INVESTIGATING THE PHYSICAL AND ECOLOGICAL DRIVERS OF CHANGE IN A COASTAL ECOSYSTEM: FROM INDIVIDUAL- TO POPULATION-SCALE IMPACTS

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Declaration

I confirm that the work presented in this thesis is my own, with the exception of:

In Chapter 2, the collection, processing and identification of benthic samples from 2009 was a collaborative effort led by Dr Roger Herbert, and part of a condition survey for Poole Harbour, funded by Natural England. The full output of this study is reported in:

Herbert, R.J.H., Ross, K., Hübner, R., Stillman, R.A., 2010. *Intertidal invertebrates and biotopes of Poole Harbour SSSI and survey of Brownsea Island Lagoon: Report to Natural England*, Poole, UK.

The collection and processing of benthic samples from 2002 was conducted by the Centre for Ecology and Hydrology and the data were collated by Dr Richard Caldow.

Species-level identification of a subset of the benthic fauna of Brownsea Island Lagoon, reported in Chapter 3, was conducted by Dr Roger Bamber and funded by the EDRF Interreg IVB project EcoSal: "Ecotourism in saltworks of the Atlantic: a strategy for integral and sustainable development" (UK partner, Bournemouth University).

The individual-based model presented in Chapter 6 was developed in collaboration with Prof. Richard Stillman.

Data on the nektonic prey abundance of Brownsea Island Lagoon were collected by Ross Wheeler.

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Investigating the physical and ecological drivers of change in a coastal ecosystem: from individual- to population-scale impacts

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Abstract

Coastal ecosystems are undergoing unprecedented rates of environmental change. Many of these changes are anthropogenically-driven and linked to long-term, climate-related phenomena. This thesis focusses on ecological change in soft sediment intertidal habitats. One of the largest harbours in Europe, Poole Harbour, is used as a case study. It contains a variety of important habitats including intertidal mudflat and non-tidal saline lagoon.

The two main themes of the thesis are 1) assessing the physical and ecological factors that determine benthic invertebrate abundance, distribution and community structure, which is examined at the scale of the whole harbour, and at the scale of individual habitats: an intertidal mudflat and a saline lagoon; and 2) predicting the response of an overwintering shorebird population, the pied avocet (*Recurvirostra avosetta*), to future environmental changes, such as sea-level rise and habitat loss. This is achieved by development of an individual-based model (IBM) and consideration of the species' unique foraging behaviour.

This study contributes to the understanding of the factors structuring soft sediment benthic communities, including the use of data from fine-scale hydrodynamic models. It offers a unique comparison of the spatial and temporal variables driving community structure of a saline lagoon and an intertidal mudflat. It also provides insight into the foraging ecology of the pied avocet at a level of detail that has not previously been considered, including a comparison of foraging behaviour in a tidal and non-tidal habitat, the importance of social foraging, and the novel application of an IBM to this species.

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List of abbreviations

A–G ratio – annelid–gastropod ratio

AONB – Area of Outstanding Natural Beauty

BEM – bioclimatic envelope modelling

BTO – British Trust for Ornithology

DBC – Dorset Bird Club

DEFRA – Department for Environment, Food and Rural Affairs

DERC – Dorset Environmental Records Centre

EDF-LNHE - Electricité de France Laboratoire National d’Hydraulique et Environnement

EEA – European Environment Agency

EIA – environmental impact assessment

EMS – European Marine Site

GAM – generalised additive model

GLM – generalised linear model

GLMM – generalised linear mixed-effects model

GPS – global positioning system

IBM – individual-based model

JNCC – Joint Nature Conservation Committee

nMDS – non-metric multidimensional scaling

ppt – parts per thousand

RNLI – Royal National Lifeboat Institution

RSPB – Royal Society for the Protection of Birds

SAC – Special Areas of Conservation

SDM – species distribution modelling

SEA – strategic environmental assessment

SMP – shoreline management plans

SPA – Special Protection Area

SSSI – Site of Specific Scientific Interest

WeBS – Wetland Birds Survey

WWT – Wildfowl and Wetlands Trust

Chapter 1: Introduction

1.1 Abstract

The purpose of this chapter is to establish the context and rationale for the proceeding body of work. Here I outline the global importance of coastal habitats and the threats to this ecosystem posed by climate change and other anthropogenic causes. Having established the need for research into the study of both the benthic invertebrate communities and overwintering shorebird populations of soft sediment coastal habitats, the remainder of this chapter provides a review of current approaches to predictive modelling, to provide theoretical background to the following chapters. I give a brief description of the study site, Poole Harbour, and the model shorebird species, the pied avocet (*Recurvirostra avosetta* [Linnaeus 1758]). Finally, I outline the main aims and objectives of the thesis, and the structure of subsequent chapters.

1.2 Wider context and rationale

The human population currently exceeds 7.1 billion, and the earth's ecosystems are undergoing unprecedented rates of environmental change (Turner et al. 1994; Pielke Sr. 2005). In this so-called 'anthropocene era', humans have significantly modified the natural world though land-use change, resource exploitation, pollution and anthropogenically-induced climate change (Crutzen 2006; Steffen et al. 2007; Zalasiewicz et al. 2008). All these factors have had significant consequences for ecosystems – such as reducing biodiversity, productivity, resilience and the ability to provide 'ecosystem services' such as nutrient cycling and carbon storage (Coleman & Williams 2002; Pauly et al. 2002; Hughes et al. 2003; Foley et al. 2005; Thompson et al. 2009). Thus, understanding the drivers and impacts of environmental change is an important goal of modern science, and a research priority within the UK (NERC 2007; BBSRC 2011).

1.2.1 The extent and importance of coastal habitats

Coastal ecosystems are among the most diverse and productive on earth (Snelgrove 1999; Holt et al. 2009; Duarte et al. 2009). As the buffer between terrestrial and marine ecosystems, they protect land from the impacts of wave energy, and filter the input of terrestrial effluent into the sea (Texier et al. 1993; Bally et al. 2004; Cochard et al. 2008; Feagin et al. 2010). Soft sediment coastal habitats are ecologically important as they act as nurseries for many species of fish and invertebrates, some of which are commercially important (Beck et al. 2001; Gillanders et al. 2003). Benthic fauna contribute to ecosystem functioning by stabilising the sediment and regulating atmospheric processes (Millennium Ecosystem Assessment 2005). They also provide an important trophic link between primary producers and higher organisms such as fish, shorebirds and wildfowl (Piersma et al. 1993; Percival et al. 1998).

In addition to conservation importance, soft sediment coastal habitats have high economic value. In terms of total value per hectare, estuaries represent the most valuable habitat on earth, valued at US$[1992] 22,832 ha^{-1} yr^{-1} due to the combined value of ecosystem services they provide, including nutrient cycling, disturbance regulation, food production, recreation and habitat refugia (Costanza et al. 1997; Snelgrove 1999).

With over 32,000 km of coastline, the British Isles contain a significant proportion of Europe's coastal habitat (Tucker & Evans 1997; Frost 2010). The total area of mudflat and sandflat within Great Britain has been estimated as 2600 km^2 (Prater 1981). This includes 133 estuaries containing at least 1 km^2 of intertidal mudflat (Prater 1981). The location of Great Britain on the East Atlantic flyway makes it a key stopover point for many migrating birds

(Rehfisch et al. 2003; Flegg 2004; Boere & Stroud 2006). The relatively mild UK winters create ideal feeding conditions for the thousands of shorebirds and wildfowl that breed in Siberia, Iceland and Northern Europe (Vellinga & Wood 2002; Flegg 2004). For this reason, many UK estuaries are designated Special Protection Areas (SPAs) and European Marine Sites (EMSs) on the basis of the bird populations they support (JNCC 2012; Holt et al. 2012).

1.2.2 Threats to coastal ecosystems

As with many of the world's ecosystems, coastal habitats are undergoing high rates of environmental change, habitat and biodiversity loss (Gray 1997; Duarte et al. 2009). These changes are driven by increased levels of human occupation and infrastructure in coastal areas, increased levels of nutrient input and eutrophication, and climate-related changes (Suchanek 1994; EEA 2006; Halpern et al. 2008). Climate-related changes in coastal ecosystems are characterised by a background level of gradual long-term change, such as sea-level rise, punctuated by extreme events such as storms (Wethey et al. 2011). Globally, sea levels are predicted to rise between 0.18 m and 5 m by 2100 (Mcleod et al. 2010). The variability in predictions is due to uncertainty surrounding the contributions of melting ice sheets and glaciers, thermal expansion of ocean water, and positive feedback from increased atmospheric temperatures (Church & White 2006; Overpeck et al. 2006; Hansen 2007; Rahmstorf 2007; Grinsted et al. 2009; Bahr et al. 2009; Nicholls & Cazenave 2010; Mcleod et al. 2010).

Secondary effects of sea-level rise include increased coastal erosion, coastal flooding and saltwater encroachment of sensitive habitats (Nicholls et al. 1999; Wolters et al. 2005). In regions where natural inland migration of habitats is possible, impacts may be lessened, but when infrastructure leads to “coastal squeeze”, significant habitat loss may occur (Taylor et al. 2004). Globally, 22% of coastal wetlands could be lost to sea-level rise by 2080, and this figure rises to 70% if other anthropogenic causes of habitat loss are taken into account (Nicholls et al. 1999). The extent of coastal wetland loss will not be uniform across the globe, with the greatest losses on the Atlantic coast of Central and North America, and in countries surrounding the Baltic and Mediterranean Seas (Nicholls et al. 1999).

Projected habitat loss within the UK is low compared with other regions, but could reach 8% by 2060 (Jones et al. 2011). Within the UK, due to the effects of vertical land movement and isotactic tilt, relative sea-level rise will be greatest in the south-east of England and least in the west of Scotland (Austin et al. 2001). The extent of habitat loss is also dependent on local geology, topography and historical land use, with low-lying areas previously reclaimed from the sea by the use of hard defences likely to have the largest impacts (Austin et al. 2001).

1.2.3 Ecological impacts of environmental change in coastal habitats

(i) Invertebrate communities

The ecological impacts of some aspects of climate change in coastal zones are relatively well understood, at least in general terms. For example, shifting distribution and abundance of invertebrate species, driven by changes in temperature (Harley et al. 2006; Lima et al. 2007a). In European waters, there has been notable shift in invertebrate species ranges, with temperate species retreating northwards and species typically associated with the Mediterranean increasing in abundance around the coasts of Britain and Ireland (Hiscock et al. 2004; Philippart et al. 2011; Jones et al. 2012; Mieszkowska et al. 2006; Herbert et al. 2003). However, uncertainty surrounds the extent and speed of responses of some species and the interactions between them (Watt et al. 2005). Furthermore, the reproduction of many coastal invertebrates is intimately linked with temperature cues and photoperiod, so fast rates of climate change may lead to local extirpations if populations do not have time to adapt (Lawrence & Soame 2004; Rehfisch & Austin 2006). This is particularly true if limited dispersal abilities or geographic barriers prevent range shifts (Lawrence & Soame 2004; Keith et al. 2011). There is growing evidence that intertidal invertebrate species in Northern Europe are undergoing a “regime shift” (i.e. a sudden change between contrasting, persistent states) (DeYoung et al. 2008; Wethey et al. 2011). However, many of the changes observed so far are gradual and not considered to bear the hallmarks of a regime shift (Spencer et al. 2011). Other likely impacts of climate change on coastal communities include an altered size structure, driven by decreases in body size of top predators and increases in the total number of organisms (Jochum et al. 2012).

(ii) Coastal bird populations

The likely impacts of climate change on coastal birds in the UK include shifting distributions due to temperature and altered habitat availability and quality due to sea-level rise (Austin et al. 2001; Austin & Rehfisch 2003). In the UK, during mild winters, the distribution of many shorebird species shifts east and north, with more birds overwintering in East Anglia and fewer in the south west (Austin et al. 2000; Austin et al. 2001; Austin & Rehfisch 2005). As such, shorebird wintering distributions are a fairly reliable indicator of environmental change (Piersma & Lindstrom 2004; Rehfisch et al. 2004). The density of birds found on estuaries is closely related to invertebrate densities (Prater 1981; Goss-Custard & Warwick 1991), therefore, a shift in invertebrate species ranges and community composition is likely to affect bird communities. Changes in estuary morphology due to rising sea levels are likely to change the nature of sediments in estuaries, which in turn will change invertebrate prey distributions (Yates & Goss-Custard 1997; Austin et al. 2001). This may benefit certain shorebird species that prefer sandier sediments, such as oystercatchers (*Haematopus ostralegus* [Linnaeus 1758]), while harming those that prefer muddy sediment such as redshank (*Tringa totanus* [Linnaeus 1758]) (Austin & Rehfisch 2003). At some sites, an increase in total intertidal area will increase in the potential number of birds supported (Austin & Rehfisch 2003).

Many estuaries and harbours are also hubs of human activity, which often conflicts with bird conservation objectives. Some high profile examples include offshore wind farms (Drewitt & Langston 2006; Chamberlain et al. 2006), tidal barrage construction (Goss-Custard & Warwick 1991; Burton et al. 2002; Clark 2006) and harvesting of natural resources (Ens 2006; Dias et al. 2008). Further impacts to local avian ecology arise through shipping (Bishop 2007; Keller et al. 2011), recreation (Burger 1986; Peters & Otis 2006; Lafferty 2001) and industry (Esselink et al. 1989). Although the impact of human activity is not always negative – estuarine organic enrichment can lead to increased numbers of birds feeding (van Impe 1985), and light pollution is thought to enhance feeding rates of visually foraging shorebirds at night (Santos et al. 2010).

Within the context of coastal management in the UK, the management strategies that are employed are likely to have a greater impact on future habitat viability than climate change itself (Richards et al. 2008). Thus, studies which improve the evidence base for management and strategic planning decisions are of vital importance (Sutherland et al. 2004; Pullin & Knight 2009).

1.2.4 Policy governing coastal habitats

Biodiversity policy within Europe is governed by a number of conventions and directives: the 1971 RAMSAR Convention on Wetlands, the 1979 Bonn Convention on the Conservation of migratory species and Bern Convention on the conservation of European Wildlife and Natural Habitats, the EC Birds Directive (79/409/EEC), the 1992 EC Habitats directive (92/43/EEC) and the 1992 Convention on Biological Diversity. Under the Birds Directive and Habitats Directive, the EU has established a large network of protected areas called Natura 2000 sites, which include Special Protection Areas (SPAs), European Marine Sites (EMSs) and Special Areas of Conservation (SACs) (European Commission 2009). Wildlife in estuaries and coastal waters is also protected under the Water Framework Directive (Pollard & Huxham 1998). Within the UK, Coastal Habitat Management Plans are in place to identify environmental changes and minimise further losses of coastal habitat at the regional scale

(Pethick 2002; Gardiner et al. 2007). In addition, Shoreline Management Plans (SMPs) for the coastlines of England and Wales are in place to minimise risk to people, property and natural environments associated with coastal processes (DEFRA 2006). Finally, under the EU Environmental Impact Assessment (EIA) Directive (85/337/EEC) and Strategic Environmental Assessment (SEA) Directive (2001/42/EC), to gain approval for any developments at coastal sites, quantitative data on how coastal bird populations will be affected by proposed changes must be provided.

Despite the commitments of the conventions to maintain environments, habitats or species in a “favourable state”, there is a general lack of consensus on how to achieve it for specific habitats or species. As much of the legislation was developed prior to the widespread recognition of climate change, there is a general lack of policy relating to climate change adaptation. For example, although intertidal habitat may be designated as an SPA, surrounding land, such as coastal grazing marsh, may also be protected under the Habitats Directive (Pethick 2001). This has created an ‘environmental paradox’, in which areas that are valued for their freshwater ecology are increasingly falling under the high tide mark and require increasingly costly and unsustainable intervention to prevent salt water incursion (Pethick 2002).

The UK government announced its mission for the next decade as:

> “to halt overall biodiversity loss, support healthy well-functioning ecosystems and establish coherent ecological networks” (DEFRA 2011).

This is in line with the EU 2020 biodiversity strategy target headline:

> "Halting the loss of biodiversity and the degradation of ecosystem services in the EU by 2020, and restoring them in so far as feasible, while stepping up the EU contribution to averting global biodiversity loss" (European Commission 2011).

As coastal biodiversity in Europe continues to diminish, there is an urgent need to understand the impacts of environmental change on biodiversity at the landscape scale, in order to design effective management strategies to halt its decline. Furthermore, as we have now moved beyond the point that climate change is preventable, policy must shift focus from mitigation to adaptation to climate change.

1.3 Predictive modelling of species distributions: a review of approaches

1.3.1 Species distribution modelling (SDM)

Understanding what determines the spatial and temporal distribution of species is a fundamental goal of ecology (Elith & Leathwick 2009). Interest in species distribution modelling (SDM) in the marine context has increased in recent years due to the potential application in climate change adaptation, marine spatial planning, and fisheries management (Thomas et al. 2004a; Leathwick et al. 2008; Valavanis et al. 2008; Maxwell et al. 2009; Elith & Leathwick 2009; Albouy et al. 2012). In this section, I review the current approaches to SDM, with a focus on the applicability to benthic invertebrate or shorebirds populations. The purpose of this section is to provide theoretical background to the methods I have employed in modelling benthic invertebrates and shorebird populations in later chapters.

There are three general approaches to modelling species distributions: niche-based models, demographic models, and process-based models (Beale & Lennon 2012).

(i) Niche-based models

Modelling the distribution of species in relation to the abiotic environment appears in the literature under various names, including *niche modelling*, *habitat association modelling* and *bioclimatic envelope modelling* (BEM). I will henceforth use the latter term. A common approach to BEM is determining the environmental requirements of a species based on its present distribution or *realised niche* (i.e. its tolerance to the present abiotic conditions combined with the effect of biotic interactions). This forms the basis for predicting the distribution of species, either under future environmental conditions or in areas where the biota have not yet been sampled (Pearson & Dawson 2003; Beale & Lennon 2012). This approach has been heavily criticised for several reasons. Firstly, because it assumes the precise nature of species interactions that determine the present species distributions will not alter in nature or strength under future conditions (i.e. *niche conservatism*) (Pearman et al. 2008). This assumption is likely to be unrealistic, but evidence of either niche conservatism (Allen & Gillooly 2006) or niche shifting (Hairston Jr & Bohonak 1998; Goldberg et al. 2005) is sparse in the marine environment. A recent study has indicated that temporal shifting of realised niches does occur in some benthic intertidal invertebrates (Kraan et al. 2012). As well as the changes in individual species' niches, competitive interactions are likely to alter under changed conditions (Poloczanska & Hawkins 2008). A further complication that may be particularly relevant in benthic invertebrates is ontogenetic changes in habitat preference, as many species have life stages with vastly differing ecological requirements (Hiddink 2003; Manzur et al. 2009).

A second criticism to BEM is that species may adapt, either via phenotypic plasticity or genetic shift, to enable them to tolerate changed climatic conditions (Pearson & Dawson 2003; Prada et al. 2008; Hoffmann & Sgrò 2011; Franks & Hoffmann 2012). Thirdly, the dispersal ability of the species is not considered in BEM (Pearson & Dawson 2003). Dispersal is a key determinant of population dynamics, but the details of dispersal is poorly understood for many marine species (Gaines et al. 2005; Cowen & Sponaugle 2009). However, studies have shown that geographical barriers to dispersal are key in determining future distributions of marine species (Lima et al. 2007b; Knutsen et al. 2013). A fourth criticism of BEM is that the observed species may not be at equilibrium with the observed climatic conditions (Pearson & Dawson 2003). A final criticism is that spatial autocorrelation may be a problem if species aggregate due to biological processes. Thus, it may be necessary to account for spatial structure within BEMs using geographically weighted regression approaches (Brunsdon et al. 1996; Dormann et al. 2007).

Much of the theoretical background to BEM has been developed in terrestrial systems. Until very recently, there have been relatively few applications of BEM in the marine context, and so the validity of this approach in many marine and coastal ecosystems is yet untested (Lima et al. 2007b; Ling et al. 2009; Elith & Leathwick 2009). Of the marine taxa, fish and mammals are the most commonly studied (Kaschner et al. 2006; Valavanis et al. 2008; Maxwell et al. 2009; Robinson et al. 2011). Studies of SDM of benthic invertebrates are less common; in spite of having several features that make them well-suited to the approach (Lima et al. 2007a; Kraan et al. 2010; Robinson et al. 2011). The occurrence of certain benthic species appears to be predictable using environmental covariates alone (Therriault & Herborg 2008); however, tests of applicability in more species and habitats are required.

Ornithological BEMs have been applied to predicting effects of sea-level rise, based on observed correlations between bird densities on estuaries and sediment properties (Yates & Goss-Custard 1997; Yates et al. 1996; Austin et al. 2001). The major criticism of this approach for predicting bird abundance is the assumption that the observed density of birds will not change if the amount of available habitat decreases; whereas in reality the birds may be able to forage as efficiently at higher density (Stillman & Goss-Custard 2010). Hence, these models tend to overestimate the effects of habitat loss on populations.

(ii) Demographic models

A second approach to modelling species distributions is the use of demographic models. These are models which relate demographic processes such as birth rates, death rates and emigration rates, to environmental variables, such as the weather. The approach has been commonly used in the study of migratory birds (Sillett 2000; Both et al. 2006; Pearce-Higgins & Yalden 2009; Pearce-Higgins et al. 2010; Renwick et al. 2012).The accuracy of predictions from this type of model is strongly dependent on the model correctly identifying the factors that limit the population. Another drawback is that unless pre-existing long term data sets are available, it may take years to collect the demographic data to produce the model. In very long-lived species, such as shorebirds, small changes in mortality rates can have large effects on populations. However, by the time that a population decline has been recognised, it may be too late prevent serious population crash through management.

Both niche-based models and demographic models are essentially correlative in nature. The link between bioclimatic variables and species distributions is a statistical model. A variety of statistical methods have been used in marine SDMs, including generalised linear models (GLMs) (Stefánsson 1996), generalised linear mixed-effects models (GLMM), generalised additive models (GAMs) (Denis 2002; Bekkby & Rinde 2008; Snickars & Sundblad 2009; Murase et al. 2009; Drexler & Ainsworth 2013), ordination-based methods (Ellingsen 2002), machine learning methods such as artificial neural networks (Berry et al. 2002; Willems et al. 2008) and regression-tree-based approaches (Lima et al. 2007b; Leaper et al. 2011; Pitcher et al. 2012), multivariate adaptive regression splines (Leathwick et al. 2005), maximum entropy models (Bučas & Bergström 2013), and Bayesian hierarchical models (Lecomte et al. 2013). However, the main drawback to correlative models is that there is a large amount of uncertainty associated with predicting outside the range of environmental conditions sampled (Zurell et al. 2012). In other words, model predictions under novel environmental conditions may not be reliable.

(iii) Process-based models

Process-based models aim to explicitly include functional traits of the organisms and the processes that determine species distributions (Beale & Lennon 2012). Thus, functional traits of organisms are linked to habitat data through a mechanistic model which captures the processes by which the organisms interacts with the environment (Kearney & Porter 2009). This approach to modelling represents a step towards a more unified approach to ecology, by which the traits of individuals are linked to population dynamics and ecosystem functioning (Loreau 2010). Understanding the mechanisms behind patterns of species occurrence in nature is essential to producing a more predictive science (Teal, 2012).

A particular class of process-based model that has been successfully used in modelling coastal bird populations is individual-based models (IBMs). Individual-based modelling (or agent-based modelling) is an approach to modelling complex systems, which has been applied to various ecological systems (Breckling et al. 2005; Grimm 1999), but has also been applied in fields as wide-ranging as the social sciences (Bonabeau 2002; Boero et al. 2008), cellular immunology (Chavali et al. 2008), and epidemiology (Roche et al. 2011).

The central tenet is that population-level characteristics (e.g. population size, mortality rate, emigration rates) are derived from the properties of individuals (e.g. behaviour and physiology) and how they interact with each other (Grimm & Railsback 2005). The models use elements of optimal foraging theory (Pyke et al. 1977) and game theory (Smith 1974), in that individuals respond to decisions made by other individuals around them in deciding where, when and on what to feed (Goss-Custard et al. 1995a). Individuals are provided with "decision rules" to maximise their fitness. Fitness-maximisation rules are grounded in the most basic concept of evolution – the genetic traits of organisms have evolved because they confer fitness to the organism (Darwin 1859; Stillman & Goss-Custard 2010).

Using fitness-maximising behaviour as the basis of prediction for how a model animal will behave under novel environmental conditions is much more likely to maintain predictive power compared with the empirical relationships of the aforementioned correlative methods. IBMs capture individual differences in foraging efficiency and social dominance, such that the least efficient foragers die first and the most efficient survive. This sets them apart from simple spatial models of prey depletion, in which all foragers must die or emigrate when prey resources become depleted (Sutherland & Allport 1994; Percival et al. 1998; Gill et al. 2001a; Stillman & Goss-Custard 2010).

IBMs have been shown to successfully predict overwinter mortality and the underlying foraging behaviour at various European sites and in various contexts, such as habitat loss (Goss-Custard et al. 1995b), sea-level rise (Durell et al. 2006), wind farm development (Kaiser 2006), shell-fishing (Stillman et al. 2001) and human disturbance (West et al. 2002).

