	100	200	0	300	200
Knot	KN	0	17,350	0	850	0
Redshank	RK	400	2,300	750	3,000	250
Grey Plover	GV	200	1,350	100	200	100
Black-tailed godwit	BW	800	1,300	1,300	200	250
Bar-tailed godwit	BA	200	1,350	100	0	0
Oystercatcher	OC	1,600	3,800	850	650	850
Curlew	CU	750	2,400	850	2,800	400
Total		6,500	41,200	5,350	25,650	3,200

Each of the eleven species has nine constants that are maintained throughout the model runs and provide a certain amount of individual variation.

i) Arrival and Departure days

In this suite of models all birds are present at the beginning of the model (*Arrival Day* = 1). The *Departure day* is also set such that birds remain in the model until the final day.

ii) Arrival, Target and Departure Energy Store

Each individual is allocated an *Arrival Energy Store* in kJ that is currently used as the *Target Energy Store* each bird aims to maintain per time step to survive to the next. This value is derived from the difference in mass in grams taken from the BTO's ringing values (Robinson 2005) less a starvation mass per species (see Table A6.1). This starvation mass was calculated from starvation weights taken from dead birds in the field (J. D. Goss-Custard pers. comm.) and using a linear relationship from these with the BTO ringing weights to work out values for other species. To convert from grams to kJ I multiplied by 34.3 per Kersten and Piersma (1987).

iii) Day and Night Efficiency

This is one of the first parameters to add individual variation to the birds as for *Day Efficiency* each individual is given a random value around a mean of 1 with a standard deviation of 0.125 based on work done on the Exe estuary (Stillman et al. 2000). *Night Efficiency* has been taken as a proportion of *Day Efficiency* from a couple of sources (Sitters 2000; Lourenço et al. 2008) for ringed plover, redshank, grey plover, black-tailed godwit and oystercatcher (see Table A6.1). For the other six species in my models an average of 82% was used apart from bar-tailed godwits where it was assumed that they had a similar value to black-tailed godwits at 81%.

iv) Dominance

Like *Day Efficiency*, *Dominance* is a point of individual variation in the modelled foragers. It is set on a uniform distribution between 0 and 1 and can be used later on in the model to rank birds and place them in a 'pecking order' with other conspecifics.

v) Lower Critical Temperature

Lower critical temperature (*LCT* in °C) is the temperature at which birds require greater energy demands to thermoregulate in addition to the energy required to meet their normal Target Stores. Using values of *LCT* for wading birds in the literature (Speakman 1984; Wood 1984; Kersten and Piersma 1987; Kelly and Weathers 2002; Scheiffarth 2003; Kvist and Lindström 2011; Ruthrauff et al. 2013) I derived a linear relationship against body mass (weight in grams) to predict the *LCT* for all my modelled species (see Table A6.1). This value is then used as a threshold for adding on additional energy costs at colder times of the model.

vi) Diets

The diets of each of the eleven waders have been developed from the categorised patch resources using literature that describes the size range of prey items taken. For nine of the species Goss-Custard et al. 2006 (see also Goss-Custard et al. 2015) was used as a good source and additional papers were used for sanderling (Masero 2003; Reneerkens et al. 2009). Turnstone proved difficult to find literature for past the species they preferred (Jones 1975) so prey sizes from the Southampton Water model were used for my models (Stillman et al. 2012). The size classes of resources that each species can consume are listed in detail in Table A6.1.

vii) Forager Variables

Seven forager variables are defined before any energetics parameters as they are used in the following equations and decision rules.

a) Free Area and Free Time

These two variables are defined as *Patch Size* and *Time Step Length* respectively and are used to aid in determining patch availability and rate of consuming diets. These hold more relevance when disturbance is included in the models so are included in this parameterisation but will not be used heavily in this thesis (see *C.H.Collop 2016 thesis*).

b) Susceptibility to interference (STI)

There are four types of *STI* in this suite of models that are used for birds feeding on specific diets. *MobilePreySTI* is for Crustacean diet with prey that can move away from foraging birds (Marine worms for visually foraging plovers and turnstones) whilst *WeakKlepSTI* applies to relatively stationary prey items from Marine worms (as hunted by tactile species), *Peringia*, Winkles, Cockles and Other Molluscs. For larger items of prey, in particular molluscs kleptoparasatism is common and so *STI* is greater between conspecifics (Wood et al. 2015b). *LargeMollKlepSTI* is for diets with large molluscs - curlew feeding on Other Molluscs and oystercatcher feeding on both Other Molluscs and Cockles. *MussKlepSTI* is for birds feeding on large mussels which mean that only oystercatchers currently use this type of *STI* in this suite of models.

The equations used to derive *STI*, and thus calculate the influence of con-specific competition on a bird's intake rate follow a similar pattern presented in the following interference functions where g = regulated density and D = con-specific density (m^{-2}), r = dominance rank and n = count of con-specifics:

$$STI = \left(\frac{\max(g, D)}{0.01}\right)^{-0.48} \qquad \text{or} \qquad STI = \left(\frac{\max(g, D)}{0.01}\right)^{-0.08+0.08*(\frac{r}{n+0.001})}$$

Specifically for this sub-model, the birds are asked if either the density of modelled birds on a patch or a set regulated density value is greater than the pre-defined threshold of 100 birds per ha (0.01) (Stillman et al. 2002). If neither prove greater than 0.01 then a value of 1 is given which means there is no effect of interference. If one of these two values is greater than the threshold then the above interference function is used to calculate the interference effect that will be used in the following submodel for the rate of consumption. In this equation, the model asks again which is greater between a set regulated density per m^2 (Table A6.1) and con-specific density on a patch before dividing them into the threshold value of 0.01 and raising them to a power defined by the strength of interference per type of STI (Stillman et al. 2002) against the dominance rank of the individual. For *MobilePreySTI* this is -0.48 alone (with no effect of dominance), for *WeakKlepSTI* -0.08 with dominance, and *LargeMollKlepSTI* is -0.5 with dominance. Oystercatchers are the only bird affects by *MussKlepSTI* and work to a slightly difference threshold of 0.00583 (Goss-Custard et al. 2006) and in addition to an effect of dominance have an effect of position in the season (0.1595+(0.0018**Day*)):

$$STI = \left(\frac{\max(g, D)}{0.00583}\right)^{(-(0.1595+(0.0018*Day))+(0.1595+(0.0018*day))*\left(\frac{r}{n+0.001}\right)}$$

Prior to this suite of models an aggregation factor had been used in place of a regulated density value and had been set to 10 bar oystercatchers feeding on mussels where it was set as 6 (Stillman et al. 2012). For this PhD I carried out field work to determine a species specific aggregation factor which was used to develop the current regulated density. This regulated density allows birds to compensate for their own plasticity in foraging densities around the average density they prefer (regulated density) whilst still being measured up against a pre-defined threshold and being affected by interference at high enough densities. The specific details of the field work to determine the species specific aggregation factor can be found in Appendix 7.

c) Feeding Efficiency

Feeding Efficiency determines whether *Day* or *Night Efficiency* should be used via checking if *Daylight* = 1 for an upcoming parameter to calculate the rate of consumption.

Now that all the previous constants and variables have been defined the rate of consumption and following behavioural rules can be parameterised.

viii) Rate of consumption

For each species there is an equation for the rate of consumption per diet it is free to consume. This follows the equations used in previous models with a few adjustments for newly named variables (Durell et al. 2006; Stillman et al. 2012). The intake rate of modelled birds is determined by the density of food in a patch and conspecific disturbance. Interference free intake rate (IFIR) is calculated from the following functional response equation:

$$IFIR = f\frac{IFIR_{max}B}{B_{50} + B}$$

For IFIR in mg s^{-1} f is the foraging efficiency of the individual, B is the patch biomass density for a prey size class and B_{50} is the prey biomass density at which intake rate is 50% of the maximum. $IFIR_{max}$ is calculated following previous work (Durell et al. 2006; Goss-Custard et al. 2006) and is written as follows where M_{spec} is the body mass of a wading bird, M_{prey} is the AFDM in mg of a prey item, r is the ratio of the size range to size in patch and 0.270 is the error mean squares:

$$\log(IFIR_{max}) = -2.082 + 0.245log_e(M_{spec}) + 0.365log_e(rM_{prey}) + (0.5 * 0.270)$$

Conspecific competition and thus interference impacts the intake rate of a modelled bird through my models' *Rate of Consumption* shown below in an example for dunlin (DN) feeding on crustacean:

Available(FreeTime/TimeStepLength)*3.6*FeedEff*MobilePreySTI**
*exp(-1.708505+0.365420*ln(1.05*1000*(DNCrustaceanDietEnergyDensity/22)))/*
((DNCrustaceanDietEnergyDensity/22)+(0.761/DNCrustaceanDietDensity))

In this sub-model the bird is asks if the patch is available, the next section is mainly for disturbance affects which are not in this model, then times 3.6 (conversion from mg/second to grams/hour), the feeding efficiency rate, add in the interference effects then the next section calculates the maximum rate of feeding dependent on prey size and bird size plus B_{50} which is the prey density half way the intake rate's maximum. Each species has its own forager coefficient derived from equations produced in previous work (Goss-Custard et al. 2006) and are listed in Table A6.1. 0.365420 is the prey coefficient and 1.05 is the ratio of size of prey consumed to size in patch (Durell et al. 2006). Dividing the energy densities by 22 in the equation turns AFDM in grams into kJ of energy (Zwarts and Wanink 1993).

Whilst testing the models it was discovered that birds were consuming earthworms at a very high rate and ignoring intertidal prey. For those birds that can forage on earthworms the rate of consumption was adjusted by an additional 0.4 (reduced to 40%) following investigations in to the energy consumption rates of my models in comparison with values found for oystercatcher and curlew in the literature (Stillman et al. 2000; Hayhow 2009). These adjustments resolved the issue.

ix) Maximum rate of consumption

This equation has remained the same as in previous models (Durell et al. 2006, 2007) with the *Maximum Rate of Consumption* per hour being set to 1000 divided by the energy density of each diet, giving a very high ceiling that will not limit intake rate.

x) Diet assimilation efficiency

Due to the indigestible chitinous parts of many prey items the actual assimilation of energy available in prey items is lower. As a result, all diets have an assimilation efficiency that reduces the kJ assimilated by foragers. For crustaceans this is set as 85% (0.85) whilst for worms, *Peringia*, cockles, mussels and Other Molluscs it is 75% (0.75) efficiency (Kersten and Piersma 1987; Goss-Custard et al. 2006). Oystercatchers have a slightly higher efficiency of 85% when feeding on cockles, winkles, Other Molluscs and mussels as they open and de-shell their prey which tends to be larger (Norton-Griffiths 1967; van de Kam et al. 2004).

xi) Feeding, resting and moving metabolic rates

The metabolic rates used in the models are specific to a species' diet and use basal-metabolic rate (BMR) and the thermostatic cost below *LCT* (kJ per °C). The energy expended is calculated for each time step by asking if the *Temperature* is above the *LCT* (defined in Forager constants) and then either giving the straight metabolic rate or adding on the thermostatic cost per degree below *LCT* (feeding and resting only). BMR is calculated per species from equations set by Kersten and Piersma (1987):

$$BMR = 437*(\text{mass in kg})^{0.729}$$

This is then multiplied by 2.1 to emulate *Feeding* and *Resting BMR* derived from 2 *x* BMR for cage metabolism expenditure (Kersten and Piersma 1987) plus an additional 10% (Zwarts et al. 1996) cost of flight (see Table A6.1 for each species' BMR). *Moving Metabolic Rate* is set at 12 *x* BMR following van de Kam et al. (2004) but not used as due to the size of the estuaries and speed of flight of wading birds all movements between patches could be made within an hour.

xii) Thermoregulatory Cost

Included in the feeding and resting metabolic rate is the thermostatic cost in kJ per degree below *LCT*. This was calculated using measurements of energy consumption per day (Kersten and Piersma 1987) above and below the *LCT* for four wading birds to calculate the thermostatic costs and then associated in a power relationship against body mass (see Table A6.1). The equation used to predict the thermostatic costs for all species is:

$$\text{Thermostatic cost in kJ} = 0.0055*(\text{body mass in g})^{1.3737}$$

xiii) Emigration fitness measure, movement time

As there is no emigration or movement in this suite of models the emigration fitness measure and movement time have both been set to 0.

xiv) Patch location rule

In my suite of models each forager can locate a patch as long as it is exposed (*Available* = 1) and *Patch Size* >1m^2.

xv) Fitness component

The fitness components are used to calculate fitness measures where foragers either survive or 'die'. In my models there is one fitness component "*Starved*" and it is measured as comparison of an individual's energy store.

I have updated this fitness measure from previously published models to allow birds to spread out across patches that are 'adequate' rather than moving to the best patch. In the previous method, termed "rate-maximising", birds would clump together on a single patch until the aggregation threshold was reach. This new method called "satisficing" allows birds to choose patches that are adequate for the birds to survive (Stillman et al. 2005b). This satisficing method has been considered in an earlier IBM on the Humber estuary (Stillman et al. 2005b) but had not been used further. The opportunity for birds to choose patches that meet their requirements rather than just go for the best quality patch allows us to escape the 'perfect knowledge' scenario of other models where the birds know the best place all the time and now allows a realistic margin of error.

Birds are asked if they are below the 95% threshold of their *Energy Target Store* or if their *Energy Assimilation Rate* is greater than their past *Assimilation Rate*. If true then they are asked if they are 'starving' or not and if again true then they get a higher value on a patch and go to the best patch, if they are not starving they go to a random adequate patch. If the bird's first response to the equation was false they go to a safe place – *Roosts* in this occasion. The full equation looks like:

*if((EnergyInitialStore<(0.95*EnergyTargetStore)) or (EnergyAssimRate>EnergyPastAssimRate),*
*(if((EnergyInitialStore<(0.95*EnergyTargetStore)),1000+EnergyAssimRate,*
1000+(EnergyAssimRate>EnergyMetabRate))),
if((Roost=1),10,0))

xvi) Feeding and resting and moving survival probability

The final parts of the parameter file ask if the birds *Energy Final Store* is greater than 0, if so they survive to the next step, if not they are removed from the model ('die').

4.2.4 Summary of major parameter updates

Table 4.4 summaries the major updates in parameters changed between previous versions of MORPH that have been parameterised for wading birds and mine (Durell et al. 2005, 2006, 2007, 2008; Stillman et al. 2005b; Stillman 2010; Ross 2013).

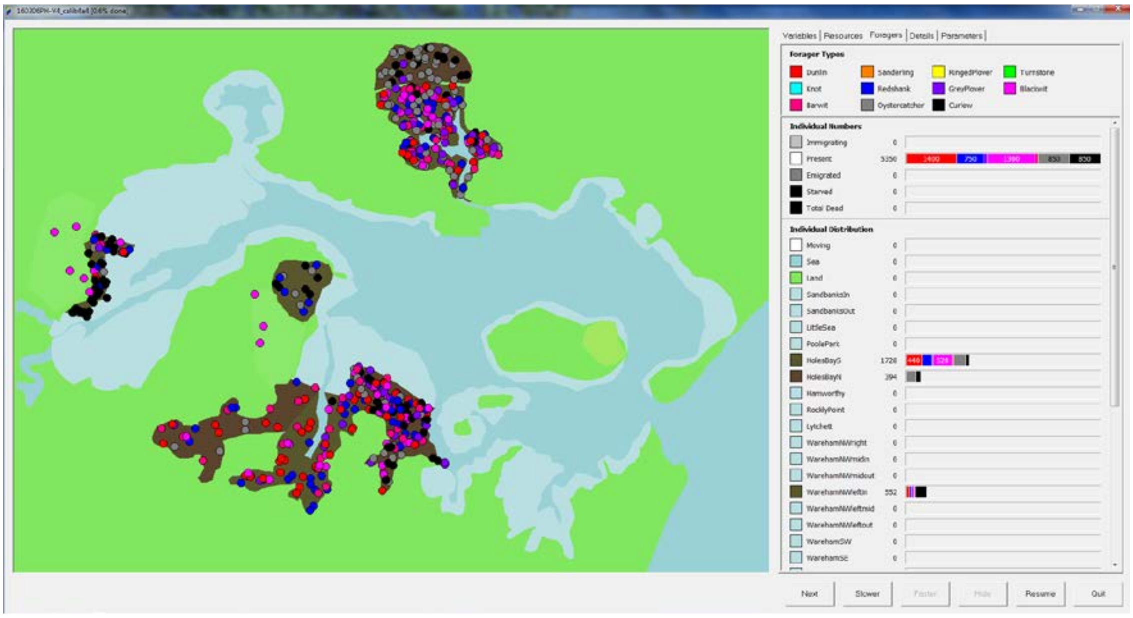
4.2.5 Observation of the model

As mentioned in the above section on Patches, a map is visible in the final viewing window of the model and it’s co-ordinates are parametrised in that entity. Additionally the various global, patch and forager variables are displayed in tables to the right of the map and can be investigated as the model runs by pausing the model at an appropriate moment (Fig.4)

At end of each section of the model parameters (Global, Patches, Foragers) it is possible to ask MORPH to save the state variables. In my models I request data to be saved at specific low tides to allow validation and interrogation of the results as needed whilst maintaining a reasonable run time. The results are saved as the model progresses and available to work with once it reaches the end of its run.

Table 4.4. Major updates to parameters in MORPH IBM for wading birds.

Section	***Parameter updated***	***Update and data source***
General	*none*	*none*
Global	Temperature (ActualTemp+ChangeTemp)	Re-added temperature with climate change option - Met Office data
Patches	Field area	23% of area observed in 0.5 km of Mean high water -OS maps
	Shoreheight	Median patch height in m^2 chart datum - HR Wallingford
	Resources	New size classes & resource categories - Invertebrate surveys/Literature
	Updating resource density	Overwinter mortality - invertebrate surveys & prior IBMs
	Resource component	AFDM - invertebrate surveys (site specific where possible)
Foragers	Number of foragers	Five-year average monthly counts of each species Oct-Feb - WeBS (BTO)
	Arrival energy store	Mass & Starvation mass in kJ - BTO & Goss-Custard data
	Lower Critical Temperature	Regression line on body mass - Multiple literature sources
	Diets	Literature
	STI	New equation, aggregation factor & regulated density - Fieldwork
	Rate of consuming diet	Species diet STI used & 40% for earthworm diets - literature research
	Metabolic rate (Resting & Feeding)	BMR & thermostatic costs updated - literature sources
	Moving metabolic rate	12*BMR from literature research
	Starved fitness measure	New satisficing equation



Individual Numbers
Immigrating 0
Present 5350 1400 750 1390 850 850
Emigrated 0
Starved 0
Total Dead 0

Individual Distribution
Moving 0
Sea 0
Land 0
SandbanksIn 0
SandbanksOut 0
LittleSea 0
PoolePark 0
HolesBayS 1728 440 328
HolesBayN 394
Hamworthy 0
RocklyPoint 0
Lytchett 0
WarehamNWright 0
WarehamNWmidin 0
WarehamNWmidout 0
WarehamNWleftin 552
WarehamNWleftmid 0
WarehamNWleftout 0
WarehamSW 0
WarehamSE 0

Figure 4.4. A screen shot of the graphical display for one of my models (Poole Harbour) with the Foragers tab visible.

4.2.6 Flexibility for investigating environmental change

It was mentioned earlier that it is possible to adjust the temperature in the model from an ‘Options’ page in the spreadsheets used to create the parameter files. This feature has also been extended to prey densities, prey energy density, habitat size, *Shoreheight* and population size. With these options it is now possible to adjust the model and simulate the effects of various environmental changes such as habitat loss, sea-level rise, climate warming/cooling and pollution. These will be used to their fullest extent in the following chapters.

4.2.7 Calibration

Once the models were parameterised and running with no errors, they were calibrated so that on average overwinter mortality of all species was <10% (due to starvation). This threshold was set from a number of sources as there is little information on overwinter mortality of wading birds in the literature and annual mortality rates include other causes of death. Using annual survival and mortality rates for multiple wader species (Goss-Custard et al. 1982; Cramp and Simmons 1983; Goss-Custard and Durell 1984; Warnock et al. 1997; Insley et al. 1997; Durell et al. 2000; Boyd and Piersma 2001; Gill et al. 2001; Brochard et al. 2002; Atkinson et al. 2003; van de Kam et al. 2004) and knowing from other avian species that overwinter survival is often higher (Blackburn and Cresswell 2016), a value of <10% mortality was deemed an appropriate threshold.

The calibration adjustments were made to the *Day Efficiency* of specific species and were specific to each estuary. This was changed from *Night Efficiency* in previous models (Durell et al. 2006, 2007) as I now have specific values to use for *Night Efficiency* (see section 4.2.3.3). A small percentage increase was applied to the mean in the normal distribution formula of *Day Efficiency* (see Table 4.5 where 1.2= 120%). This calibration accounts for the lack of larger invertebrates seen on some estuaries (see Tables A3.3a-e) that may have arisen from coarser invertebrate surveys.

Calibration of the *STI* regulated density was also investigated but even at 50% of the original value no change was seen in the final mortality numbers.

Table 4.5. Calibration values applied to the Day Efficiency of various species per estuary.

Model name **Species**	**Exe estuary**	**Humber estuary**	**Poole Harbour**	**Severn estuary**	**Southampton Water**
Grey Plover		1.1			
Black-tailed godwit		1.3		1.2	
Bar-tailed godwit	1.125	1.425			
Oystercatcher				1.2	
Curlew		1.35		1.2	
No. birds calibrated	1	4	0	3	0

4.2.8 Model validation

As recommended in the pattern-orientated modelling strategies of Grimm, Railsback and colleagues (Grimm and Railsback 2005; Grimm et al. 2005) it is best to validate IBMs against as many observations as possible. For this suite of models habitat usage and proportion of time spent feeding have been used to validate against due to the limited availability of energetic data. For these two sets of validation WeBS survey data has been used in the former and observational data from C.H.Collop (*unpublished thesis 2016*) in the latter.

After parameterisation and calibration, the final five models predict that birds will survive to the end of the model run with less than 10% mortality averaged over 10 runs. As specific mortality data were not available to test the models, I used WeBS Low Tide counts (Holt et al. 2015) for each of the estuaries obtained from the British Trust for Ornithology (BTO) to validate habitat usage. The available years are listed below in Table 4.6.

With so many smaller patches created from abiotic divisions, I joined several patches on each estuary together to create ‘rough’ areas that could be used to compare to the WeBS low tide counts. These new composite areas were mapped onto the Low Tide count areas following receipt of GIS shapefiles from the BTO. Using the statistical software package R (R Development Core Team 2015) I was able to graphically compare the percentage of time each of the eleven species spent in each area to see how similar they were to observations.

Table 4.6. Dates of low tide surveys for each of the five estuaries

Estuary	**Date of latest Low Tide Survey**
Exe estuary	2006/07
Humber estuary	2011/12
Poole Harbour	2004/05
Severn estuary	2008/09
Southampton Water	2000/01

4.2.9 Sensitivity analysis

An analysis of the sensitivity of the models to important parameters was carried out. Each parameter value analysed was changed by ± 25% (leading to 75% and 125% of normal parameter values) and multiple runs (5) were carried out to determine an average effect. The sensitivity to each parameter was measured as change to percentage mortality (Stillman et al. 2000) and proportion of time spent feeding compared to 10 default runs of an unaltered version of the model. As mentioned in previous modelling work (Ross 2013), having a second output to compare with survival is important as the low mortality rates following calibration mean that major changes (reductions in particular) are not as easily observed from slight ones.

As the following two chapters study environmental change effects using a number of parameters that would normally be included in a sensitivity analysis, I decided to not to include these in the analysis within this chapter. The parameters adjusted in the sensitivity analysis are listed in Table 4.7.

Table 4.7. Parameters changed for sensitivity analysis

Parameter to be changed	**How change will be adjusted**
Arrival Energy Store	± 25% *x* Starvation mass
Day Efficiency	± 25% *x* (normal distribution)
STI	± 25% *x* (Inside equation for birds affected by STI)
Rate of Consumption	± 25% *x* (rate of consumption)
Assimilation Efficiency	± 25% *x* Assimilation Efficiency
Metabolic Rate	± 25% *x* (Metabolic rates – Feeding and Resting)

4.3 Results

4.3.1 Validation of habitat usage

Comparing each estuary on a species by species basis it was clear that the models replicated observed habitat usage, but more accurately on a rougher scale of areas. The graphs seen in Figure 4.5 show an example set of validation graphs for dunlin across the five estuaries. It should be noted that confidence intervals were removed from the validation graphs due to lack of data for WeBS confidence intervals. As well as ‘rough’ areas I created ‘less rough’ areas that were finer grained but in some estuaries these did not replicate the WeBS patterns as well as when I use broader areas that may have been less visited on the observation dates. All ‘rough area’ validation graphs are available in Appendix 8.

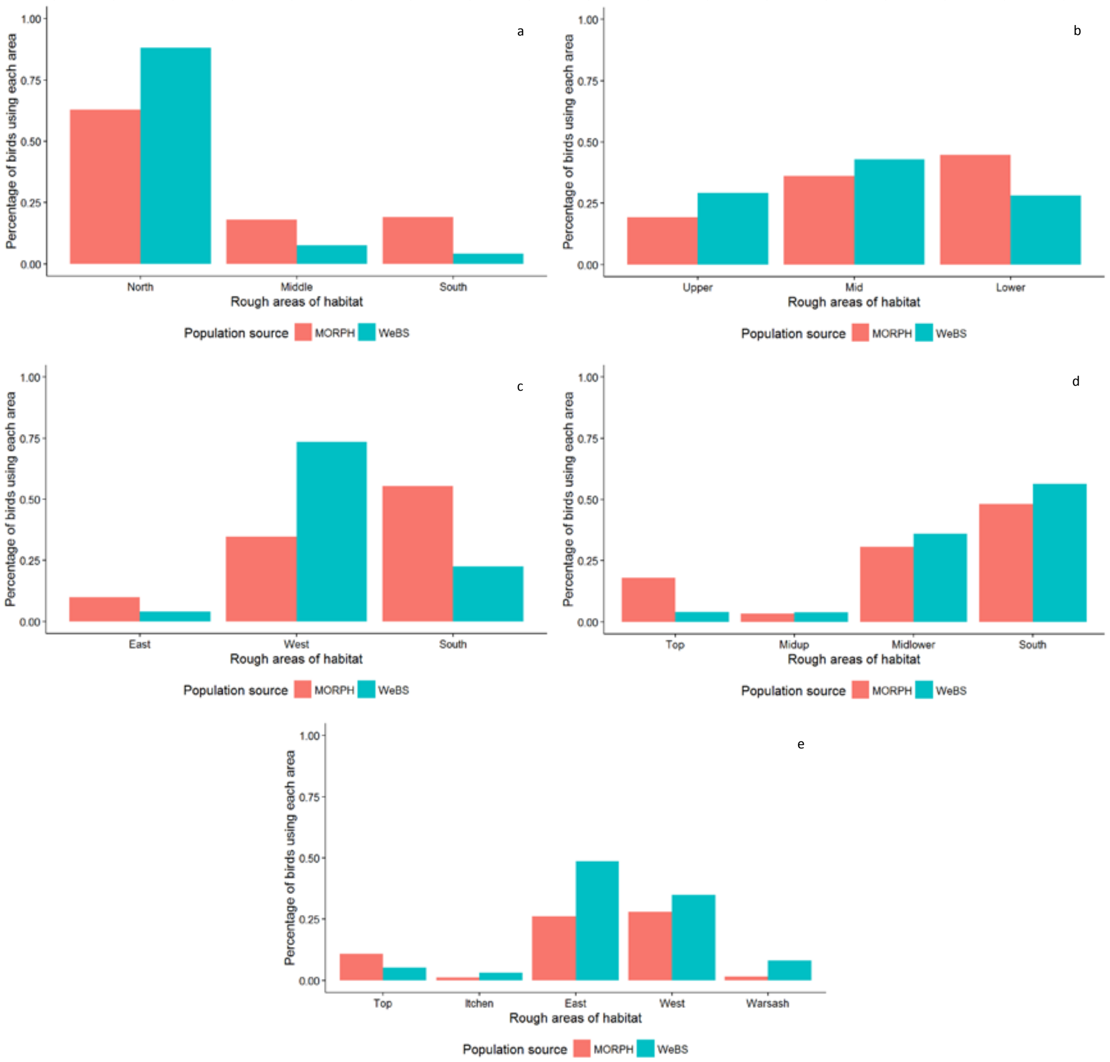


Figure 4.5. Proportion habitat usage comparison between MORPH predictions and WeBS data for ***dunlin*** *on each of the five modelled estuaries a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) Severn estuary and e) Southampton Water where red = MORPH results and blue = WeBS data. Error bars indicate the 95% confidence intervals of replicate values.*

Whilst the rough areas showed that the MORPH birds were generally distributing themselves similarly to the observed data there were still some cases in which predictions and observations differed. These discrepancies usually occurred when a species was not that common (closer to the modelling limit of 100 birds per winter), was not as susceptible to interference. Additionally on estuaries with coarser quality invertebrate surveys some species such as the bar-tailed godwits may be lacking part of their diet from their greater reliance on lugworms which are hard to survey (and few were present in the surveys used). In particular, black-tailed godwit tend to not match WeBS on the Humber and Severn estuaries which have coarser invertebrate survey data. Also in the wild this species may feed on intertidal areas closer to terrestrial habitat (on which they also forage), an interaction not included in my models. Turnstone were another species that did not always match the WeBS data as closely as others, possibly because this species tends to feed on habitats (e.g. strandlines) that are not that well covered in estuarine invertebrate surveys.

For black-tailed godwits alone, a study in Ireland looking at field foraging also recorded variation in proportion of time spent feeding in fields being a good 20% higher than that of birds on intertidal areas and always over 80% (Hayhow 2009). A crude averaging of these two values gives a figure closer to my MORPH results than Collop's observations potentially indicating a closer validation if field feeding was removed (*C.H.Collop 2016 thesis*). This does not work for all species, as only half feed in fields, but indicates that with additional time and computer power it might be possible to record all results for all time steps (time is a limiting factor in generating results files) and get a patch specific value.

4.3.2 Validation of proportion of time spent feeding

The latter validation has been made possible due to field work carried out on a parallel PhD on Poole Harbour (*C.H.Collop 2016 – unpublished data*). The proportion of time spent feeding by ten species was collected and compared to the results of the 10 default replicates of the suite of models. Figure 4.6 shows the comparison between my results alongside Collop's work and values taken from another paper (Goss-Custard and Stillman 2008). For the species present in Poole Harbour it can be seen that there is quite a lot of variation between my results and the observed data but only widely different in a few species. My results cover the whole period of foraging in the model runs and are not as variable as the observed data (no confidence intervals were available for Goss-Custard and Stillman 2008). Additionally it should be noted that the majority of model birds feed for longer than seen from observational data and suggest they are having issues meeting their energy demands. The reasons behind this may be related to missing invertebrate data such as larger more mobile worms that may be missed from core sampling.

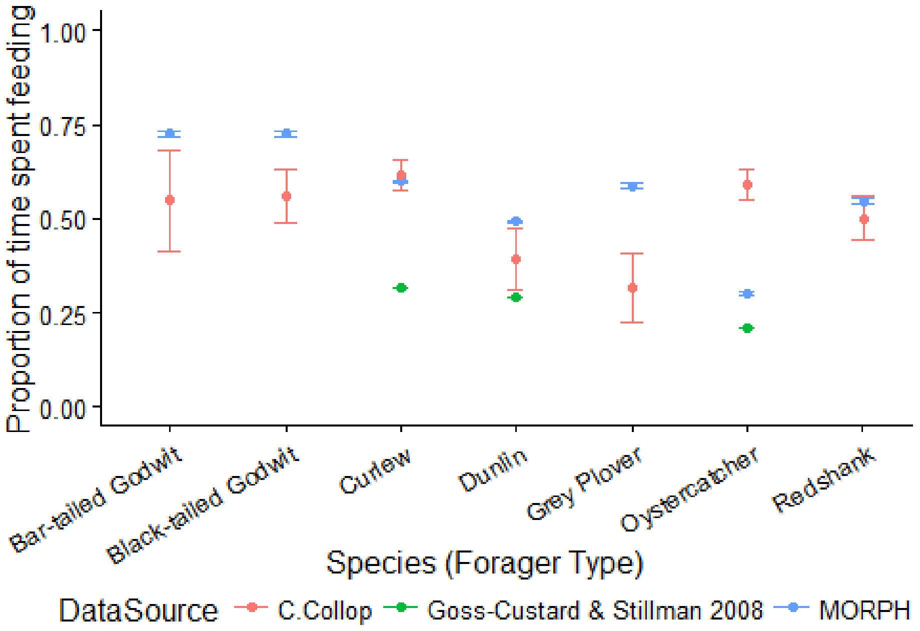


Figure 4.6. Proportion of time spent feeding of wading birds in Poole Harbour from three data sets (1 modelled and 2 observed). Error bars indicate the 95% confidence intervals of replicate values.

As with habitat usage, an observed value for proportion of time spent feeding in fields was only available for black-tailed godwits. From this one study that included proportion of time spent feeding when on fields (Hayhow 2009) I saw a similar value for black-tailed godwits in my models.

From this I can be broadly confident that my models are replicating the real world in regards to the proportion of time spent feeding but not as confident as with the habitat usage. In future these issues can be addressed through larger studies into proportion of time spent feeding as the limited data available may not be as accurate when compared to a whole modelled winter's results.

4.3.3 Sensitivity Analysis

The sensitivity of the models to the six chosen parameters showed a high variance in their effects on the percentage mortality predicted from the models, although within each species the proportion of time spent feeding was similar between estuaries. For the waders that showed the most variation (in amplitude) across the estuaries during validation (such as the bar and black-tailed godwits) a similar pattern was seen in sensitivity to changes in parameter values. All graphs are available in the appendices (Appendix 9) where negative sensitivity bars are presented in black and positive sensitivity bars in white.

4.3.3.1 Sensitivity to percentage mortality

Of the eleven species in the models some birds showed a strong response to the change in parameters whilst others only were affected on specific estuaries (Appendix 9, Figures A9.1-11). With many species mortalities sitting close to 0% mortality in the neutral runs the 75% sensitivity had the greatest effect on five of the changed parameters whilst *Metabolic Rate* increased mortality of the 125% change. In general, *Assimilation Efficiency* had the greatest effect on predicted mortality, often causing over 50% mortality in a species population. Decreases in *Rate of Consumption*, *Day Efficiency* and *Metabolic Rate* also increased mortality although at slightly decreasing rates respectively. In general, *Starvation Mass* and *STI* had little effect on the mortality of the birds (see example Figure 4.7 for grey plover) except for bar-tailed (Figure 4.8) and black-tailed godwits (Figure A9.2) which were strongly affected by *STI* on all estuaries they were modelled in. It should be noted that in these species (godwits) the birds were already highly aggregated so the reduction found in -25% *STI* increased the negative effect on the godwits whereas other species had little or no change.

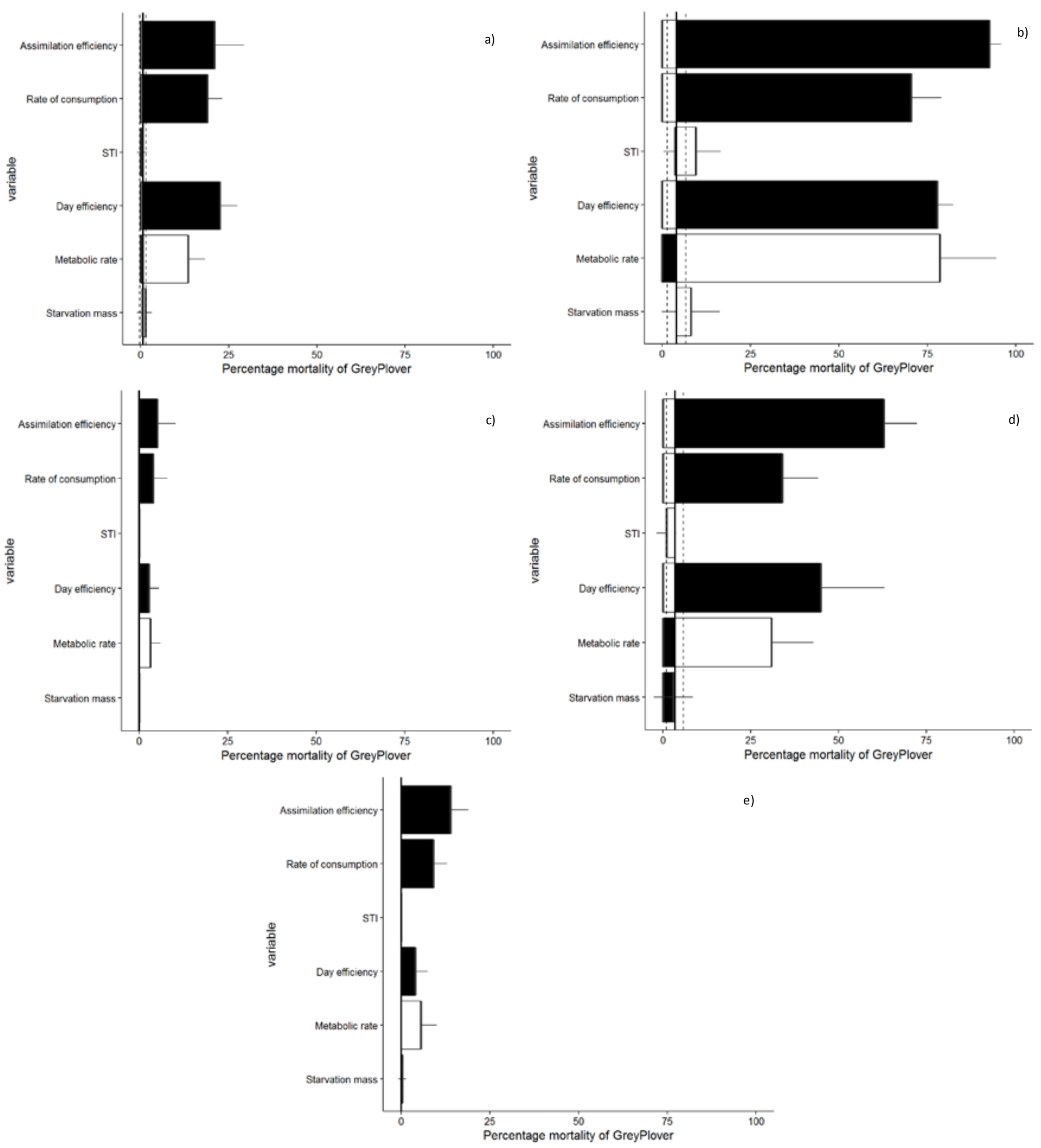


Figure 4.7. A sensitivity analysis of the effects of six parameters set to 75% (black) and 125% (white) of their default values on ***grey plover*** *percentage mortality for five sites - a) Exe estuary, b) Humber* estuary, *c) Poole Harbour, d) Severn estuary and e) Southampton Water. The solid black line shows the mean of 10 replicates of the 100% parameters with the dashed lines either side being the 95% confidence intervals. The error bars indicate the 95% confidence intervals of 5 model replicates.*

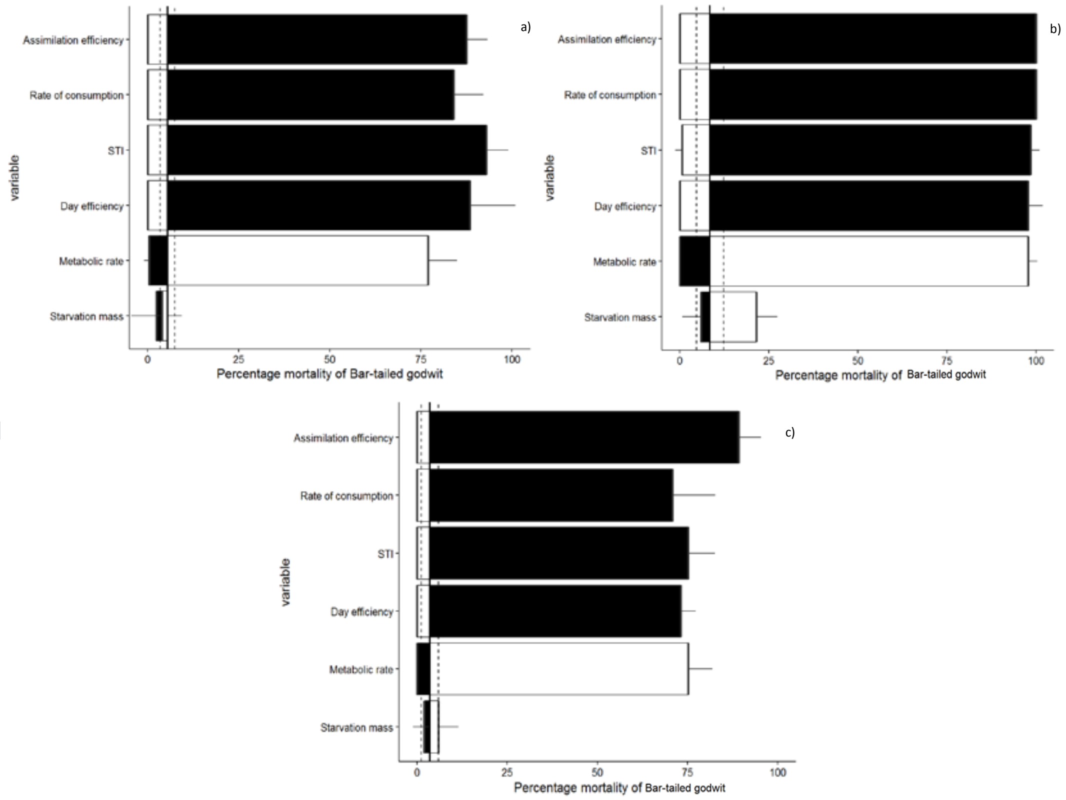


Figure 4.8. A sensitivity analysis of the effects of six parameters set to 75% (black)and 125% (white) of their default values on ***bar-tailed godwit*** *percentage mortality for three sites this species is present on - a) Exe estuary, b) Humber* estuary *and c) Poole Harbour. The solid black line shows the mean of 10 replicates of the 100% parameters with the dashed lines either side being the 95% confidence intervals. The error bars indicate the 95% confidence intervals of 5 model replicates.*

When I look broadly at the absolute difference from the default results in all the +25% sensitivity analyses of each species across all modelled estuaries (Figure 4.9a), *Metabolic Rate* at 125% was the only parameter to be affected in anyway and was quite variable. In the -25% analyses (Figure 4.9b) more species were affected although the higher percentages in efficiency and rate of consumption are mainly ordered from the larger species down to the smallest in size of effect. The two godwit species were affected by *STI* as explained above.

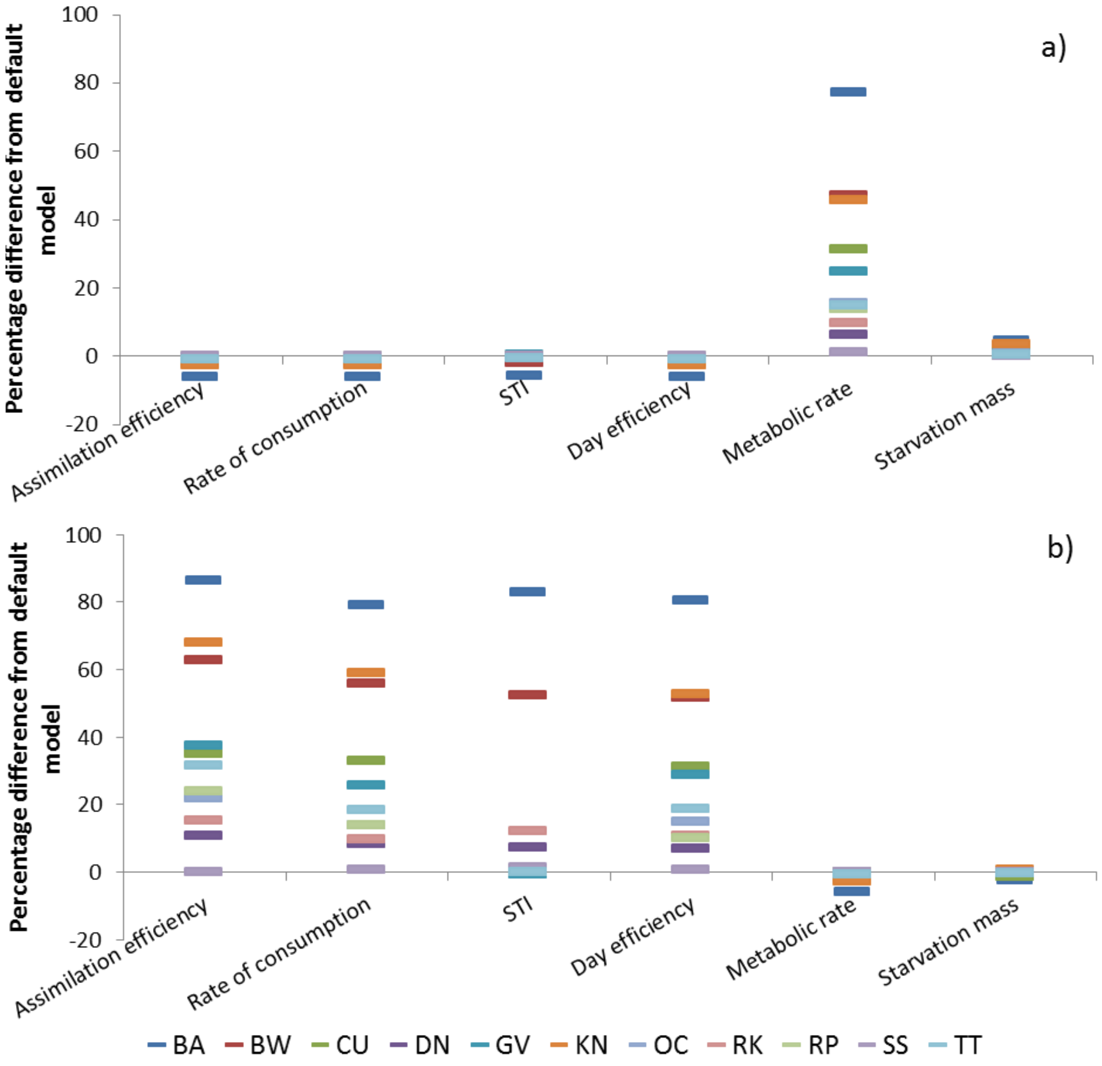


Figure 4.9. Percentage difference from the default results for a) +25% sensitivity analysis and b) -25% sensitivity analysis results averaged on all species across all estuaries. Species are designated by BTO two letter codes (see Table 4.3).

4.3.3.2 Sensitivity to proportion of time spent feeding

The results of sensitivity analysis on the effect of proportion of time spent feeding are not as dramatic in their differences as seen in percentage mortality (Figures A9.12-22). All birds responded to 75% and 125% in a similar way, with 75% resulting in increased and 125% decreased the percentage of time spent feeding for all parameters bar *Metabolic Rate* which was reversed. The effect size was within 25% either way and <30% for a total effect combining + and -. *Metabolic Rate* had the greatest effect in decreasing the percentage of time spent feeding but was closely followed by *Assimilation Efficiency*, *Rate of Consumption* and *Day Efficiency*.

For increasing feeding time no one parameter had the greatest effect although all were as mention before <25% in effect (see Figure 4.10 for an example on curlew). Over all *Starvation Mass* had no effect for 75% and only a small increase in percentage of time spent feeding for dunlin at 125% of parameter values. *STI* only affected half of the species investigated, although still with a lower amount that the other parameters with the exception of *Starvation Mass*. Of the species affected by *STI* they included bar and black-tailed godwits, dunlin, redshank and sanderling. Of the last of these populations, it should be mentioned again that it is only present on the Humber estuary which reduces our full understanding of their sensitivity to my chosen parameters.

The predicted results of proportion of time spent feeding are quite stable across the wader species modelled in my study and there is no site effect as with percentage mortality.

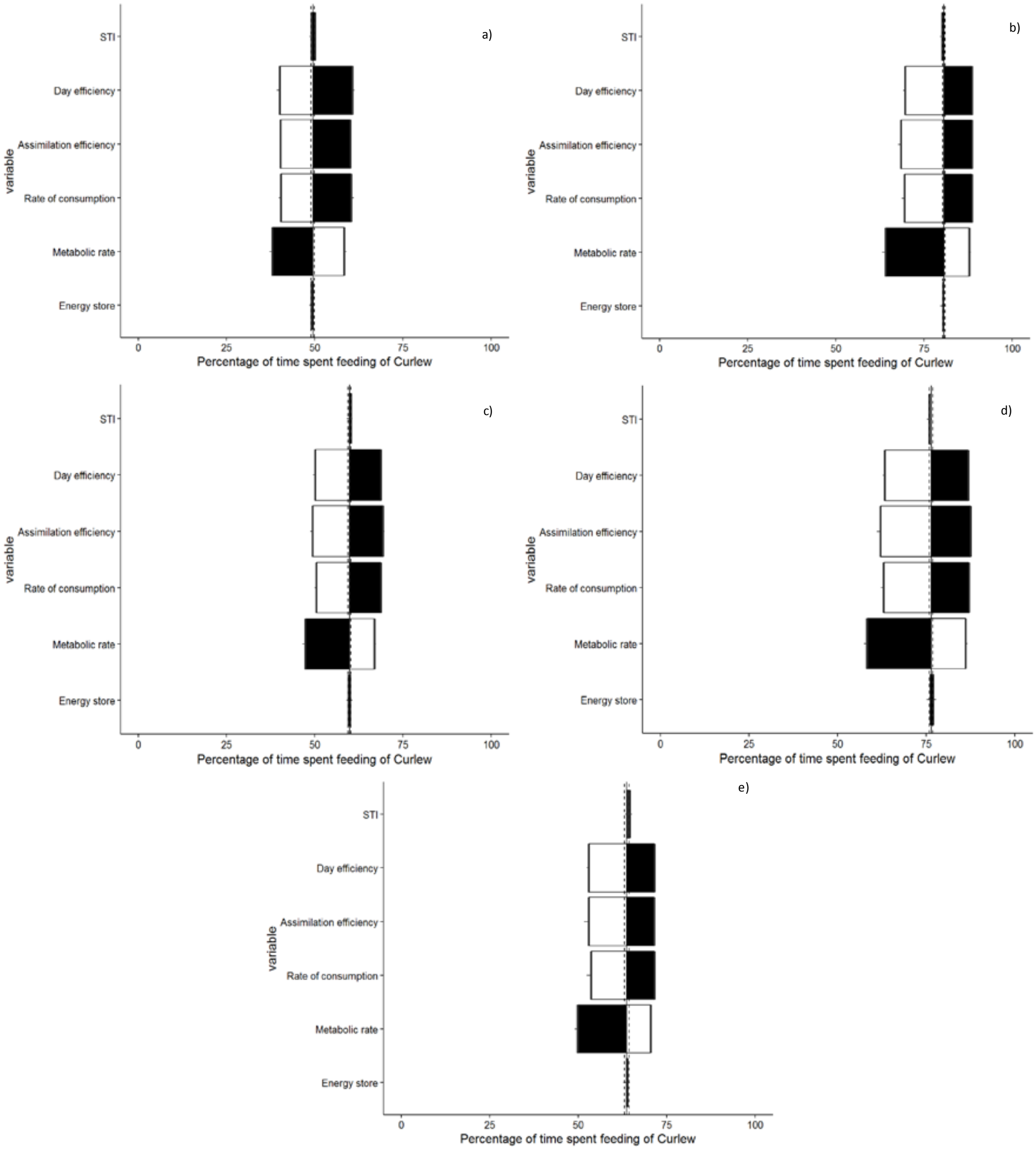


Figure 4.10. A sensitivity analysis of six parameters set to 75% (black), 100% and 125% (white) and their effects on ***grey plover*** *percentage of time spent feeding five - a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) Severn estuary and e) Southampton Water. The solid black line shows the mean of 10 replicates of the 100% parameters with the dashed lines either side being the 95% confidence intervals. The error bars indicate the 95% confidence intervals of 5 model replicates.*

4.4 Discussion

Using the MORPH platform I have developed a set of standardised models for five UK estuaries. This new suite of models predicts habitat distribution for wading birds that is generally similar to the observed patterns of wild birds. In addition, the proportion of time spent feeding by modelled waders is relatively close to those expected from empirical data. The comparison of the predictions with observed data gives confidence that the future use of the models to predict how birds survive and behave in relation to environmental change.

4.4.1 Overview of the benefits of additional parameters added to the model

During the development of the models I chose to improve and add several parameters that had previously been unexplored. The processes involved have added extra options for investigations in environmental change and allow for more detailed analyses of habitat usage.

By adding in the effects of temperature and its associated forager energetic parameters (*Lower Critical Temperature* and *Thermostatic Cost*) model birds now regulate their prey consumption to their thermoregulatory needs. Temperature is parameterised as the average daily value over 50 years and now allows the exploration of the impacts of extreme climates through simple adjustments to the parameters files. In future it will be interesting to investigate the effects of daytime vs. night time fluctuations (Irving 1955) but extremes of temperature are known to have major importance in the survival of birds through reduction in overnight feeding efficiency (Klaassen 1990; Kelly et al. 2002).

Accurately representing the exposure of patches has been improved in these models. Whilst percentage of time available of each square metre of habitat would be the best way of representing the harbour (see previous models (Stillman et al. 2005b, 2012)), the method I have employed works just as well in terms of habitat usage using a set median *Shoreheight* with a binary value of Available. This simplification allows for direct use with any winter tidal cycle. Additionally it allows for quicker analysis of sea-level rise by direct manipulation of *Shoreheight* rather than re-running multiple hydrodynamic models.

One of the most significant changes I made was to the way that the density of birds on patches was calculated. Previously, an aggregation factor was used which multiplied the density of birds (i.e. number of birds divided by patch area) by a fixed amount to account for aggregated distributions of birds. Instead, from my field data I calculated the regulated density, which assumed that birds self-regulated their density if patch area was sufficiently large. This mimics more closely the processes drawing birds closer together (e.g. predator avoidance, aggregated food), with those pushing them apart (e.g. competition).

Using the older rate-maximising fitness measure makes understanding distribution a little trickier as birds tended to clump together. The new ‘satisficing’ method improves this fitness component, with bird’s now spreading out further to any patch that on which energy assimilation rate is adequate to allow them to survive. This more varied approach to how birds utilise the foraging areas of an estuary allows for better predictions of bird distribution and prevents birds from having the unrealistic characteristic of ‘perfect knowledge’.

4.4.2 Limitations in model development and subsequent simplifications.

During the development of this suite of models the limitations of suitable data and what level of complexity to include have become quite apparent. A major limitation has been the availability of detailed invertebrate data; many surveys are available through published literature and reports but the formats are not compatible. Invertebrate data have been shown to be a critical factor in developing models throughout this thesis, and in particular the lack of relationship between the actual diversity and densities of size classes of prey items to the real systems cause major issues in validating model outputs. I have been able to compensate for these with calibration but only through awareness of the work in the second chapter of this thesis is it hoped that more surveys will be carried out that both measure the abundance and size distribution of invertebrates throughout sites. From such detailed surveys comes better awareness of the food supply of waders whether through the use of IBMs or otherwise. Additionally the ways fields have been incorporated has been simplified as there is a lack of information on the distance birds fly to reach fields from an estuary and type of fields they will use. Future work to expand on this issue will help us understand the exact importance of fields in the context of environmental change.

4.4.3. Validation of the models and their sensitivity to their parameters

Following calibration, validation was carried out for all modelled estuaries in regards to species habitat usage. Although a few locations and species might not match as well as others (due to low numbers or coarser invertebrate surveys) there is scope for improvements in future models. Species that are not matching the observed distributions as closely as others tend to be species with smaller populations or more specific diets. In particular, the distributions of species with limited diets are less well predicted from the coarser invertebrate surveys of the Humber and Severn estuaries. For field usage, some validation was possible for black-tailed godwits alone, but as mentioned above, more work on this area would be greatly valued to aid in understanding the role of fields.

Proportion of time spent feeding was not predicted that closely in all cases, but was limited to data available for Poole Harbour. This is again an understudied area, with few papers available that could be used for validation (e.g. Goss-Custard and Stillman 2008). Other studies investigate short bouts of feeding instead of a full daylight period (Heppleston 1971; Sheehan et al. 2012) or were expressed in more general terms (Townshend 1981b).

Testing the model's sensitivity to a range of parameters has shown that whilst mortality rate is highly variable for several species, proportion of time spent feeding tends to not be as affected. The responses of the different wader species were highly estuary-dependent with adjusted parameters only causing higher mortalities on certain estuaries. The Humber and Severn estuaries had increased mortality in species that on the other three estuaries produced little or no response. Clearly the variation in the individual ecosystems of each estuary has a bigger effect on how species respond to the sensitivity testing that individual species themselves. The largely unaffected *STI* parameter justifies the improvement of the species specific regulated density and aggregation factor.

That the models were highly sensitive to energetic parameters (*Metabolic Rate*, *Day* and *Assimilation Efficiency*) follows results of previous wader models (Stillman et al. 2000; Ross 2013). *Assimilation efficiency* is higher in species that can remove the flesh of prey from their exoskeletons/shells. High sensitivity to *Metabolic Rate* means that variation in temperature is likely to affect birds, so the importance of gaining true LCT values and including temperatures in models is shown. The comparatively small changes observed through proportion of time spent feeding indicate that individuals were able to compensate for the ±25% change in parameter values, and / or that they had little potential to increase the proportion of time spent feeding (e.g. due to tidal exposure of patches and daytime-only availability of fields).

4.4.4 Final thoughts and future directions

This validated suite of wading bird IBMs is an important tool in the prediction of environmental change effects on estuarine environments and should extend the use of such models in management and planning scenarios. The following chapters will expand on this chapter with examples of how different environmental changes affect the birds with comparison across five estuaries. In future, improvements that can be made with better invertebrate surveys will also add to the utility of the models.

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5. Can estuaries support increased populations of waders? An investigation of population change using individual-based models.

This chapter uses the new suite of IBMs (Chapter 4) to investigate how each estuary can support increasing populations of waders, the relationship to previously designated numbers and implications for the future.

5.1 Introduction

Schemes exist to aid the protection and conservation of avian populations, from small scale local Nature Reserves (Fournier-Origgi and Herrera de Fournier 1979) through to the Global Flyway Network (Boere and Stroud 2006; Piersma 2007) each playing a vital role in the conservation of many species. In Europe the Special Protection Area (SPA) classification, protects areas of high importance for rare and vulnerable populations of migratory birds (Stroud et al. 2001). By protecting these areas many more species benefit from the limited developments that can occur providing an 'umbrella' of security to many communities (Roberge and Angelstam 2004). From its inception in 1979 as part of the EC Birds Directive, 270 SPAs exist (correct 24th May 2016) in the UK (JNCC 2016a) with many more across Europe (5,572 as of February 2016) covering over 12% of the 28 European Union countries (European Commission 2016). Of the UK SPAs, approximately 30% are set over estuarine regions (correct 24th May 2016), with populations of wintering waders the main conservation objective featuring highly in designation criteria (JNCC 2016b).

The bird numbers used to justify these SPA designations in the UK were inferred from Wetland Bird surveys (WeBS) taken in the first half of the 1990s, with the exception of the Humber estuary which used values from the end of the same decade (Stroud et al. 2001). The majority of SPAs existing at those times were updated in 1999 but no further updates of designated population sizes have been carried out (bar the Humber in 2007). During the same period, wading birds have faced a decline in numbers throughout the globe (International Wader Study Group 2003; Wetlands International 2012), with rapid changes to their environments both in and out of their breeding range from both anthropogenic (Sutherland et al. 2012; van Roomen et al. 2012; Melville et al. 2016) and climatic sources (Rehfisch et al. 2004; Bairlein et al. 2007; Maclean et al. 2008). There are a few species that have increased, often with the aid of conservation programs, but in general the numbers of birds currently recorded on SPAs is lower than the numbers recorded at the time of designation.

The estuaries themselves have also changed since the early years of designation. Developments related to both industry and climate are now having greater impacts on waders and their ecosystems, with terms such as ‘coastal squeeze’ aptly describing their effects (Mander et al. 2007). Whether an estuary can support the populations it was designated for is a now pertinent question given the extent of changes seen across the UK (Evans 2007). If estuaries are still able to support the SPA designated numbers in their current states but populations are still declining across the region, it implies that declines are due to impacts on the migrating (Evans et al. 1991; Yang et al. 2011) and breeding stages (Rehfisch and Crick 2003; Norris et al. 2004; Perkins et al. 2016) of wader annual lifecycles.

This chapter will use the new suite of individual-based models of five estuaries (see Chapter 4) to investigate whether these habitats can support increased numbers of waders and compare these with past peaks and designations of wading bird populations.

5.2 Methods

To understand whether estuaries can still support SPA numbers, my previously developed suite of individual-based models was parameterised to simulate up to a 500% increase in current bird numbers. The five models (Exe, Humber, Poole Harbour, Severn and Southampton Water) were initially parameterised with WeBS 2009/10-2013/14 five year average winter populations (October-February) with corresponding tides and daylight (Holt et al. 2015). A full detailed explanation of the models can be found in Chapter 4. Table 5.1 reports the current population sizes for each of the five modelled estuaries; a minimum cut-off for inclusion in models of 100 birds was applied to all WeBS average counts to restrict predictions to the most abundant species.

To simulate an increase in population size, models were run with these numbers (Table 5.1) multiplied by 2, 3, 4 or 5. For simplicity all species were increased together. The maximum investigated increase of 500% was set following comparison of current average populations to past peaks (see Table A10.1) showing an average of 423% difference (maximum 580%). A 500% increase allowed for comparison with past peaks, averages and SPA designations. These past peaks come from winter periods during 1994-1999 and correspond with the years of designation for each site; although the Humber estuary has been updated recently (2007) the designations are still calculated from the previous designation years (Table A10.1).

Table 5.1. Current (2009-2014) mean over-winter numbers of birds within the SPAs on each of the five estuaries based on BTO WeBS count data (Holt et al. 2015).

Model name	**BTO code**	**Exe estuary**	**Humber estuary**	**Poole Harbour**	**Severn estuary**	**Southampton Water**
Dunlin	DN	2,450	10,850	1,400	17,550	1,150
Sanderling	SS	0	300	0	0	0
Ringed Plover	RP	0	0	0	100	0
Turnstone	TT	100	200	0	300	200
Knot	KN	0	17,350	0	850	0
Redshank	RK	400	2,300	750	3,000	250
Grey Plover	GV	200	1,350	100	200	100
Black-tailed godwit	BW	800	1,300	1,300	200	250
Bar-tailed godwit	BA	200	1,350	100	0	0
Oystercatcher	OC	1,600	3,800	850	650	850
Curlew	CU	750	2,400	850	2,800	400
Total		6,500	41,200	5,350	25,650	3,200

Ten replicate simulations were run for each combination of parameter values and an average response calculated for each simulation. The numbers of birds supported to the end of the simulation and their use of the habitats and diets were recorded. Confidence in these outputs can be found from the validation and sensitivity analyses of the base model parameterisations for each estuary (Sections 4.3.1-4.3.2, Chapter 4). A *population increase threshold* for each species per estuary was taken as the population increase at which the numbers of birds supported was less than 90% of that at the start of the model. This corresponds with the calibration threshold used in Chapter 4 based on a range of annual survival and mortality rates for multiple wader species. These *population increase thresholds* are used to investigate the development of predictive conservation rules through linear regression against forager and estuaries characteristics.

It should be noted that the thresholds found from these IBMs should not be presented directly as absolute values of change that can occur for management advice. As seen in an earlier chapter (Chapter 2), wading birds are able to compensate for changes to their environment with different diets, densities of conspecifics and alternative foraging areas. With this behavioural plasticity, birds can be seen to be shifting from their preferred locations and diets earlier than the modelled threshold, thus indicating that they are 'stressed' or 'under pressure'. Using the points at which large shifts in diet are noticed based on a predefined value (i.e. 25% more of a less preferred diet), a lower threshold can be developed for practical management use. When presenting thresholds developed from IBMs this difference in values must be made to all stakeholders and the new buffered threshold should be used to aid discussions of mitigation and potential environmental change developments.

5.3 Results

5.3.1 Proportion of species supported following increased population

In general, increasing the population sizes of birds on each estuary resulted in the subsequent decline in the percentage supported. Considering all bird species and estuaries together a significant linear relationship ($y = 118.752-0.184x$) was found (Figure 5.1). On some estuaries survival rates declined more rapidly with increased population size (Figure 5.2). As a result of the simulated increases, populations in the Humber estuary were the first to decline strongly, followed by the Severn estuary and then Poole Harbour (Figure 5.2). The Exe estuary and Southampton Water still maintained over 40% survival of their birds even when with 500% of the original bird numbers.

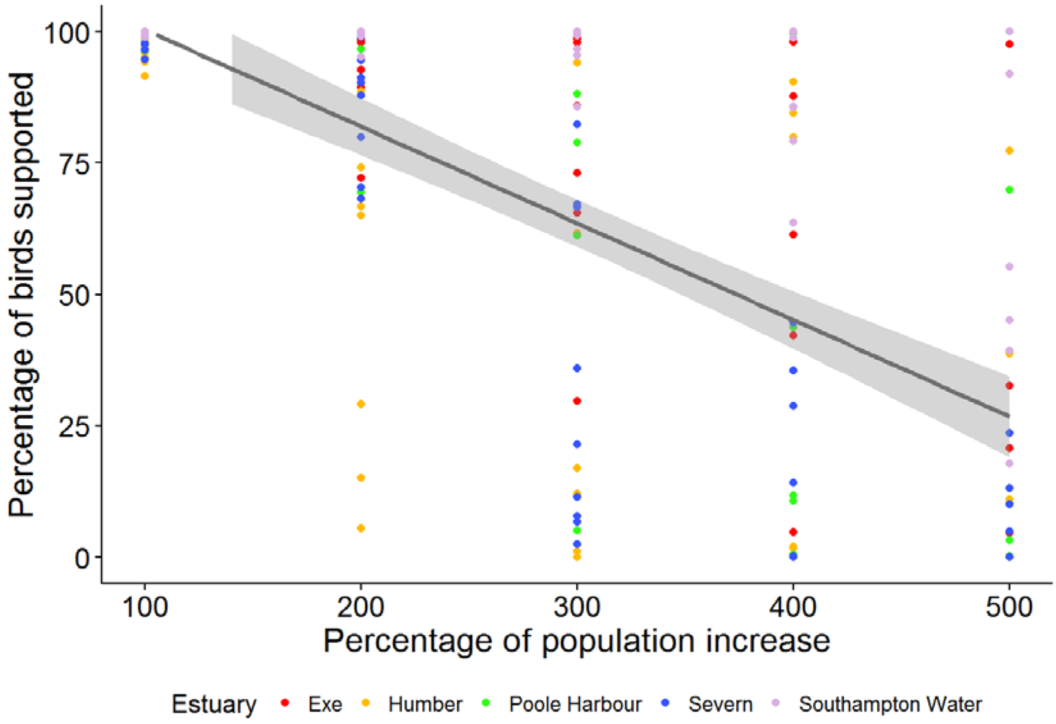

Figure 5.1. Percentage of birds supported to the end of winter for up to a 500% population increase split by estuary. The black line indicates the significant linear relationship of these results ($F_{(1,203)}=132.5$, $p=<0.001$, $r^2=0.3949$) and the shaded area is the 95% confidence interval.

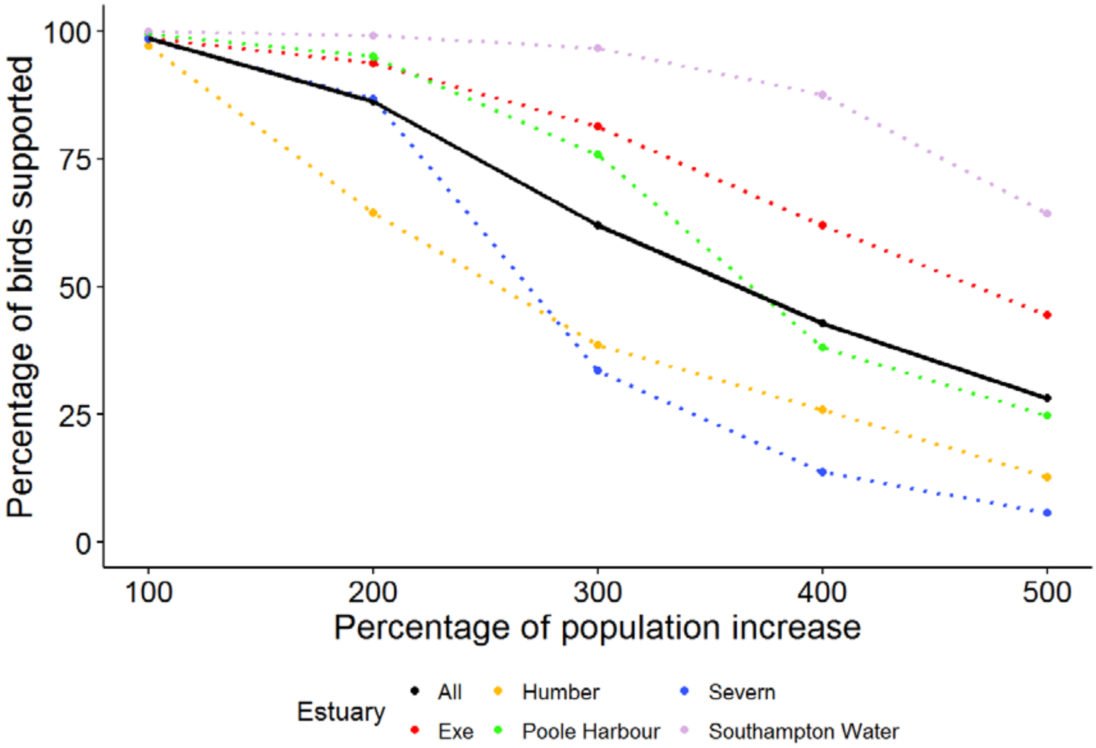

Figure 5.2. Percentage of birds supported to the end of winter for up to a 500% population increase split by estuary. The central solid line indicates an averaged number supported across all five estuaries.

With simulated population increases, species with more restricted diets (see Appendix 6 for dietary preferences), such as the bar-tailed godwit (*Limosa lapponica*), declined first, but others declined in a site-specific sequence (Figures A11.1a-e). Of the other species, some followed similar trends across the estuaries; as a result of a simulated increase of 300%, numbers of black-tailed godwit (*Limosa limosa*) fall below 90% on all estuaries. Others were very site-specific, such as the redshank (*Tringa totanus*) which had high survival on Southampton Water, even with an increase of 500%, but had low survival on the Humber estuary by 300% (Figures A11.1a-e).

On the Exe estuary and Poole Harbour, with up to a 200% increase, all birds except bar-tailed godwit maintained a greater than 90% survival compared to their starting populations, whilst over three-quarters of the species in the Humber and Severn estuaries fell below the *population increase threshold*. Southampton Water could support an increase of over 300% of all species except the black-tailed godwit before population declines were predicted.

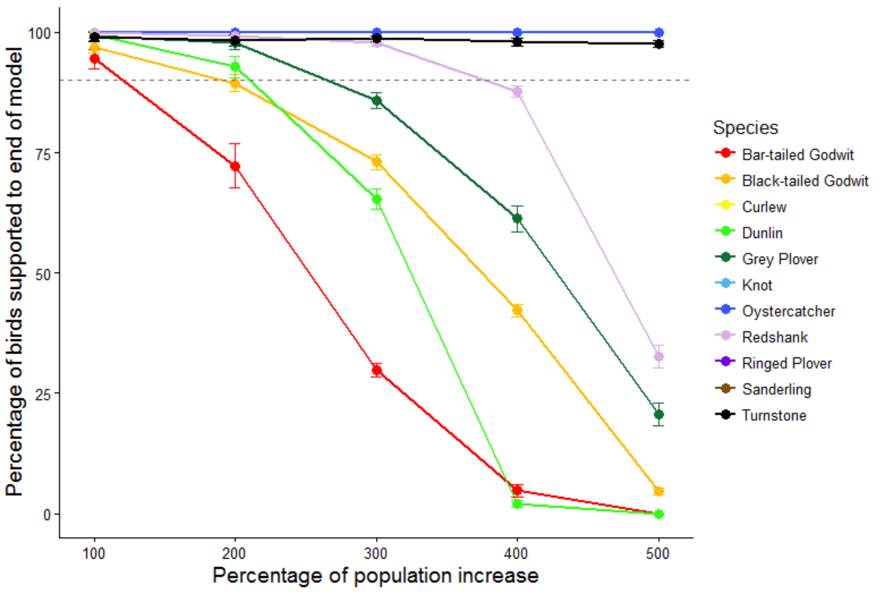

Figure 5.3 Percentage of birds supported when faced with population increase on the Exe estuary.

Table 5.2. Percentage increase in time feeding across all estuaries and species after experiencing a 500% increase in population. A colour legend is displayed below the table.

Model name	**Exe**	**Humber**	**Poole Harbour**	**Severn**	**Southampton Water**
Bar-tailed godwit	0.01	1.13	6.95		
Black-tailed godwit	2.72	2.84	9.42	11.03	5.46
Curlew	0.97	3.5	9.56	7.9	1.84
Dunlin	11.29	18.16	23.8	26.87	14.16
Grey Plover	1.56	3.44	15	6.78	7.16
Knot		8.46		7.59	
Oystercatcher	0.26	8.94	7.86	6.34	3.90
Redshank	8.38	5.75	19.29	21.95	10.24
Ringed Plover				14.74	
Sanderling		15.36			
Turnstone	-0.14	8.56		16.72	5.28

Percentage	0-5%	5-10%	10-15%	15-20%	20+%

Even when the model populations were increased substantially, the proportion of time different birds were required to spend feeding was relatively similar on all estuaries (Table 5.2). However, some larger increases were predicted for a few species on the Severn estuary and Poole Harbour (Table 5.2; Figures A12.1a-e). Following a simulated increase of 500% in the population of redshank and dunlin (*Calidris alpina*), both species were required to increase their feeding time by between 19-27%, whilst increases in most other species remained below 10%. Dunlin always showed the greatest increase (Table 5.2) but on Poole Harbour and the Severn estuary the largest increases were predicted (see Severn estuary example Figure 5.4).

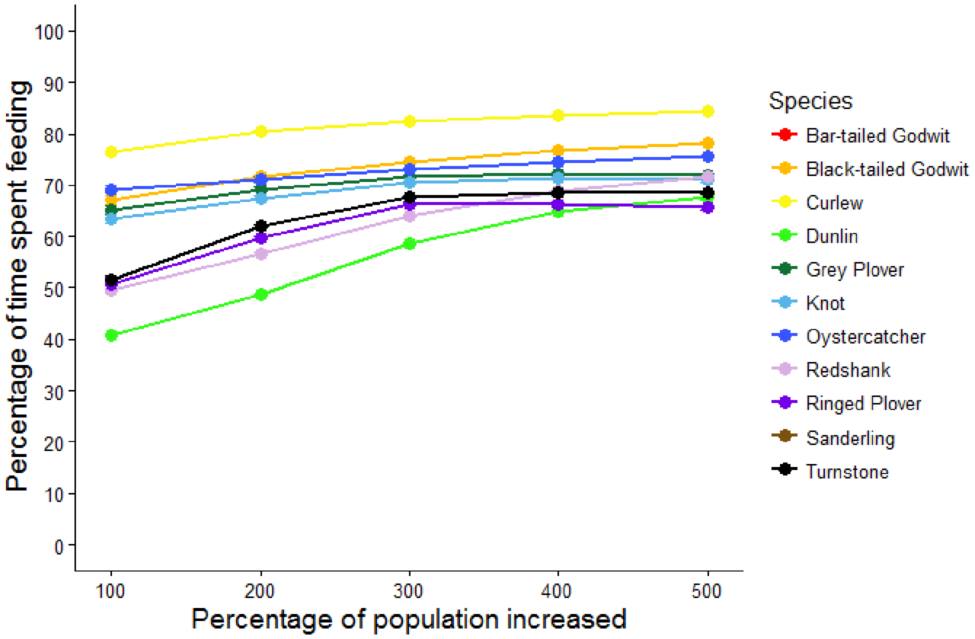

Figure 5.4 Percentage of time birds are required to spend feeding when faced with population increase on the Severn estuary.

Considering dietary changes (see Appendix 13) to explain the population declines in more detail, with population increases of 500%, except for additional crustacea in Poole Harbour and the Exe estuary for black-tailed godwit, both black-tailed and bar-tailed godwit did not greatly change their diets, thus showing the lack of flexibility in diet of these species. Only curlew (*Numenius arquata*) altered their diets greatly on the Severn estuary when marine worms were reduced to less than 50% of biomass intake, having started out at close to 60% in the default model (see Figure A13.4b).