1.4 Study site: Poole Harbour

1.4.1 General geography

Poole Harbour is one of the largest natural harbours in the world, covering roughly 3600 ha at High Water Spring Tides (Humphreys & May, 2005). It is located on the south coast of Dorset, UK (Figure 1.1), approximately equidistant between Portland Bill to the west and the Isle of Wight to the east. There are 5 islands within the harbour, the largest being Brownsea Island. The main drainage channels are influenced by the islands, which prevent the tide draining in a uniform front, as it does in other estuaries such as the Dee or Morecombe Bay in the northwest of England (Gray 1985; Marker 1967). Maintenance dredging is undertaken bi-annually in the main shipping channels between the harbour mouth and the northern ports at Poole and Hamworthy, and sediments are deposited offshore (PHC 2004). In addition, the main shipping channel was also deepened from 6 to 7.5 m and widened from 80 to 100 m during the winter of 2005-6 (HR Wallingford 2004).

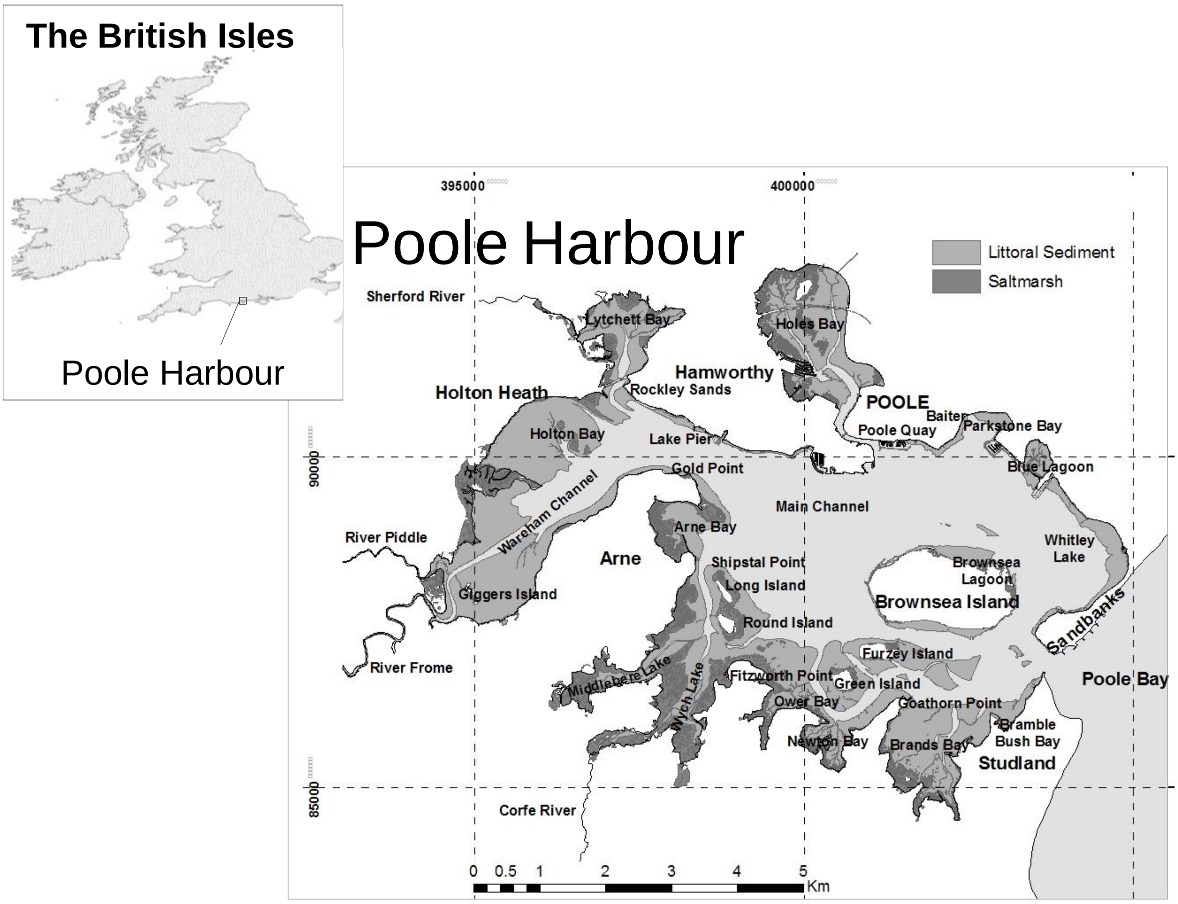


Figure 1.1 Map of Poole Harbour (modified from Herbert *et al.*, 2010), showing location within the UK.

The tidal range is 1.8 m during springs and 0.6 m during neaps, and the tide undergoes an unusual ‘double high water’ that causes it to remain above the mean level for 16 out of 24 hours (Humphreys & May 2005). Fresh water flows into Poole Harbour via four rivers: the Frome and Piddle flow into the Wareham Channel, the Sherford flows into Lytchett Bay and Corfe River flows into Wych Lake. The combined fluvial discharge is ~10 m^3s^{-1} (PHC 2004), which contributes to the brackish character of parts of the harbour. Salinity throughout the harbour is generally 20–30 ppt, with relatively little seasonal variation, apart from the Wareham Channel in which salinities are lower and more variable (10–25 ppt) (Dyrynda 2005). The site receives 835 mm rain per year, 28% less than the UK average, and temperatures are a few degrees warmer than the UK average (minimum 1.2ºC in February and maximum 22.1ºC in July) (Met Office 2011). Winds are most commonly west or southwesterly (Humphreys & May 2005).

The harbour is situated in a densely populated area of commercial importance – 30,000 people live along its northern shores, it is a popular destination for tourism, and the largest onshore oilfield in Western Europe is situated on one of its smaller islands. Ferries to Cherbourg, St. Malo, Guernsey and Jersey operate out of the harbour and a number of inshore fisheries operate in the area. The Poole Harbour Commissioners introduced an Aquatic Management Plan for the area in 1994, which aims to keep conflicting activities distant from each other and minimise the strain on natural ecosystems (Drake & Bennett 2011).

1.4.2 Ecological significance

Poole Harbour is an area of considerable ecological significance. The intertidal zone contains an array of habitats, including extensive areas of mud and sandflats, often bordered by saltmarsh or reed bed. These habitats regularly support >20,000 wildfowl, as well as internationally important numbers (i.e. >1% of the total population) of both migratory species such as black-tailed godwit (*Limosa limosa* [Linnaeus 1758]) and shelduck (*Tadorna tadorna* [Linnaeus 1758]*),* and species listed under Annex 1 of the Birds Directive, including pied avocet (*Recurvirostra avosetta*), Mediterranean gull (*Larus melanocephalus* [Temminck 1820]) and common tern (*Sterna hirundo* [Linneaus 1758]). For this reason, Poole Harbour was designated a SPA and EMS in 1999, under Article 4.1 of the EU Birds Directive (79/409/EEC), and a RAMSAR site (Natural England 2012; JNCC 2008). A number of other UK statutory designations have been applied to the harbour, including Area of Outstanding Natural Beauty (AONB), Site of Special Scientific Interest (SSSI), and a Heritage Coast designation for Studland Bay (Humphreys & May 2005). The Dorset Wildlife Trust (DWT) and Royal Society for the Protection of Birds (RSPB) both operate reserves in the vicinity of the harbour.

The situation of Poole Harbour, north of the English Channel, is biogeographically significant. The English Channel is the primary link between southern and northern seas, and has been considered a biogeographic barrier or 'hybrid zone' (Hilbish et al. 2012). It represents the southern range limit for many northern invertebrate species and *vice versa* (Wethey et al. 2011). Furthermore, there is evidence that the hybrid zone has shifted up to 100 km eastwards in the past two decades in response to warming climate (Hilbish et al. 2012), and significant changes in invertebrate community assemblages and species range limits have been observed (Southward et al. 1995; Mieszkowska et al. 2006; Hawkins et al. 2009). As such, data on invertebrate species abundance within this region are of wider significance.

A number of surveys of the benthic fauna of the intertidal mudflats of Poole Harbour have been conducted since the 1970s. Generally, the harbour is dominated by numerous species of annelid worm. There are indications that the nature of the harbour has changed significantly in recent decades. Historical surveys indicate that prior to 1990s, the fauna comprised a much higher density of bivalves (Caldow et al. 2005). However, little has been done to date to synthesise the findings of these independent studies and examine the drivers and mechanisms of ecological change in the harbour. There is also a lack of studies linking data on changing food resources to the impacts on bird populations. Although, some of the climate-related changes to invertebrate prey resources have been shown to have positive impacts on birds in Poole Harbour (Caldow et al. 2007).

1.4.3 Brownsea Island Lagoon

Brownsea Lagoon is a 17.8 ha non-tidal saline lagoon, situated on the north-eastern edge of Brownsea Island, in the centre of Poole Harbour. It was constructed in the 1850s when a sea wall was built, enclosing an area formerly known as St. Andrews Bay, to provide grazing land for cattle. When the pumps controlling water levels fell into disuse, the area was flooded and the present lagoon habitat was created (National Trust, 2011). It is currently managed by the Dorset Wildlife Trust, and in the summer the small artificial islands within the lagoon provide nesting habitat for internationally important numbers of migrants such as common tern and sandwich tern (*Sterna sandvicensis* [Latham 1787]), and resident breeding birds such as black-headed gulls (*Chroicocephalus ridibundus* [Linneaus 1766]) and Mediterranean gulls. Throughout the winter it is an important feeding habitat for internationally important numbers of shorebirds, such as avocet and black-tailed godwit, and waterfowl. Despite its conservation interest as a Special Protection Area (SPA) and Site of Special Scientific Interest (SSSI), Brownsea Lagoon was not included in previous UK lagoon surveys conducted in the 1980s and 1990s, so very little was known about its fauna.

1.5 Focal species: the pied avocet (*Recurvirostra avosetta)*

1.5.1 Population trends

The pied avocet (*Recurvirostra avosetta* [Linneaus 1758]) re-established its UK breeding population on shallow brackish coastal lagoons in Suffolk in 1947, after previously being driven to extirpation in the UK in the 1840s due to habitat loss, and egg collecting (Hill & Carter 1991). Since the 1970s, the population has expanded its range, and breeding colonies are now found in Norfolk, Essex, Kent, Cambridgeshire, Hampshire, Worcestershire and as far north as Teesside (RSPB 2010). This expansion been facilitated by the creation of suitable breeding habitat in the form of coastal saline lagoons, and the success of its re-colonisation prompted the RSPB to adopt its image for their logo (RSPB 2013a). While the avocet is not red-listed as a globally or nationally threatened species, its range within the UK is restricted to areas of suitable habitat, which are in themselves scarce, granting it amber status (Eaton et al. 2009; IUCN 2013; RSPB 2013b).

The pied avocet is one of four species of Recurvirostridae – with other species located in South America (the Andean avocet, *R. andina* [Philippi & Landbeck 1861]), North America (the American avocet *R. Americana* [Gmelin 1789]), and Australasia (red-necked avocet, *R. novaehollandiae* [Vieillot 1816]).The global population of pied avocet is estimated as 280,000–495,000 individuals, and the species is found in Europe, Africa and Asia (Wetlands International 2012; Birdlife International 2013). The Western European population is roughly 90,000, with an estimated 29,658 breeding pairs, the majority of which breed in The Netherlands, Germany, Spain and Denmark (Hötker & West 2006).

1.5.2 Wintering behaviour

Outside of the breeding season, UK estuaries provide important overwintering sites for the UK breeding population, as well as Northern European breeding birds (Blomert et al. 1990). From the late 1980s to mid-1990s, the number of wintering avocets in the UK increased by 122%, more than any other shorebird species (Rehfisch et al. 2003). The British wintering population now represents ~8% of the European population (Hötker & West 2006; Holt et al. 2012). European avocets migrate south between August and October, and return to breeding grounds between March and May; however, some Western European and African populations are non-migratory (Hayman et al. 1986; del Hoyo et al. 1996). Pied avocet have a large latitudinal wintering range (Cramp & Simmons 1983). The average temperature within the wintering ranges of the Western European avocet population is 12.9ºC (Godet et al. 2011), suggesting the UK is at the colder extreme of the wintering range. Wintering populations may consist of amalgamations of breeding populations from different countries, and similarly, individuals from the same breeding colony overwinter at different sites (Hötker 1998).

Preferred wintering habitats of avocets are coastal and inland saline lakes, lagoons, pools, saltpans, river deltas, flood plains, and sandy beaches; they are also rarely found on inland freshwater lakes and rivers (Birdlife International 2013). Avocets most commonly feed on small invertebrates, such as annelid worms and crustaceans, which they capture using a unique foraging method, by sweeping their long upturned bill across the surface of muddy sediments (Cramp & Simmons 1983). They can hunt individually, or in large social groups (see Figure 1.2).

Figure 1.2 (L–R) Solitary avocet visually foraging on ragworm *Hediste diversicolor*, and avocet flock socially foraging on pelagic prey at Brownsea Island Lagoon. Photographs courtesy of Chris Moody.

1.5.3 The Poole Harbour avocet population

The first mention of avocets at Poole Harbour in the Wetland Birds Survey (WeBS) is 1986–7, for which 56 individuals were recorded (Salmon et al. 1988). At this time only 530 avocets wintered in the entire UK, and the Ore/Butley/Havergate Estuary complex in Suffolk and the Exe in Devon were the main wintering sites (Salmon et al. 1987). The number of overwintering avocet in Poole Harbour increased steadily from 59 individuals in 1986–87 to a peak of 1893 in 2001–02. Since then the numbers have fluctuated around a mean of ~1300 (see Figure 1.3). Based on WeBS data from 2010–11, Poole Harbour now supports 9.6% of the UK wintering population, and roughly 1.5% of the European population (Holt et al. 2012;

Hötker & West 2006). It is the third most important UK wintering site for avocet, surpassed by the Thames Estuary and Alde Complex in Suffolk (Holt et al. 2012). Breydon Water and Berney Marshes in Norfolk and the Humber Estuary in North Lincolnshire are the only other UK sites with internationally important wintering populations of avocet (Holt et al. 2012).

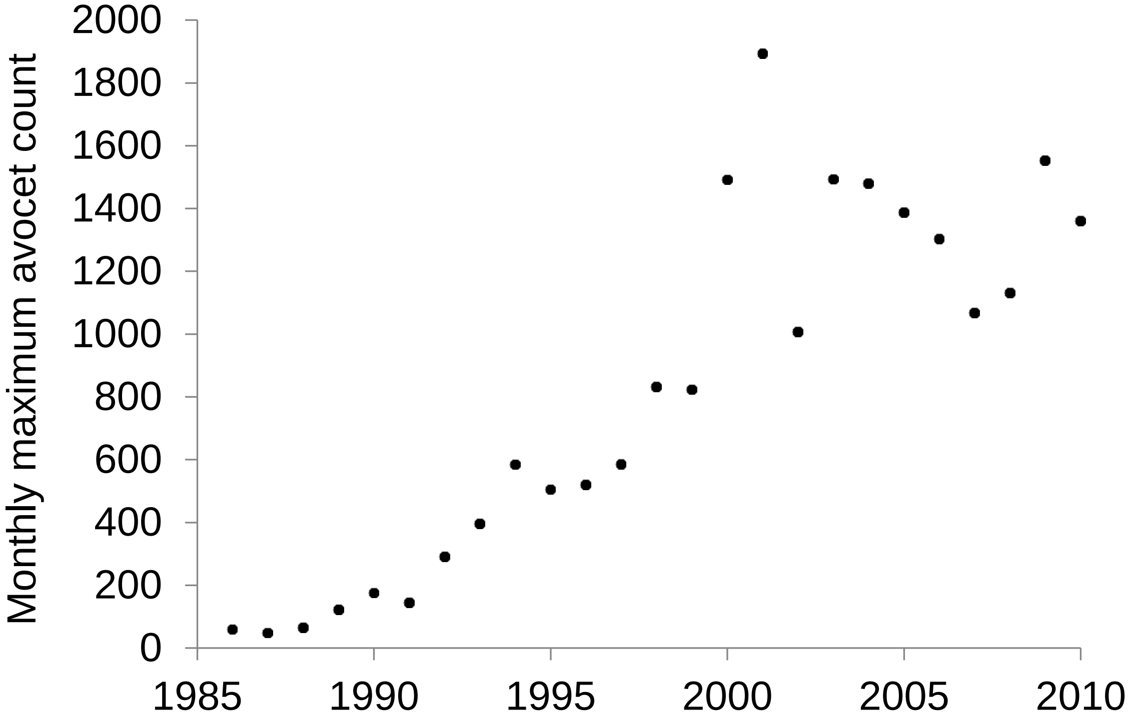


Figure 1.3 The number of overwintering avocets in Poole Harbour, based on Wetland Bird Survey (WeBS) data (Salmon et al. 1988; Kirby et al. 1992; Cranswick et al. 1997; Pollitt et al. 2003; Musgrove et al. 2007; Holt et al. 2012).

All UK sites with internationally important numbers of overwintering avocets have experienced increases in population sizes since the mid-1990s (Cranswick et al. 1997; Pollitt et al. 2003; Musgrove et al. 2007; Holt et al. 2012). As there is potential for a larger number of sites within the UK becoming internationally important overwintering sites for avocet, there is a need for more research into winter habitat use and foraging behaviour to ensure that sites can be managed appropriately for this species.

1.6 Scope of thesis

1.6.1 Aims and objectives

The overall aim of this thesis is to develop an individual-based model to assess the effect of sea-level rise on the overwintering avocet population of Poole Harbour. In pursuit of this overall aim, the project has several subsidiary aims and objectives:

- to determine the extent to which spatial variation in soft sediment benthic faunal abundance can be explained by physical and biological factors;
- to compare the extent of seasonal and annual variation in the soft sediment benthic fauna of an intertidal mudflat and a non-tidal saline lagoon;
- to develop a mechanistic model of avocet foraging strategies, including the functional response;
- to determine the effects of a range of physical and biological drivers on avocet foraging behaviour;
- to assess the importance of social foraging in avocet winter foraging ecology.

1.6.2 Thesis structure

A brief summary of the contents of each chapter are provided below, with a conceptual diagram of the main themes and interconnections in Figure 1.4. The specific aims of each chapter are discussed in further detail within the chapters.

Chapter 1: Introduction

- Provides rationale and scope of thesis. Reviews predictive modelling approaches. Outlines relevant background to study site (Poole Harbour) and focal species (*Recurvirostra avosetta*).

Chapter 2: Explaining broad-scale invertebrate distribution in soft sediment intertidal habitats: insights from machine learning

- Compares two analytical approaches for determining associations between environmental variables and invertebrate species distributions within Poole Harbour, and assesses the extent of inter-year variability.

Chapter 3: A comparison of macrobenthic invertebrate communities in a saline lagoon and an intertidal mudflat: implications for foraging birds.

- Compares the seasonal and spatial variability of benthic communities, and the relationship with abiotic variables at a tidal and non-tidal site, and discusses the implications for foraging birds using the sites.

Chapter 4: A mechanistic model of avocet (*Recurvirostra avosetta*) foraging

- Uses data from field observation of foraging behaviour to develop functional response models for avocet feeding strategies and determine intake rates for the study site, and discusses the conditions under which each strategy is profitable.

Chapter 5: A comparison of avocet (*Recurvirostra avosetta*) foraging behaviour in tidal and non-tidal foraging habitats

- Investigates several aspects of avocet overwinter foraging behaviour at a tidal and non-tidal site, in relation to seasonal changes in invertebrate abundance, tidal variation, and weather, to determine which factors had the greatest effect on behaviour. Also discusses the importance of social foraging in avocet overwinter foraging ecology.

Chapter 6: Predicting the effects of sea-level rise on the avocet (*Recurvirostra avosetta*) population of Poole Harbour

- Develops an individual-based model of avocet foraging behaviour to predict the effects of rising sea levels and habitat loss on the body condition and winter mortality of the Poole Harbour avocet population.

Chapter 7: Overall discussion and conclusions

- Synthesises the findings of the thesis, discusses management implications and suggests further work.

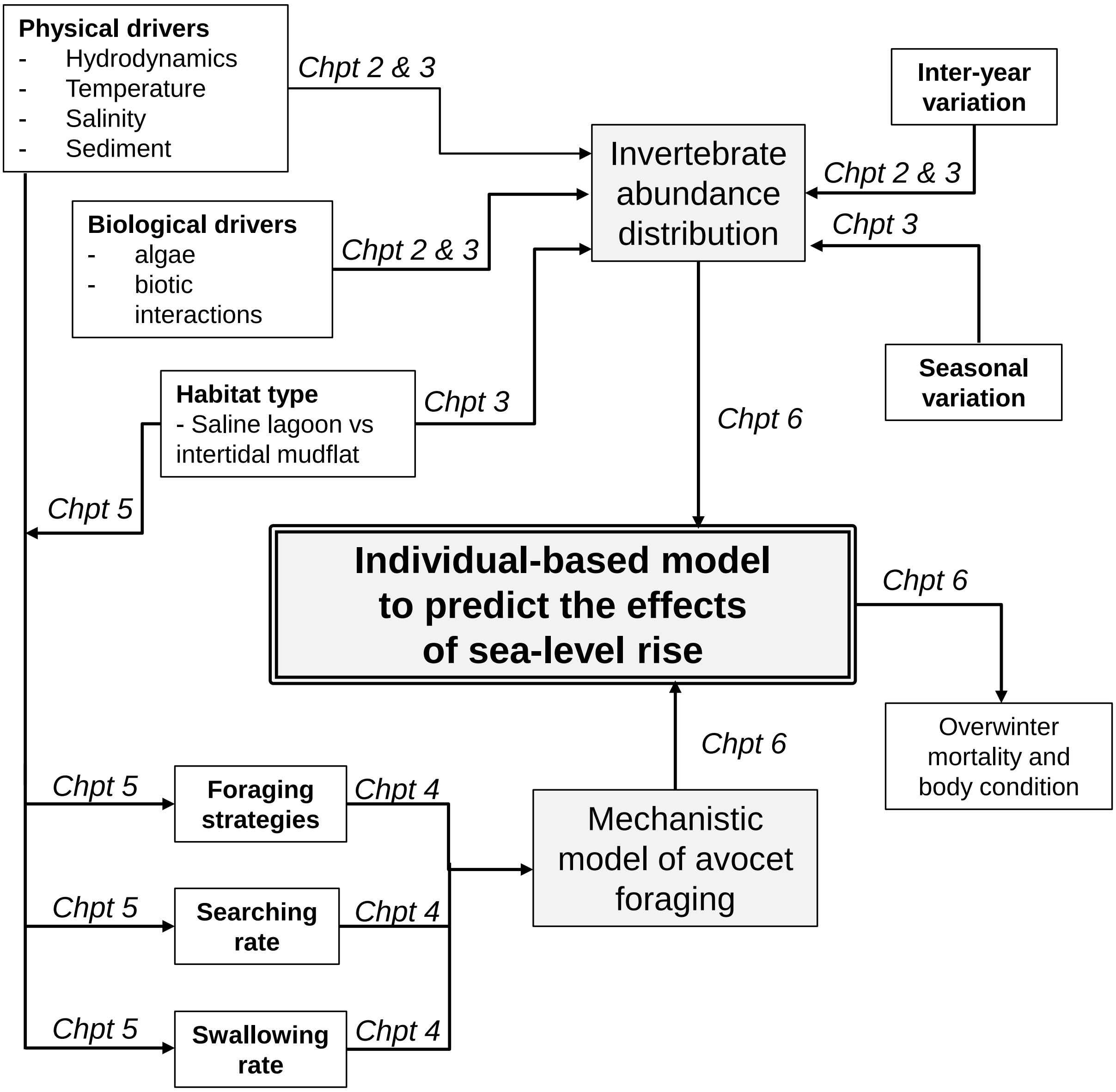


Figure 1.4 Schematic diagram of thesis data chapters. Solid boxes represent the main themes discussed, hollow boxes represent physical and ecological drivers affecting the system, and the arrow linkages indicate the chapters in which the various drivers and themes are discussed.

Chapter 2: Explaining broad-scale invertebrate distribution in soft sediment intertidal habitats: insights from machine learning

2.1 Abstract

I compared two analytical approaches (BIO-ENV and Gradient Forest) to determine if the distribution and abundance of invertebrates in intertidal benthic communities can be explained using environmental variables derived from hydrodynamic models and sediment analysis. I collected benthic cores in 2009, from 80 sites on a 500 x 500 m grid (which had previously been surveyed in 2002), within the intertidal zone of Poole Harbour. I examined community composition in relation to environmental variables derived from a 2-dimensional depth-integrated hydrodynamic model (depth, velocity, salinity, wave height), sediment cores (organic content, sediment particle size, sorting and kurtosis) and from visual assessment (algal cover). Organic content and median sediment particle size were the most important environmental predictors for both methods. The order of importance of the remaining predictors varied between methods. Using Gradient Forest, I found two different and potentially important thresholds in key variables (wave height 8 cm and organic content 2%), above which considerable change in benthic community structure occurred. In conclusion, Gradient Forest is a useful tool for both predicting and explaining benthic invertebrate distributions in soft sediment habitats. Identification of threshold values in environmental gradients is a valuable new capability which is particularly relevant to the assessment of biodiversity distribution, marine spatial planning, and ecosystem function. This approach can be used to identify appropriate sites or species for monitoring environmental change within a harbour or estuary and thus can aid in planning further experiments or field data collection.

2.2 Introduction

A central aim of ecology is to understand the spatial distribution and abundance of species in relation to environmental variables (Whittaker 1967). Ecological point surveys sample only a small fraction of an area. Therefore, to understand species distributions in relation to environmental surrogates, which are less expensive and easier to measure than the biota itself, is desirable. Accurate predictions of species distribution and abundance are required to manage natural resources effectively and infer the effects of climate change on species.