Where dunlin numbers declined steeply (after a 200-300% increase), they included *Peringia* in their diets on the Exe and Severn estuaries (see Figures A13.1d and A13.4.4c) whilst adding more molluscs in Poole Harbour (Figure A13.3d). These three estuaries had the highest densities of *Peringia* and mollusc resources (as 'Other Molluscs' see Figures A15.6 and A15.4). The more obvious shifts in diet composition were in redshank, where they increased their intake of either crustaceans or earthworms. These were seen for the estuaries where they declined the most (Severn, Exe, Poole Harbour, Southampton Water) suggesting a link to lower resource options on these sites (Figure 5.5 and Figures A5.4). The decline on the Humber estuary has no corresponding change in redshank's dietary preferences (Figure A13.2h).

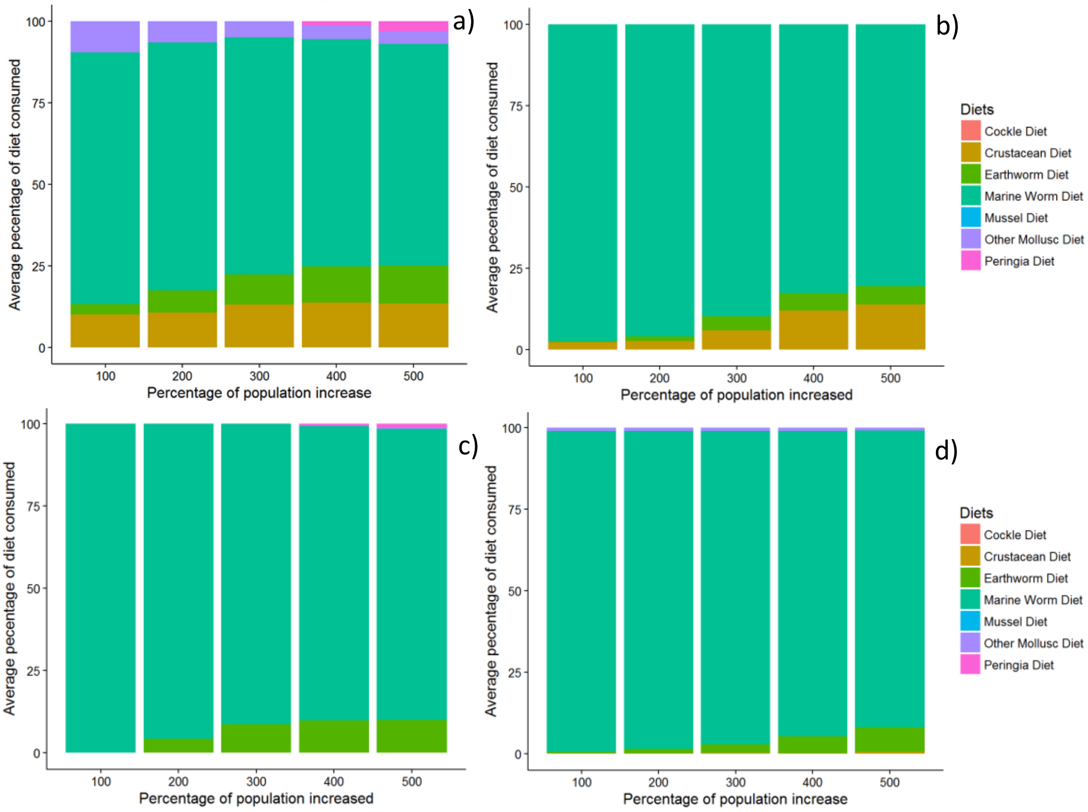

Figure 5.5 Dietary preferences of redshanks when faced with increased populations on the a) Exe estuary, b)Poole Harbour, c) Severn and d) Southampton Water.

5.3.2 Abilities of estuaries to support designated SPA population numbers and past maximums from WeBS surveys.

Having investigated responses to population increases in each estuary, the numbers of birds given within SPA designations were considered alongside current and past maximums. Table 5.3 shows the current differences between estuary SPA designations for each species and values used to parameterise MORPH (from 2009-2014 winter averages). Appendix 14 contains graphs for all species included on the modelled estuaries with comparisons to their SPA designations, WeBS averages and peaks.

For almost all species and estuaries, the winter peak numbers from the years of designation (1994-1999) were higher than the current values (winter 2009/14 averages) used to model the birds. The differences between current and SPA designated numbers could have a big impact when assessing an estuary's capacity in the face of environmental change. An example of this is seen on the Exe estuary where dunlin (Figure 5.6a) are currently present in lower numbers on average (2,450) than the average number seen at the time of designation (2,998) and much lower than the peak mean that they were designated for (5,740) which is 234% greater than current levels. Similar scenarios were seen for grey plover (*Pluvialis squatarola*) and oystercatcher (*Haematopus ostralegus*) on the Exe estuary (SPA 235.5% and 266.6% larger respectively than current averages). It should be noted that oystercatcher on the Exe estuary did not experience any declines when simulated populations increased to 500%, indicating that a maximum population has not been reached.

Table 5.3 Percentage difference between designated SPA numbers (JNCC 2016) *and values from current winter averages for each species (2009/2014), which are used in the MORPH simulations. SPA percentages in **Bold** are less than current averages.*

Site	**Species**	**2009/14 winter averages (used in MORPH)**	**SPA numbers**	**SPA as a percentage of values used in MORPH**
Exe estuary	Black-tailed Godwit	800	533	**66.6**
	Dunlin	2450	5740	234.3
	Grey Plover	200	471	235.5
	Oystercatcher	1600	4265	266.6
Humber estuary	Bar-tailed Godwit	1350	2752	203.9
	Black-tailed Godwit	1300	1113	**85.6**
	Curlew	2400	3253	135.5
	Dunlin	10850	22222	204.8
	Grey Plover	1350	1704	126.2
	Knot	17350	28165	162.3
	Oystercatcher	3800	3503	**92.2**
	Redshank	2300	4632	201.4
	Ringed Plover	0	403	*(too low 2009/14)*
	Sanderling	300	486	162.0
	Turnstone	200	629	314.5
Poole Harbour	Black-tailed Godwit	1300	1576	121.2
Severn estuary	Dunlin	17050	44624	261.7
	Redshank	3000	2330	**77.7**
Southampton Water	Black-tailed Godwit	250	1125	450.0
	Ringed Plover	0	552	*(too low 2009/14)*

The reverse is seen for the Exe estuary's black-tailed godwits (see Figure 5.6b) where the SPA was designated for 533 wintering birds but since designation in 1999 (updated from the original in 1992) current averages are 53% higher than the original designation (now 816; Table A10.1). This highlights the need for updating totals used for SPA designations. The maximum peaks of birds seen over the same years as the SPAs were designated, compared to the most recent five years, also indicate a need to be aware of the variation in numbers that an estuary can support. In this case, at a 200% increase of current populations, black-tailed godwits could not be supported in the estuary.

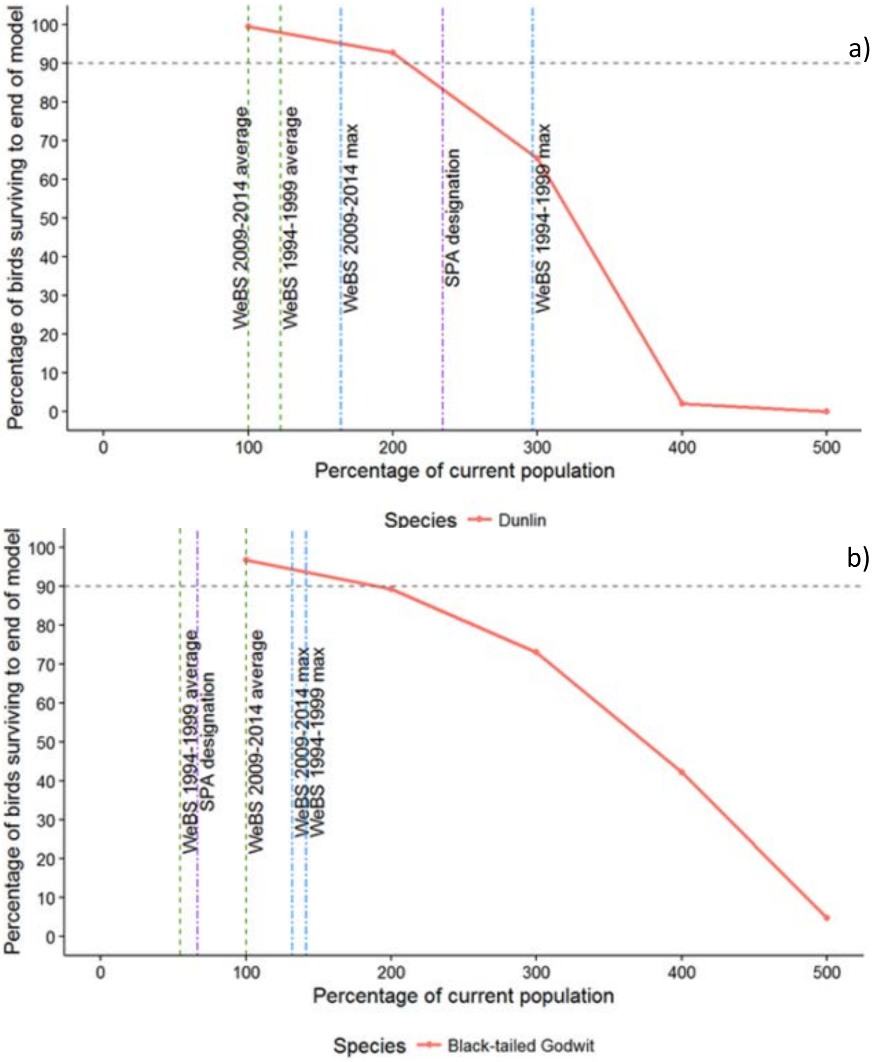

Figure 5.6. Comparing the percentage of modelled birds supported when faced with increased populations on the Exe estuary - a) dunlin, b) black-tailed godwit.

In Poole Harbour, black-tailed godwits were the only wader (used in these models) listed under the SPA designation and this sits only slightly above the current number (121%) as are both the peak maximums. Bar-tailed godwits drop considerably down to 70% of the population supported when close to the latest peak maximum.

All modelled species on the Humber estuary were included in the SPA designation, along with ringed plover (*Charadrius hiaticula*) that are currently in too low numbers to be included in my models. Of these ten modelled waders, only oystercatcher and black-tailed godwits are currently at populations greater than their SPA designations (SPA 92.2 and 85.6 lower than

2009/14 averages). For the other waders the SPA values are all above current populations and for four species (bar-tailed godwit, curlew, redshank and turnstone (*Arenaria interpres*)) are higher than the recent peak maximum. Bar-tailed godwit, dunlin and turnstone are the most different from current numbers, (205, 205 and 315% above current populations respectively).

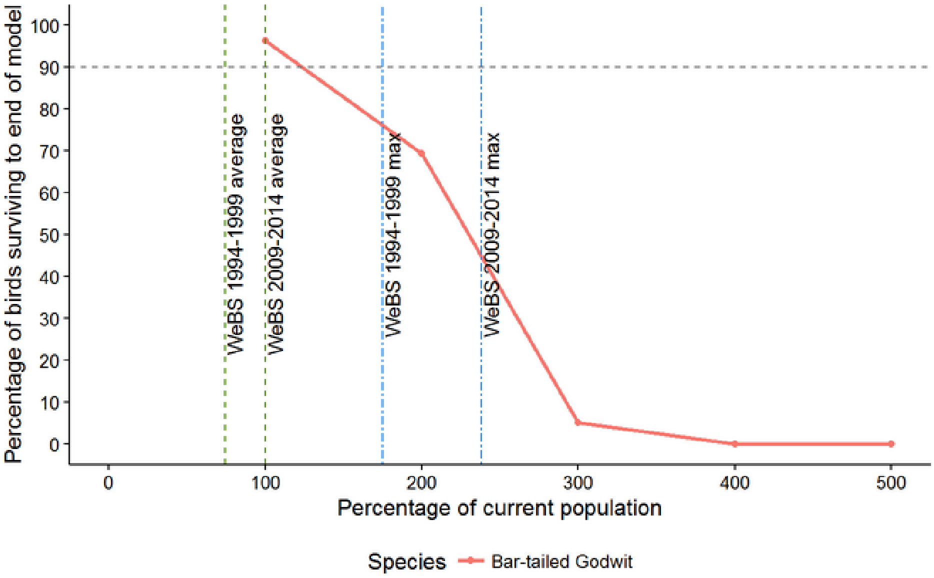

Figure 5.7. Comparing the percentage of bar-tailed godwit supported when faced with increased populations on Poole Harbour.

Two species, dunlin and redshank, are included in the Severn estuary SPA, and whilst the latter is slightly above the listed population (2009/14 average; 28% greater than SPA), dunlin numbers are well below previous populations and the SPA designation (2009/14 average to 1994/99 peak 297%, to SPA 262%). For the Severn estuary, increases in populations mean that once dunlin were at the numbers designated for the SPA, they do poorly with around 50% being supported indicating that invertebrate resources within the estuary would not be able to support these numbers. Other species on the Humber do not respond well to increasing populations; black-tailed godwit, grey plover, knot (*Calidris canutus*), oystercatcher, ringed plover and turnstone all drop beneath the *population increase threshold* when the numbers in the models are increased above current averages. One of the most dramatic impacts are seen in ringed plover, that are only supported up to 200% and are currently well below the maximum numbers seen on the estuaries in the past 20 years and thus left out of the Severn estuary IBM.

Finally the results for Southampton Water show that black-tailed godwit are supported at levels well below those designated for the SPA and when the estuary contains enough birds to match that population only 50% of the birds are supported. Other species tend to be quite well supported until closer to 400%, so the estuaries could support the peak maximum populations over a winter. In particular, no influence was found on up to 500% of oystercatcher and curlew populations, so further parameterisation will be needed to determine their *population increase thresholds*. As with the Severn estuary, ringed plover have declined to the extent that they were not included in the IBMs; less than 100 birds were seen on average in the past five years (Holt et al. 2015).

5.3.3 Development of predictive conservation rules for increasing wader populations

Having looked at the individual species responses on five estuaries, a set of *population increase thresholds* for each species and estuary have been predicted (Table 5.4). Variation in these thresholds is now related to species and site characteristics.

Using R version 3.2.3 (R Development Core Team 2015) and the ggplot2 package (Wickham 2009) the relationships between species and estuary characteristics and the *population increase thresholds* were investigated using a linear regression, with 95% confidence intervals portrayed on the plots. The thresholds found for each wader species per estuary can be viewed in Figure 5.8. For species that did not cross the *population increase threshold* within the scale of environmental change investigated, the maximum value (500% population increase) was used to allow for their inclusion in the modelling.

Table 5.4. Threshold of population increase above which the percentage supported fell below 90%. Cells with "supported" indicate that the percentage supported did not fall below 90%, even with the greatest increase in population size, and were given a value of 500% in the analysis.

Species	**Exe estuary**	**Humber estuary**	**Poole Harbour**	**Severn estuary**	**Southampton Water**
Bar-tailed Godwit	120	102	124		
Black-tailed Godwit	192	121	219	202	254
Curlew	*supported*	117	433	119	*supported*
Dunlin	210	349	245	212	368
Grey Plover	265	109	284	139	361
Knot		184		126	
Oystercatcher	*supported*	112	*supported*	178	*supported*
Redshank	377	127	313	205	*supported*
Ringed Plover				254	
Sanderling		401			
Turnstone	*supported*	343		201	333

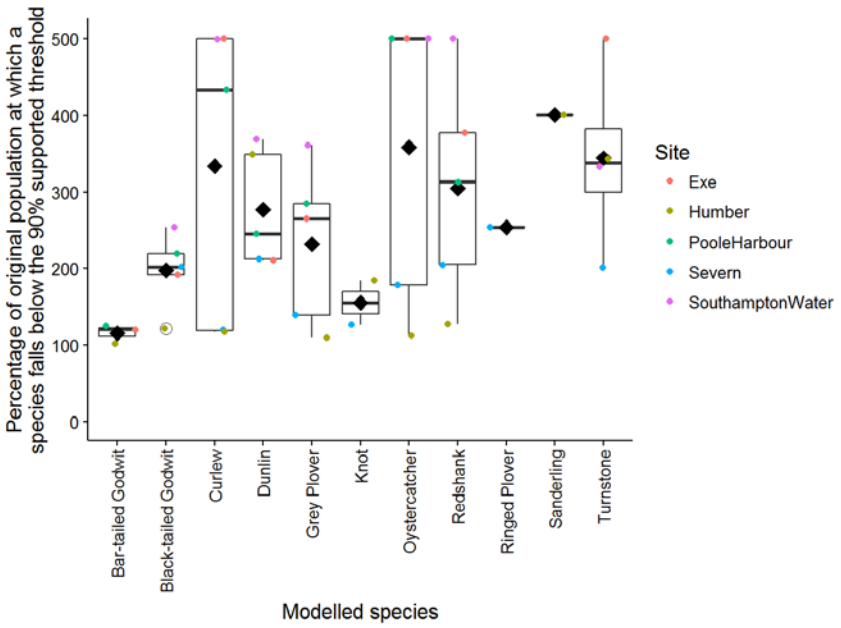

Figure 5.8. Comparison of population increase thresholds (less than 90% of the population supported) found for eleven species when faced with population increases up to 500%.

The variables used are those for which a mechanism for affecting the threshold population increase could be determined. For forager variables, the list included: body mass (g), regulated density (m^{-2}), count of resource types (Marine worms, Other Molluscs, crustaceans etc.) and count of size classes that could potentially be consumed. Estuarine variables were: Percentage (mean) exposure of intertidal habitat (over model run), Average food per bird (kg AFDM), Density of birds on estuary (m^{-2}), number of resource types, number of resource size classes and average length of invertebrates (Marine worms or Other Molluscs in mm) on the site.

Only one species characteristic was significantly related to the *population increase thresholds* (using modelled linear regression) – the number of resource types a species can consume (marine worm, other mollusc, crustacean etc. to a maximum of seven). This positive relationship shows that birds with a broader potential diet can be supported at higher population sizes (Table 5.5 and Figure 5.9). No other relationships were significant, but count of marine worm resources in diet and count of other mollusc resources were close to significance (Table 5.5). Other regressions against weight, regulated density and average length of invertebrates in bird's diets were non-significant.

Table 5.5. Linear regression of forager characteristics against population increase threshold.

Forager characteristic investigated	**F**	**Degrees of freedom**	**r^2**	**P value**	**Direction of relationship**
Count of types of resource in diet	4.899	1,39	0.1116	0.0328	Positive
Count of marine worm resources in diet	3.96	1,39	0.0922	0.0689	Negative
Count of other mollusc resources in diet	3.638	1,39	0.0853	0.0619	Positive

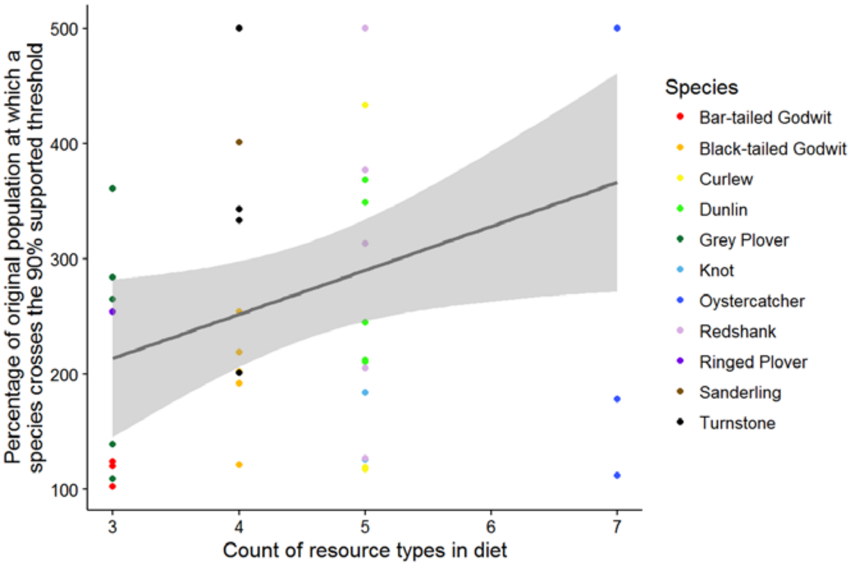

Figure 5.9. Linear regression of count of resource types a forager can consume against the population increase threshold.

Significant linear relationships were found with estuarine resource characteristics (Table 5.6). There are four positive relationships with variables measuring the diversity and size of an estuary's resources, showing that with increasing resource types and numbers of size classes, as well as larger average invertebrate sizes, larger increases in population size can be supported (Figures 5.10b-d). The negative trend of the average food per bird is not as expected; the influence of the Severn and Humber results will be explained in the context of their invertebrate diversities in the discussion (Figure 5.10a). Linear regression with percentage of time an estuary's intertidal habitat is exposed, and the initial density of birds were non-significant related to population increase thresholds.

Table 5.6. Linear regression of estuarine characteristics against population increase threshold.

Estuarine characteristic investigated	**F**	**Degrees of freedom**	**r^2**	**P value**	**Direction of relationship**
Average food per bird (kg)	11.27	1,39	0.2241	0.00177	Negative
Count of resource types available	11.18	1,39	0.2228	0.00184	Positive
Count of size classes available	14.14	1,39	0.2661	0.000557	Positive
Average size of marine worm (mm)	16.29	1,39	0.2946	0.000246	Positive
Average size of other mollusc (mm)	14.48	1,39	0.2708	0.000488	Positive

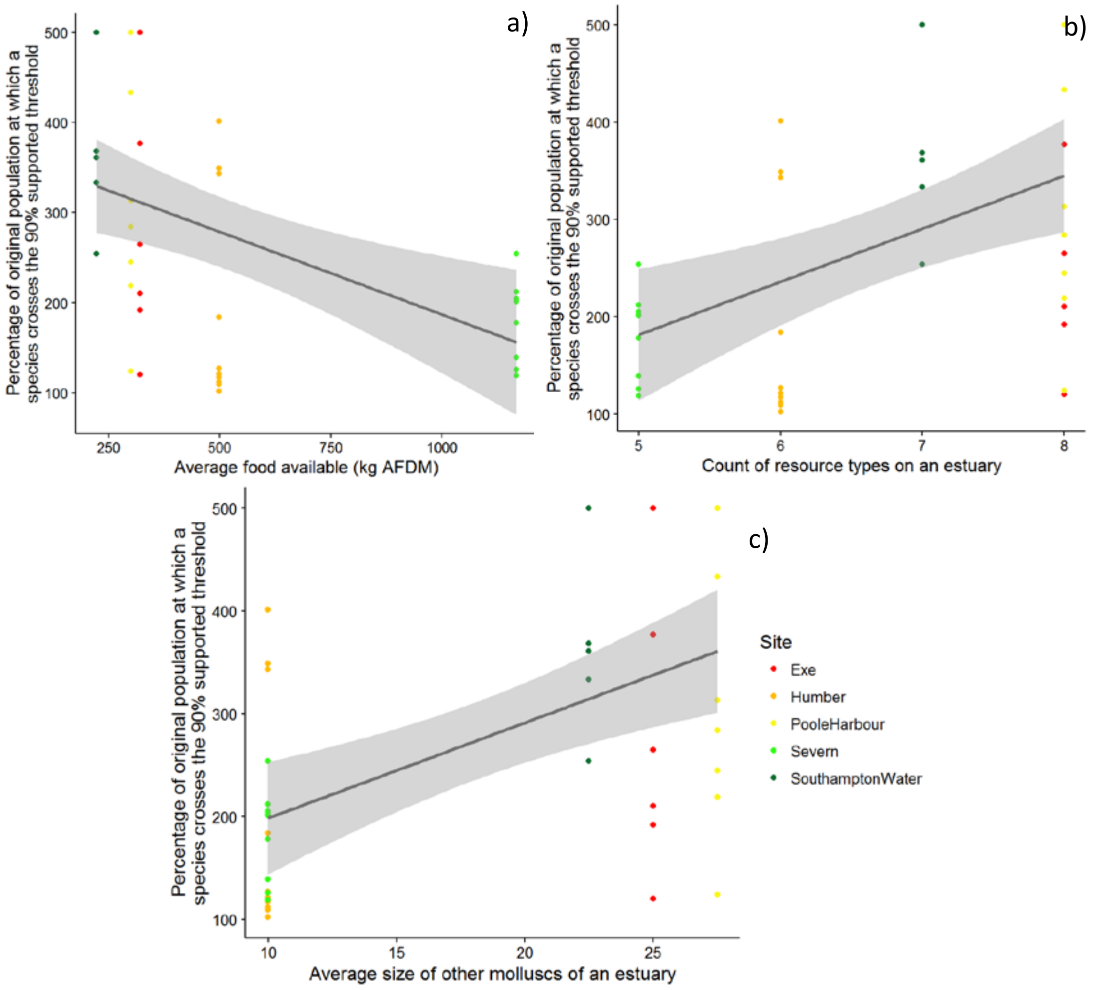

Figure 5.10. Linear regression of a) average food available for each bird, b) count of resource types available and c) average size of other molluscs (mm) against the population increase threshold.

5.4 Discussion

Increasing the populations of wading birds on estuaries within individual-based models has shown that for most species a limit, or carrying capacity is reached when up to a 500% increase in population size is simulated. There is a certain amount of variation in each estuary's ability to hold a larger population, but once past a certain point – around 226% increase on average – survival rate in almost all species is predicted to decline. Most estuaries have seen declines in populations of waders and, of those with SPA designated species; half are predicted to be unable to support more than 90% of the parameterised populations when at designated numbers. This is consistent with previous research that showed that survival rates of wader species are density-dependent and thus affected by increasing numbers of conspecifics (Durell et al. 2000; Ryan et al. 2016).

Several of the eleven wading birds studied had similar patterns of decline across the five estuaries, showing a similar response to the depletion of resources and competition for space. Although differences are observed for the starting point of the declines, birds like bar-tailed godwit, black-tailed godwits and dunlin all had similar trends, whilst curlew had a clear division between the southern estuaries. Given the lack of invertebrate diversity on the Seven and Humber, this indicates a link between site quality and the increase in population that could be supported. Grey plover, oystercatcher, redshank and turnstone had very different patterns of decline on different estuaries, although all showed rapid declines on the Humber and Severn. Unusually, the pattern of decline of Humber estuary turnstones remained between those predicted on the Exe estuary and Southampton Water, whilst the pattern on the Severn estuary was more like that predicted for ringed plover, and is likely due to the lack of crustaceans which formed an important part of the turnstone's diet when under population pressure.

When populations were increased, the lack of change in time spent feeding and slight changes in diet (Appendices 12 and 13), indicates that most species are not able to compensate for increased competition effectively by exploiting alternative food sources, or for feeding for longer. Only a few birds, such as turnstone and ringed plover greatly altered their diets to include additional resources (such as crustaceans and *Peringia*). Oystercatcher had more subtle shifts that align with their steady population maintenance throughout all increases in population. The wide variety of diets seen in knot and oystercatcher indicates that the changes in dietary preferences are quite different between estuaries.

Differences between the three southern estuaries and the Severn and Humber are species-specific and given the poorer invertebrate diversity on the latter two estuaries (Appendices 5.6 and 5.7) are likely to be driving the differences. Moreover, high energy tidal systems such as

Severn estuary are characterised by smaller invertebrate species (Emerson 1989; Kaiser 2005). Further investigations into the importance of invertebrate diversity and population size frequencies will improve model accuracy.

5.4.1. SPA number comparisons

The results of population increases compared to SPA designated numbers of individuals and related maximums have proven highly informative for conservation and management. Only four out of the twenty designations now fall below the 2009-2014 averages, whilst the other values all sit higher than current average.

Looking at the five-year averages and peaks, most 1994-1999 peaks are greater than the current numbers seen but only half of the five-year averages were higher. The majority of the peaks were quite different from each other in terms of magnitude and often essentially unchanged in observed population size. This illustrates the decline in wader populations over the fifteen year period (Holt et al. 2015; Frost et al. 2016) and also highlights that fact that many SPAs designations are well above current averages. Currently, predictions indicate that some estuaries will not be able to support peak numbers of species previously recorded, with six of the ten modelled waders on the Humber declining below 90%of their original populations. For the other estuaries, declines of waders range between 29-44% of their previous peak numbers. However this is only for the maximum number of birds seen; only two species the dunlin on Poole Harbour and redshank on the Humber are not supported at previous average populations.

Of the other species that had higher SPA designations than the current averages, there is an equal split of birds that drop beneath the *population increase threshold*. No clear difference can be seen between those above or below the threshold for the current population that the old SPA value sits, the relationships must be due to the estuaries and the species own particular characteristics. It should be noted that in the case of ringed plover, the current populations on the Humber estuary and Southampton Water are too low for inclusion in the MORPH models (<100 individuals over the past five winters) and these need to be. As such, new models can be developed to include these to assess how well they would cope with the previous populations.

The outcome of all these observations is that the SPA designations should be re-examined. For some species where the populations have increased (black-tailed godwit on the Exe and Humber, and oystercatcher on the Humber and redshank on the Severn) the designations should be raised to be in line with the current averages. Where the SPA designations are higher than averages a more careful approach should be taken, looking into where peak populations lie in relation to the previous numbers, but also into whether it is predicted that an estuary can no longer support such large numbers.

5.4.2. Making more general predictions for population increase effects on waders

Individually, each wader on a modelled estuary can be used to make predictions for how conservation and management can be carried out. Whilst these estuary-specific predictions are in themselves useful to future conservation efforts, being able to predict the effects of population increases from general characteristics would be very advantageous.

Even with all species being parameterised similarly between the five sites, there were few forager characteristics that were close to being significantly related to population increase thresholds. The positive relationship between those species with wider diets (greater numbers of resources accessed) is consistent with the idea that generalist birds tend to be better able to cope with the impacts of environmental changes than specialists (Caldow et al. 2007; Ma et al. 2009). That the relationships between average lengths of Marine worms and Other Molluscs consumed were close to significance, signify that with future work on other estuaries it may be possible to say if the size range of a diet plays an important role in ability to cope with population increases.

Of the various linear regressions that were significant for estuarine characteristics, the most understandable relationships are seen for resource variables. The less diverse Severn and Humber estuaries (Appendices 5.6 and 5.7) are not able to support as many birds following the population increases. These estuaries did have a higher amount of (average) food per bird than the other sites, however their lack of supportiveness was mainly due to their greater sizes reducing the density of these resources. Wading birds have been seen to preferentially choose better quality sites over poorer quality sites (Gill et al. 2001) and the models add to this understanding by showing how less able these sites are to support greater population increases.

5.4.3 General conclusions

Overall, these models have both brought to light the inconsistencies between SPA designation numbers and the inability of the estuaries to support increasing populations. Dietary generalists do better than those species with more limited diets but only in estuaries with broader resources available. As such, the predictions will be useful for future work on appropriate SPA designations and aid the understanding of inter-estuarine relationships between species. Any general conservation rules of how wading birds will respond to population increases requires better understanding of the importance of invertebrate diversity for a greater variety of bird species in different sites. Future work on the combined effects of population increases and environmental change will expand the understanding of how the carrying capacity of estuaries is important in the conservation of waders and their ecosystems.

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6. Using individual-based models to predict how wading birds will be affected by environmental change.

This chapter uses the new suite of IBMs (Chapter 4) to predict the effects of habitat loss and sea-level rise on wading birds. Bird’s survival and fitness are analysed in the event of such environmental change and conservation rules for management and mitigation are explored.

6.1 Introduction

Rapid environmental change due to rising a human population, development and associated habitat loss and climatic change, is occurring at a unprecedented rate (Hoekstra et al. 2005; Bindoff et al. 2007; Hanna et al. 2013; Toth and Szigeti 2016), and ecosystems such as estuaries and the species that live on them are no longer as diverse as they used to be (Lotze et al. 2006). To slow the rate of these changes, and even reverse them, conservationists, industry and governing bodies need to work together to ensure future development is sustainable.

Estuarine ecosystems are found globally along almost every coastline (Dürr et al. 2011) and of the many species that live within their bounds, wading birds (Charadrii) are an important group. These birds live at the higher reaches of the trophic levels of an estuary (Fujii 2012) and are good indicator species for the health of an estuary (Furness and Greenwood 1993; Rehfisch et al. 2004). But, as mentioned in Chapter 2, individual responses of birds can be quite varied, given their adaptability to compensate for changes in their environment. Without knowing what is happening on an individual basis, we could easily miss detrimental changes to an estuary until sudden changes in population size occur, with no opportunity to introduce mitigating management measures. A way to understand subtle effects of environmental change, and account for adaptive shifts in behaviour is to use simulation models, such as individual-based models, that account for the variation between birds (Stillman et al. 2003, 2014; Grimm and Railsback 2005).

Predicting the effects of future changes on an environment can be complex. In the past, predictions have been made using experimental studies (Piersma et al. 2001; Ruthrauff 2014), transposing reactions of other sites (Goss-Custard et al. 1991), and statistical modelling (Austin and Rehfisch 2003; Hunter et al. 2015). These all have their benefits, when understanding the potential damage to a section of habitat (no matter how small), but they might be flawed in their assumptions over why birds in different sites respond in different ways, or oversimplify the responses populations to change. As mentioned in previous chapters (Chapter 4 & 5), individual-based models (IBMs) follow the decisions of individuals (such as individual birds) and allow observed behaviours to emerge from basic decisions based on individual characteristics. IBMs provide a perfect opportunity to investigate the impacts of environmental changes through small manipulations to the simulated environments that modelled wading birds have to accommodate and respond to.

Wading birds are affected by many environmental changes (see Chapter 3). Of these, the most published scenarios include habitat loss (Evans et al. 1979; Burton et al. 2006; Moores et al. 2016), sea-level rise (Norris and Atkinson 2000; Austin and Rehfisch 2003; Fujii 2012), temperature change (Irving 1955; Davidson 1982; Nebel and Thompson 2005) and pollution (Frederick et al. 2002; Alves et al. 2012; Agoramoorthy and Pandiyan 2016). The impacts of these changes can be easily incorporated into an IBM, as they directly affect either the environment or the energetics of an individual.

Habitat loss and sea-level rise both affect the foraging space and time than an individual can access. Global examples of intertidal area loss and impacts on waders include the Cardiff Bay barrage (Burton et al. 2006; Ferns and Reed 2009), removal of the majority of intertidal areas in Saemangeum, Korea (Moores et al. 2008, 2016), intertidal reclamation for aquaculture and industry in China (Yang et al. 2011; Melville et al. 2016) and loss of foraging areas to shellfishing in the Wash, UK (Atkinson et al. 2010).

With rising global temperatures (Trenberth et al. 2007) the risk of sea-level rise from loss of ice sheets is increasing and current projections to the end of the 21st century (UKCP09) predict up to a 0.59 m increase globally (Lowe et al. 2009). Birds will also come into conflict with humans and other species and compete for available space. Depending on the rate of sea-level rise, and the availability of suitable habitat, the preferred prey species of birds may adapt to changing tide levels and redistribute to higher shore levels (Fujii 2012). Finally, sea-level rise could alter the percentage of time birds have to access intertidal foraging areas (Goss-Custard et al. 1991; Stillman 2009), creating another pressure on already stressed populations.

This chapter will investigate the impacts of habitat loss and sea-level rise on wintering wading birds using a suite of IBMs. The thresholds of environmental change leading to negative effects on the birds will be identified and related to species and site characteristics. These relationships will be used to determine conservation rules to identify species and sites that may be more vulnerable to environmental change.

6.2 Methods

Using the previously developed suite of individual-based models (see Chapter 4) for the Exe estuary, Poole Harbour, Southampton Water, the Humber estuary and the Severn estuary, I altered specific parameters to simulate environmental change. Following work carried out during my literature review (see Chapter 3), I found that of the many environmental changes impacting wading birds, apart from direct human disturbance, most studies have considered the effects of habitat loss, sea-level rise, temperature change and pollution. As a result, the environmental changes parameterised in this chapter look into the effects of the first two issues, habitat loss and sea-level rise.

To simulate habitat loss, a stepwise removal of intertidal patch areas, in 10% increments, was implemented with an upper limit of 90%, as 100% removal would have eliminated any species that cannot feed on terrestrial habitats. Sea-level rise was simulated in accordance with the latest predictions (UKCP09). It is reported that there could be up to a 0.76 m increase in sea-level around the United Kingdom by 2095 (Lowe et al. 2009) under the highest emissions scenario. Using these as a guideline, sea-level rise increases were applied up to 0.8 m through increases of the *Shoreheight* in metres Chart Datum (CD) of each patch (Table 6.1). This reduced the percentage of time that patches were exposed compared to current sea-level.

Table 6.1 Mean and Max Shoreheights in metres Chart Datum (CD) across all patches used in the default IBMs from the bathymetry models of HR Wallingford.

Estuary	**Mean Shoreheight (m CD)**	**Max Shoreheight (m CD)**
Exe Estuary	1.6	2.6
Humber Estuary	4.1	5.9
Poole Harbour	1.2	2.0
Severn Estuary	4.0	8.7
Southampton Water	2.5	3.7

Each simulated environmental change was run ten times for each of the five estuaries and the mean response calculated. The numbers of birds of each species supported to the end of each model run were analysed to determine the threshold environmental change at which the percentage of birds supported declined below 90% (see Chapter 4). Confidence intervals and linear regressions were used to develop conservation rules using the statistical software R (R Development Core Team 2015) and the ggplot2 package (Wickham 2009). For species for which the percentage supported did not decline below 90%, within the range of environmental change simulated, the maximum value of environmental change simulated was used in the analysis.

To determine conservation rules, a set of species and site characteristics were related to the environmental change (i.e. habitat loss or sea-level rise) thresholds. These characteristics were limited to those for which the link (mechanism) between the characteristic and potential susceptibility to environmental change could be identified. Species characteristics were: body mass (g) (i.e. energy demands), regulated density (m^{-2}) (i.e. susceptibility to interference), maximum number of resource types that can be consumed (Marine worms, Other Molluscs, crustaceans etc.), average length of invertebrates consumed (mm) and maximum number of size class that can be consumed (i.e. potential number of alternative resources available). Site characteristics were: mean *Shoreheight* (m CD) (i.e. amount of shore that may remain available after sea-level rise), percentage exposure of intertidal habitat throughout a simulation (i.e. amount of habitat available), average biomass of food per bird (kg AFDM) (i.e. amount of food available for each individual bird), density of birds on site (m^{-2}) (i.e. potential susceptibility to increased density and competition), number of resource types available, number of resource size classes available (i.e. potential number of alternative resources), and average length of invertebrates (Marine worms or Other Molluscs mm).

As mentioned in Chapter 5, before the thresholds found from these IBMs are used by conservationists and managers, they should be buffered down to a lower value of environmental change. Bird’s abilities to compensate for environmental changes prevent direct population declines until they are unable to find alternative energy sources, at which point the modelled threshold will have been reached. These lower thresholds should be produced against predefined values of dietary shifts or increases in time spent feeding.

6.3 Results

When environmental changes were applied to the suite of modelled estuaries, the majority of species reacted to both of the environmental changes, with habitat loss having the greatest impact. The Humber estuary showed the greatest number of predicted negative effects, with the least number of effects on Southampton Water. Due to the extensive nature of these models, the full graphical results are found in the appendices (see Appendices 16-21) whilst the following text contains pertinent examples.

6.3.1 Habitat Loss

Loss of habitat resulted in a wide variety of responses by each of the modelled species (Figures A16.1a-e). Most of the five estuaries showed little overall decline in bird populations below the 90% threshold (termed *habitat loss threshold* for this environmental change) until nearly 60% of the habitat was removed (Figure 6.1a). The Humber estuary showed a high level of variability in mortality with, for example, between 10-62% of turnstone (*Arenaria interpres*) still being supported at 10% of the original habitat (Figure 6.1b). At 90% habitat loss only a few species on particular estuaries survived in any large numbers. These were curlew (*Numenius arquata*) and oystercatcher (*Haematopus ostralegus*) on the Exe estuary and turnstone on the Exe and Humber estuaries. Numbers of all other species were reduced to none or very few birds.

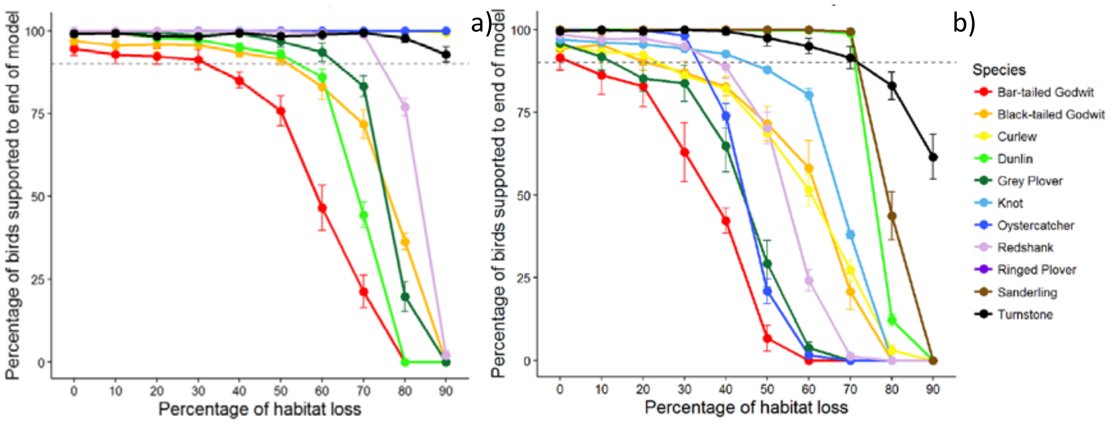

Figure 6.1. Percentage of birds supported in relation to habitat loss on a) the Exe estuary and b) the Humber estuary.

Looking at individual species (Figure 6.2), all except the curlew tend to have steep declines in populations when a *habitat loss threshold* is reached, with a few species on some estuaries (knot, curlew and both godwits), having more gradual changes. With the exception of the Humber estuary, visually there seems to be a similar trend in the population decline profiles of several species between estuaries. This is most visible in the case of bar-tailed (*Limosa lapponica*) and black-tailed godwit (*Limosa limosa*), dunlin (*Calidris alpina*) and redshank (*Tringa totanus*).

Table 6.2 shows the *habitat loss thresholds* leading to 90% of birds being supported. Leaving aside the Humber and Severn estuaries, which had limited invertebrate diversity (see Figures 5.4a-e) and size classes, most bird species could have between 50 and 80% of the habitat removed before populations dropped below the *habitat loss threshold*. In particular, curlew, oystercatcher and redshank showed little change in numbers until higher values of habitat loss were simulated. On the Exe and Severn estuaries, bar-tailed godwit reached the threshold at 30% habitat loss, declining relatively steadily compared to other species (Figure 6.2a).

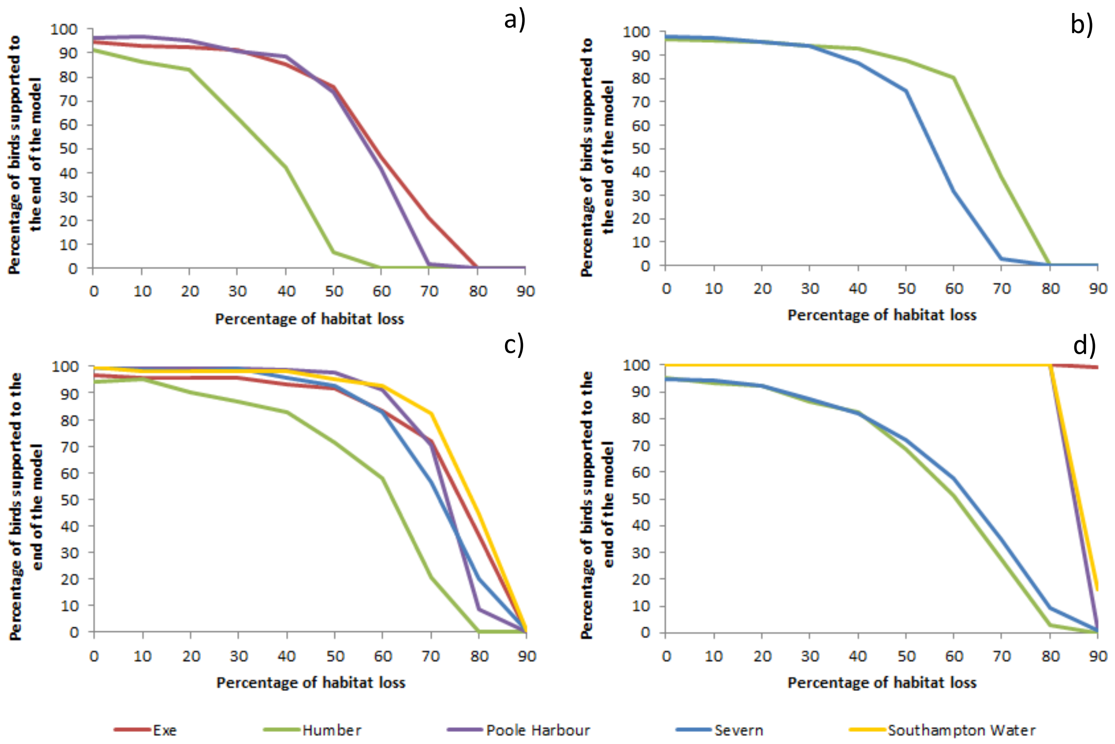

Figure 6.2 Percentage of birds supported in relation to habitat loss a) bar-tailed godwit, b) knot, c) black-tailed godwit and d) curlew.

Table 6.2. Threshold percentage of habitat loss after which populations dropped below 90% of their original population. Cells with "above" indicate the population did not drop below the habitat loss threshold and were given a value of 90% habitat loss for the following linear regressions.

Species	**Exe Estuary**	**Humber Estuary**	**Poole Harbour**	**Severn Estuary**	**Southampton Water**
Bar-tailed Godwit	32	2.9	33		
Black-tailed Godwit	51.8	21.1	60.5	52.7	62.5
Curlew	*above*	23.8	81	24.9	81.2
Dunlin	54	71	62.1	56.9	71.1
Grey Plover	63.4	12.8	65.1	43	71.3
Knot		45.7		35.2	
Oystercatcher	*above*	33.4	81.2	46.5	81
Redshank	74	37.9	71.6	63.1	80.6
Ringed Plover				51.3	
Sanderling		71.7			
Turnstone	*above*	71.8		50	71.4

Whilst for most species the percentage of time spent feeding appears to remain pretty constant throughout the run of models (Figure A17.1a-e), a closer inspection shows that an upward trend is seen in over half of the species on each estuary and mainly when the majority of habitat is removed. Dunlin, redshank, and oystercatcher showed the greatest responses by increasing feeding time by 15-28% on over half of the estuaries they were present on; the largest increase being redshank on the Severn estuary that increased feeding time by 28.2%. With the exception of the Humber estuary, these three species showed the most consistent patterns in simulations of habitat loss. Other species increased feeding time to a maximum of 18% on one estuary each but in general was below 10% change in proportion of time spent feeding through to 90% habitat loss. Bar-tailed godwit and knot were the only two species that had little change in their time spent feeding, both being less than 5.5%. Poole Harbour and the Severn estuary had the largest increases in percentage of time spent feeding followed by Southampton Water, with over three quarters of the birds present increasing by at least 8%. All three of these estuaries have the lowest ratio of total bird numbers to total usable foraging habitat (excluding fields), although differences are slight (respectively 0.039, 0.033 and 0.0034 m^{-2}).

The dietary preferences add an extra layer of understanding to the effects of habitat loss. Bar-tailed godwit showed very little change (e.g. Figure A18.1a) as only a slight difference is seen by the greater loss of habitat. This is very different from that seen in the diets of black-tailed godwits where, as seen on the Severn estuary, marine worm usage reduces from over 60% to 40% of total diet (Figure 6.3). The decline in curlew consumption of marine worm is more severe, and food resources are supplemented with additional species; both crustacea and *Peringia* use increases, although this is dependent on estuary (e.g. Figure A18.1c). Apart from the Severn estuary, where large molluscs are relatively scarce, oystercatchers exploit cockles and mussels and little change in survival was seen in these estuaries until the least amount of habitat remained, when they added earthworms and crustaceans to their diet (Figure 6.4).

Of the other species, dunlin, grey plover (*Pluvialis squatarola*) and redshank do compensate for the marine worm decline by exploiting *Peringia* and Other Molluscs (earthworms and crustaceans for redshank) but only by less than 25%. In the case of grey plover they increased marine worm usage on the Humber estuary and Southampton Water. Knot (*Calidris canutus*) behaved in opposite ways on the two estuaries they were found on, increasing marine worm usage on the Humber estuary and increasing Other Molluscs on the Severn estuary.

Turnstone’s ability to survive on the Exe and Humber estuaries looks to be in part due to their preference for crustaceans, which are little used by other species, and the dramatic shifts are seen towards the greatest habitat loss indicates (Figure 6.5).

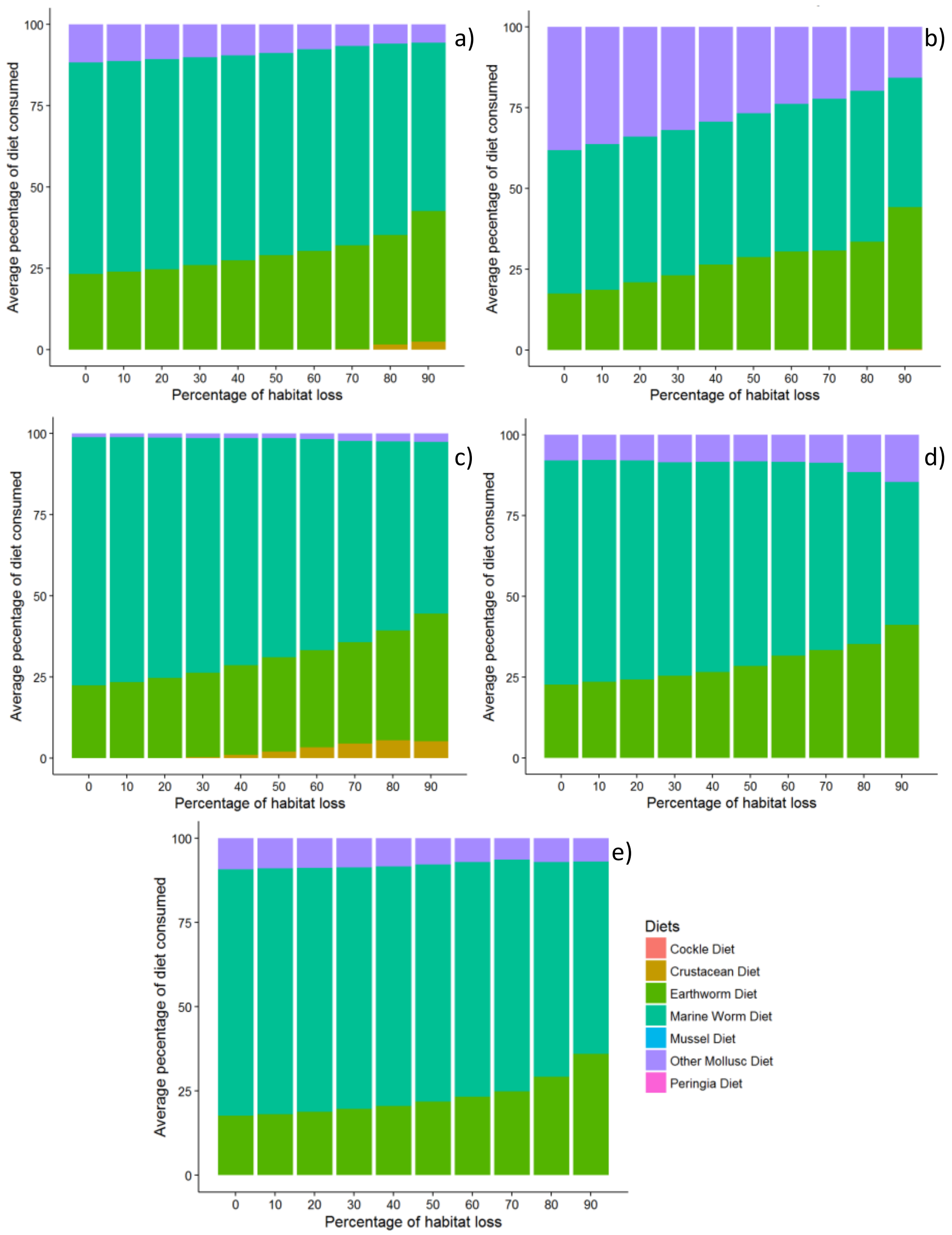

Figure 6.3 Dietary preferences of black-tailed godwit supported in relation to habitat loss on the a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) Severn estuary and e) Southampton Water.

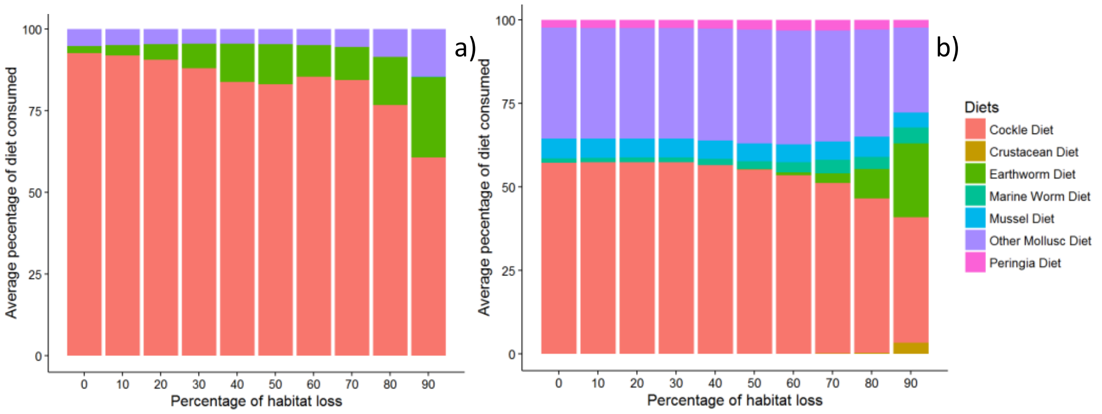

Figure 6.4 Dietary preferences of oystercatcher when faced with habitat loss on the a) Humber estuary and b) Poole Harbour.

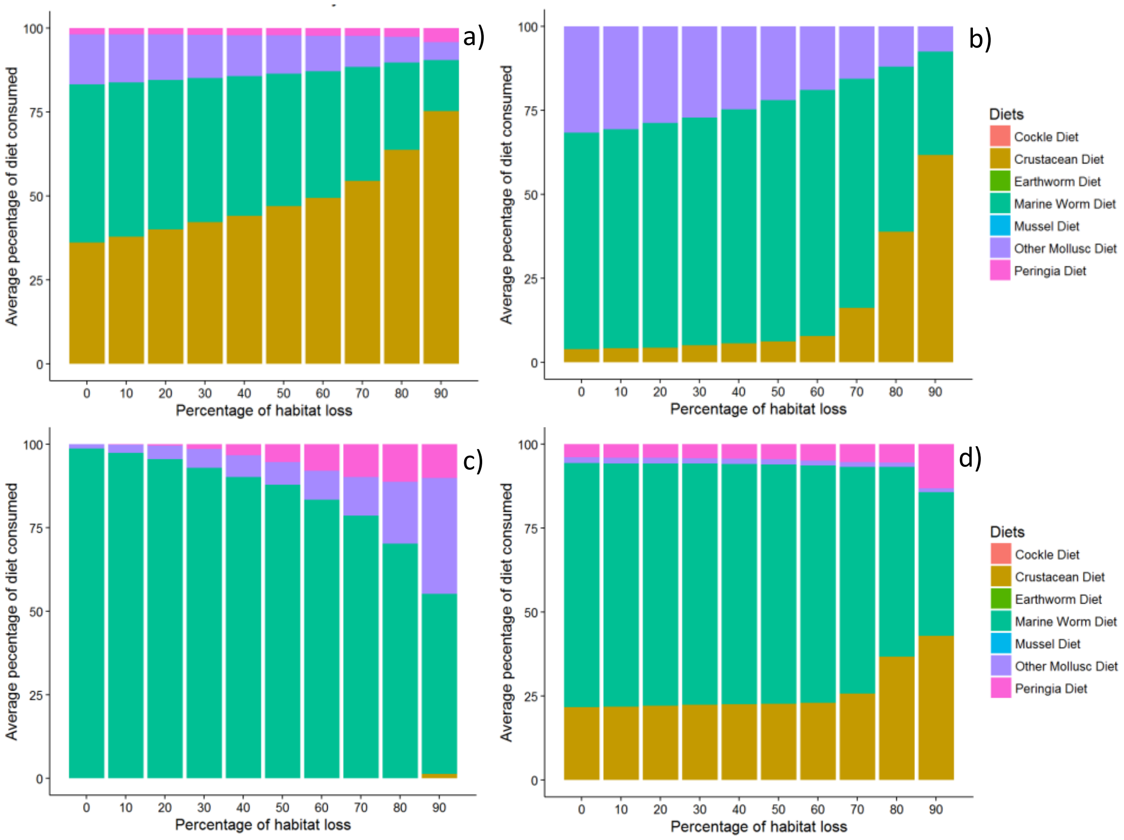

Figure 6.5 Dietary preferences of turnstone in relation to habitat loss on the a) Exe estuary, b) Humber estuary, c) Severn estuary and d) Southampton Water.

6.3.1.1 Comparisons with data from literature

Following from Chapter 3, a comparison between the overall responses of birds to habitat loss (regardless of which estuary they were modelled on) and empirical data from the literature was performed.

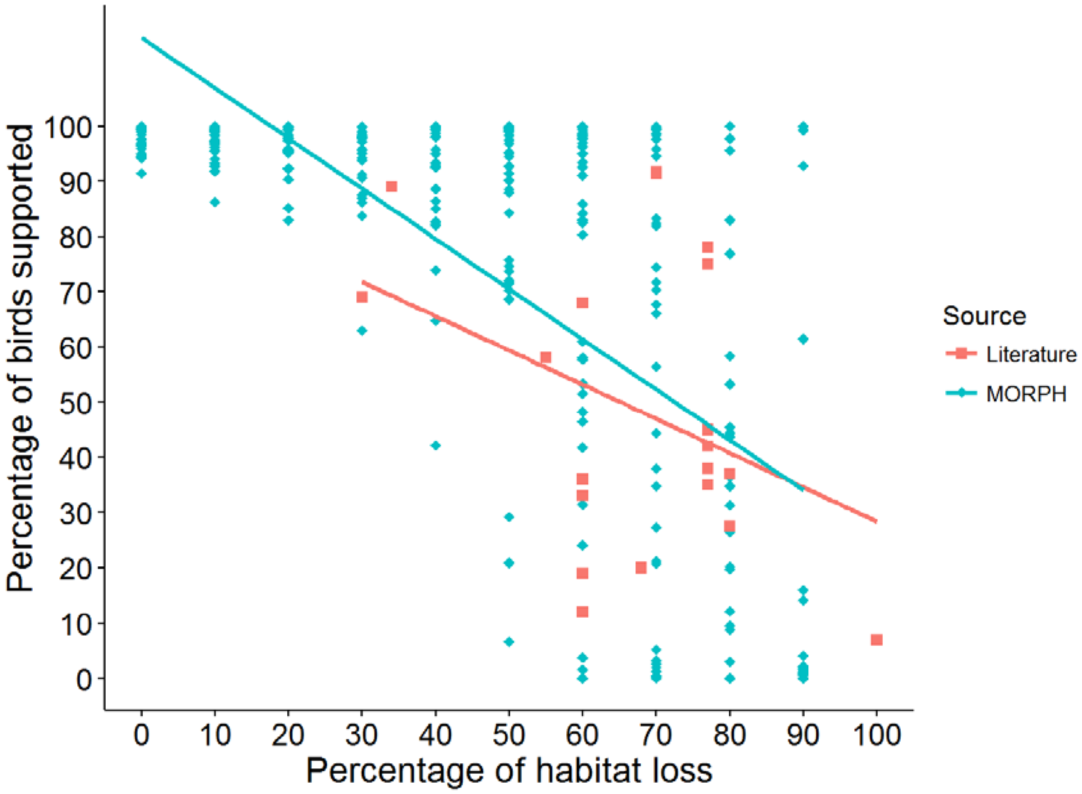

Figure 6.6 Percentage of birds supported to the end of the models when faced with increasing habitat loss derived from MORPH models and literature searches.

Twenty points were found from the literature (Evans 1978/79.; Prater 1981; Schekkerman et al. 1994; Atkinson et al. 2003, 2010; Dare et al. 2004; Burton 2006; Piersma et al. 2007; Burton and Armitage 2008; Duriez et al. 2009; Kraan 2010; Kraan et al. 2010; Yang et al. 2011) that recorded the effect of habitat loss on wading bird survival (see Appendix 22). These were plotted with those from MORPH and the regression lines compared. Figure 6.6 shows that visually there is a large overlap in the points, and the regression gradients are not dissimilar. An analysis of covariance (ANCOVA) in R version 3.2.3 (R Development Core Team 2015) on Arcsine transformed data showed that there was no significant difference (F=0.671, df=1, p=0.413) when including an interaction of source (literature or MORPH).

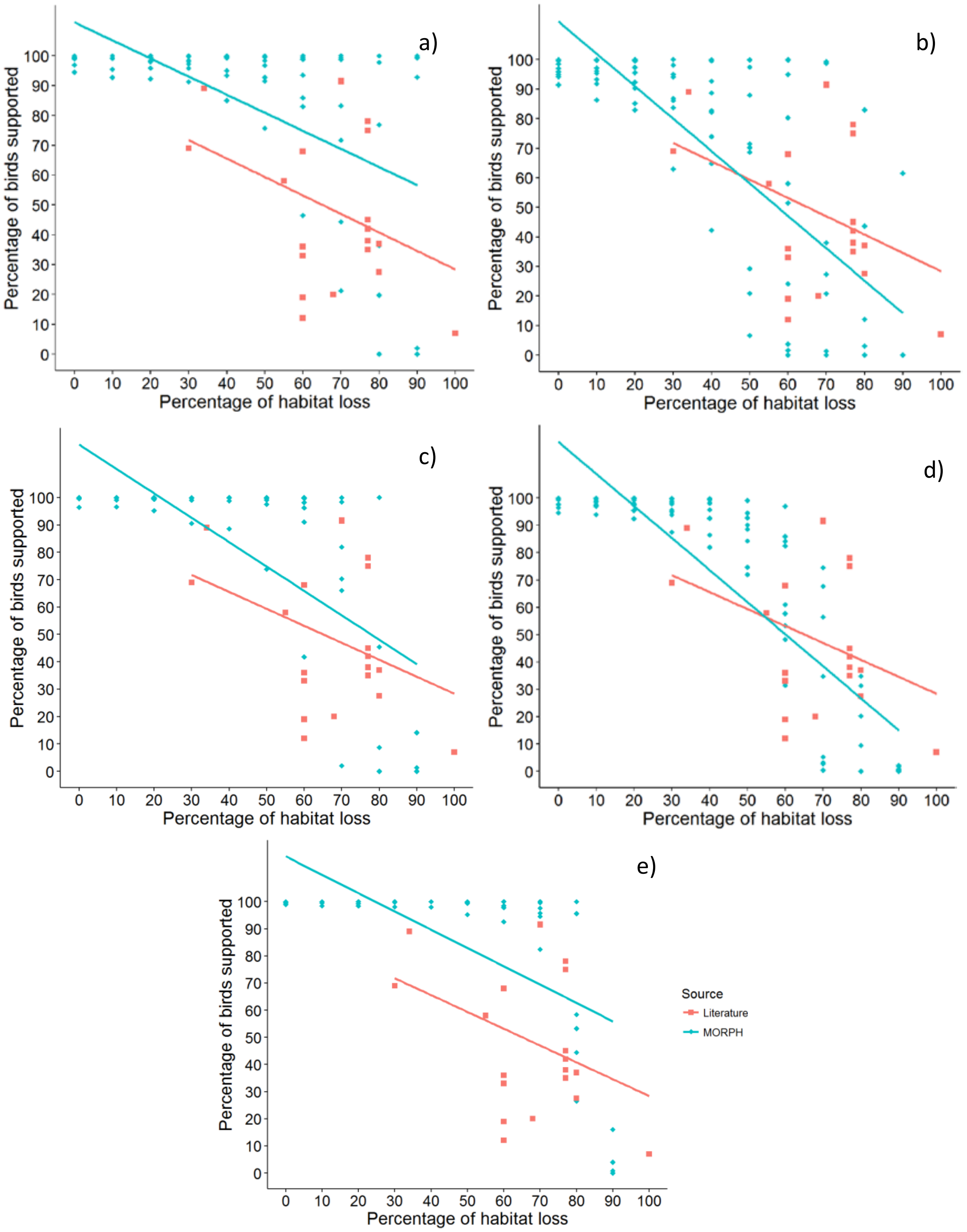

Figure 6.7 Percentage of bird's surviving to the end of the models when faced with increasing habitat loss on five estuaries - a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) Severn estuary and e) Southampton Water

To investigate differences between estuaries, similar analyses between literature and MORPH results were carried out (Figure 6.7). The Humber and Severn estuaries follow similar patterns of mortality with overall habitat loss whilst data points from the two analyses on are relatively well separated. Differences in linear regression lines between MORPH and literature in all five estuaries are not-significant when investigating linear regressions with the interaction term of source (Table 6.3).

Table 6.3. ANCOVA on Arcsine transformed percentage of birds supported to the end of the models when faced with increasing habitat loss derived from MORPH models and literature searches percentage.

Estuary	**F**	**Degrees of freedom**	**r^2**	**P value**
Exe Estuary	21.21	3,96	0.3986	0.9136
Humber Estuary	43.52	3,116	0.5295	0.2040
Poole Harbour	26.77	3,86	0.4829	0.4093
Severn Estuary	63.94	3,106	0.6441	0.0922
Southampton Water	29.73	3,86	0.5091	0.6957

6.3.1.2 Development of predictive conservation rules for habitat loss scenarios

In the previous descriptive sections, the models have predicted the effect of habitat loss, but for single estuaries alone. To investigate if more general predictions can be made, without the data required for a specific individual-based model, another approach needs to be taken. To make these general conservation rules, the *habitat loss threshold* is related to forager and estuary characteristics using linear regression.

For habitat loss, there are three significant relationships between forager characteristics and the habitat loss thresholds (Table 6.4): (i) the number of resources (size-classes) of Marine worms potentially consumed; (ii) the number of crustaceans that a species can potentially consume and (iii) the total number of resource types (Marine worms, Other Molluscs, cockles, etc) that a species can potentially consume. The confidence intervals and spread of the data are quite wide for these linear regressions (Figure 6.8). Additional regressions against body mass and regulated density were both non-significant, as were average lengths of Marine worms and Other Molluscs in bird's diets.

Table 6.4. Linear regression of forager characteristics against habitat loss thresholds.

Forager characteristic	**F**	**Degrees of freedom**	**r^2**	**P value**	**Direction of relationship**
Count of types of resource in diet	4.299	1,39	0.0993	0.0448	Positive
Count of marine worm resources in diet	5.152	1,39	0.1167	0.0288	Negative
Count of crustacean resources in diet	4.411	1,39	0.1016	0.0422	Positive

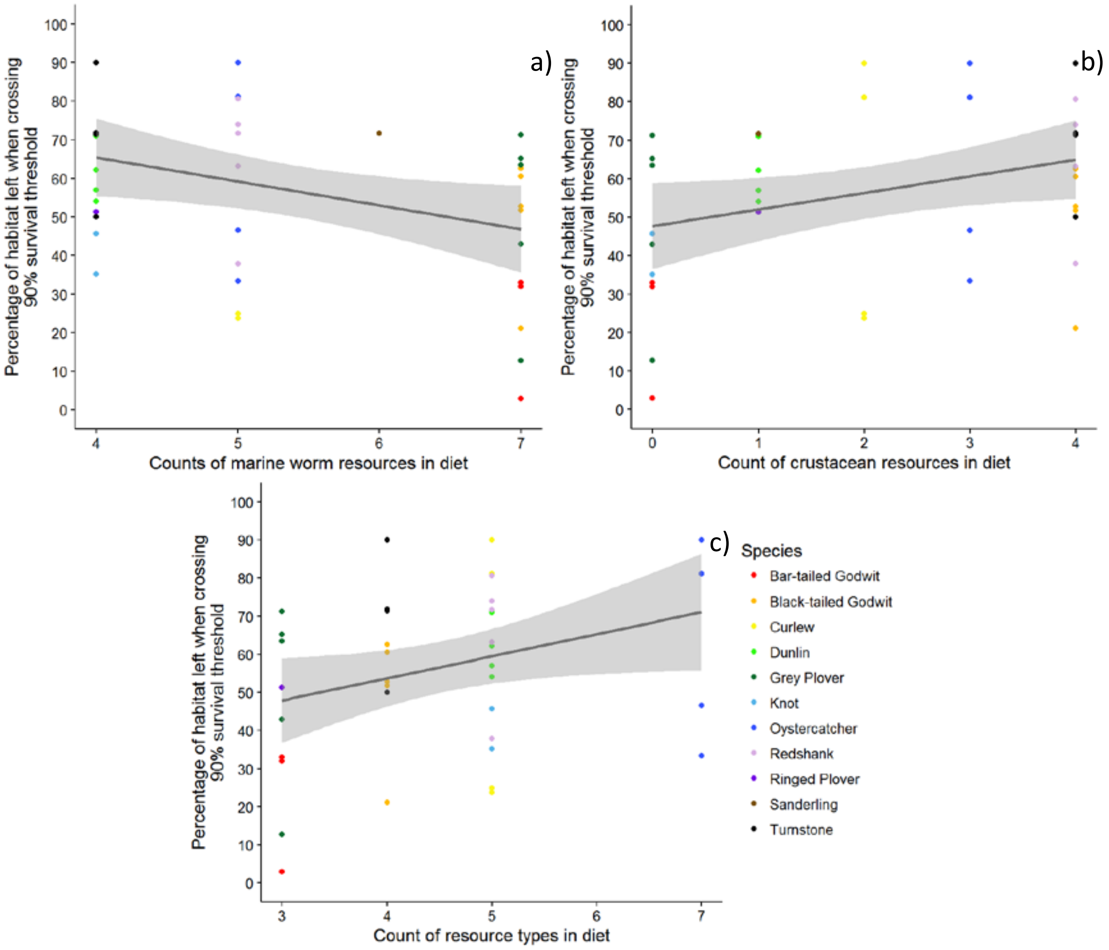

Figure 6.8 Linear regression of a) count of marine worm resources, b) count of crustacean resources and c) count of resource types in diet against the habitat loss threshold.

Looking at the relationships with estuarine characteristics, there are significant relationships with several variables such as count of resource types and size classes of each estuary, and the average length of Marine worms and Other mollusc size classes available (Table 6.5). These relationships have in general better confidence intervals and higher r^2 values (Figure 6.9) than the other two estuarine characteristics. Mean *Shoreheight* and average food available per bird (kg ash-free dry mass) were both negatively associated with *habitat loss thresholds* though it should be noted that the Severn and Humber estuary values have the lowest threshold values (Figure 6.10). The impact of this will be considered in the discussion. One additional regression was carried out against density of birds (m^{-2}) but was found to be non-significant.

Table 6.5. Linear regression of estuarine characteristics against habitat loss threshold.

Estuarine characteristic investigated	**F**	**Degrees of freedom**	**r^2**	**P value**	**Direction of relationship**
Mean *Shoreheight* (m CD)	16.03	1,39	0.2913	0.00027	Negative
Average food per bird (kg AFDM)	6.62	1,39	0.145	0.014	Negative
Count of resource type	11.33	1,39	0.2251	0.00172	Positive
Counts of resource size classes	15.5	1,39	0.2845	0.00033	Positive
Average length of marine worm (mm)	22.7	1,39	0.3685	0.000026	Positive
Average length of other mollusc (mm)	17.92	1,39	0.3148	0.000136	Positive

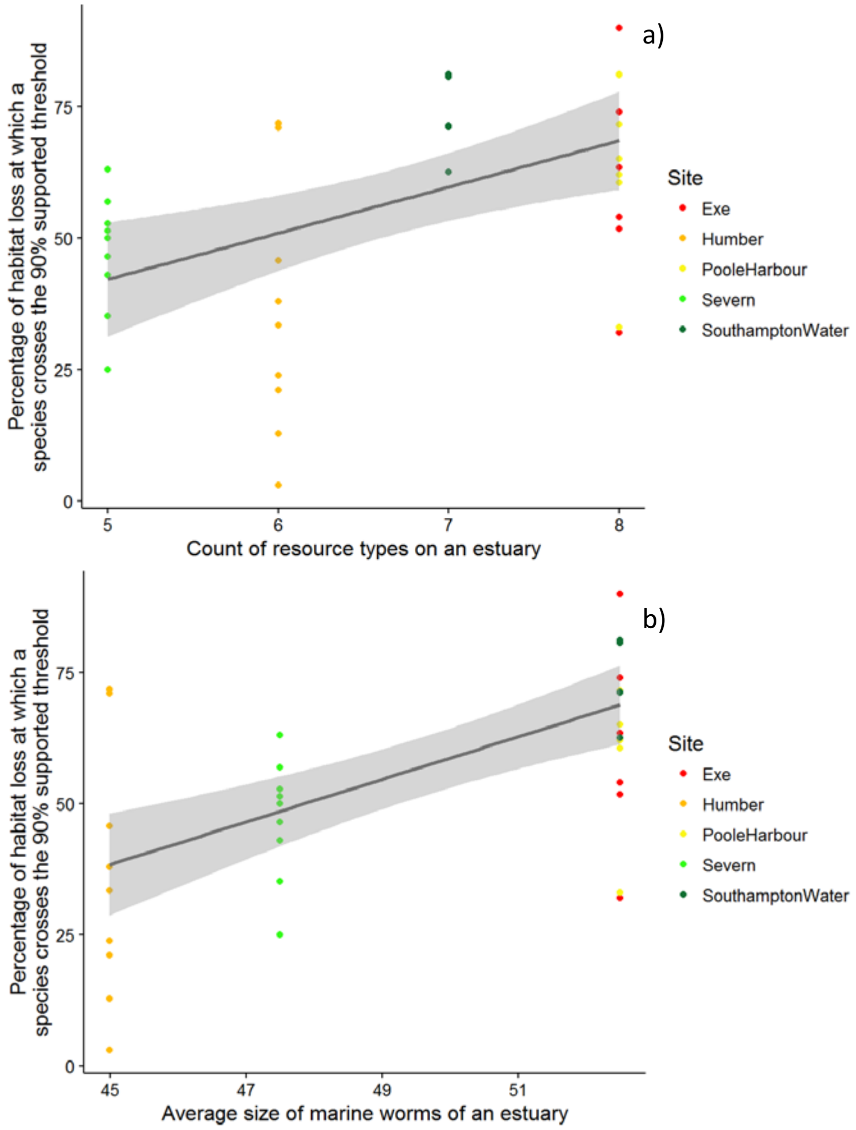

Figure 6.9 Linear regression of a) count of resource types on an estuary and b) average length of Marine worms (mm) in an estuary's intertidal foraging areas against the habitat loss threshold.

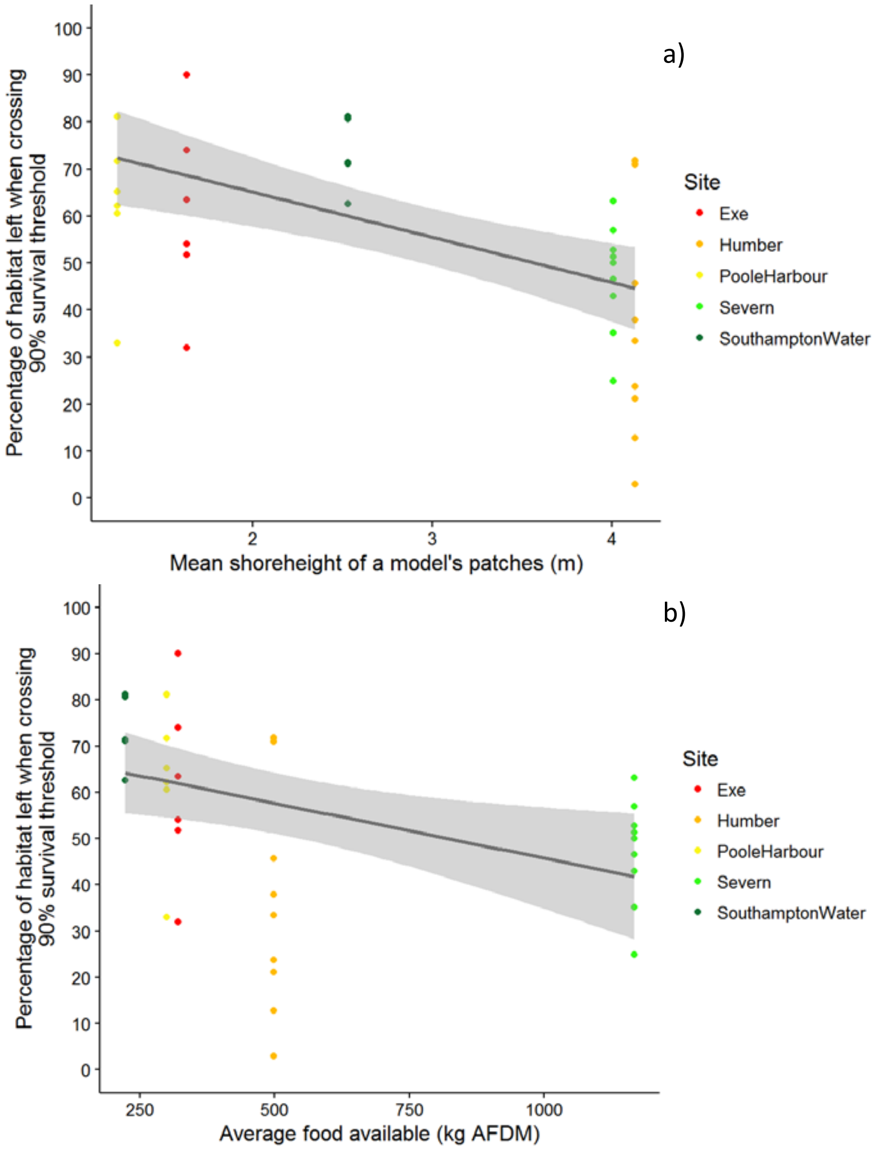

Figure 6.10 Linear regression of a) mean Shoreheight (m CD) and b) Average food per bird (kg AFDM) against the habitat loss threshold.

6.3.2 Sea-level rise

As with habitat loss, sea-level rise reduced the availability of foraging patches for wading birds enough to cause declines on most if not all estuaries (Figures A19.1a-e). The threshold values in Table 6.6 show the variation in thresholds of the species (termed sea-level rise threshold for this environmental change). Bar-tailed godwits are sensitive to the smallest increase in sea-level rise whilst oystercatchers are able to be supported on most estuaries under this scenario. The shallower estuaries, such as Poole Harbour and the Exe estuary (median *Shoreheight* 1.2m and 1.6m Chart Datum respectively), were most affected under these simulations and results showed sudden declines in bird numbers, whilst the remaining three estuaries had smooth declines if any (e.g. Figure 6.11). This is also shown in more detail although the species specific graphs of Figure 6.12.

Table 6.6. Threshold of sea-level rise (metres Chart Datum) after which populations dropped beneath 90% of their original population. Cells with "above" indicate the population did not drop below the sea-level rise threshold and were given a value of 0.8m (CD) sea-level rise for the following linear regressions.

Species	**Exe estuary**	**Humber estuary**	**Poole Harbour**	**Severn estuary**	**Southampton Water**
Bar-tailed Godwit	0.07	0.02	0.01		
Black-tailed Godwit	0.12	0.43	0.11	*above*	0.59
Curlew	*above*	0.33	0.41	0.69	*above*
Dunlin	0.25	*above*	0.12	*above*	*above*
Grey Plover	0.3	0.15	0.13	0.78	0.79
Knot		0.35		0.62	
Oystercatcher	*above*	*above*	0.61	*above*	*above*
Redshank	0.5	*above*	0.22	*above*	*above*
Ringed Plover				*above*	
Sanderling		*above*			
Turnstone	0.24	*above*		*above*	0.49

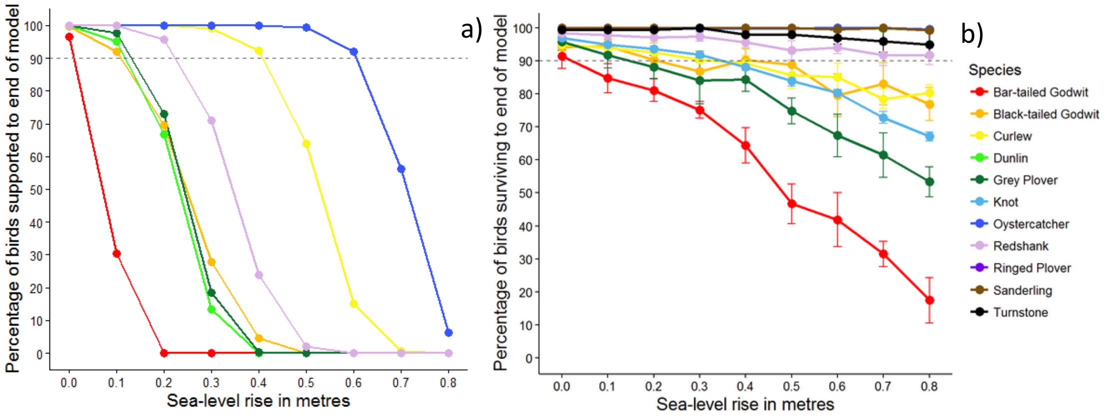

Figure 6.11. Percentage of birds supported when faced with sea-level rise on a) Poole Harbour and b) the Humber estuary.

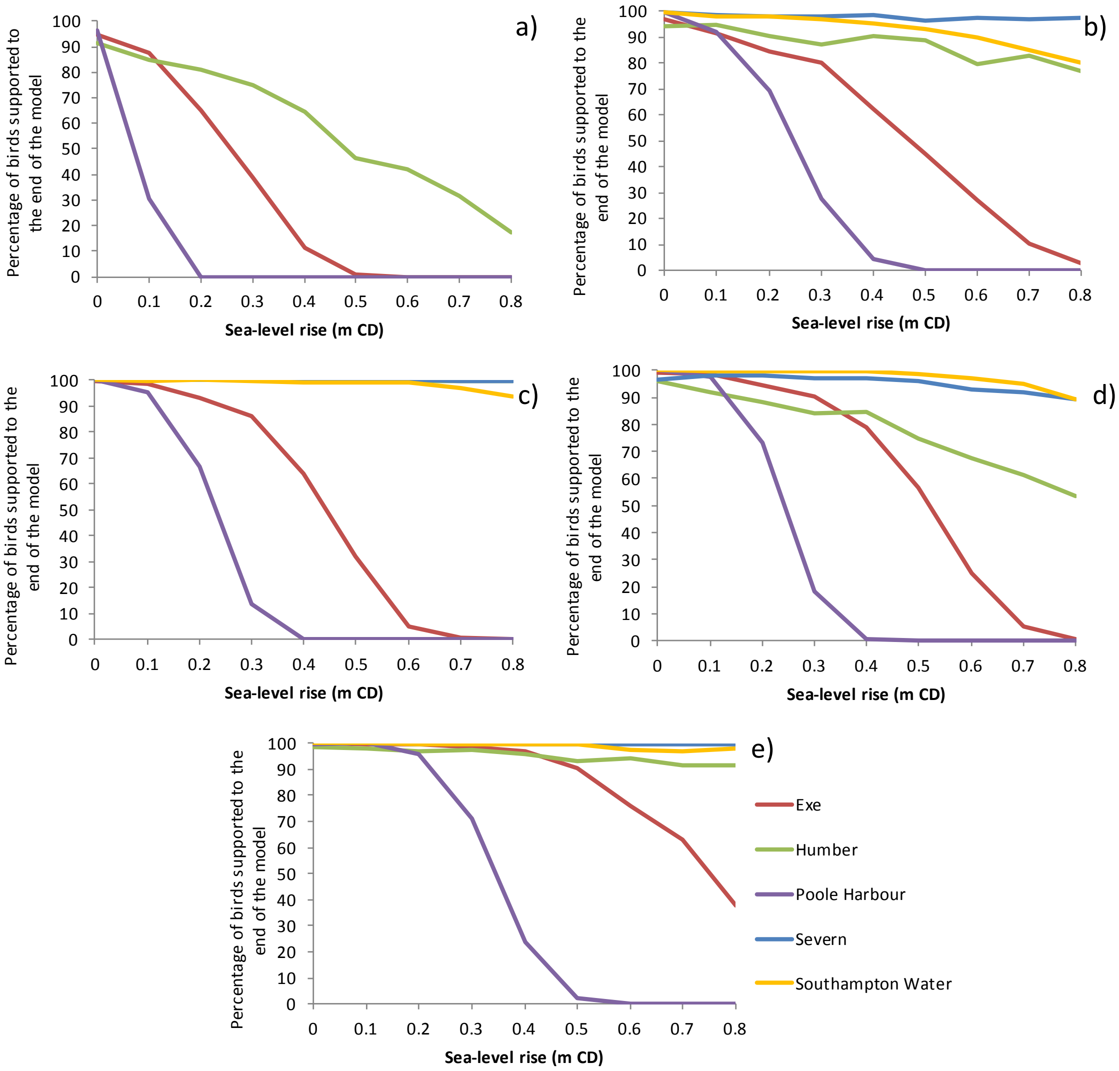

Figure 6.12. Percentage of birds supported when faced with sea-level rise on each estuary for a) bar-tailed godwit, b) black-tailed godwit, c) dunlin, d) grey-plover and e) redshank.

Considering the percentage of time spent feeding, the largest variations are seen for the Exe estuary and Poole Harbour. Following the population declines, any remaining individuals of each species sharply reduce the percentage of time spent feeding significantly once there is little conspecific competition (Figures A20.1a-e).

Shifts in dietary preferences are quite dramatic with a variety of changes occurring. Some species switch to a new food source quite sequentially whilst others quickly shift between invertebrate species. For all estuaries the biggest shift is to earthworms in fields, for the species that can consume them, although oystercatchers tend to include Marine worms first (Figures 6.13a-e).

There are some species that include crustaceans, most noticeably the turnstone, (e.g. Figure A21.1h). A few species are apparently unable to shift their diets enough to maintain populations, such as bar-tailed godwit on Poole Harbour and the Humber estuary (Figures A21.2a and A21.3a), and as such the sharp declines in numbers are explained through dietary restrictions.

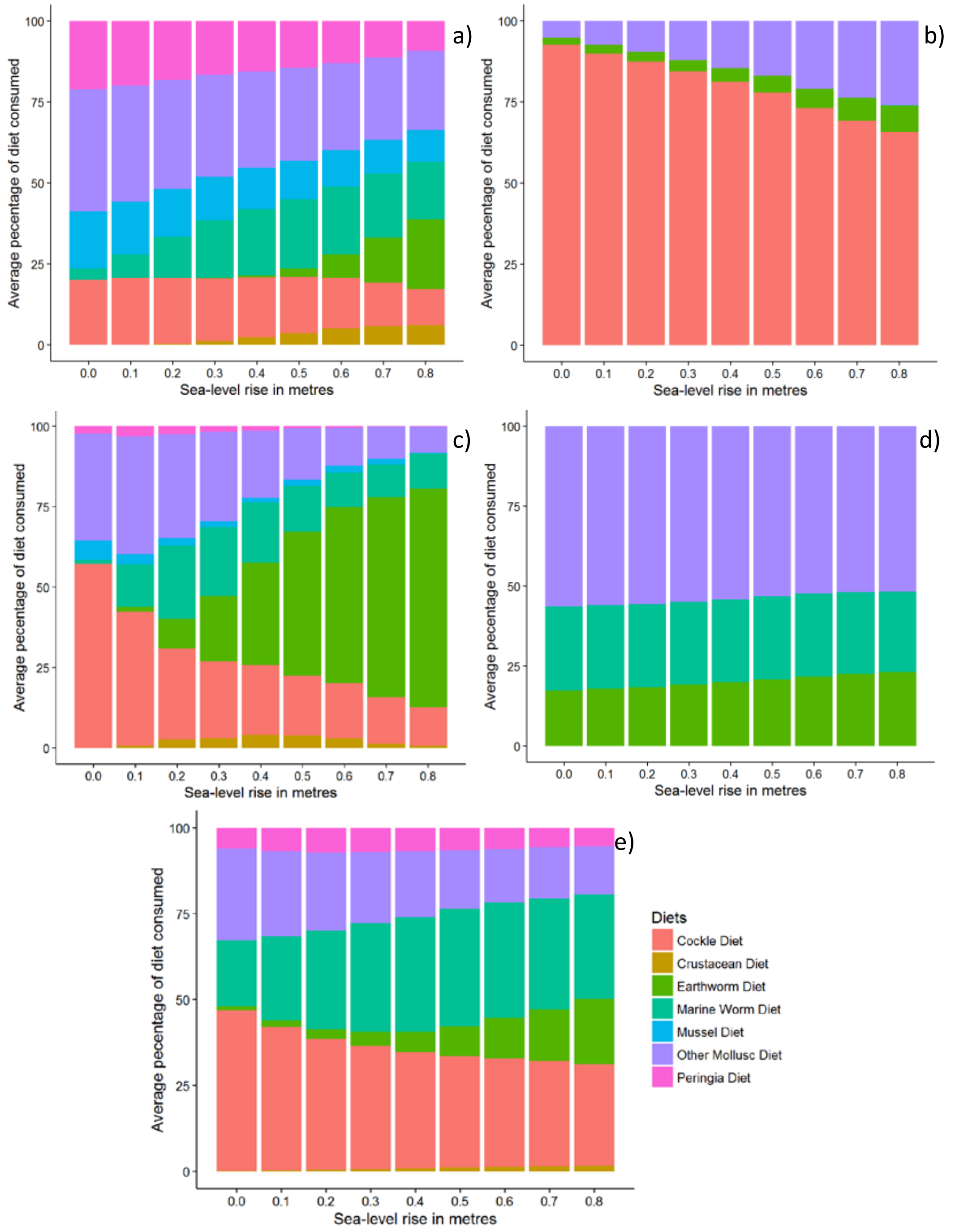

Figure 6.13. Dietary preferences of oystercatchers in relation to sea-level rise on the a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) Severn estuary and e) Southampton Water.

With rising sea-level, there is an increasing use of field habitat. For half the species in Poole Harbour there is a visible shift towards the Wareham patches in the west of the harbour before the overwhelming movement to the fields is visible (Figure 6.14).

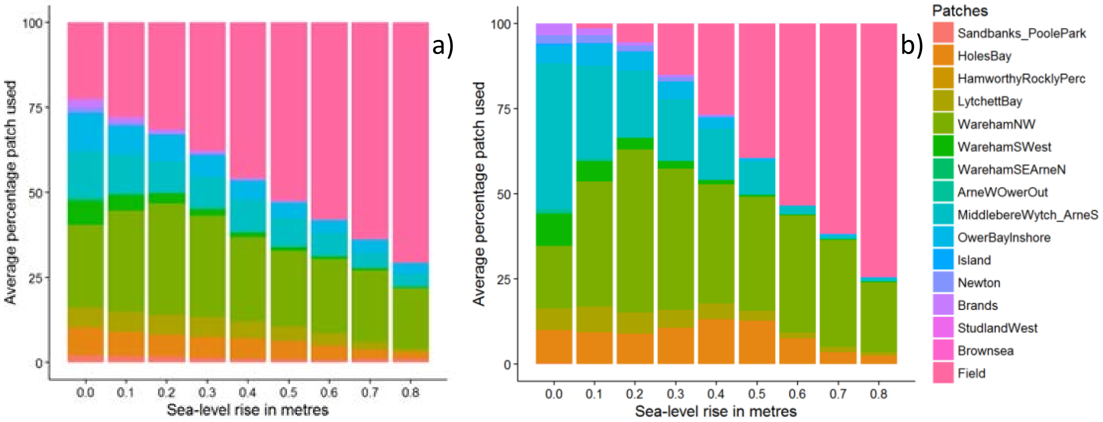

Figure 6.14 Habitat preferences on Poole Harbour for a) black -tailed godwit and b) dunlin.

6.3.2.1 Development of predictive conservation rules for sea-level rise scenarios

When considering forager characteristic's under increasing sea-level rise, three values were significantly related to the *sea-level rise threshold* (Table 6.7); (i) the number of types of resource (ii) numbers of size classes of other molluscs, which were both positive in their relationships with sea-level rise threshold, and (iii) number of marine worm resources in diet, which was unexpectedly negative (Figure 6.15). Additional regressions against body mass, regulated density and average lengths of invertebrates in a bird's diets were non-significant.

Table 6.7. Linear regression of forager characteristics against sea-level rise threshold.

Forager characteristic investigated	**F**	**Degrees of freedom**	**r^2**	**P value**	**Direction of relationship**
Count of types of resource in diet	8.63	1,39	0.1813	0.0055	Positive
Count of marine worm resources in diet	6.88	1,39	0.1499	0.0124	Negative
Count of other mollusc resources in diet	4.13	1,39	0.0958	0.0489	Positive

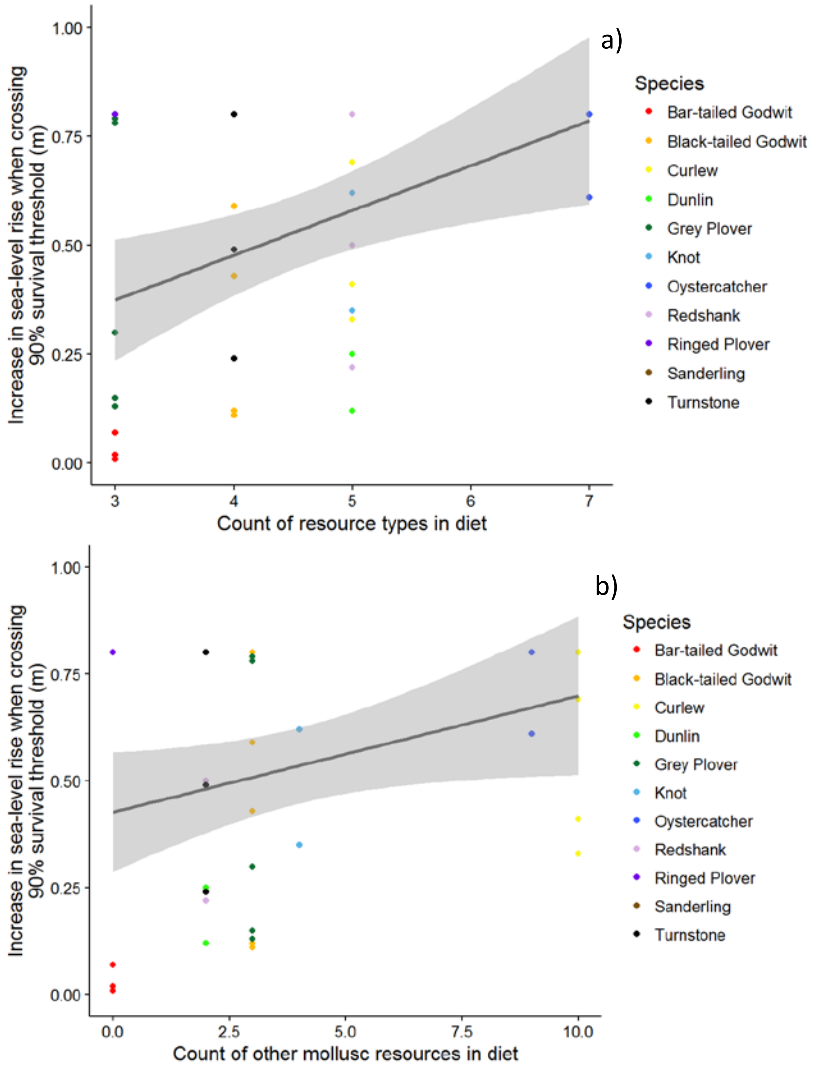

Figure 6.15 Linear regression of a) count of resource type in diet and b) count of other mollusc resources in diet against sea-level rise threshold.

Table 6.8. Linear regression of estuarine characteristics against sea-level rise threshold.

Estuarine characteristic investigated	**F**	**Degrees of freedom**	**r^2**	**P value**	**Direction of relationship**
Mean *Shoreheight* (m CD)	11.65	1,39	0.23	0.00151	Positive
Average food per bird (kg)	7.52	1,39	0.1617	0.00916	Positive
Density of birds on estuary (m^{-2})	5.76	1,39	0.1288	0.0212	Negative
Count of resource type	15.62	1,39	0.2859	0.00032	Negative
Counts of resource size classes	9.18	1,39	0.1905	0.00433	Negative
Average length of other mollusc (mm)	8.94	1,39	0.1865	0.00481	Negative

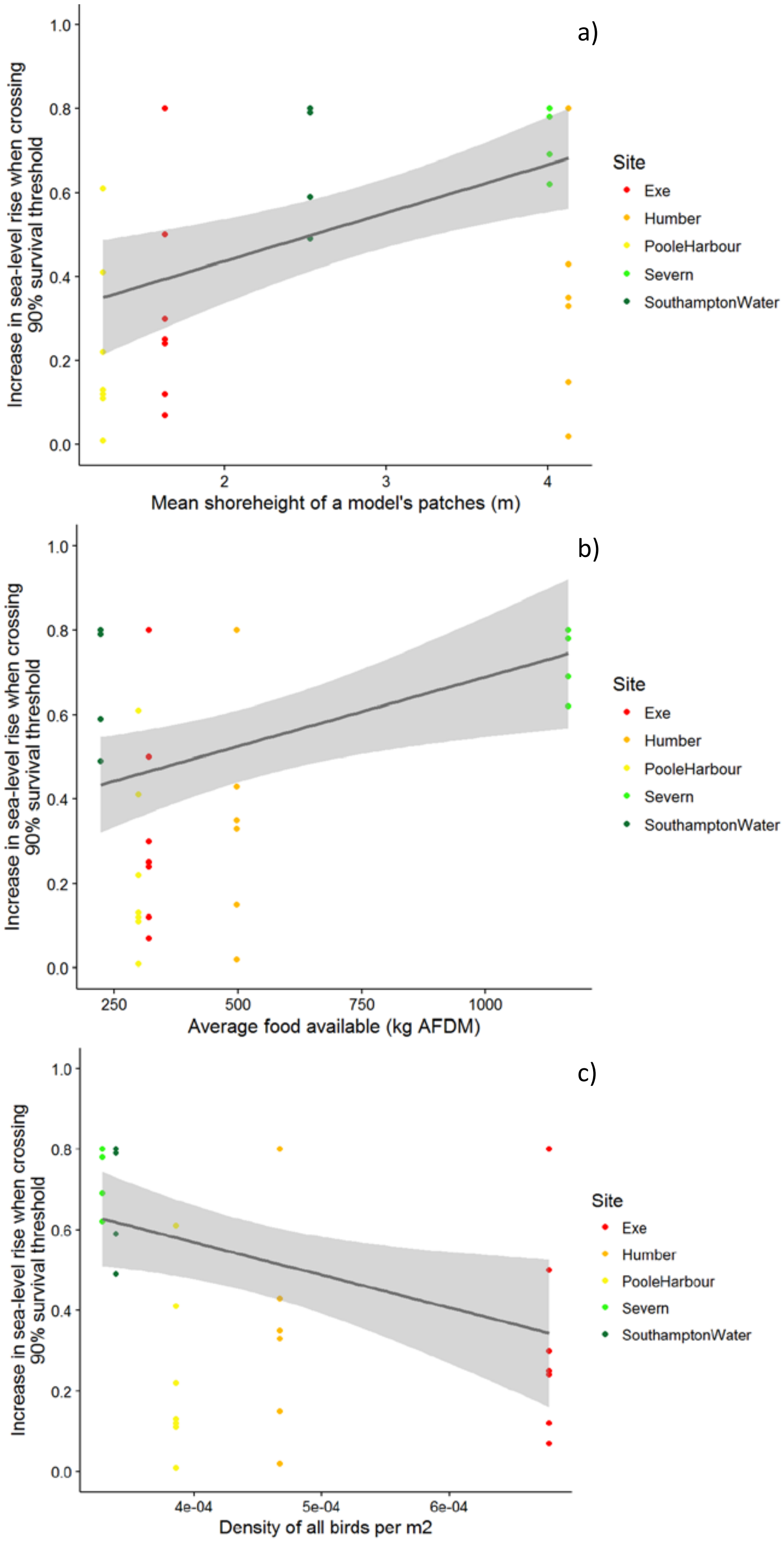

Figure 6.16 Linear regression of a) mean Shoreheight (m CD), b) average food per bird (kg AFDM) and c) density of birds (m^{-2}) of an estuary against sea-level rise threshold.

Several estuarine characteristics were significantly related to the threshold sea-level rise,and help explain the importance of site-specific factors in supporting larger populations of wading birds (Table 6.8). Significant positive relationships with mean *Shoreheight* and average food per bird (kg AFDM) were found (Figure 6.16a and b). The effect of bird density was negatively related to sea-level rise thresholds, predicting that estuaries with greater initial densities of birds were less able to support them under increasing sea-levels (Figure 6.16c). Unexpected negative relationships were found when considering the resources that estuaries contain (Figure 6.17). The Seven and Humber estuaries once again had the lowest thresholds, and the impact of these will be considered in the discussion.

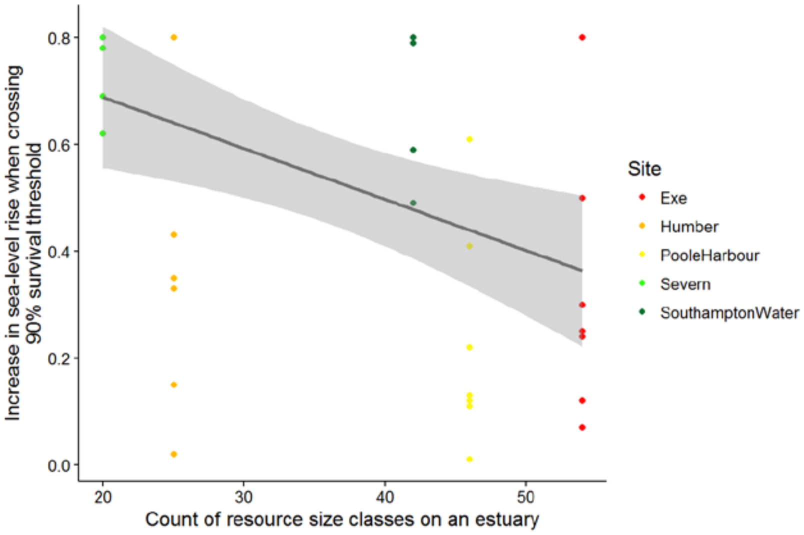

Figure 6.17 Linear regression of count of resource size classes of an estuary against sea-level rise threshold.

6.4 Discussion

6.4.1 General conclusions from the model outputs

The suite of models has shown that wading birds can adapt to environmental change up to a threshold when populations become unsupportable. The extent of change that can occur before a threshold is reached is specific to each species and site, but understanding the reasons for differences has led to approximate conservation rules that can be used for other non-modelled estuaries. These thresholds and predictive models are a positive outcome for future conservation management.

Of the two types of environmental change modelled, habitat loss caused the proportion supported to fall below 90% for more than three quarters of all species. Sea-level rise affected a little over half of all species by the time the worst case scenario (highest sea-level rise) was modelled. Future work on combined environmental change scenarios (e.g. sea-level rise with field loss) will allow greater understanding of the importance of monitoring changes with weak individual effects alone.

There was little similarity between how species responded to each set of changes (looking across the five estuaries) although both godwit species had similar profiles in their modelled population declines. The greater similarity between certain estuaries, as seen in the simulations of rising sea-level, emphasises the importance of physical conditions rather than forager physiology for the impact of these scenarios. Often, the responses for the Humber and Severn estuaries were quite similar, suggesting that the restricted invertebrate diversity on these sites might be driving some of differences between these and the more invertebrate-diverse estuaries. This is confirmed by graphs of species' diet showing how some species were unable to switch diets compared to populations on other sites. Future work to improve the spread and detail of the invertebrate surveys for these two estuaries will also be important and allow more detailed individual-based models to be developed.

The increase in percentage of time spent feeding indicates how model birds responded to increasing environmental change. Differences are seen between the two types of scenarios with habitat loss resulting in larger increases to percentage of time feeding than those seen under sea-level rise. Sea-level rise had a lower impact on bird's feeding rates and thus the stress they experience.

The shifts in dietary choices are quite revealing in terms of the modifications in behaviour and decisions birds make when affected by environmental change. The relationships between shifts in diets and population declines are not always consistent, with each species having their own levels of resilience and adaptability to compensate for each scenario. Whilst some changes can be explained by movements in habitat, such as increased earthworms in diets when moving onto fields, many are more subtle. The main switches between Marine worms for Other Molluscs and vice versa emphasises the importance of these two diets. Turnstone's increasing need for crustaceans stands out across several of the imposed conditions showing the importance of these invertebrates for this species and follows previous studies (Jones 1975). Given the difficulties observing intake of this prey type in the field (Martins et al. 2013) these models provide additional insight into adaptability under stress.

Some species with more limited dietary options suffered more when attempting to compensate for change with alternative diets. Both godwits were generally the first to be affected by change across all estuaries and environmental changes. Bar-tailed godwit were only able to access three types of resources (Appendix 6), whilst oystercatcher had over seven types to choose from and thirty-seven size classes. The dietary shifts are not the same across all populations but give a general indication of the likelihood of a species to respond. Future use of the dietary results will be highly valuable when looking into the compensatory abilities of birds and using the points of dietary shifts as an early-warning threshold in place of the point of decline (Rehfisch et al. 2004; Bowgen et al. 2015).

The general environmental effects that were modelled emphasise that, although birds do shift their within-site patch preference (area of estuary they prefer), this is driven more by diet in most scenarios. The declining exposure time of intertidal areas when sea-level rise was implemented showed the main shifts towards elevated patches and fields. The importance of patch usage will play a greater role when investigating patch-specific habitat loss.

6.4.2 Comparisons with empirical studies

The lack of comparable results on the effects of environmental change on birds has reduced the ability to compare many of the effects modelled with observed effects. The way in which previous empirical studies have reported results vary between listing general effects – "a decline was seen" – through to details of energy requirements – "daily energy requirements increased by *n* kJ". This makes general comparisons difficult and limited the empirical comparisons to habitat loss. A more concerted effort should be made in the future to ensure that environmental change studies are published in such a way that their data can be used for between-study investigations as well as the aims of the individual studies.

Therefore, it was gratifying to find that the predicted effects of habitat loss on the birds fitted well with empirically-derived results. The lack of papers publishing work on small-scale habitat loss effects on waders does leave a gap that IBMs can fill, with the underlying processes of compensation for these stress (e.g. dietary shifts) providing vital information.

6.4.3 General conservation rules for environmental change effects on wading birds

This is the first time that five IBM models have been developed in concert with each other, all foragers following the same rules, minimal site-specific calibration, and answering the same questions. This is a vital important step for developing a widespread understanding of how individual wading birds are supported in the face of environmental changes.

The results of the linear regression for conservation rules revealed the wide range of factors affecting wading bird's responses. The importance of multi-factor effects of forager diet, energetics and behaviour on specific resource-containing habitats that are exposed to birds in a site-specific way mean that relatively little of the variation was explained by forager and estuary characteristics. That there are some significant trends gives support to using a general rule in conjunction with several others to predict potential effects of environmental change for wading birds on estuaries without IBMs.

The most promising way of linking bird characteristics to habitat loss and sea-level rise thresholds was through diets. The numbers of resources accessed, alongside average invertebrate size consumed and count of accessible size classes were the most significant factors across the environmental changes, again signifying the importance of diet in predictions of this kind.

Estuarine characteristics had a greater number of relationships to habitat loss and sea-level rise thresholds, but the negative relationship for many of these variables but lower thresholds were consistently found on the Humber and Severn estuaries. These lower thresholds for the two more northerly estuaries can be explained through the lack of prey diversity and size on these two sites. These models have shown that the diversity of prey on an estuary's intertidal habitat is most important when explaining sensitivity to environmental change.

The results of the sea-level rise scenarios generally follow what would be expected. It can be easily seen that with greater mean *Shoreheight* more habitat is exposed under the same sea-level rise across the estuaries, indicating that average shore level of an estuary can be used to predict the potential effect of sea-level rise. Sea-level rise thresholds alone were related to the density of birds across the estuaries. The loss of exposed habitat from sea-level rise is more severe for estuaries with higher levels of initial bird density which would be expected. The only positive relationship with average food per bird was found with sea-level rise thresholds, and follows previous work on the importance of food density as a predictor of estuaries ability to support wader populations (West et al. 2005; Stillman 2009; Stillman and Wood 2013).

6.4.4 Final conclusions

The number of prey resources consumed by a species and the number of prey resources available in a site are key in determining the effect of environmental change. This emphasises the importance of having a good understanding of the state of an estuary's invertebrate populations and diversity. For habitat loss, 90% of the modelled species crossed the *habitat loss thresholds,* whilst 60% crossed the *sea-level rise threshold*.

Future work for this suite of models includes updating the invertebrate prey surveys for the two more northern estuaries and investigating the impacts of concurrent environmental changes. The impact of habitat loss associated with other types of environmental change is a real possibility, such as increasing pollution with harbour expansions for industry or nuclear power stations along coastal sites (Garcia et al. 2011; Wang et al. 2014), where there is also the risk of contaminant levels increasing in the water column and sediment. It is already known that the reasons behind a species' decline rarely come from a single source but is often the culmination of multiple factors (Dekshenieks et al. 2000; Fujii 2012; van Roomen et al. 2012). Individual-based modelling provides a clear way to investigate these multiple effects and provides a simple way to analyse the outcomes. Having a suite of models such as the set created here allows us to answer these questions in a timely manner and provide answers to many conservation questions.

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7. Overall discussion and conclusions

7.1 Introduction and thesis overview

The use of simulations such as individual-based models (IBMs) provides highly informative predictions to help manage changing ecosystems. Being able to investigate the impacts of environmental change on wading birds swiftly, and quantitatively, will aid conservationists and stakeholders facing difficult management decisions. Through the use of a previous model, this thesis has emphasised the importance of invertebrates and their size classes in wading bird IBMs and has urged caution in the use of waders as bioindicators (Chapter 2). By analysing the current literature on waders and environmental change, it has been possible to understand empirically how habitat loss affects wading bird populations, but the lack of comparable studies has also been made evident (Chapter 3). This thesis' development of a suite of comparable IBMs (Chapter 4) has shown that it is possible to derive a greater understanding of estuaries abilities to support changing wader populations (Chapter 5) and predict the effects of losing foraging habitat (Chapter 6). The creation of general predictive relationships for several scenarios (population increases, habitat loss and sea-level rise) allows for simple predictions for sites without IBMs, and emphasises the importance of diversity in both diet and estuarine resources (Chapters 5 & 6). These wading bird IBMs will be able to provide results that can fill knowledge gaps, and speed up conservation processes and management. The increasing need for adequate communication between researchers and stakeholders (Wood et al. 2015; Cartwright et al. 2016) means that this suite of models comes at an appropriate time. The following discussion will interpret each of the chapter's findings within the overall context of wading bird ecology and conservation.

7.2 Discussion of thesis findings

7.2.1 The importance of invertebrate size and wading populations

Predictions of the impacts of environmental change on organisms' survival need to consider the energetic needs of species, as well as the diversity of energy available in the habitat they inhabit (Sibly et al. 2013). For estuarine wading birds this requires detailed surveys of intertidal invertebrates and a good understanding of the prey sizes and species that waders consume (Bryant 1979; Goss-Custard et al. 2006; Goss-Custard and Zwarts 2015). In Chapter 2 I investigated the impact of regime shifts of marine worms and bivalves to understand how changing invertebrate size affects wading birds abilities to support themselves. Birds with high energy requirements and those with more specialist diets were found to be unable to compensate enough once their preferred prey items were reduced, or to be able to move to alternative foraging such as nearby fields. Whether biomass was redistributed or not, some species were still unable to be supported and the largest prey items in a bird's diet were found to be highly important. This chapter also makes that point that the ability of birds to switch to alternative species means that their use as direct bioindicators is called into question. For birds to be used as bioindicators in an estuarine ecosystems they must respond directly with declines in their environment or prey (Furness 1993; Piersma and Lindström 2004). The masking compensatory abilities of birds (e.g. changing prey) make it necessary to use additional indicators, together with changing wader numbers, to fully understand the health of an ecosystem.

In addition to this thesis' results regarding bird's use as bioindicators, the importance of invertebrate sizes must not be overlooked. With invertebrate surveys being highly labour intensive and with no associated requirement in the littoral Common Standard Monitoring guidance (JNCC 2004), there is often a lack of measurements taken for invertebrate length, leading to the predictive capabilities of IBMs being hindered.

7.2.2 Determining the importance, impact and roles of previous studies

In Chapter 3 I showed that whilst a large number of publications on wading birds have considered the effects of environmental change, few studies use comparable results. When developing relationships of environmental change against population change only habitat loss provided results in similar units and suitable numbers. It should also be noted that the habitat loss relationship is lacking the effect of small changes, a knowledge gap which IBMs can fill.

When looking at the differences between previous studies on environmental change and wading birds, disturbance was the most investigated. Scenarios surrounding disturbance are quite well publicised in the public eye but methods to measure its impacts on wading bird numbers are less well known (Sutherland 2007; Sutherland et al. 2012). As a result most papers consider disturbance impacts on individual birds rather than whole populations (Stillman et al. 2007). That this environmental change tops the list of most published studies raises a question over its relative importance compared to other types of change. Habitat loss, pollution, climate change and weather all have similar amounts of published papers for wading birds and have better measures for population effects (even if not directly comparable between studies). With more directly comparable measurements of environmental change it should be possible to investigate the relative impacts on wader populations of different types of change.

7.2.3 Advantages of the development of a suite of wading bird models

Most modelling studies tend to investigate a single scenario, site or species. Whilst such models will provide highly valuable results, their flexibility to answer more general questions is limited. The production of this PhD's suite of models was carried out with cross comparisons in mind, as each of the five estuaries were modelled following the same methodology, and foragers were parameterised in the same way between sites. Sensitivity analysis of the models helped identify key parameters in relation to the modelled bird's mortality and percentage of time spent feeding. Bigger impacts were seen for mortality than for time spent feeding in these analyses. These results were highly estuary-dependent, with the two estuaries with the lowest invertebrate diversities being most sensitive to changes in parameter values. In line with previous studies (Stillman et al. 2000; Ross 2013), energetic requirements had the biggest impact on mortality. In addition, the models are less sensitive to variations in regulated density than the previously used aggregation factor (Stillman et al. 2000).

The creation of the new species-specific regulated density now more closely mimics the behaviours seen in wading birds. This new sub-model assumes that birds self-regulate their density on mudflats unless the amount of space available reduces to the point at which density must increase. The final improvement to MORPH-based IBMs is a new satisficing method (minimum requirement or adequate, see Chapter 4) for bird's fitness calculations that spreads out individuals more realistically over foraging areas. The resulting validation of these models against BTO low tide surveys has been gratifying.

7.2.4 The ability of estuaries to support increasing bird populations

Chapter 5 predicted the ability of different estuaries to support increased populations of birds. With recent declines of wading birds (Holt et al. 2015; Frost et al. 2016) there are noticeable differences in assemblages of birds on UK estuaries, and in particular this chapter draws attention to the large differences in numbers of birds seen since Special Protection Areas (SPAs) were designated. Each of the five estuaries were able to support a certain increase in bird populations for the majority of species before a limit was reached, but then quite rapid declines were observed. Some similarities between species indicated similar responses to increasing competition for resources and space, although the Severn and Humber estuaries did have bigger differences compared to the more resource diverse southern sites. Birds were able to compensate for increasing populations through their diets as they shifted their percentage use of different resources rather than increase their time spent feeding. Oystercatchers (*Haematopus ostralegus*), the most generalist (diet) species, were supported past the 500% maximum increases of this set of models. The general outcomes of this chapter indicated that updates need to be considered for SPA designations to match recent wader populations and that the five estuaries cannot always support increasing populations. Predictions from this suite of models will be highly useful for the evidence base to justify new SPA designations and will help understand the capacities of different estuaries

It should also be noted that peak counts are used to define SPA designated numbers but these unusually high occurrences only last for short periods at a site (Frost et al. 2016). For my modelled estuaries to be able to support these extreme populations over the course of a whole winter is an overestimation to test the carrying capacity of a site. Future work could include short-term peak populations to investigate how such peak populations can be supported.

7.2.5 Comparisons of environmental change impacts across estuaries

As mentioned previously, a novel element of this PhD has been the development of a comparable suite of models that have been parameterised to allow prediction of a range of environmental change impacts. Using more than one model provides greater insight into the differences between species and sites. Investigations into habitat loss have shown that thresholds of habitat loss leading to negative effects on the birds can be found for almost all modelled species and have the potential to be used in conservation management and mitigation methods. Sea-level rise also affected many waders, but a lower percentage of birds (60%) crossed the pre-defined threshold, with quite a few birds moving to surrounding fields to feed on earthworms. This follows previous studies that stress the importance of surrounding fields for foraging and roosting of wading birds (Navedo et al. 2013; Furnell and Hull 2014). Sea-level rise simulations predicted less birds increasing their percentage of time spent feeding than habitat loss simulations, reflecting differences in the pressure that birds experience under each scenario. We can take from this that many species should have the ability to cope with rising sea-levels as long as the scenarios stay below the highest predictions (Bindoff et al. 2007; Lowe et al. 2009), although the potential impacts of multiple environmental changes might have more detrimental effects.

As seen for regime shifts, the different changes in dietary preferences observed in the modelled birds were highly informative of the way in which species could compensate for large scale environmental changes. The increases in earthworm diets during sea-level rise are consistent with birds availing themselves of an alternative non-tidal foraging habitat (fields) as mentioned above (Heppleston 1971; Townshend 1981a; Smart and Gill 2003). For other species in both scenarios some significant changes in diets were seen when a population dropped below the sea-level rise threshold (<90% of population supported to the end of the models).

The previously developed empirical relationship between habitat loss and wading bird survival (Chapter 3) was compared to a relationship predicted for all five estuaries to add an extra validation of the predictive capabilities of these models. That the two relationships were not significantly different was pleasing and increases confidence in the ability of IBMs to predict environmental change effects. As mentioned above, IBMs can be used to predict the effect of relatively small-scale habitat loss, missing from empirical studies.

7.2.6 General predictions and conservation rules

Using the environmental change thresholds predicted in final two data chapters (Chapter 5 and 6), it was possible to develop general predictions of the effects of environmental change on wading birds. Where IBMs and other studies are not available or where there is a lack of time to develop models before an environmental change might occur, a general predictive model provides an initial solution. In general, all generalist foragers did better than specialists under the three investigated scenarios. This follows previous research in which generalist bird species are more resilient to change (Davey et al. 2012) compared to specialists, which are more restricted in their choices and abilities to compensate through diet change. When looking at estuarine variables during habitat loss and population increases, even those waders classed as dietary generalists did less well on estuaries with lower levels of resource diversity. This explains why the larger sites (e.g. the Humber or Severn estuaries) were more likely to have lower thresholds for many wader populations. Sea-level rise thresholds had stronger relationships with mean *Shoreheight* of a site (a simple measure of shallowness) as well as sites with high initial densities of birds. This showed that with reduced exposure time, and therefore available foraging habitat, these are the best characteristics to consider when making predictions for newly threatened sites. Sea-level rise predictions follow the results of previous investigations where shallower estuaries suffer more from climate change (Newton et al. 2014), and in which the amount of food available for birds affects how many can be supported (West et al. 2005; Stillman and Wood 2013). Overall the characteristics of estuaries explain more of the variation in thresholds than forager’s themselves and so, in future studies, these should be considered first before including species specific variables.

7.3 Limitations and future research

As with all simulation models, validation to the real world is a key goal to engender confidence in the outputs and predictions (Robinson 1997; Grimm and Railsback 2005; Goss-Custard and Stillman 2008). My IBMs have been validated against observed behaviours and distributions of birds but there is always room for improvement. In future iterations of these models it would be ideal to collect more extensive ‘percentage time spent feeding’ observations of a wide range of species across multiple sites. This emergent behaviour (Grimm and Railsback 2005) of birds is known to relate to the way a bird responds to changing environmental conditions (Goss-Custard et al. 1977). The improvements in tracking of individual birds through GPS and VHF (Bridge et al. 2011) will aid in the observations of true habitat use in addition to the long term WeBS surveys (Frost et al. 2016).

The invertebrate surveys of the estuaries investigated were of a suitable level of detail to enable IBMs to be developed. Additional estuaries were considered but with a lack of appropriate surveys it was deemed not possible to create comparable models for these sites. It is known that birds prefer particular lengths and sizes of their prey (Goss-Custard et al. 2006), and so any models that are created must account for any available biomass by size classes rather than numerical densities alone (Chapters 2 and 5). Such detailed invertebrate surveys can be expensive, time consuming and have resulted in the dearth of sites that can be immediately modelled. Future IBMs will investigate the number of cores and degree of measurement required to maintain reliable predictions. In addition, it would be interesting to compare a range of surveys over time to see if changes in populations or assemblages of birds can be related to changing habitats. My investigation into regime shifts was based on previous studies that reported changes in the invertebrate communities (van Roomen et al. 2005; Weijerman et al. 2005; Atkinson et al. 2010), and by linking these to bird numbers it might be possible to find new explanations for wading bird declines.

With these new models planned it would be remiss to not state that the investigations of new species and sites will improve the understanding of general conservation rules. The linear models developed in previous chapters (Chapter 5 & 6) were derived from eleven species across five estuaries, and as is known in any basic statistical text - the greater the number of samples the better the accuracy (Blainey et al. 2014). In addition, better understanding of the regulated density would be advantageous, for example through investigation of the spacing of multiple species across multiple sites.

After initial completion of these models, calibration adjusted for some high mortality in certain estuaries that was might be due to missing invertebrate data e.g. lack of data for lugworms (*Arenicola marina*) and larger species (Chapter 4). The threshold of 10% overwinter mortality was derived from a number of sources as there is a lack of data across wading bird species (e.g. Goss-Custard et al. 1982; Cramp and Simmons 1983; Insley et al. 1997; Warnock et al. 1997). Collaborations with researchers and amateurs studying overwinter wading birds would hopefully provide a better estimate of survival that could be used to calibrate future models in two directions – the maximum and minimum expected mortalities for a population.

There are also additional environmental changes to be investigated in the model that were parameterised but not presented in the thesis - the effects of temperature change and pollution. With the world’s climate predicted to be warming over the next hundred years (Trenberth et al. 2007; Murphy et al. 2009), there could be positive impacts on wading birds through decreasing energy costs over the winter, but this could also be detrimental to invertebrates. As mentioned in my previous chapter (Chapter 3), we know that range extensions of native species are occurring, but also that previous populations are dwindling through warming waters (Beukema et al. 2009; Kröncke et al. 2013; Schückel and Kröncke 2013) all of which will impact on wading birds. The impact of cold winters should not be forgotten too, as even in the past decade one of the coldest winters in the UK for 30 years was experienced (Osborn 2011), and the loss of access to fields and mudflats (Goss-Custard 1969; Townshend 1981b; Beukema 1990; Strasser et al. 2001), as well as physiological impacts on bird energetics, will play their part in regulating populations (Kersten and Piersma 1987; Zwarts et al. 1996). The impacts of both increases and decreases of ambient temperature should be investigated to fully understand the effects on wader populations.

The impact of pollution of human origin through waste and by-products in the marine environment is documented (Roessler and Tabb 1974; Kennish 2002; Smith and Shackley 2006; Elliott and Elliott 2013; Langston et al. 2015), and is well represented in the wading bird literature (Chapter 3). Though little is fully known of the direct impacts of pollution on bird physiology (Bryan and Langston 1992), they experience indirect effects through alterations in their prey species. Prey will decline or increase depending on the location and type of pollution (Moore et al. 1991; Cabral et al. 1999; Alves et al. 2012; Wright et al. 2013; Langston et al. 2015) and so again, investigating these through IBMs will allow repeatability and understanding that would not be readily available through traditional studies.

With these additional environmental changes parameterised, future investigations into cumulative effects of multiple events is now possible. My research has shown that 40% of modelled species were not predicted to be affected by current predictions of sea-level rise. However, sea-level rise in combination with other scenarios (e.g. habitat loss, pollution or severe winters) may negatively affect these species. These in-combination events will be highly important for future conservation planning of wading birds as anthropogenic change will still be occurring whilst climate change develops.

All of these investigations look at the ranging impacts on the same numbers of birds and densities of invertebrates. Whilst I can justify these through extreme changes in temperature cause higher levels of ice-melt in a single year (Nghiem et al. 2012), or the total loss of foraging habitat through implementation of a barrage (Burton 2006; Moores et al. 2016), the reality is often these changes will be gradual year on year. A potential future study would be to investigate the sequential impact of an environmental change event using the resultant populations (birds and prey) to parameterise the next model year. Also the impacts of sudden peak populations (Chapter 5) or levels of emigration when an individual reaches a certain month and mass (Pienkowski et al. 1979; Gill et al. 2014) could be implemented to again replicate a more ‘real’ scenario.

7.4 Conclusions

This thesis has shown that individual-based models are an important tool to understand and predict the effects of environmental change on wading birds. The suite of five models has shown how it is possible to simulate a set of estuaries in parallel to create general conservation rules. The importance of the correct empirical data cannot be discounted, as without thorough invertebrate surveys none of this modelling would be possible. Finally, the amazing compensatory abilities of waders to support themselves in taxing scenarios means that we must be careful in using them as bioindicators. They are, however, as important a part of the estuarine ecosystem at the sediment itself.

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Appendix 1. Results showing the percentage of birds supported during models run from modified parameter files where AFDM was redistributed.

Table A1.1. Averaged percentage survival results for all models used. Those listed under R (redistributed) were from models that retained any removed biomass and redistributed it proportionally across the remaining diets, NR (non-redistributed) results had the biomass removed entirely during parameterisation.

Model description (sizes = mm)	**Percentage of birds supported during the non-breeding season**									
	Dunlin		**Redshank**		**Black-tailed godwit**		**Oystercatcher**		**Curlew**	
	R	**NR**	**R**	**NR**	**R**	**NR**	**R**	**NR**	**R**	**NR**
Original	99.2		99.78		100		100		95.67	
Phylum extinction										
No worms	93.60	-	23.11	-	0.40	-	100	-	0	-
No bivalves	99.84	-	100	-	76.00	-	39.17	-	5.83	-
No worms at all	77.04	-	2.67	-	0	-	100	-	0	-
No bivalves at all	98.80	-	99.56	-	38.40	-	7.50	-	0	-
Negative directional shift: reducing maximum worm size available										
worms ≤104.99	98.64	98.48	98.44	98.44	99.40	99.40	100	100	81.83	67.50
worms ≤ 89.99	98.88	98.08	98.00	98.44	99.60	99.60	100	100	82.83	69.83
worms ≤ 74.99	99.28	98.64	94.89	92.44	46.80	26.40	99.83	100	0	0
worms ≤ 59.99	98.88	99.12	84.67	77.56	7.60	1.20	99.83	100	0	0
worms ≤ 44.99	96.80	95.76	59.78	54.00	0.20	0	99.83	100	0	0
worms ≤ 29.99	83.04	83.84	2.67	4.22	0	0	100	99.83	0	0
worms ≤ 14.99	82.40	81.60	4.00	2.22	0	0	100	100	0	0
worms ≤ 4.99	80.80	82.80	2.89	2.22	0	0	100	100	0	0
Positive directional shift: increasing minimum worm size available										
all worms ≥ 5.00	99.92	98.72	100	99.56	100	100	100	100	99.50	94.17
all worms ≥ 15.00	100	99.84	100	99.78	100	100	100	100	99.50	94.50
all worms ≥ 30.00	100	98.24	100	99.56	100	100	100	100	99.50	96.17
all worms ≥ 45.00	100	94.56	100	99.78	100	100	100	100	99.67	94.67
all worms ≥ 60.00	76.80	77.84	100	98.44	100	99.80	100	100	100	88.33
all worms ≥ 75.00	76.80	78.32	100	97.78	100	99.80	100	100	99.67	90.33
all worms ≥ 90.00	76.16	76.72	100	76.44	100	32.20	100	100	96.83	3.50
all worms ≥ 105+	77.68	75.92	100	78.44	100	31.60	100	100	97.67	5.67

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Negative directional shift: reducing maximum bivalve size available										
all bivalves ≤49.99	98.72	98.80	99.56	99.56	99.80	100	100	100	95.00	95.17
all bivalves ≤44.99	99.20	98.80	99.56	99.56	100	100	100	100	97.50	92.67
all bivalves ≤39.99	99.04	98.96	99.33	99.56	100	100	100	99.83	97.17	93.50
all bivalves ≤34.99	99.04	98.72	99.56	98.89	100	98.40	100	99.50	97.33	57.83
all bivalves ≤29.99	98.48	98.96	99.56	99.11	100	96.20	100	97.67	98.83	34.50
all bivalves ≤24.99	98.96	98.80	99.78	99.33	100	58.60	100	35.83	97.00	0.50
all bivalves ≤19.99	99.28	98.48	99.11	98.67	100	39.80	77.83	6.50	97.00	0
all bivalves ≤14.99	99.92	98.88	100	98.22	88.40	35.80	19.00	8.67	11.67	0.17
all bivalves ≤9.99	99.92	98.88	99.56	98.67	43.40	34.60	9.33	6.83	0	0
Positive directional shift: increasing minimum bivalve size available										
all bivalves ≥ 10.00	99.04	99.12	99.33	99.78	100	100	100	100	94.83	95.17
all bivalves ≥ 15.00	99.36	99.04	99.78	99.33	100	100	100	100	96.00	95.00
all bivalves ≥ 20.00	99.12	99.28	99.56	99.56	99.80	100	100	100	94.67	96.33
all bivalves ≥ 25.00	99.12	98.48	100	99.33	100	100	100	100	94.17	87.67
all bivalves ≥ 30.00	98.56	98.96	99.33	99.33	100	99.80	100	100	87.67	76.83
all bivalves ≥ 35.00	98.80	98.88	99.56	99.78	99.80	99.60	100	100	94.00	71.83
all bivalves ≥ 40.00	99.20	99.20	99.33	99.33	100	87.60	100	82.00	84.00	15.00
all bivalves ≥ 45.00	98.80	98.88	99.33	99.11	100	57.00	100	19.17	86.50	1.00
all bivalves ≥ 50.00	99.12	98.56	99.56	98.89	98.80	36.00	100	7.33	56.83	0.50
Converging worm biomass										
5-104.99 worms	100	98.56	100	97.56	100	98.80	100	100	98.17	69.17
15-89.99 worms	100	100	100	98.22	100	99.40	99.83	100	98.00	71.50
30-74.99 worms	100	99.36	100	94.00	99.80	25.80	100	100	93.50	0
45-59.99 worms	100	92.80	98.22	57.56	100	0	100	99.50	92.00	0
Diverging worm biomass										
≠ 45-59.99 worms	96.56	96.40	99.78	99.33	100	99.80	100	100	95.83	95.33
≠ 30-74.99 worms	85.12	82.40	98.67	97.56	100	100	100	100	98.67	90.83
≠ 15-89.99 worms	82.56	79.84	92.67	80.22	87.80	31.60	100	100	38.17	5.00
≠ 5-104.99 worms	84.32	81.84	95.11	77.78	95.00	34.00	100	100	48.83	3.33
Converging bivalve biomass										
10-49.99 bivalves	98.96	99.68	100	99.33	99.80	100	100	100	94.83	93.83
15-44.99 bivalves	99.28	98.72	99.11	98.89	100	100	100	100	97.00	94.67
20-39.99 bivalves	99.04	99.04	99.11	99.56	100	100	100	100	97.67	92.33
25-34.99 bivalves	99.12	99.04	99.11	99.11	99.40	97.20	100	99.33	94.83	30.17
Diverging bivalve biomass										
≠ 25-34.99 bivalves	98.96	98.96	99.56	99.56	100	99.80	100	100	95.33	78.17
≠ 20-39.99 bivalves	98.64	99.04	99.11	99.56	99.80	88.40	100	81.50	86.17	21.50
≠ 15-44.99 bivalves	98.72	98.32	99.11	99.78	100	56.80	100	20.50	86.17	1.67
≠ 10-49.99 bivalves	99.12	98.24	99.56	98.44	98.40	38.00	100	7.67	51.67	0.17

Appendix A2. Additional figures to explain results.

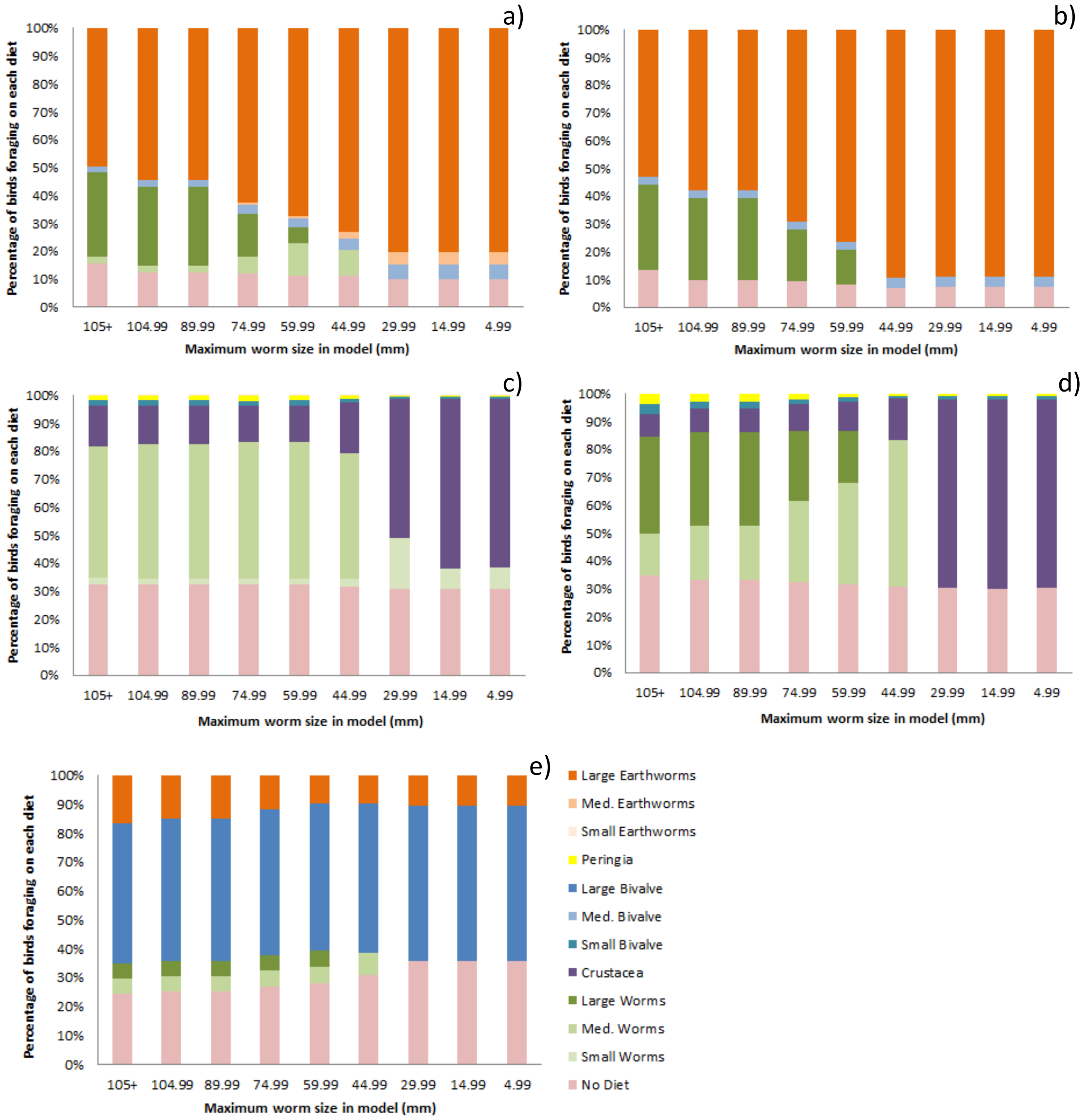

Figure A2.1. Percentage of diets consumed with decreasing worm biomass size for a) black-tailed godwit, b) curlew, c) dunlin, d) redshank and e) oystercatcher.

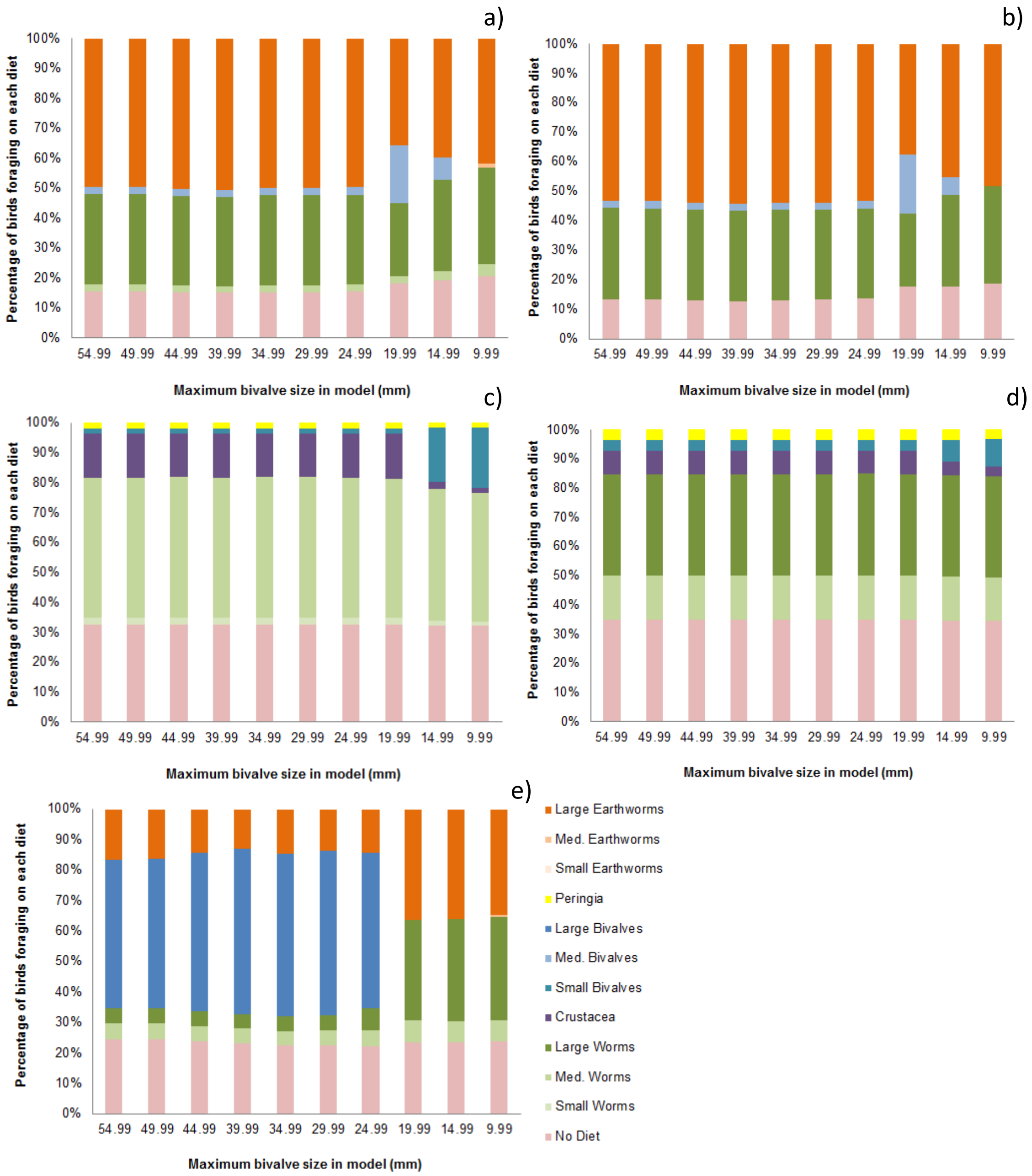

Figure A2.2. Percentage of diets consumed with decreasing bivalve biomass size for a) black-tailed godwit, b) curlew, c) dunlin, d) redshank and e) oystercatcher.

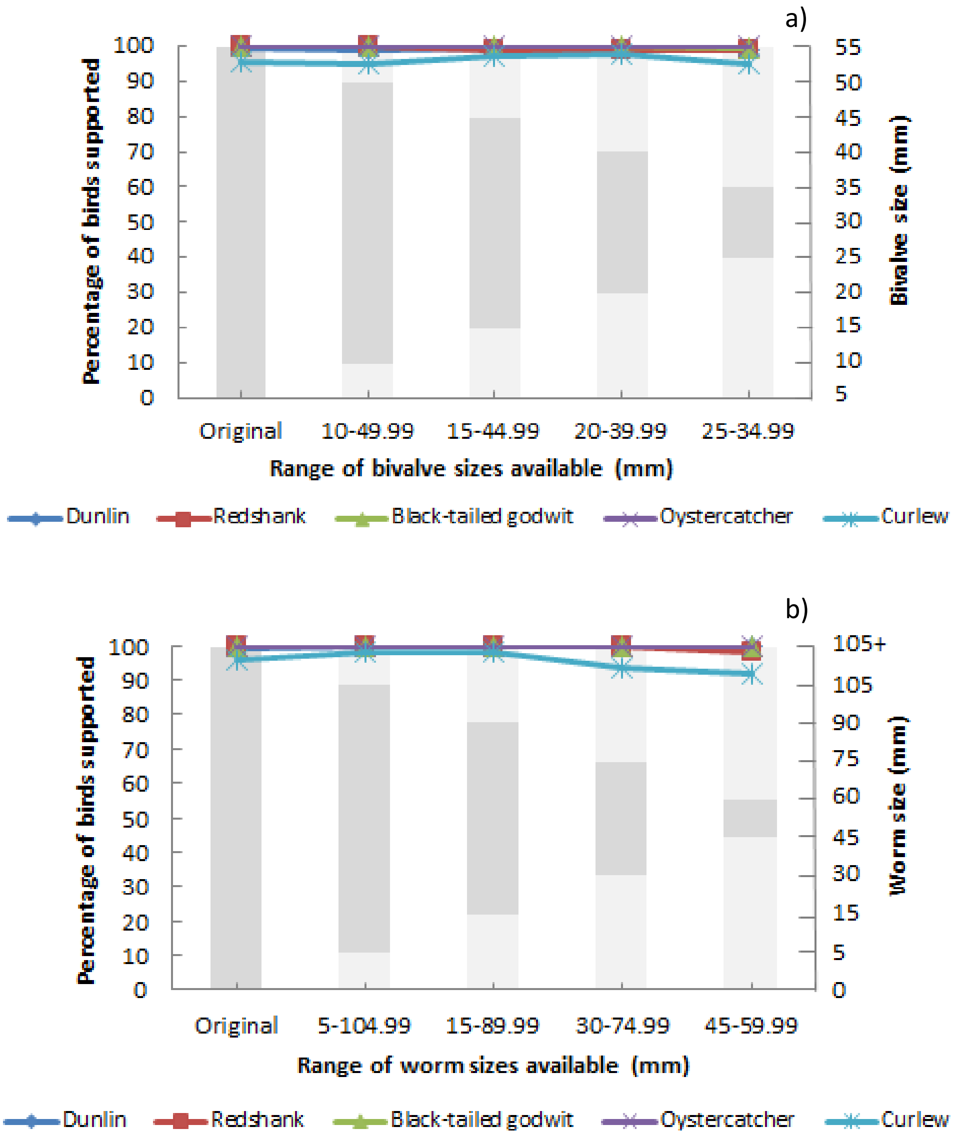

Figure A2.3. Percentage of birds supported with converging biomass size of a) bivalves and b) worms plotted against a right hand axis showing the biomass of prey present by size and length in each model run (dark grey for present and light grey for removed).

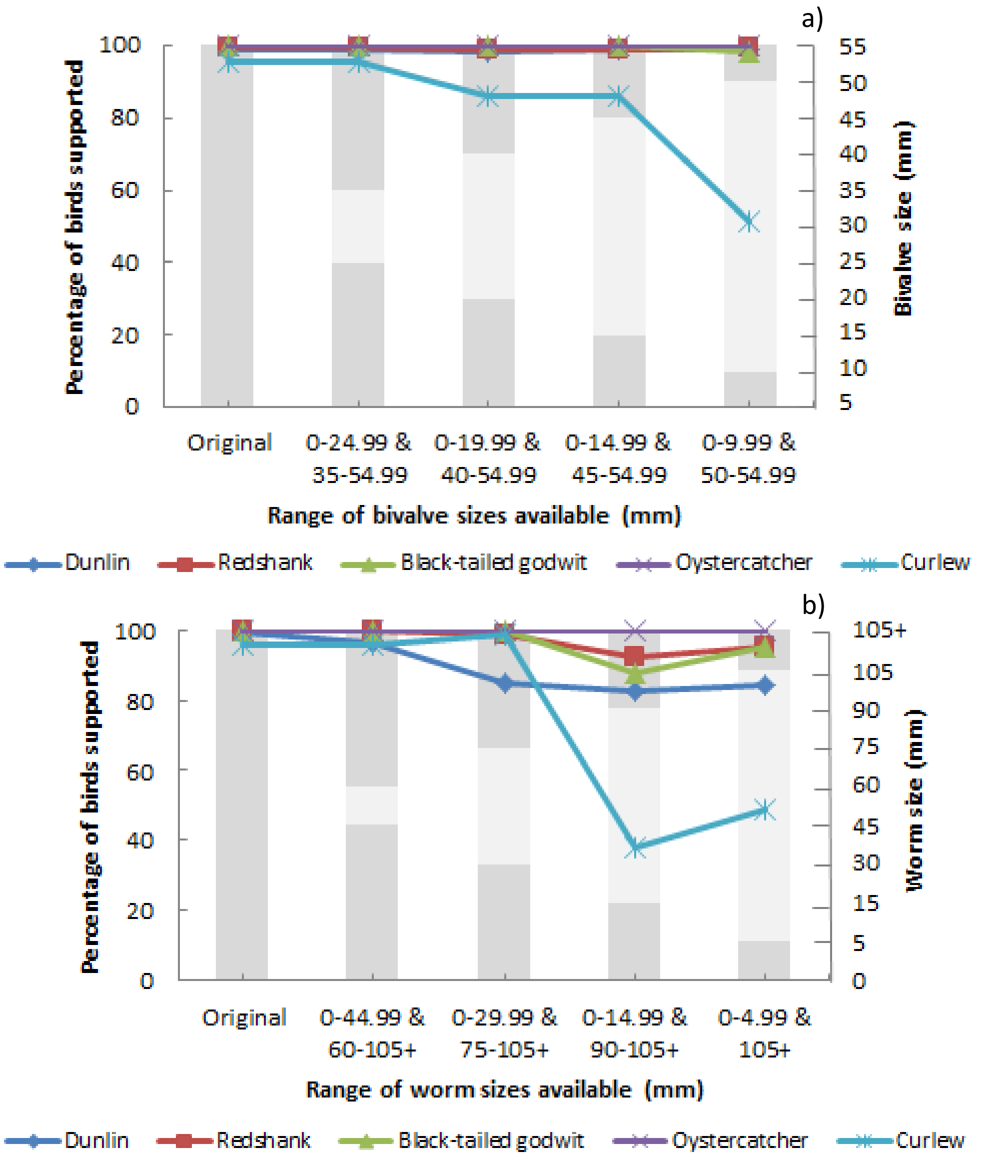

Figure A2.4. Percentage of birds supported with diverging biomass size of a) bivalves and b) worms plotted against a right hand axis showing the biomass of prey present by size and length in each model run (dark grey for present and light grey for removed).

Appendix 3. Patch names for all five modelled estuaries

Table A3.1. Details for all patches found in each of the five modelled estuaries.

Estuary name	**Poole Harbour**	**Exe estuary**	**The Humber**
Patches	34	29	22
Accessible patches with resources	31	25	18
Patch names **(name=location)**	Sea Land	Sea Land	Sea Land
3	SandbanksIn	WestTopsham	Blacktoft
4	SandbanksOut	PowderhamSand	Ferriby
5	LittleSea	StarcrossNorth	BartonUponHumber
6	PoolePark	StarcrossSand	Hull
7	HolesBayS	Cocklewood	BarrowHaven
8	HolesBayN	WarrenNorth	EastHalton
9	Hamworthy	BullHillBank	Immingham
10	RocklyPoint	ShellyBank	PaulltoCherryCobbUp
11	Lytchett	CockleSandEast	PaulltoCherryCobbOut
12	WarehamNWright	CockleSandNorth	SunkIsland
13	WarehamNWmidin	LympstoneSouth	SpurnBightOut
14	WarehamNWmidout	LympstoneWest	SpurnBightMid
15	WarehamNWleftin	LympstoneNorth	SpurnBightUp
16	WarehamNWleftmid	EastTopshamSouth	NorthCleethorpesUp
17	WarehamNWleftout	EastTopsham	NorthCleethorpesOut
18	WarehamSW	MidTopsham	SouthCleethorpes
19	WarehamSE	MussBed1	DonnaNookUp
20	ArneN	MussBed2	DonnaNookOut
21	ArneW	MussBed3	
22	OwerBayOut	MussBed4	
23	ArneS	MussBed5	
24	Middlebere	MussBed6	
25	WytchLake	MussBed7	
26	OwerBayIn	MussBed8	
27	Islands	ExmouthBeach	
28	NewtonBay		
29	BrandsBay		
30	StudlandW		
31	BrownseaS		
32	BrownseaN		
	Roosts	Roosts	Roosts
	Fields	Fields	Fields

Continued on next page

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Table A3.1. Details for all patches found in each of the five modelled estuaries.

Estuary name	**The Severn estuary**	**Southampton Water**
Patches	20	23
Accessible patches with resources	17	16
Patch names **(name = location)**	Sea	Sea
	Land	Land
3	NEtopFretherne	MarchwoodIPFreemantle
4	NELydney	MarchwoodMarchwoodIP
5	NEShepperdine	HythePierMarchwood
6	NEMathern	CadlandCrHytheUpper
7	NEAust	CadlandCrHytheLower
8	NEmidchannel	FawleyCadlandCrUpper
9	EPortishead	FawleyCadlandCrLower
10	WRedwick	CalshotCFawleyUpper
11	WNewportCardiffIn	CalshotCFawleyLower
12	WNewportCardiffMid	InchmeryCalshotC
13	WNewportCardiffOut	AnglingClubGlickickerPoint
14	EWSMareIn	HillHeadAnglingClub
15	EWSMareMid	WarsashHillHead
16	EWSMareOut	HambleRiceWarsash
17	EBurnhamIn	HambleLRHambleRice
18	EBurnhamOut	OceanVHambleLeRiceUpper
19		OceanVHambleLRLower
20		ItchenBridgeSwaything
21		FreemantleOceanV
22		
23		
24		
25		
26		
27		
28		
29		
30		
31		
32		
	Roosts	Roosts
	Fields	Fields

Appendix 4. Shoreheight determination through HR Wallingford tidal models

Determining the median *Shoreheight* for every patch involved a visit to HR Wallingford (match funding partner based in Wallingford, Oxfordshire, UK) to gain access to their in-house hydrodynamic models for four of the five estuaries being modelled (a model for the Exe estuary was unavailable). The hydrodynamic models are based on a two-dimensional tidal flow model (TELEMAC-2D (Hervouet 2007)) that predicts the flows and tidal heights across a defined estuarine system for a given tidal cycle. These flow models outputs are viewed in the post-processing software MERMAID (Benson 2016) at allowed the placement of patch shapes as boundaries over the estuary within which to then extract percentage of time the water depth was <0.01 m (therefore considered “dry”). Using this value of how much of the time during a tide a patch should be exposed (“dry”) the predicted median *Shoreheight* of a patch was determined to allow this exposure time. To account for the lower shore that is not usually exposed, a ‘mask’ was placed over the patches to prevent any data being used from areas below chart datum (approximately the lowest astronomical tide level). It should be noted that as the models are set up to Ordnance Datum (Newlyn) which is a flat datum, compared to Chart Datum which varies spatially with the tide, all values for *Shoreheight* have been adjusted by their appropriate conversion value to Chart Datum found in TideWizard (Smartcom Software 2009) for the tidal point closest to each patch.

Before the final *Shoreheights* were determined MERMAID was used to extract the tide curve in metres for the modelled cycles and compare a series of point locations down the shore to the sea (Figure A4.1). If there was a difference of greater than 1 hour for exposure time, it was judged that the patch should be split at the nearest bathymetry contour so that the intertidal mudflat in that area exposed more gradually. This allowed for a graduated exposure of the shore between the hourly time steps the models run to. In models with smaller time steps, i.e. 30 mins, the need to sub divide patches would need to be re-calculated.

In addition to grading the intertidal areas the simulated tide curve was again used to compare the tidal exposure around the estuaries as for some, Poole Harbour in particular, there were no Tide Wizard tidal curves available beyond a representative point in the middle and the tide shape varied significantly over the area. As a result the differences in lowest tidal level predicted by the model were used to adjust the available tidal curves to simulate lags in exposure. In Poole Harbour there were a few areas where water was funnelled through a narrow low water, drainage channel during the ebb tide which impeded the flow and slowed intertidal exposure in comparison to other areas.