Methods for evaluating the relationship between environment and species occurrence fall into three main categories: “predict-first-assemble-later”, “classification-then-modelling” and “assemble-and-predict-together” (Ferrier & Guisan 2006). The first class models abundance distributions for single species then aggregates or classifies afterwards (Ferrier et al. 2002). The second class includes models that classify community structure into a univariate measure, such as species richness or diversity (Gray 2001), and then relate it to environmental variables using generalised linear models or generalised additive models (Martínez et al. 2012; Garza-Pérez et al. 2004). The third class utilises techniques such as multivariate adaptive regression splines and multivariate regression trees to model multispecies responses to environmental variables in an integrated fashion (De’Ath 2002; Leathwick et al. 2005). The methods in this final class can be described as ‘machine learning’ methods, whereby a computationally intensive algorithm is used to quantify complex relationships between environmental variables and species occurrence, and the identified relationship is used to make predictions about species occurrence for altered or projected environmental conditions. Machine learning methods have gained much credibility recently and have been successfully employed in various fields such as speech recognition (Anusuya & Katti 2009), animal behaviour (Guilford et al. 2009), ecology (Olden et al. 2008) and sub-tidal algal community analysis (Leaper et al. 2011).

In this study, the objectives are fourfold – (i) to examine the relationship between environmental variables and broad-scale biodiversity patterns in a soft sediment intertidal habitat; (ii) to assess the utility of environmental data generated by hydrodynamic models for predicting species distributions in this habitat; (iii) to contrast the outputs of two existing statistical models: the BIO-ENV routine in PRIMER v6 (an example of the “classification-then-modelling” approach) and Gradient Forest (an example of a multispecies “assemble-and-predict-together” approach); (iv) to examine the temporal stability of these associations by comparing the results from similar surveys, conducted 5 years apart.

I address several key knowledge gaps in this study. Firstly, there are few studies available in soft sediment habitats at the spatial scale of an individual harbour. The majority of studies address either very large-scale (Ellis et al. 2000; Kraan et al. 2010), or small-scale patterns (Ieno et al. 2006; Herman et al. 2001). Insight into species distribution patterns and drivers of biodiversity change at this intermediate scale are important, as management decisions tend to occur at this scale (e.g. Drake & Bennett 2011). Secondly, there are very few studies which directly assess the impact of hydrodynamic variables on multi-species distribution and abundance patterns in intertidal habitats. Determining the way in which climate change is altering oceanographic conditions and the impacts to marine ecosystems has been earmarked as an important research target (Sutherland et al. 2006). In addition, many published environment-biota relationships are based on surveys taken at a single time point (Kraan et al. 2010; Warwick et al. 1991), which provide little information about many of the important processes affecting species distributions. And finally, there is a need for testing associations between environmental variables and species assemblages in a variety of contexts using various sampling methodologies, as different systems yield contradictory results (McArthur et al. 2010; Pitcher et al. 2012).

2.3 Methods

2.3.1 Study site

The study was conducted on the intertidal zone of Poole Harbour, one of Europe's largest lowland estuaries, on the south coast of England, Dorset, UK. The harbour is designated a site of special scientific interest (SSSI) and a special protection area (SPA) due to internationally important overwintering populations of wildfowl and shorebird. It also supports various anthropogenic activities, such as commercial shipping and recreation (Humphreys & May 2005). The intertidal habitat includes sandflats, mudflats and mixed sediment, an area totalling 1800 ha. Previous surveys have shown that the harbour biota is dominated by annelid worms (Caldow et al. 2005).

2.3.2 Benthic community and sediment data collection

I collected benthic data from 80 sites on a 500 x 500 m sampling grid (Figure 2.1) within the Poole Harbour site of special scientific interest (SSSI), between mean high water springs (HWS) and low water springs (LWS). Samples were collected between October 4th and November 20th 2009. Most sites were accessed at LWS by hovercraft, and the remaining sites were accessed by foot or small boat. Sites were located using a global positioning system (GPS).

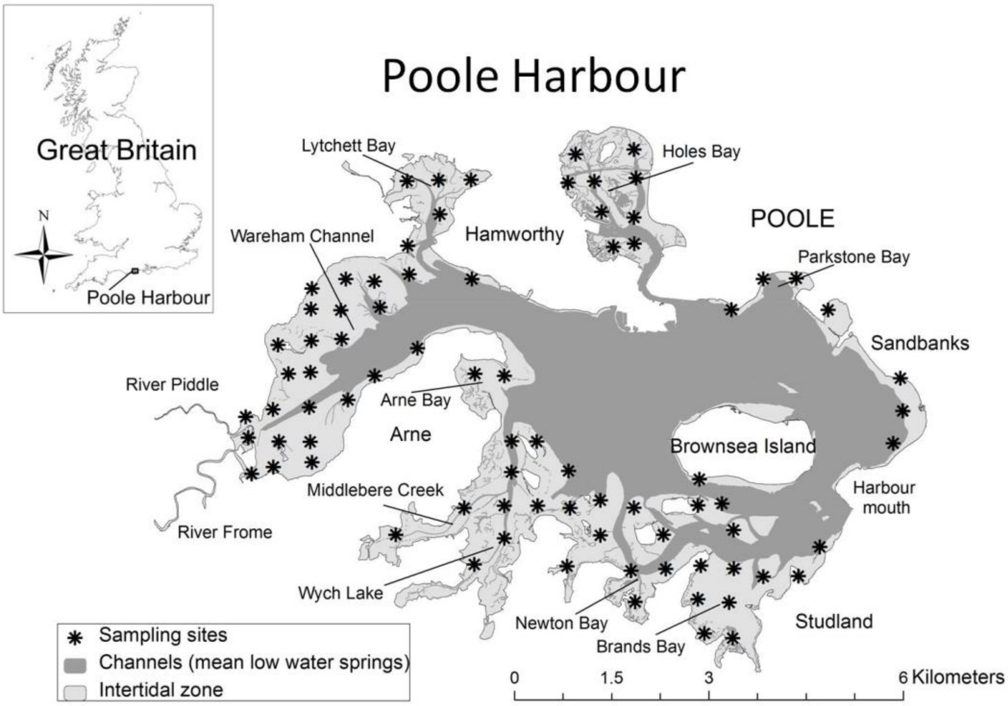


Figure 2.1 Location of study: Poole Harbour, Dorset, UK, and sampling site location.

At each site, 5 cores of 10 cm diameter and 15 cm depth were obtained with a hand corer to determine macrofaunal community composition. In addition, 3 plots of roughly 25 cm^2 were dug at each site to examine the sediment for signs of larger rarer species. Algal percentage cover and number of lugworm (*Arenicola marina* [Linnaeus 1758]) casts per m^2 were assessed visually.

A similar survey was conducted in October 2002 on the same sampling grid (reported in Thomas et al. 2004b); however, only a single core and a single 25 cm^2 plot were used at each site.

2.3.3 Macrofaunal processing

The cores were sieved within 24 h of collection, through a 500 μm mesh to remove excess sediment. The retained macrofaunal fraction was fixed in 10% formal saline (Fisher Scientific), and subsequently transferred it to 70% industrial methylated spirits (Fisher Scientific). Macrofauna were identified to species level where possible using nomenclature specified in the World Register of Marine Species (Appeltans et al. 2012), and numerical densities for each species were determined.

2.3.4 Sediment processing

An additional smaller core (6 cm diameter) was taken at each sampling site for sediment analysis and these cores were frozen within 24 h to minimise organic decomposition. Samples were thawed and homogenised to determine organic content, shell fragments were removed, samples were dried for 48 h at 37˚C, and mass loss on ignition for 12 h at 450˚C was recorded. Particle size of the remaining sediment was determined by wet sieving through a column of sieves (mesh sizes: 2 mm, 1 mm, 500 μm, 250 μm, 125 μm and 63 μm) and weighing the resultant fractions. I calculated statistics to describe the particle size distribution using the RYSGRAN package in R v2.15.0 (de Camargo et al. 2011). Comparable cores were not taken in the 2002 survey, so I used sediment data from 2009 for the analysis of both years.

2.3.5 Hydrodynamic modelling

I extracted hydrodynamic data for each sampling point from a tidal flow model based on the TELEMAC-2D depth-averaged flow model (TELEMAC-MASCARET 2012), developed by EDF-LNHE (Electricité de France Laboratoire National d'Hydraulique et Environnement). The 2-dimensional local model is driven by a larger model of Poole Bay. The extent and resolution of the model are provided in Figure 2.2. It consists of a finite element triangular grid across Poole Harbour, which allows for variable model resolution, ranging from 20 m to 100 m. It is based on the TELEMAC modelling system (Hervouet 2007). Bed elevation (bathymetry) for each node is interpolated from survey or chart data to establish the model. Values for bed roughness, duration of time-step and length of run guide the computation and are calibrated by comparison of the model against observations of tidal level and current. The model solves shallow water equations at the nodes of the triangular grid and calculates water depth, free surface level and the u and v velocity components at the model nodes with these variables assumed to vary linearly in the spaces between nodes. This model has been used for several previous modelling studies at Poole since 1998, including the prediction of post-dredging effects on the hydrodynamics of Poole Harbour for the most recent channel deepening (HR Wallingford 2004). The model was developed and calibrated using a combination of existing bathymetric and flow data, obtained from the Poole Harbour Commission, and newly collected data, and was originally designed to predict the effects of channel deepening on the hydrodynamics and sediment flows in Poole Harbour (HR Wallingford 2004). Salinity was modelled using the DELWAQ transport modelling tool, developed by Deltares, which uses flows from the TELEMAC-2D simulation and solves the advection-diffusion equation over a hexagonal mesh based on the TELEMAC mesh, in order to simulate water quality. Further details are reported in Herbert et al. (2011). The data presented in this study represent summary statistics (e.g. mean, range) for two spring/neap tidal cycles.

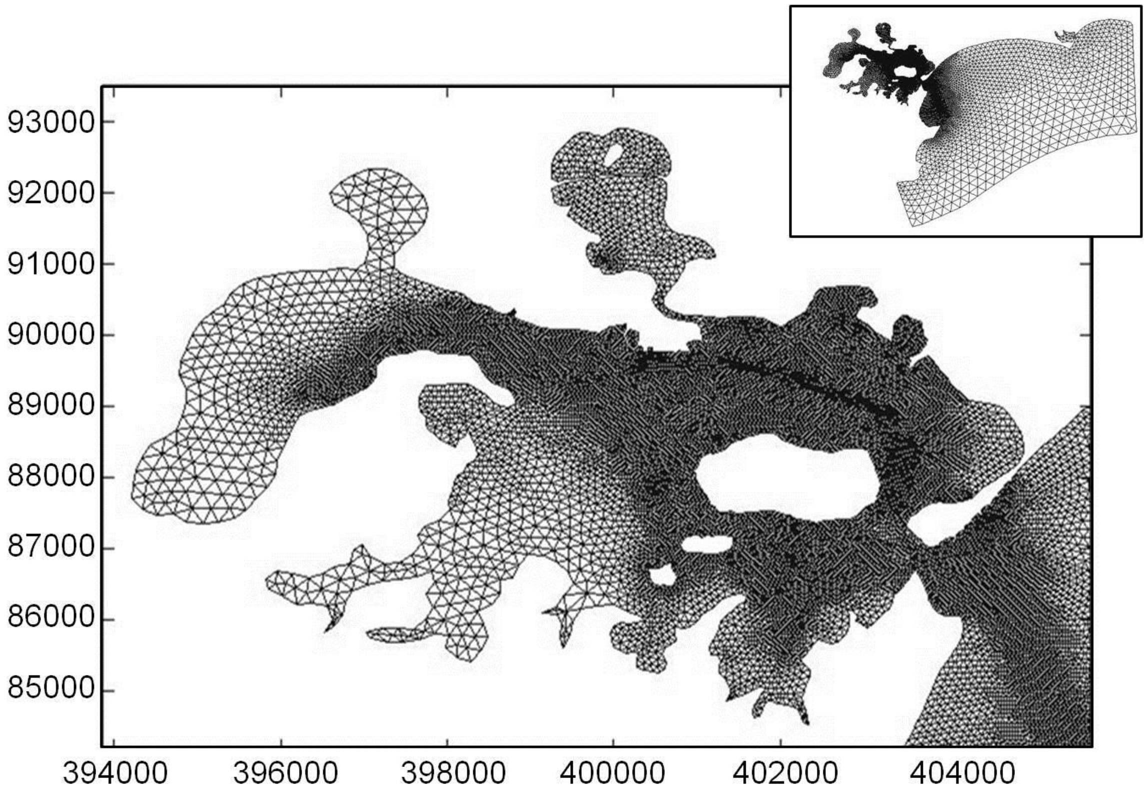


Figure 2.2 Resolution and extent of Poole Harbour hydrodynamic model.

2.3.6 Statistical models

In this study I compare the outputs of two statistical models – the BIO-ENV routine in PRIMER v6 (Warwick & Clarke 1993), and the Gradient Forest model (Pitcher et al. 2011), implemented in R v2.15.0 (R Core Development Team 2012). The former has been widely used in industry and marine research for the past two decades, while the latter is a relatively new and novel approach to analysing community data.

BIO-ENV matches multispecies assemblages to subsets of environmental variables by optimising the Spearman correlation coefficient (ρ). It performs a full search over all environmental variables alone, and in combination, to determine which variable or variables maximise ρ. The abundance data are represented by a Bray-Curtis dissimilarity matrix of fourth-root-transformed data (to account for over-dispersion in the data, as per Field et al. (1982), and environmental variable subsets are represented by a Euclidean distance matrix of transformed, normalised variables.

Gradient Forest is a new type of classification and regression approach based on machine learning, which is computationally intense but runs comfortably on a modern desktop pc. Like its predecessor, Random Forest (Breiman 2001), Gradient Forest randomly re-samples the data many times in a process known as 'bagging' to build thousands of regression trees (hence 'forest'). Each regression tree explains variation in the response variable (species abundance) by splitting the data, using combinations of environmental variables, to minimise the sum of squared residuals of the resulting groups. Aggregation of the results from all the trees in the forest forms the final model output. As there is no prior assumption of structure in the data, the analysis is not sensitive to variable transformation. Gradient Forest extends the Random Forest single species model, to a multiple species model, and as such is well-suited to the analysis of benthic community data.

Prior to running the analyses, a pairwise draftsman plot and Spearman correlation matrix were used to determine the degree of co-linearity between variables, and variables with correlations >0.6 were omitted. This reduced the initial number of input variables from 23 to 10. I tabulated a description of these 10 environmental variables to show the range of values (Table 2.1).

Table 2.1 The environmental variables in this study, details of how the data were obtained and the range of values sampled.

Name	Description	Source	Sampled range
Depth mean	Depth of water, averaged over 2 spring/neap tidal cycles	Poole Harbour water model (HR Wallingford)	0.07–2.11 m
Depth range	Maximum difference in depth between high tide and low tide for an average spring tide	Poole Harbour water model (HR Wallingford)	0.36–1.7 m
Maximum flow velocity	Maximum depth-averaged water flow velocity	Poole Harbour water model (HR Wallingford)	0.008–0.199 (ms^{-1})
Salinity range	Difference between highest and lowest salinity observed during 2 spring/neap tidal cycles	Poole Harbour water model (HR Wallingford)	1.6–35.5 ppt
Wave height mean	Wave height modelled as a function of fetch, assuming a southwesterly wind of 8 ms^{-1}, averaged over 2 spring/neap tidal cycles	Poole Harbour water model with superimposed wave model (HR Wallingford)	0.001–0.176 m
Algal cover	% cover of macrophyte visible within a 5 m radius of sampling site	Benthic survey 2009	0–95%
Sediment organic content	% of mass loss on ignition, representing % organic content of sediment	Benthic survey 2009 and 2002	0.31–18.29%
Sediment median particle size	The value of ϕ_{50} on the cumulative frequency curve of % mass against ϕ. $\phi=-\log_2$ (particle size in mm)	Benthic survey 2009	0.97–4.49 ϕ
Sediment sorting	Represents uniformity or homogeneity of sediment, calculated as: $(\phi_{84} - \phi_{16})/4 + (\phi_{95} - \phi_{5})/6.6$	Benthic survey 2009	0.31–2.33
Sediment kurtosis	Represents the range of particle sizes present in the sample, calculated as: $(\phi_{90} - \phi_{5})/2.44(\phi_{75}-\phi_{25})$	Benthic survey 2009	0.45–1.85

*Due to conservation of mass, the model predicted unreasonably high salinities on exposed mudflats. Therefore, maximum salinity was artificially capped at 36 ppt.

2.4 Results

2.4.1 Environmental variables

(i) Hydrodynamics

The deepest parts of the harbour were in and around the main shipping channels and near the harbour mouth, where greatest mean depth was ~20 m and tidal range was 1.8 m (Figure 2.3a (i)). However, none of the invertebrate sampling points occurred in the sub-tidal channels. Most of the bays were quite shallow, for example Wareham Channel had mean depths of 0.08–1.16 m. In contrast, Newton Bay, Brands Bay and Lytchett Bay were deeper, particularly Lytchett Bay (mean depth 1.65–2.00 m). Depth range generally decreased with distance from the harbour mouth, and bays exhibited a more restricted range than the central harbour (Figure 2.3a (ii)). Lytchett Bay and Arne Bay had very little depth fluctuation. The greatest flow velocities occurred in the unsampled sub-tidal channels, and flow velocities were lower in the bays, (e.g. maximum flow velocity of Brands Bay was 0.28 ms^{-1}) (Figure 2.3a (iii)). Faster flows occurred around 'pinch points' including the narrow outflow channels of Holes Bay (0.80 ms^{-1}) and Lytchett Bay (0.66 ms^{-1}), and the narrowest part of Middlebere Creek (0.68 ms^{-1}). The wave model predicted maximum wave heights of 0.21 m, which occurred in the north-east corner of the harbour, and minimum wave heights of <1 cm occurred in the sheltered areas such as Holes Bay and Middlebere Creek (Figure 2.3a (iv)).

(ii) Salinity

A general increase in mean salinity occurred from west to east, with minimum salinities in the Wareham Channel (0.4–21.4 ppt), and maximum salinities near the harbour mouth (30.5–36 ppt; Figure 2.3a (v)). Salinity was high in the shallow bays and channels due to evaporation from the mudflat at low tide. In contrast, salinity range was greatest at the outflow of Wareham Channel, where low salinity channel water flushes into the higher salinity water of the central harbour (Figure 2.3a (vi)).

(iii) Sediment

Most intertidal sediment of Poole Harbour is classified as 'mud' according to the Joint Nature Conservation Committee (JNCC) Marine Habitat Classification (Connor et al. 2004), or a mixture of silt and clay according to the Wentworth scale (Wentworth 1922), with a median particle size of <63 μm. Fine sediments dominated the north-western end of the harbour. Larger sediment fractions, including sand and muddy sand dominated the north-east, close to its mouth and to the south of Brownsea Island (Figure 2.3b (i)). Mixed sediments, including sand and gravel, were found throughout the harbour, especially close to the islands

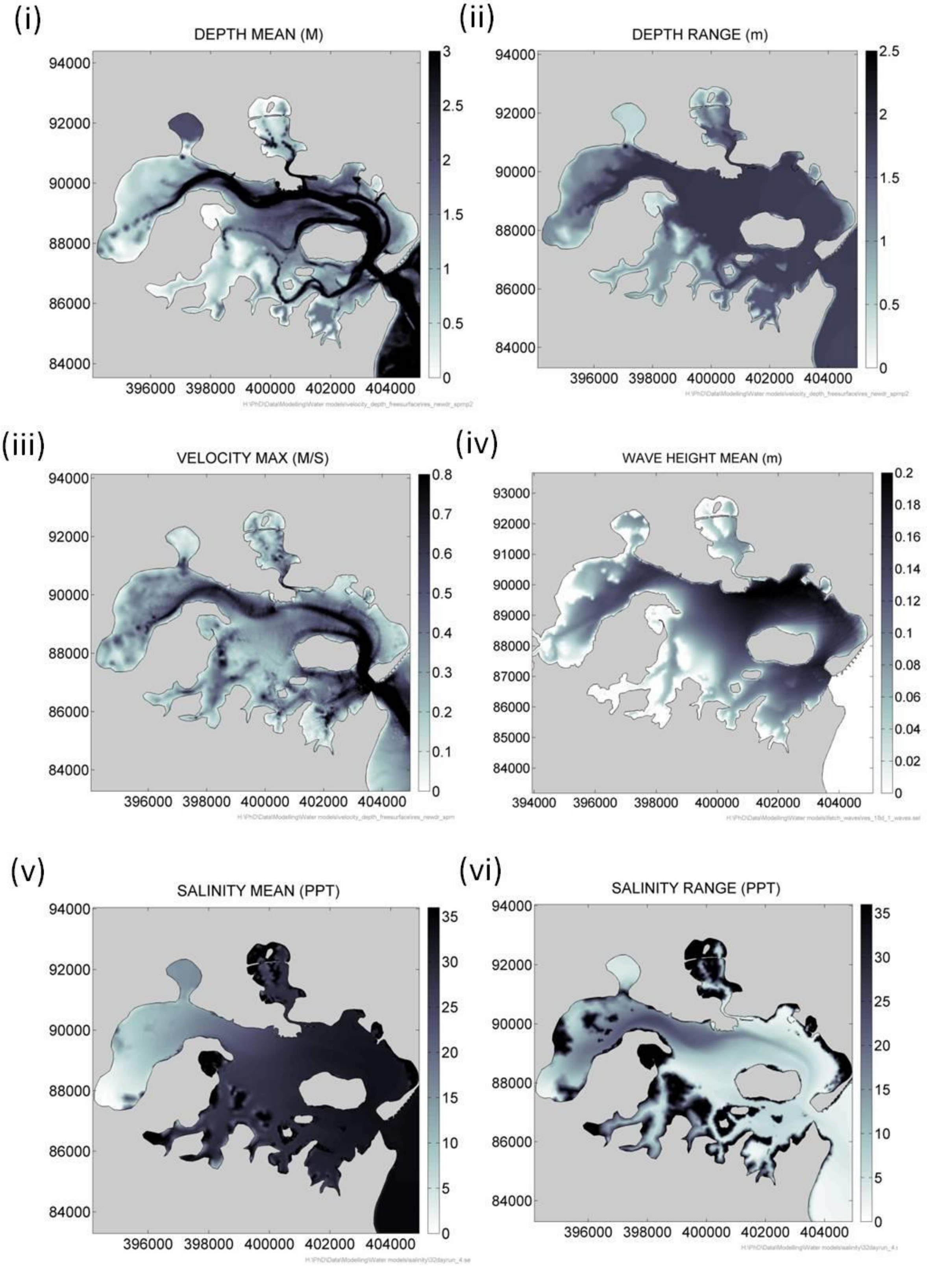


Figure 2.3a Hydrodynamic and salinity variables included in the analysis: (i) mean depth, m; (ii) depth range, m; (iii) velocity maximum, ms^{-1}; (iv) mean wave height, m; (v) mean salinity, ppt; (vi) salinity range, ppt.

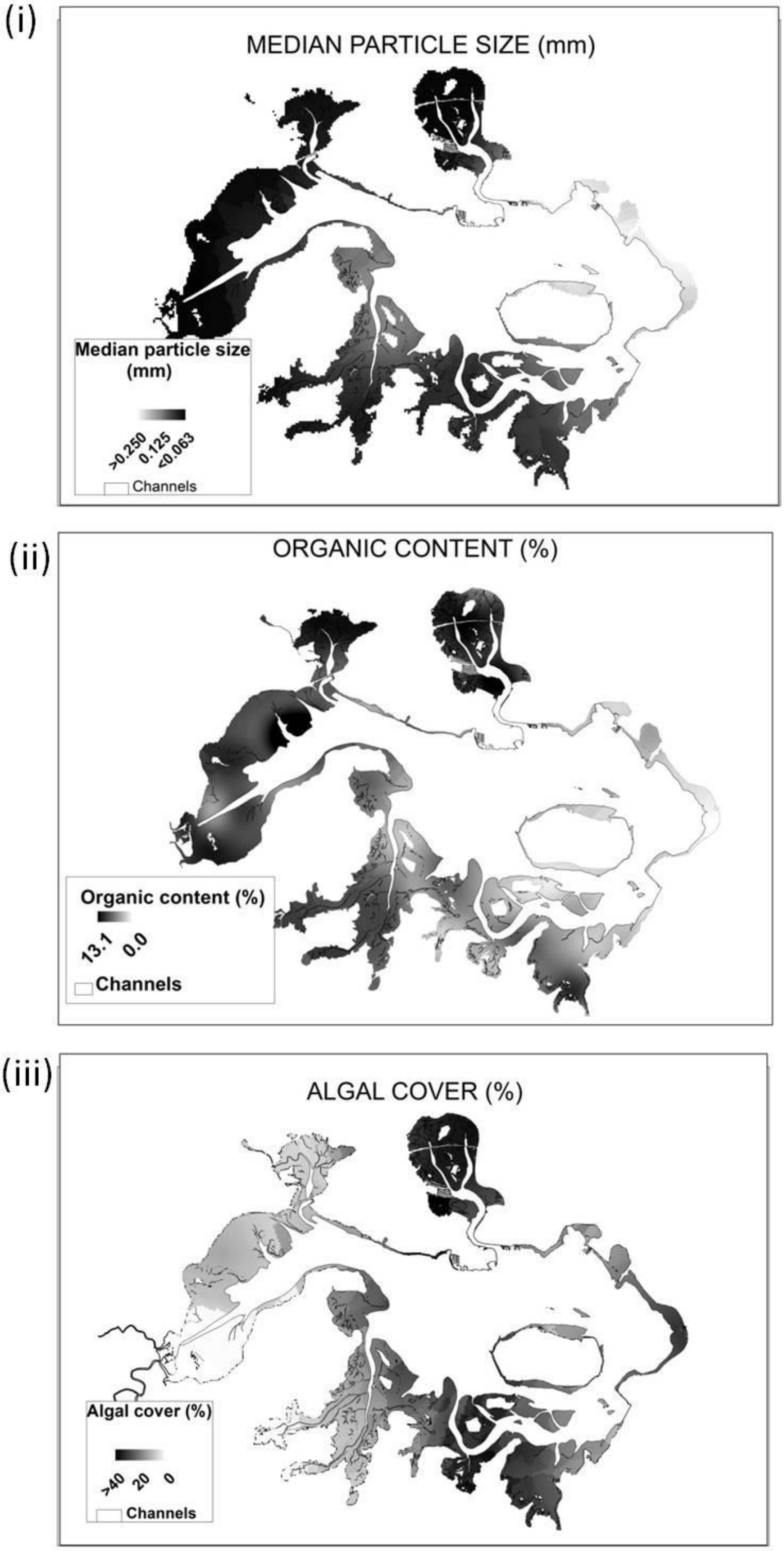


Figure 2.3b Sediment variables included in the analysis: (i) median particle size, (ii) % organic content and (iii) % algal cover.

and in Brands Bay. Organic content was greatest within the sheltered areas, including Holes Bay, Lytchett Bay, Brands Bay, Wych Lake and Wareham Channel (Figure 2.3b (ii). Most areas of the harbour had dense patches of algal mats, composed primarily of *Ulva* spp., with the highest % coverage occurring in Holes Bay and the sheltered creeks north of Newton Bay (Figure 2.3b (iii). Nine percent of sites surveyed had >70% coverage. Further details of sediment data are reported in Herbert et al. (2010).