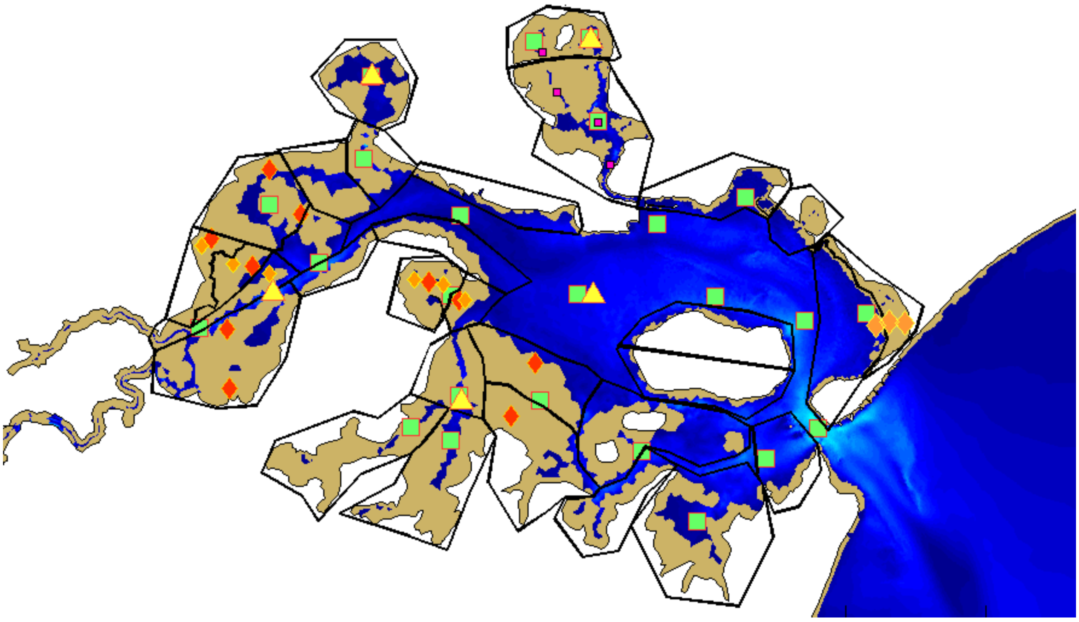


Figure A4.1. A screen shot of the Poole Harbour hydrodynamic model in Mermaid with the tide comparison points analysed.

Appendix 5. Resource parameters for all IBMs

Table A5.1. A complete list of resource parameters included in the MORPH models (all except Humber estuary where a site specific AFDM was available). (1) Please see Table A5.3 for full description of all species included in each estuaries resource. (2) Equations and their sources for AFDM are can be found in Table 5.2.

Resource name	**Prey type/species**	**Size class (mm)**	**Overwinter mortality (Percent)**	**AFDM (g) (2)**
Cerast0to5	*Cerastoderma edule*	0-4.99	0.58	0.00007236
Cerast5to10	*Cerastoderma edule*	5-9.99	0.58	0.00277373
Cerast10to15	*Cerastoderma edule*	10-14.99	0.32	0.01509652
Cerast15to20	*Cerastoderma edule*	15-19.99	0.13	0.04607399
Cerast20to25	*Cerastoderma edule*	20-24.99	0.11	0.10601351
Cerast25to30	*Cerastoderma edule*	25-29.99	0.16	0.20621593
Cerast30to35	*Cerastoderma edule*	30-34.99	0.13	0.35881282
Cerast35to40	*Cerastoderma edule*	35-39.99	0.13	0.5766573
Cerast40to45	*Cerastoderma edule*	40-44.99	0	0.87324485
Muss5to10	*Mytilus edulis*	5-9.99	0.06	0.0042
Muss10to15	*Mytilus edulis*	10-14.99	0.06	0.0171
Muss15to20	*Mytilus edulis*	15-19.99	0.06	0.0432
Muss20to25	*Mytilus edulis*	20-24.99	0.06	0.070375
Muss25to30	*Mytilus edulis*	25-29.99	0.06	0.1525
Muss30to35	*Mytilus edulis*	30-34.99	0.06	0.271875
Muss35to40	*Mytilus edulis*	35-39.99	0.06	0.424
Muss40to45	*Mytilus edulis*	40-44.99	0.06	0.6005
Muss45to50	*Mytilus edulis*	45-49.99	0.06	0.7925
Muss50to55	*Mytilus edulis*	50-54.99	0.06	0.991375
Muss55to60	*Mytilus edulis*	55-59.99	0.06	1.190375
Litt5to10	*Littorina littorea*	5-9.99	0.75	0.00511366
Litt10to15	*Littorina littorea*	10-14.99	0.6	0.03206383
Litt15to20	*Littorina littorea*	15-19.99	0.45	0.10741796
Litt20to25	*Littorina littorea*	20-24.99	0.45	0.264982
OtherMoll0to5	Additional molluscs (1)	0-4.99	0.26	0.00389322
OtherMoll5to10	Additional molluscs (1)	5-9.99	0.26	0.00389322
OtherMoll10to15	Additional molluscs (1)	10-14.99	0.19	0.01435073
OtherMoll15to20	Additional molluscs (1)	15-19.99	0.19	0.03388385
OtherMoll20to25	Additional molluscs (1)	20-24.99	0.23	0.06436568
OtherMoll25to30	Additional molluscs (1)	25-29.99	0.23	0.10743603
OtherMoll30to35	Additional molluscs (1)	30-34.99	0.24	0.16457602
OtherMoll35to40	Additional molluscs (1)	35-39.99	0.24	0.23714929
OtherMoll40to45	Additional molluscs (1)	40-44.99	0.24	0.32642782
OtherMoll45to50	Additional molluscs (1)	45-49.99	0.03	0.4336093
OtherMoll50to55	Additional molluscs (1)	50-54.99	0.03	0.55982963
Crust0to3	Crustaceans (1)	0-2.99	0	0.00001596

Crust3to10	Crustaceans (1)	3-9.99	0	0.00081206
Crust10to20	Crustaceans (1)	10-19.99	0	0.00761565
Crust20to40	Crustaceans (1)	20-39.99	0	0.04866828
Crust40plus	Crustaceans (1)	40+	0	0.1051207
Peringia0to5	*Peringia ulvae*	0-4.99	0.39	0.0005695
Peringia5to10	*Peringia ulvae*	5-9.99	0.39	0.00207347
MarineWorms0to5	Annelida sp.(1)	0-4.99	0.15	0.00119
MarineWorms5to15	Annelida sp.(1)	5-14.99	0.12	0.00068074
MarineWorms15to30	Annelida sp.(1)	15-29.99	0.13	0.0031283
MarineWorms30to45	Annelida sp.(1)	30-44.99	0.2	0.00817442
MarineWorms45to60	Annelida sp.(1)	45-59.99	0.2	0.01538895
MarineWorms60to75	Annelida sp.(1)	60-74.99	0.25	0.02468413
MarineWorms75to90	Annelida sp.(1)	75-89.99	0.43	0.0359974
MarineWorms90to105	Annelida sp.(1)	90-104.99	0.57	0.04928038
MarineWormsover105	Annelida sp.(1)	105+	0.57	0.11427061
Earthworms5to15	Terrestrial Oligochaeta	5-14.99	0	0.0009
Earthworms15to30	Terrestrial Oligochaeta	15-29.99	0	0.0054
Earthworms30to45	Terrestrial Oligochaeta	30-44.99	0	0.0165
Earthworms45to60	Terrestrial Oligochaeta	45-59.99	0	0.0346
Earthworms60to75	Terrestrial Oligochaeta	60-74.99	0	0.0601
Earthworms75to90	Terrestrial Oligochaeta	75-89.99	0	0.0935
Earthworms90to105	Terrestrial Oligochaeta	90-104.99	0	0.135
Earthwormsover105	Terrestrial Oligochaeta	105+	0	0.194

Table A5.2. AFDM equation and source for each resource parameter included in the MORPH models (except Humber estuary where a site specific AFDM was available).

Prey type/species	**Size class (mm)**	**Equation**	**AFDM Equation source**
Cerastoderma edule	0-44.99	EXP(-5.68+3.315*LN(x) +0.5*0.046)	Thomas et al. 2004 - *C.edule*
Mytilus edulis	5-19.99	Direct from paper source	Durell et al. 2007
Mytilus edulis	20-59.99	Direct from survey results	Stillman et al. 2014
Littorina littorea	5-24.99	EXP(-5.6481+3.59194*LN(B12) +0.5*0.09)	Thomas et al. 2004 - *L.littorea*
Additional molluscs (1)	0-54.99	EXP(-3.8521+2.5525*LN(x) +0.5*0.14)	Thomas et al. 2004 – *Scrobicularia sp.*
Crustaceans (1)	0-40+	EXP(-5.2531+2.6753*LN(x) +0.5*0.0787)	Thomas et al. - *Gammarus sp*.
Peringia ulvae	0-9.99	EXP(-1.6752+1.1748*LN(x) +0.5*0.0762)	Thomas et al. - *Peringia sp.*
Annelida sp.(1)	0-4.99	0.00119g	Herbert et al. 2010
Annelida sp.(1)	5-105+	EXP(-4.8+1.88*LN(x) +0.5*0.175	Thomas et al. - *Hediste diversicolor*
Terrestrial Oligochaeta	5-105+	Direct from survey results	Durell et al. 2006

Table A5.3. A full list of species included in all five estuaries MORPH resources (Species names correct April 2016).

Poole Harbour 2009 survey		
Cerastoderma edule & glaucum	*Urothoe pulchella*	*Oligochaeta indet*
Mytilus edulis	***Peringia ulvae***	*Parapionosyllis minuta*
Littorina littorea	**Marine worms <5mm**	*Phyllodoce mucosa*
Other molluscs:	*Ampharete baltica*	*Nematoda*
Abra tenuis	*Ampharete grubei*	*Nemertea*
Dosinia lupinus	*Aonides oxycephala*	*Polychaeta sp.*
Limecola balthica	*Aphelochaeta marioni*	*Polycirrus sp.*
Mya arenaria	*Capitella capitata*	*Polydora cornuta*
Parvicardium exiguum	*Chaetozone zetlandica*	*Polydora sp.*
Retusa obtusa	*Chaetozone christiei*	*Pseudopolydora paucibranchiata*
Ruditapes philippinarum	*Cirratulidae indet*	*Pygospio elegans*
Scrobicularia plana	*Cirriformia tentaculata*	*Sabella pavonina*
Solen marginatus	*Cossura longocirrata*	*Scolelepis sp.*
Venerupis corrugata	*Desdemona ornata*	*Scoloplos (Scoloplos) armiger*
Crustaceans:	*Eteone longa*	*Serpulidae sp.*
Ampelisca brevicornis	*Eumida cf. sanguinea*	*Spio martinensis*
Austrominius modestus	*Eumida punctifera*	*Spionidae sp.*
Carcinus maenas	*Glycera tridactyla*	*Spirobranchus lamarcki*
Corophium volutator	*Hediste diversicolor* <=5mm	*Streblospio shrubsolii*
Crangon crangon	*Hypereteone foliosa*	*Tubificoides benedii*
Cyathura carinata	*Janua pagenstecheri*	*Tubificoides pseudogaster*
Gammarus locusta	*Malacoceros tetracerus*	*Tubificoides sp.*
Idotea balthica	*Mediomastus fragilis*	**Marine worms >5mm**
Idotea chelipes	*Melinna palmata*	*Alitta virens*
Liocarcinus navigator	*Microphthalmus cf. similis*	*Arenicola marina*
Melita palmata	*Nemertea*	*Hediste diversicolor*
Microdeutopus gryllotalpa	*Neoamphitrite figulus*	*Nephtys hombergii*
Microprotopus maculatus	*Notomastus latericeus*	*Nephtys kersivalensis*
Severn 2010/2011 surveys	**Humber 2009/2010 surveys**	
Other molluscs:	***Cerastoderma sp.***	**Marine worms:**
Macoma sp.	**Other molluscs:**	*Arenicola sp.*
Crustaceans:	*Eteone sp.*	*Nephtys sp.*
Corrophium sp.	*Macoma sp.*	
Peracarida sp.	**Crustaceans:**	
Peringia	*Corrophium sp.*	
Hydrobia	***Peringia***	
Marine worms:	*Hydrobia*	
Hediste sp.		

Continued on next page

Continued from previous page

Exe 2001 survey

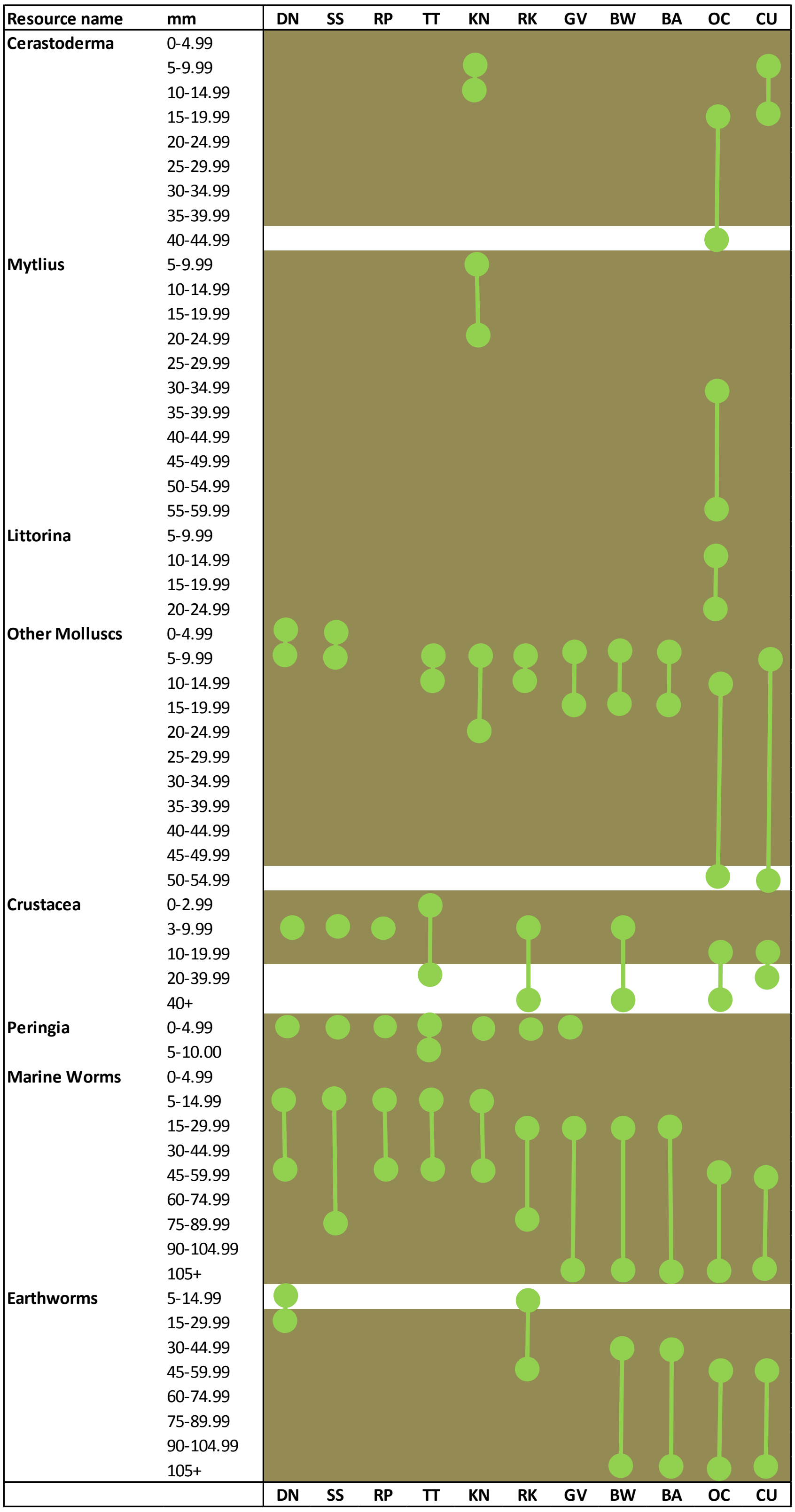
Cerastoderma edule
Mytilus edulis
Littorina sp.
Other molluscs:
Abra alba
Angulus tenuis
Crepidula fornicata
Gibbula umbilicalis
Lepidochitona cinerea
Limecola balthica
Mya arenaria
Ruditapes decussatus
Scrobicularia plana
Crustaceans:
Bathyporeia pelagica
Bathyporeia sarsi
Carcinus maenus
Chironomid larvae
Corophium arenarium
Corophium spp.
Corophium volutator
Crangon crangon
Cyathura carinata
Dipteran larva
Eurydice pulchra
Gammarus locusta
Idotea chelipes
Idotea pelagica
Jaera albifrons
Melita palmata
Neomysis integer
Praunus flexuosus
Sphaeroma serratum
Tanaidacea
Urothoe poseidonis
Peringia ulvae
Marine worms:
Ampharete grubei
Arenicola marina
Capitella capitata
Cirratulid spp.
Eteone longa
?Eteone sp.
Euclymene lombricoides
Glycera tridactyla
Harmothoe sp.
Hediste diversicolor
Heteromastus filiformis
Lanice conchilega
Lysidice unicornis
Malacoceros fuliginosus
Nematoda
Nemertea
Nephtys hombergii
Ophelia bicornis
Phyllodoce maculata
Psamathe fusca
Pygospio elegans
Scolelepis squamata
Scoloplos (Scoloplos) armiger
Spio spp.
Tubificidae

Southampton Water 2003 survey

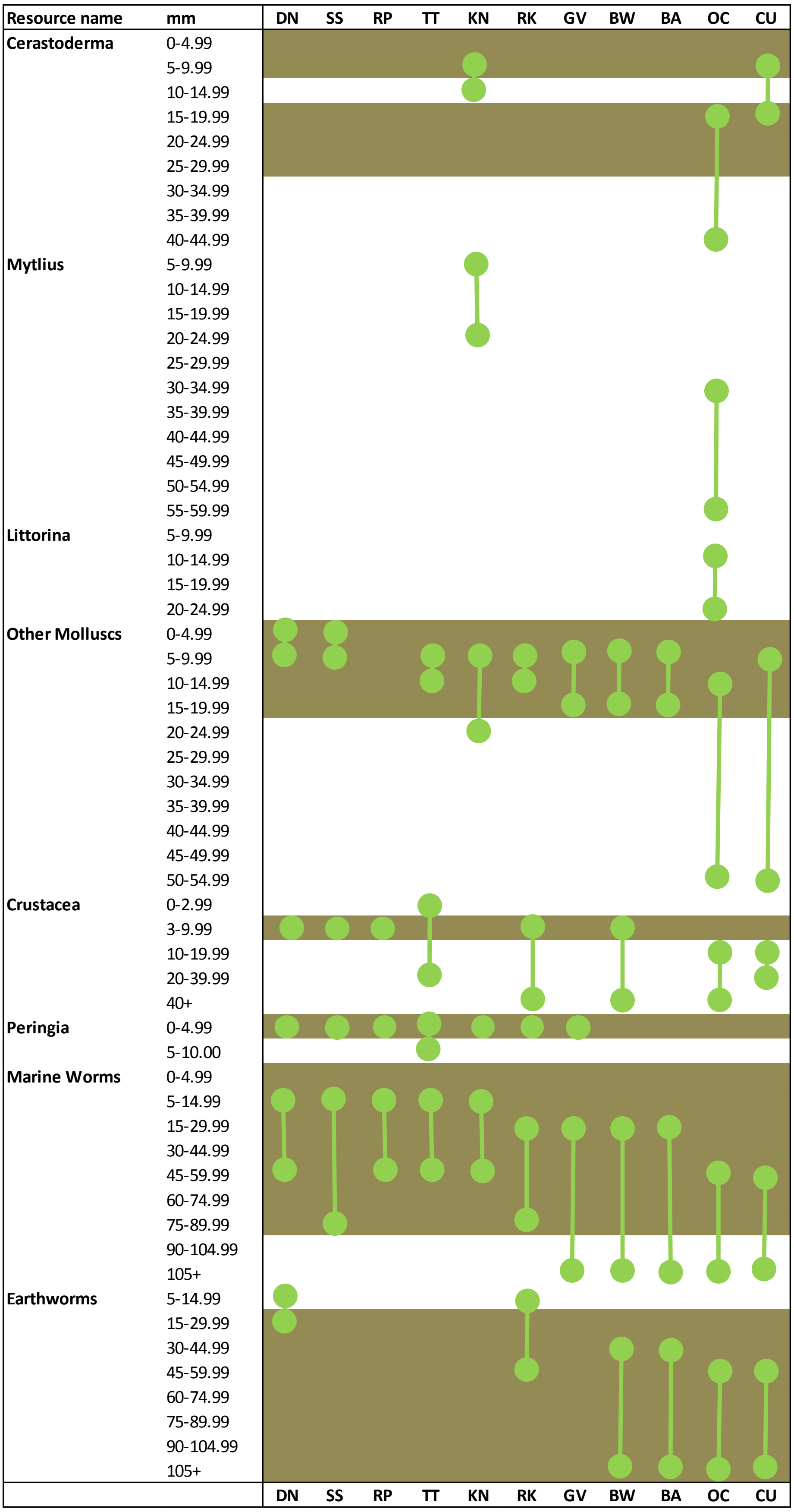
Cerastoderma edule
Littorina
Littorina sp.
Littorina littorea
Littorina saxatilis
Other molluscs:
Abra alba
Corbula gibba
Crepidula fornicata
Gibbula umbilicalis
Limecola balthica
Mactridae sp.
Mya arenaria
Parvicardium exiguum
Scrobicularia plana
Tellinidae sp.
Veneridae sp.
Crustaceans:
Amphipoda indet
Anthura gracilis
Carcinus maenas
Corophium volutator
Crangon crangon
Decapoda indet
Sphaeroma serratum
Peringia ulvae
Marine Worms:
Alitta virens
Ampharetidae indet
Aphroditidae indet
Cephalothrix rufifrons
Cirratulidae sp.
Cirratulus cirratus
Cirriformia tenteculata
Eteone sp.
Hediste diversicolor
Lanice conchilega
Marphysa sanguinea
Nephtyidae sp.
Nephtys caeca
Nephtys cirrosa
Nereididae sp.
Phyllodoce maculata
Phyllodocidae sp.
Terebellidae - Amphitrite sp.
Tharyx sp.
Tubificoides benedii

Tables A5.4.a-e. Species specific dietary choices in relation to available resources for each estuary per size class. Green bars indicate dietary size classes accessed by each species. Brown boxes show resources present on one or more patches of an estuary.

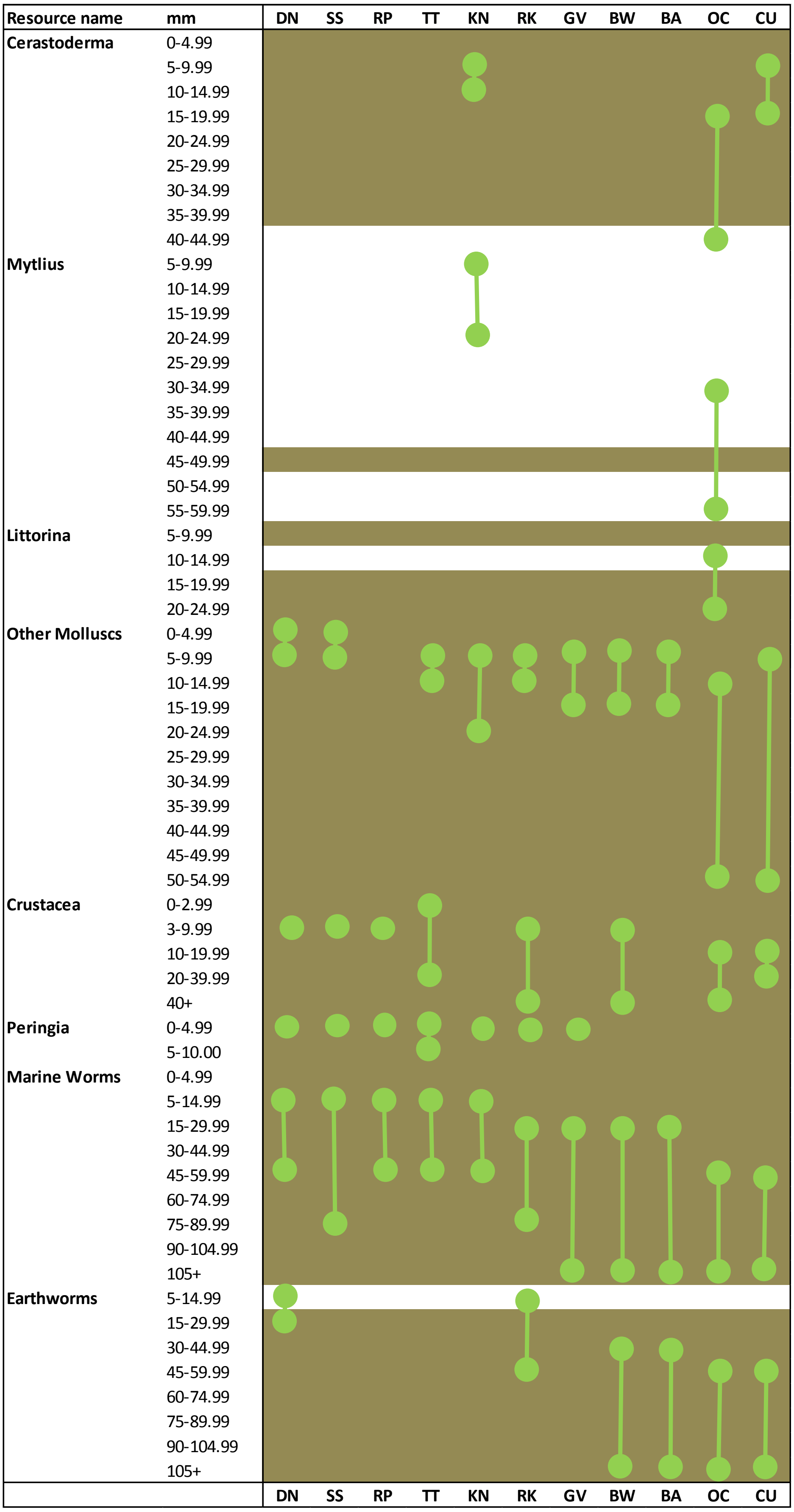
a) Exe estuary



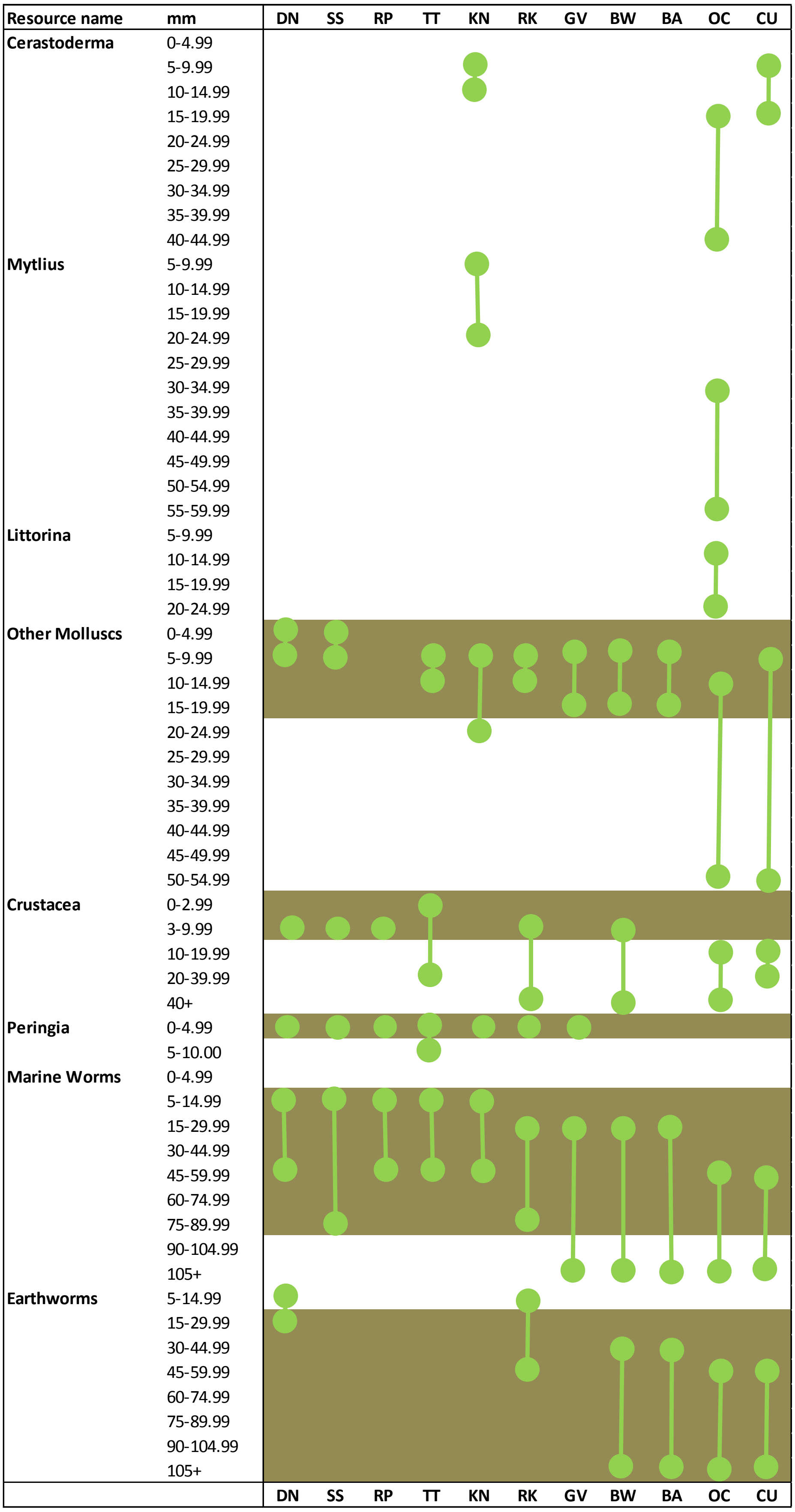
b) Humber estuary



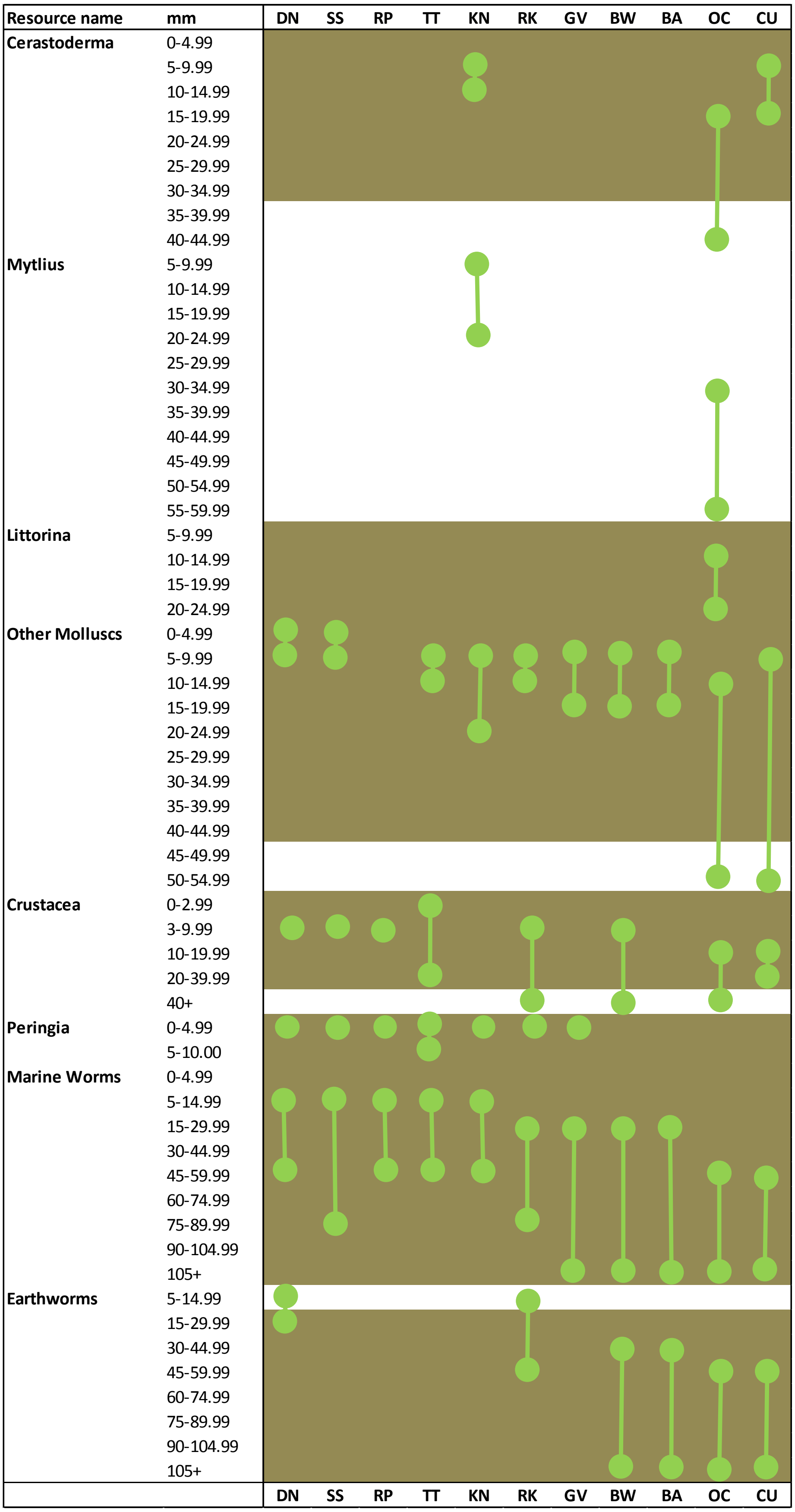
c) Poole Harbour



d) Severn estuary



e) Southampton Water



Appendix 6 Forager details

Table A6.1 Forager variables and constants – *continued on next page*

	Species	Dunlin	Sanderling	Ringed Plover	Turnstone	Knot	Redshank
	BTO codes	DN	SS	RP	TT	KN	RK
Diets consumed by size (mm)							
Cerastedorma	0-44.99					5-14.99	
Mussel	5-59.99					5-24.99	
Littorina	5-24.99						
Other Molluscs	0-54.99	0-9.99	0-9.99		5-14.99	5-24.99	5-14.99
Crustacean	0-40+	3-9.99	3-9.99	3-9.99	0-39.99		3-40+
Peringia	0-4.99	0-4.99	0-4.99	0-4.99	0-10	0-4.99	0-4.99
Marine Worms	0-105+	5-59.99	5-89.99	5-59.99	5-59.99	5-59.99	15-89.99
Earthworms	5-105+	5-29.99					5-59.99
Bird values							
Mass (g)	BTO ringing data	50.01	57.68	67.68	107.7	138.1	153.3
Starvation mass (g)	Goss-Custard work	39	30.4	37	61.8	93	90.5
Arrival Energy Store (g)	*y = 34.4*(mass-stavation mass)*	377.643	935.704	1052.324	1574.37	1546.93	2154.04
Day Efficiency		Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000
Day Eff *calibration values*	Exe estuary	-	-	-	-	-	-
	The Humber	-	-	-	-	-	-
	Poole harbour - no calirbation needed	-	-	-	-	-	-
	Severn estuary	-	-	-	-	-	-
	Southampton Water - no calirbation needed	-	-	-	-	-	-
Night Efficiency	*y = DayEff * x*	0.82	0.82	0.49	0.82	0.82	0.95
Aggregation factor	KMB	1378	1378	88	88	1	167
Regulated density no/m^2	KMB	0.65	0.65	0.0054	0.0054	1	0.0319
STI for each species per diet							
CockleDiet						WeakKlepSTI	
CrustaceanDiet		MobilePreySTI	MobilePreySTI	MobilePreySTI	MobilePreySTI		MobilePreySTI
EarthwormDiet		WeakKlepSTI					WeakKlepSTI
WinkleDiet							
MarineWormDiet		WeakKlepSTI	WeakKlepSTI	MobilePreySTI	MobilePreySTI	WeakKlepSTI	WeakKlepSTI
MusselDiet						WeakKlepSTI	
OtherMolluscDiet		WeakKlepSTI	WeakKlepSTI		WeakKlepSTI	WeakKlepSTI	WeakKlepSTI
PeringiaDiet		WeakKlepSTI	WeakKlepSTI	WeakKlepSTI	WeakKlepSTI	WeakKlepSTI	WeakKlepSTI
		DN	**SS**	**RP**	**TT**	**KN**	**RK**
Function response							
Forager coefficients	*y = (-2.802+(0.245*LN(mass))-(0*0.227)+(0.5*0.27)*	-1.708505	-1.673547	-1.634376	-1.520559	-1.459645	-1.434063
Coeff for OC on mussels	*y = (-2.802+(0.245*LN(mass))-(1*0.227)+(0.5*0.27)*						
Metabolic costs							
LCT	*y= -0.0216*(mass g)+21.896*	20.8	20.7	20.4	19.6	18.9	18.6
Thermostatic costs °C	*y = 0.0055*(mass g)^1.3737*	1.2	1.4	1.8	3.4	4.8	5.5
Basal Metabolic Rate kJ/day	*y = 437*(mass kg)^0.729*	49.215	54.61	61.36	86.093	103.201	111.363
Feeding BMR kJ/day	*y = BMR*2.1*	103.3515	114.681	128.856	180.7953	216.7221	233.8623
Flying BMR kJ/day	*y = BMR*12*	590.58	655.32	736.32	1033.116	1238.412	1336.356

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	Species	Grey Plover	Black-tailed godwit	Bar-tailed godwit	Oystercatcher	Curlew
	BTO codes	GV	BW	BA	OC	CU
Diets consumed by size (mm)						
Cerastedorma	0-44.99				15-44.99	5-19.99
Mussel	5-59.99				30-59.99	
Littorina	5-24.99				10-24.99	
Other Molluscs	0-54.99	5-19.99	5-19.99	5-19.99	10-54.99	5-54.99
Crustacean	0-40+		3-40+		10-40+	10-39.99
Peringia	0-4.99	0-4.99				
Marine Worms	0-105+	15-105+	15-105+	15-105+	45-105+	45-105+
Earthworms	5-105+		30-105+	30-105+	45-105+	45-105+
Bird values						
Mass (g)	BTO ringing data	243.4	298.5	304.45	546.2	783.9
Starvation mass (g)	Goss-Custard work	127	161	185.5	350	489
Arrival Energy Store (g)	*y = 34.4*(mass-stavation mass)*	3992.52	4716.25	4079.985	6729.66	10115.07
Day Efficiency		Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000	Normal(1,0.125,0,1000
Day Eff *calibration values*	Exe estuary	-	-	1.125	-	-
	The Humber	1.1	1.3	1.425	-	1.35
	Poole harbour - no calirbation needed	-	-	-	-	-
	Severn estuary	-	1.2	-	1.2	1.2
	Southampton Water - no calirbation needed	-	-	-	-	-
Night Efficiency	*y = DayEff * x*	1	0.87	0.87	0.81	0.82
Aggregation factor	KMB	25	868	868	88	25
Regulated density no/m^2	KMB	0.0024	0.205	0.205	0.0054	0.0024
STI for each species per diet						
CockleDiet					LargeMollKlepSTI	WeakKlepSTI
CrustaceanDiet			MobilePreySTI		MobilePreySTI	MobilePreySTI
EarthwormDiet			WeakKlepSTI	WeakKlepSTI	WeakKlepSTI	WeakKlepSTI
WinkleDiet					WeakKlepSTI	
MarineWormDiet		MobilePreySTI	WeakKlepSTI	WeakKlepSTI	WeakKlepSTI	WeakKlepSTI
MusselDiet					MussKlepSTI	
OtherMolluscDiet		WeakKlepSTI	WeakKlepSTI	WeakKlepSTI	LargeMollKlepSTI	LargeMollKlepSTI
PeringiaDiet		WeakKlepSTI				
		GV	**BW**	**BA**	**OC**	**CU**
Function response						
Forager coefficients	*y = (-2.802+(0.245*LN(mass))-(0*0.227)+(0.5*0.27)*	-1.320797	-1.270801	-1.265966	-1.122769	-1.034251
Coeff for OC on mussels	*y = (-2.802+(0.245*LN(mass))-(1*0.227)+(0.5*0.27)*				-1.349769	
Metabolic costs						
LCT	*y= -0.0216*(mass g)+21.896*	16.6	15.4	15.3	10.1	5
Thermostatic costs °C	*y = 0.0055*(mass g)^1.3737*	10.4	13.8	14.2	31.7	52
Basal Metabolic Rate kJ/day	*y = 437*(mass kg)^0.729*	155.994	181.016	183.639	281.197	365.93
Feeding BMR kJ/day	*y = BMR*2.1*	327.5874	380.1336	385.6419	590.5137	768.453
Flying BMR kJ/day	*y = BMR*12*	1871.928	2172.192	2203.668	3374.364	4391.16

Appendix 7 – Fieldwork to determine new species specific aggregation factor and thus regulated density

Following a decision to improve the previous aggregation factor to account for a wider range of species in my models field work was planned and carried out over the winter of 2013/14. Three estuaries along the south coast – Exe, Poole Harbour and Chichester – were visited and two locations sourced on each that provided good views of intertidal areas and were populated with the five main species common to all models – dunlin, redshank, black-tailed godwit, oystercatcher and curlew. For the months of November, December, January and February each site was visited at the lowest available daylight tide for two hours (one before low tide and one after) and all birds of these five species were counted and then as many as possible if not all were assessed for how far apart they were from their nearest neighbour.

A visual count of bird body lengths between nearest individuals was taken either as an exact number of lengths or category of lengths (0-5,5-10,10-20,20-30,30+) using a Swarovski STM 80 HD telescope with a 20–60x eyepiece. These lengths were converted to metres using the average length of a bird (Robinson 2005). The locations at which observations were made were predetermined before the observations started in November and then areas were calculated using OS Vector Map District ‘Foreshore’ areas in ArcGIS (ESRI 2012).

Following ESRI calculations (ESRI 2014) the Average Nearest Neighbour ratio is given as

$$ANN = \frac{\overline{D}_O}{\overline{D}_E}$$

Where D_O is the observed mean distance and D_E is the expected mean distance. These are calculated as follows where d_i = distance between a bird and its nearest neighbour, n is the total number of birds and A is the size of the observed patch:

$$\overline{D}_O = \frac{\sum_{i=1}^{n} d_i}{n} \qquad \overline{D}_E = \frac{0.5}{\sqrt{n/A}}$$

The ANN ratio is worked out by:

$$ANN = \frac{\overline{D}_O - \overline{D}_E}{SE} \quad \text{where } SE = \frac{0.26136}{\sqrt{n^2/A}}$$

To calculate and aggregation factor I determined Average Nearest Neighbour Distance using R (R Development Core Team 2015) to work out the expected distance.

In R the packages “maptools”, “rgdal” and “spatstat” (Braddeley and Turner 2005; Bivand and Lewin-Koh 2015; Bivand et al. 2015) were used to load in ArcGIS shapefiles of the observed patches and randomly populate them with the number of individuals seen on each survey date for each site for 1000 repetitions to find the expected median nearest neighbour distance (NND) between individuals (D_E). The average D_E for each species per month and site were then calculated. To work out the ANN the average of the observed NND (D_O) in metres was squared (as working in areas) and divided by the average D_E^2; this was then divided into 1 and averaged for all species to give the new aggregation factor (Table A7.1)

Table A7.1 New aggregation factors for five species of UK overwintering wading birds.

Species	**Black-tailed Godwit**	**Curlew**	**Dunlin**	**Oystercatcher**	**Redshank**
Aggregation Factor	868	25	1378	88	167

To account for observer error, calibration fieldwork was carried out in May 2014 to determine my accuracy of measuring NND in body lengths. Five pairs of life-size and pre-measured cardboard cut-outs of each of the five species were created (see Figure A7.1) and two field assistants (R.H.Bowgen and M.K.Bowgen) stood at 230m distance from my observation point and measured the exact distance and angle between each pair multiple times whilst I took my own observations. It should be noted that 230m was the greatest distance possible on a flat plain in the local area to carry out this calibration and was a reasonable approximate to the minority of birds observed. The results of both observations and real distances were analysed through correlation to get an accurate linear relationship (Poole et al. 2006; Murray et al. 2013). This resulting equation (measured distance = 1.2342*(estimated distance); R^2=0.6376) was then used to adjust the median D_O of my fieldwork before the above aggregation factors were determined.

Figure A7.1 Life-size cut-out of dunlin used for calibration

Following discussions on the accuracy of this new aggregation factor (and trial runs of the model) it was decided to update the submodel and subsequent parameterisation of *STI* by using the new aggregation factor to create regulated density values instead. The actual density of birds seen for each species on each month at each site was calculated then multiplied by the new aggregation factors (see Table A7.1) and averaged for each species. This new value is the regulated density that birds experience per m^2 (See Table A7.2).

Table A7.2 New regulated density for five species of UK overwintering wading birds.

Species	**Black-tailed Godwit**	**Curlew**	**Dunlin**	**Oystercatcher**	**Redshank**
Regulated Density	0.205	0.0024	0.650	0.0054	0.0319

To account for the previous difference of oystercatcher's feeding on mussel beds, values from work by John Goss-Custard (pers. comm.) were used to derive a new regulated density value of 0.00289. This was then used for the *MussKlepSTI* values in the forager variables section of the models.

References for Appendix 7

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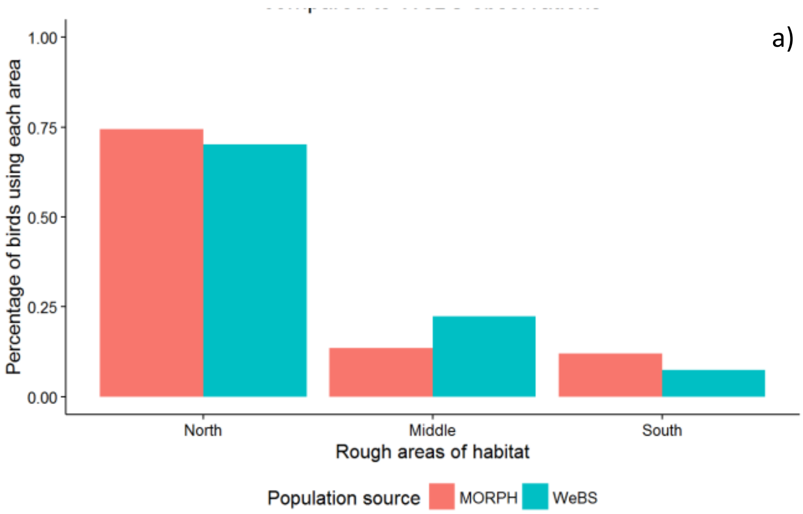
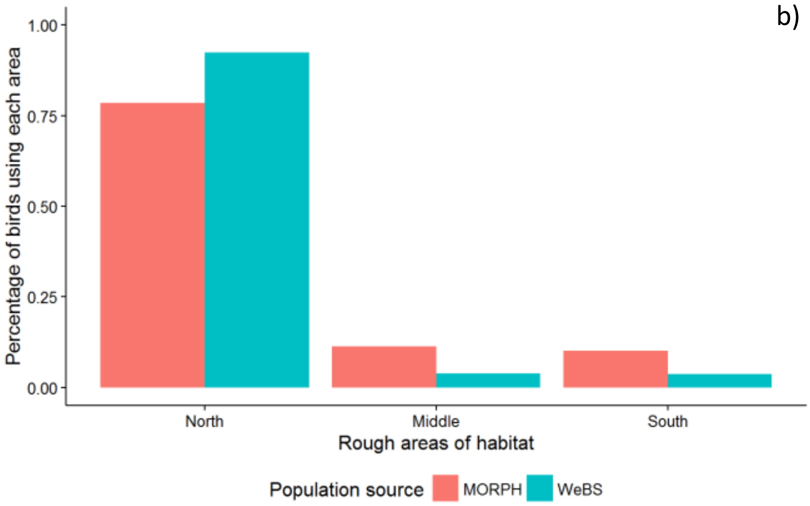
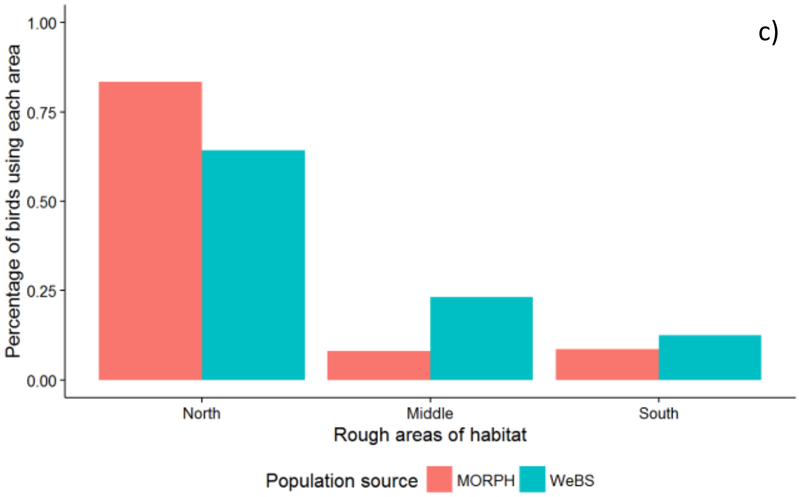
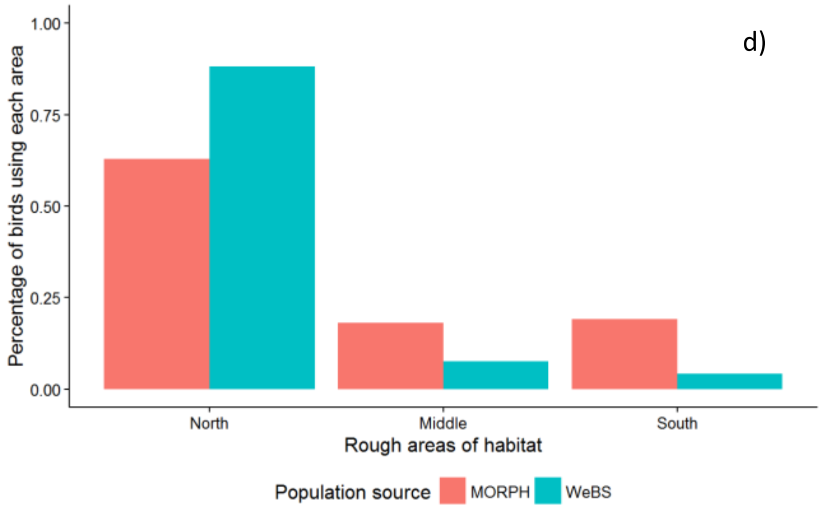
Appendix 8 Validation of wading birds IBMs

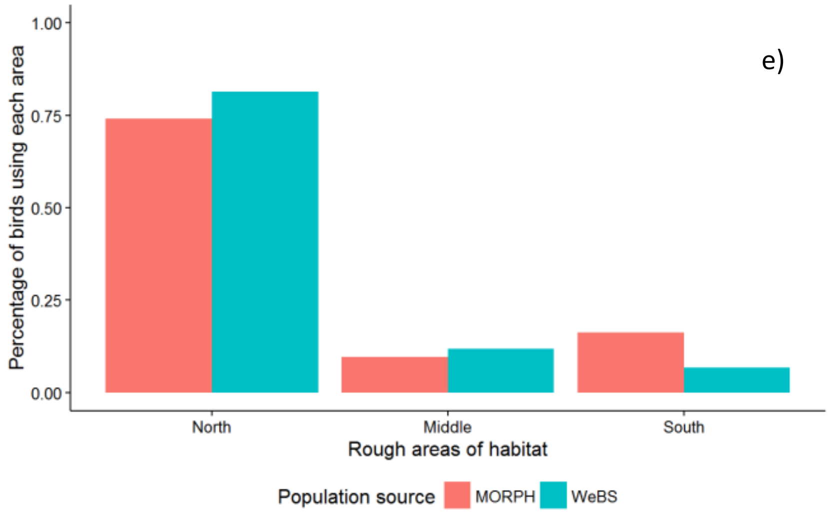
Figures A8.1 a-h. Percentage of each species using ‘rough’ areas of the ***Exe estuary****: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher, g)redshank and h)turnstone.*

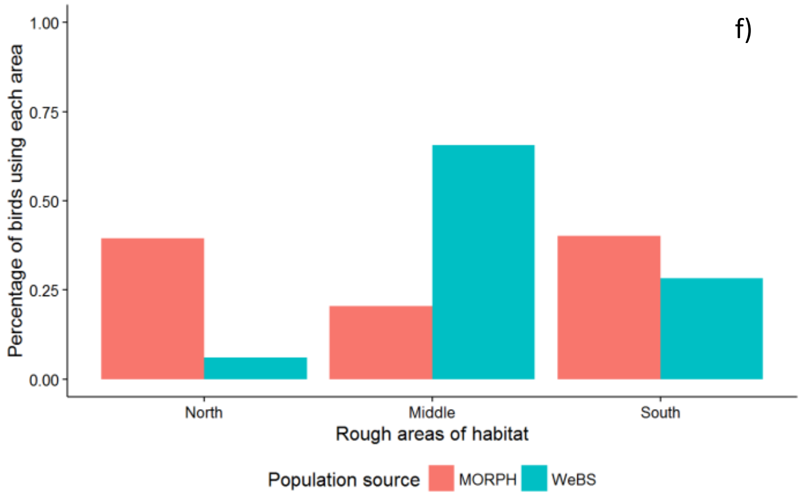


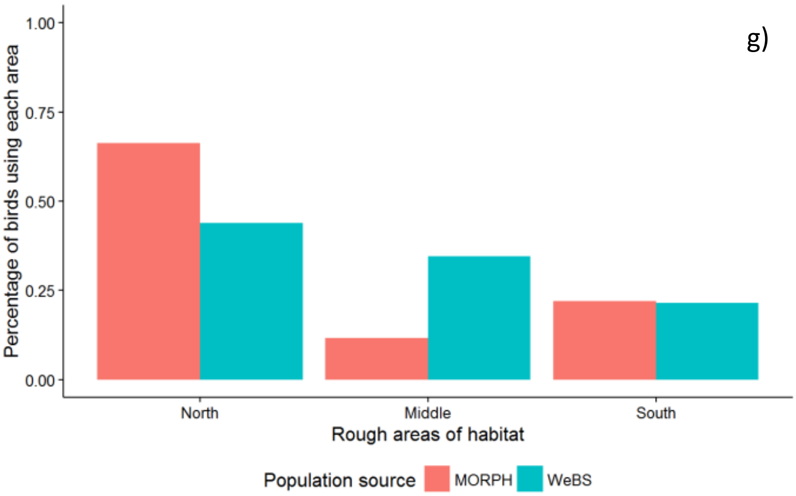


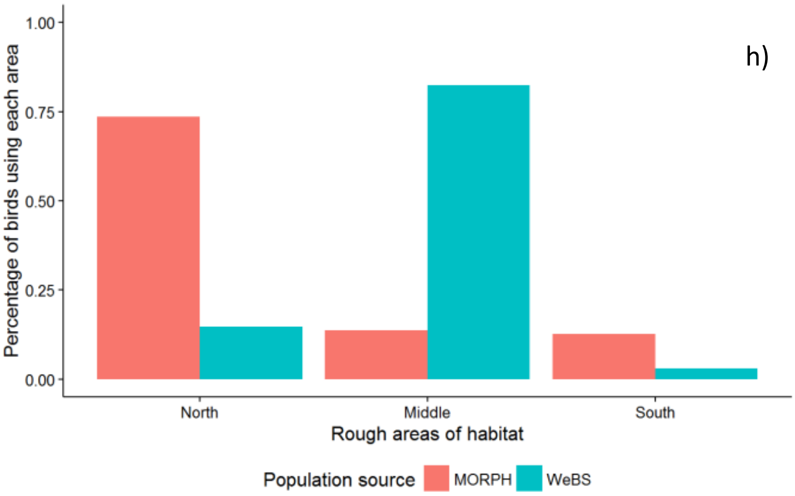



d)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
North
Middle
South
Rough areas of habitat
Population source
MORPH
WeBS

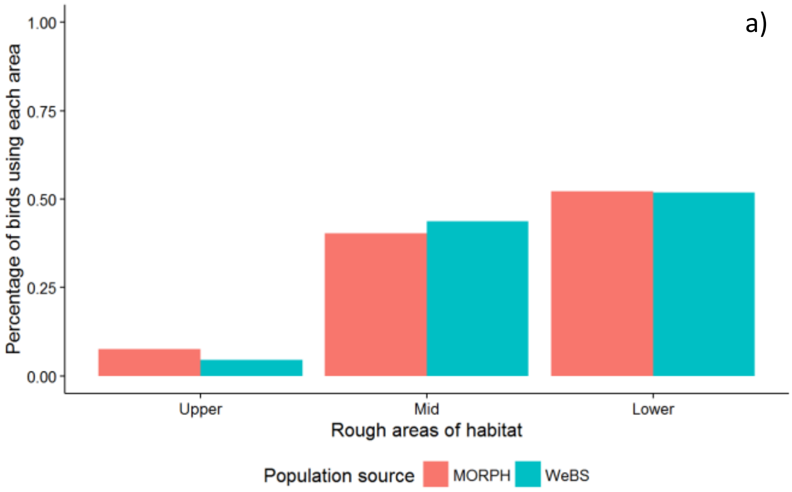

e)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
North
Middle
South
Rough areas of habitat
Population source
MORPH
WeBS

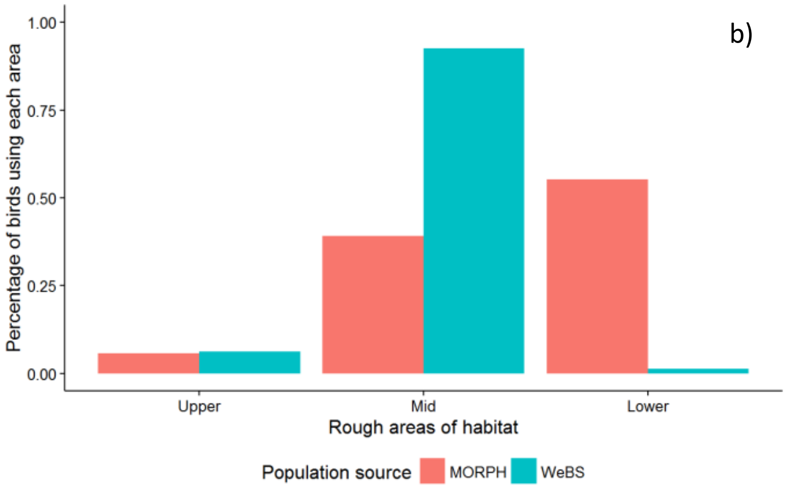

f)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
North
Middle
South
Rough areas of habitat
Population source
MORPH
WeBS

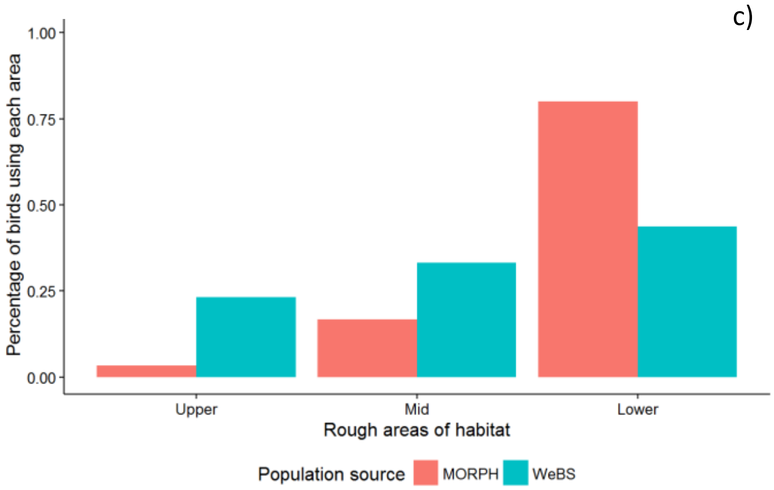


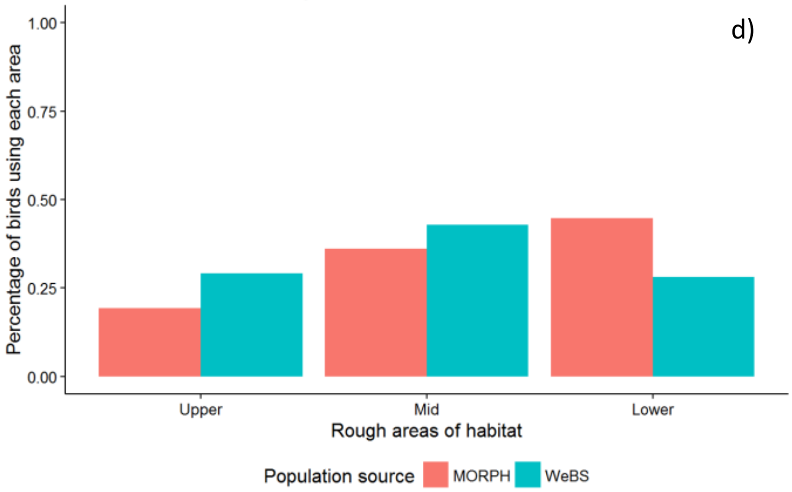


Figures A8.2 a-j. Percentage of each species using 'rough' areas of the ***Humber estuary****: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)knot, g)oystercatcher, h)redshank, i)sanderling and j)turnstone.*

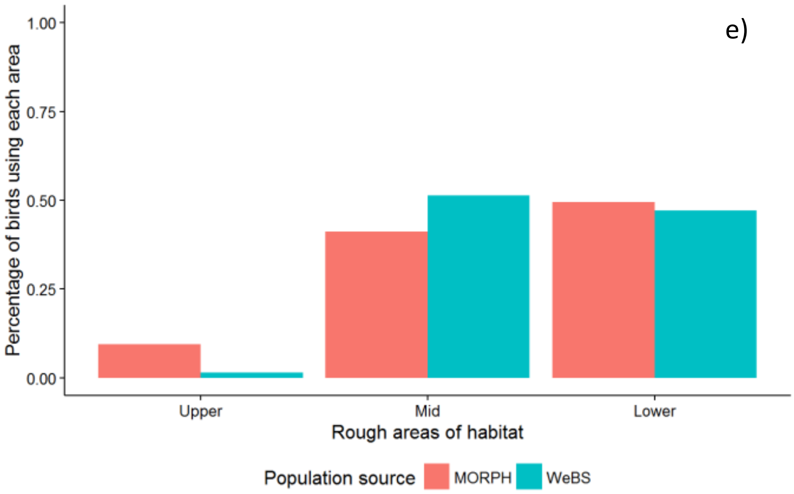



b)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

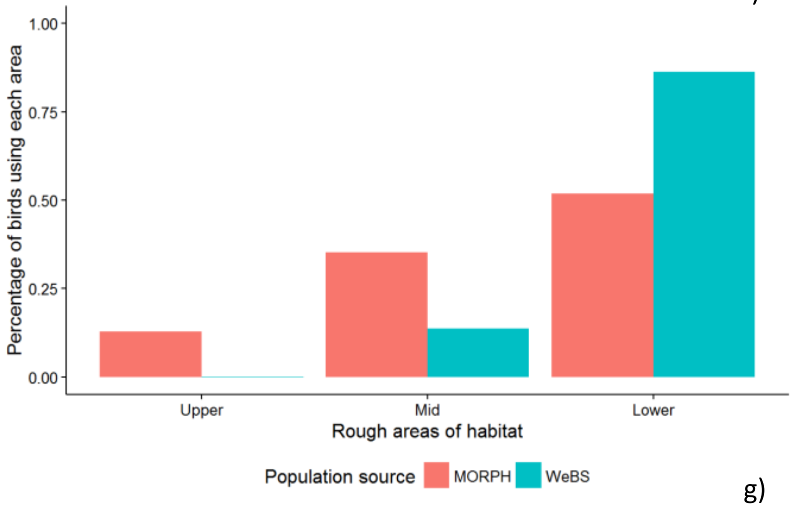

c)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS


d)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

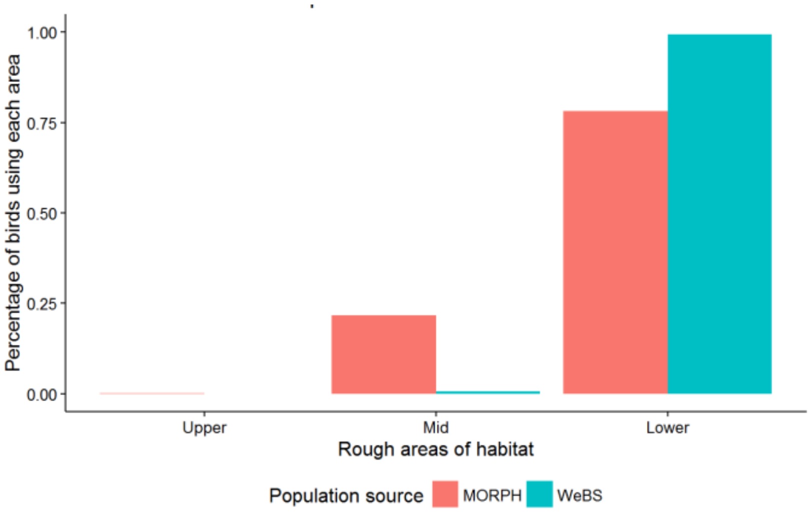
e)


Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

f)


Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

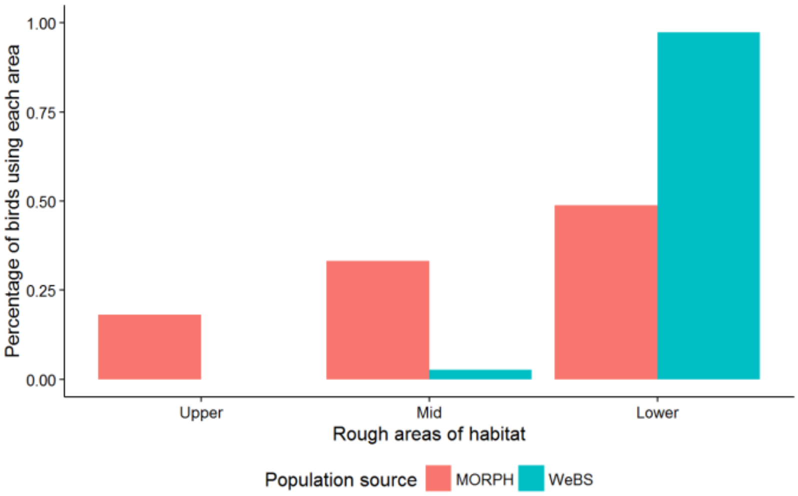
g)


Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

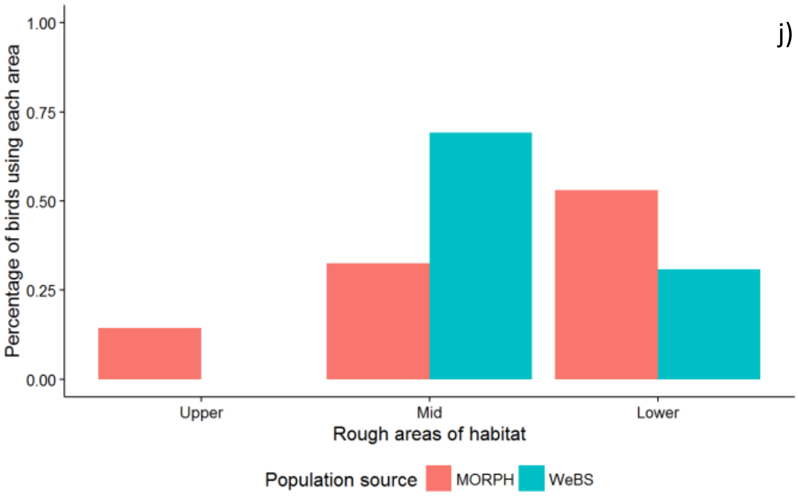
h)


Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

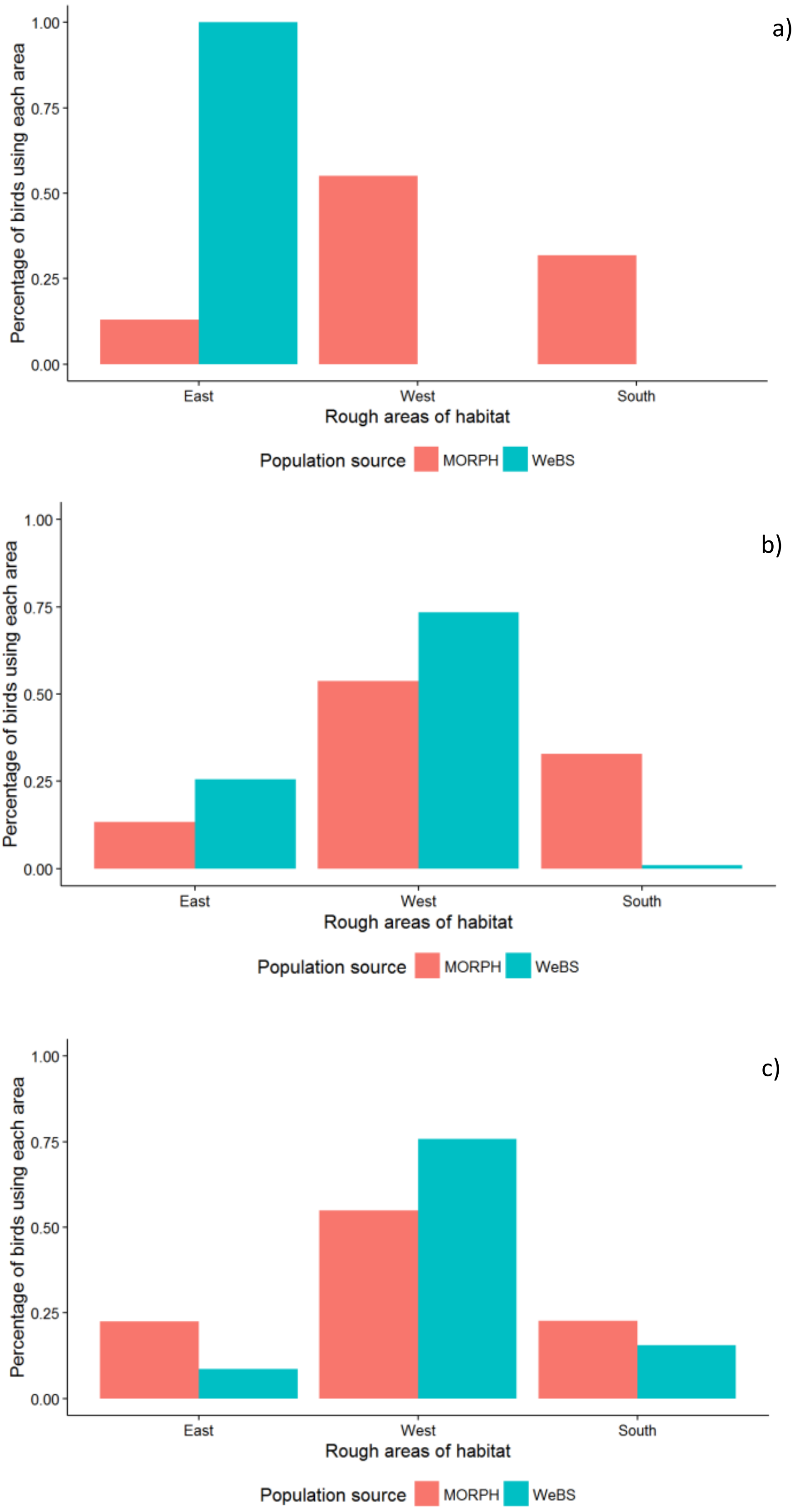
i)

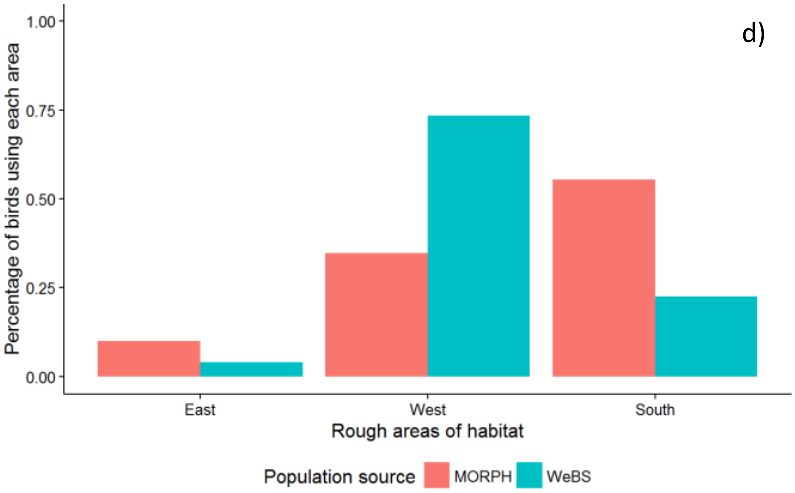

Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

j)

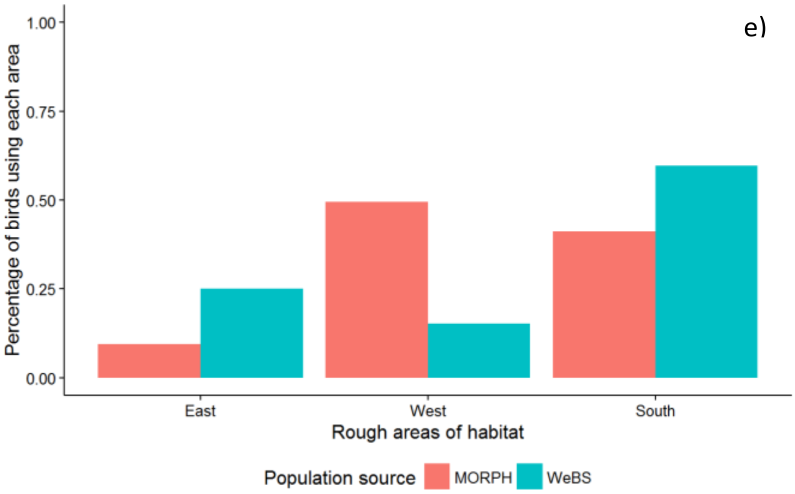

Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Upper
Mid
Lower
Rough areas of habitat
Population source
MORPH
WeBS

Figures A8.3 a-g. Percentage of each species using 'rough' areas of ***Poole Harbour****: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher and g)redshank.*

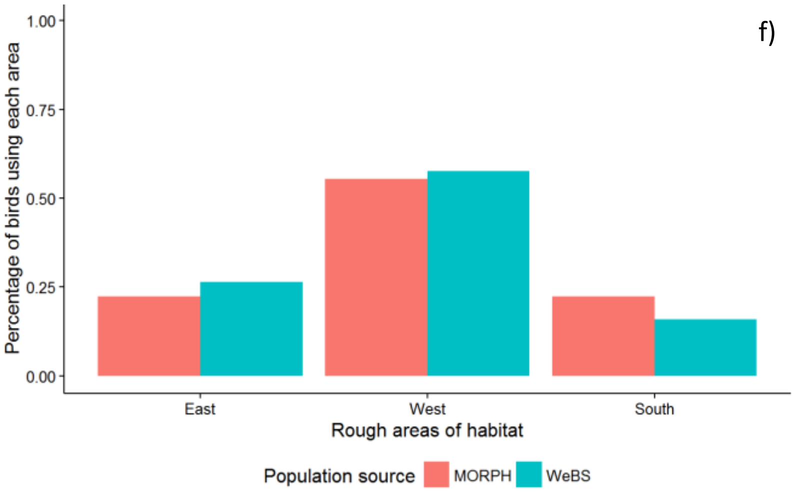



d)

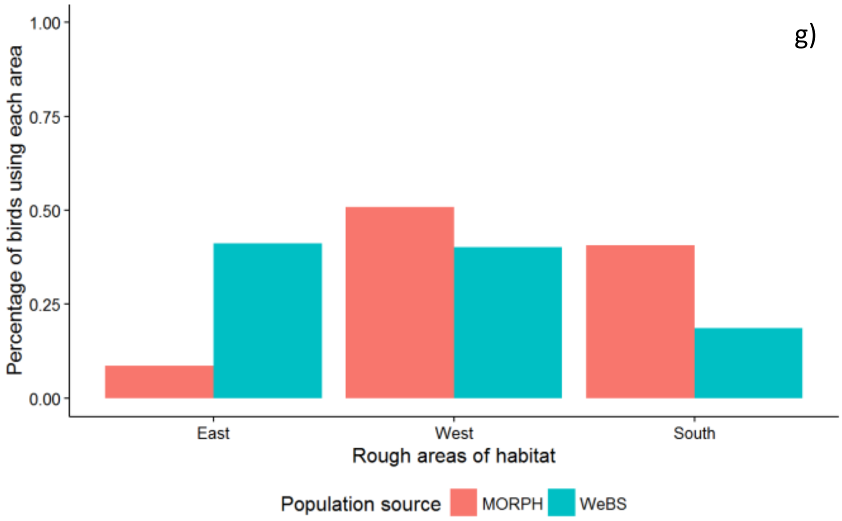
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
East
West
South
Rough areas of habitat
Population source
MORPH
WeBS


e)

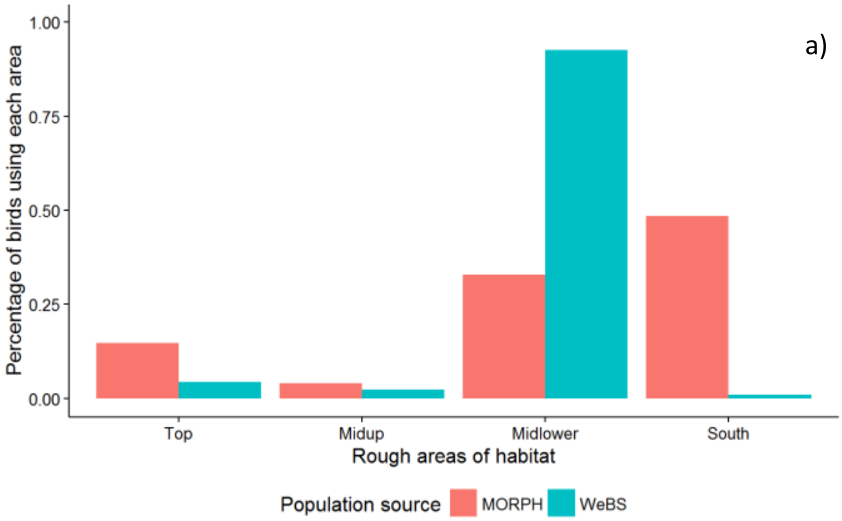
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
East
West
South
Rough areas of habitat
Population source
MORPH
WeBS

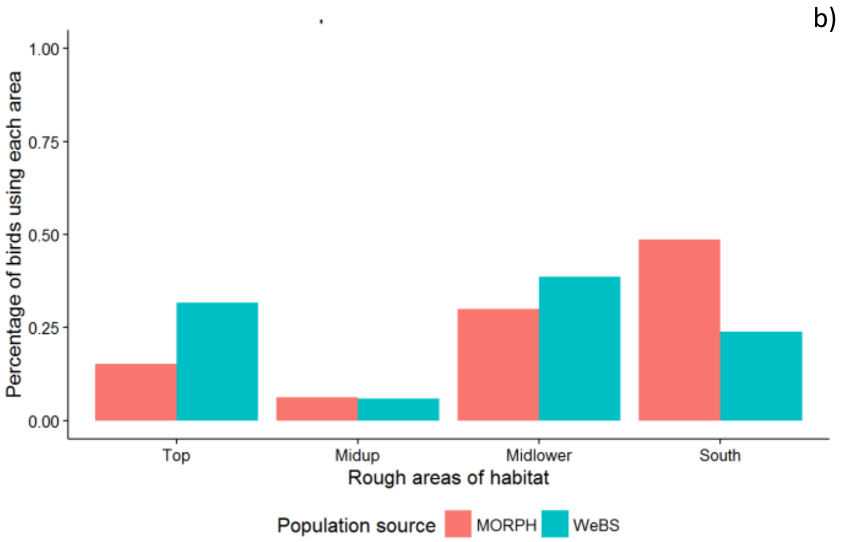

f)

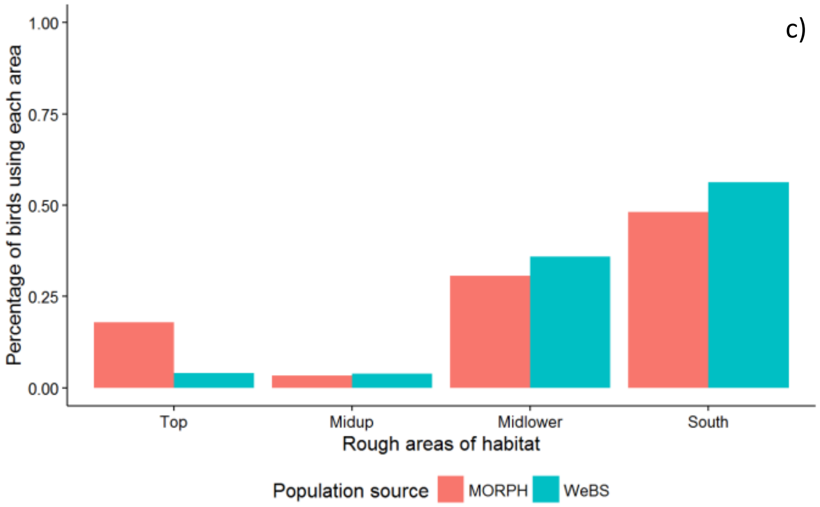
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
East
West
South
Rough areas of habitat
Population source
MORPH
WeBS

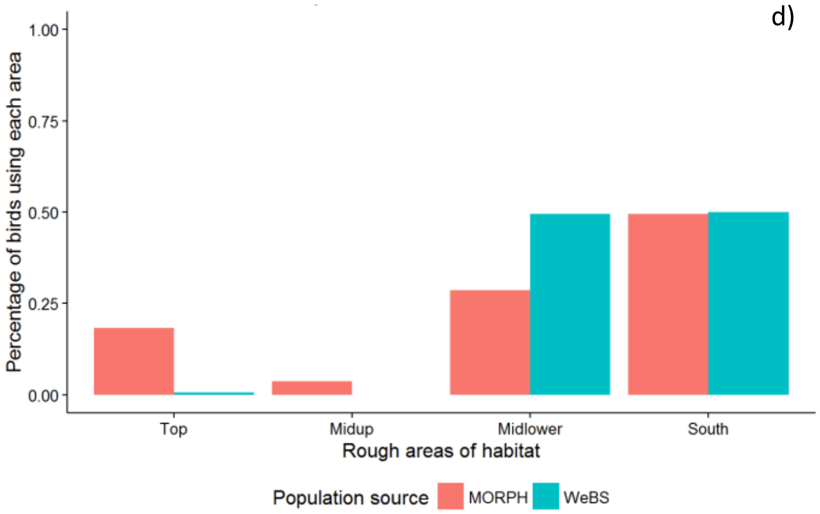


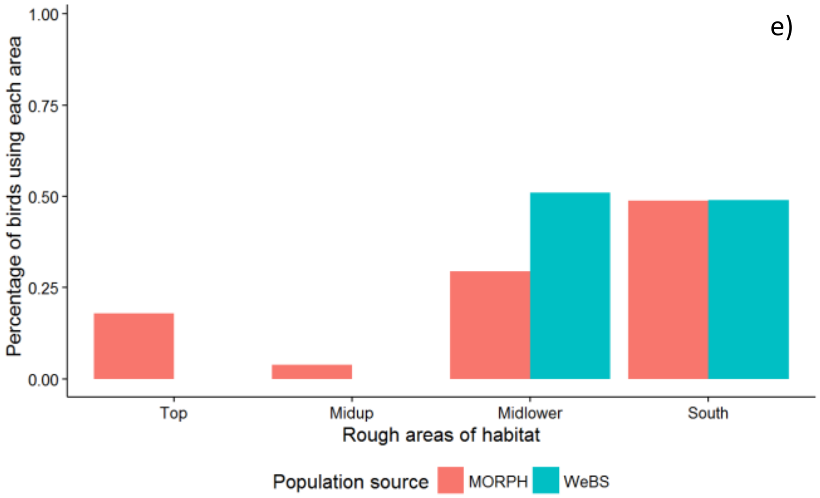
Figures A8.4 a-i. Percentage of each species using 'rough' areas of the ***Severn estuary:*** *a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)knot, f)oystercatcher, g)redshank, h)ringed plover and i)turnstone.*

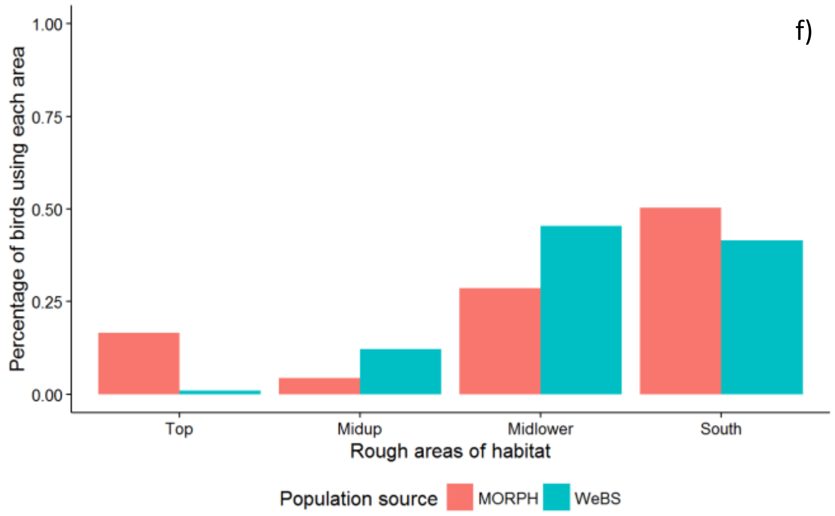


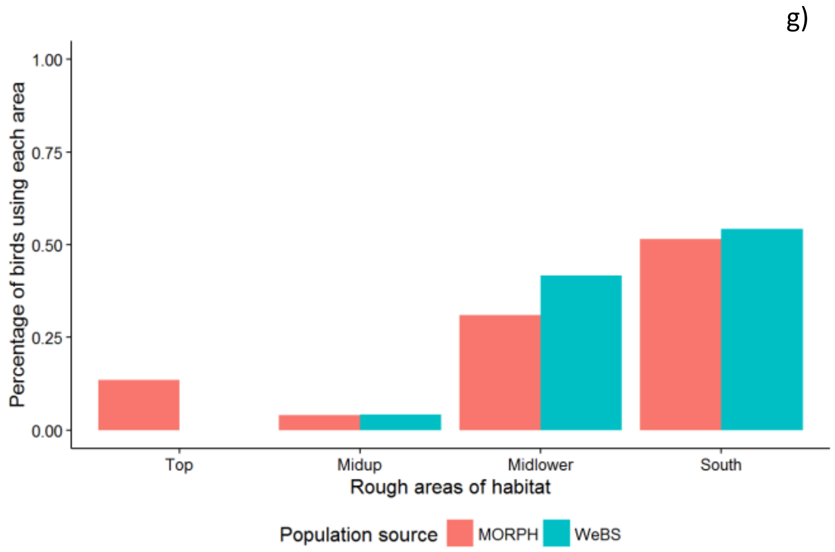


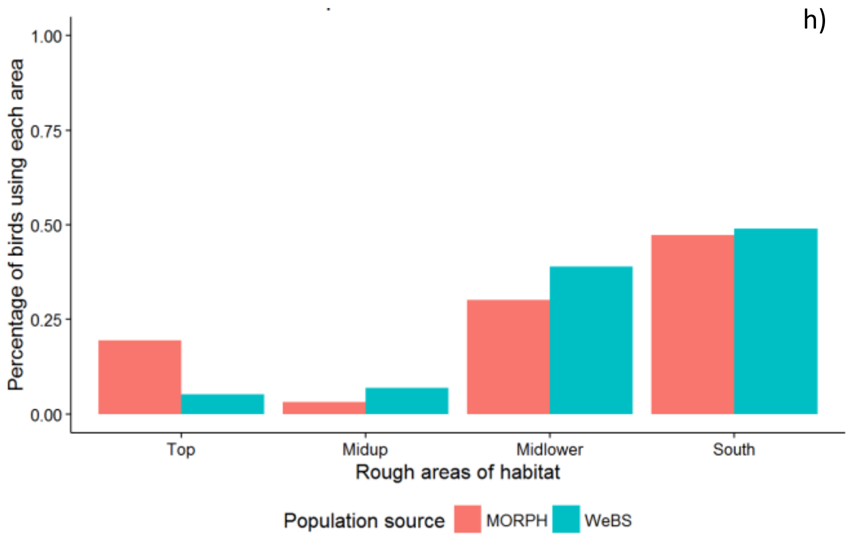

c)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Midup
Midlower
South
Rough areas of habitat
Population source
MORPH
WeBS

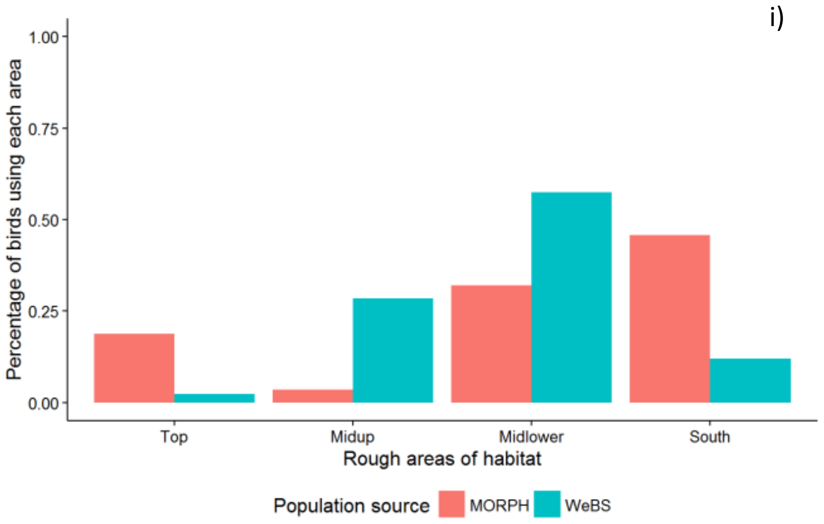

d)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Midup
Midlower
South
Rough areas of habitat
Population source
MORPH
WeBS


e)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Midup
Midlower
South
Rough areas of habitat
Population source
MORPH
WeBS

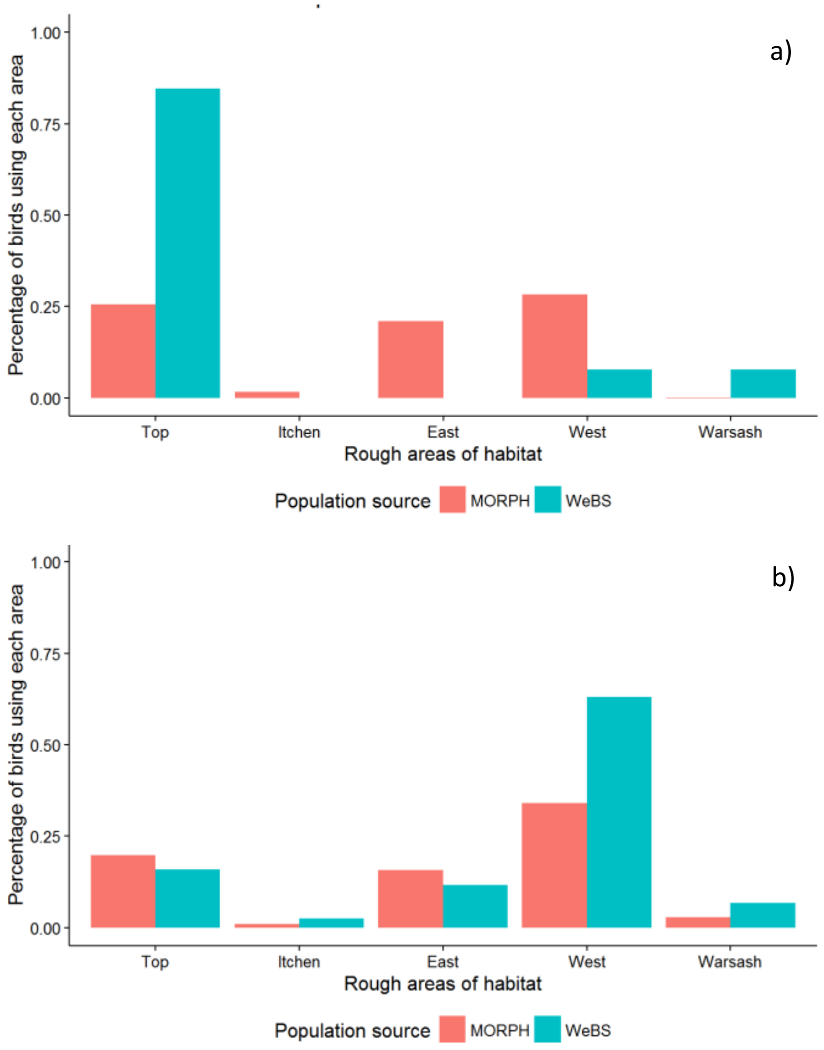

f)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Midup
Midlower
South
Rough areas of habitat
Population source
MORPH
WeBS

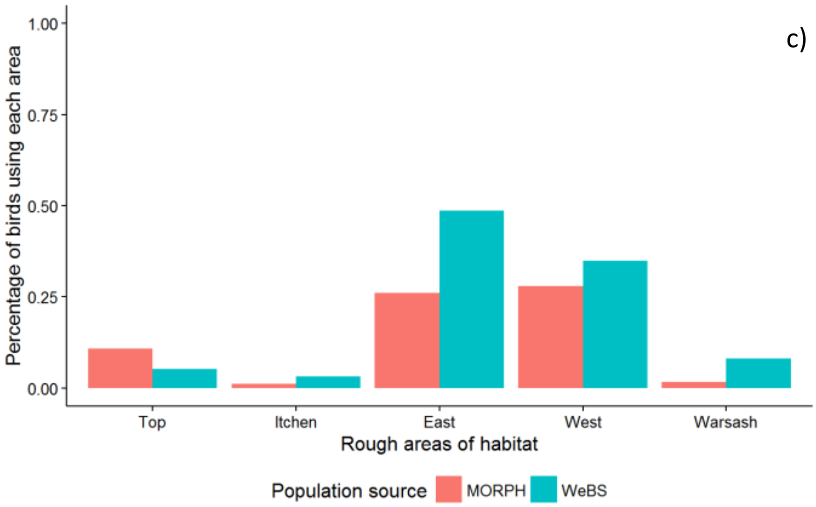

g)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Midup
Midlower
South
Rough areas of habitat
Population source
MORPH
WeBS

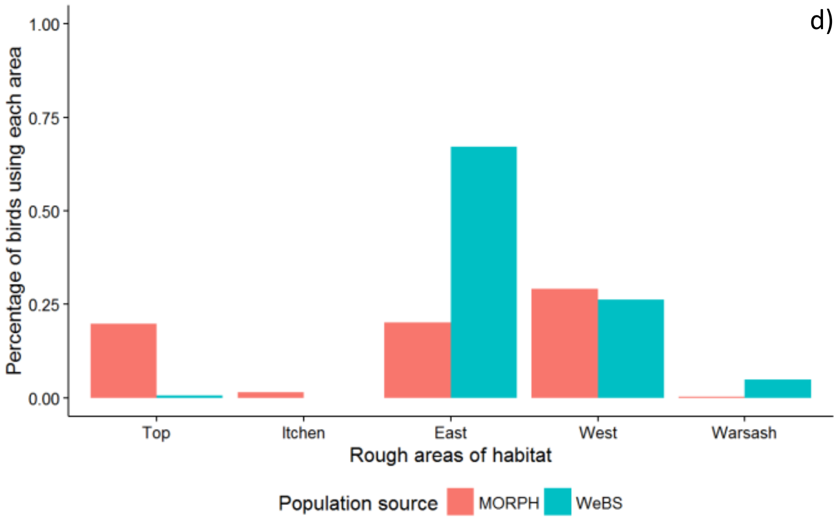

h)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Midup
Midlower
South
Rough areas of habitat
Population source
MORPH
WeBS

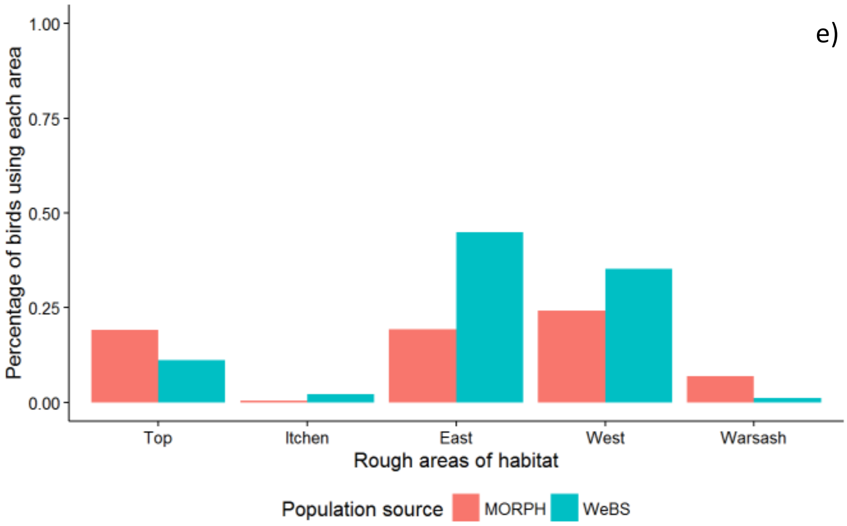


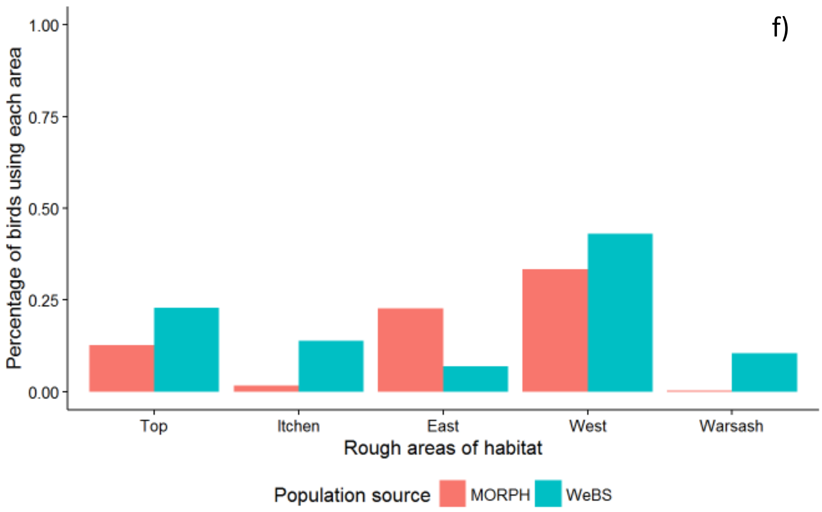
Figures A8.5 a-g. Percentage of each species using 'rough' areas of ***Southampton Water****: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)oystercatcher, f)redshank and g)turnstone.*

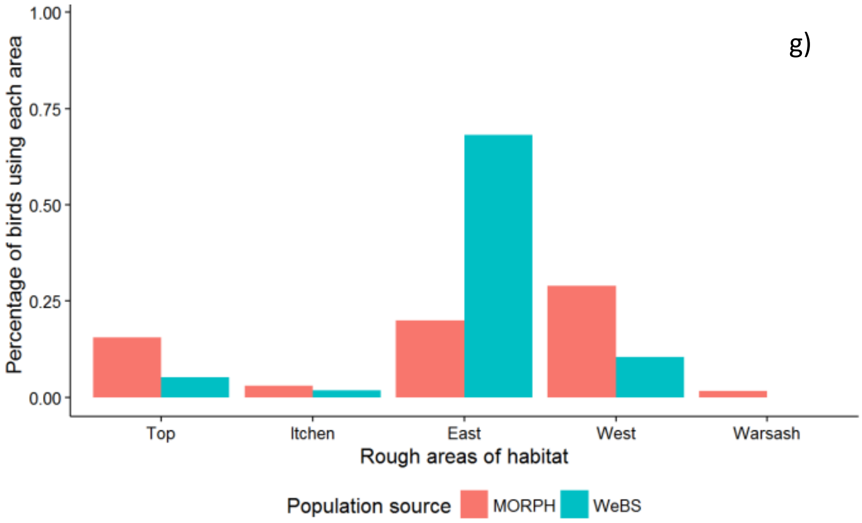



c)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Itchen
East
West
Warsash
Rough areas of habitat
Population source
MORPH
WeBS


d)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Itchen
East
West
Warsash
Rough areas of habitat
Population source
MORPH
WeBS

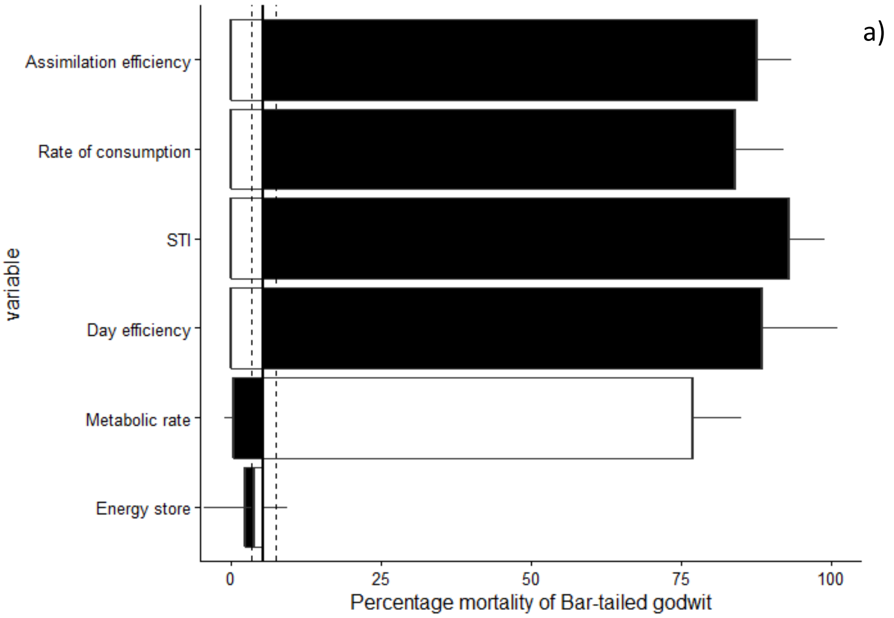

e)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Itchen
East
West
Warsash
Rough areas of habitat
Population source
MORPH
WeBS

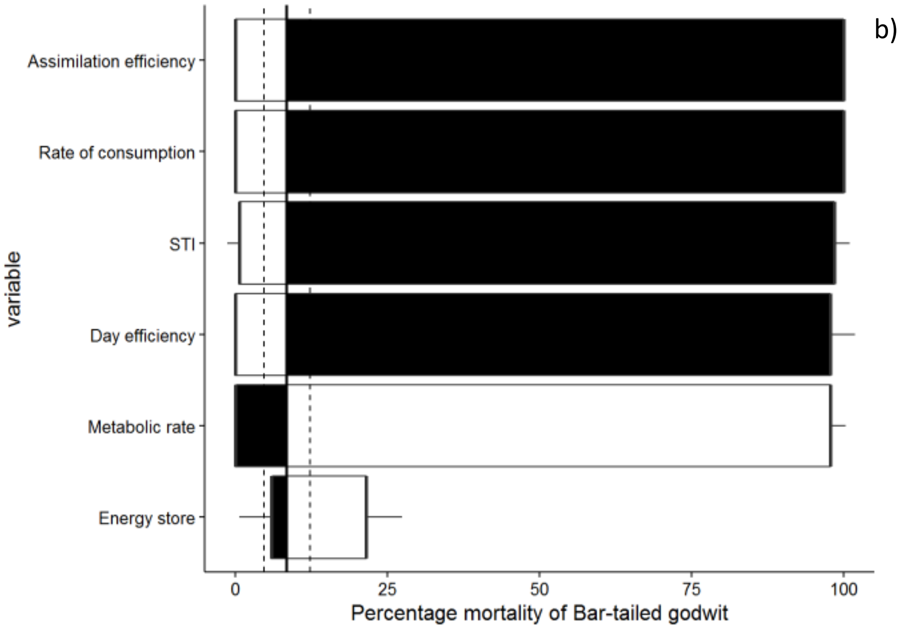

f)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Itchen
East
West
Warsash
Rough areas of habitat
Population source
MORPH
WeBS

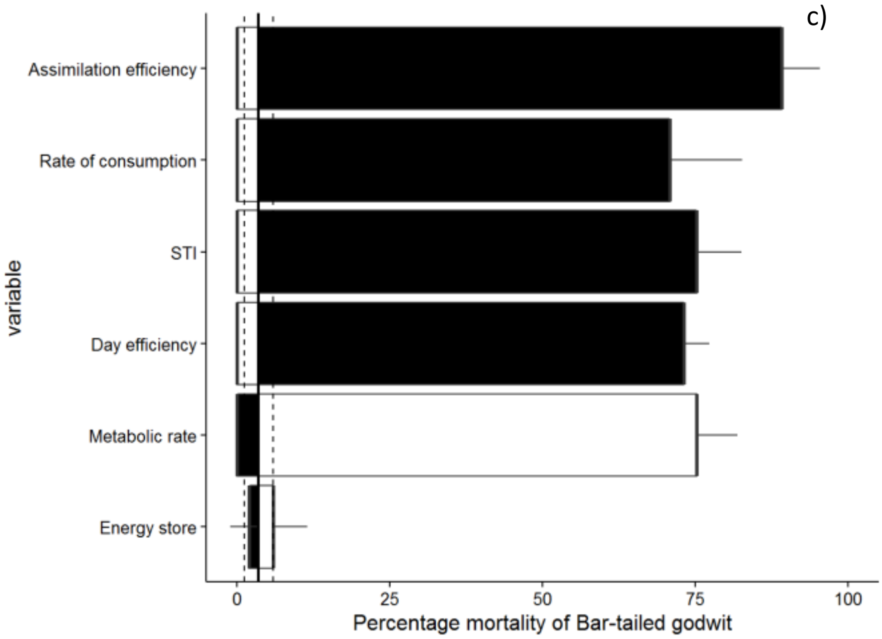

g)
Percentage of birds using each area
1.00
0.75
0.50
0.25
0.00
Top
Itchen
East
West
Warsash
Rough areas of habitat
Population source
MORPH
WeBS

Appendix 9 Sensitivity analysis of wading birds IBMs

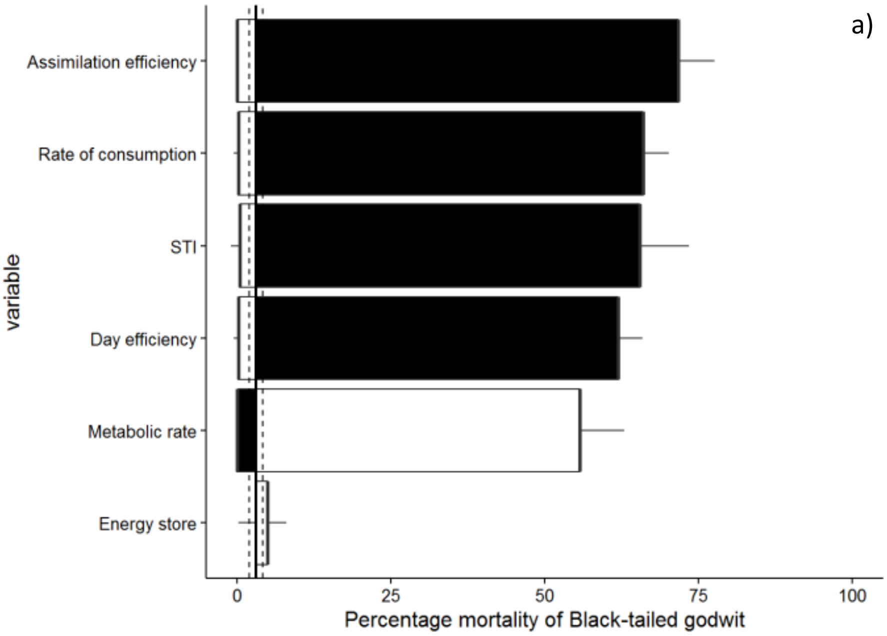
Figures A9.1. Sensitivity analysis for percentage mortality of ***bar-tailed godwit*** *on the a) Exe estuary, b) Humber and c) Poole Harbour*

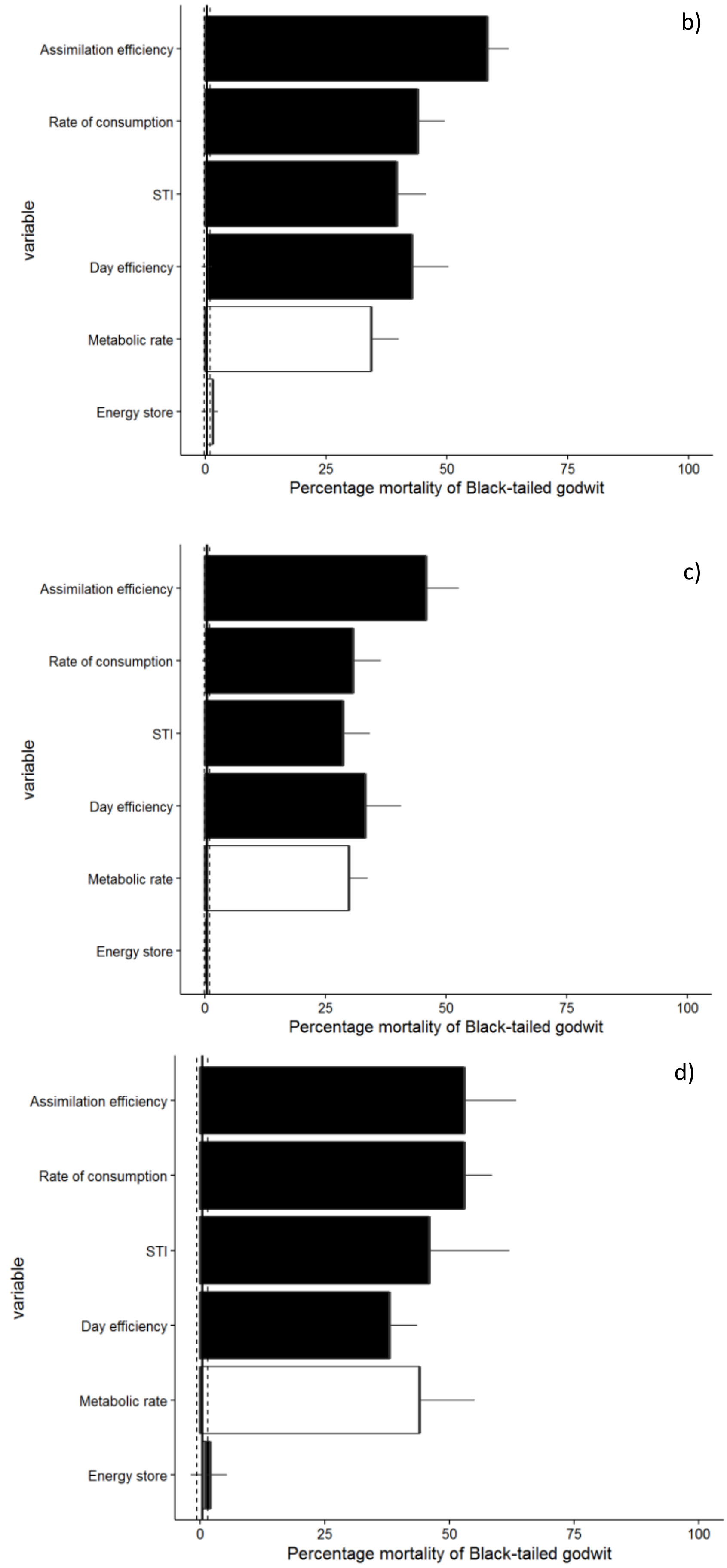


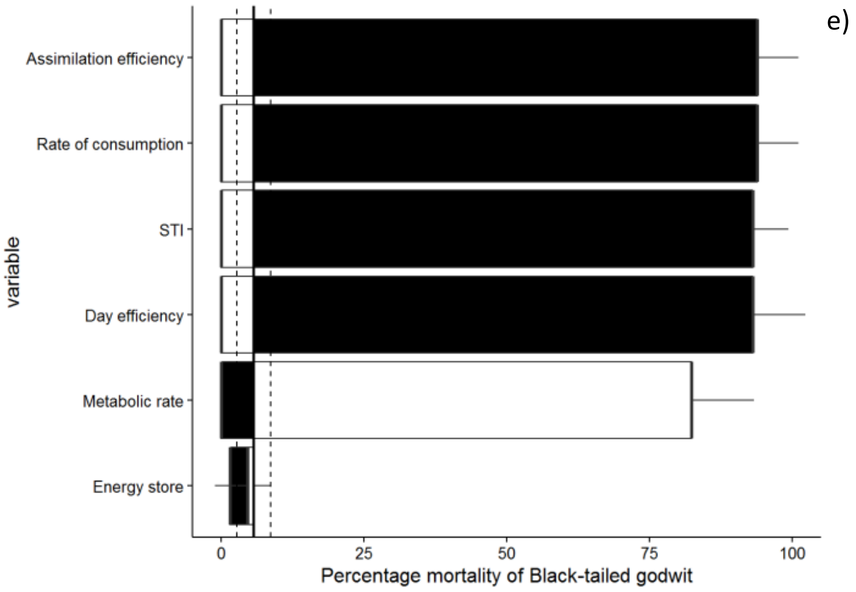




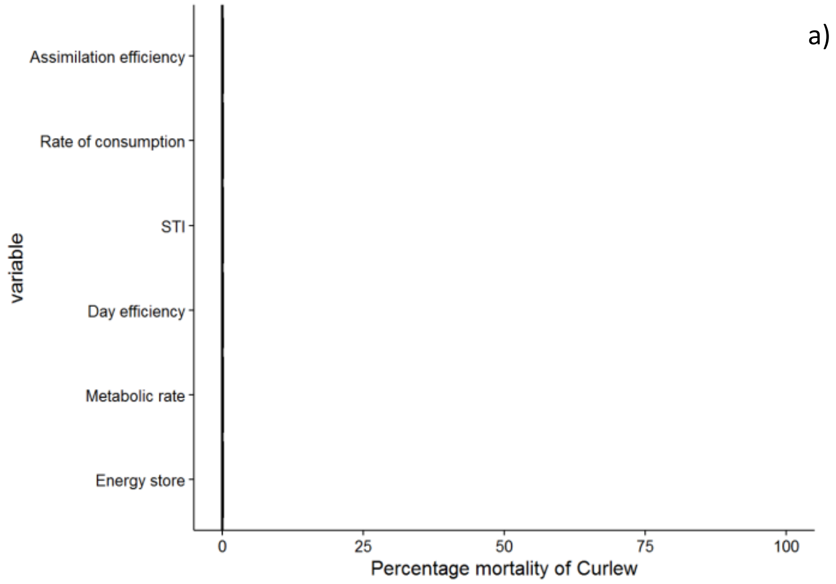
*Figures A9.2. Sensitivity analysis for percentage mortality of **black-tailed godwit** on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*

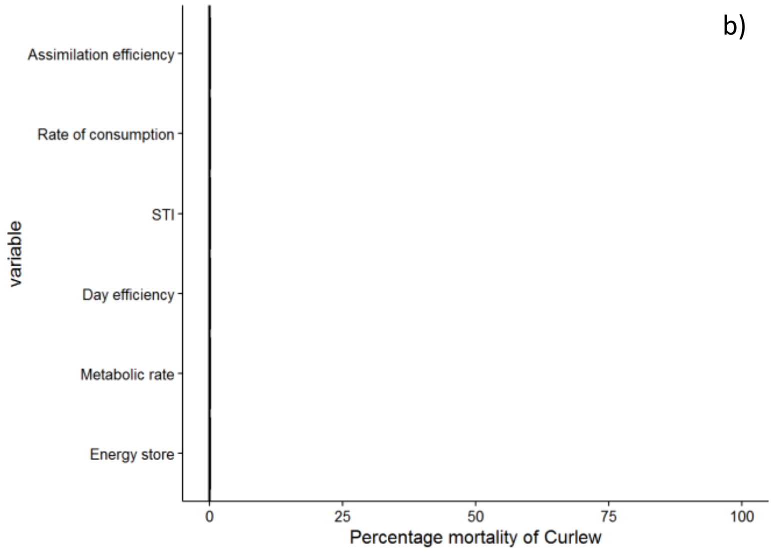


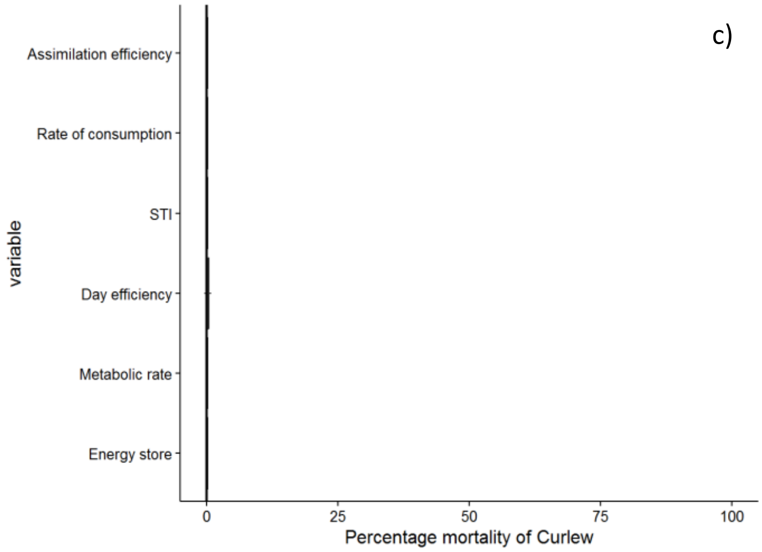

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Black-tailed godwit
c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Black-tailed godwit
d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Black-tailed godwit

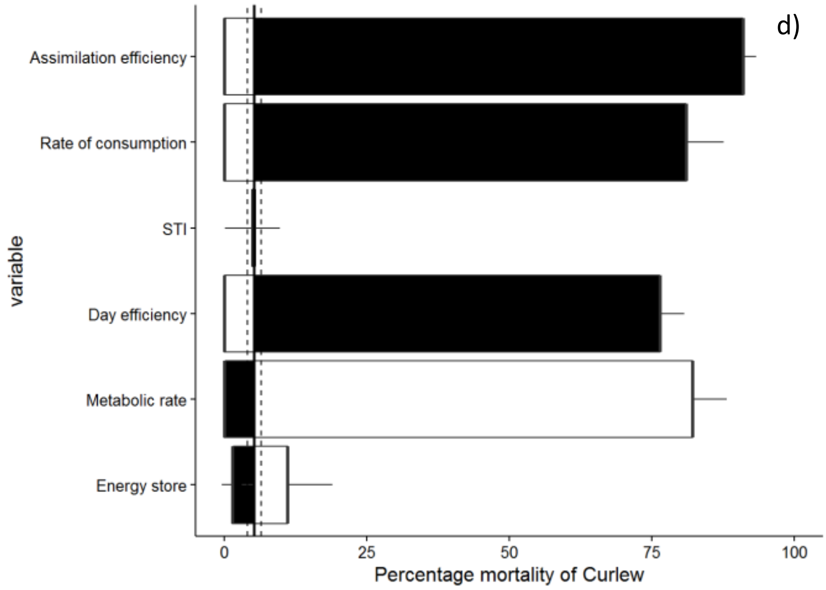


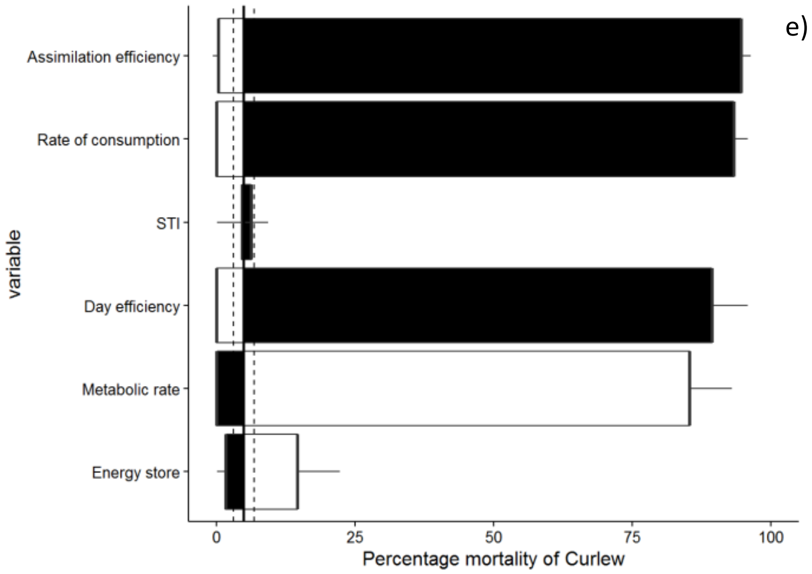
Figures A9.3. Sensitivity analysis for percentage mortality of ***curlew*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



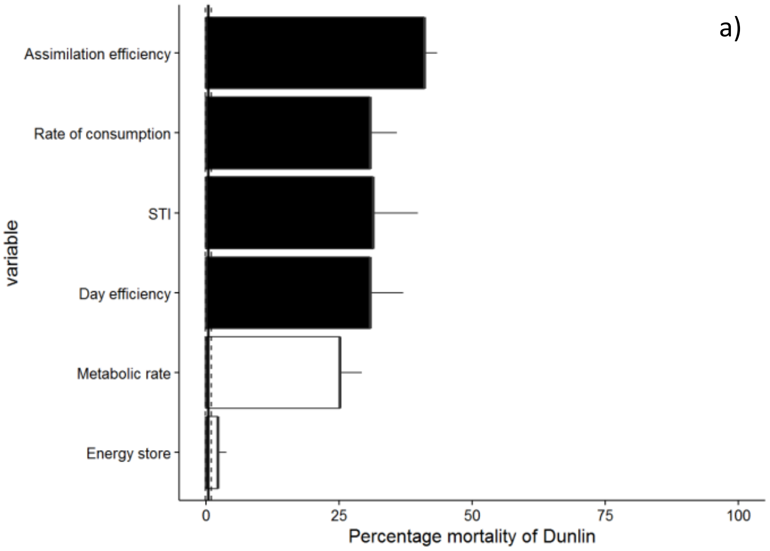

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Curlew

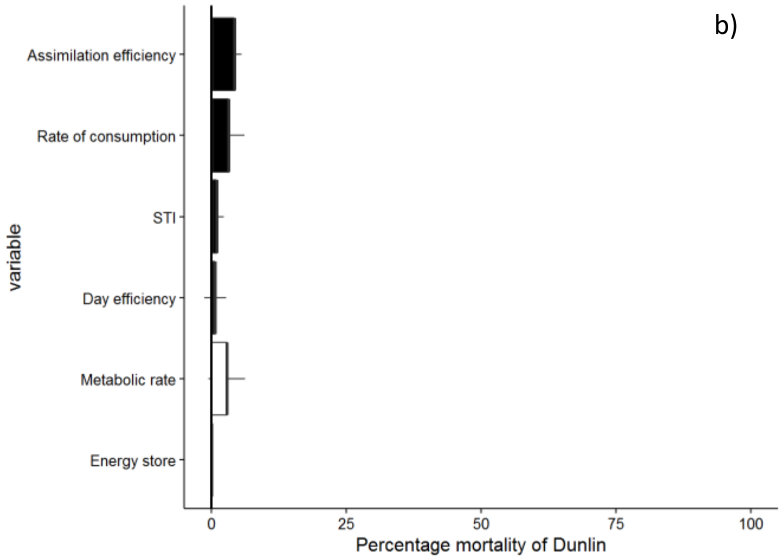

c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Curlew

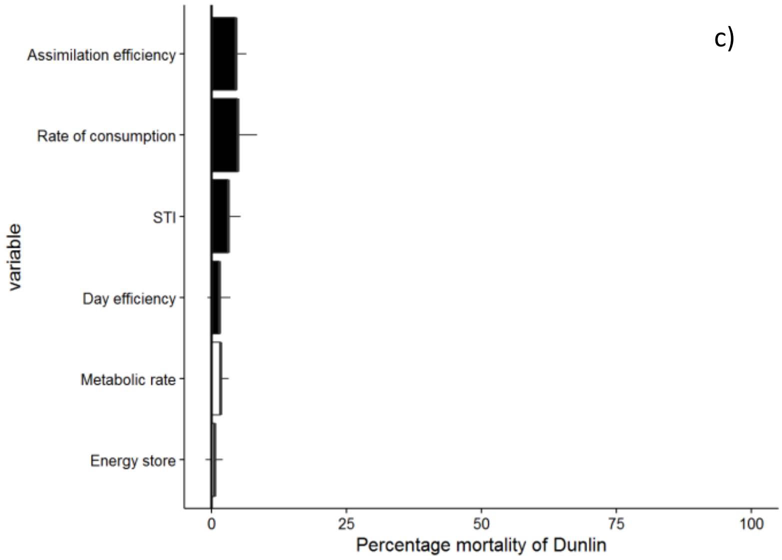

d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Curlew

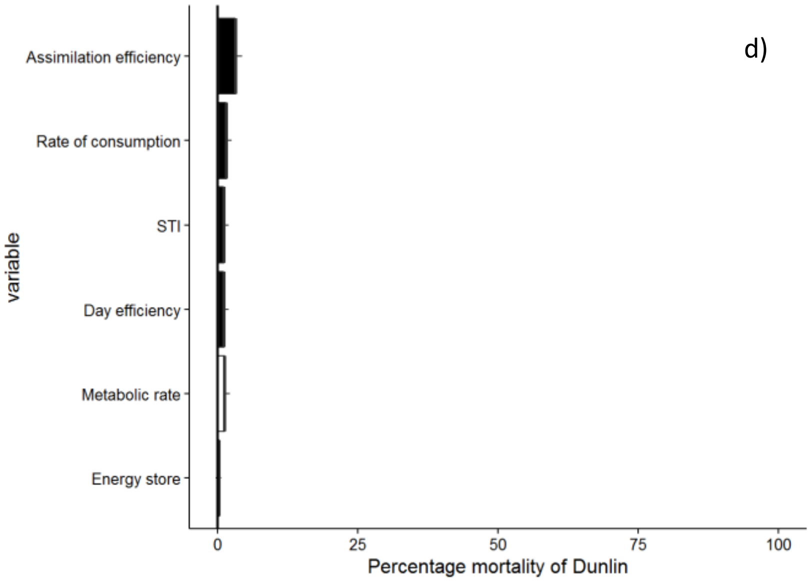


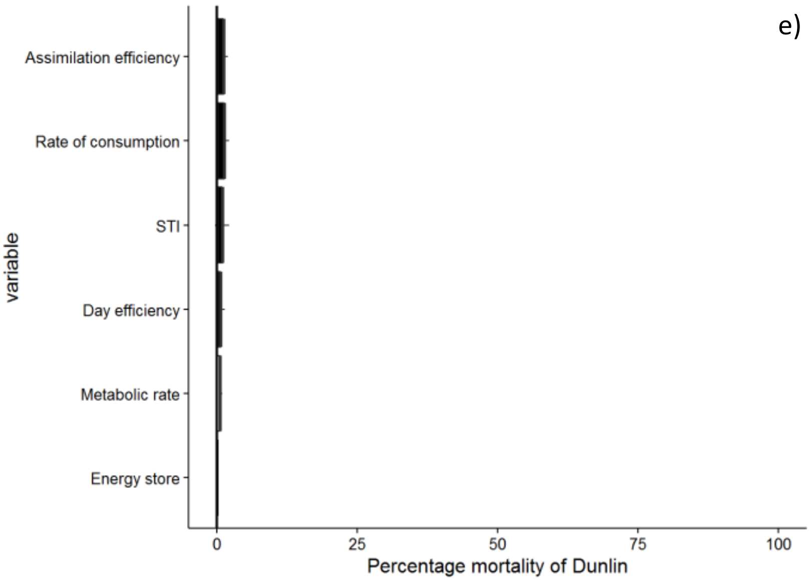
Figures A9.4. Sensitivity analysis for percentage mortality of ***dunlin*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



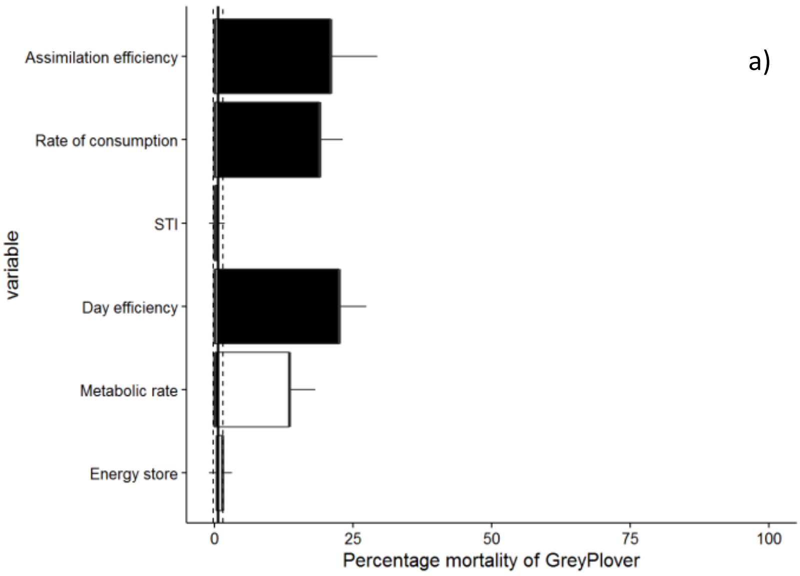

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Dunlin

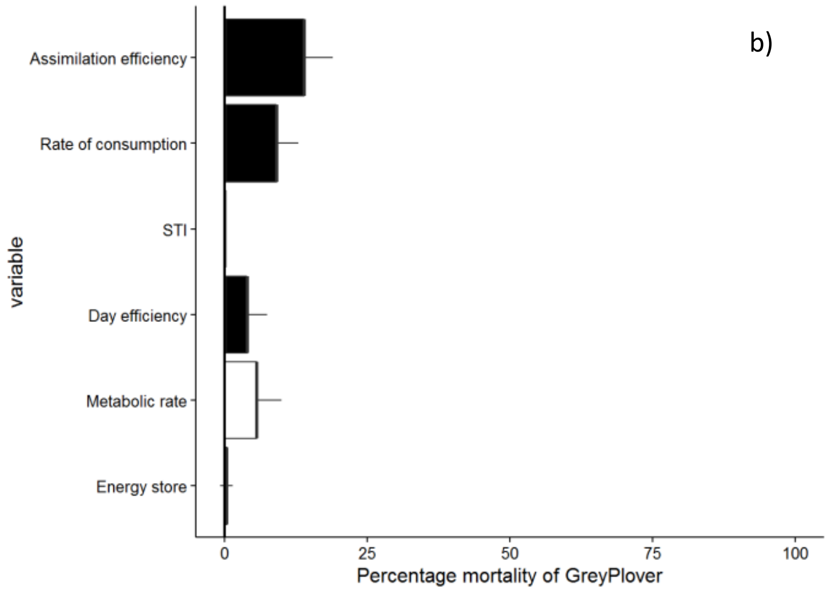

c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Dunlin

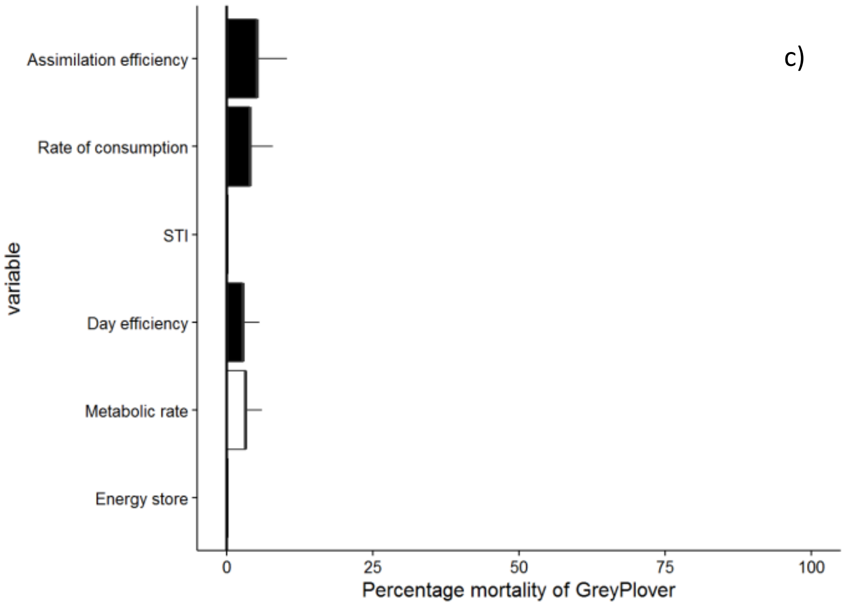

d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Dunlin

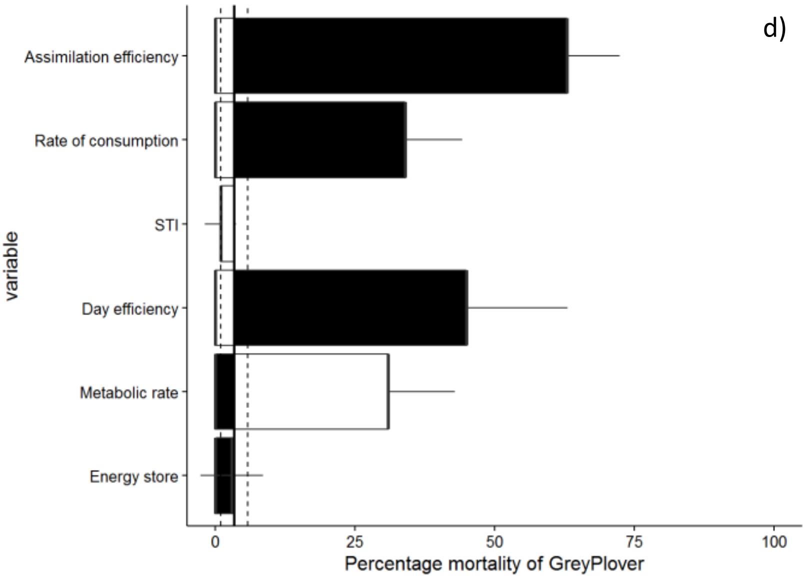


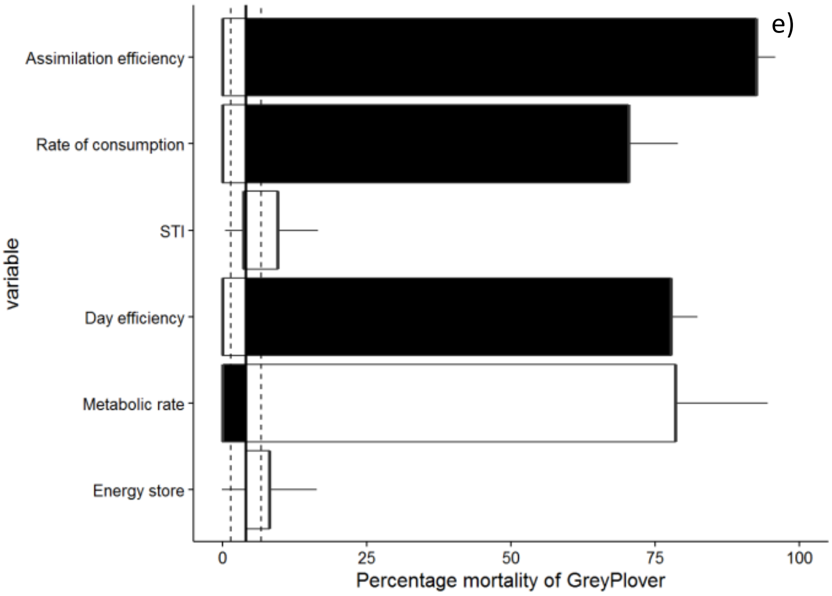
Figures A9.5. Sensitivity analysis for percentage mortality of ***grey plover*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



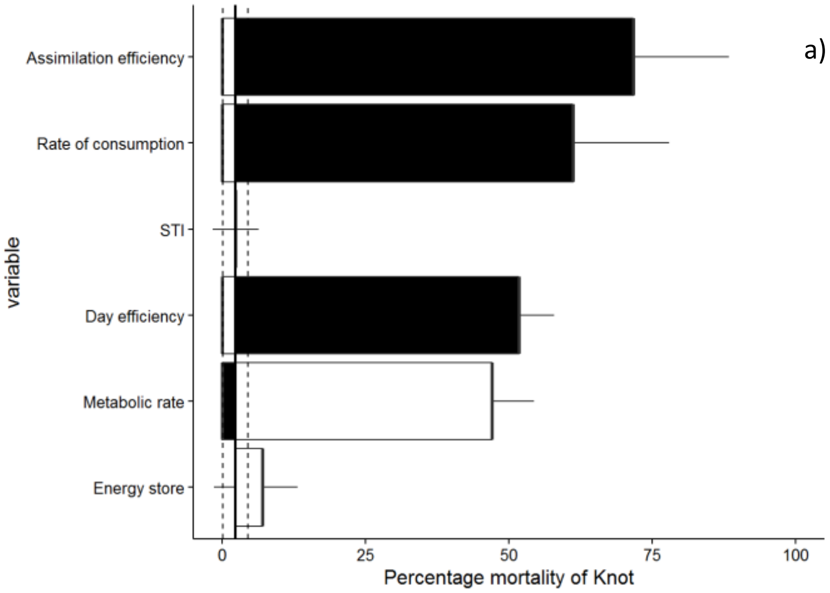

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of GreyPlover

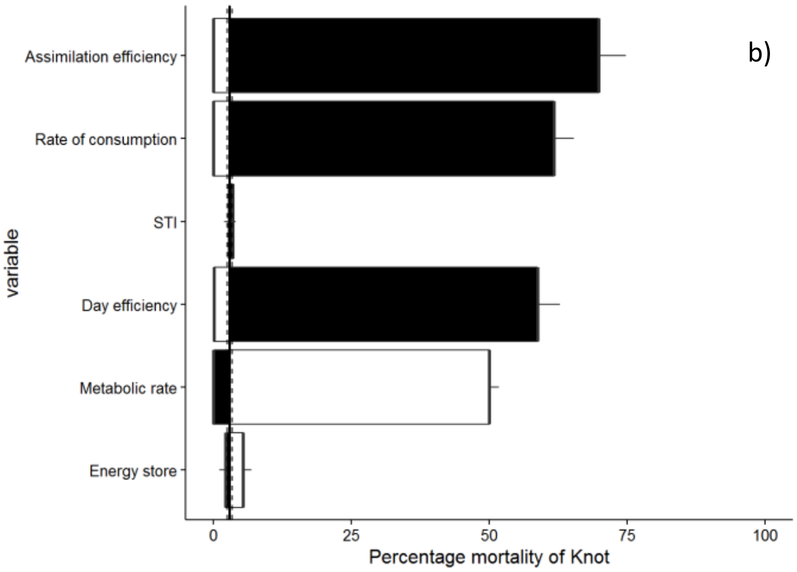

c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of GreyPlover


d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of GreyPlover

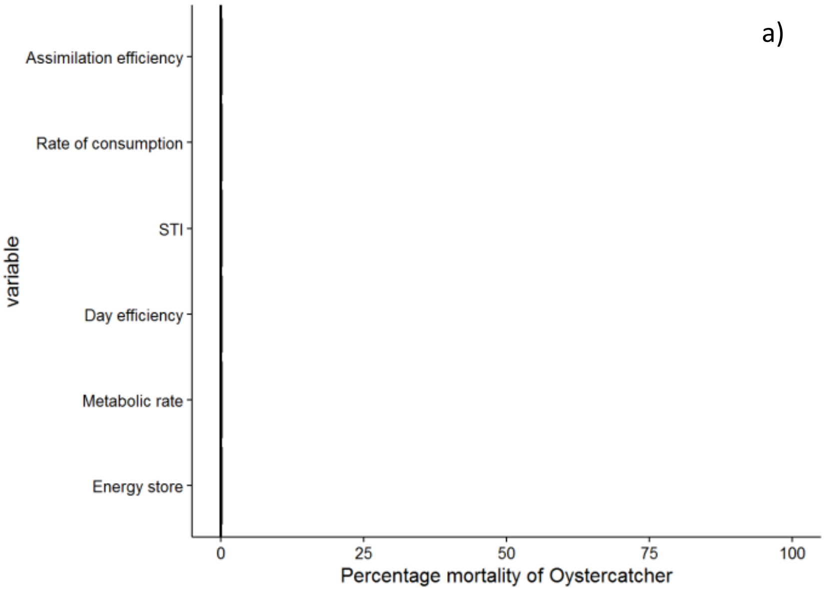


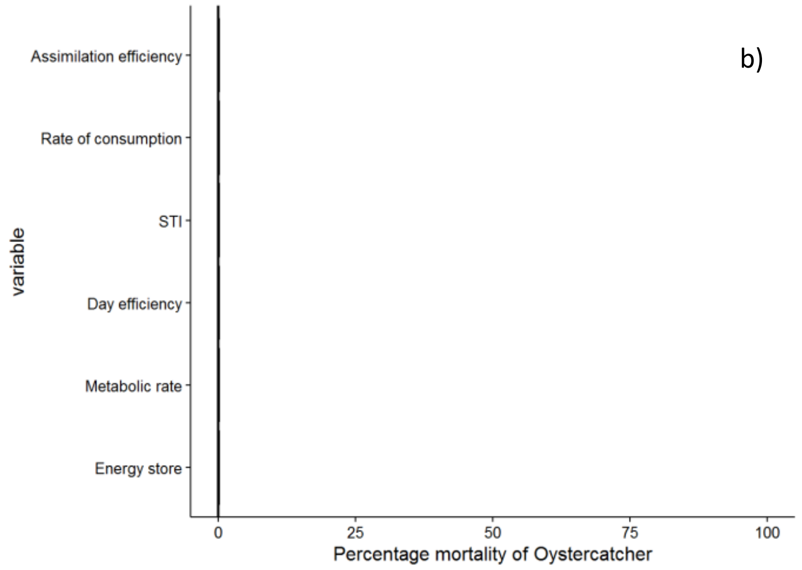
Figures A9.6. Sensitivity analysis for percentage mortality of ***knot*** *on the a) Severn estuary and b) the Humber*

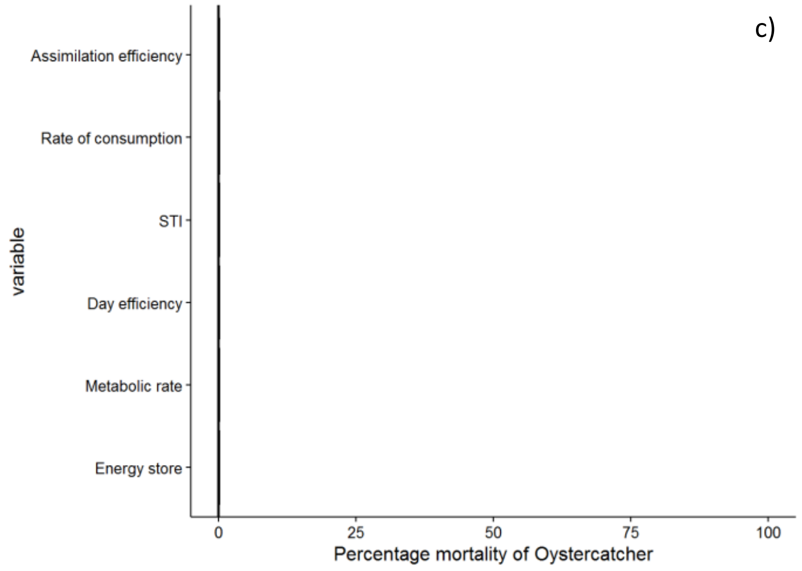


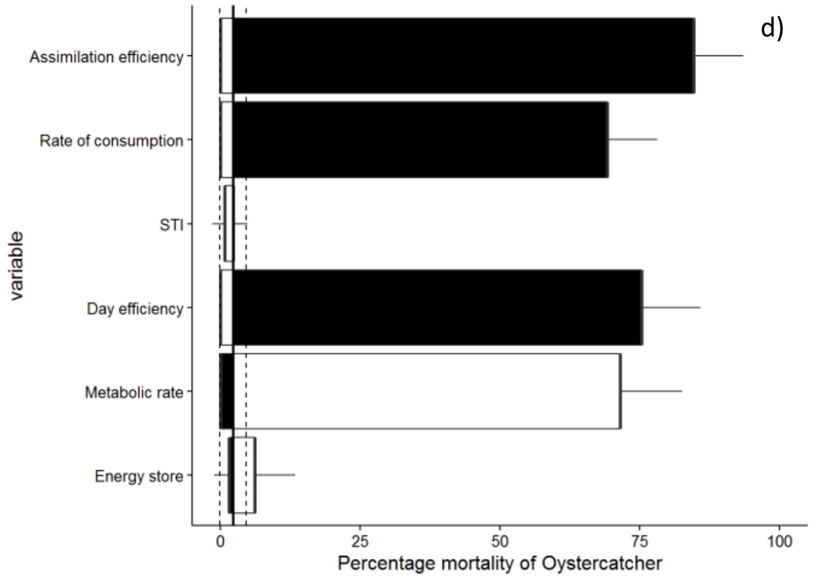


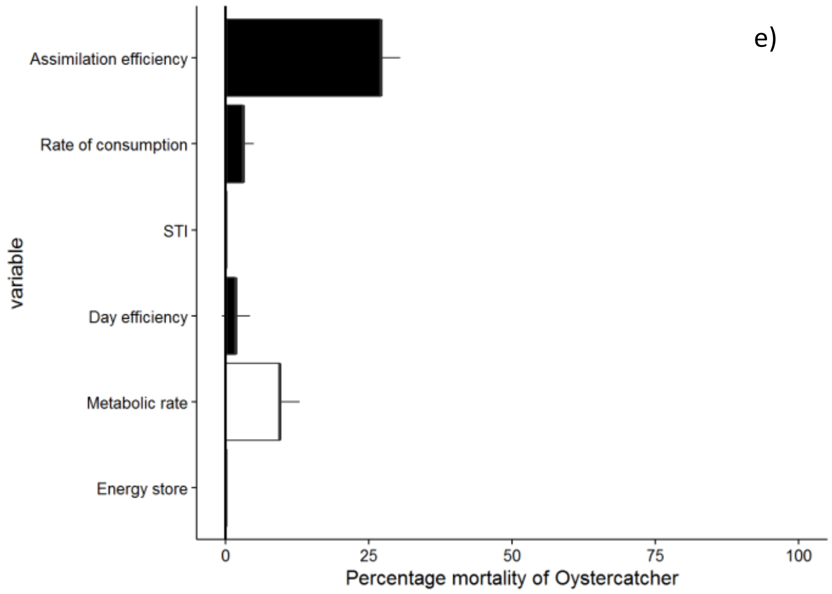
Figures A9.7. Sensitivity analysis for percentage mortality of ***oystercatcher*** *on a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



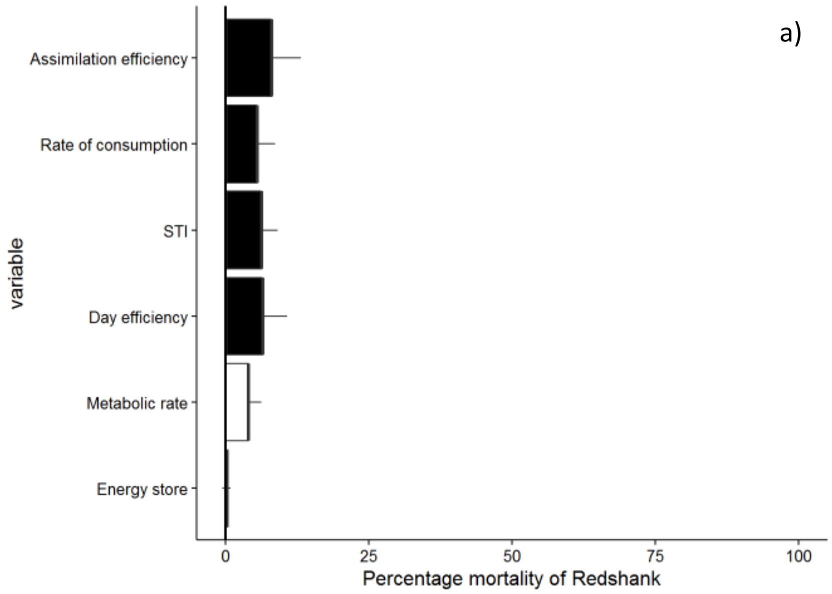

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Oystercatcher

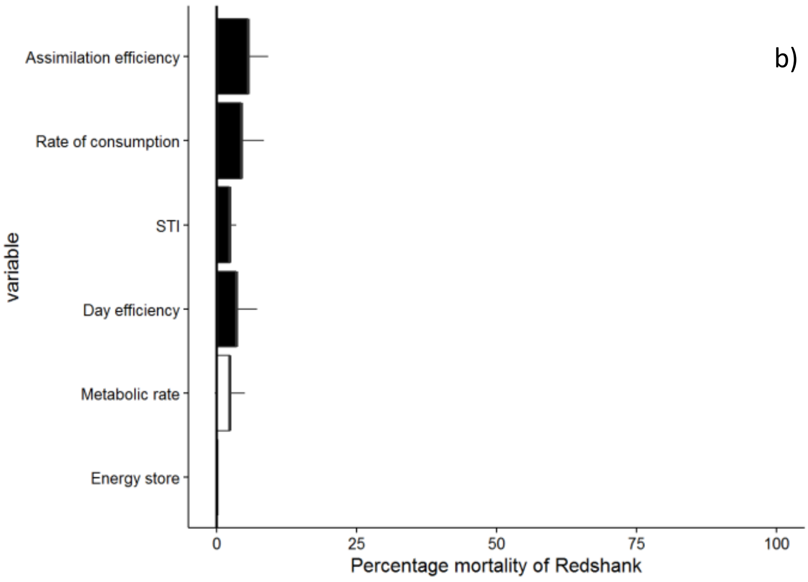

c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Oystercatcher

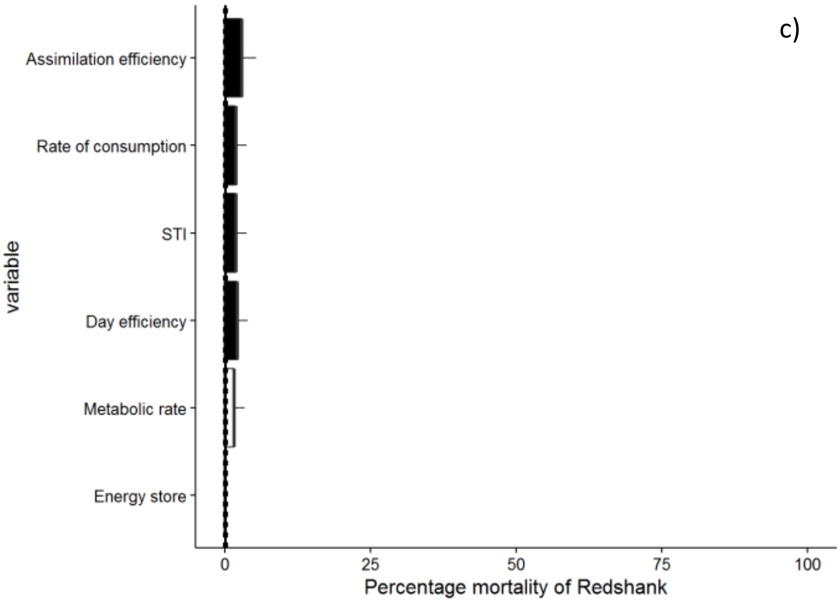

d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Oystercatcher

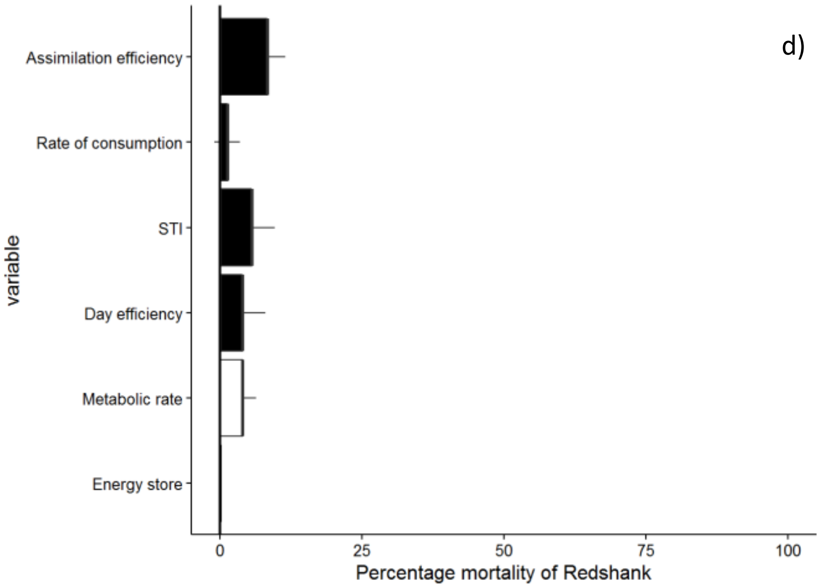


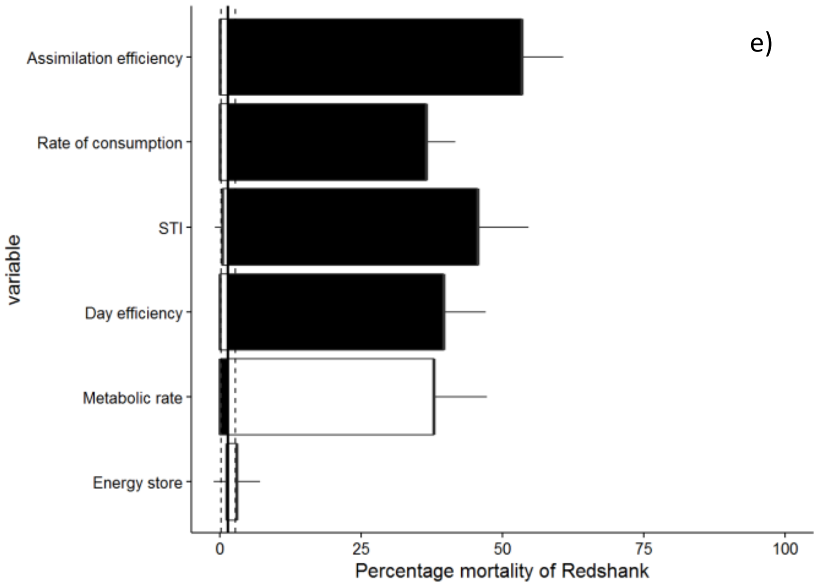
Figures A9.8. Sensitivity analysis for percentage mortality of ***redshank*** *on a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