2.4.2 Benthic community data

The 2009 survey yielded 95 benthic species, whereas the 2002 survey showed a lower number of species overall, due to the reduced sampling effort. The taxa found in each year are presented in Table 2.2. Species distribution maps for 2009 and 2002 for four species: *Cyathura carinata* [Krøyer 1847], *Hediste diversicolor* [Müller 1776], *Nephtys hombergii* [Savigny & Lamarck 1818] and *Scoloplos armiger* [Müller 1776] are presented in Figure 2.4.

Table 2.2 Taxa recorded in benthic cores in 2009 and 2002.

Phyla	Taxa	2009	2002
Total		**95**	**61**
Annelida		**45**	**20**
	Hirudinea	1	0
	Oligochaeta	3	1
	Polychaeta	41	19
Arthropoda		**22**	**19**
(subphylum: Crustacea)	Amphipoda	8	8
	Copepoda	1	0
	Decapoda	3	4
	Isopoda	3	3
	Mysida	0	4
	Ostracoda	2	0
	Sessilia	2	0
	Tanaid	1	0
Mollusca		**22**	**14**
	Bivalvia	15	7
	Gastropoda	7	7
Other		**7**	**5**
	Actinaria	0	1
	Actinopterygii	1	0
	Ascidia	0	1
	Bryozoa	1	0
	Echinodermata	1	0
	Insecta	3	1
	Nematoda	1	1
	Nemertea	1	1

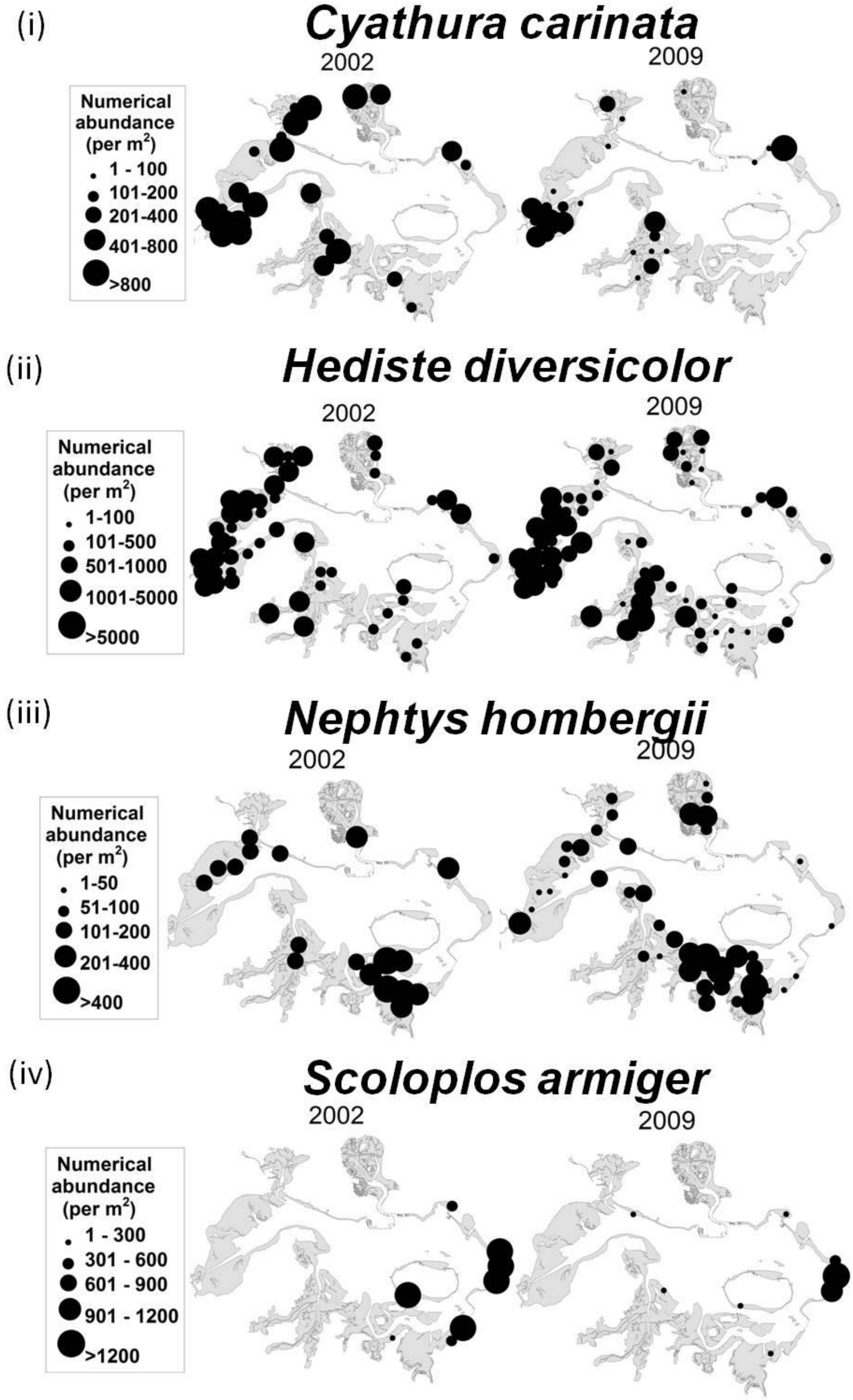


Figure 2.4 Species distribution maps showing the numerical abundance in 2002 and 2009 within Poole Harbour intertidal zone of (a) *Cyathura carinata*, (b) *Hediste diversicolor*, (c) *Nepthys hombergii*, (d) *Scoloplos armiger*.

(i) How well did environmental variables explain species distribution for each year?

The proportion of variation in species abundance distribution explained by the BIO-ENV and Gradient Forest models was modest. For BIO-ENV, a combination of organic content, median particle size, wave height, depth range and algal cover explained 40.0% of the variation for the 2009 data. For 2002, the same combination of environmental predictors, excluding depth range, was the best combination of environmental variables, explaining 24.9% of the variation. For Gradient Forest, 14 of the 94 species (15%) gave positive R^2 values (i.e. showed some predictable relationship with environmental variables). Averaging across all species with a positive R^2, the mean R^2 was 0.138 (range 0.004–0.470). Table 2.3 presents the R^2 values for those species that were ‘predictable’ to some extent (i.e. had an R^2 value greater than 0). For 2009, they include 9 annelids, 5 arthropods and 1 mollusc, (20%, 22% and 4%, respectively, of the total numbers of these phyla recorded). In 2009, annelids were the phyla with the most explicable distribution according to the environmental variables used and molluscs were the least well-explained phyla. In contrast, for 2002, the species for which the environmental variables had the greatest explanatory power included 3 annelids, 3 arthropods, and 2 molluscs (15%, 16% and 14%, respectively). The fact that R^2 values are generally higher for 2009 reflects the fact that sediment data (median particle size and organic content) were collected in 2009, and are thus more closely matched to the 2009 biota, compared with the 2002 biota.

Table 2.3 Performance of Gradient Forest in explaining species distributions and frequency of occurrence for each species (% of sites at which each species was recorded) in 2009 and 2002.

Species	**Phylum**	**R^2**	**Frequency of occurrence**
	2009		
Scoloplos armiger	Annelida	0.470	10.0
Urothoe brevicornis	Arthropoda	0.303	3.8
Haminoea navicula	Mollusca	0.231	5.0
Eusarsiella zostericola	Arthropoda	0.223	10.0
Caulleriella zetlandica	Annelida	0.174	3.8
Nephtys hombergii	Annelida	0.147	52.5
Nephtys kersivalensis	Annelida	0.145	15.0
Notomastus latericeus	Annelida	0.144	6.3
Cyathura carinata	Arthropoda	0.087	31.3
Ampelisca brevicornis	Arthropoda	0.070	5.0
Eteone longa	Annelida	0.068	38.8
Hediste diversicolor	Annelida	0.061	81.3
Anaitides mucosa	Annelida	0.042	18.8
Ostracoda sp.	Arthropoda	0.035	32.5
Eteone foliosa	Annelida	0.004	2.5
	2002		
Scoloplos armiger	Annelida	0.390	10.0
Hediste diversicolor	Annelida	0.171	60.0
Cyathura carinata	Arthropoda	0.123	33.8
Nematoda sp	Nematoda	0.079	3.8
Actinaria sp	Actinaria	0.060	30.0
Arenicola marina	Annelida	0.050	16.3
Crepidula fornicata	Mollusca	0.020	7.5
Corophium volutator	Arthropoda	0.016	12.5
Nassarius reticulatus	Mollusca	0.011	2.5
Microdeutopus gryllotalpa	Arthropoda	0.001	11.3

(ii) Which environmental variables were important?

Table 2.4 presents a comparison of variable importance for BIO-ENV and Gradient Forest. BIO-ENV indicated that the factors that were most important in structuring invertebrate community assemblages were organic content (0.353), median particle size (0.318), and wave height (0.191). The combination of variables that gave the greatest explanatory power was depth range, mean wave height, median particle size, % algae and % organic content (0.400). In comparison, Gradient Forest also indicated that median particle size (R^2 0.028) and organic content (R^2 0.030) were important. It is essential to note that the R^2 values are not directly comparable between the two methods; it is the order of variable importance determined by each method and the relative importance of variables for each method that is of interest here. Spearman's rank test indicated that the rank order of variables predicted by BIO-ENV and Gradient Forest respectively were significantly correlated (r=0.482, p=0.05), and the top two most important variables for 2009 were the same for both methods. The order of variable importance predicted by BIO-ENV for 2009 and 2002 was strongly correlated (r=0.836, p <0.01); however, the correlation in variable importance between years for Gradient Forest was weaker but still significant (r=0.582, p=0.05).

Table 2.4 A comparison of variable importance, as determined by BIO-ENV and Gradient Forest models.

	BIO-ENV				Gradient Forest					
Variables	Ranked importance*		Weighted Spearman's Rank Correlation		Ranked importance*		R^2 weighted importance		Accuracy importance	
	2009	2002	2009	2002	2009	2002	2009	2002	2009	2002
organic	1	1	0.353	0.224	1	1	0.03	0.031	1.88	-0.97
median particle size	2	2	0.318	0.18	2	9	0.028	0.003	1.63	35.72
mean wave height	3	3	0.191	0.106	8	5	0.007	0.008	-0.17	25.88
depth range	4	4	0.16	0.068	6	4	0.011	0.01	13.05	21.05
sorting	5	8	0.097	0.03	3	7	0.027	0.005	7.92	17.29
algal cover	6	6	0.09	0.048	11	11	0.002	0.002	1.87	-2.30
kurtosis	7	9	0.088	0.025	10	8	0.005	0.003	6.49	5.30
depth mean	8	5	0.075	-0.055	5	3	0.011	0.01	5.27	51.33
salinity mean	9	11	-0.03	-0.005	4	2	0.012	0.013	10.97	21.50
salinity range	10	7	0.03	0.038	7	6	0.008	0.007	8.84	10.78
velocity max	11	10	0.028	0.03	9	10	0.005	0.002	0.05	4.90

*Rank order with 1 indicating greatest importance and 11 indicating least importance.

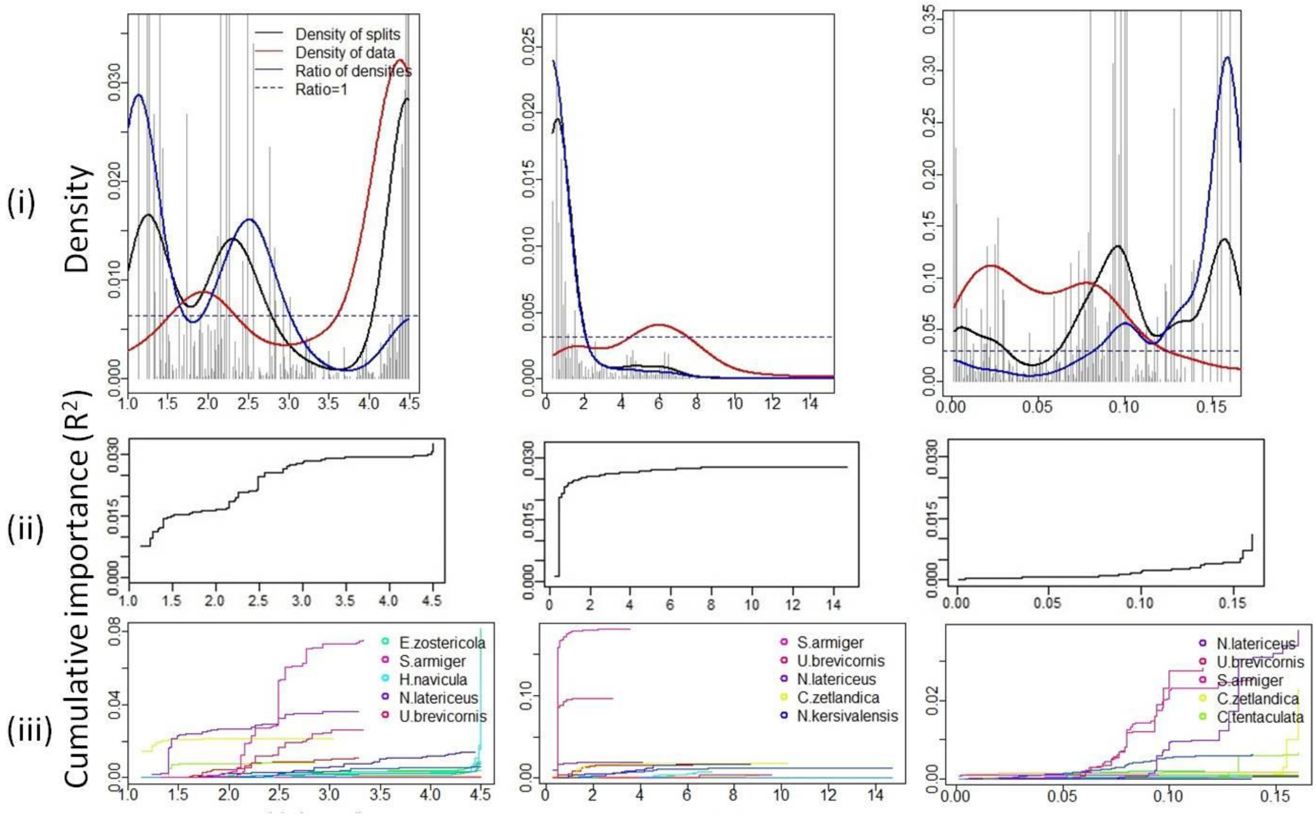
Figure 2.5 shows how the changes in multispecies assemblage vary across the environmental gradients, as predicted by Gradient Forest. These figures show the locations along the environmental gradient where the highest density of splits in the regression tree occur (standardised to the density of data collected). For example, median particle size is only an influential predictor when φ is <3 (equivalent to particle size of <250 µm) and organic content is influential when % organic content is <2% (Figures 2.5a(i) and 2.5b(i), respectively). Notably, wave height is an important predictor when wave height is >8 cm. The cumulative density plots for all species (Figure 2.5 (ii)) show the cumulative increase in R^2 for all species along the environmental gradient, thus emphasise the non-linear response in rates of change of community composition.

(iii) Which species were driving the changes in community structure?

Plots of cumulative R^2 importance for individual species show which species were driving the changes in community structure along each environmental gradient (Figure 2.5(iii)). For example, for median particle size, the most influential species were the ostracod *Eusarsiella zostericola* [Cushman 1906], the amphipod *Urothoe brevicornis* [Bate 1862] and the orbinid worm *Scoloplos armiger*, the latter two of which increased in numbers at intermediate median particle sizes (Figure 2.5a (iii)). *S. armiger* and *U. brevicornis* also increased in density between 0 and 2% organic content (Figure 2.5b (iii)). The wave height gradient was dominated by an increase in the numbers of the capitellid worm *Notomastus latericeus* [Sars 1851] and the cirratulid worm *Caulleriella zetlandica* [McIntosh 1911] at sites with wave height >8 cm (Figure 2.5c (iii)). Such plots can be used to generate ‘sensitivity’ maps, highlighting sites which have environmental variables close to threshold values, which could be used to target monitoring efforts or enhance management efficiency (e.g. Figure 2.6).

(iv) Spatial structuring of data

Including latitude and longitude as predictors in the BIO-ENV analysis increased the overall variance explained from 0.400 to 0.421. Latitude and longitude alone accounted for 0.27 and 0.096 of variance explained. Similarly, including latitude and longitude as predictors in Gradient Forest, the R^2 values were 0.023 and 0.015, respectively, making them the 2nd and 5th most important predictors, respectively.



(a) Median particle size (ϕ) (b) Organic content % (c) Wave height mean (m)

Figure 2.5 Key graphical outputs from Gradient Forest analysis of the three environmental variables that had R^2 weighted importance greater than 0.05 – (a) median particle size, (b) % organic content, and (c) mean wave height. The density plots (i) show the location and importance of splits (grey histogram), the density of splits (black line), the number of observations (red line), and the density of splits standardised by the number of observations (blue line). Where the standardised splits density is >1 (above the dotted line), the predictor is an important determinant of community structure for those values. Species abbreviations: *E. zostericola, Eusarsiella zostericola; S. armiger, Scoloplos armiger; H. navicula, Haminoea navicula; N. latericeus, Notomastus latericeus; U. brevicornis, Urothoe brevicornis; C. zetlandica, Caulleriella zetlandica; N. kersivalensis, Nephtys kersivalensis; C. tentaculata, Cirriformia tentaculata.*

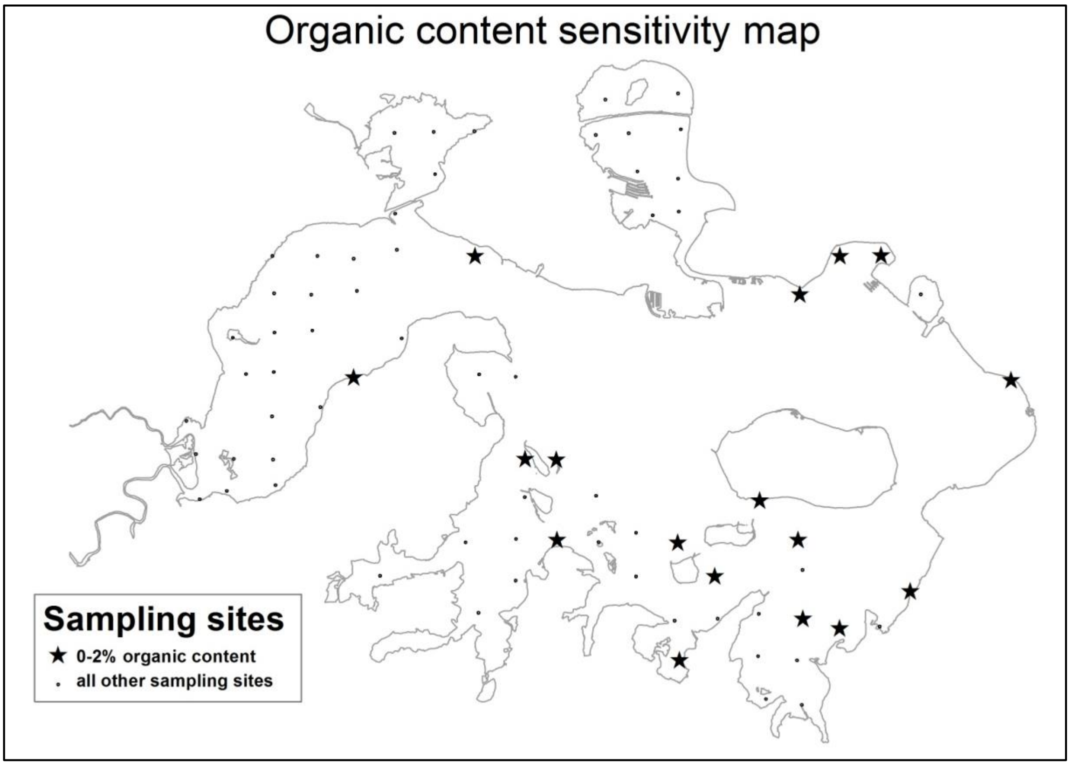


Figure 2.6 Map identifying sites within the Poole Harbour sampling grid where benthic communities are most likely to be impacted by increasing organic content.

2.5 Discussion

I have demonstrated that benthic invertebrate abundance and distribution can be predicted with improved accuracy, deriving more information from survey data, through use of a more computationally intense machine learning application (Gradient Forest), compared with a simpler correlative method (BIO-ENV). In particular, the results establish how machine learning can expose biologically relevant thresholds in environmental gradients that may prove useful and informative as indicators of species abundance and distribution patterns. Threshold identification is not available using BIO-ENV, the older, simpler, and more popular method. I also showed the potential of well-resolved hydrodynamic models to allow subtle but important new conclusions to be drawn from sparse data. For instance, I identified that wave height is potentially a valuable predictor for certain species and that there may exist a high threshold (~8 cm) which is relevant to benthic community data, and can be relatively easily modelled or measured over wide areas. I showed that nutrient availability may also impact the species abundance and distribution; in this case with a low threshold (2% organic content). This finding is of particular importance in harbours and coasts with widespread human-induced nutrient enrichment, including agricultural run-off, urban rainwater discharge, and sewage, all of which may be exacerbated by climate change and sea-level rise and which, crucially, may present initially at very low thresholds. The results suggested that benthic communities may be particularly susceptible to small changes around a low threshold. Overall, the study demonstrated how machine learning (Gradient Forest) can be used to deduce more complex information from notoriously tricky benthic survey data, but that its efficacy will only be established if the subtle threshold indications are confirmed through targeted observations and designed experiments.

Sediment variables had better explanatory power than hydrodynamic variables. However, as the range of hydrodynamic conditions found on intertidal mudflats in Poole Harbour are relatively homogeneous, and the majority of variation in depth and velocity is found in the deeper sub-tidal areas, it is likely that stronger associations between hydrodynamic variables and biotic assemblages would be detected if the sub-tidal sites had also been sampled. The relatively low predictive ability of salinity in both methods probably reflects the fact that the hydrodynamic model did not take into account seasonal fluctuation in salinity, which is likely to be biologically important (Bemvenuti & Netto 1998; Montague & Ley 1993).

The degree of variation in benthic community structure that was explained by environmental conditions was relatively low, but comparable to that obtained in studies of other habitats, which generally achieve maximum correlations of 30% (e.g. Leaper et al. (2011) for subtidal rocky reefs; Compton et al. (2012) for topographically diverse continental margins; and

Pitcher et al., (2012) for meso-scale patterns of seabed biodiversity). While it is feasible that some of the remaining variation could be attributed to other environmental variables that were not measured in this study such as temperature, primary production or pore-water nutrients (Magni & Montani 2006), even studies which have utilised fairly comprehensive suites of around 30 environmental variables, do not achieve much stronger correlations (Pitcher et al. 2012). Therefore it is more likely that the unexplained variation is attributable to internal ecosystem-based factors such as biotic interactions. These may include intraspecific competition between adults (Lawrie et al. 2000), effects of adult density on juvenile recruitment (Thrush et al. 2000; Bartol et al. 1999), predation (Como et al. 2004), chemical/mechanical reworking of the sediment by certain macrofauna rendering it uninhabitable to other organisms (Magni & Montani 2006; Hansen & Kristensen 1997), or spatial competition. In addition, historical disturbance events (Zajac et al. 1998; Ellis et al. 2000), temporal variation in niche preference or patch structure (Parry et al. 2003; Kraan et al. 2012), weather-related factors (van der Meer 1999) and natural population fluctuations of individual species (Hughes 1970; Barbeau et al. 2009; Whitlatch 1977) play a role in structuring communities, and could account for the unexplained variation in the models. Interaction between benthic macroalgae and sedimentation are unstable and potentially chaotic processes which may lead to the formation of multiple stable states, favouring different community structures existing in areas with similar environmental conditions (Herman et al. 2001).