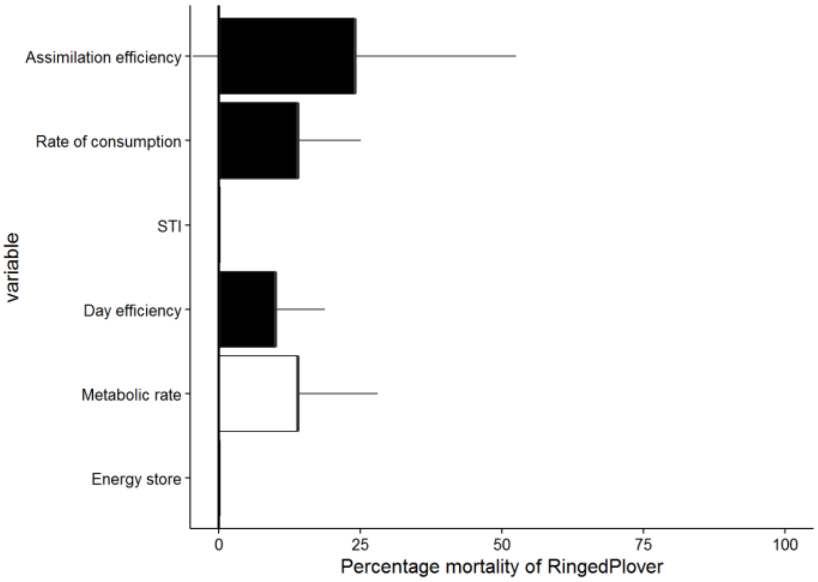

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Redshank


c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Redshank

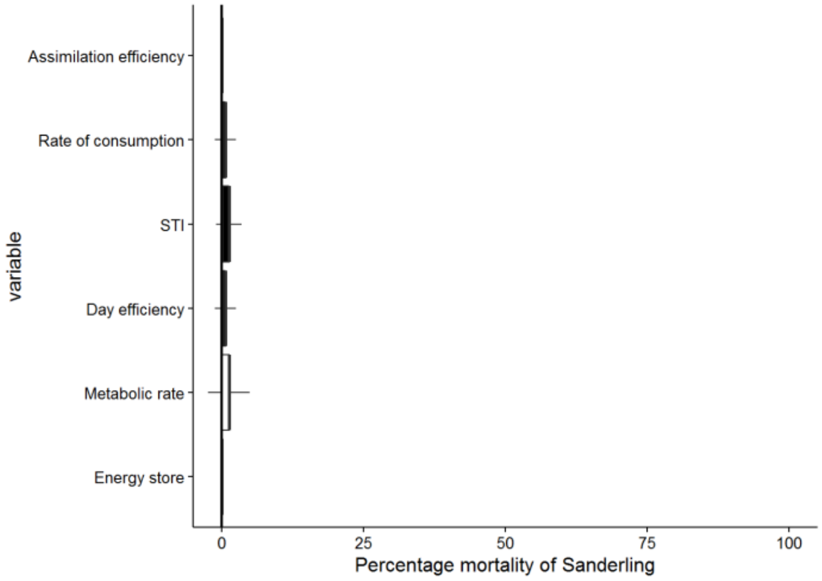

d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Redshank



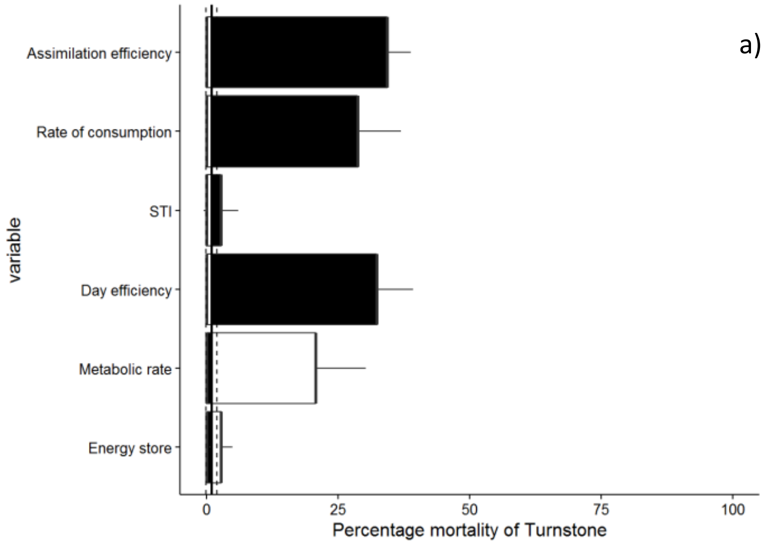
Figures A9.9 Sensitivity analysis for percentage mortality of ***ringed plover*** *on the Severn estuary*

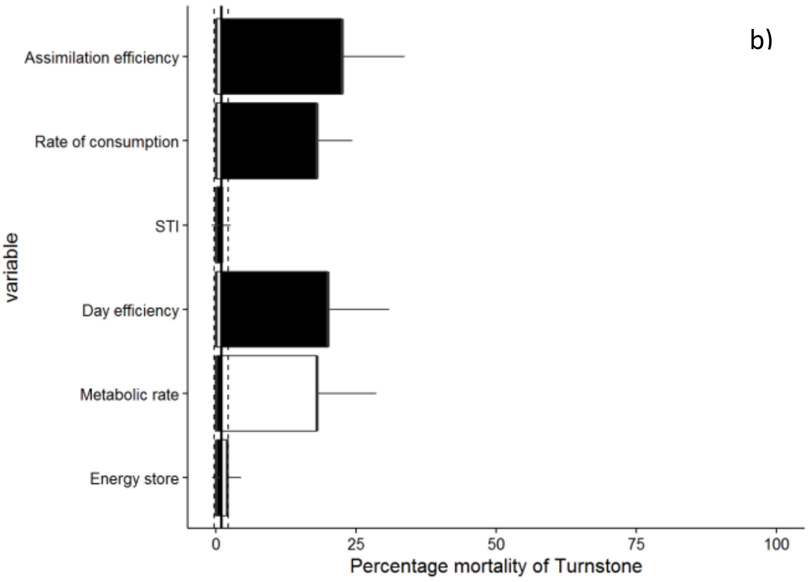


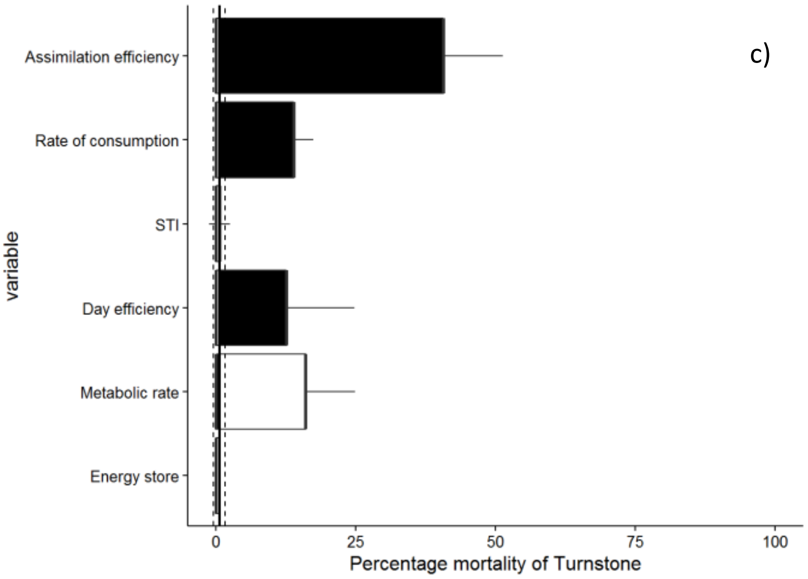
Figures A9.10. Sensitivity analysis for percentage mortality of ***sanderling*** *on the Humber*

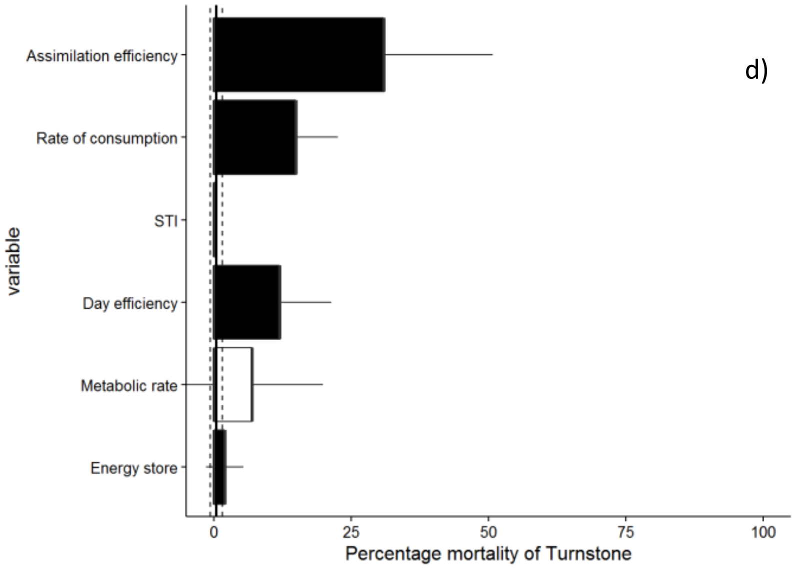


Figures A9.11. Sensitivity analysis for percentage mortality of ***turnstone*** *on the a) Exe estuary, b) Southampton water, c) Severn estuary and d) the Humber*



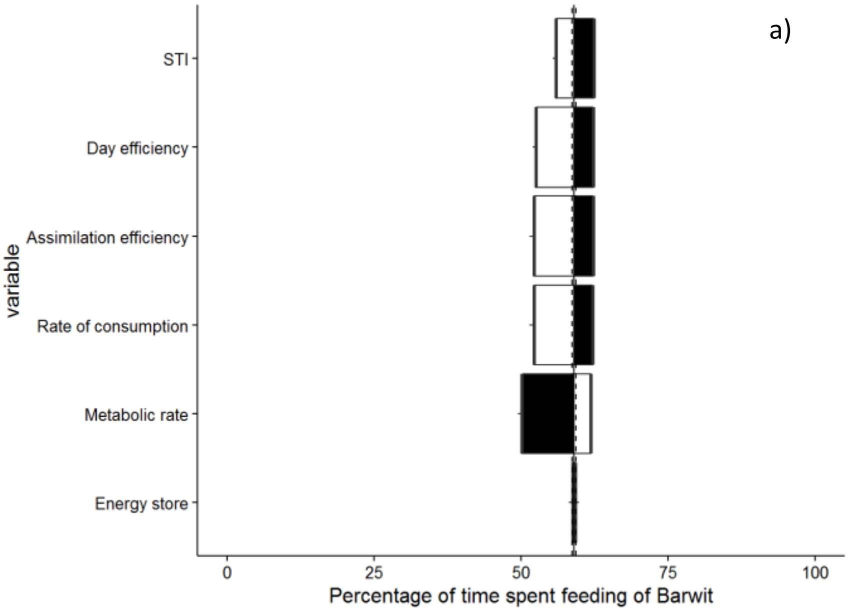

b)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Turnstone

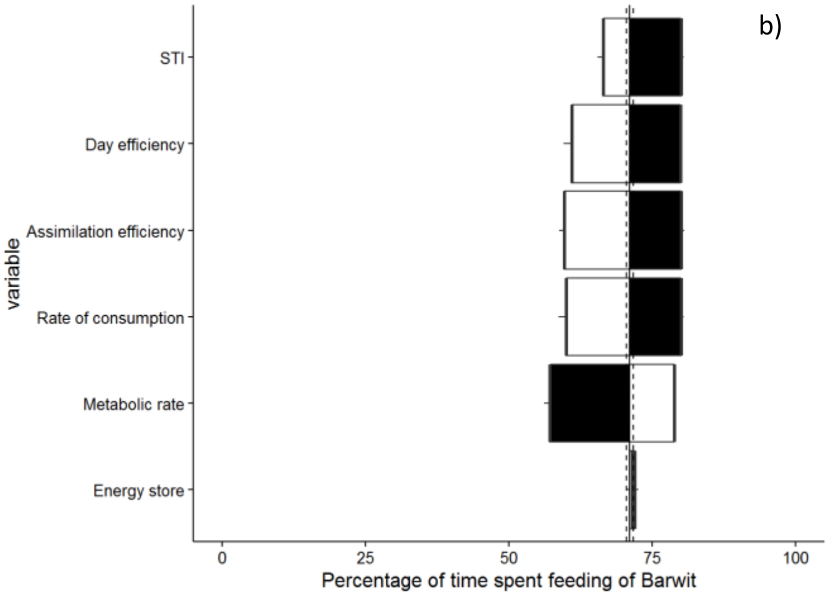

c)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Turnstone

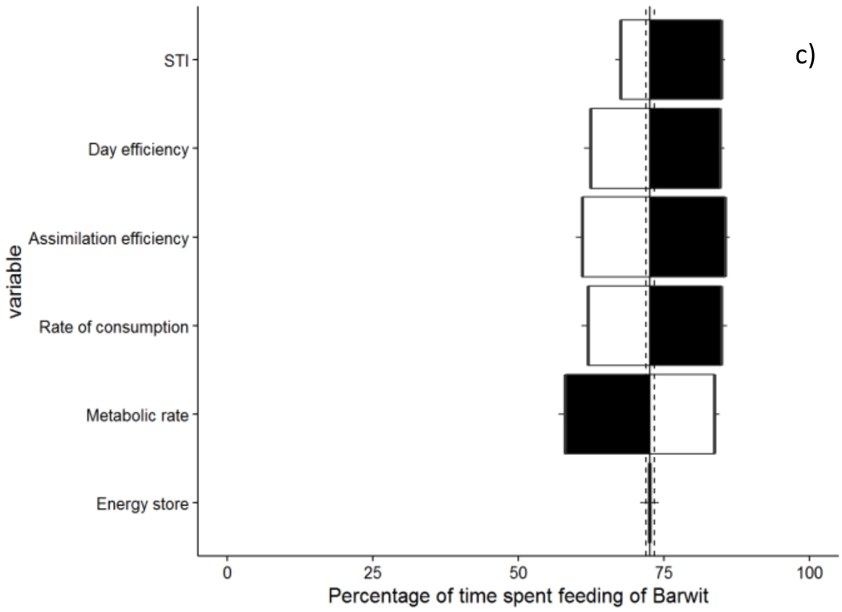

d)
variable
Assimilation efficiency
Rate of consumption
STI
Day efficiency
Metabolic rate
Energy store
0
25
50
75
100
Percentage mortality of Turnstone

Sensitivity analysis for Proportion of time spent feeding

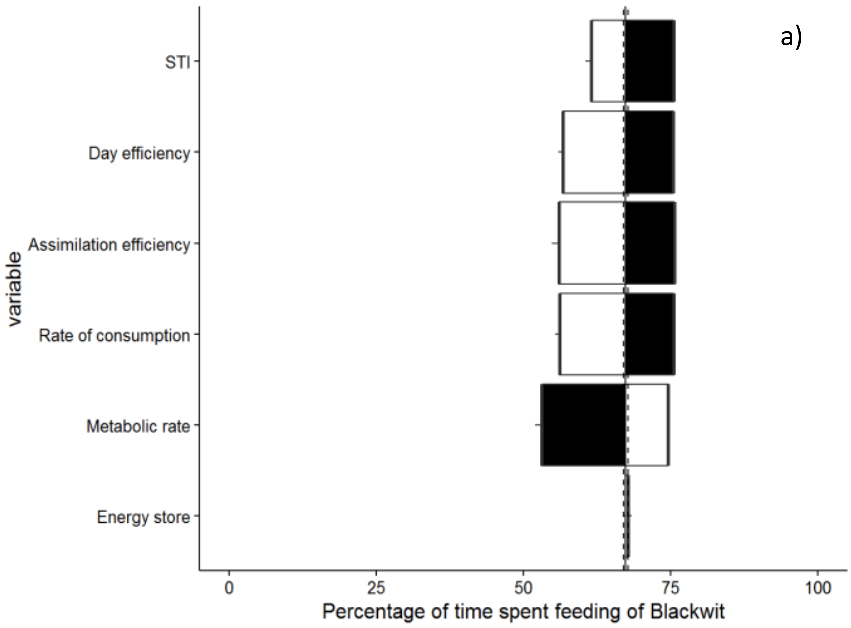
Figures A9.12. Sensitivity analysis for percentage of time spent feeding of ***bar-tailed godwit*** *on the a) Exe estuary, b) Humber and c) Poole Harbour*

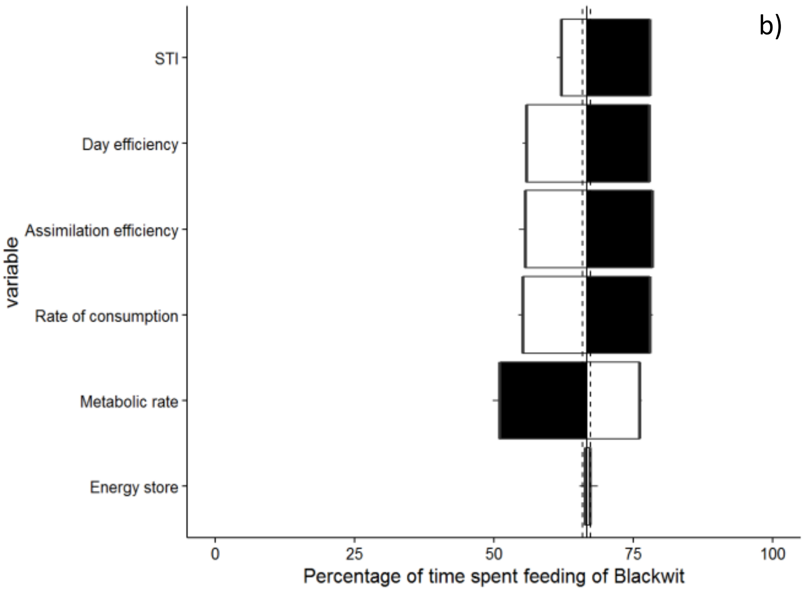


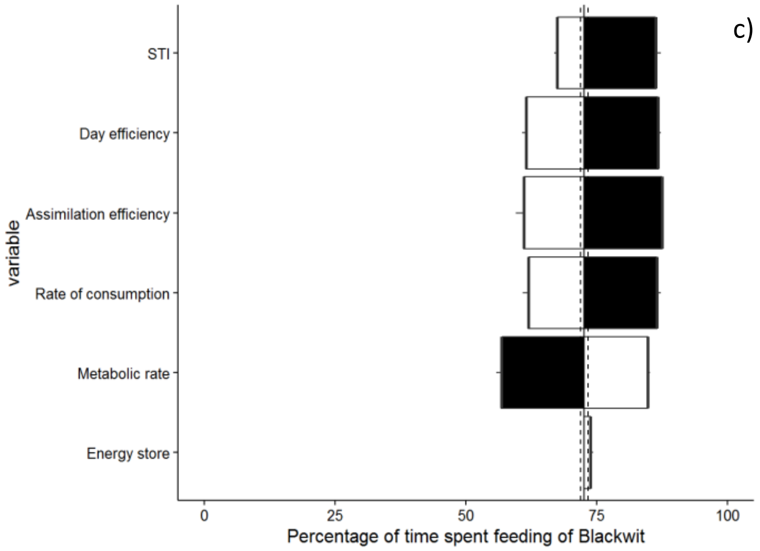


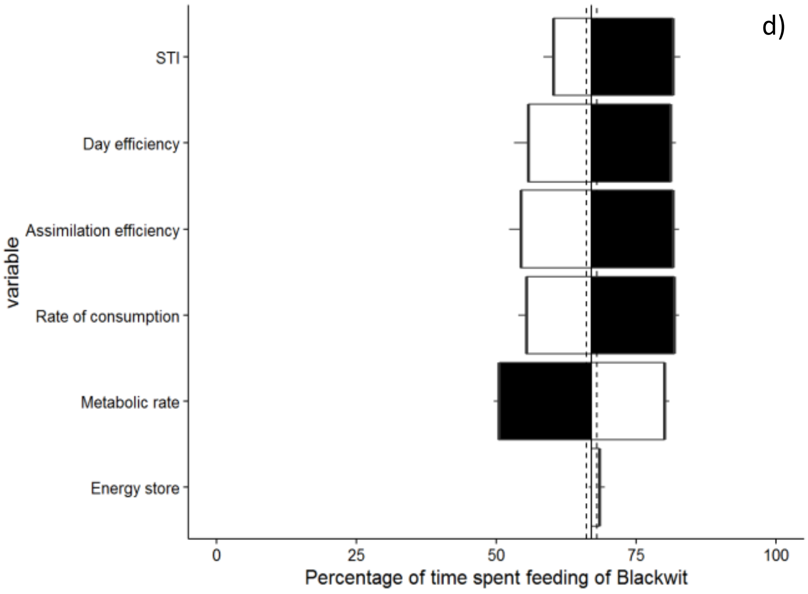


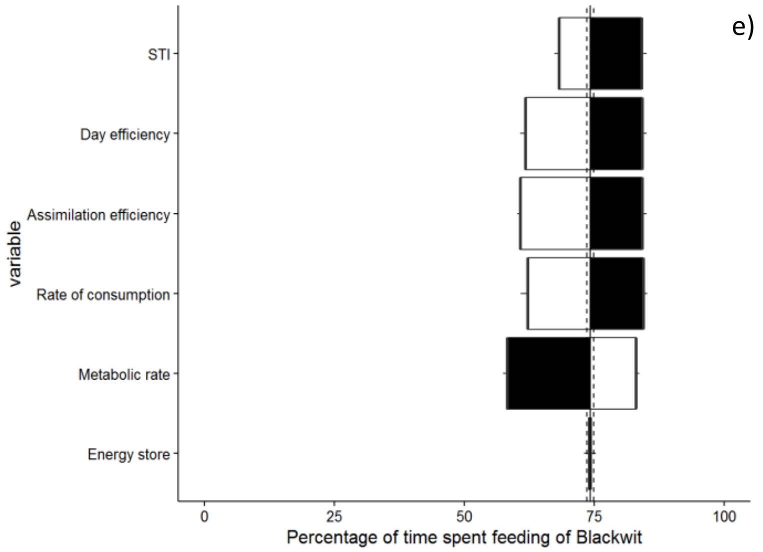
Figures A9.13. Sensitivity analysis for percentage of time spent feeding of ***black-tailed godwit*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



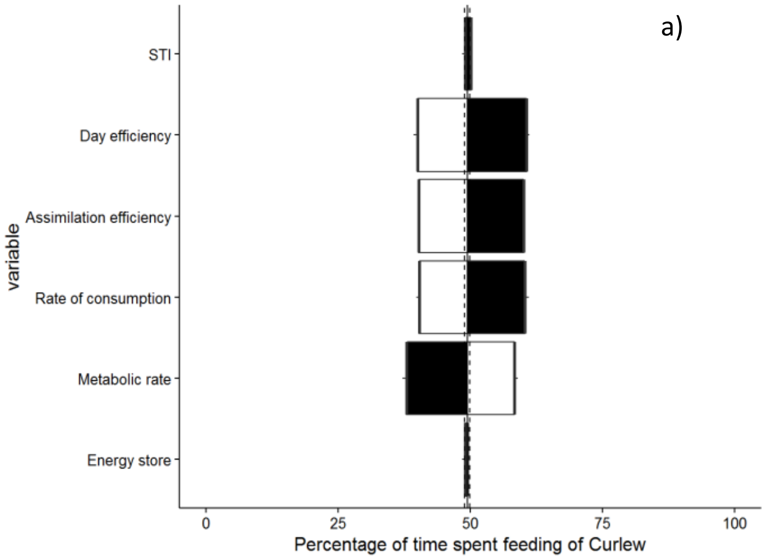

b)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Blackwit

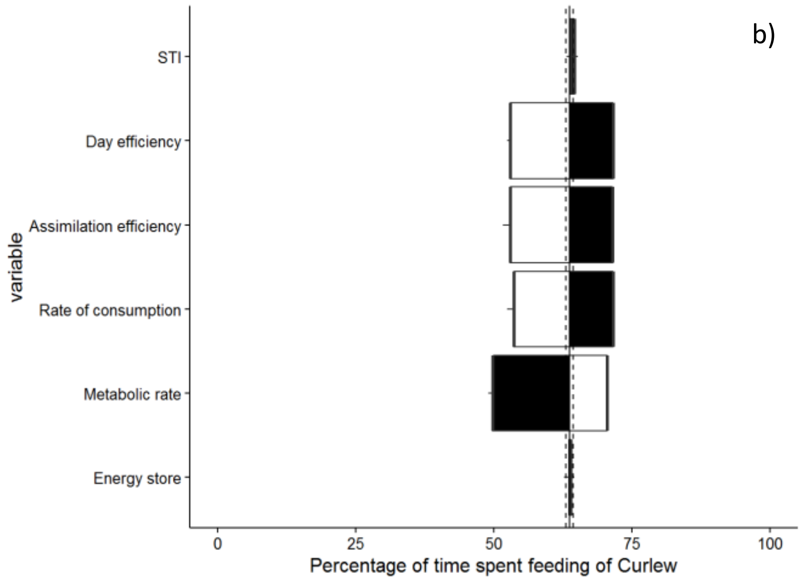

c)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Blackwit

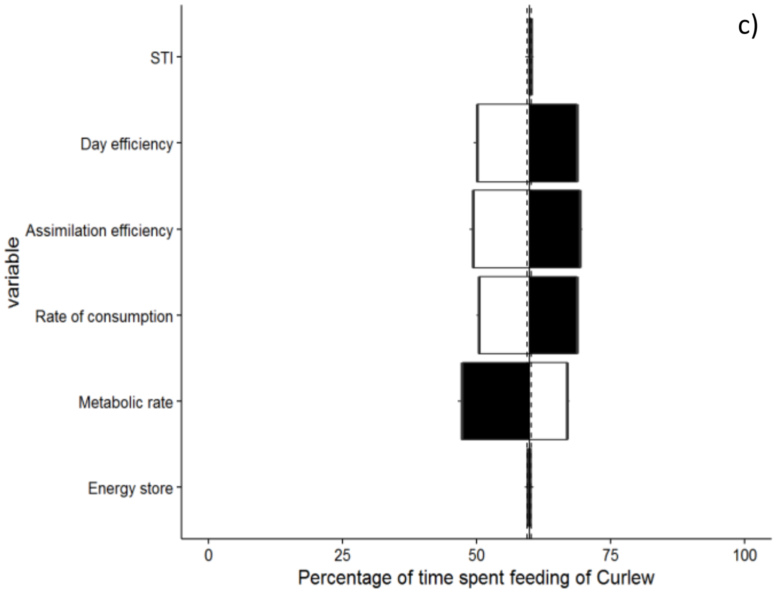

d)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Blackwit

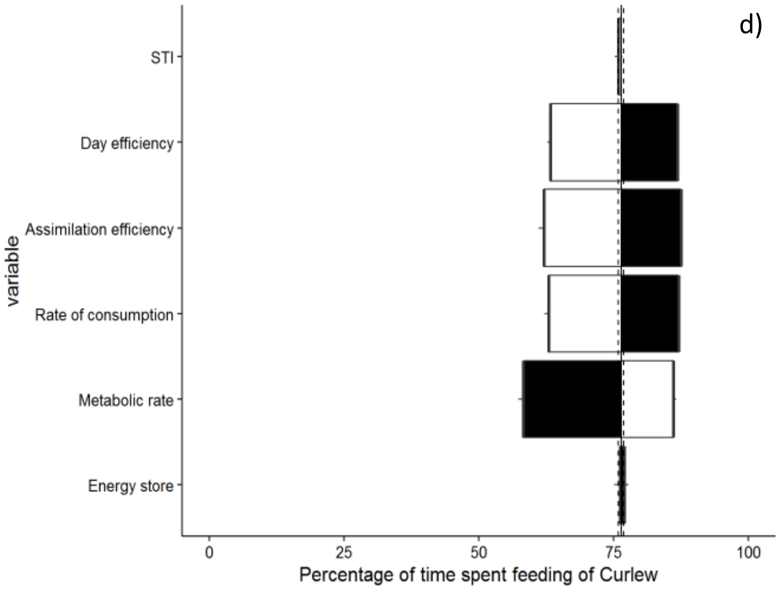


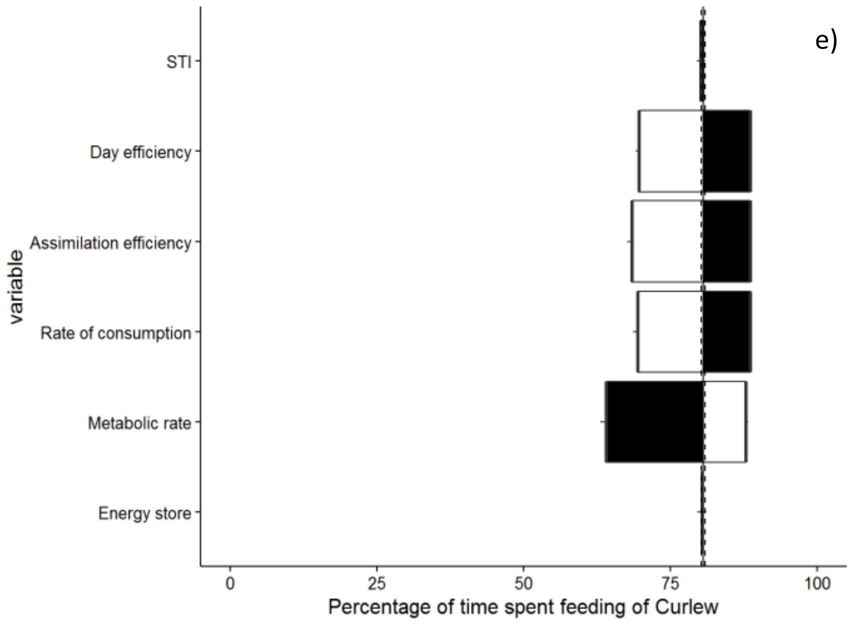
Figures A9.14. Sensitivity analysis for percentage of time spent feeding of ***curlew*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



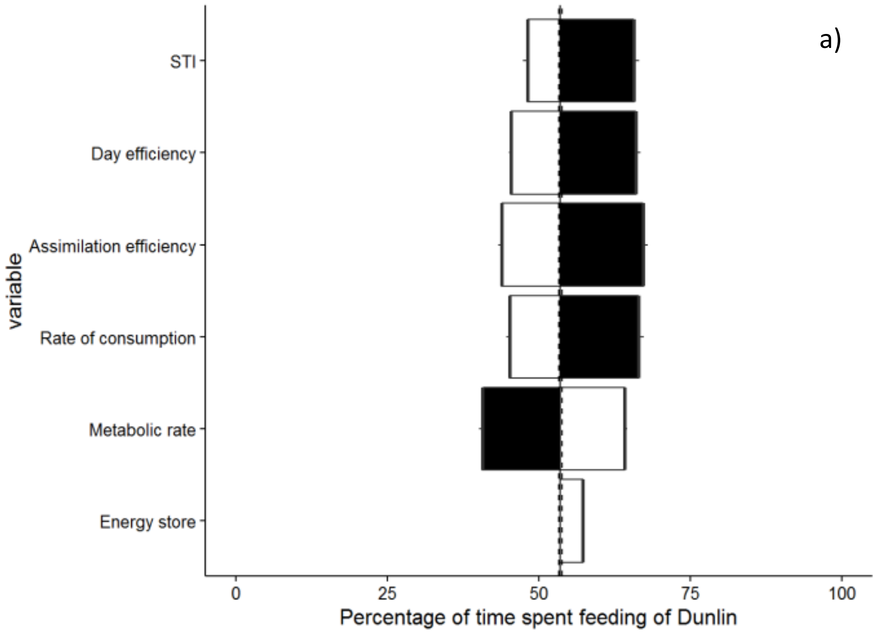

b)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Curlew

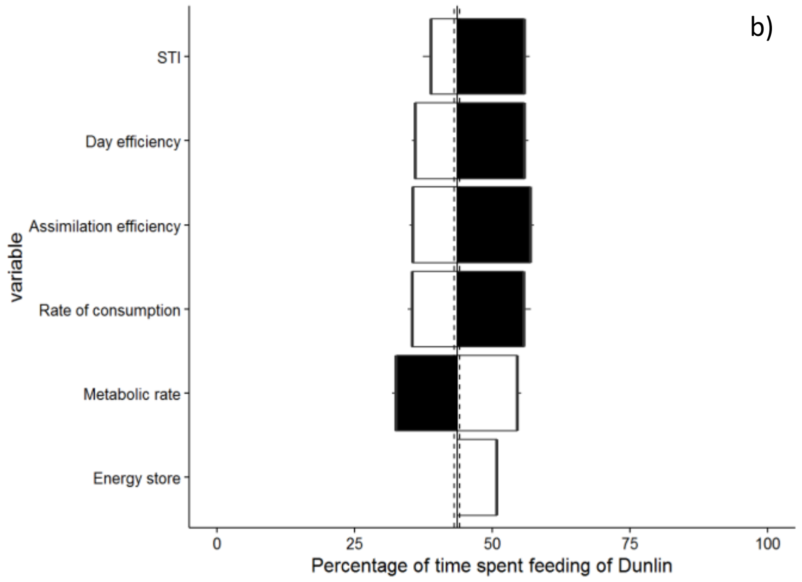

c)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Curlew

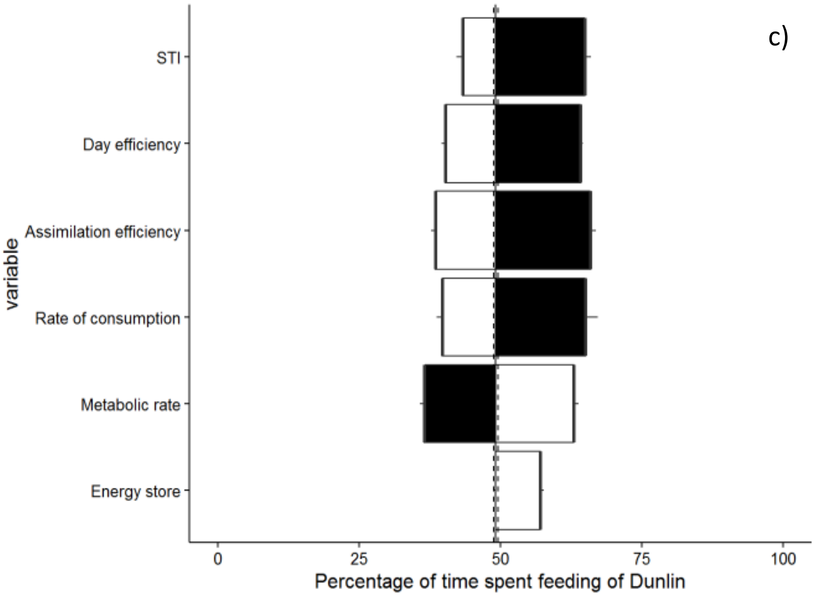

d)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Curlew

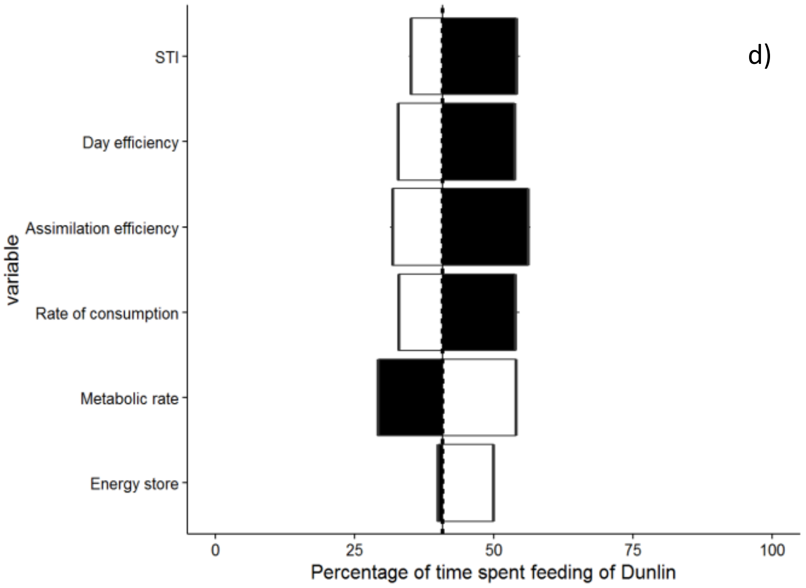


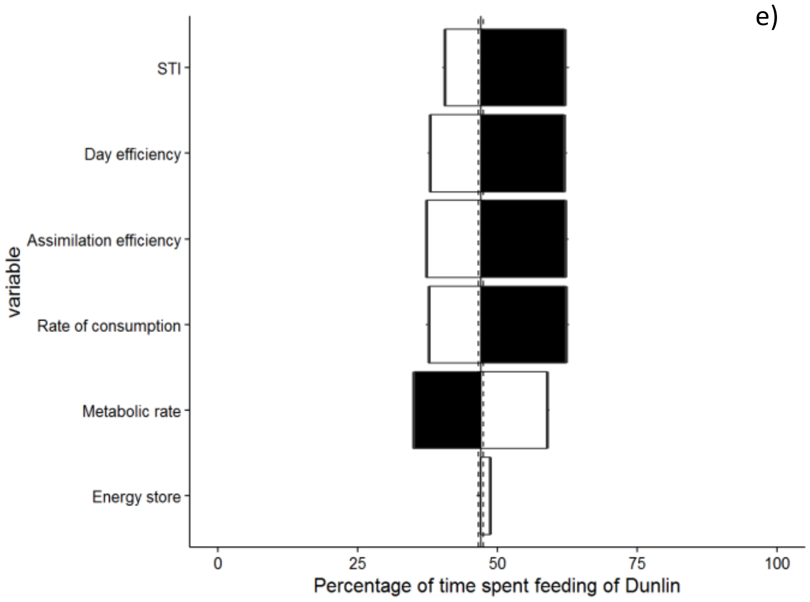
Figures A9.15. Sensitivity analysis for percentage of time spent feeding of ***dunlin*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



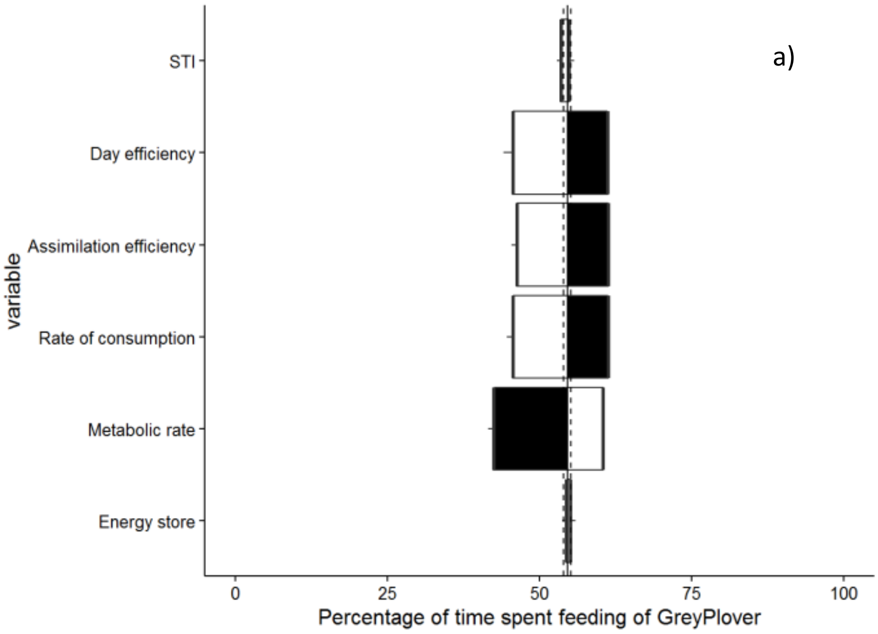

b)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Dunlin

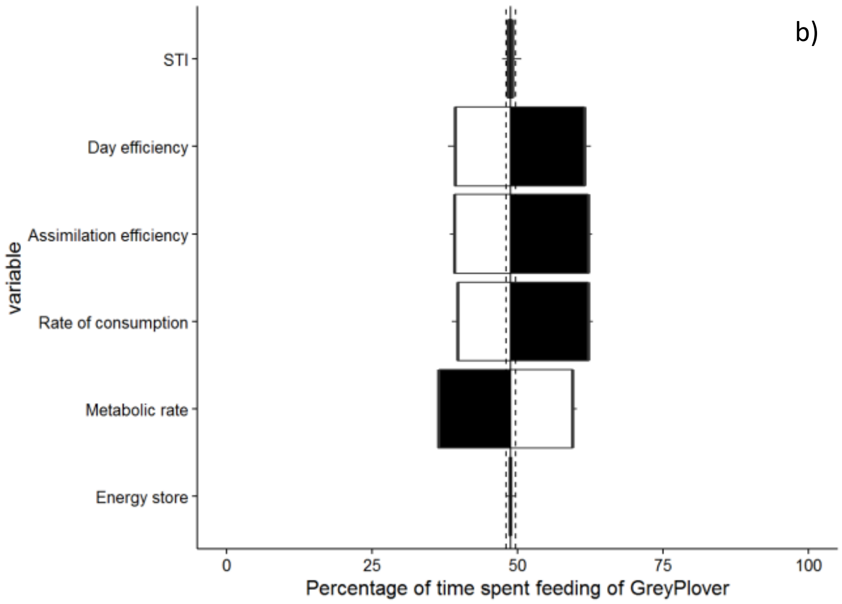

c)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Dunlin

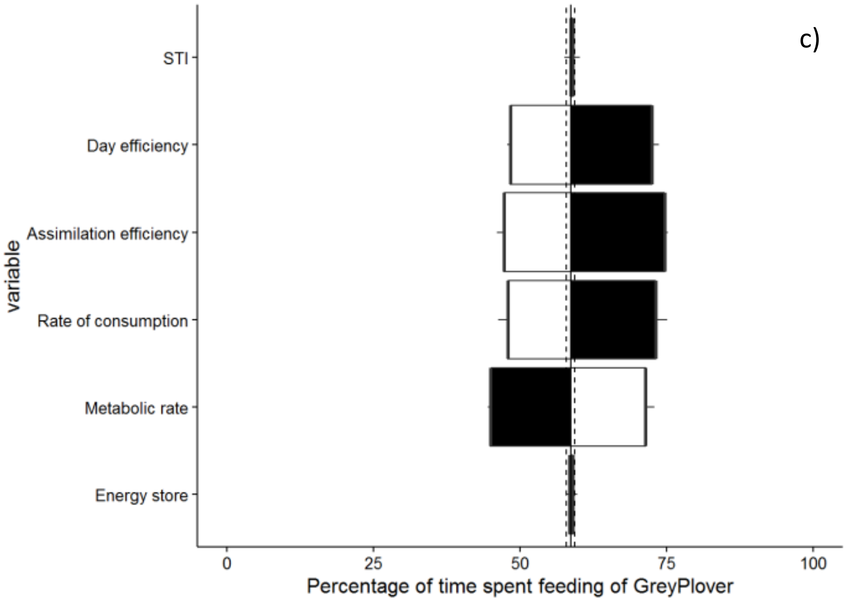

d)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Dunlin

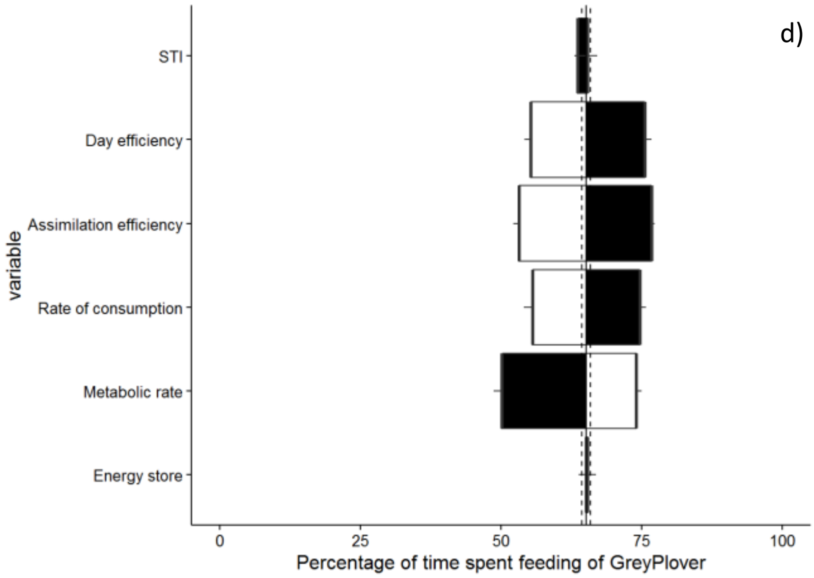


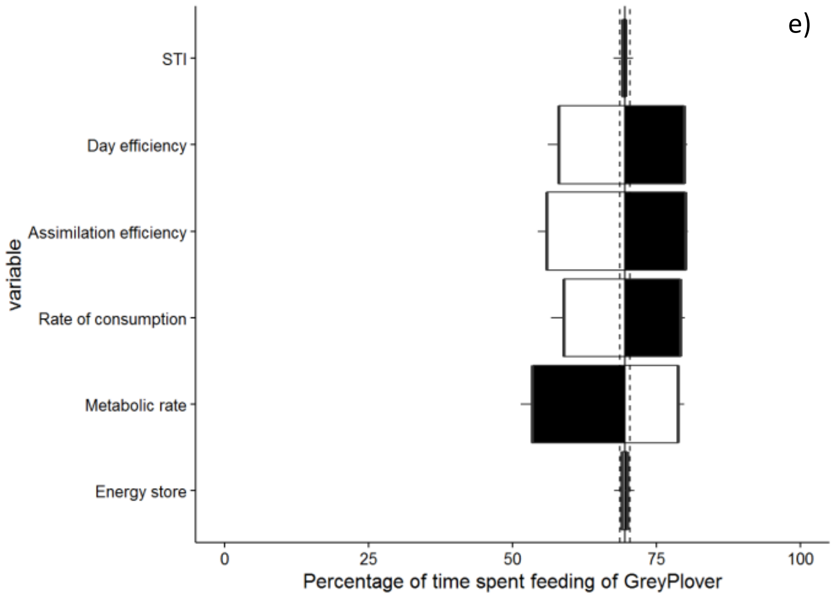
Figures A9.16. Sensitivity analysis for percentage of time spent feeding of ***grey plover*** *on the a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



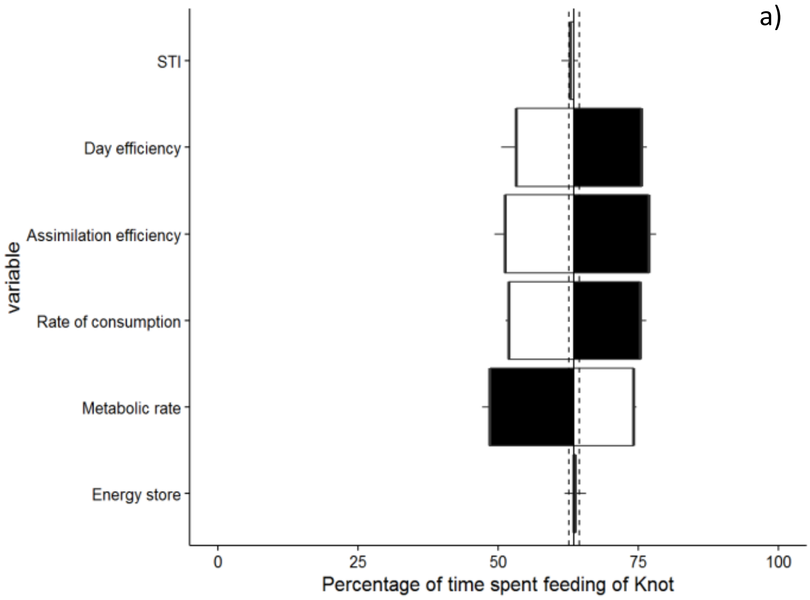

b)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of GreyPlover

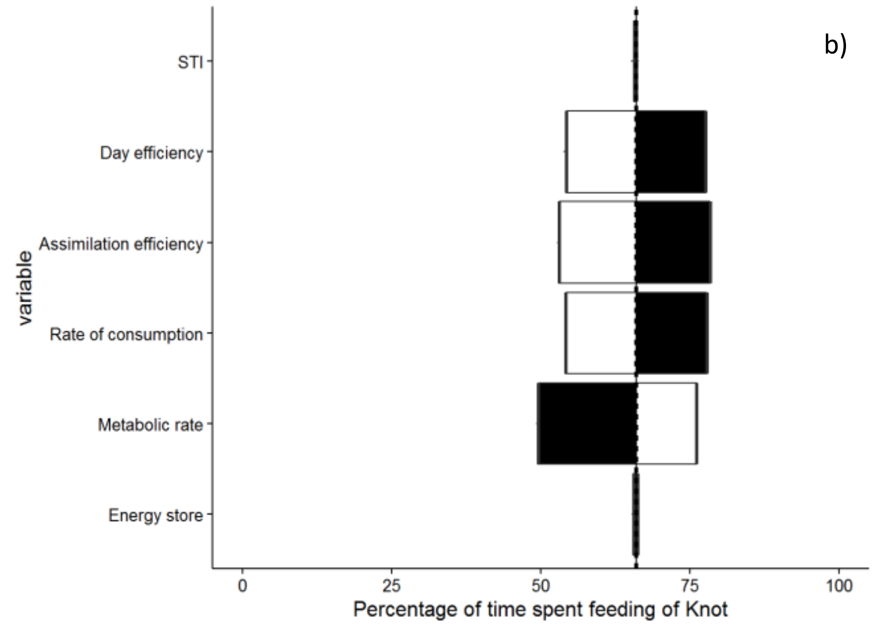

c)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of GreyPlover


d)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of GreyPlover

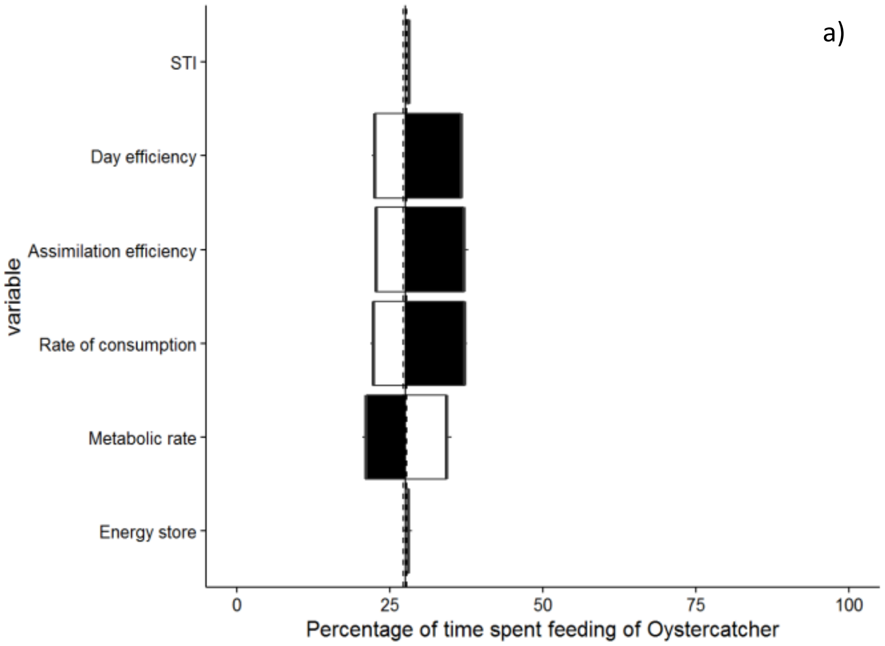


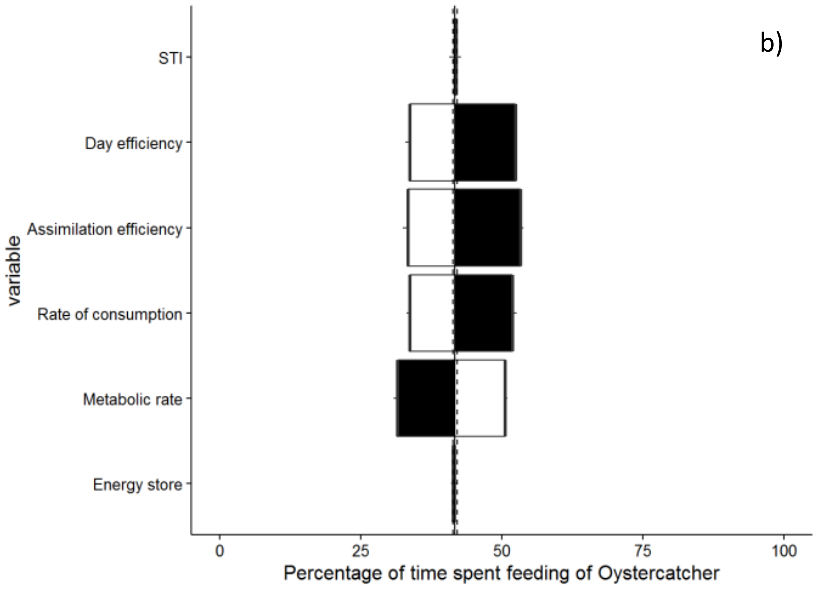
Figures A9.17. Sensitivity analysis for percentage of time spent feeding of ***knot*** *on the a) Severn estuary and b) the Humber*

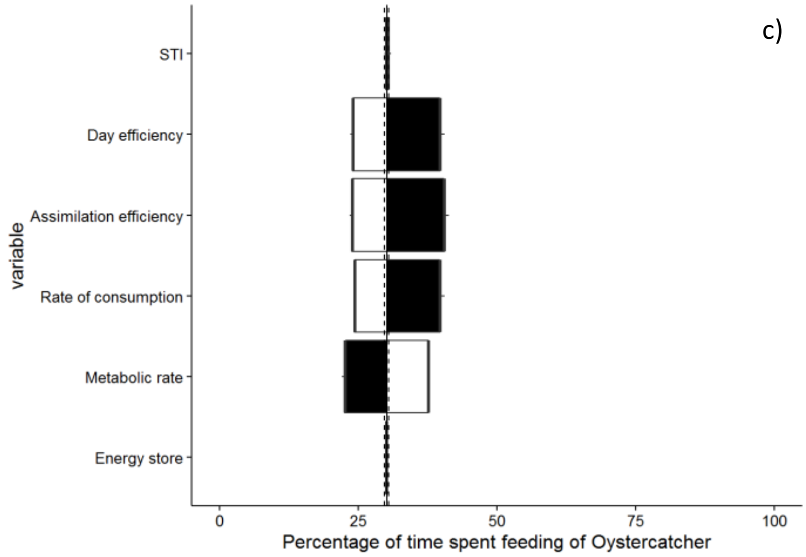


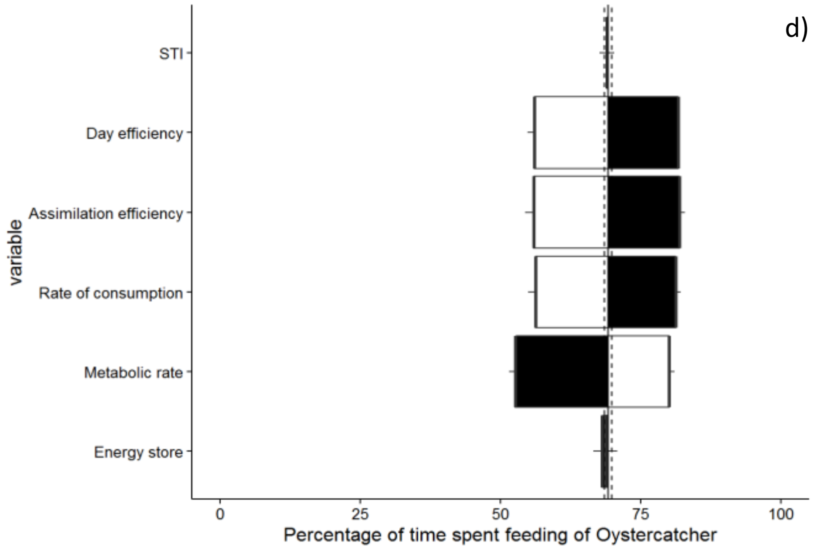


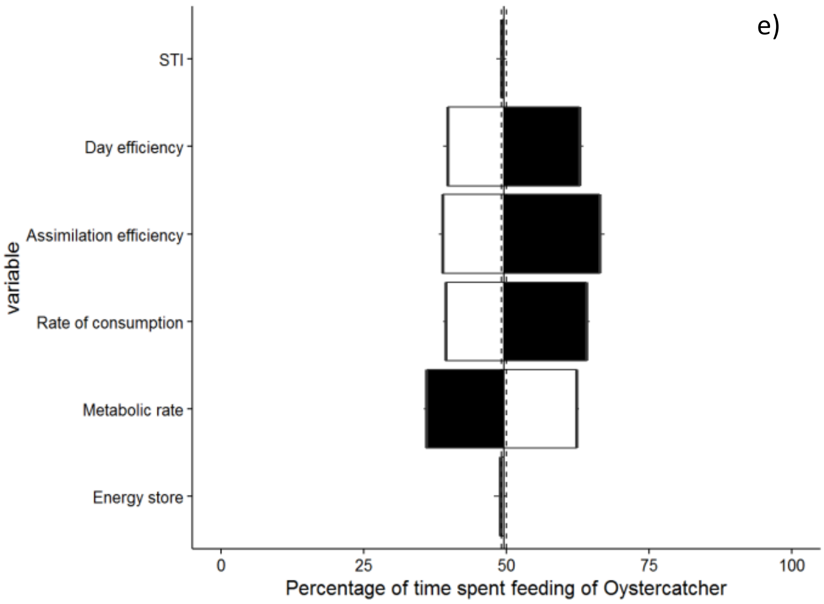
Figures A9.18. Sensitivity analysis for percentage of time spent feeding of ***oystercatcher*** *on a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



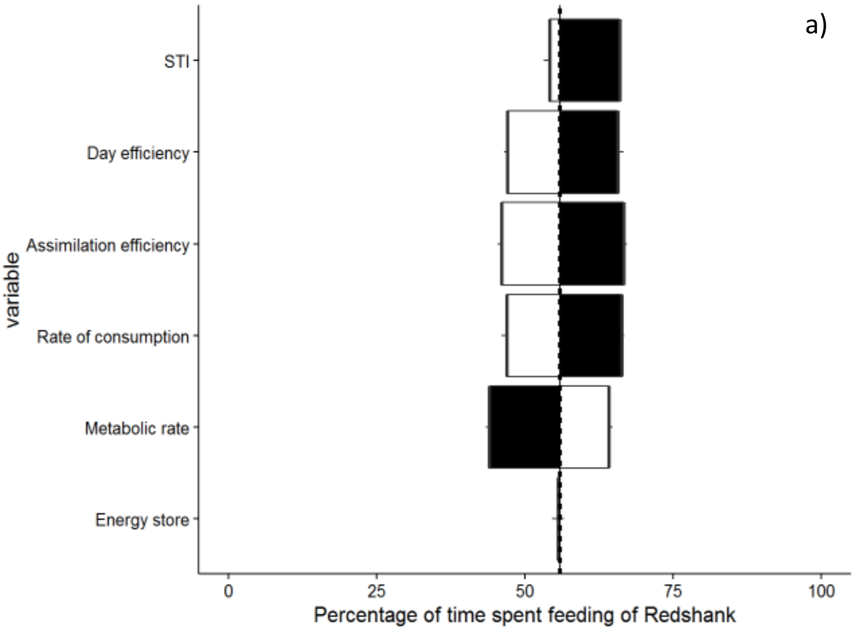

b)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Oystercatcher

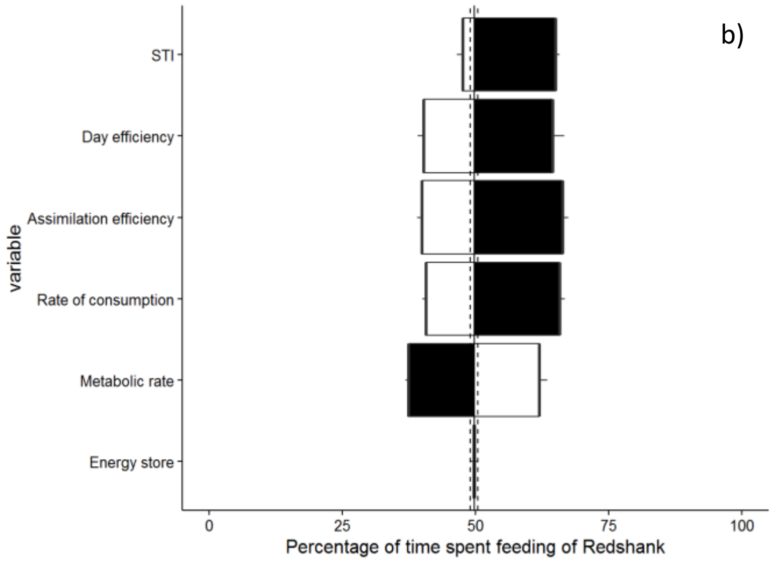

c)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Oystercatcher

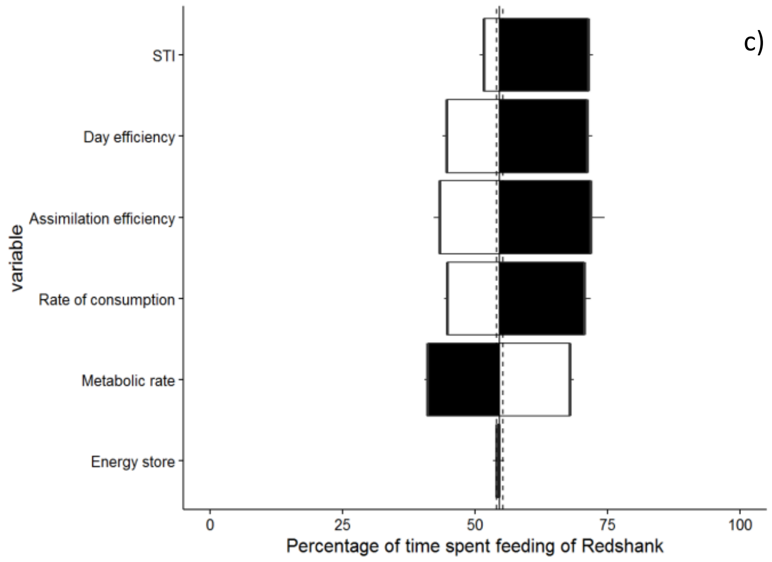

d)
variable
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
0
25
50
75
100
Percentage of time spent feeding of Oystercatcher

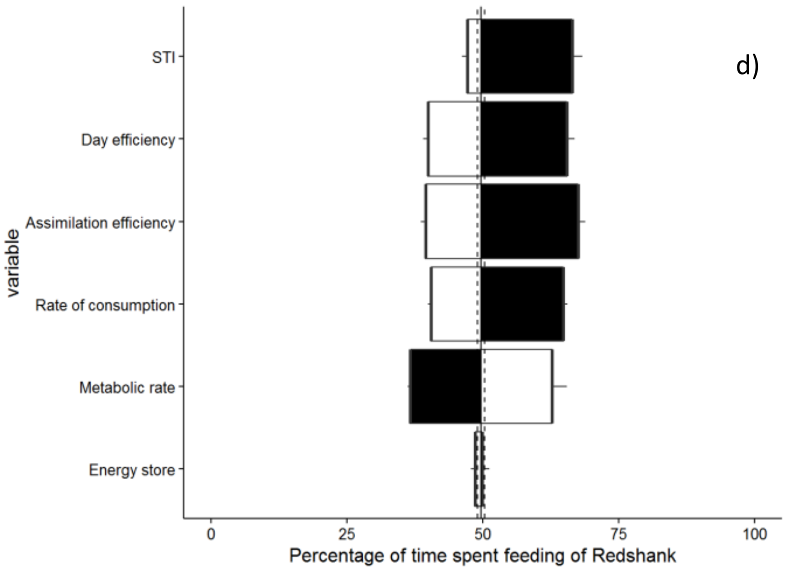


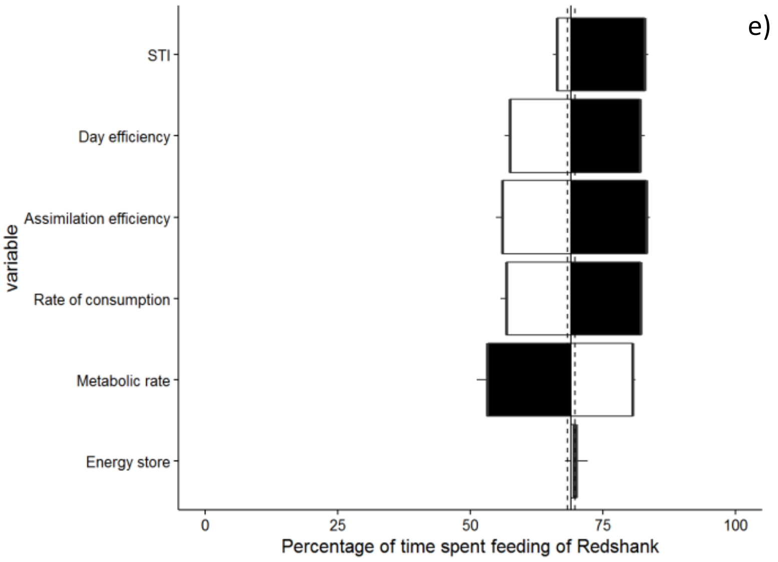
Figures A9.19. Sensitivity analysis for percentage of time spent feeding of ***redshank*** *on a) Exe estuary, b) Southampton water, c) Poole Harbour, d) Severn estuary and e) the Humber*



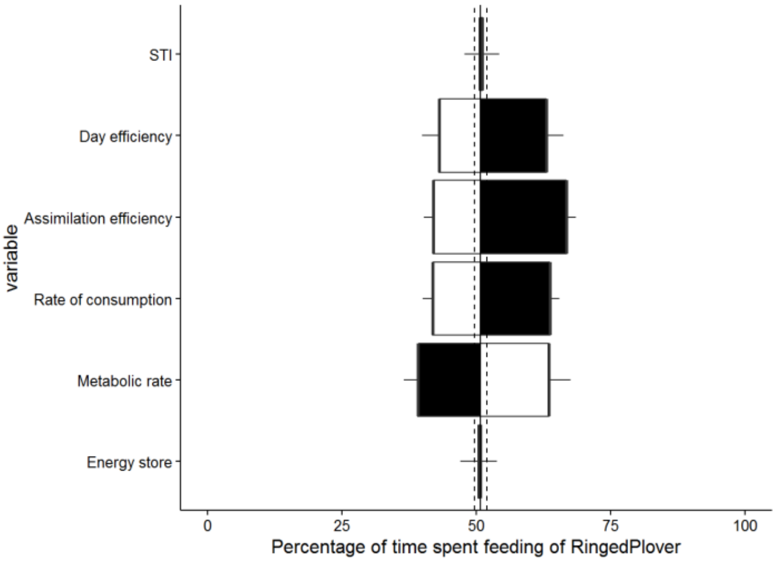

b)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Redshank


c)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Redshank

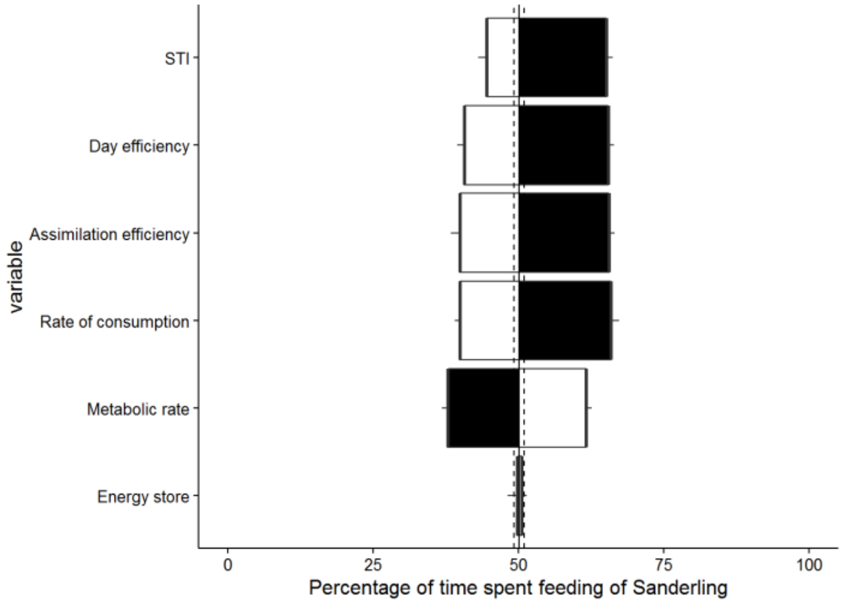

d)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Redshank



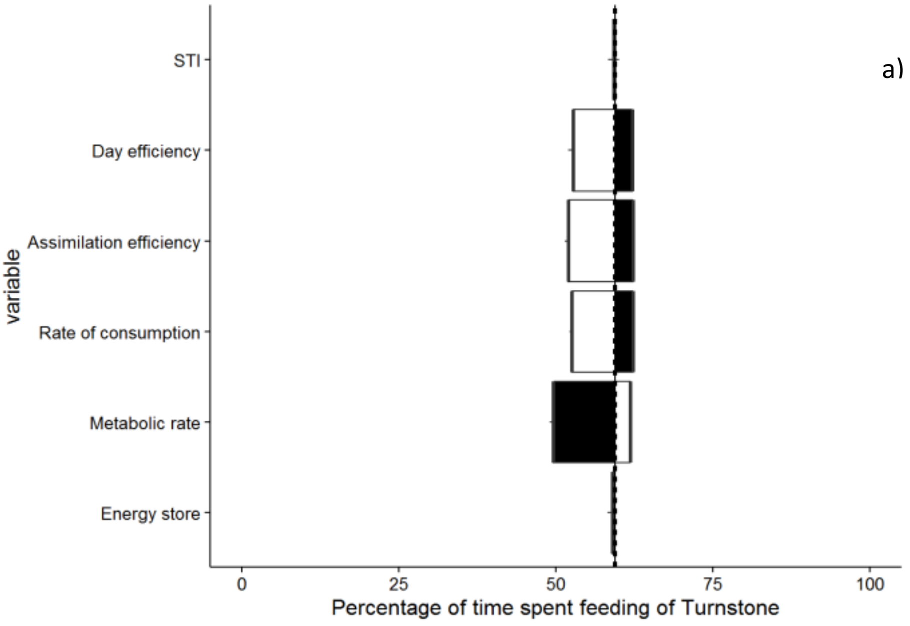
Figures A9.20. Sensitivity analysis for percentage of time spent feeding of ***ringed plover*** *on the Severn estuary*

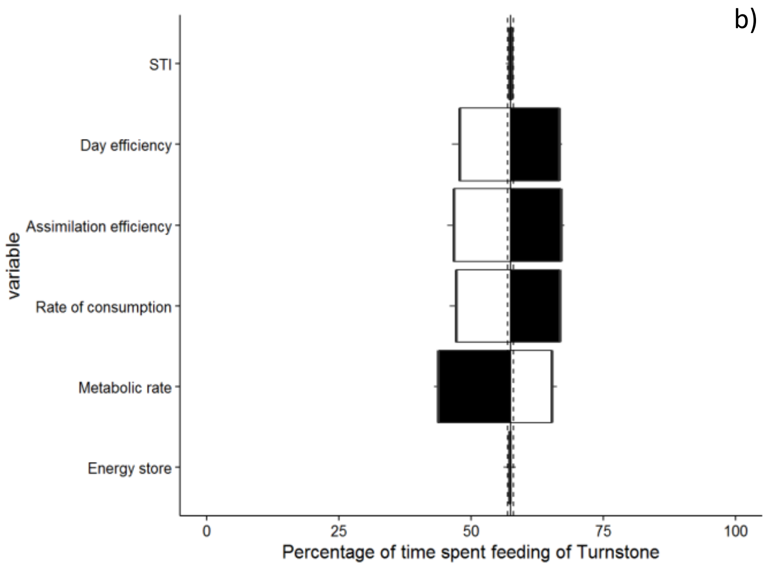


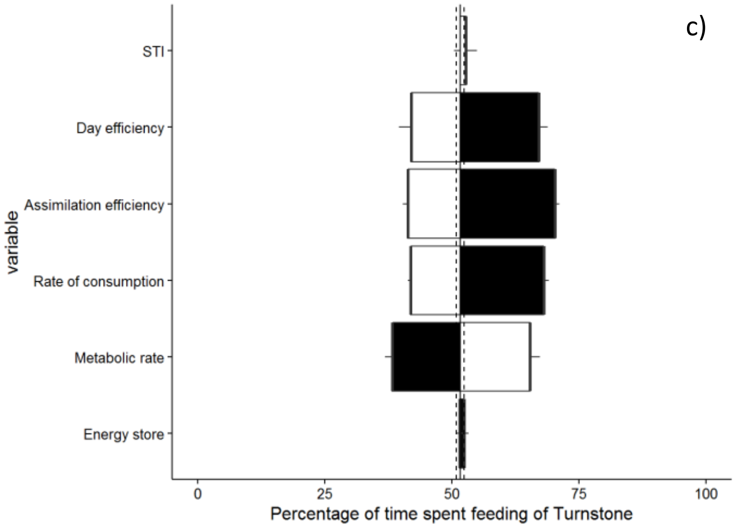
Figures A9.21. Sensitivity analysis for percentage of time spent feeding of ***sanderling*** *on the Humber*

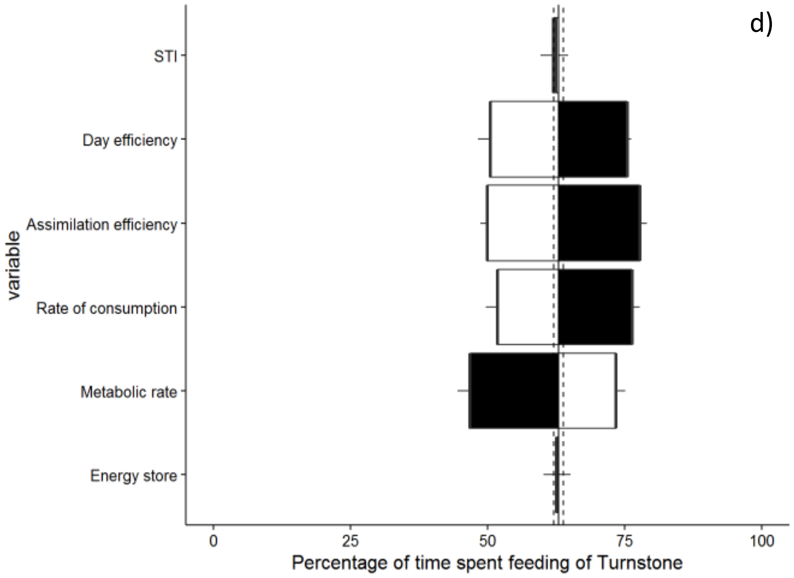


Figures A9.22. Sensitivity analysis for percentage of time spent feeding of ***turnstone*** *on the a) Exe estuary, b) Southampton water, c) Severn estuary and d) the Humber*




b)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Turnstone


c)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Turnstone


d)
STI
Day efficiency
Assimilation efficiency
Rate of consumption
Metabolic rate
Energy store
variable
0
25
50
75
100
Percentage of time spent feeding of Turnstone

Appendix 10. Species numbers and averages across five estuaries used for model development and analysis

Table A10.1. Table of species population averages and peaks for two five-year periods and SPA designations for each estuary.