The study emphasised the importance of organic content in determining benthic community structure. High organic content is likely to result from a combination of marine and fluvial deposits, live and detrital algae, saltmarsh debris and enrichment from terrestrial sources. It was concentrated in the bays, especially those in close proximity to the built-up area of Poole. Organic enrichment causes increased growth of algal mat and subsequent eutrophication, and thus may favour species tolerant of hypoxic conditions (Gamenick et al. 1996). While the effects of sediment characteristics on soft sediment intertidal invertebrates are well established, the importance of wave energy in this habitat is less well-understood. It has long been recognised that extreme disturbance by high-energy wave conditions can affect benthic community structure (Rees et al. 1977), but more recently it has been suggested that gentle wave action, such as that generated by wind or by passing craft, may also impact benthic community structure (Emerson 1989; Bishop 2007). Mechanisms may include modified habitat topography, altered food availability, and altered feeding behaviour of benthic infauna (Turner & Miller 1991; Thrush et al. 2000; Dolphin et al. 1995; Miller et al. 1984; Jones & Frid 2009). Near-bed flow and sediment stability may also be important determinants of settlement rate (St-Onge & Miron 2007). Both wave action and flow velocity have been found to be important structuring factors in intertidal mussel beds (Brinkman et al. 2002), but perhaps in a worm dominated community such as Poole Harbour, the effects are less profound. Links between hydrodynamic processes and benthic invertebrate abundance have been demonstrated (Butman 1987) but much remains to be discovered about the scale at which these processes operate, and the interaction with other environmental factors.

2.5.1 Comparison of methods

Both BIO-ENV and Gradient Forest describe the extent to which environmental variables can predict species distribution, and the relative importance of each environmental predictor. However, only Gradient Forest explores the shape and magnitude of changes in community structure along each environmental gradient, and identifies threshold values for certain predictors that lead to large changes in community composition (Pitcher et al. 2012). I found two different and potentially important thresholds in key variables (wave height and organic content) which are helpful in planning further designed experiments and field data collection. In addition, unlike BIO-ENV, Gradient Forest is insensitive to transformation of predictor variables and is able to detect non-linear responses. This is a key benefit as the fourth-root-transformation often employed by BIO-ENV is extreme, and suppresses potentially valuable information while often increasing the likelihood of a false positive correlation. Thus, the discrepancies in variable importance indicated by each method are likely to result from procedural differences in the models, such as the way they deal with correlated variables, rather than any genuine differences in variable importance.

2.5.2 Explaining species associations with environmental gradients

A key difficulty in analysing ecological data sets is that environmental variables are often highly collinear. I minimised collinearity by excluding variables which had a correlation coefficient of >0.6 and by inclusion of a range of hydrodynamic variables, which were modelled with a high resolution across the entire study area, and which were pared down to wave characteristics as the single most informative variable. Thus this study shows that developing approaches using a wide variety of environmental data from different sources can reduce the probability of collinearity biasing results and can lead to new signals in the data which are potentially fruitful lines of new enquiry.

In observational studies, linking observed patterns to process to determine causal links is a challenge as the observed associations may be indirect drivers or proxies for the true physical drivers of change. Indeed, one can never definitively determine which processes give rise to an observed pattern, as more than one process may be responsible for generating the same spatial pattern (Fortin & Dale 2005). True tests of the association between the environmental factors implicated in this study can come only from carefully designed experiments, of which there is an extreme paucity in the scientific literature. In the absence of such evidence, inference as to whether the observed associations are likely to be true cause and effect can be made through careful consideration of the species' physiology and ecology. For example, the species which increased in abundance at sites with wave height >8 cm were mainly capitellid and spionid worms. Both these families consist of opportunistic, fast growing species that rapidly colonise disturbed sediments (Borja et al. 2000). Thus, their presense in sediments frequently disturbed by wind and wave action is likely. *Urothoe brevicornis* feeds by cleaning microorganisms from sediment grains and favours medium to fine sand with low silt or clay content; *Scoloplos armiger* is a detritus feeder which preferentially targets medium grain sizes, and sandier sediments with lower organic content provide ideal conditions for burrowing (Degraer et al. 2006), hence their association with particle size and organic content. *Eusarsiella zostericola* was introduced to European waters unintentionally in association with the American oyster *Crassostrea virginica* [Gmelin 1791], which is an estuarine species and thus associates with finer sediments (Bamber 1987; Bartol et al. 1999); however, it is worth noting that as these ostracods are very small, they may have been undersampled with the 500 μm sieve mesh size.

2.5.3 Spatial structure

Neither of the approaches utilised in this study deal explicitly with spatial structure in community composition or quantify the degree of spatial autocorrelation (Legendre 1993) The presence of spatial autocorrelation in community data can impact statistical inference due to lack of independence of observations, which is inherent in ecological studies, since the structure of the community at a given site could, in theory, have an effect on the community structure at neighbouring sites (Fortin & Dale 2009). The inclusion of longitude and latitude in the models indicated that there is a spatial component to the data that is not accounted for in the environmental variables used. This variation may be driven by some external factor that has a spatial component on the scale of the entire study area such as human activity, or distribution of avian or aquatic predators, or any of the complex interactions between them.

2.5.4 Future research directions

As organic content and sediment particle-size are so influential in driving community structure, a topic for further investigation is how sea-level rise in Poole Harbour will affect these properties. Furthermore, as organic enrichment from terrestrial sources is currently cause for concern in Poole Harbour, and many other harbours, especially in terms of its effects on higher trophic levels (such as commercially important fish or protected shorebirds and wildfowl), a tool that detects subtle changes in biotic communities is valuable for monitoring and management. Gradient Forest identifies species that may be particularly sensitive to changes in the levels of environmental predictors and pinpoints sites which are close to environmental gradient thresholds which may be used for monitoring changes within a site. The extent to which the important species and gradients identified in this study will hold true for other harbours and estuaries is an area that warrants further research.

Chapter 3: A comparison of macrobenthic invertebrate communities in a saline lagoon and an intertidal mudflat: implications for foraging birds

3.1 Abstract

Lagoons are ecologically important within the UK on account of their rarity and importance in supporting protected species, including shorebirds and waterfowl. Additionally, lagoon habitat creation has been proposed as a mitigation measure to offset the loss of intertidal habitat due to sea-level rise. However, there are no studies directly comparing the seasonal abundance and community composition of invertebrates in saline lagoons and intertidal mudflats. This comparison is essential for determining how well lagoons can compensate for intertidal mudflats loss, and support shorebird populations that depend on them.

The spatial and temporal variation in macrobenthic communities were examined over two winters (2009–10 and 2010–11) within a macrotidal lagoon (Brownsea Island Lagoon), and a nearby tidal creek (Middlebere Creek). I collected samples with a 10 cm diameter benthic corer and passed them through a 0.5 mm mesh sieve. I also collected a sediment sample at each station to determine organic content and particle size distribution, and measured salinity and water temperature. Seasonal and spatial variation in community and environmental parameters were compared using standard univariate (ANOVA, Kruskal-Wallis) and multivariate (nMDS, ANOSIM) techniques. The relationship between the biota and environmental variables was determined by two methods: BIO-ENV and Gradient Forest.

There were clear differences in faunal composition between the tidal and non-tidal sites. While the sites shared a number of species, they varied in the relative importance of taxa, the size-frequency of species and the timing of peak abundance. The lagoon habitat was defined by a patchy distribution that was driven by biotic interactions rather than environmental gradients. Its fauna was dominated by annelids and gastropods that were highly abundant, but with individually low biomass. This faunal distribution may be better suited to generalist foragers. At Middlebere, the fauna was more spatially predictable, relating to distance downstream, and biomass was dominated by large bivalves, which may be better suited to specialist foragers hunting for large prey by sight.

3.2 Introduction

Estuaries and lagoons are shallow bodies of water with permanent or ephemeral connection to the sea, collectively referred to as “transitional waters” (McLusky & Elliott 2007). They are characterised by soft sediments, high turbidity and variable salinity and temperatures. The fauna of these habitats originate from marine and terrestrial sources, and have high intrinsic tolerance to variable conditions. However, lagoons differ from estuaries in their degree of isolation from the sea, often separated by a shingle barrier, beach, spit or sea wall, which allows limited exchange of sea water (Barnes, 1987; Bamber, 1992). Some lagoons are partially tidal, whilst others are totally isolated and only connected to the sea by means of a managed sluice gate (Bamber et al. 1993; UK BAP 2008). Soft sediment habitats receive nutrient input from several sources - groundwater, surface water run-off, and the ocean, so they exhibit high rates of primary production and secondary production of benthic invertebrates, compared with other aquatic environments (Nixon & Buckley 2002).

3.2.1 The importance of lagoon and estuary habitats to coastal birds

The high productivity of soft sediment coastal habitats makes them suitable as feeding grounds for many species of birds (Granadeiro et al. 2004). Within the UK, soft sediment habitats are particularly important for passage migrant and resident birds during the winter (Vellinga & Wood 2002; Rehfisch et al. 2003). For this reason, many UK estuaries are designated as Special Protection Areas under the EC Directive on the Conservation of Wild Birds 79/409/EEC. Within Europe, lagoon habitat supports more priority bird species than any other habitat type, and estuaries and mudflats support the second highest number of priority species (Tucker & Evans 1997). Thus, as tidal mudflats become increasingly threatened by sea-level rise, artificial non-tidal habitats will become increasingly important for maintaining bird populations. Creation of artificial lagoon habitats has been proposed as a mitigation strategy to offset the loss of feeding areas (Bamber et al. 2001).

However, there is currently very little research directly comparing the invertebrate availability throughout the year in these two habitats. Understanding the distribution and quality of the invertebrate food resource is a crucial stage in building models to predict the effects of habitat change on bird populations (Stillman 2008). Therefore, it is essential to understand how these two habitat types differ in invertebrate community structure and how spatial and temporal fluctuations in abiotic conditions affect these communities (Ysebaert & Herman 2002; Carvalho et al. 2005). An understanding of these processes is crucial for both design of effective artificial habitats in the future and management of current habitats (Bamber et al. 1992; Bamber et al. 2001).

3.2.2 The conservation importance of lagoons

On a European scale, lagoons are relatively widespread along the microtidal shores of the Mediterranean, Baltic and Black Seas, but occur far less frequently along the macrotidal North Atlantic coasts (Barnes 1989; Mistri et al. 2001a; Carvalho et al. 2011; Tucker & Evans 1997). The total extent of lagoon habitat within the UK was estimated as 5480 ha in 2007, with over half of this area occurring in Scotland, and only 1480 ha occurring within England (JNCC 2007). Individual lagoons vary in size from less than 1 ha to 800 ha (the largest being the Loch of Stenness, Orkney) (Barnes 1989). Lagoons have a protected status within the UK. They are listed under Annex 1 of the EC Habitats Directive as a priority habitat (92/43/EEC). Saline lagoons were also included in the list of priority habitats in the UK Biodiversity Action Plan (BAP), which was superseded in 2012 by the UK post-2010 Biodiversity Framework (JNCC and DEFRA 2012). Within England, saline lagoons are listed in the Habitats of Principal Importance list (Natural England 2010). Forty-seven per cent of UK lagoon habitat occurs within Special Areas of Conservation (SAC), and many lagoons are designated as Special Protection Areas (SPA) and RAMSAR sites. All lagoons are designated as Sites of Special Scientific Interest (SSSIs). Of the 37 'lagoon specialist' species listed by the JNCC, thirteen are protected under Wildlife and Countryside Act (1981), including two plants, nine invertebrates and two birds, protected under Schedules 8, 5 and 1, respectively (JNCC 2004).

3.2.3 Lagoon macrobenthic communities

There is a paucity of knowledge on the relative importance of factors that structure lagoon communities, both spatially and temporally (Joyce et al., 2005). Important environmental factors include salinity (Joyce et al. 2005; Falk et al. 1994; Ayadi 2004; Barron et al. 2002), degree of light penetration (Casabianca & Posada 1998), substrate composition (Millet & Guelorget 1994; Wilson 1991; Arias & Drake 1994; Joyce et al. 2005; Schiller 2006) and macroalgal abundance (Arias & Drake 1994; Mistri et al. 2000). Lagoon size and degree of water exchange are also important (Nicolaidou et al. 2006; Bamber et al. 1993; Carvalho et al. 2005; Reizopoulou & Nicolaidou 2004).

Lagoon salinity is intermediate between marine and freshwater ecosystems, so lagoons support species typically associated with marine and freshwater habitats, as well as specialist lagoon species. Generally, lagoon biodiversity is low, limited to species tolerant of variable environmental conditions (Falk et al. 1994). However, the invertebrate species able to withstand these variable abiotic conditions are among the most important prey species for shorebirds, including *Hediste diversicolor* [Müller 1776] and *Corophium volutator* [Pallas

1766] (Falk & Nøhr, 1994). Previous work has shown that salinity determines the distribution of species within lagoons, typically with marine species located at the seaward end (Joyce et al. 2005; Falk et al. 1994). However, in some studies, salinity does not play a significant role in determining species distribution within lagoons (Lardicci et al. 2001).

The nature of the sediment is important; however, studies have drawn differing conclusions on the precise relationship between sediment variables and community structure (Reizopoulou & Nicolaidou 2004; Carvalho et al. 2005). The percentage of fine sediments is important for relatively sessile, tube building organisms (Wilson 1991; Arias & Drake 1994). In terms of biomass production, dominance of fine sediments benefits crustaceans, whereas coarser sediments benefit molluscs (Millet & Guelorget 1994). Furthermore, larger sediment particles may interfere with the feeding mechanisms of tactile foraging shorebirds, thus altering the predation pressure on the invertebrate communities (Quammen 1982). The degree of habitat heterogeneity, for example due to the presence of 'ditch grass' *Ruppia sp.* or cobbles and pebbles, may affect community structure by altering faunal recruitment rates ((Boström & Bonsdorff 2000; Joyce et al. 2005; Schiller 2006). High levels of organic content in the sediment may favour the proliferation of opportunistic species, such as polychaetes of the Capitellid family (Reizopoulou & Nicolaidou 2004). Organic enrichment may also lead to the proliferation of macroalgae, and subsequent eutrophication may favour hypoxia-tolerant species, such as hydrobiid gastropods and chironomids (Reizopoulou & Nicolaidou 2004; Gray et al. 2002).

However, the majority of the studies to-date have been conducted in meso- or microtidal areas such as the Mediterranean, which differ in species composition from the macrotidal lagoons of the Atlantic (Maci & Basset 2009; Magni et al. 2008; Magni et al. 2005; Mistri et al. 2000; Mistri et al. 2001a; Carvalho et al. 2011; Lardicci et al. 2001). Most surveys of lagoon benthic life in the UK have either been limited to either a few months of the year, generally focussing on the summer (e.g. Joyce et al. 2005; Mason 1986), or have sampled a limited number of sites within the lagoon with a bias towards sites close to the shore, giving little indication of spatial variation within the lagoon (e.g. Healy 1997). Notable exceptions include the detailed surveys of the Keyhaven-Lymington lagoons (Bamber 2000). Other studies have included only presence-absence data so have limited utility in understanding secondary production (Bamber et al. 2000). The lack of understanding of spatial and temporal variation in invertebrate communities limits the ability to fully understand the importance of British lagoon resources for stop-over migrants or overwintering birds.

In comparison to lagoon habitat, the community composition of intertidal soft sediment benthic habitats is comparatively better studied, and is discussed in detail in Chapter 2.

3.2.4 Aims and objectives

The overall aim of this chapter is to determine the seasonal and spatial variability of the benthic community within Brownsea Island Lagoon, an artificial non-tidal saline lagoon within Poole Harbour. This is compared with the seasonal and spatial variation of the benthic community of a nearby intertidal mudflat, Middlebere Creek. In order to ensure that newly created lagoon habitat is ‘fit for purpose’, it is essential to understand how environmental variables, such as sediment properties, impact the invertebrate communities, both in terms of abundance and the biomass density.

The specific objectives of this chapter are:

- to compare the seasonal and spatial variation in community structure in a non-tidal lagoon and an intertidal mudflat habitat, in terms of species abundance and biomass;
- to describe seasonal and spatial variation in salinity and sediment properties in each habitat;
- to determine if there is a relationship between abiotic environmental factors and benthic community structure within each habitat;
- to discuss the implications for foraging birds at each site.

3.3 Methods and materials

3.3.1 Study sites

Brownsea Lagoon is a 17.8 ha non-tidal saline lagoon, situated on the north-eastern edge of Brownsea Island, in the centre of Poole Harbour, UK, 50.692° N, 1.959° W. Middlebere Creek is an intertidal mudflat in the southwest corner of Poole Harbour, 50.681° N, 2.035° W, immediately south of the Arne Royal Society for the Protection of Birds (RSPB) Nature Reserve (Figure 3.1).

3.3.2 Study design

I conducted a preliminary survey of 3 sites within Middlebere Creek in October 2009 and 6 sites around the periphery of Brownsea Lagoon in November 2009 to assess species diversity and abundance. I collected further samples from 15 stations at each study site (see Figure 3.1), in August 2010, November 2010, and February 2011 and also from Middlebere in April 2011. A reduced number of sites were sampled at Brownsea in April 2010 and 2011, to minimise disturbance to the breeding colonies of common and sandwich terns.

3.3.3 Sampling

As preliminary surveys indicated the presence of the starlet sea anemone, *Nematostella vectensis* [Stephenson 1935], which is protected under Schedule 5 of the Wildlife and Countryside Act (1981), I obtained a licence from Natural England to take biotic samples. I collected three benthic core samples (10 cm diameter, 15 cm deep) from each station to analyse biota, using a purpose-built suction corer (Figure 3.2), which enabled sampling of the intertidal sites at high tide. I collected a smaller (6 cm diameter) core for sediment particle size and organic content analysis. Within 24 hours of collection, I sieved the biotic cores through a 500 µm mesh and preserved the retained fraction in 10% formal saline (Fisher Scientific) for at least 2 weeks. Subsequently, I separated the organisms from the residual sediment and transferred them into 70% industrial methylated spirits (Fisher Scientific). In the preliminary survey, biota were identified to the species level where possible to determine diversity indices for the samples (although annelids of <5 mm were not identified further than class); however, for the main survey, organisms were grouped into taxa to determine trends in biomass. For the Brownsea fauna, a subsample of 10 stations from each time point (B1, B2, B3, B4, B5, B6, B7, B11, B14 and B15) were identified to species level in order to determine diversity indices, and the relationship between biota and the environment.

I froze the small sediment cores within 24 hours of collection. I conducted particle size and organic content analysis by the methodology outlined in Chapter 2. Salinity and temperature measurements were also taken at each site using a handheld salinity meter (YSI salinity conductivity and temperature meter model 30). The percentage cover of macroalgae within a 5 m radius of the sample core was visually assessed at Brownsea, but could not be assessed at Middlebere as samples were collected at high tide. Presence of macroalgae in cores was also recorded.

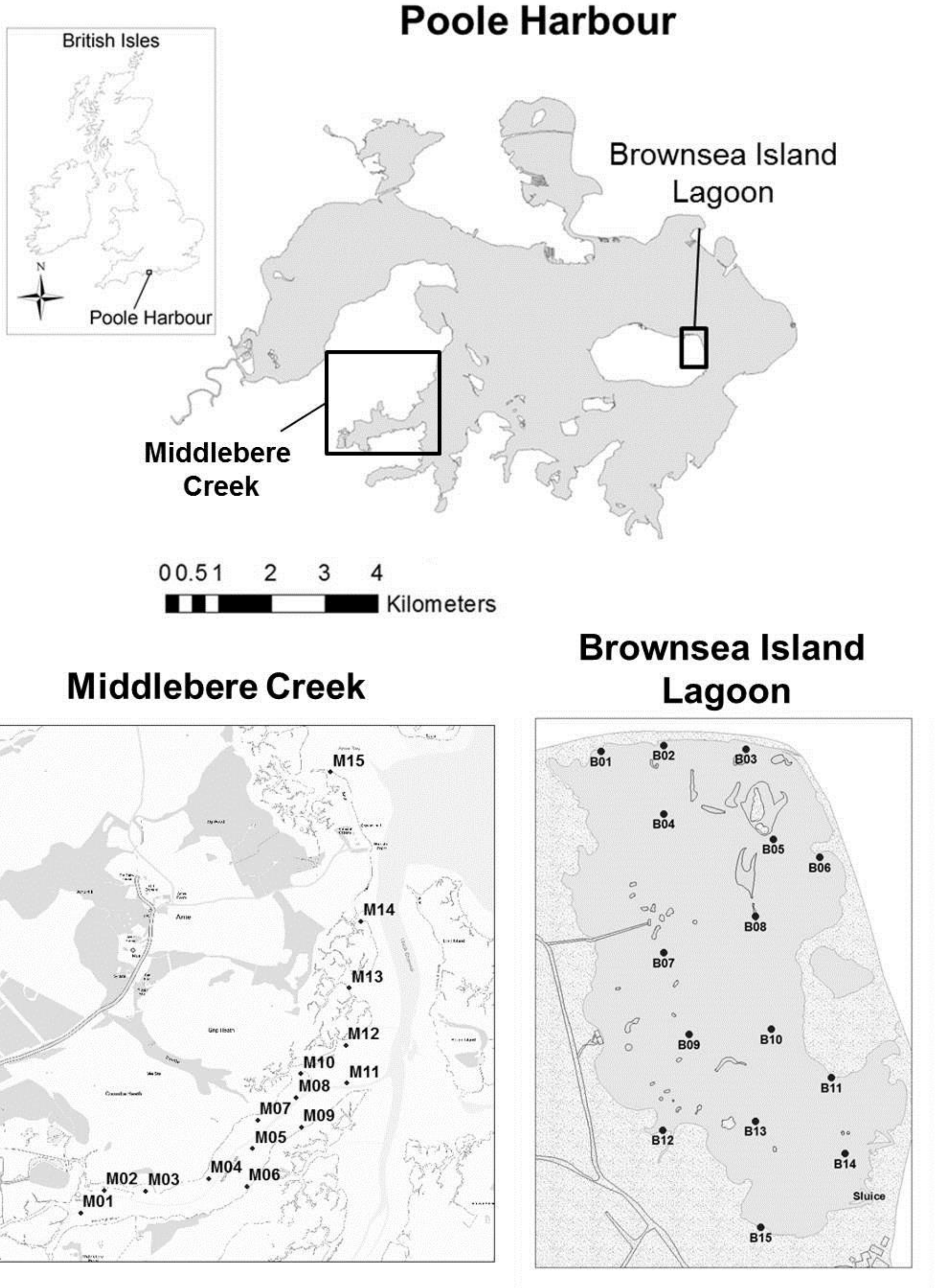


Figure 3.1 Map of study sites and sampling stations.

Figure 3.2 Annotated diagram of suction corer used for benthic sampling.

3.3.4 Biomass quantification

I calculated biomass for the most numerically abundant invertebrates. For the species *H. diversicolor*, *C. volutator* and *Idotea chelipes* [Pallas 1766], I collected fresh specimens in November and December 2011, measured the total length and determined the ash-free dry mass (AFDM) of individuals by loss of mass on combustion. The raw data were $\log_e$ transformed, and I fitted type II linear models to the data using Reduced Major Axis regression to account for the uncertainty in both length and AFDM measurements. I used the regression equations to estimate the biomass of preserved specimens. For fragmented *H. diversicolor* specimens, length was estimated using the relationship between head width and body length, which I determined from a sample of 48 intact fresh worms (see Appendix 1). To estimate the relaxed length of live *H. diversicolor* I used the unpublished method of McGrorty and West, by which live worms were placed alongside a ruler on a cold, wet tray, shielded from bright light. Worms adopt a relaxed, stationary posture against the angle of the ruler within roughly one minute, at which time body length was recorded. For small taxa (small annelids, small bivalves and *Nematostella*), I calculated an average value for the specimens collected. Small annelids and *Nematostella* were too small to determine AFDM of individual organisms, so ten organisms were pooled and an average value was calculated. I determined the AFDM for all *Corophium* using *C. volutator* (which were more abundant at the time of sample collection than *Monocorophium insidiosum* [Crawford 1937]). I determined the AFDM of ‘small bivalves’ from a sample of 7 *Abra tennuis* [Montagu 1803]; however, as this species was not abundant in the samples, only an approximation of biomass per organism was necessary. I did not collect enough large *Cerastoderma glaucum*

[Linneaus 1758] to produce an adequate regression line, so I used a previously reported relationship for *Cerastoderma edule* [Linneaus 1758] (N. S. Thomas et al. 2004). A previously reported length—biomass relationship for *Hydrobia ulvae* [Pennant 1777] (synonymised to *Peringia ulvae*) was used to determine AFDM for *P. ulvae* and the related gastropod *Ecrobia ventrosa* [Montagu 1803] (N. S. Thomas et al. 2004).

3.3.5 Data analysis

I calculated average abundance and biomass figures over one year, using the data from August and November 2010 and February and April 2011 surveys. I calculated a selection of univariate indices to describe benthic community structure in PRIMER v6 (Clarke & Gorley 2006): numerical abundance (N), number of species (S), Margalef's species richness (d), Pielou's evenness (J') and Shannon-Wiener species diversity using log base e (H'), taxonomic diversity (Δ), and taxonomic distinctness (Δ*). For taxonomic diversity and distinctness I used the full taxonomy, aggregating from species to phylum (Warwick & Clarke 1995) . These indices were calculated for each station and time period.