	Exe estuary	**Humber estuary**	**Poole Harbour**	**Severn estuary**	**Solent & Southampton Water**
WeBS 09/10-13/14 Five-year winter peak counts of each species					
Bar-tailed Godwit	318	2126	238	19	19
Black-tailed Godwit	1054	3556	2093	409	351
Curlew	865	3168	1036	3425	451
Dunlin	4022	15012	2500	25281	1867
Grey Plover	322	3511	201	302	178
Knot	171	28706	59	2130	35
Oystercatcher	2006	4634	1248	752	1012
Redshank	463	3058	975	3462	312
Ringed Plover	36	176	40	120	75
Sanderling	20	420	25	120	10
Turnstone	208	352	79	358	282
WeBS 1994-1999 Five-year winter peak counts of each species					
Bar-tailed Godwit	379	786	175	10	6
Black-tailed Godwit	1132	2970	2046	115	1450
Curlew	892	3980	1783	5307	583
Dunlin	7270	40121	6816	50638	5177
Grey Plover	573	3368	476	767	253
Knot	162	34663	64	3135	1
Oystercatcher	4733	4201	1487	915	903
Redshank	696	6109	1356	2526	613
Ringed Plover	159	382	121	161	326
Sanderling	74	665	10	46	1
Turnstone	274	481	20	428	283

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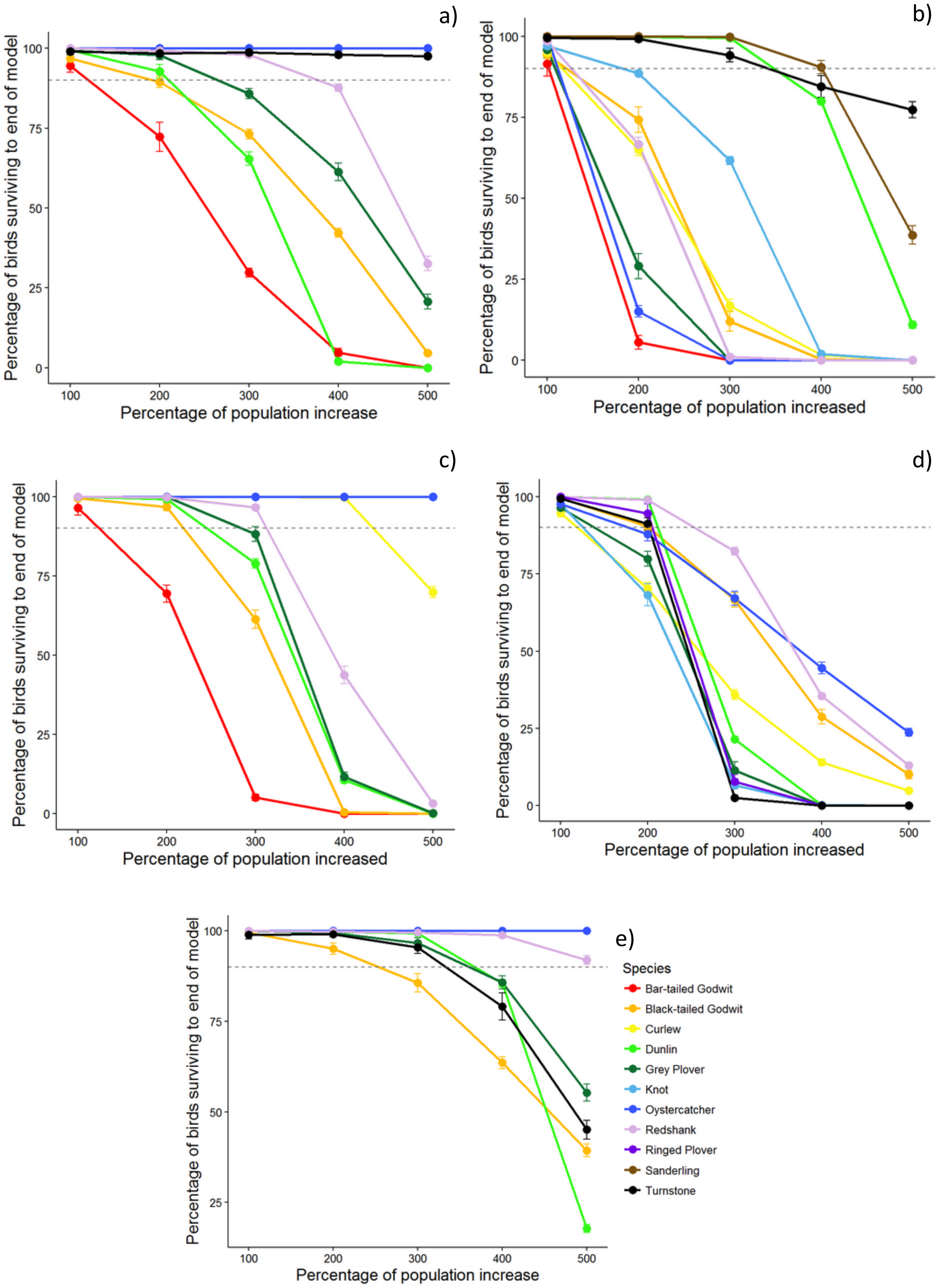
WeBS 2009/10-2013/14 Five-year average monthly counts of each species (Oct-Feb, used for MORPH)					
Bar-tailed Godwit	179.8	1344.2	100	10	7
Black-tailed Godwit	816.2	1318	1298	218.4	257
Curlew	747.8	2414	828	2781.2	402
Dunlin	2445.2	10836.2	1392	17057.4	1160.4
Grey Plover	176.8	1360	104	205.6	106.2
Knot	59.8	17367.2	29	859.6	11.4
Oystercatcher	1590	3797.2	871	673.2	857.2
Redshank	383.6	2307.6	742	2997.4	246.8
Ringed Plover	22.8	91.4	12	103.6	55.8
Sanderling	6.6	285.4	11	55.2	5.2
Turnstone	116.4	231	37	276	195.2
WeBS 1994/95-1998/99 Five-year average monthly counts of each species (Oct-Feb)					
Bar-tailed Godwit	206.2	889.2	74.4	6.2	0.4
Black-tailed Godwit	438.6	651.8	1041.4	104	338
Curlew	739.8	1635.2	1324.4	2214	361.2
Dunlin	2998.2	17329.4	4105.6	20709.2	2618.8
Grey Plover	298.6	946.8	161.4	219.6	103.2
Knot	50.8	15151.2	19.6	672.2	0.2
Oystercatcher	3256.8	2417.8	1265.4	456	668.8
Redshank	362.8	3361.8	965	1554.2	422.2
Ringed Plover	82.6	265.2	43.2	82.2	126.2
Sanderling	37.8	312.6	2.6	17.2	0.2
Turnstone	135.2	293.8	7.8	222.8	141.8
SPA numbers - Winter Annex 1 birds and migratory birds					
Bar-tailed Godwit	0	2752	0	0	0
Black-tailed Godwit	533	1113	1576	0	1125
Curlew	0	3253	0	0	0
Dunlin	5740	22222	0	44624	0
Grey Plover	471	1704	0	0	0
Knot	0	28165	0	0	0
Oystercatcher	4265	3503	0	0	0
Redshank	0	4632	0	2330	0
Ringed Plover	0	403	0	0	552
Sanderling	0	486	0	0	0
Turnstone	0	629	0	0	0

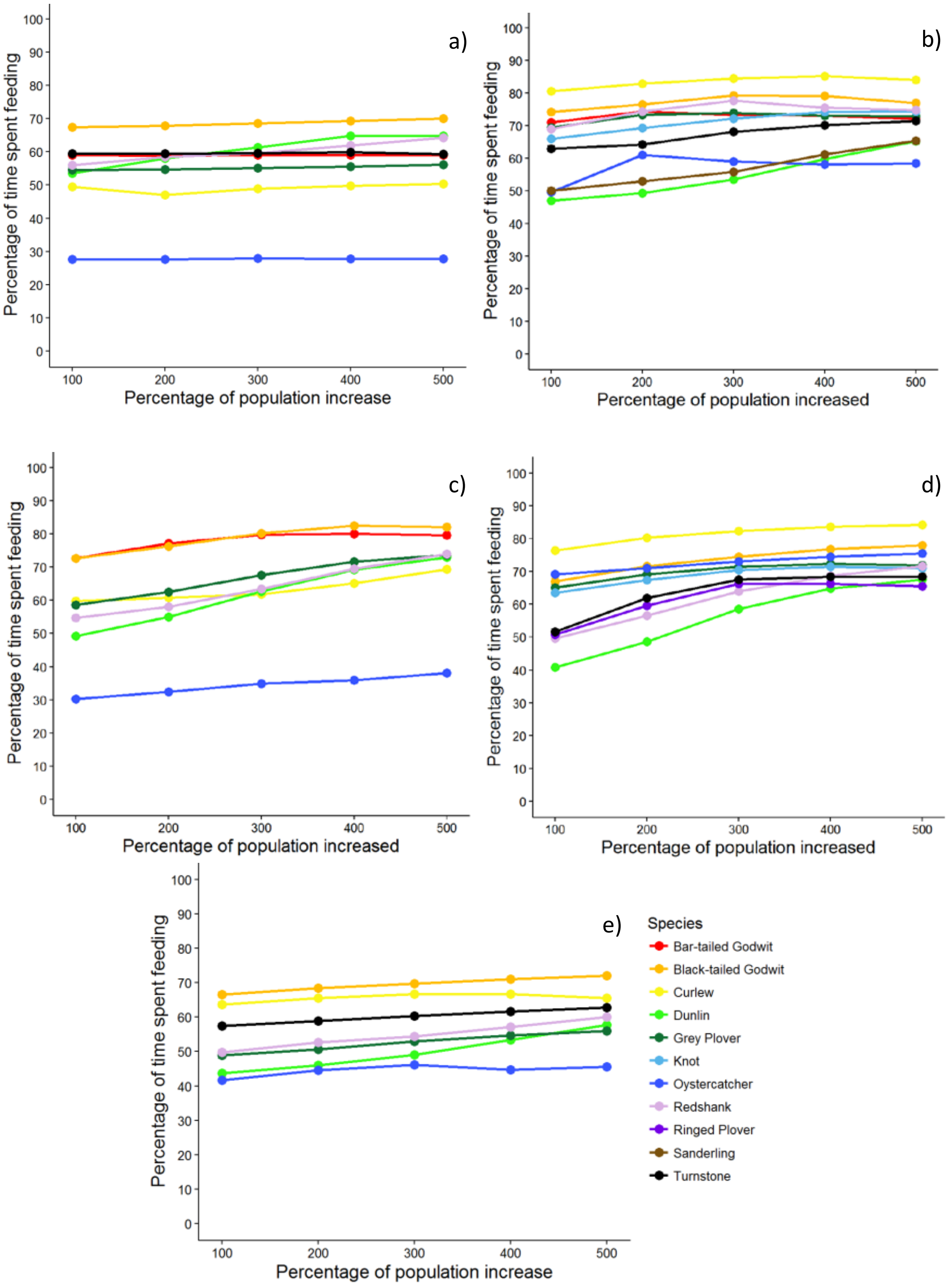
Appendix 11. Estuary specific numbers supported when faced with increasing populations.

Figures A11.1a–e. Percentage of birds of eleven species supported to the end of a winter modelling period for five estuaries whilst affected by increased populations. a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) The Severn estuary and e) Southampton Water.



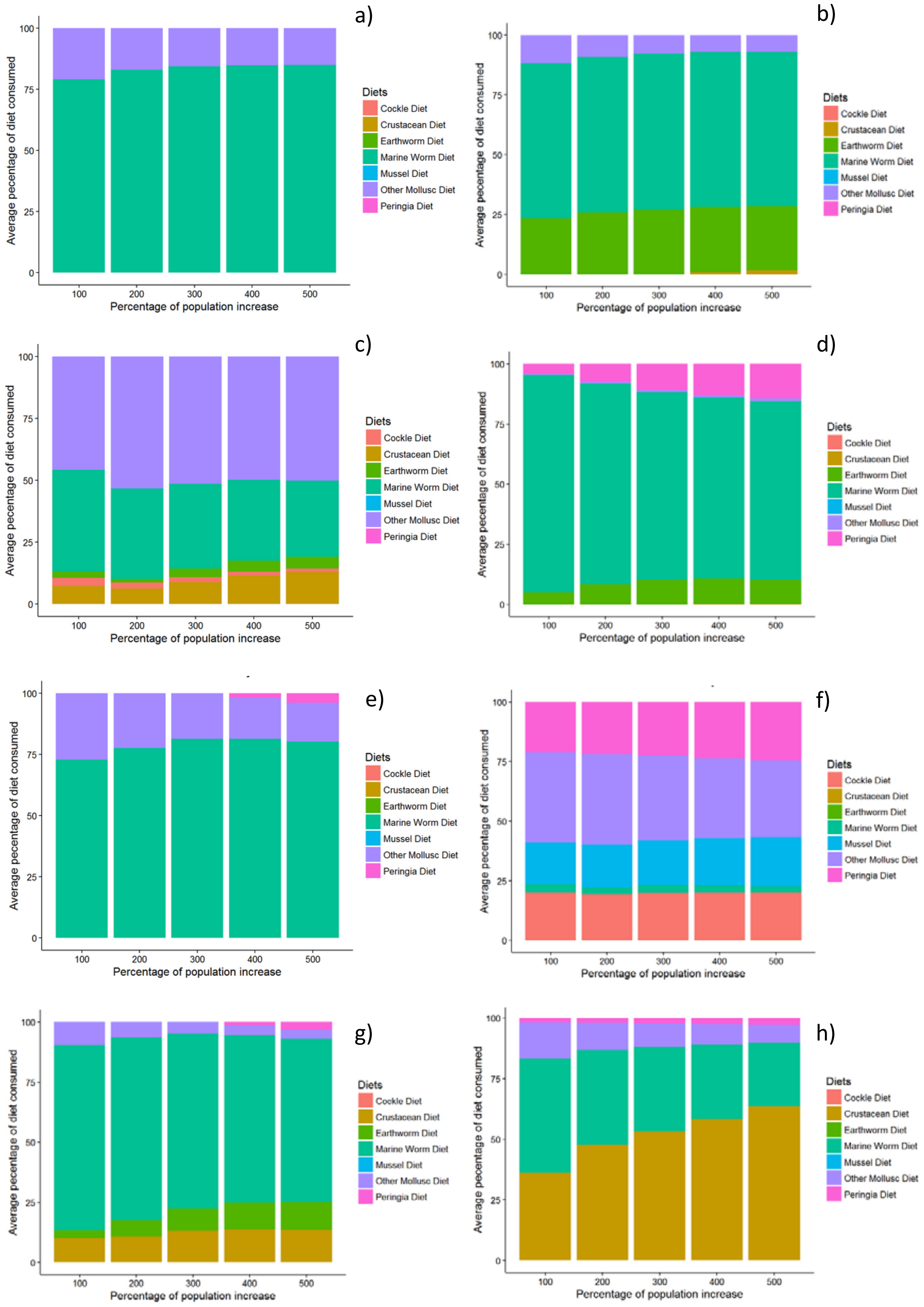
Appendix 12. Estuary specific percentage of time spent feeding when faced with increasing populations.

Figures A12.1a – e. Percentage of time spent feeding for eleven species on five estuaries whilst affected by increased populations. a) Exe estuary, b) The Humber estuary, c) Poole Harbour, d) The Severn estuary and e) Southampton Water.

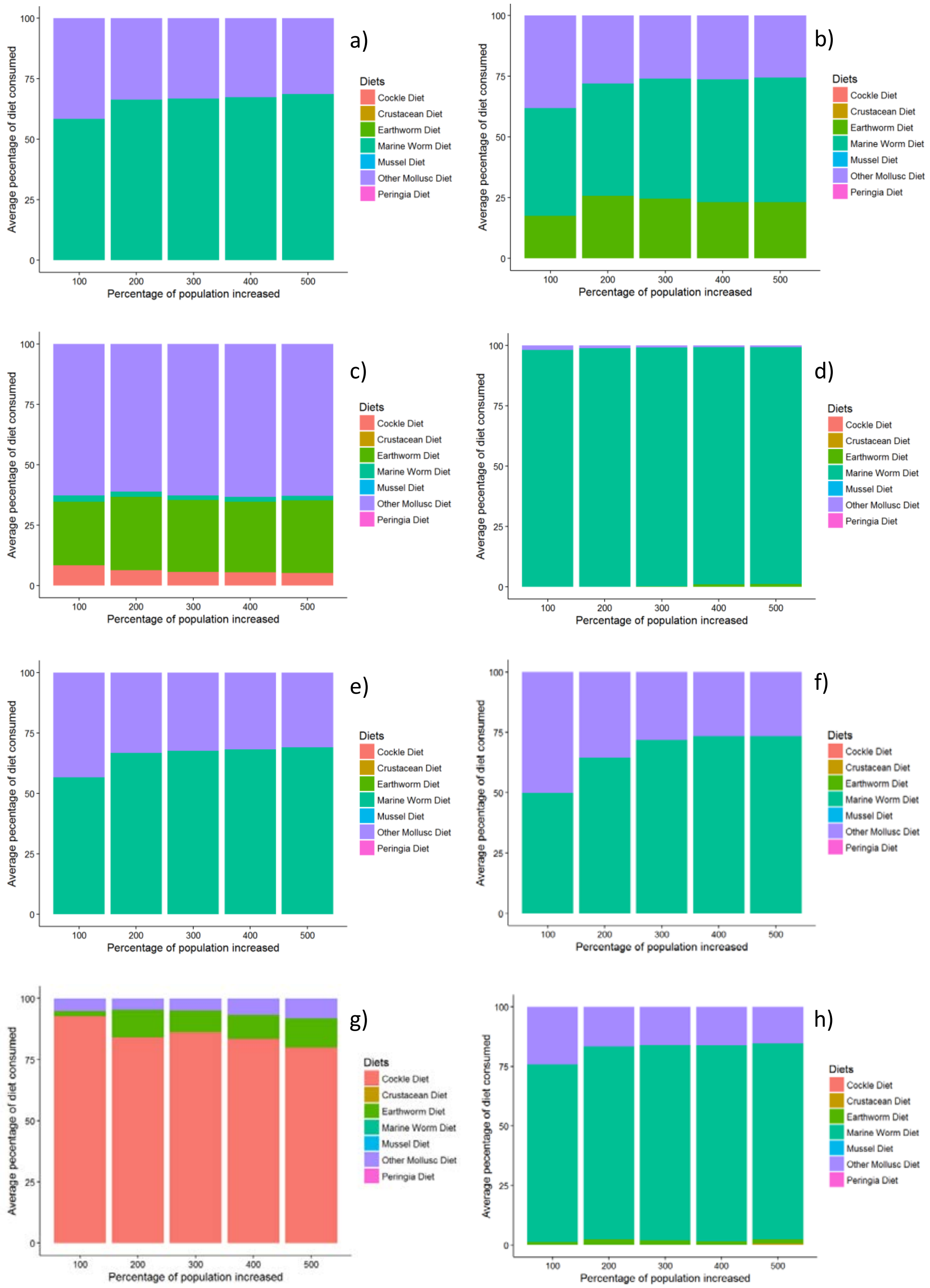


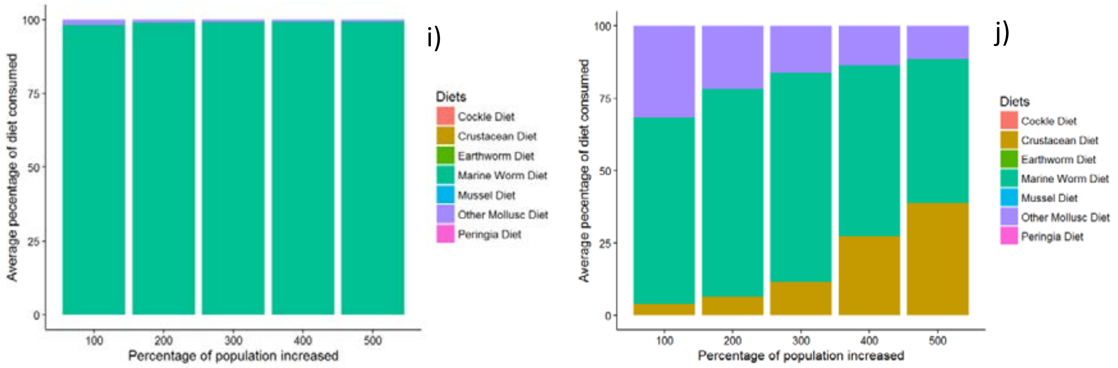
Appendix 13. Dietary shifts in each species on an estuary when faced with increasing populations.

Figures A13.1a-h. Dietary preferences of wading birds on the ***Exe estuary*** *when faced with increased populations: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher, g)redshank and h)turnstone.*

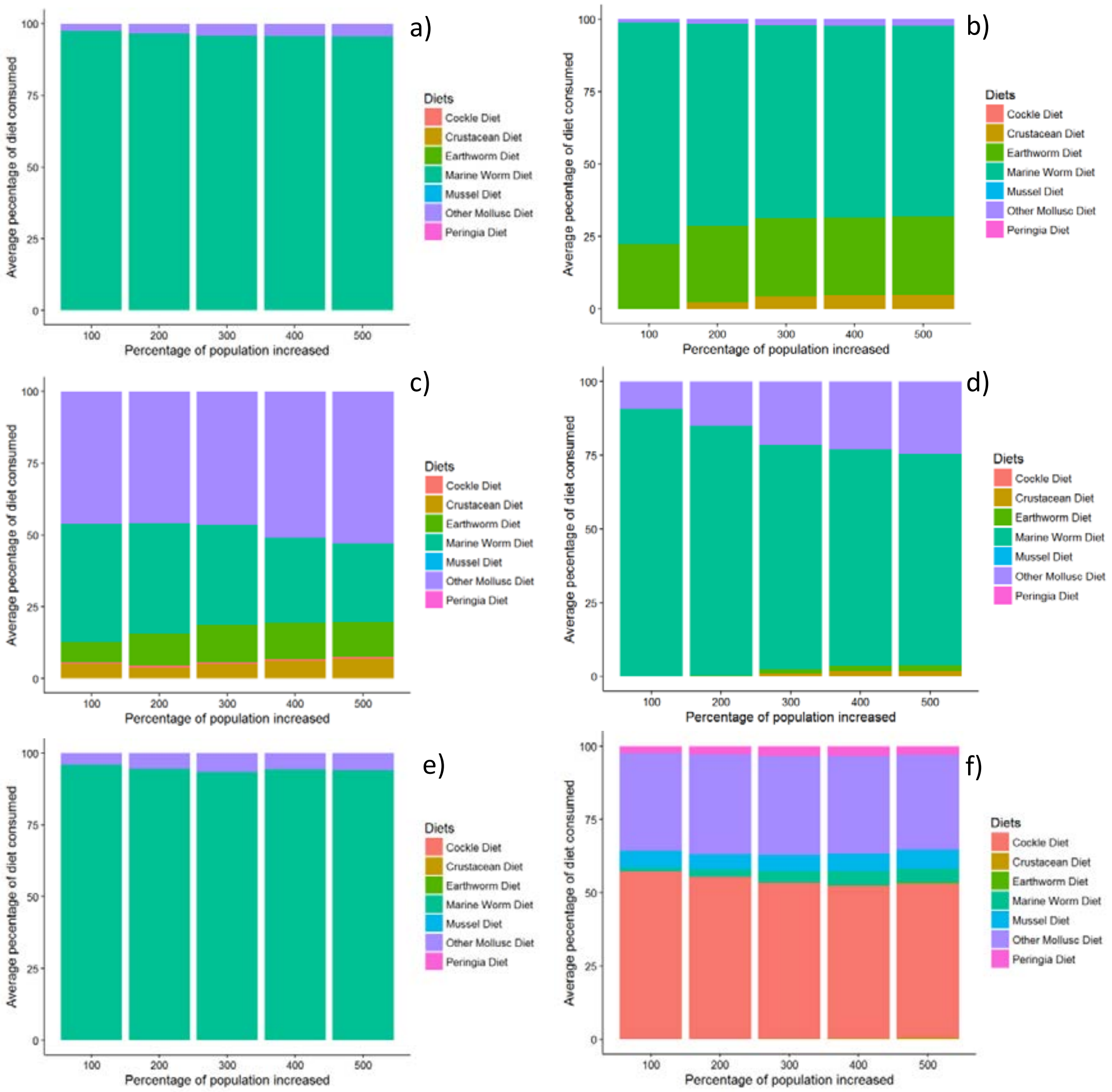


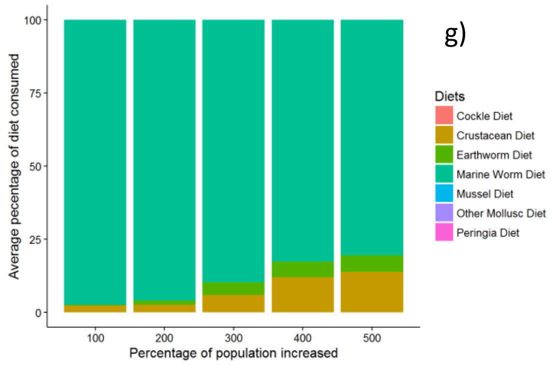
Figures A13.2a-j. Dietary preferences of wading birds on the ***Humber*** *estuary when faced with increased populations: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)knot, g)oystercatcher, h)redshank, i)sanderling and j)turnstone.*



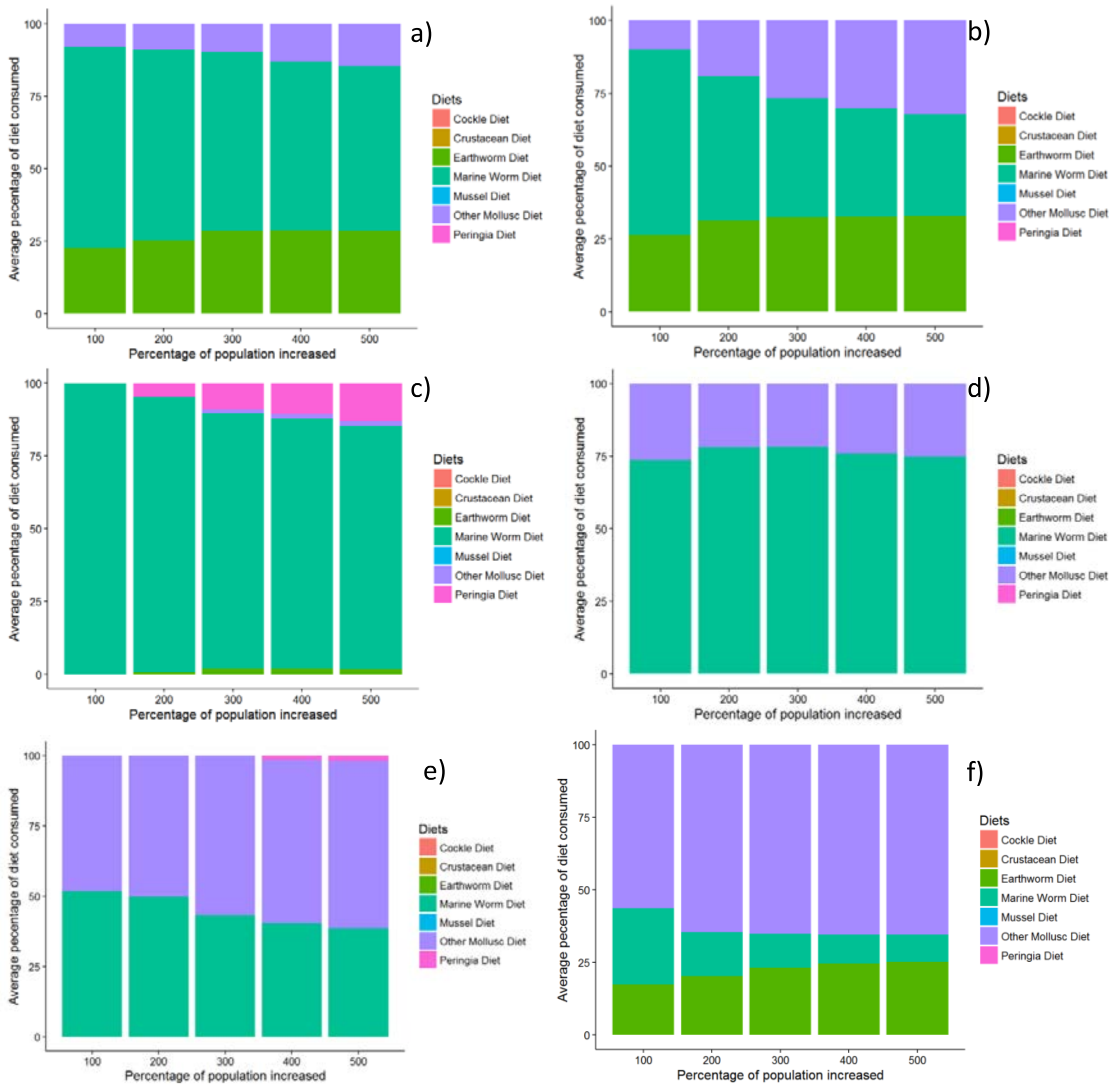


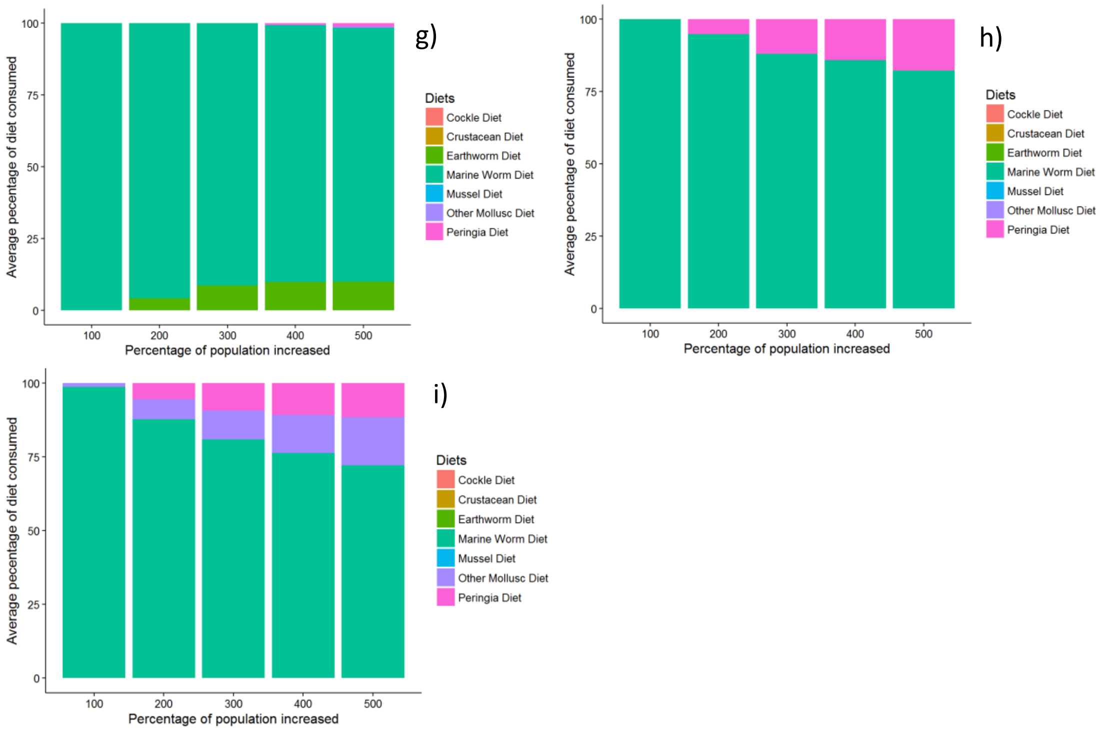
Figures A13.3a-g. Dietary preferences of wading birds on ***Poole Harbour*** *when faced with increased populations: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher and g)redshank.*



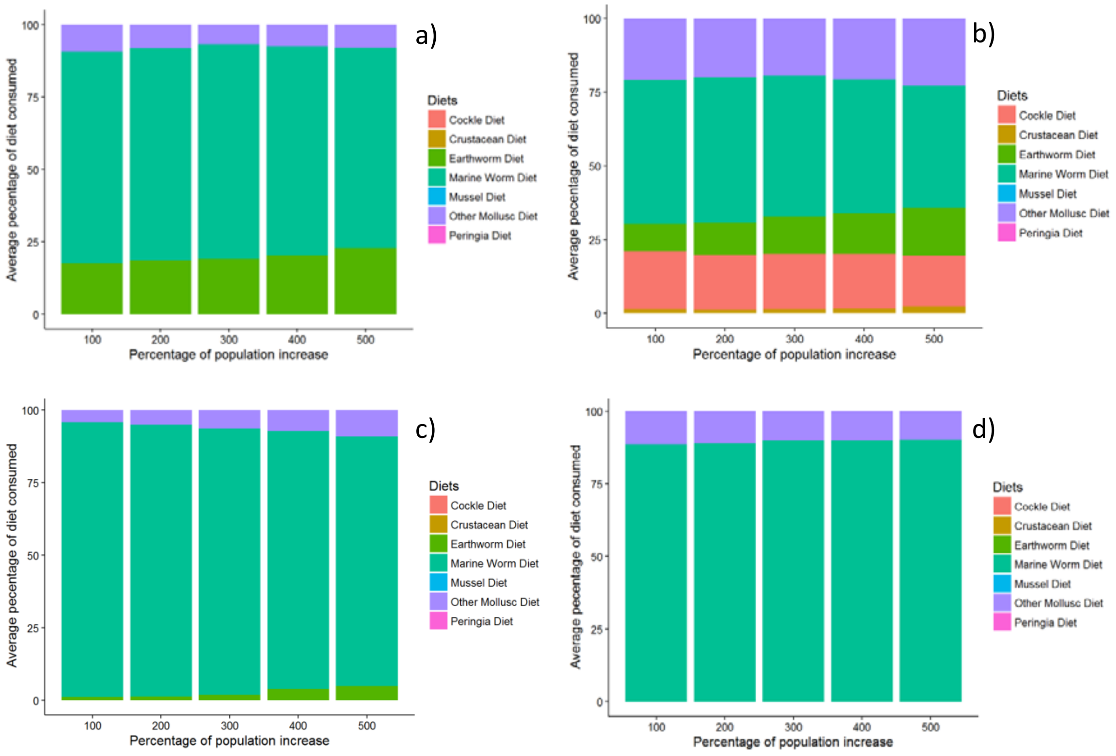


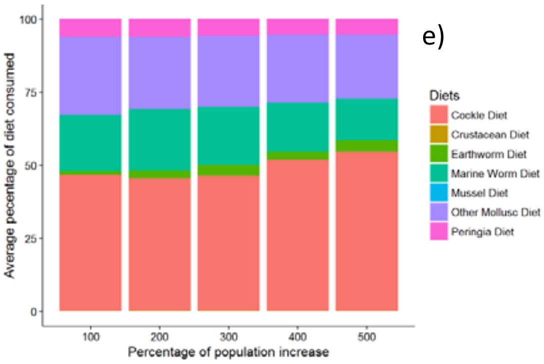
Figures A13.4a-i. Dietary preferences of wading birds on the ***Severn estuary*** *when faced with increased populations: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)knot, f)oystercatcher, g)redshank, h)ringed plover and i)turnstone.*



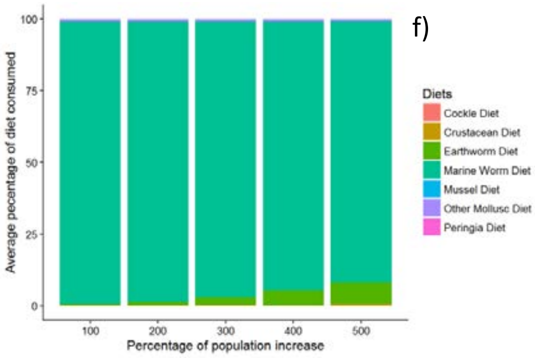


Figures A13.5a-g. Dietary preferences of wading birds on ***Southampton Water*** *when faced with increased populations: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)oystercatcher, f)redshank and g)turnstone.*

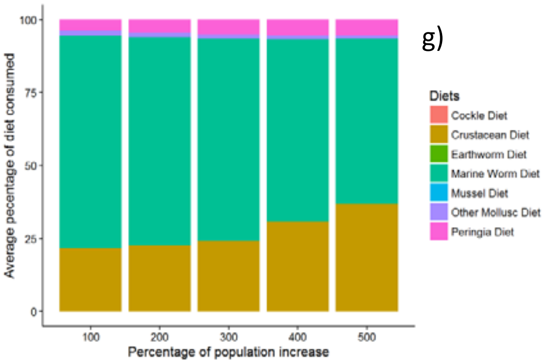



e)

Average pecentage of diet consumed
100
75
50
25
0
100
200
300
400
500
Percentage of population increase
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet


f)

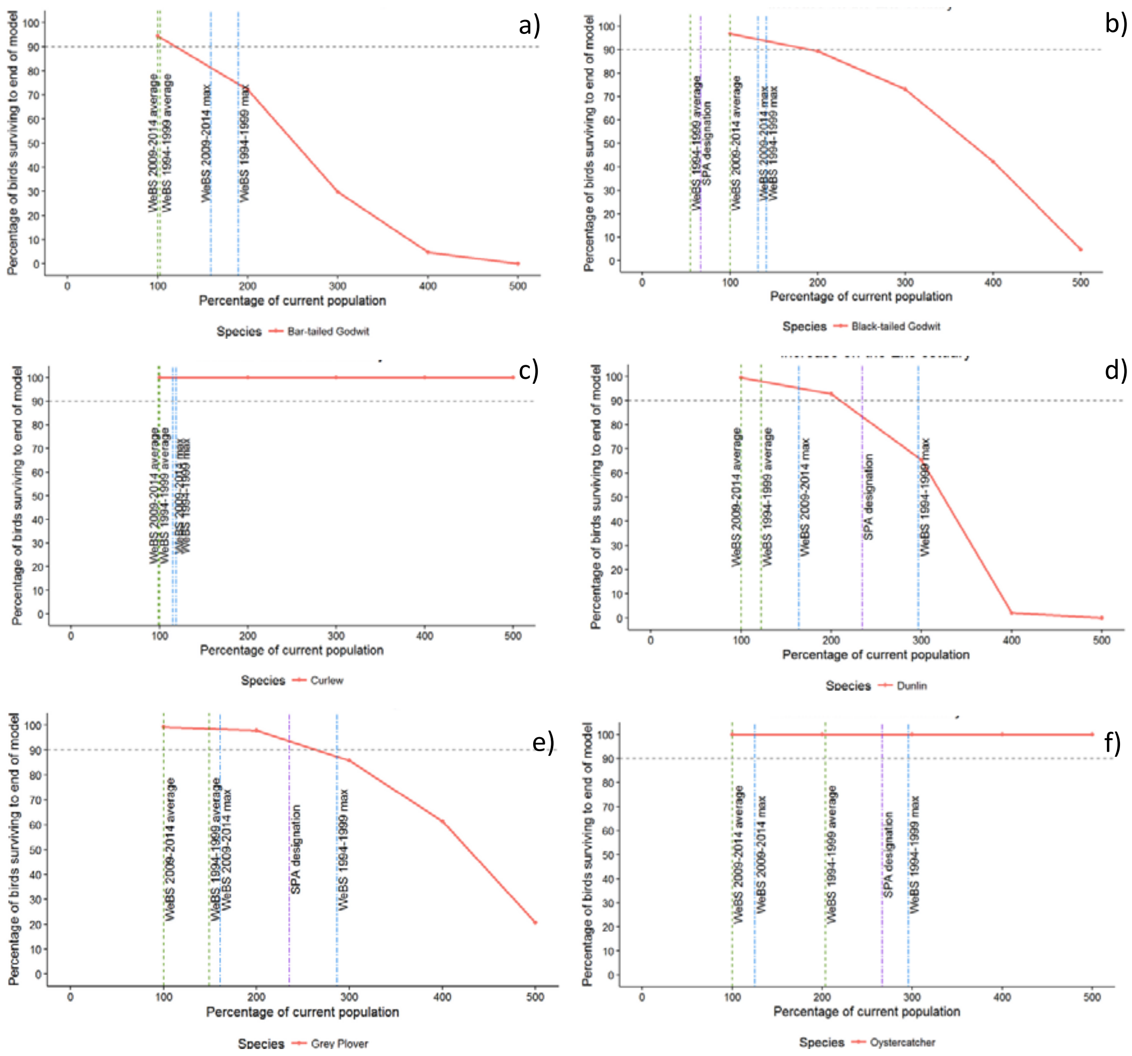
Average pecentage of diet consumed
100
75
50
25
0
100
200
300
400
500
Percentage of population increase
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet

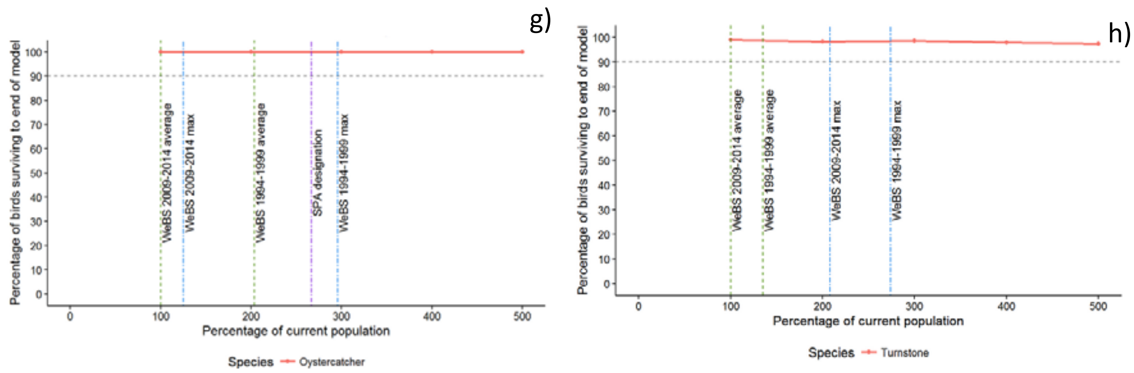

g)

Average pecentage of diet consumed
100
75
50
25
0
100
200
300
400
500
Percentage of population increase
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet

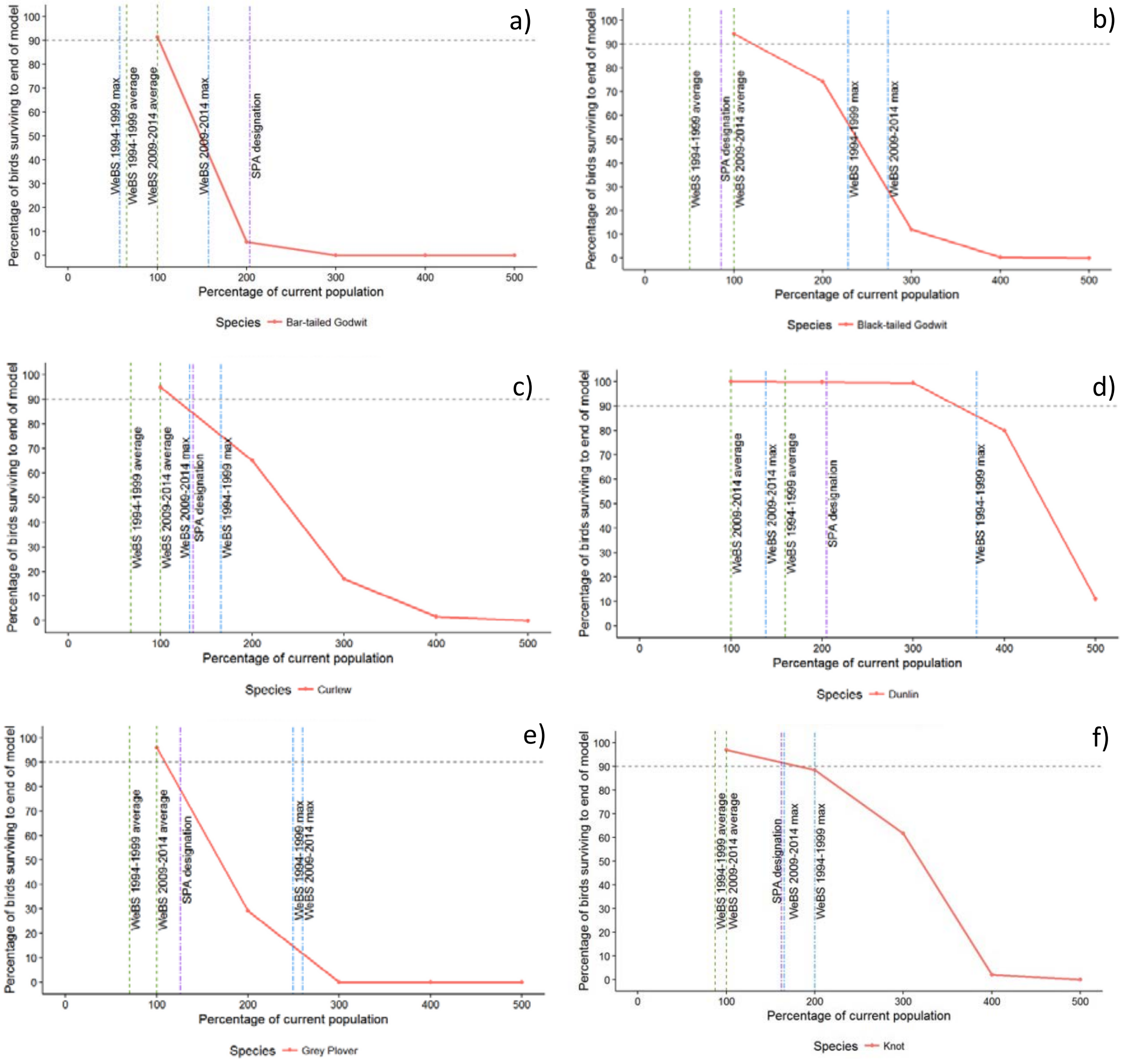
Appendix 14. Species specific population responses to increasing populations and comparisons with WeBS averages, peaks and SPA designated numbers.

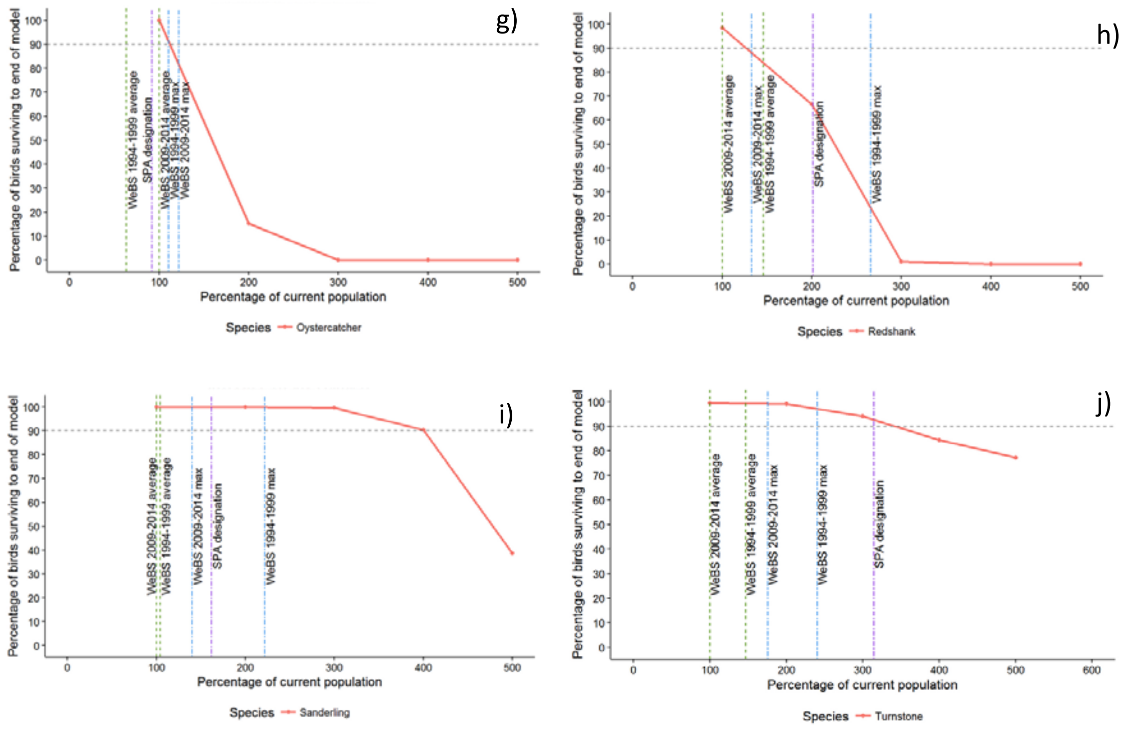
Figures A14.1 Percentage of birds supported to the end of the model when faced with population increases on the Exe estuary. a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher, g)redshank and h)turnstone. Vertical lines indicate where SPA designated numbers and WeBS winter averages and peaks fall in relation to current averages (2009/10-2013/14).



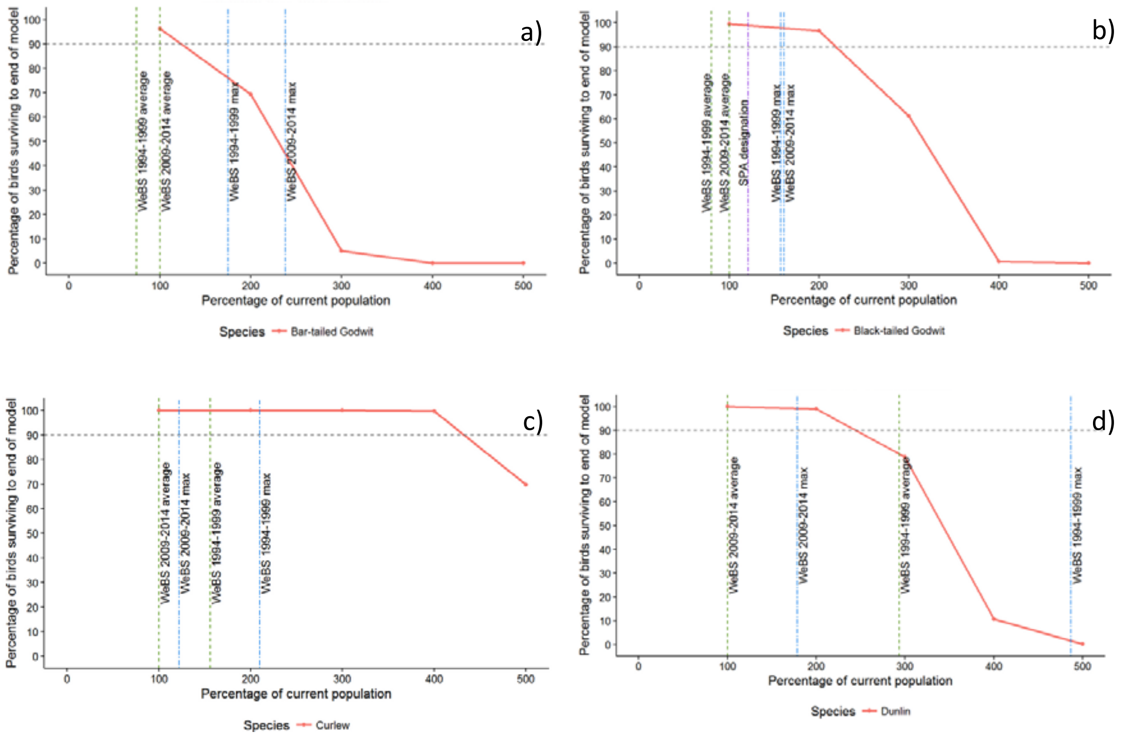


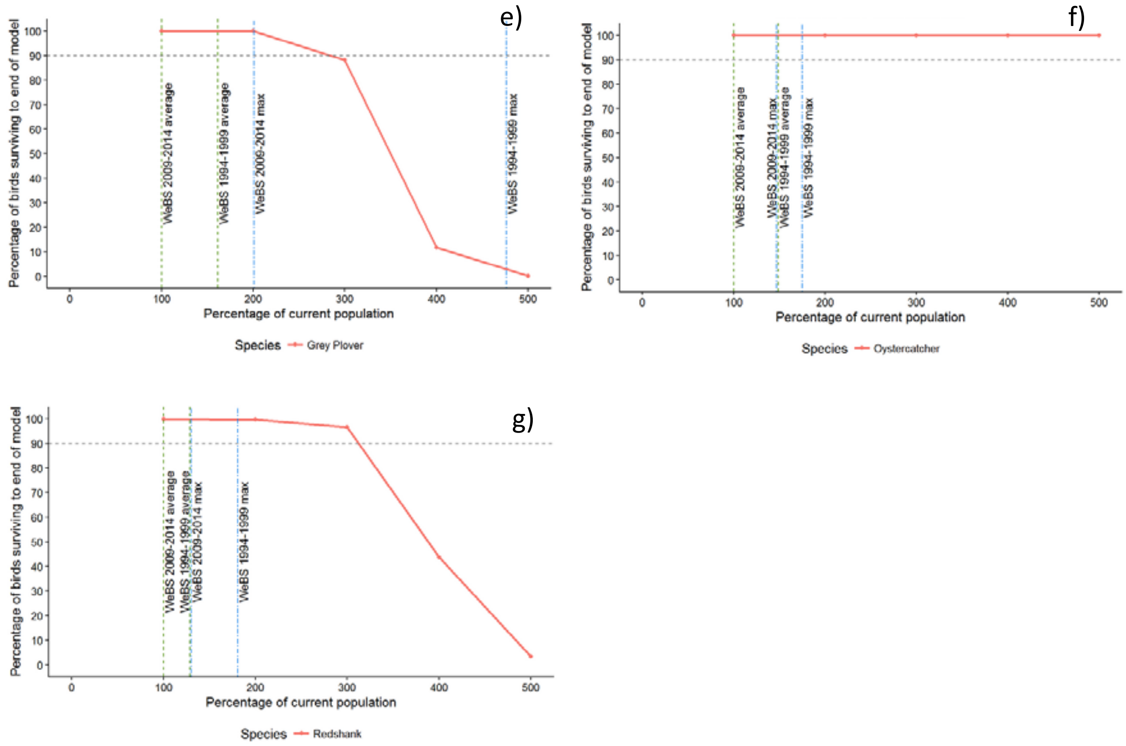
Figures A14.2 Percentage of birds supported to the end of the model when faced with population increases on the Humber estuary. a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)knot, g)oystercatcher, h)redshank, i)sanderling and j)turnstone. Vertical lines indicate where SPA designated numbers and WeBS winter averages and peaks fall in relation to current averages (2009/10-2013/14).



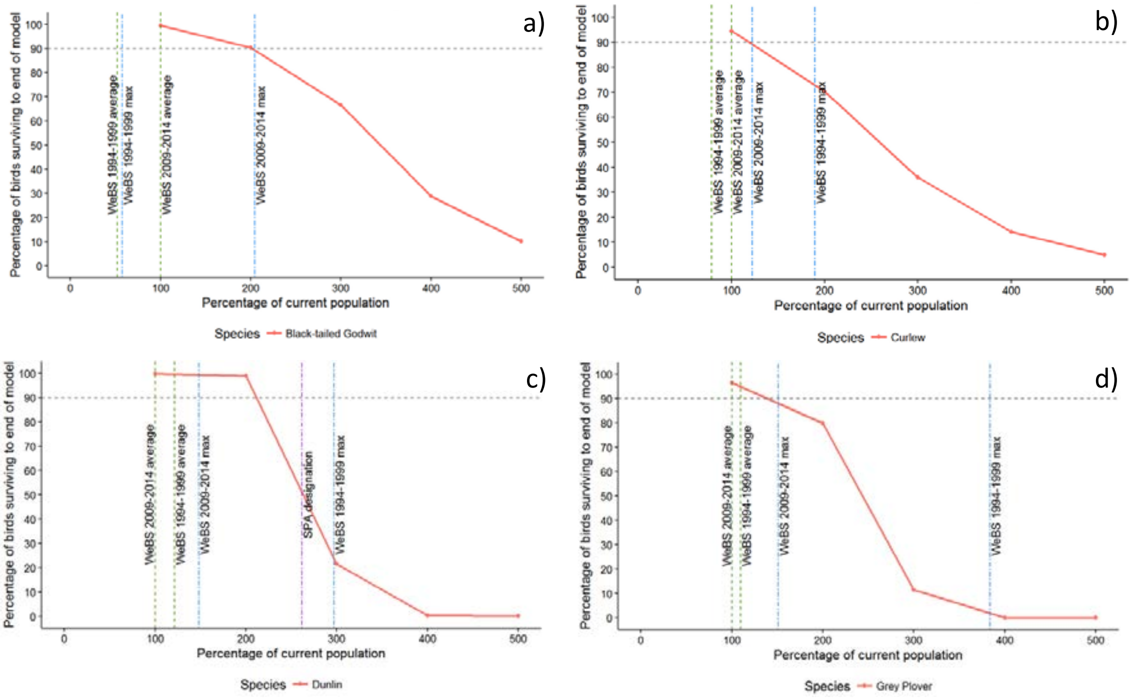


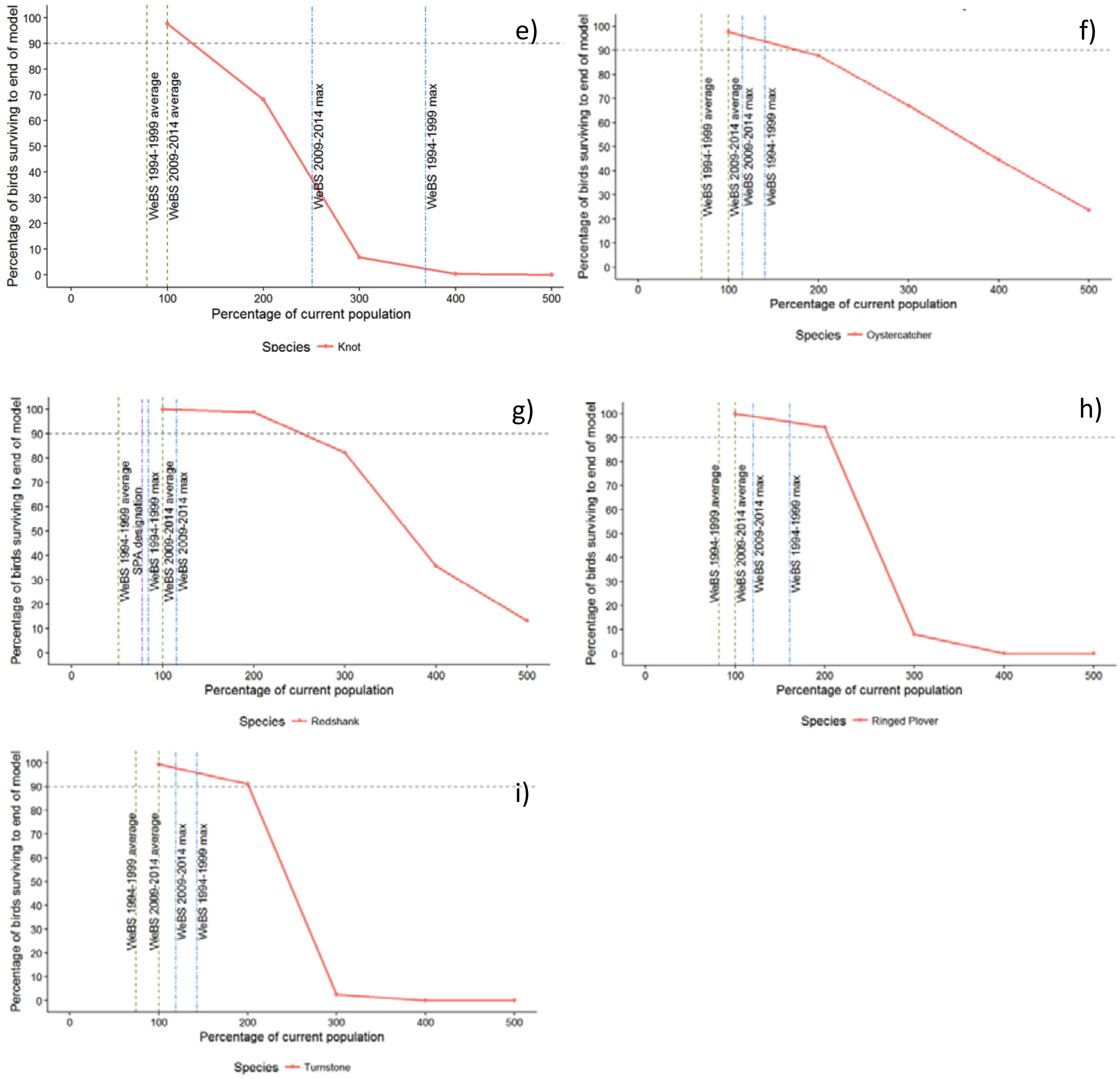
Figures A14.3 Percentage of birds supported to the end of the model when faced with population increases on Poole Harbour. a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher and g)redshank. Vertical lines indicate where SPA designated numbers and WeBS winter averages and peaks fall in relation to current averages (2009/10-2013/14).



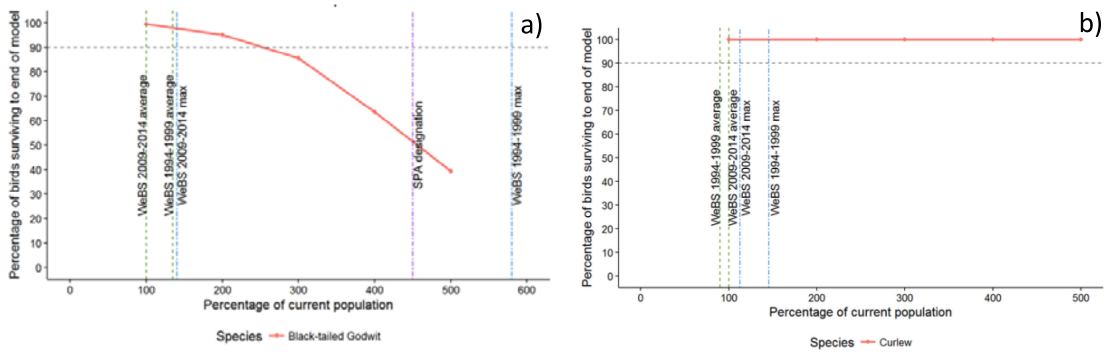


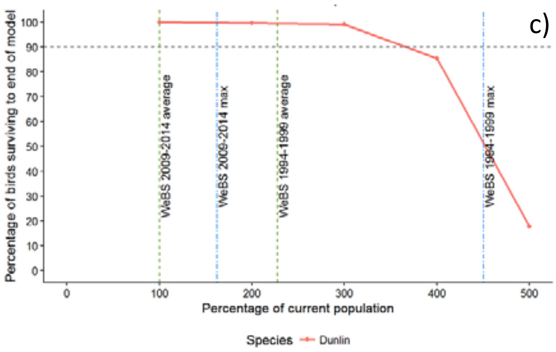
Figures A14.4 Percentage of birds supported to the end of the model when faced with population increases on the Severn estuary. a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)knot, f)oystercatcher, g)redshank, h)ringed plover and i)turnstone. Vertical lines indicate where SPA designated numbers and WeBS winter averages and peaks fall in relation to current averages (2009/10-2013/14).

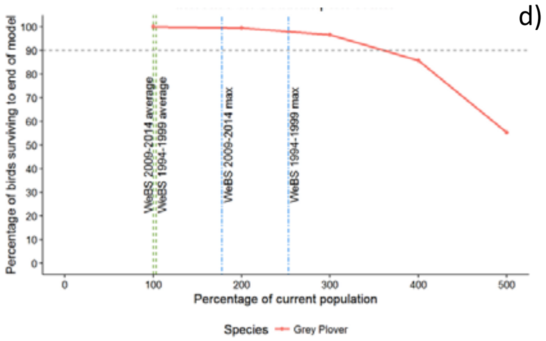


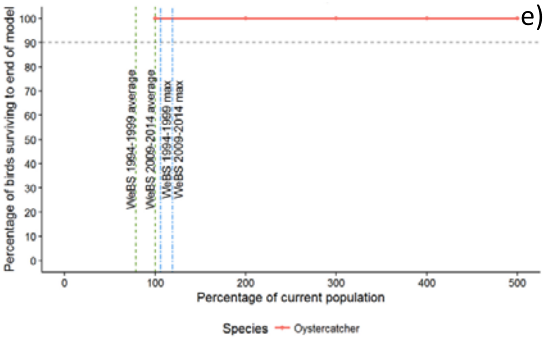


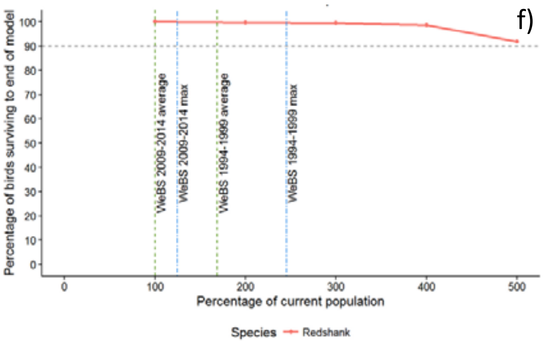
Figures A14.5 Percentage of birds supported to the end of the model when faced with population increases on Southampton Water. a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)oystercatcher, f)redshank and g)turnstone. Vertical lines indicate where SPA designated numbers and WeBS winter averages and peaks fall in relation to current averages (2009/10-2013/14).

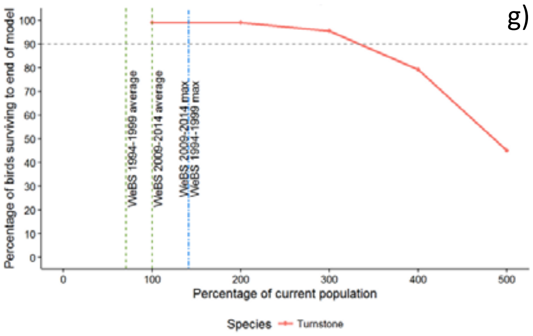



c)
Percentage of birds surviving to end of model
100
90
80
70
60
50
40
30
20
10
0
WeBS 2009-2014 average
WeBS 2009-2014 max
WeBS 1994-1999 average
WeBS 1994-1999 max
0
100
200
300
400
500
Percentage of current population
Species — Dunlin


d)
Percentage of birds surviving to end of model
100
90
80
70
60
50
40
30
20
10
0
WeBS 2009-2014 average
WeBS 1994-1999 average
WeBS 2009-2014 max
WeBS 1994-1999 max
0
100
200
300
400
500
Percentage of current population
Species — Grey Plover


e)
Percentage of birds surviving to end of model
100
90
80
70
60
50
40
30
20
10
0
WeBS 1994-1999 average
WeBS 2009-2014 average
WeBS 1994-1999 max
WeBS 2009-2014 max
0
100
200
300
400
500
Percentage of current population
Species — Oystercatcher


f)
Percentage of birds surviving to end of model
100
90
80
70
60
50
40
30
20
10
0
WeBS 2009-2014 average
WeBS 2009-2014 max
WeBS 1994-1999 average
WeBS 1994-1999 max
0
100
200
300
400
500
Percentage of current population
Species — Redshank


g)
Percentage of birds surviving to end of model
100
90
80
70
60
50
40
30
20
10
0
WeBS 1994-1999 average
WeBS 2009-2014 average
WeBS 2009-2014 max
WeBS 1994-1999 max
0
100
200
300
400
500
Percentage of current population
Species — Turnstone

Appendix 15. Percentage area that contains one or more prey item per size class on each modelled estuary.

Figures A15.1-7 Percentage of usable areas of an estuary containing prey items from specific size classes of a resource.

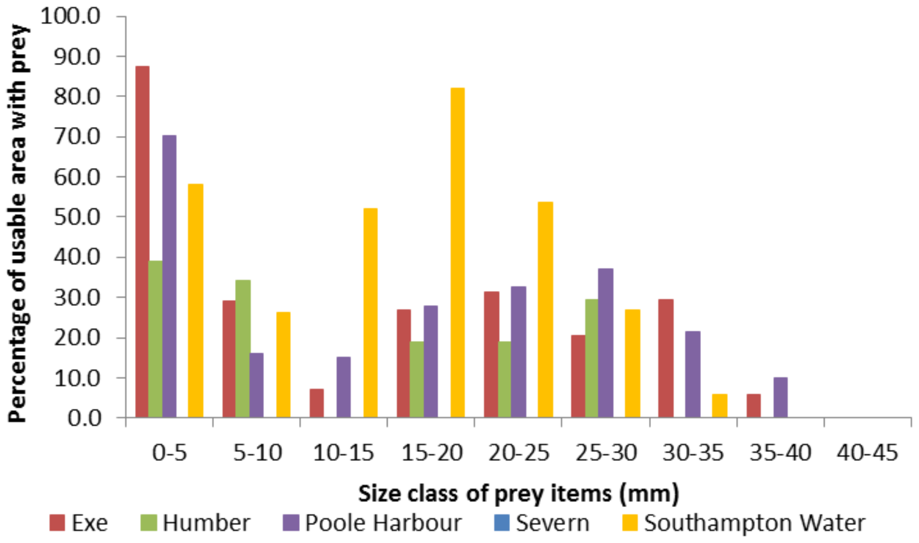


Figure A15.1 Percentage of usable area of an estuary containing Cerastoderma.

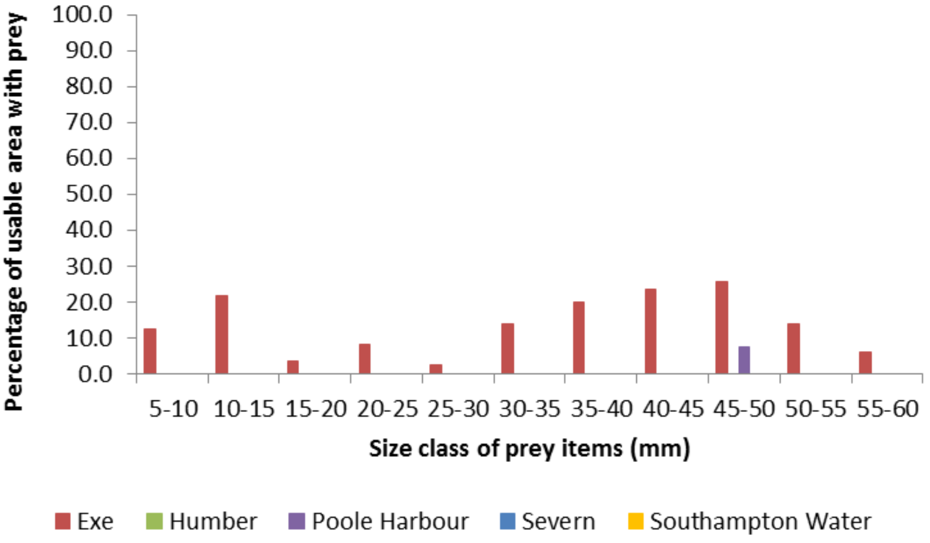


Figure A15.2 Percentage of usable area of an estuary containing mussels.

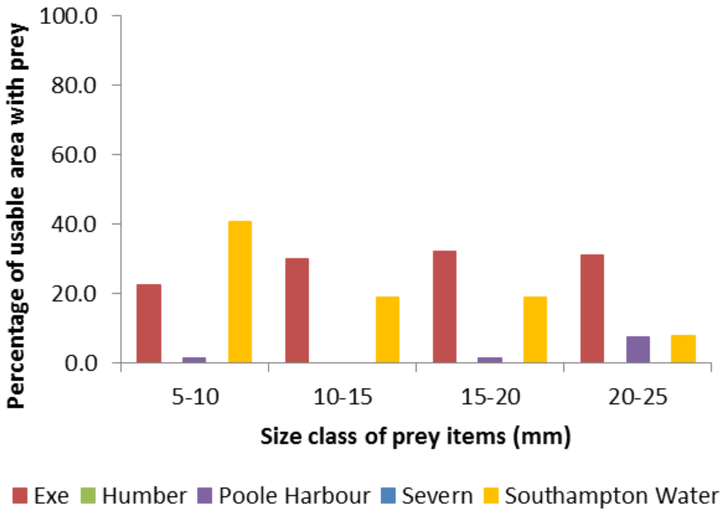


Figure A15.3 Percentage of usable area of an estuary containing Littorina.