Differences between community assemblages and sediment particle size composition were tested using a 2-way crossed ANOSIM (Clarke 1993). SIMPER analysis was used to determine species that were highly influential in determining community structure (Clarke 1993). Spatial and seasonal differences in abundance and biomass of taxa and environmental variables were assessed using Kruskal-Wallis and Mann-Whitney U tests, using IBM SPSS Statistics 20 (IBM Corp 2011). In cases where data were normal with homogenous variance, shown by the Shapiro-Wilk and Levene statistics, respectively, 1-way ANOVA was used.

The relationship between biotic assemblages and environmental variables was tested using the BIO-ENV routine in PRIMER v6 on dispersion-weighted, square-root-transformed biotic data and suitably transformed and normalised environmental variables (Clarke et al. 2006; Clarke & Warwick 2001). Associations were tested independently using the Gradient Forest method implemented in R (R Core Development Team 2012; Pitcher et al. 2011). The latter two methods are described fully in Chapter 2. I tested the degree to which numerically abundant taxa could predict the abundance distribution of all other species by removing them from the site-by-species matrix and including them as an environmental variable in both BIO-ENV and Gradient Forest analyses. Sediment characteristics such as median particle size, sorting, skewedness, kurtosis and % gravel, sand and silt were determined from particle size fractional abundance data collected for each site using the R package RYSGRAN (de Camargo et al. 2011).

3.4 Results

3.4.1 Macrobenthic communities

Overall, 27 species were identified in the samples from Brownsea Island Lagoon - 11 annelids, 10 arthropods, 4 molluscs, 2 insects, an actinarian and a nematode. These included seven lagoon specialist species: the starlet sea anemone *Nematostella vectensis*; the lagoon mudsnail *Ecrobia ventrosa*; the lagoon cockle *Cerastoderma glaucum*; the ostracod *Cyprideis torosa* [Jones 1850]; two isopods, the lagoon slater *Idotea chelipes* and *Lekanosphaera hookeri* [Leach 1814]; and the amphipod *Monocorophium insidiosum* (formerly *Corophium insidiosum*). At Middlebere, 29 species were identified, including 12 annelids, 5 arthropods, 9 molluscs, an insect, an actinarian, a nematode and a nemertean. The full species lists are provided in Appendix 2. Univariate community measures, based on the initial survey of Brownsea and Middlebere, conducted in November and October 2009, respectively, are provided in Table 3.1. Species richness, number of species per core, and species diversity were higher at Brownsea compared with Middlebere, and species evenness was higher at Middlebere. Furthermore, the mean number of individuals per core was 6.6 times greater at Brownsea.

Figure 3.3 shows the non-metric multidimensional scaling (nMDS) plot of dispersion-weighted square-root-transformed community data at Brownsea and Middlebere, grouped by sampling date. Each point represents the average of three cores. Sample B12 from February 2011 was omitted from the Brownsea plot as it was extremely anoxic and species poor and strongly skewed the plot. A 2-way crossed ANOSIM test showed a significant difference in community assemblages at Brownsea between sampling dates, (R=0.517, P=<0.001) and between stations (R=0.622, P=<0.001). SIMPER analysis indicated that the similarity in community structure between sampling dates was driven by the abundance of the same three species: *Ecrobia ventrosa*, *Hediste diversicolor* and the small oligochaete worms *Tubificoides sp*. Significant differences were also found at Middlebere between sampling dates (R=0.433, P=0.001) and stations (R=0.475, P=0.001), but the smaller R values indicated that the differences were not as pronounced as those observed at Brownsea. As with Brownsea, the similarity of community structure between sampling dates was driven by a hydrobiid gastropod, *Peringia ulvae*, and *H. diversicolor*.

Table 3.1 Univariate community measures for Brownsea and Middlebere, surveyed in November and October 2009, respectively.

	Index (95% Confidence interval)	
	Brownsea	Middlebere
Mean number of species (S)		
Per core	9.7 (8.8–10.6)	5.3 (4.4–6.1)
Mean number of individuals (N)		
Per core	270 (204–336)	41 (21–61)
Per m^2	34321 (25876–42766)	5870 (3297–8443)
Margalef species richness (d)	1.61 (1.46–1.76)	1.44 (1.16–1.73)
Shannon-Wiener diversity (H’)	1.53 (1.38–1.67)	1.24 (1.06–1.41)
Pielou’s Evenness (J’)	0.67 (0.62–0.72)	0.77 (0.72–0.83)
Simpson diversity ($1 - \lambda'$)	0.70 (0.65–0.76)	0.65 (0.59–0.72)
Taxonomic diversity (Δ)	66.6 (61.7–71.5)	60.0 (53.1–66.9)
Taxonomic distinctness (Δ*)	94.5 (92.3–96.7)	90.8 (88.0–93.6)

$d = (S-1)/logN$ where S is the total number of species and N is the total number of individuals in the sample; $H' = -\sum_i p_i \log(p_i)$, where p_i is the proportion of the total count arising from the i^{th} species; $J = H'/\log S$;$1 - \lambda' = 1 - \{\Sigma_i N_i\,(N_i - 1)\}/\{N(N-1)\}$; $\Delta = [\Sigma\Sigma_{i<j}\omega_{ij}\, x_i x_j]/[N(N-1)/2]$ where the double summation is over all pairs of species i and j and ω_{ij} is the taxonomic distance between species i and j (ie. the average ‘taxonomic distance’ apart of two randomly chosen individuals); $\Delta^* = [\Sigma\Sigma_{i<j}\omega_{ij}\, x_i x_j]/[\Sigma\Sigma_{i<j}\, x_i x_j]$ is the expected taxonomic distance apart of any two individuals chosen at random, provided they are not from the same species (Clarke & Warwick 2001).

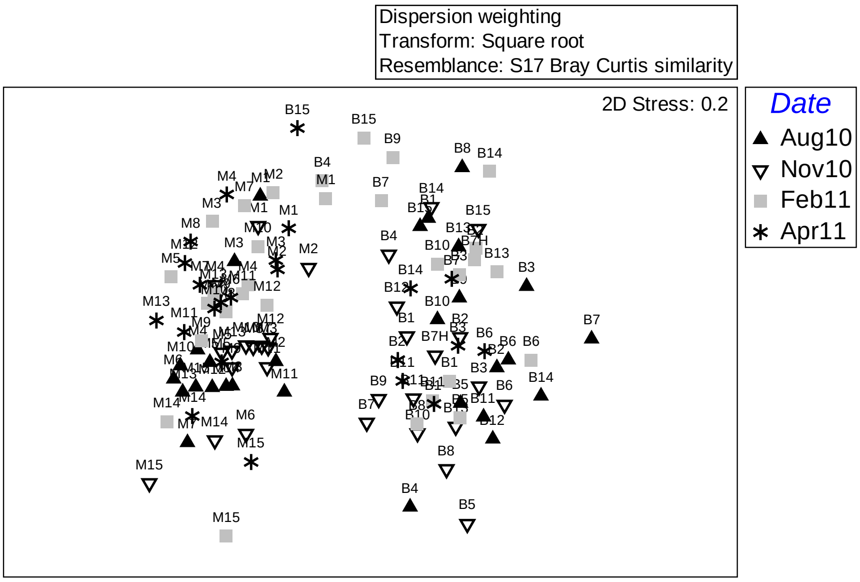


Figure 3.3 Non-metric multidimensional scaling (nMDS) plot of dispersion-weighted square-root-transformed community data from sampling sites at Brownsea Island Lagoon (B) and Middlebere Creek (M). Each point represents the average of three benthic cores.

3.4.2 Seasonal variation in invertebrate abundance

The seasonal variation in the absolute and relative abundance of taxa is presented in Figure 3.4. All taxa were more abundant at Brownsea compared with Middlebere, except bivalves, for which there was no significant difference between the sites. At both study sites, the highest absolute abundance of all organisms was observed in November. At Brownsea, this was largely due to a higher number of gastropods and crustaceans in November, with annelids comprising a smaller proportion of the organisms compared with other months; however, at Middlebere it was due to higher numbers of all taxa.

At Brownsea there was a significant seasonal variation in abundance of all taxa except annelids and crustaceans, and in total organismal abundance ($p<0.05$). The most abundant taxa for all sampling periods except November 2010, was annelid worms. This group was dominated by the ragworm *H.diversicolor* and the tubificid oligochaete worms *Tubificoides benedii* [Udekem 1855] and *Tubificoides pseudogaster* [Dahl 1960]. Annelids comprised more than half the organismal abundance in February and April 2011, but less than a third of the overall abundance in August and November 2010. The second most abundant taxon overall (and most abundant in November 2010) was the gastropods, comprised of the prosobranch molluscs, *E. ventrosa* and *P. ulvae*. There was also a clear seasonal pattern in the numbers of *Nematostella vectensis*, with high abundance in August and November of both years (peak abundance 16736 m^{-2} in November 2009), and low abundance in February and April of both years of (lowest abundance of 25 m^{-2} in February 2011).

At Middlebere, the seasonal variation in abundance was significant for all taxa except chironomids ($p<0.05$). At Middlebere, annelids were numerically dominant for all sampling periods, except August, when gastropods dominated. The relative dominance of annelids peaked in February.

There was minimum variation in trophic structure between study periods. At Brownsea, deposit feeders were consistently dominant, comprising between 68–89% of the numerical abundance, with predators comprising between 12–24% and suspension feeders comprising 3–8%. At Middlebere, deposit feeders were also dominant (43–78%), but there was a proportionally higher number of suspension feeders compared with Brownsea (4–40%) and a slightly higher proportion of predators (17–29%).

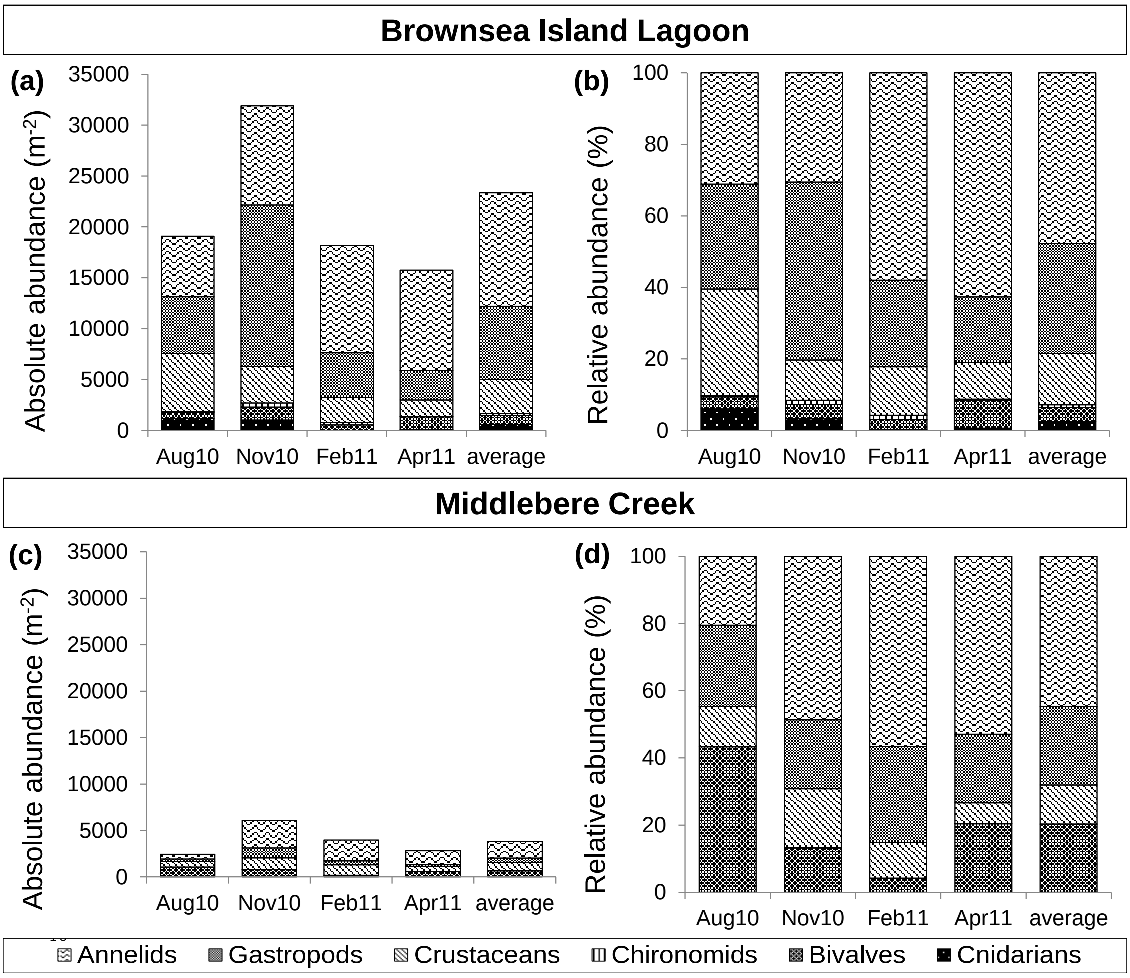


Figure 3.4 Seasonal variation in absolute and relative abundance of invertebrate taxa at Brownsea Island Lagoon (a,b) and Middlebere Creek (c,d).

3.4.3 Spatial variation in invertebrate abundance

As well as seasonal heterogeneity, there were differences between sampling stations within the study sites. The spatial variation in absolute abundance of taxa, averaged over one season (August 2010, November 2010, February 2011, April 2011) is presented in Figure 3.5. At Brownsea, there were significant differences between stations in all taxa except cnidarians, and in total organismal abundance. Some sites were consistently dominated by annelids (e.g. B3), while others were dominated by gastropods and crustaceans (e.g. B11). In addition some sites had consistently high organismal abundance (e.g. B5). Conversely, at Middlebere, there was much less variability in organismal abundance, and relative abundance of taxa between sites. There were significant differences between stations for crustaceans ($p<0.001$) and gastropods ($p<0.001$), but differences in annelids were not statistically significant ($p=0.136$) and differences in bivalves ($p=0.028$) and chironomids ($p=0.039$) were barely significant. The abundances recorded for each sampling period, separately, are provided in Appendix 3.

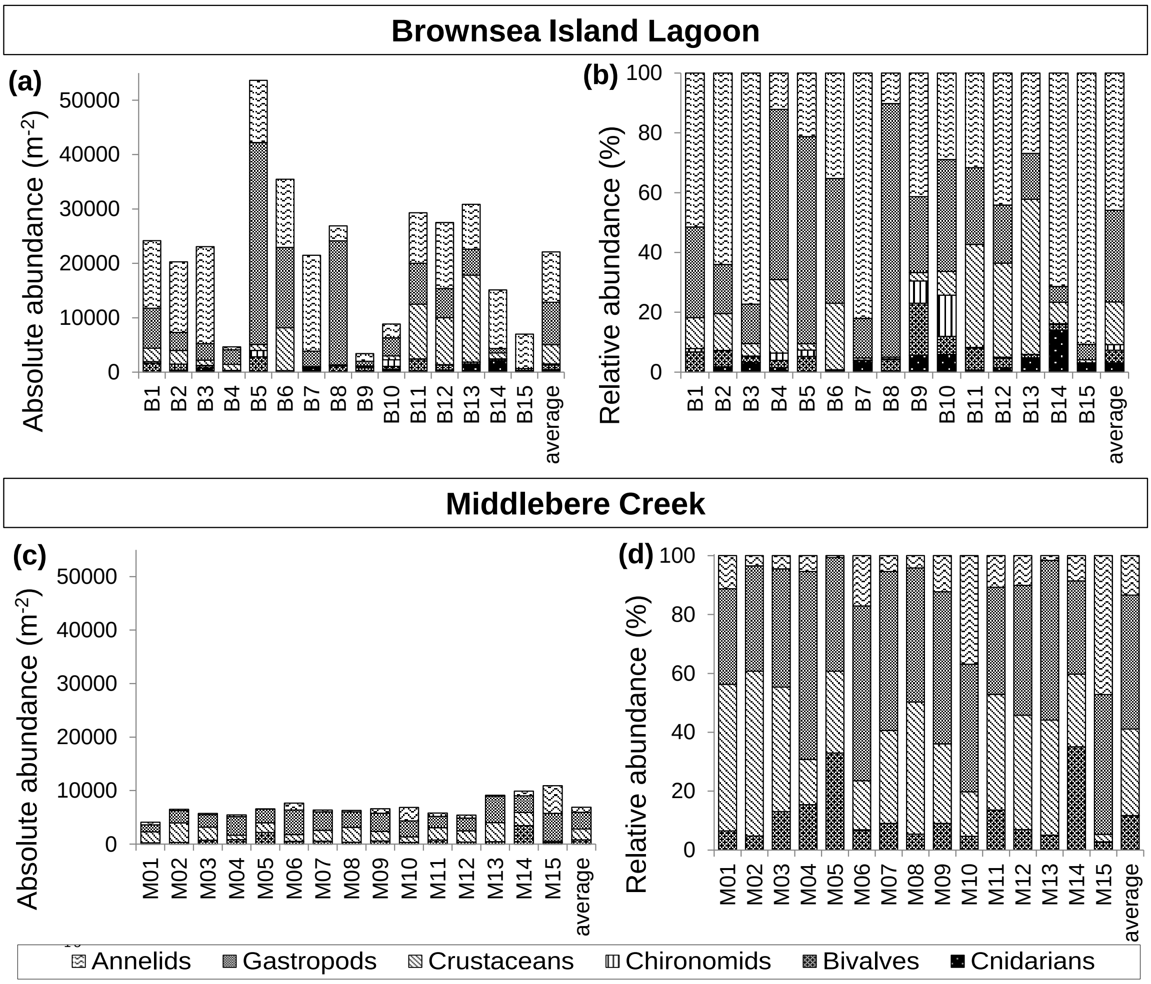


Figure 3.5 Spatial variation in absolute and relative abundance of invertebrate taxa at Brownsea Island Lagoon (a,b) and Middlebere Creek (c,d).

3.4.4 Seasonal variation in biomass

I calculated the biomass of the main benthic taxa: annelids, gastropods, crustaceans, bivalves and cnidarians. Chironomids were excluded due to negligible abundance. The allometric equations used to determine the biomass of large species are given in Table 3.2, and the biomass per organism for small taxa is given in Table 3.3.

The seasonal variation in biomass contributed by each taxon is presented in Figure 3.5. At Brownsea, 2-way crossed ANOSIM test showed significant difference in community biomass structure between dates (R=0.484, p=0.001); however, the degree of similarity between was greater than that determined using species abundance. There were significant seasonal differences in biomass of all taxa except crustaceans and bivalves, and in total biomass. Averaged across all dates, annelids comprised 47.5% of total biomass, and dominated the biomass during all sampling periods except November. During November, only 16.1% of biomass was contributed by annelids, and 66.5% was contributed by gastropods.

The biomass of all taxa were significantly lower at Middlebere, compared with Brownsea ($p<0.001$). At Middlebere, there were significant differences in community biomass structure between dates ($R=0.317$, $p=0.001$). There were significant seasonal differences in all taxa, and in total biomass. The biomass at Middlebere was dominated by bivalves in all sampling periods, comprising on average 63% of the biomass. Annelids comprised 19–48% of the biomass and gastropods and crustaceans combined comprised only 2–8% of the total biomass.

Table 3.2 Allometric equations used to relate ash-free dry mass (AFDM) in mg (A) to total length in mm (TL) for large prey species.

Species	**n**	**Allometric equation**	**Pearson's R**	**R^2**	**P (2-tailed)**
Hediste diversicolor	23	$lnA = 2.032408 \times ln(TL) - 5.487573)$	0.696	0.485	<0.001
Idotea chelipes	13	$lnA = 2.120569 \times ln(TL) - 4.203262)$	0.944	0.891	<0.001
Corophium volutator[1]	28	$lnA = 2.010116 \times ln(TL) - 4.637604)$	0.629	0.395	<0.001
Cerastoderma glaucum[2]	41	$lnA = 3.3147 \times ln(TL) - 5.6799)$	Not reported	0.958	<0.001
Peringia ulvae[3,4]	68	$lnA = 1.1748 \times ln(TL) - 1.6752)$	Not reported	0.371	<0.001

[1]Also used to calculate AFDM for *M. insidiosum*. [2]Regression equation for *C. edule* taken from Thomas et al. (2004). [3]Regression equation for *H. ulvae* was taken from Thomas et al. (2004). [4]Also used to calculate AFDM for *Ecrobia ventrosa*.

Table 3.3 Ash-free dry mass (AFDM) per individual, for small species.

Taxa	**n**	**mg AFDM (mean±s.d.)**
Nematostella vectensis	10	0.22†
Small annelids	30	0.23±0.06
Abra tennuis	6	2.11±0.90

†No standard deviation was available for this figure as only 10 individuals were used to determine ash-free dry mass.

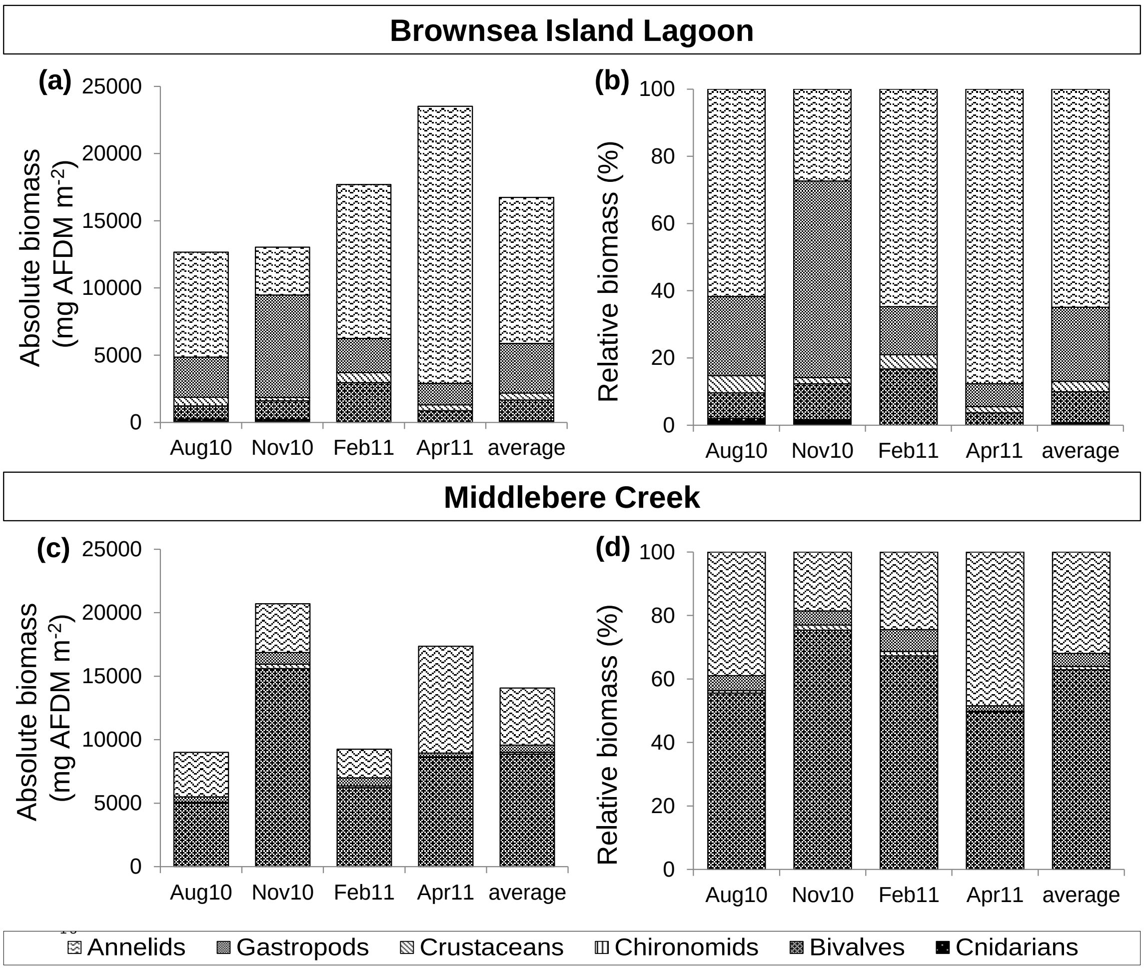


Figure 3.6 Seasonal variation in absolute and relative biomass of invertebrate taxa at Brownsea Island Lagoon (a,b) and Middlebere Creek (c,d). AFDM=ash-free dry mass.

3.4.5 Spatial variation in biomass

The spatial variation in biomass is given in Figure 3.7. The sampling stations are numbered as in Figure 3.1. There were significant differences in community biomass structure between stations at Brownsea (R=0.492, p=0.001) and Middlebere (R=0.386, p=0.001). At Brownsea, there were significant between-station differences in biomass of all taxa, except cnidarians; and at Middlebere there were significant differences for all taxa except annelids. Generally, as with organismal abundance, the variability in biomass between stations was higher at Brownsea compared with Middlebere, as was the proportion of biomass contributed by each taxon. At Middlebere, there was a more predictable trend of biomass increase from upper to lower creek. This increase was due to an increasing number of large bivalves toward the mouth of the creek. There was also a clear increase in biomass of crustaceans at the freshwater end of the Creek, at stations M01 and M02, due to the occurrence of large *C. volutator* at these sites. The spatial distribution of biomass for each time period is provided in Appendix 4.

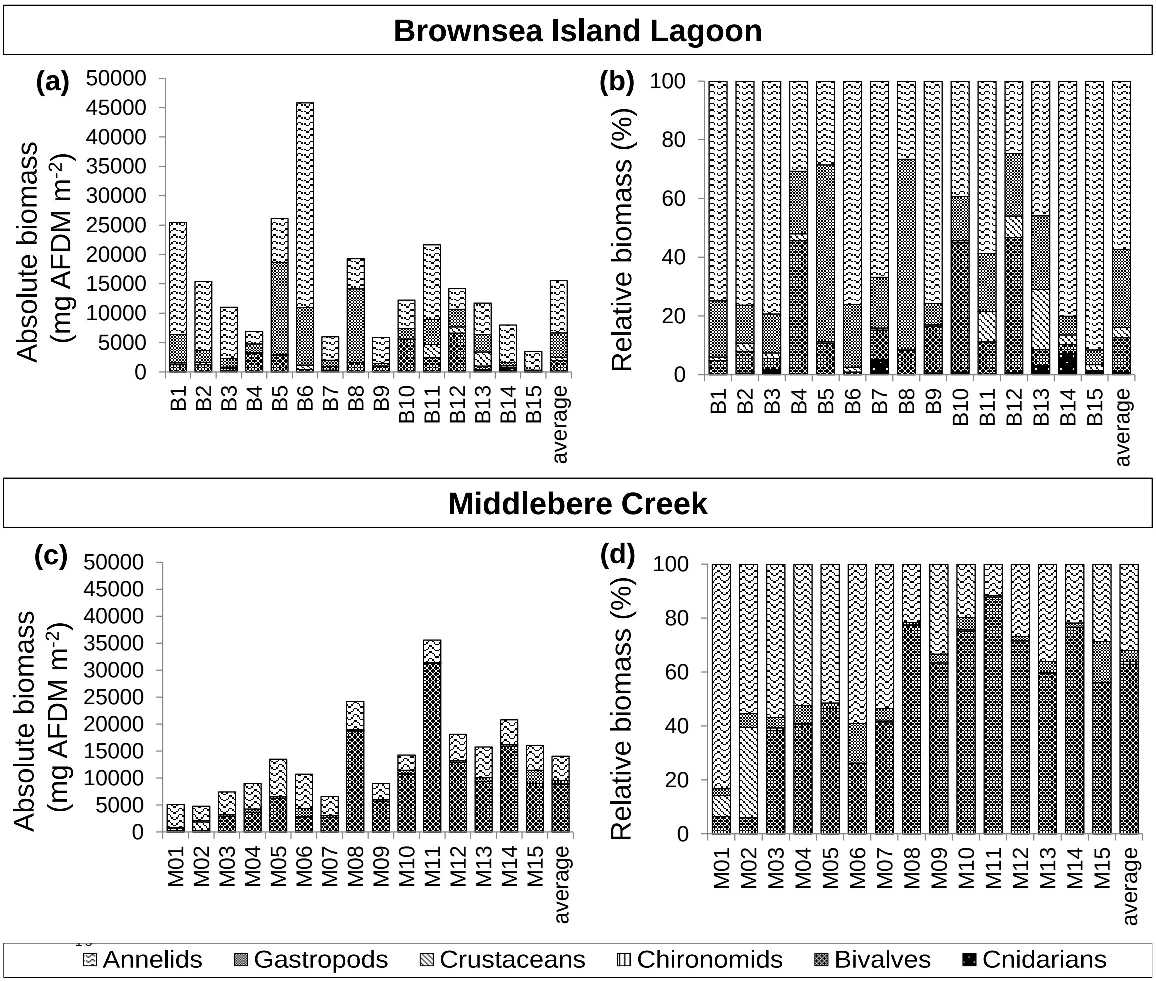


Figure 3.7 Spatial variation in absolute and relative biomass of invertebrate taxa in Brownsea Island Lagoon (a,b) and Middlebere Creek (c,d). AFDM=ash-free dry mass.

3.4.6 Size frequency distributions of selected taxa

To interpret the differences in the patterns of abundance and biomass observed between Brownsea and Middlebere, it is necessary to consider the size frequencies of the main taxa at each site. For *H. diversicolor*, there was a dramatic increase in the number of <1 cm individuals in November, but very few worms in larger size classes in this month. Similarly, there was an increase in <1 cm individuals at Middlebere, but there were also individuals in larger size classes present. In February and March, worms in larger size classes were present at Brownsea.

The difference in size class structure for *Corophium* between sites was in part due to the presence of *M. insidiosum* and *C. volutator* at Brownsea, whereas all individuals at Middlebere were *C. volutator*. *M. insidiosum* was on average 4.4 times more abundant than *C. volutator* at Brownsea. Here, *Corophium* was most abundant in August, but the majority of individuals were very small ≤3 mm. By contrast, the *Corophium* at Middlebere peaked in abundance in November, and while the overall abundance was roughly a tenth of that at Brownsea, a much higher proportion of the *Corophium* were larger in size (5–12 mm).

For bivalves, with the exception of three large lagoon cockles (*Cerastoderma glaucum*) found in February, all bivalves at Brownsea were ≤10 mm in length, and all were either A*bra tennuis* or *C. glaucum*. At Middlebere, the majority of bivalves were ≤10 mm, but larger size classes, up to 50 mm in length were observed in all sampling periods. Furthermore, a greater diversity of species were identified at Middlebere, including *A. tennuis*, *C. edule*, *C. glaucum*, *Macoma balthica* [Linnaeus 1758], *Mya arenaria* [Linnaeus 1758], *Scrobicularia plana* [da Costa 1778] and the manila clam *Venerupis philippinarum* [Adams & Reeve 1850].

The size frequency distributions for *H. diversicolor*, *Corophium* spp. and Bivalvia are presented in Appendix 5.

3.4.7 The annelid-gastropod biomass ratio

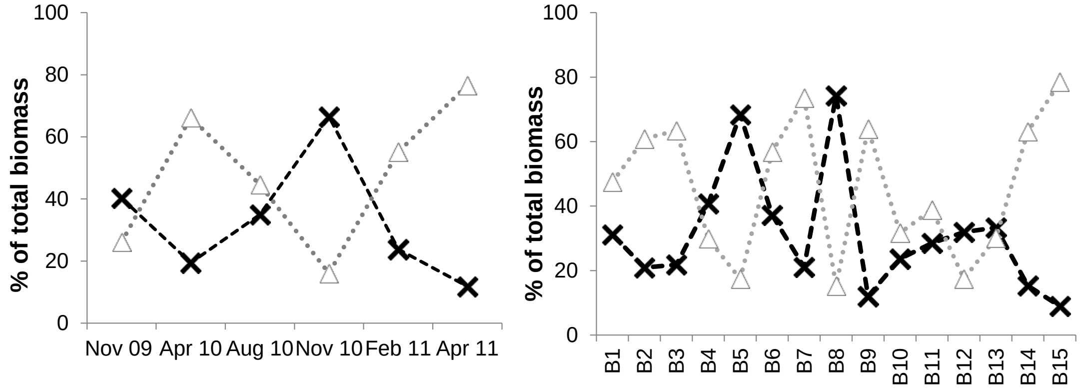
Figure 3.8 shows the relative biomass contributed by annelids and gastropods at each time point and each station. At Brownsea, in terms of biomass, annelids were dominant in August, February and April, and gastropods were dominant in November (Figure 3.8a). Furthermore, the biomass was dominated by annelids at ten of fifteen stations (Figure 3.8b). At Middlebere, however, annelid biomass always exceeded gastropod biomass.

The median annelid-gastropod ratio (A-G ratio) of biomasses was 1.6 at Brownsea and 4.4 at Middlebere and the difference between sites was significant (Mann-Whitney U (141,180) 10886, Z=-2.189, p=0.03). There were statistically significant differences in A-G ratios between sampling periods at Brownsea (Kruskal-Wallis H (3) 47.33, p<0.001) and Middlebere (Kruskal-Wallis H (3) 16.10, p=0.001). The highest A-G ratios occurred in April at both sites, and the lowest occurred in November at Brownsea and February at Middlebere.

Brownsea Island Lagoon

(a) by date

(b) by station



Middlebere Creek

(c) by date

(d) by station

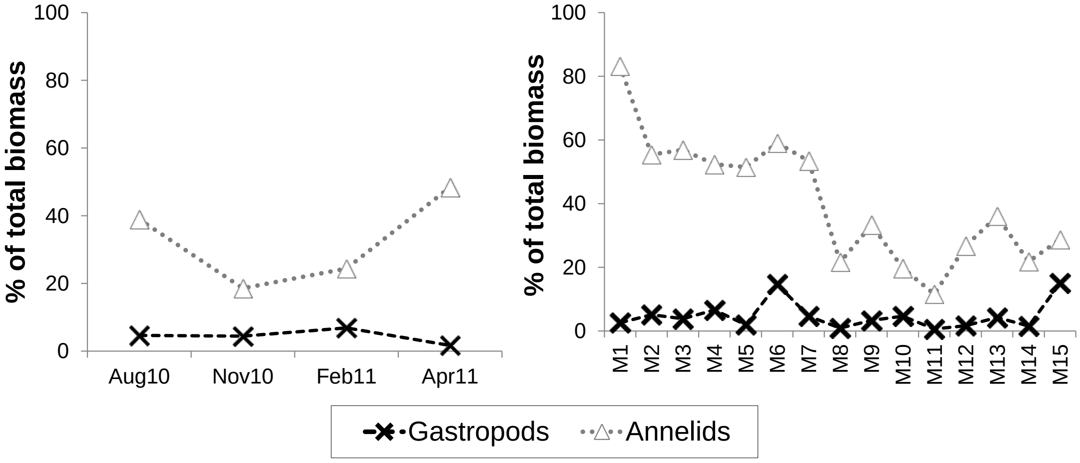


Figure 3.8 The proportion of biomass contributed by annelids and gastropods for each sampling period, averaged over all stations sampled (a,c); and for each station, averaged over 4 sampling periods (b,d), for Brownsea Island Lagoon and Middlebere Creek, respectively.

3.4.8 Environmental variables

(i) Sediment composition

Sediment composition differed significantly between Brownsea and Middlebere both in terms of % of fine (<63 µm) sediments (Mann-Whitney U (54,54) 221, Z=-7.6, $p<0.001$) and % of coarse (>500 µm) sediments (Mann-Whitney U (54,54) 308 Z=-7.1, $p<0.001$). At Brownsea, sediment median particle size ranged from <63 to 460 µm, or course silt to medium sand on the Wentworth Scale (Wentworth 1922), and the sediments were generally classified as ‘mud’ or ‘muddy sand’ according to the Joint Nature Conservation Committee (JNCC) Marine Habitat Classification (Connor et al. 2004). There was no seasonal variation in sediment particle size composition (ANOSIM R=-0.026, p=0.56; Figure 3.9a); however there was considerable heterogeneity between stations in the lagoon, in terms of median particle size, sorting, kurtosis, and percentage gravel (ANOSIM R=0.169, p=0.01; Figure 3.9b). The stations closer to the lagoon periphery had a higher proportion of coarse sediment. At Middlebere, the sediment consisted of >95% fine sediment (<63 µm). There was no seasonal variation in sediment particle size composition (ANOSIM R=-0.007, p=0.46; Figure 3.9c). There was far less variability between stations, compared with Brownsea (ANOSIM R=0.317, p=0.09). However, stations M14 and M15, which were taken from the mouth of the creek and Arne Bay, respectively, contained a higher percentage of coarse sediment (Figure 3.9d). Sediment grain-size composition for each station and each sampling time are given in Appendix 6.

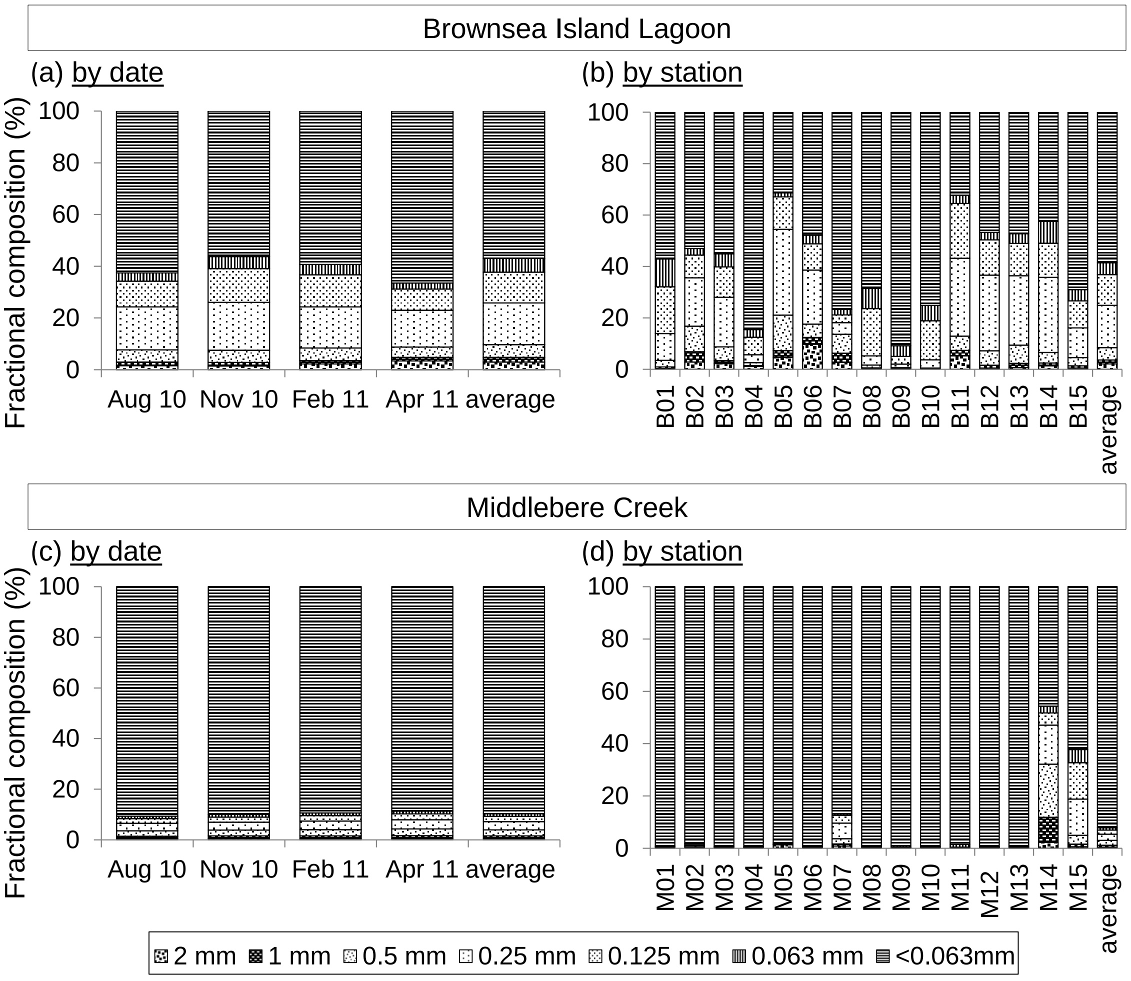


Figure 3.9 Sediment grain size composition by date, averaged over 4 sampling periods (a,c); by station, averaged over all dates (b,d), for Brownsea Island Lagoon and Middlebere Creek, respectively.

(ii) Organic content

The mean organic content of Brownsea Lagoon was 5.8%±0.4%, ranging from 1.0 to 15.8%. There was a significant seasonal variation (1-way ANOVA F(3,50) 5.55, p=0.002; Figure 3.10a). Differences between stations were not statistically significant (1-way ANOVA F(15,38) 1.57, p=0.129; Figure 3.10b). Mean organic content was 2.6% higher at Middlebere compared with Brownsea (t(106) -4.877, p<0.001). Mean organic content at Middlebere was 8.4%±0.3%, ranging from 2.5 to 13.9%. There were significant seasonal differences (1-way ANOVA F(3,49) 5.16, p=0.004; Figure 3.10c), and as with Brownsea, the highest organic content was observed in April. There were significant differences between stations (1-way ANOVA F(14,39) 2.68, p=0.008; Figure 3.10d), largely driven by the low organic content at M14 and M15.

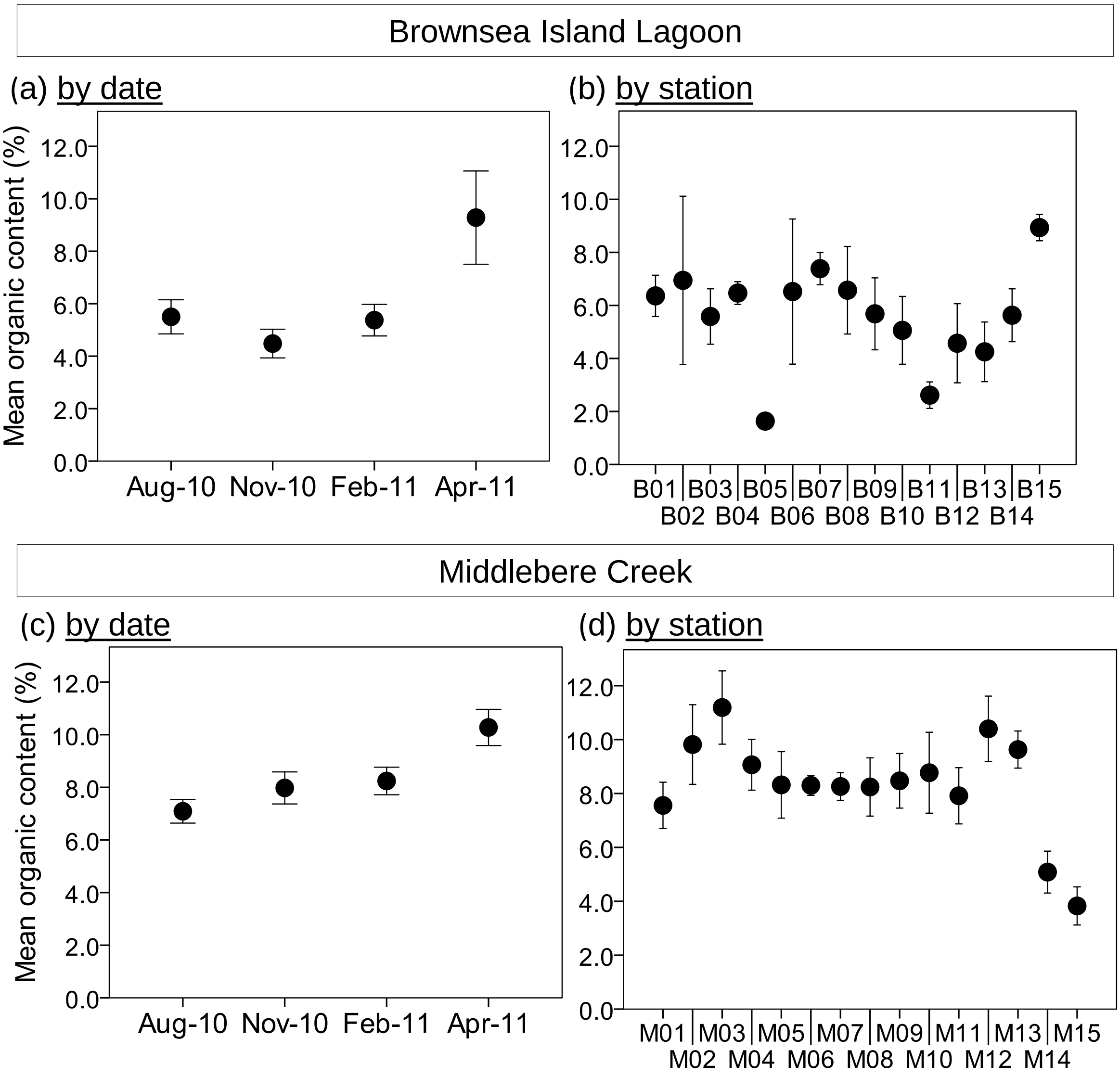


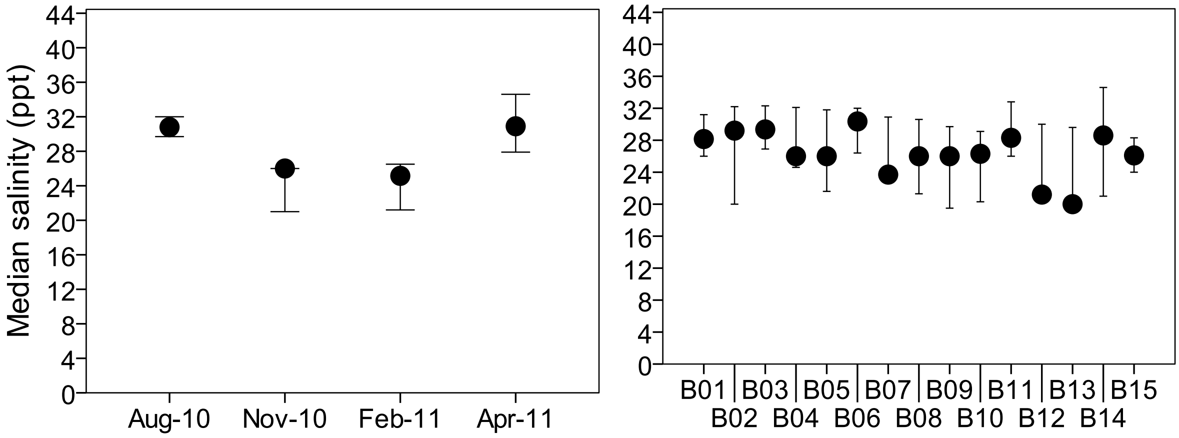
Figure 3.10 Mean organic content for each sampling period, averaged over all stations (a,c); for each station, averaged over 4 sampling periods (b,d), for Brownsea Island Lagoon and Middlebere Creek, respectively. Error bars represent standard errors of the mean.

(iii) Salinity

The median salinities at Brownsea (28.3 ppt) and Middlebere (26.9 ppt) were not significantly different and were characteristic of a 'brackish' environment. A significant seasonal variation in salinity was observed at Brownsea (Kruskal-Wallis H (3) 37.6, $p<0.001$; Figure 3.11a) and Middlebere (Kruskal-Wallis H (3) 43.0, $p<0.001$; Figure 3.11c). At Brownsea, salinity was highest in April 2011 and August 2010, but at Middlebere was highest in November and April. There were no significant differences in salinity between stations at Brownsea (Figure 3.11b) or Middlebere (Figure 3.11d).

Brownsea Island Lagoon

(a) by date (b) by station



Middlebere Creek

(c) by date (d) by station

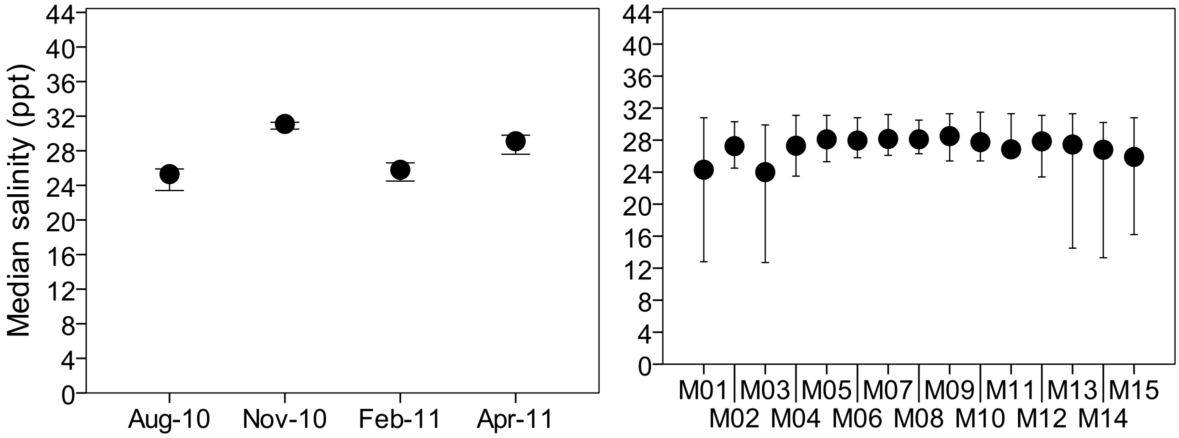


Figure 3.11 Median salinities recorded at each sampling period, averaged over all stations (a,c); at each station, averaged over 4 sampling periods (b,d), for Brownsea Island Lagoon and Middlebere Creek, respectively. Error bars represent 95% confidence intervals.

(iv) Macroalgae

The percentage cover of macroalgae at Brownsea, determined by visual assessment is shown in Figure 3.12. The most common species was the lagoon specialist *Chaetomorpha linum* [Müller 1845]; *Graciliariopsis longissima* [Gmelin 1995] occurred frequently in floating clumps and *Ulva lactuca* [Linnaeus 1753] was occasionally present. Algal cover could not be assessed visually at Middlebere; however, *U. lactuca* was present in 24 of 180 cores, 18 of which occurred in August, suggesting the overall extent of macroalgal cover was minimal during the other months of the year.