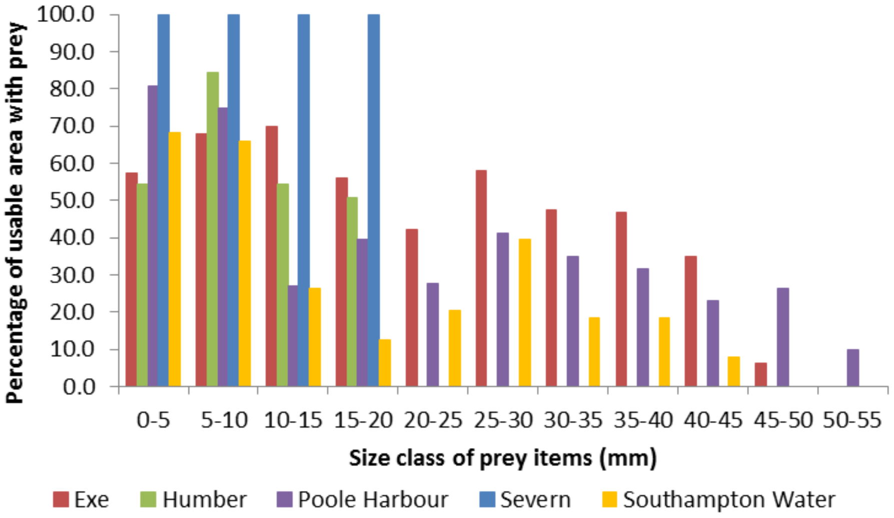


Figure A15.4 Percentage of usable area of an estuary containing Other Molluscs

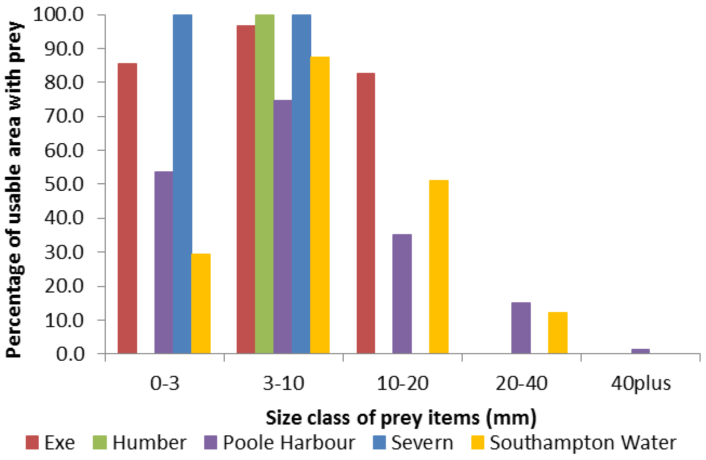


Figure A15.5 Percentage of usable area of an estuary containing crustaceans

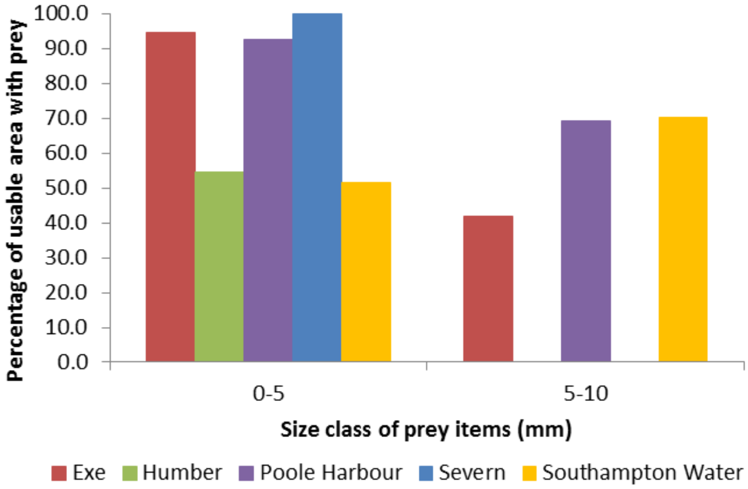


Figure A15.6 Percentage of usable area of an estuary containing Peringia

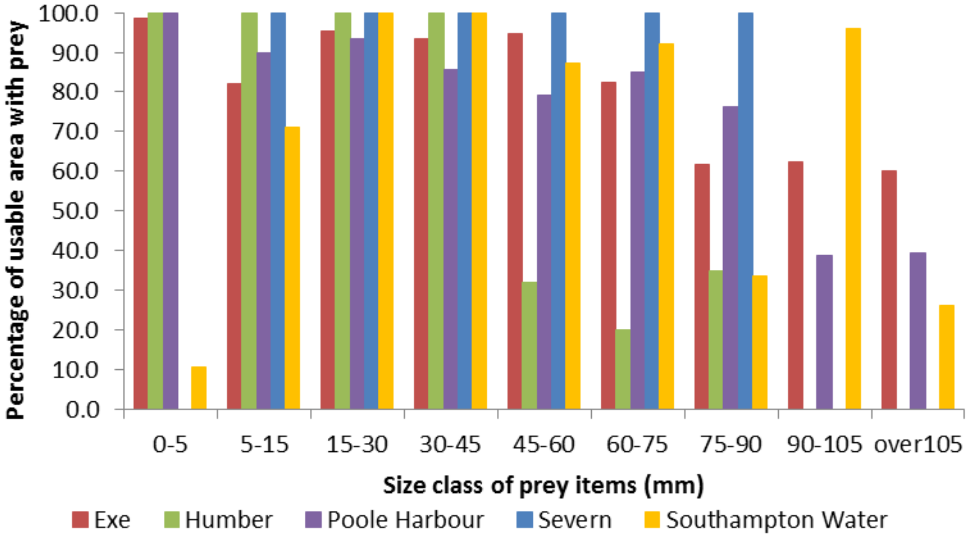
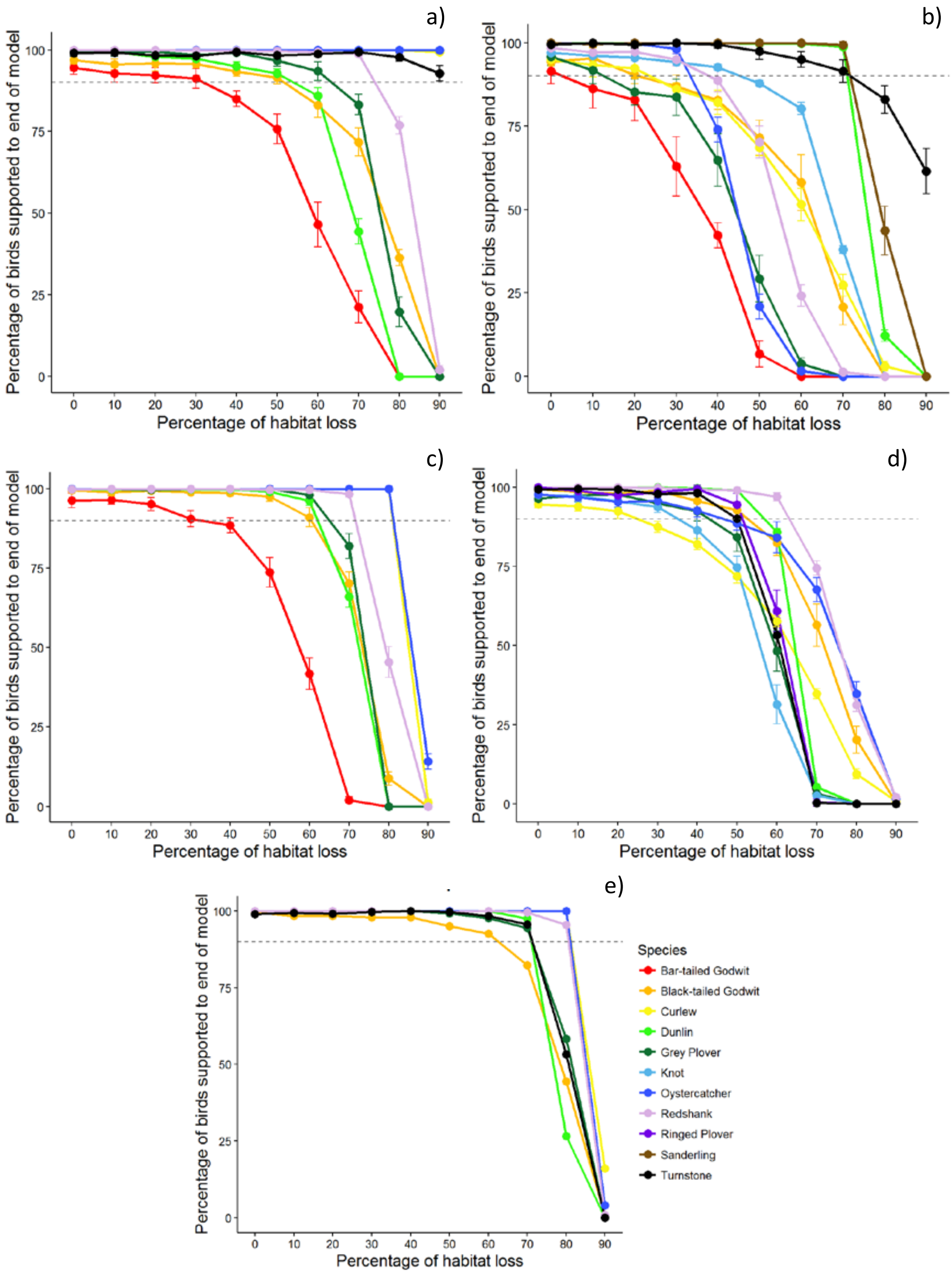


Figure A15.7 Percentage of usable area of an estuary containing marine worms

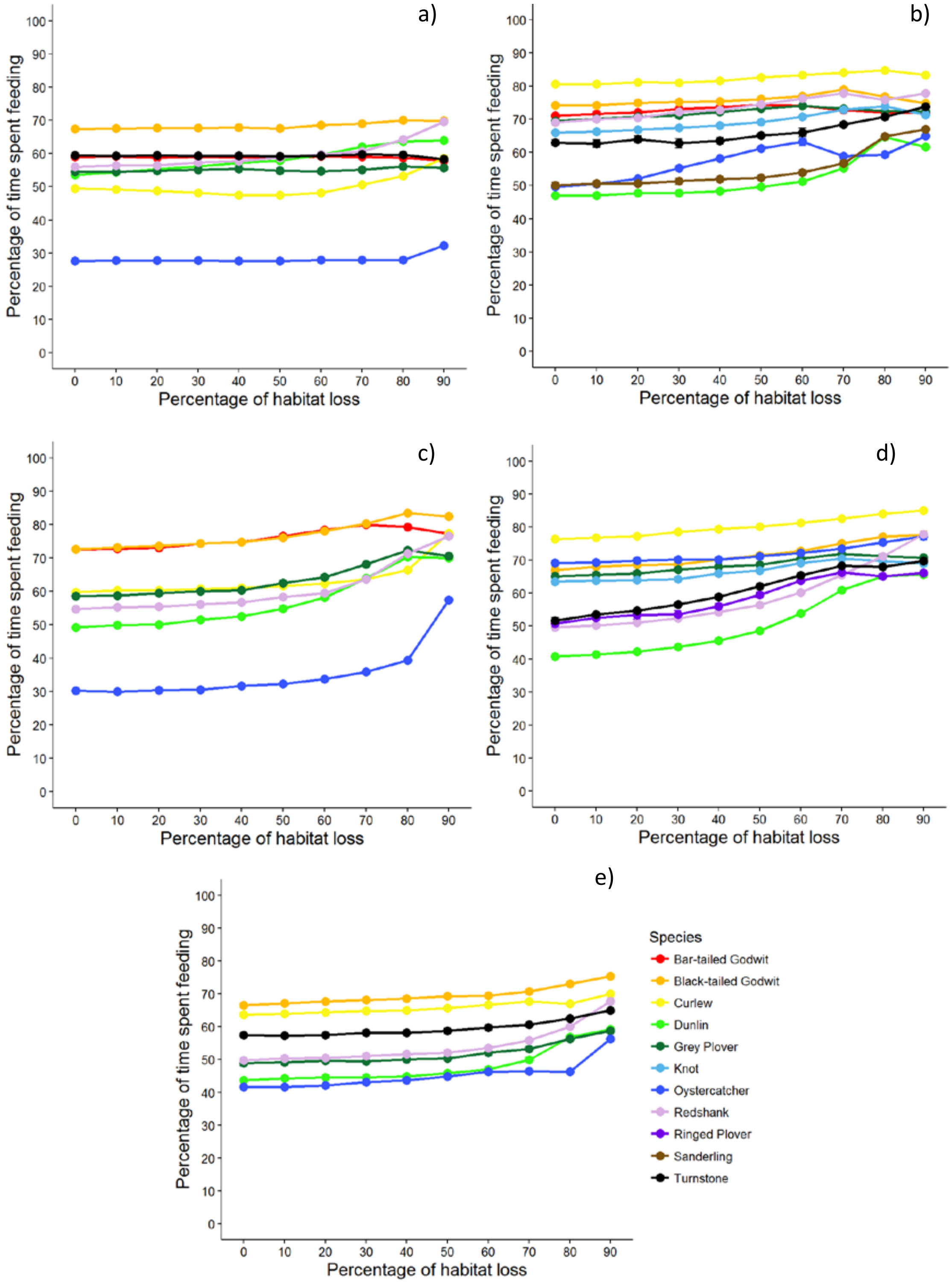
Appendix 16. Estuary specific numbers supported when faced with habitat loss.

Figures A16.1a–e. Percentage of birds of eleven species supported to the end of a winter modelling period for five estuaries whilst affected by habitat loss. a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) The Severn estuary and e) Southampton Water.



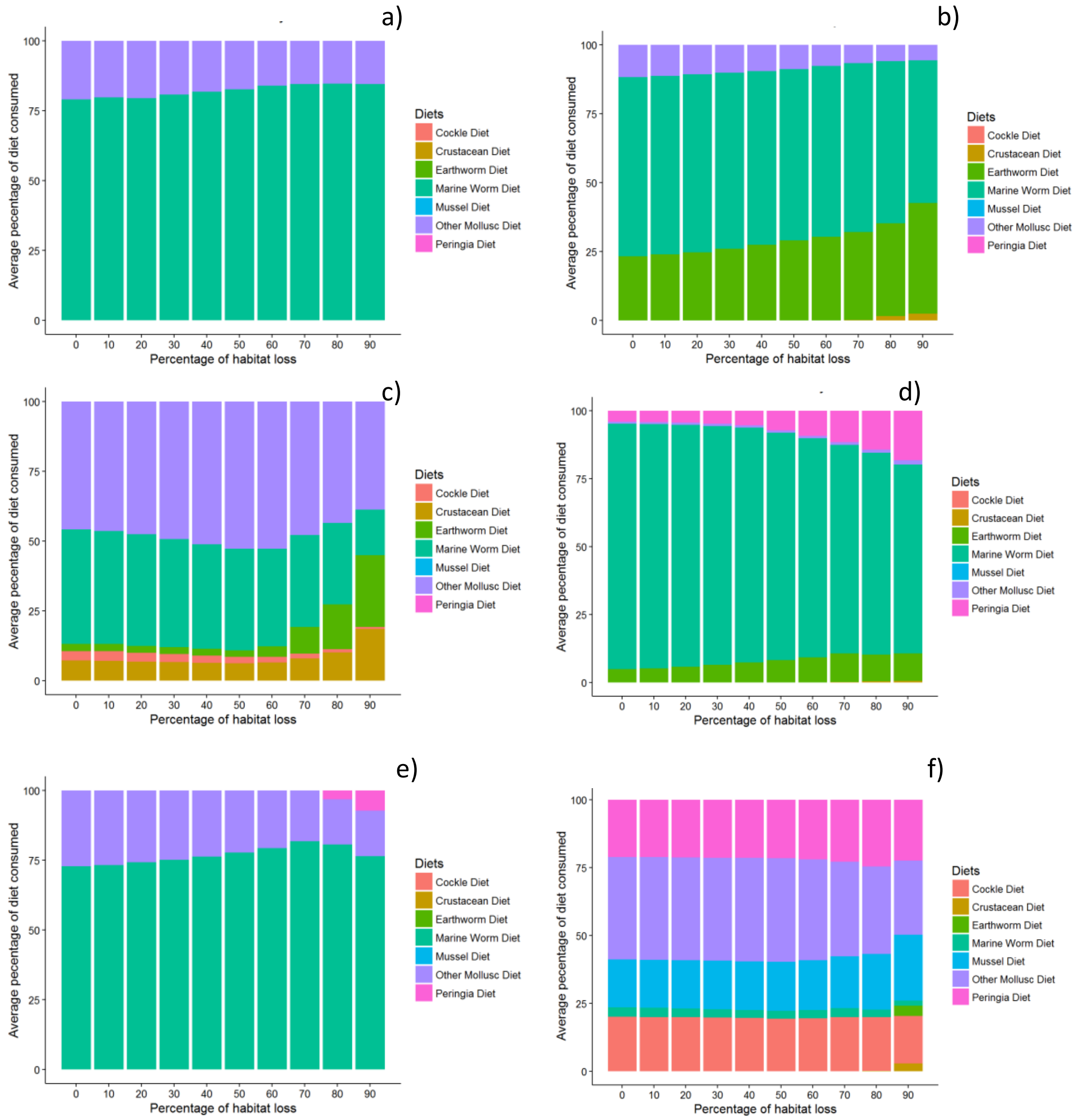
Appendix 17. Estuary specific percentage of time spent feeding when faced with habitat loss.

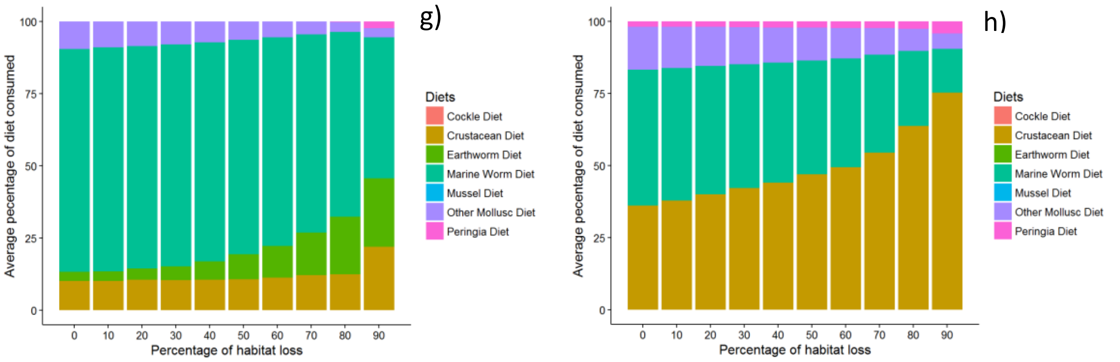
Figures A17.2a–e. Percentage of time spent feeding for eleven species on five estuaries whilst affected by habitat loss. a) Exe estuary, b) The Humber estuary, c) Poole Harbour, d) The Severn estuary and e) Southampton Water.



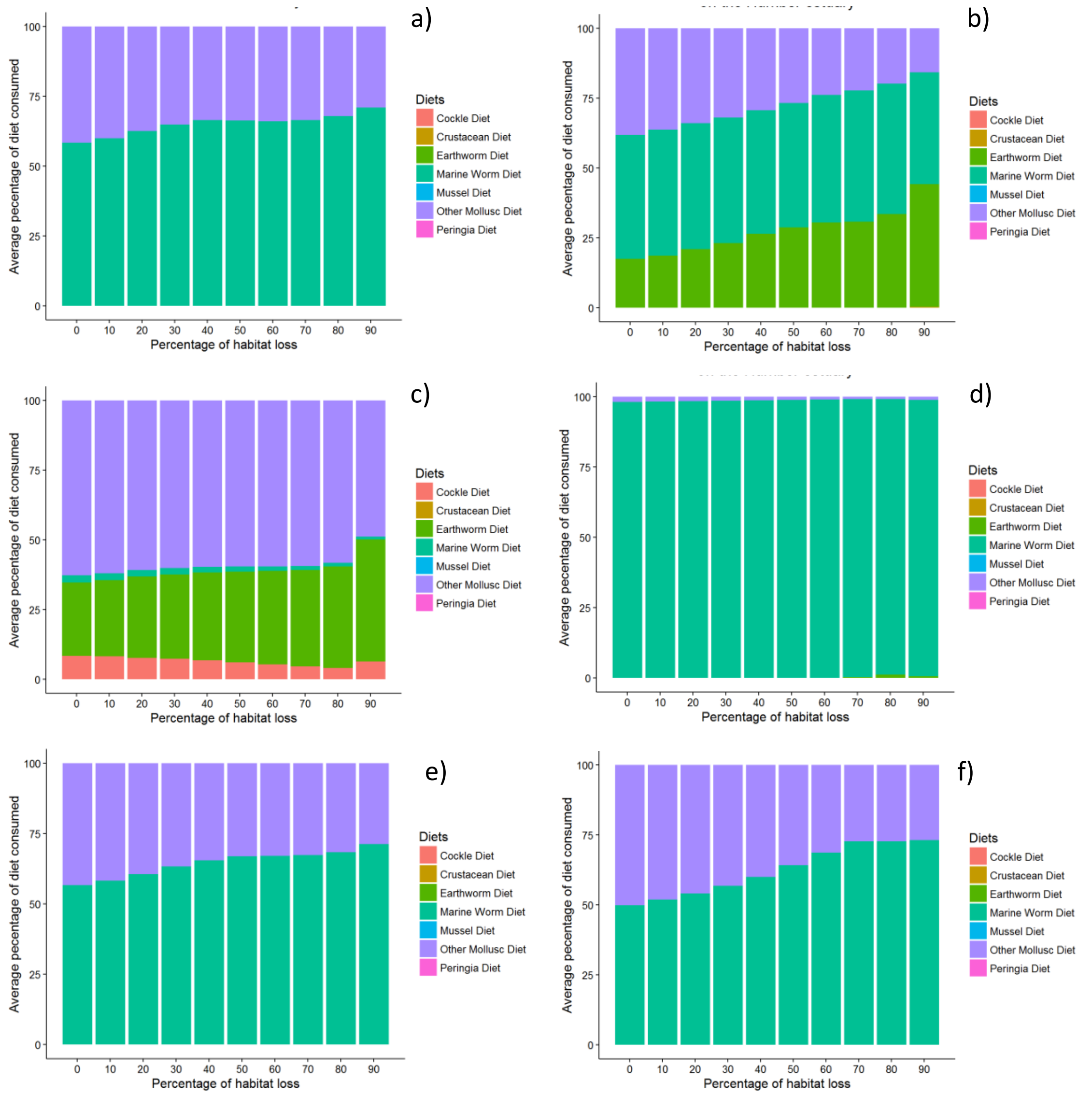
Appendix 18. Dietary shifts in each species on an estuary when faced with habitat loss

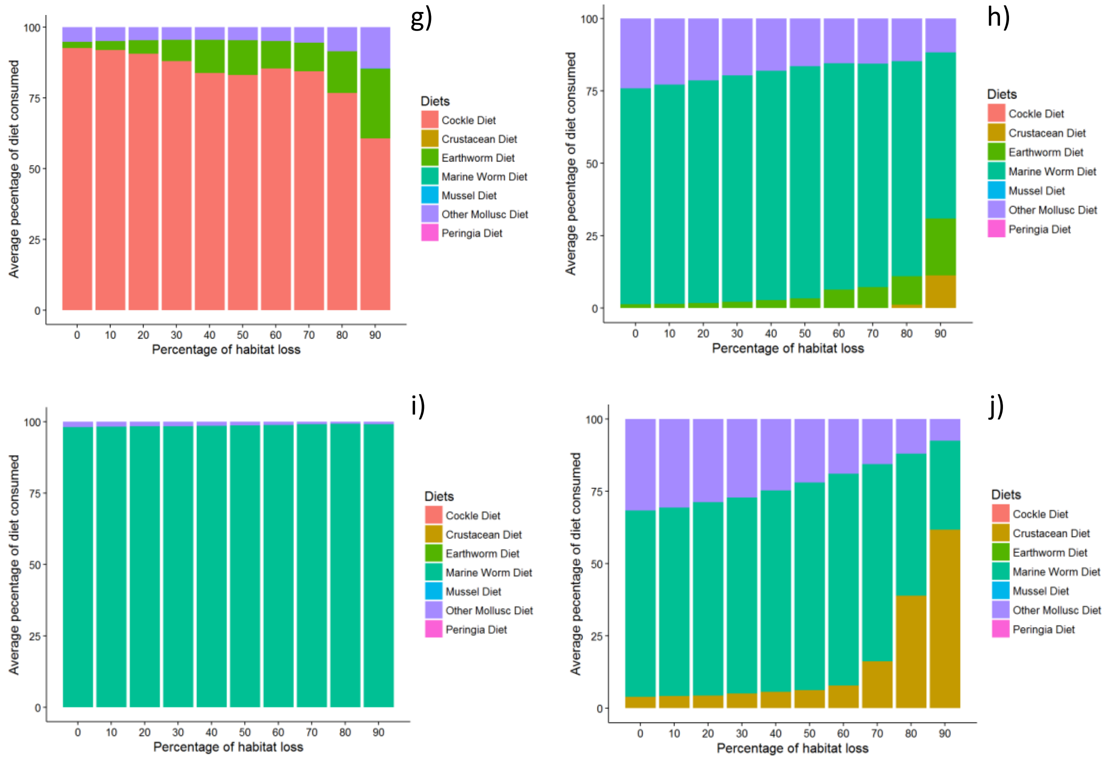
Figures A18.1a-h. Dietary preferences of wading birds on the ***Exe estuary*** *when faced with habitat loss: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher, g)redshank and h)turnstone.*



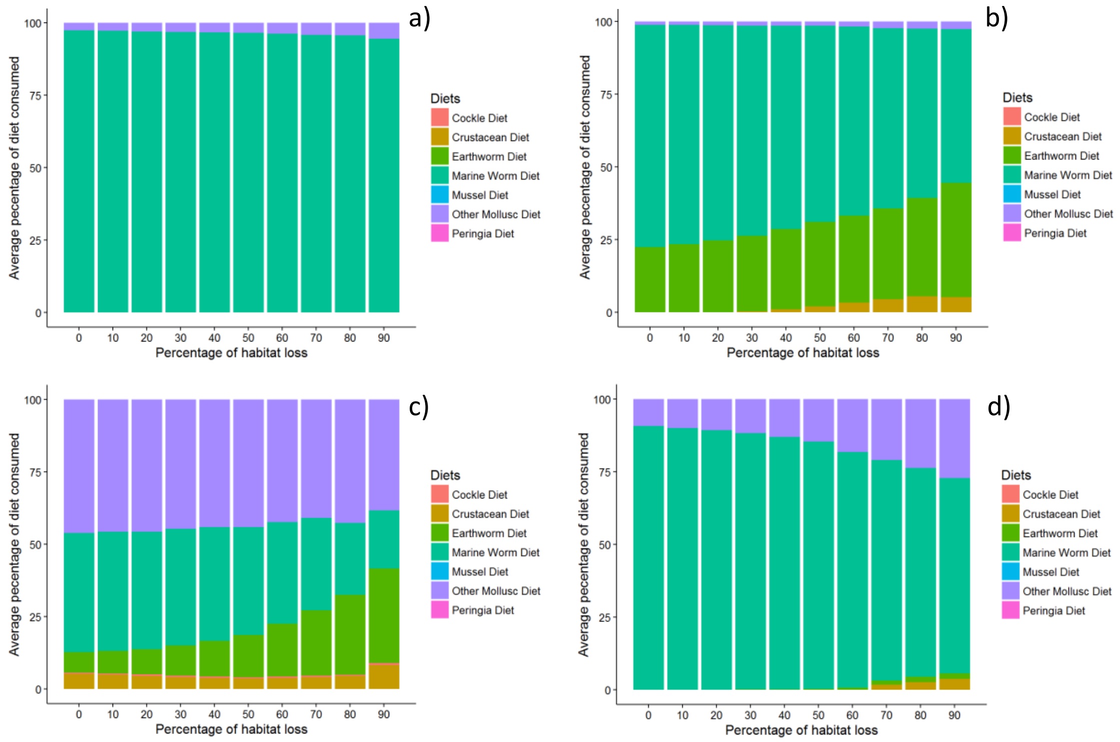


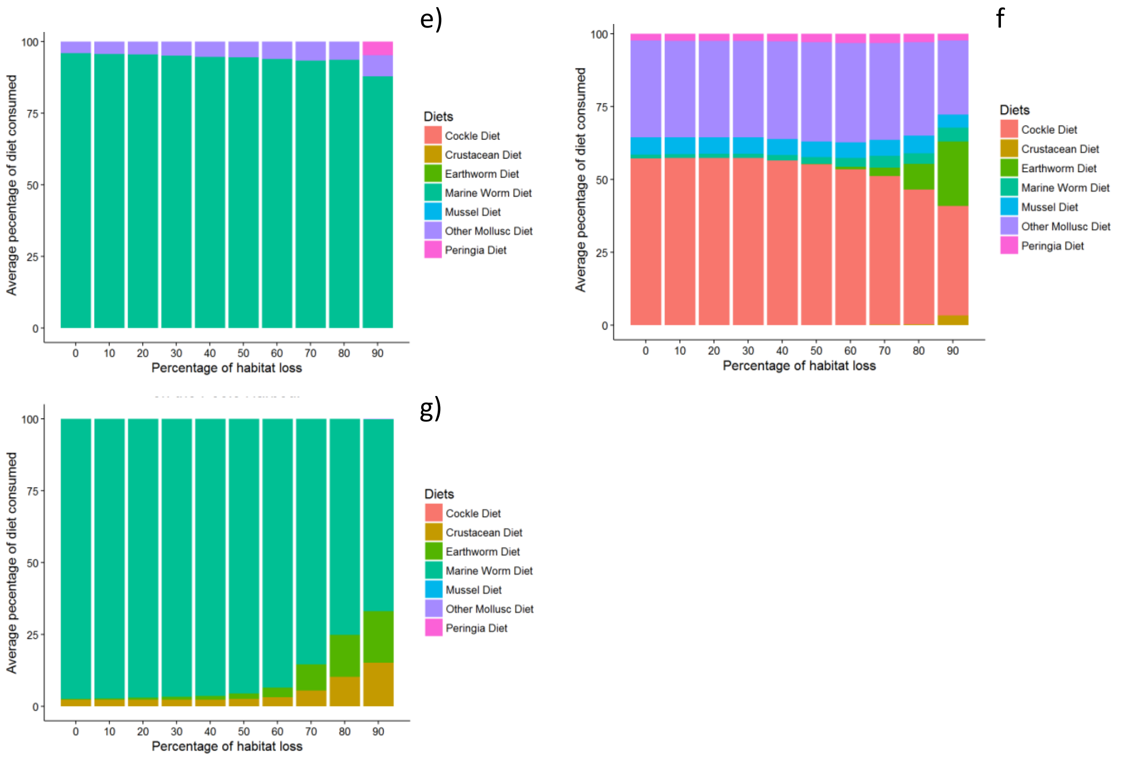
Figures A18.2a-j. Dietary preferences of wading birds on the ***Humber*** *estuary when faced with habitat loss: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)knot, g)oystercatcher, h)redshank, i)sanderling and j)turnstone.*



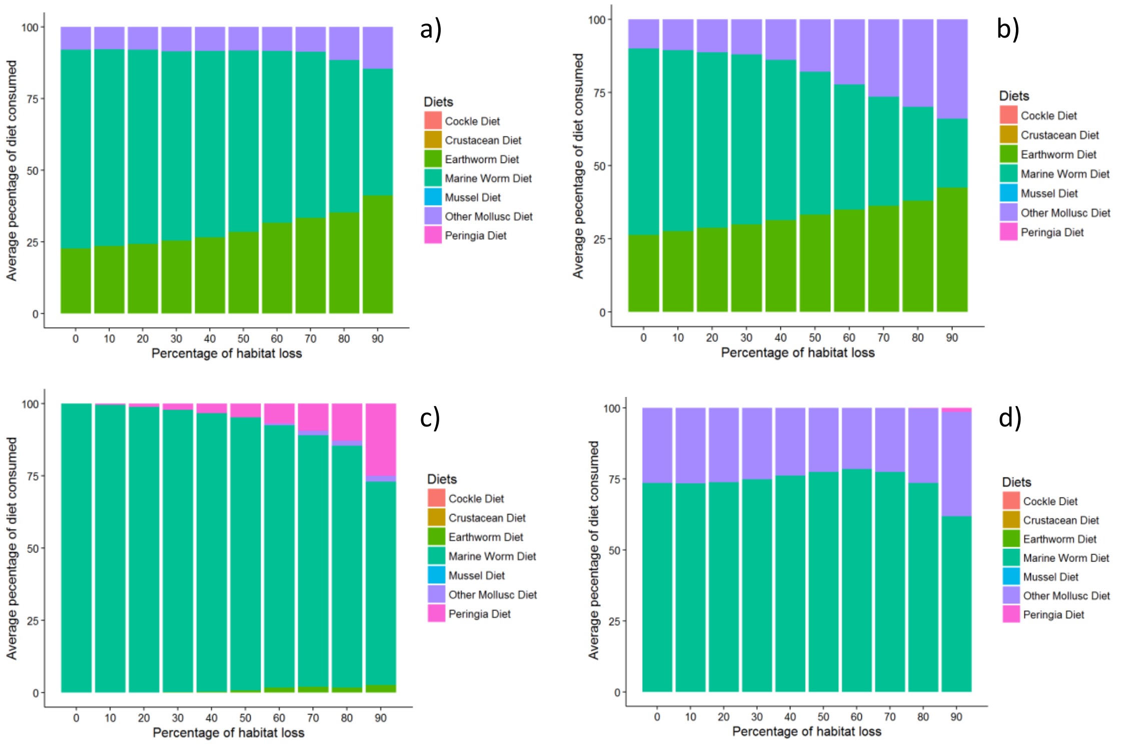


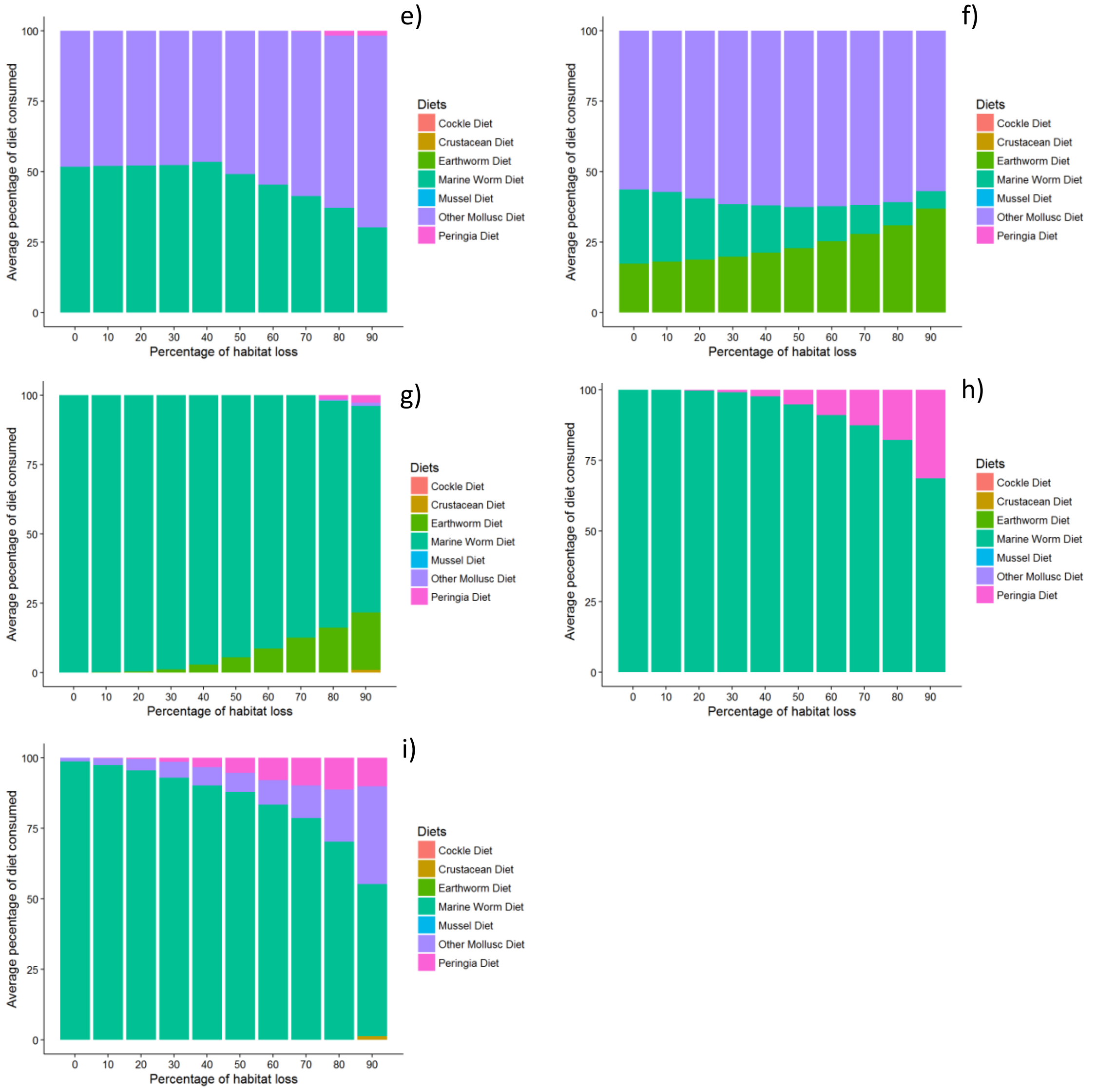
Figures A18.3a-g. Dietary preferences of wading birds on ***Poole Harbour*** *when faced with habitat loss: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher and g)redshank.*



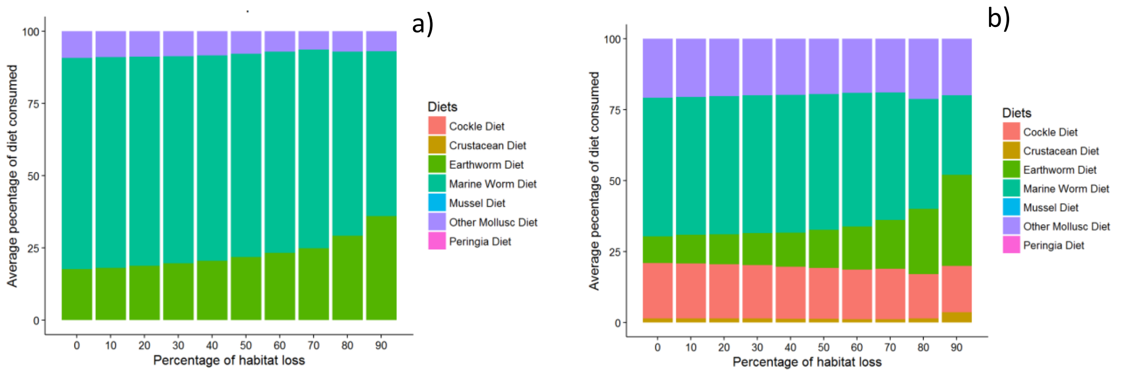


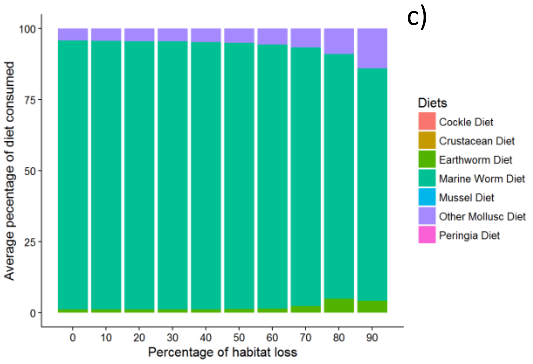
Figures A18.4a-i. Dietary preferences of wading birds on the ***Severn estuary*** *when faced with habitat loss: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)knot, f)oystercatcher, g)redshank, h)ringed plover and i)turnstone.*

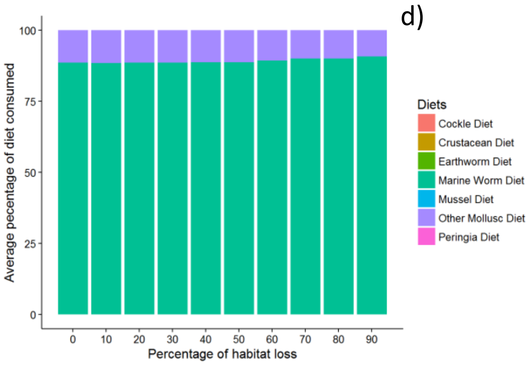


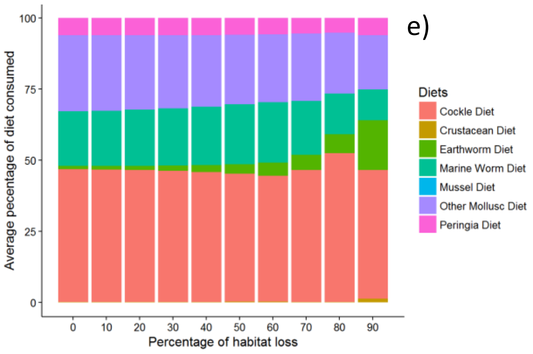


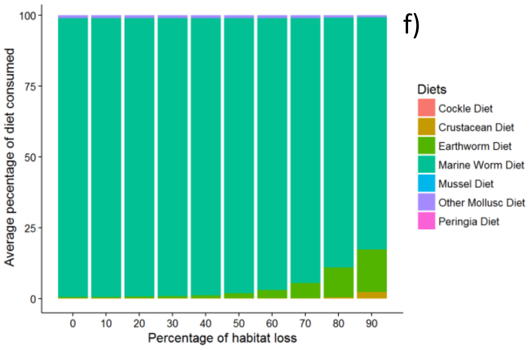
Figures A18.5a-g. Dietary preferences of wading birds on ***Southampton Water*** *when faced with habitat loss: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)oystercatcher, f)redshank and g)turnstone.*

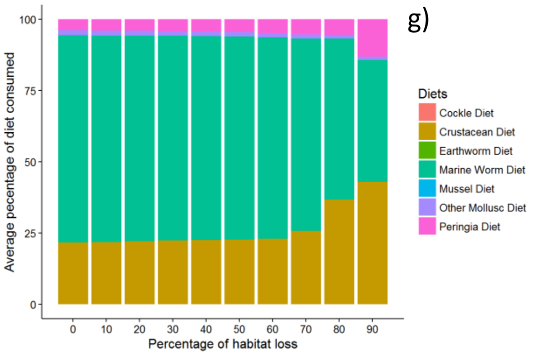



c)
Average pecentage of diet consumed
100
75
50
25
0
0
10
20
30
40
50
60
70
80
90
Percentage of habitat loss
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet


d)
Average pecentage of diet consumed
100
75
50
25
0
0
10
20
30
40
50
60
70
80
90
Percentage of habitat loss
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet

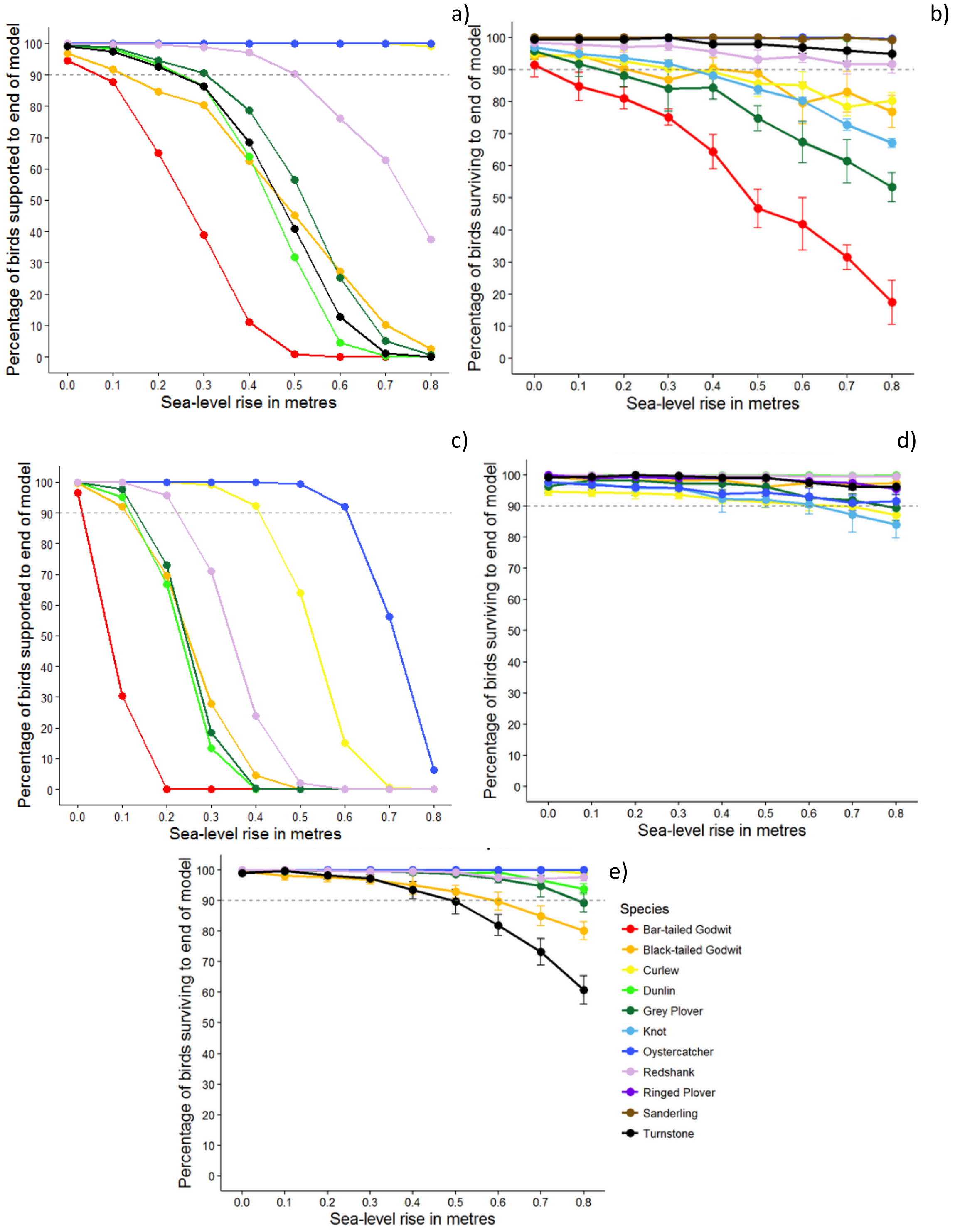

e)
Average pecentage of diet consumed
100
75
50
25
0
0
10
20
30
40
50
60
70
80
90
Percentage of habitat loss
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet


f)
Average pecentage of diet consumed
100
75
50
25
0
0
10
20
30
40
50
60
70
80
90
Percentage of habitat loss
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet


g)
Average pecentage of diet consumed
100
75
50
25
0
0
10
20
30
40
50
60
70
80
90
Percentage of habitat loss
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet

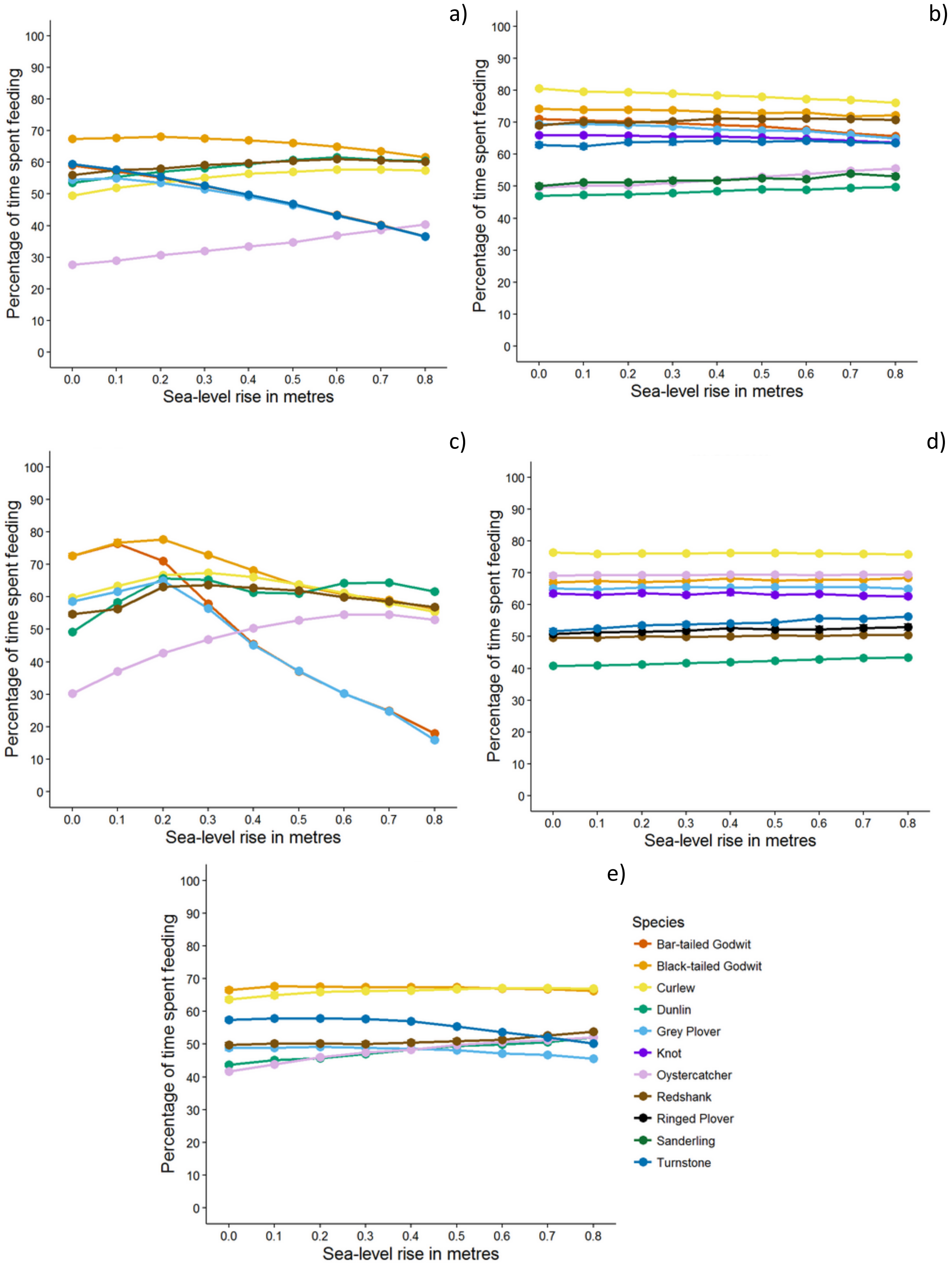
Appendix 19. Estuary specific numbers supported when faced with sea-level rise.

Figures A19.1a–e. Percentage of birds of eleven species supported to the end of a winter modelling period for five estuaries whilst affected by sea-level rise. a) Exe estuary, b) Humber estuary, c) Poole Harbour, d) The Severn estuary and e) Southampton Water.



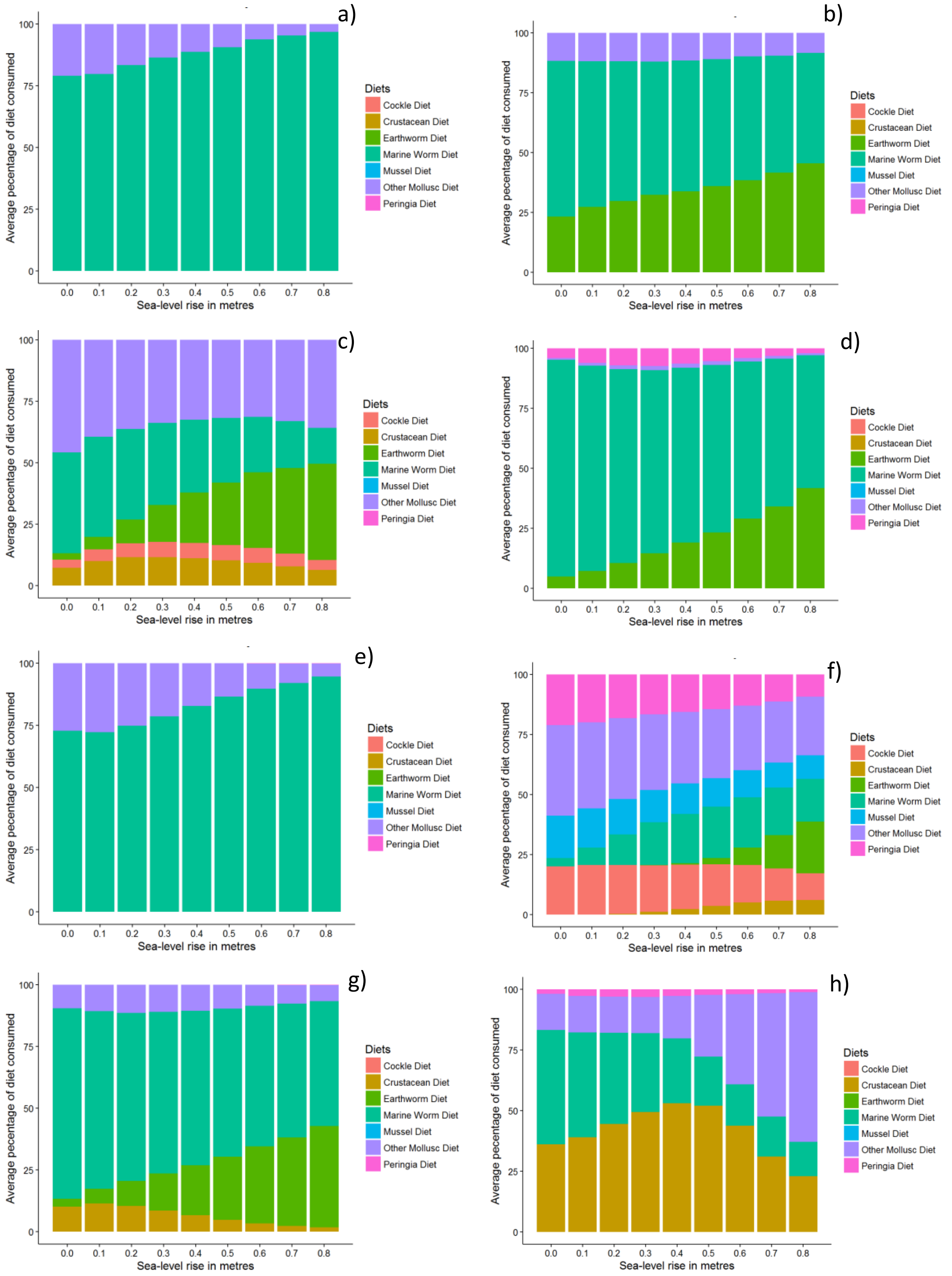
Appendix 20. Estuary specific percentage of time spent feeding when faced with sea-level rise.

Figures A20.1a–e. Percentage of time spent feeding for eleven species on five estuaries whilst affected by sea-level rise. a) Exe estuary, b) The Humber estuary, c) Poole Harbour, d) The Severn estuary and e) Southampton Water.

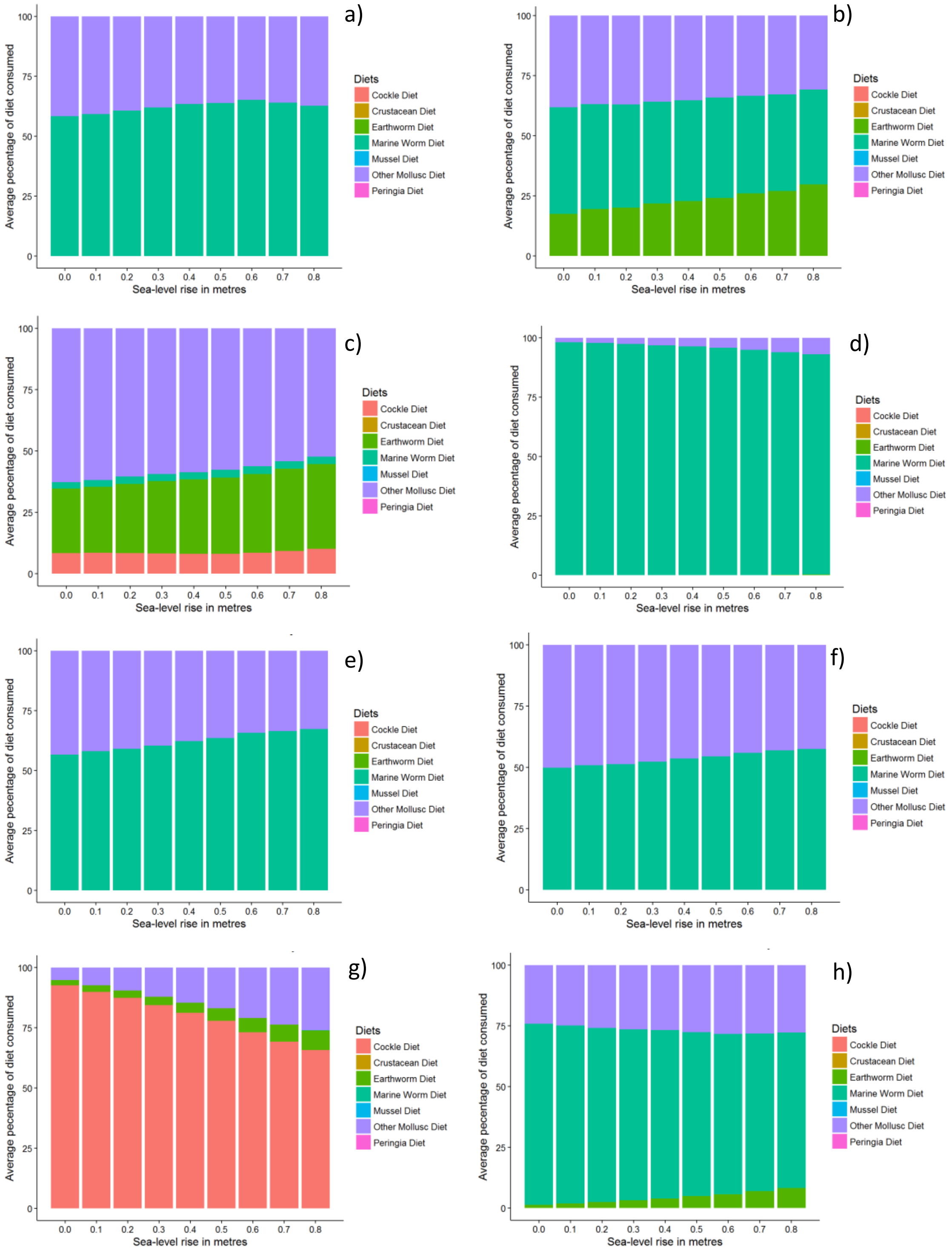


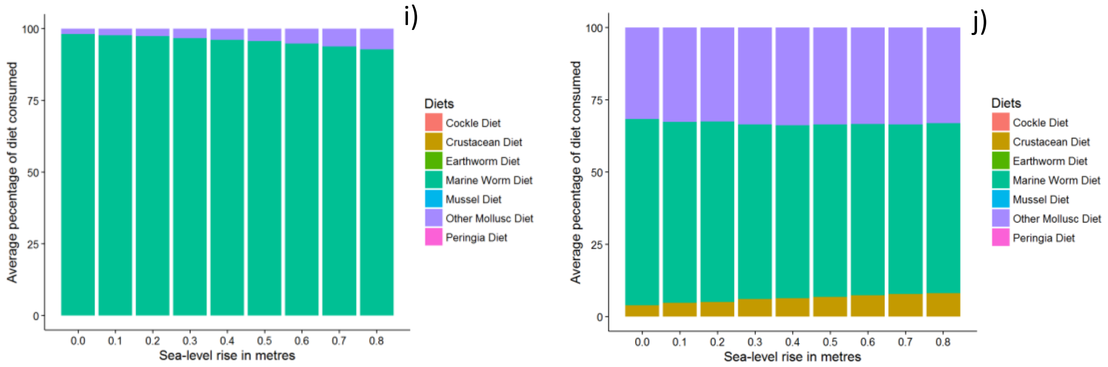
Appendix 21. Dietary shifts in each species on an estuary when faced with sea-level rise

Figures A21.1a-h. Dietary preferences of wading birds on the ***Exe estuary*** *when faced with sea-level rise: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher, g)redshank and h)turnstone.*

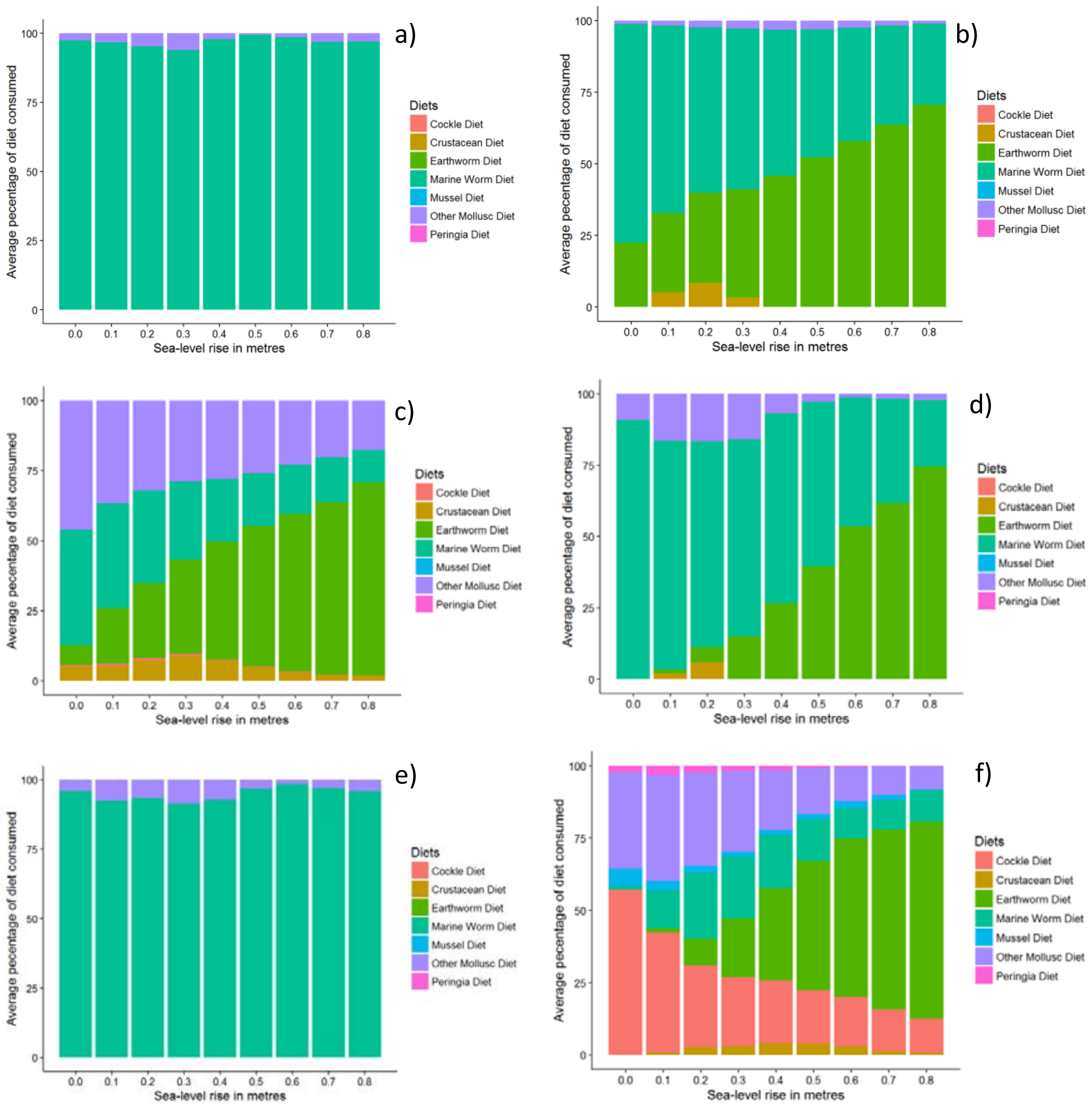


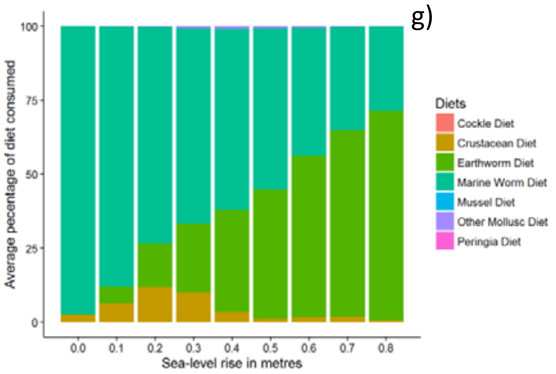
Figures A21.2a-j. Dietary preferences of wading birds on the ***Humber*** *estuary when faced with sea-level rise: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)knot, g)oystercatcher, h)redshank, i)sanderling and j)turnstone.*



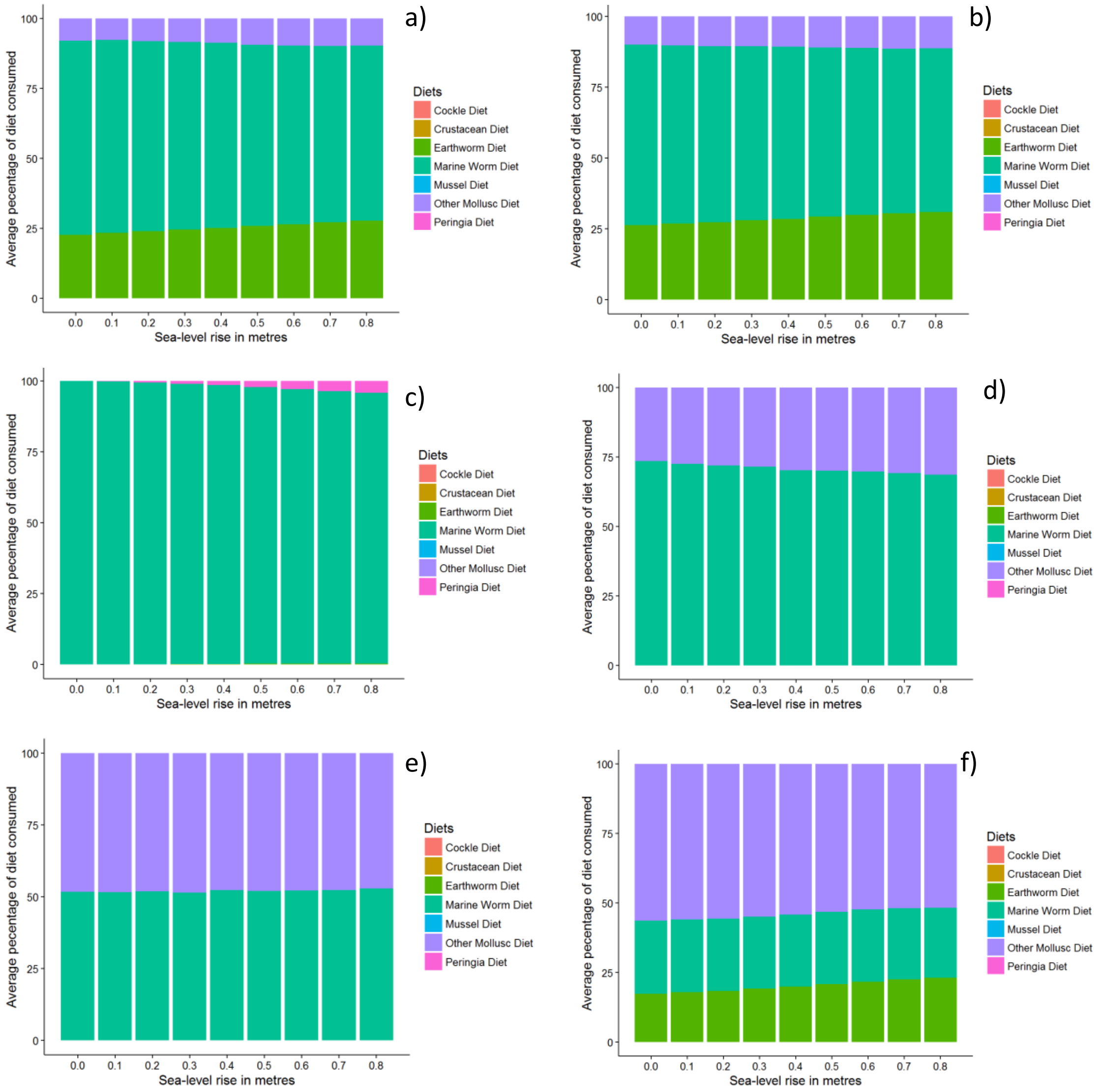


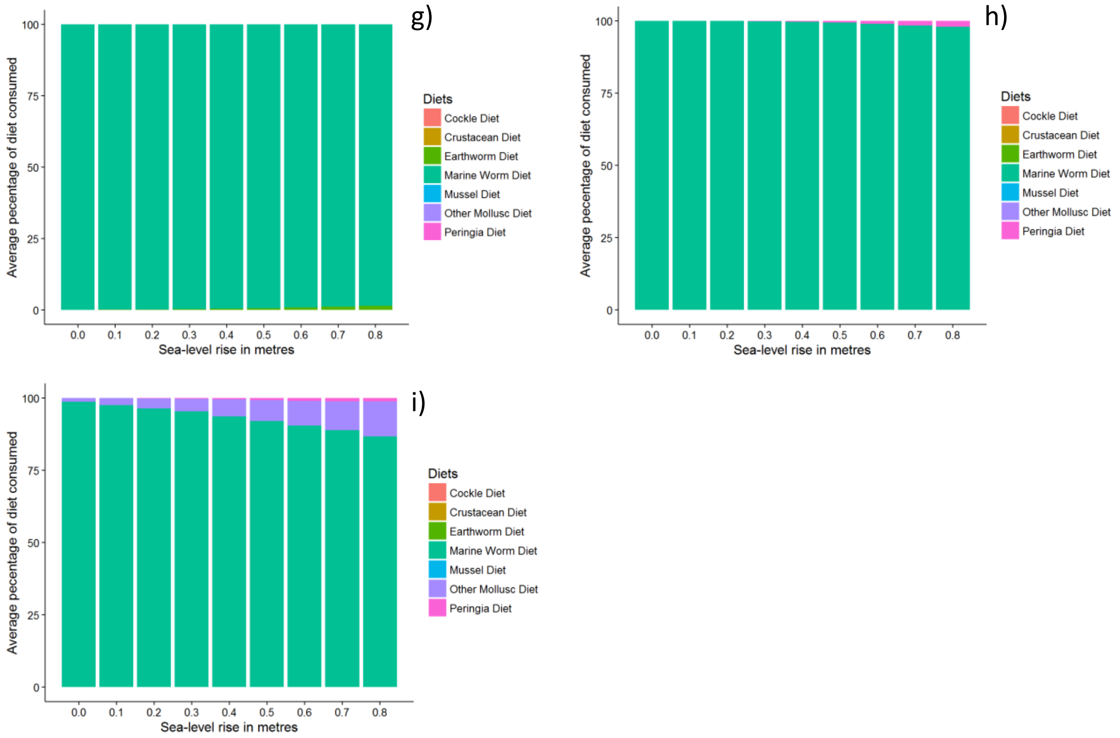
Figures A21.3a-g. Dietary preferences of wading birds on ***Poole Harbour*** *when faced with sea-level rise: a)bar-tailed godwit, b)black-tailed godwit, c)curlew, d)dunlin, e)grey plover, f)oystercatcher and g)redshank.*



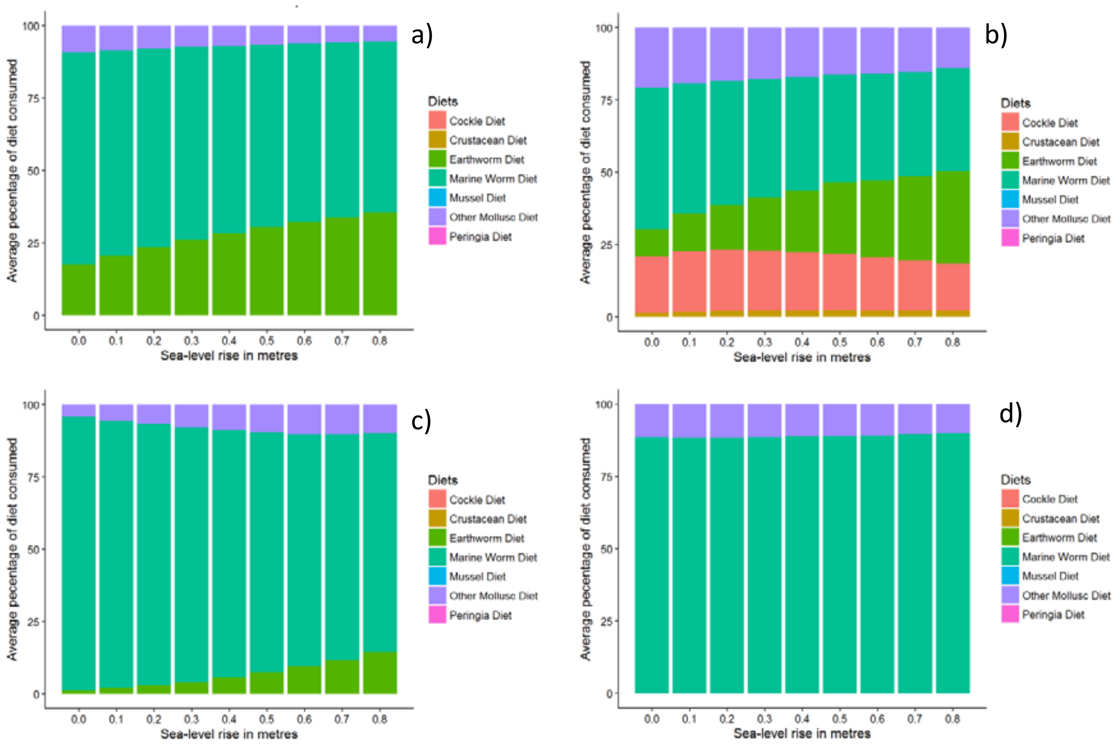


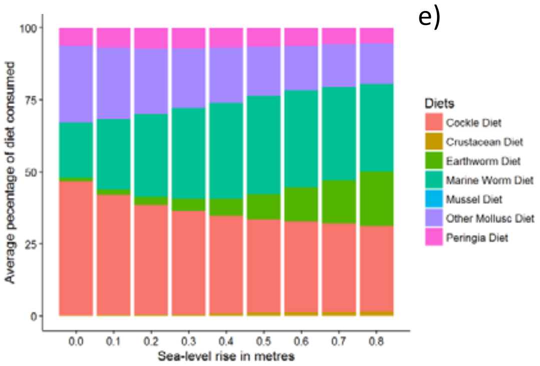
Figures A21.4a-i. Dietary preferences of wading birds on the ***Severn estuary*** *when faced with sea-level rise: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)knot, f)oystercatcher, g)redshank, h)ringed plover and i)turnstone.*

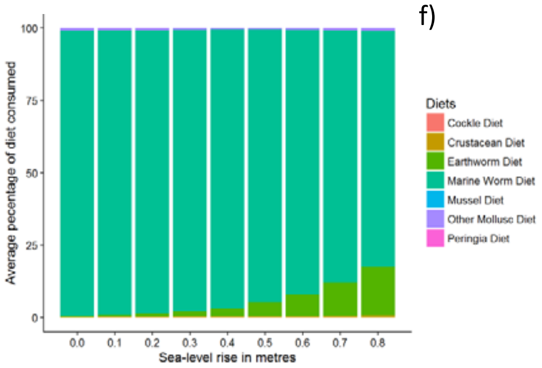


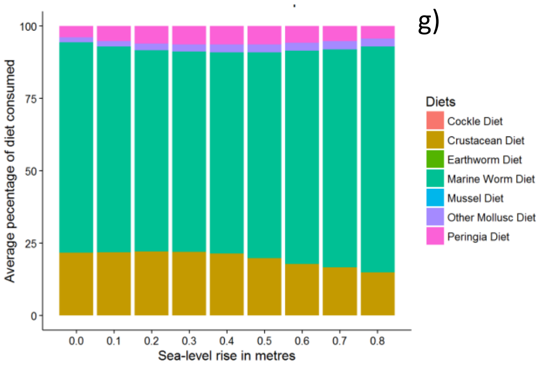


*Figures A21.5a-g. Dietary preferences of wading birds on **Southampton Water** when faced with sea-level rise: a)black-tailed godwit, b)curlew, c)dunlin, d)grey plover, e)oystercatcher, f)redshank and g)turnstone.*




e)
Average pecentage of diet consumed
100
75
50
25
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Sea-level rise in metres
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet


f)
Average pecentage of diet consumed
100
75
50
25
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Sea-level rise in metres
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet


g)
Average pecentage of diet consumed
100
75
50
25
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Sea-level rise in metres
Diets
Cockle Diet
Crustacean Diet
Earthworm Diet
Marine Worm Diet
Mussel Diet
Other Mollusc Diet
Peringia Diet

Appendix 22. Values of habitat loss and associated population declines in wading birds from the literature.

Table A22.1. Empirical sources for habitat declines and associated wading bird population declines from the literature.

Habitat loss type	Location	Species affected	Latin	Dates	Habitat loss (%)	Population remaining (%)	References
Land reclaimation	Teesmouth, UK	Dunlin	Calidris alpina	1970-1977	77	75	Prater 1981
Land reclaimation	Teesmouth, UK	Oystercatcher	Haematopus ostralegus	1970-1977	77	78	Prater 1981
Land reclaimation	Teesmouth, UK	Redshank	Tringa totanus	1970-1977	77	45	Prater 1981
Land reclaimation	Teesmouth, UK	Curlew (Eurasian)	Numenius arquata	1970-1977	77	42	Prater 1981
Land reclaimation	Teesmouth, UK	Bar-tailed godwit	Limosa lapponica	1970-1977	77	38	Prater 1981
Land reclaimation	Teesmouth, UK	Knot	Calidris canutus	1970-1977	77	35	Prater 1981
Land reclaimation	Teesmouth, UK	Dunlin	Calidris alpina	1972-1974	60	33	Evans 1978
Land reclaimation	Teesmouth, UK	Grey plover	Pluvialis squatarola	1972-1974	60	36	Evans 1978
Land reclaimation	Teesmouth, UK	Bar-tailed godwit	Limosa lapponica	1972-1974	60	12	Evans 1978
Land reclaimation	Teesmouth, UK	Redshank	Tringa totanus	1972-1974	60	19	Evans 1978
Land reclaimation	Teesmouth, UK	Shelduck	Tadorna tadorna	1972-1974	60	68	Evans 1978
Dredging	The Wash, UK	Oystercatcher	Haematopus ostralegus	1981-2003	70	91.7	Atkinson et al. 2010
Dredging	The Wash, UK	Knot	Calidris canutus	1981-2003	70	91.4	Atkinson et al. 2010
Dams	Oosterschelde, NL	Waders	*unspecified*	1986-1987	30	69	Schekkerman et al. 1994, Duriez 2009
Overfishing	The Wash, UK	Knot	Calidris canutus	1990-1992	80	37	Atkinson et al. 2003, Dare et al. 2004
Overfishing	The Wash, UK	Oystercatcher	Haematopus ostralegus	1990-1999	80	27.5	Atkinson et al. 2003, Dare et al. 2004
Land reclaimation	Bohai Bay, CN	Curlew (Eurasian)	Numenius arquata	1994-2010	34	89	Yang et al. 2011
Overfishing	Wadden Sea, NL	Knot	Calidris canutus	1996-2005	55	58	Kraan 2010
Dredging	Wadden Sea, NL	Knot	Calidris canutus	1997-2003	68	20	Piersma 2007
Barage	Cardiff Bay, UK	Redshank	Tringa totanus	1999-2000	100	7	Burton & Armitage 2008, Burton 2006