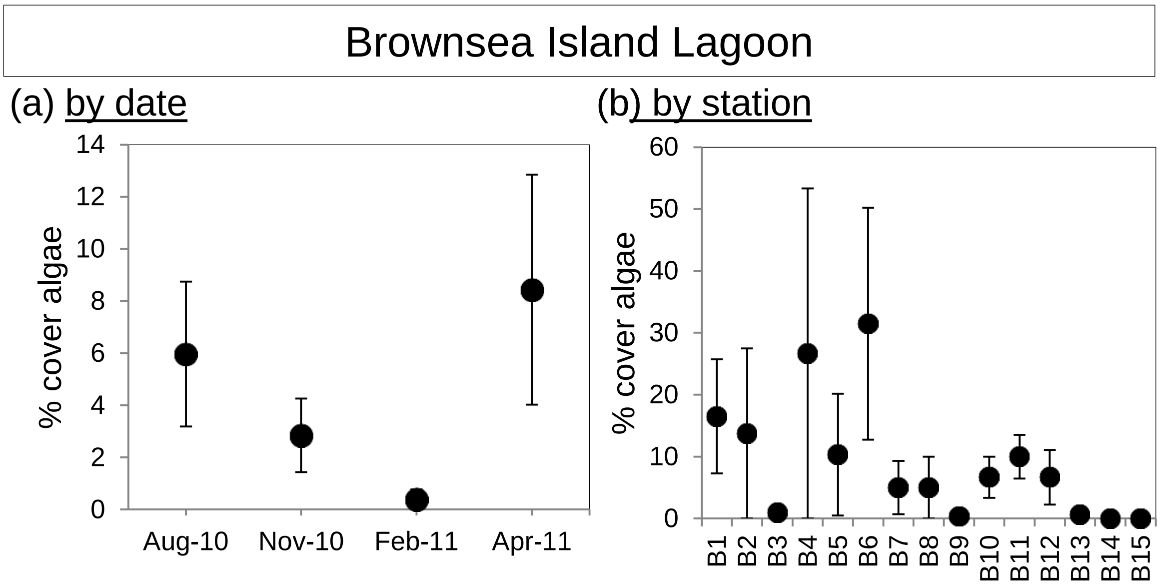
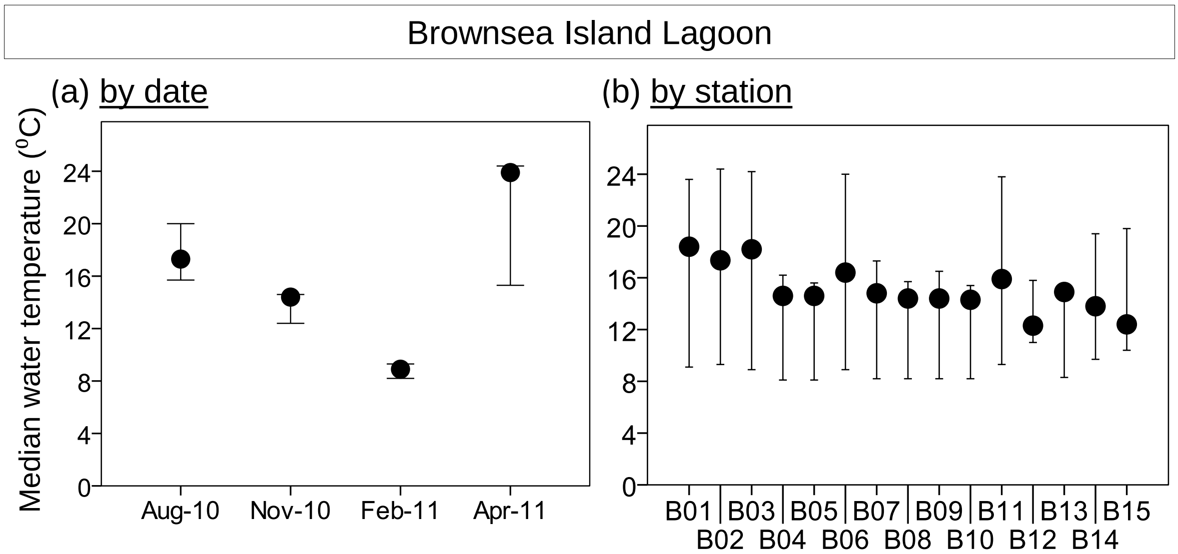


Figure 3.12 Percentage cover of algae at Brownsea Island Lagoon at each sampling period, averaged over all stations (a); at each station, averaged over 4 sampling periods (b). Error bars represent standard errors of the mean.

(v) Water temperature

There was significant seasonal variation in water temperatures at both sites, with lowest temperatures observed in February and highest temperatures in August and April. However, there were no significant differences between stations at either site (Figure 3.13). The inter-station temperature variability was higher Brownsea due to daily fluctuations in temperature. This is reflected in the relatively high temperature recorded in April 2011, for which the readings were taken later in the day compared with other sampling periods.



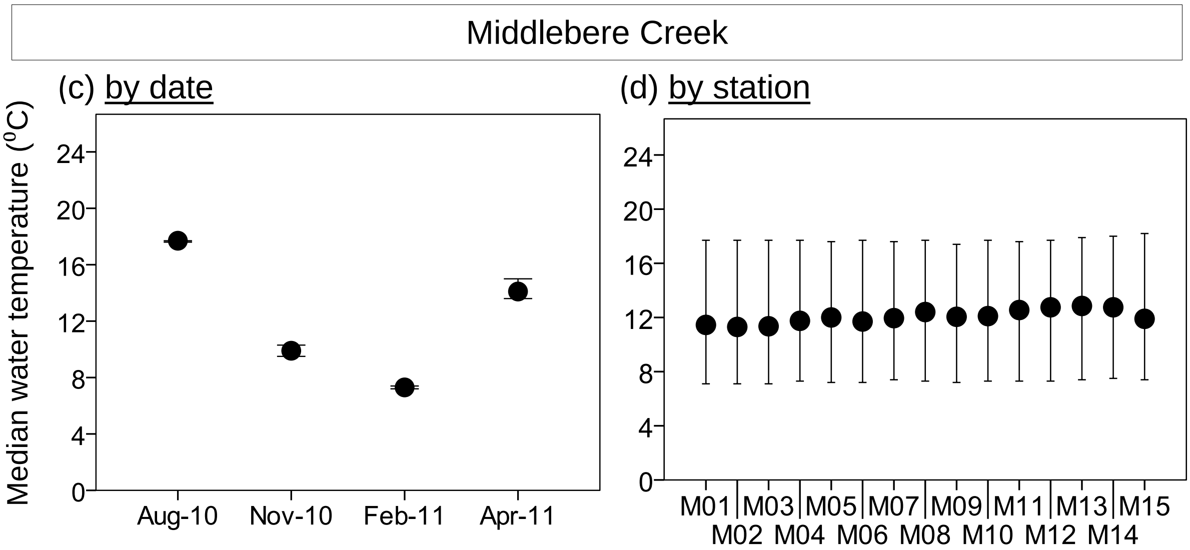


Figure 3.13 Median water temperatures recorded at each sampling period, averaged over all stations (a,c); at each station, averaged over 4 sampling periods (b,d), for Brownsea Island Lagoon and Middlebere Creek, respectively. Error bars represent 95% confidence intervals.

(vi) Weather during study period

Table 3.4 gives the temperature and rainfall data for each of the months in which surveys were conducted, and a comparison with the 20 year-mean figure for that month, to determine whether any atypical weather patterns may have influenced the results. There was significantly less rainfall in April 2011, compared with 2010, which was reflected in the lagoon salinity being higher in April 2011 compared with April 2010 (Figure 3.11). November and February 2011 were slightly colder than average with a higher than average number of frost days.

Table 3.4 Weather data (mean daily maximum temperature, number of frost days and rainfall in mm) during the survey months. Figures in brackets represent a comparison with the 20-year average data for that month (negative values mean the survey data were lower than the 20-year average).

Survey month	Mean daily max temp, ^{0}C	Frost, no. of days	Rainfall, mm
November 2009	12.9 (-2.1)	0 (-4.7)	163.2 (+91.7)
April 2010	14.6 (-0.4)	5 (+0.2)	34.4 (-36.3)
August 2010	21.0 (+6.0)	0 (-4.8)	94.8 (+23.8)
November 2010	9.8 (-5.1)	12 (+2.2)	107.4 (+36.1)
February 2011	10.4 (-4.5)	8 (+3.1)	75.8 (+4.5)
April 2011	18.3 (+3.3)	0 (-4.9)	6.8 (-64.1)

Data were taken from the Hurn weather station, 50.779 ^{o}N 1.835^{o}W (Met Office 2011).

(vii) Lagoon depth

Water levels in the lagoon are controlled by the Dorset Wildlife Trust on an *ad hoc* basis. The average water depth of the sampling stations in the lagoon was 16.5 cm, ranging from 10 to 20 cm, with the exception of B15, which was particularly shallow (between 2 and 5 cm). Depths did not vary significantly between sampling periods.

3.4.9 Relating biota to environment

A BIO-ENV procedure was performed on dispersion-weighted square-root-transformed abundance data and a suite of normalised environmental data from all stations in August 2010, November 2010, February 2011 and April 2011. The environmental data included in the analysis were organic content, temperature, salinity, median particle size, log (% gravel) and distance from the sluice. Particle skewedness, sorting, % sand and % silt were excluded from the analysis as they were correlated >0.7 with other factors. The combination of factors which gave the best match between the biotic and environmental data at Brownsea was median particle size (MPS) and salinity, which explained 13.0% of the variation in community structure.

Greater concordance between biotic and environmental data was achieved when each sampling period was analysed separately. The variation in community structure for individual sampling periods varied between 24.9% in August (for which MPS and distance from the sluice were the most important variables) and 41.2% in February (for which MPS and temperature were the most important variables). MPS was important during all sampling periods except April (which was likely due to fewer sites being sampled in April).

At Middlebere there was a higher degree of association between the biota and the environment, compared with Brownsea, with 50.1% of the variance explained by the combination of distance downstream and MPS. Distance downstream on its own accounted for 46.4% of the variance. Distance downstream was the most important variable in all sampling periods, but the amount of variance explained differed by period, with a maximum in April (84.9%) and minimum in August (14.7%).

If hydrobiid abundance was removed from the abundance matrix and used as an environmental predictor, the variance explained at Brownsea increased 83.1%, whereas at Middlebere it only increased 6.9%.

The Gradient Forest procedure, using the environmental variables organic content, salinity, median particle size, sorting, % gravel, % sand, % silt, and distance from sluice, also had low predictive ability, and only four taxa showed positive R^2 values (i.e. their abundance showed some predictable relationship with one or more environmental variables). These were *Pygospio elegans*, R^2 0.05, *Tubificoides pseudogaster,* R^2 *0.04,* Chironomidae, R^2 0.03, and *Monocorophium insidiosum,* R^2 *0.02*). If date and sampling station were included as environmental variables, the predictive ability of the model increased, with 7 species having positive R^2 values ranging from 0.11–0.03. In contrast to the BIO-ENV procedure, distance from sluice and % gravel was important in determining species distribution. However, both of these factors were only important at the extreme values for the environmental gradient, rather than across the whole range of values (see Figure 3.14a(i) and 3.14c(i)).

Gradient Forest also indicated that the association between the environmental variables and the biota was stronger at Middlebere than at Brownsea. Six taxa had positive R^2 values: *H. diversicolor,* R^2 0.26; *Corophium* sp., R^2 0.18; *Retusa obtusa,* R^2 0.10; *Peringia ulvae,* R^2 0.08; *Ostracoda* sp, R^2 0.06; and *Cyathura carinata,* R^2 0.13. As with the BIO-ENV procedure, distance downstream was by far the most important explanatory variable, and temperature and salinity were also important (Figure 3.15).

As with BIO-ENV, removing Hydrobiidae from the species abundance matrix and using it as an environmental predictor resulted in higher explanatory power than any other environmental variables a Brownsea, increasing the R^2 for all species from 0.14 to 0.36. However, at Middlebere hydrobiid abundance had less explanatory power than the environmental predictors: distance downstream, temperature and salinity, and only increased the overall R^2 from 0.71 to 0.77.

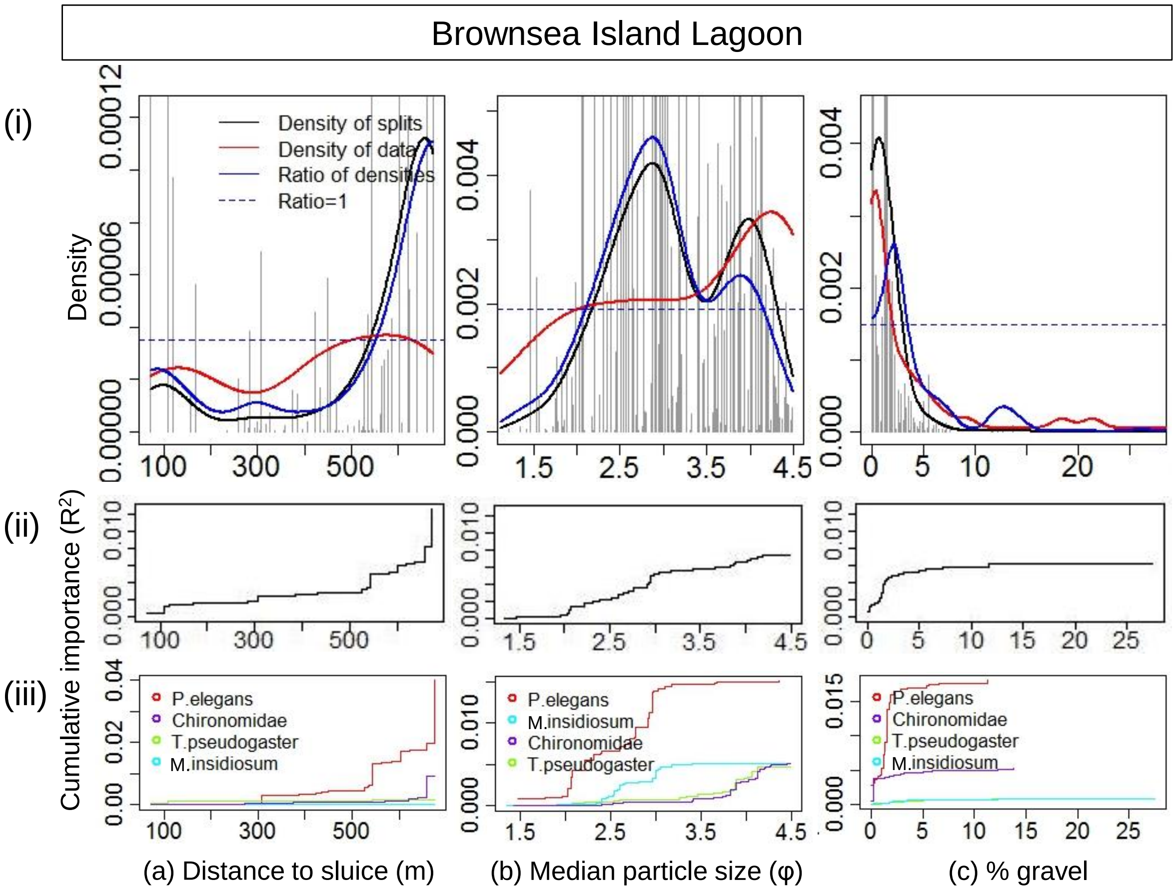
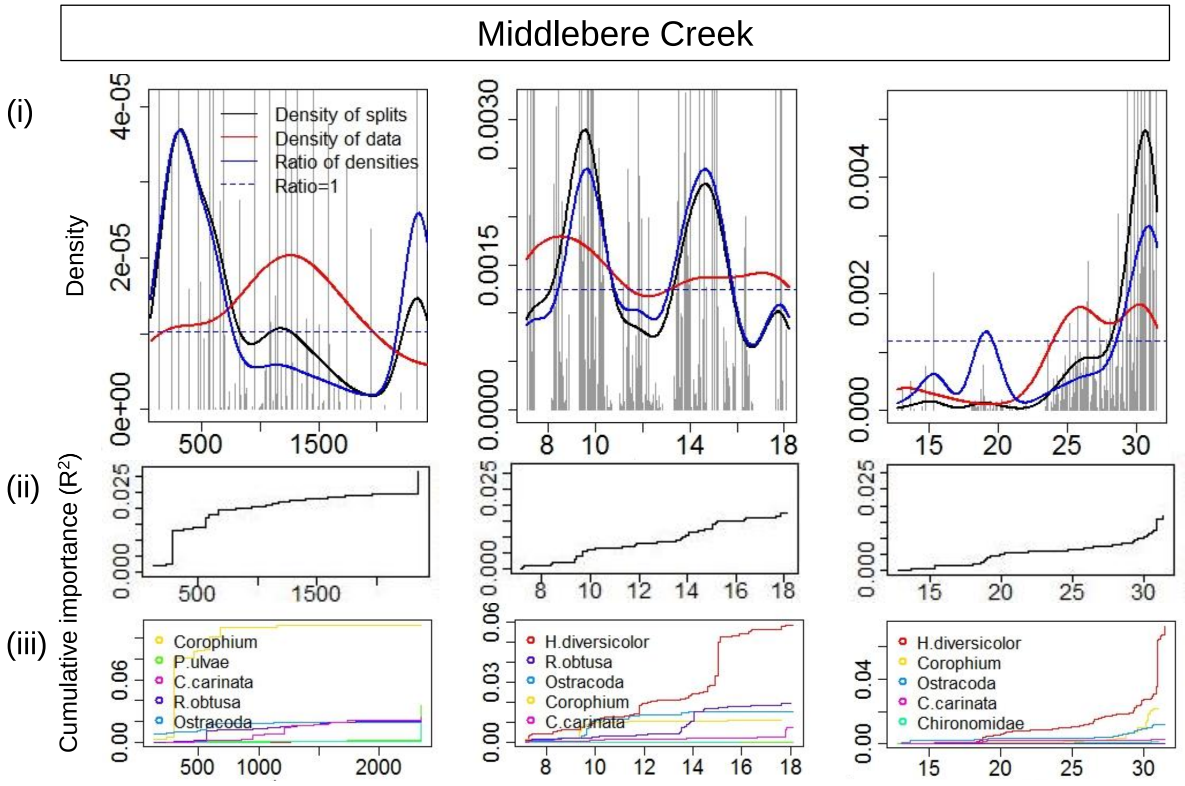


Figure 3.14 Key graphical outputs from Gradient Forest analysis of the three environmental variables with the highest R^2 weighted importance at Brownsea – (a) Distance to sluice in m, (b) Median particle size, in ϕ units, and (c) % gravel. The density plots (i) show the location and importance of splits (grey histogram), the density of splits (black line), the number of observations (red line), and the density of splits standardised by the number of observations (blue line). Where the standardised splits density is >1 (above the dotted), the predictor is an important determinant of community structure for those values. (ii) predictor cumulative plots show cumulative change in community composition along the environmental gradients. (iii) Species cumulative plots show the cumulative change in abundance of individual species along the environmental gradients. Species abbreviations: *P elegans, Pygospio elegans; T. pseudogaster,Tubificoides pseudogaster; M. insidiosum, Monocorophium insidiosum.*



(a) Distance downstream (m) (b) Temperature (ºC) (c) Salinity (ppt)

Figure 3.15 Key graphical outputs from Gradient Forest analysis of the three environmental variables with the highest R^2 weighted importance at Middlebere Creek – (a) Distance downstream in m, (b) Temperature in ^{0}C, and (c) Salinty in ppt. The density plots (i) show the location and importance of splits (grey histogram), the density of splits (black line), the number of observations (red line), and the density of splits standardised by the number of observations (blue line). Where the standardised splits density is >1 (above the dotted), the predictor is an important determinant of community structure for those values. (ii) predictor cumulative plots show cumulative change in community composition along the environmental gradients. (iii) Species cumulative plots show the cumulative change in abundance of individual species along the environmental gradients. Species abbreviations: *P.ulvae, Peringia ulvae; C. carinata, Cyathura carinata; R.obtusa, Retusa obtusa; H. diversicolor, Hediste diversicolor.*

3.5 Discussion

3.5.1 Site differences in biota and implications for foraging birds

In this chapter I have shown there are clear differences in faunal composition in an artificial saline lagoon and a tidal mudflat. While the sites shared a number of species, the two habitats varied in the relative importance of taxa, the size-frequency of species and the timing of peak abundance. Each of these factors has important implications for bird species utilising these habitats.

The fauna at Brownsea is most likely to favour generalist feeders. An average ‘scoop’ of Brownsea mud contains higher biomass due to the high numbers of small annelids, and hydrobiids present. This should be especially favourable to species that ‘scoop’ or scrape the mud such as avocet, shelduck, teal and shoveler (*Anas clypeata* [Linneaus 1758]).

In addition, the spatial distribution of prey at the two sites was different – at Brownsea prey was highly clustered in a patchy distribution, whereas the prey at Middlebere was more uniform, with community structure that varied gradually with distance downstream (Figure 3.5). These different distributions may favour different search strategies at each site.

Brownsea had very few large bivalves, whereas these were abundant at Middlebere. Furthermore, at Middlebere the bivalves exhibited a predictable spatial pattern, with higher numbers of large bivalves occurring further downstream, making this area particularly well suited to oystercatchers (*Haematopus ostralegus* [Linneaus 1758]) searching for large, profitable prey by sight. Brownsea had a much higher numerical abundance of annelids compared with Middlebere. However, the size distribution of worms at Middlebere was different, with higher proportion of worms in larger size classes. In addition, the distribution of worms at Middlebere was less predictable spatially than bivalves. Brownsea had high abundance of hydrobiid snails, making it exceptionally good habitat for wildfowl that feed on this taxa, such as shelduck (*Tadorna tadorna* [Linneaus 1758]) and teal (*Anas crecca* [Linneaus 1758]). Finally, the relative biomass contributed by small crustaceans was low at both sites, but this group showed strong spatial dependence at Middlebere, clustering at the freshwater end of the creek. Furthermore, *Corophium* at Middlebere were much larger than those at Brownsea.

3.5.2 Environmental variability within study sites

While both intertidal mudflat and lagoon are considered ‘transitional waters’, suggesting an ephemeral and changeable nature, there are key abiotic differences between the two habitats. In the case of Brownsea Lagoon, which is non-tidal, exchange with the sea water is controlled via a sluice system. Therefore, with the exception of wind-induced mixing, which is minimal due to the shelter from the prevailing winds conferred from Brownsea Island, there is relatively little movement of water within the lagoon. This enables the creation of a heterogeneous ‘patchy’ habitat with semi-stable microhabitats within. The mudflat at Middlebere, on the other hand, represents a relatively homogeneous habitat, with a definite environmental gradient (most likely driven by salinity) down its length.

A certain amount of heterogeneity within the lagoon arises from the variability in sediment composition, which may be due in part to the historical use of the land as a grazing pasture, which created channels and ruts in the ground. Over time, fine sediment has accumulated and smoothed over the ruts, but in places the firm substratum is not far from the surface. In addition, coarser sediments tended to occur closer to the edge of the lagoon which may be due to proximity to the sandy harbour sediments. However, this heterogeneity is maintained within the lagoon due to the lack of tidal movement. In contrast, there was also very little variation in sediment composition down the length of the creek, apart from the sandier sites around Arne Bay (M14 and M15).

There was a notable variation in organic content in the creek, with the sandier Arne Bay sediments containing the lowest organic content. But with the exception of these two stations, the variation in organic content between stations was not as great as that recorded at Brownsea. The spatial variation in organic content at Brownsea was related to sediment particle size – the sandier stations such as B05 and B11 were consistently low in organic content. However, the temporal variation in organic content was different between Brownsea and Middlebere – generally increasing from August through to April at Middlebere, but remaining consistently low at Brownsea from August through to February, then rising in April. The organic component of the sediment includes the macrobenthos as well as meiobenthos, microorganisms, living and decaying macrophytes and saltmarsh debris. At Middlebere, seasonal variation may be linked to variations in organic content of fluvial runoff.

The greater spatial variability in salinity and temperature at Brownsea was related to small scale variations in depth between sampling stations. However, the apparent higher variability at sites B01, B02, B03, B06, B11, B14 and B15, was a sampling artefact due to these sites being sampled in April, while the other sites were omitted to avoid disturbance to the breeding tern colony. The salinity at Brownsea may be more temporally variable, in response to rainfall for example. The salinity was particularly low in November 2010, which was a particularly wet month (see Table 3.4). Salinity at Middlebere, however, is likely to be much more variable at low tide than was evident from the data, which were collected at high tide. There was some variability in salinity in the stations at the freshwater end of the creek (M01 and M03), as well as the stations close to the periphery of the saltmarsh and in Arne Bay (M13, M14, M15), but generally, the water in Middlebere Creek was well-mixed.

3.5.3 The importance of biotic interactions

There was a high degree of spatial variability in the biota at Brownsea, which is a common characteristic of lagoons (Joyce et al. 2005). The patchiness in individual species distributions in lagoon habitat has been termed “spot endemism” (Schlacher et al. 1998). The relative lack of predictability of soft sediment habitat, compared with other habitats is perhaps in part due to the fact that the physical environment can change over short time scales. The sediment particles are small compared with the infaunal communities, and the activity of these organisms can change the nature of the substrate biogeochemistry (Wilson 1991). While a small proportion of the community variation could be attributed to differences in the sediment, most of the variation could not be attributed to any of the environmental variables measured. Furthermore, the hierarchy of importance of variables appeared to vary seasonally. A survey of a brackish lagoon in Ireland reported a similar lack of concordance between a matrix of species presence to a matrix on environmental parameters, but only checked associations within a single time point (Healy 1997).

It has been hypothesised that biotic interactions may not be very important in brackish environments, as the species diversity is low (Joyce et al. 2005); however, the finding that the abundance of hydrobiid snails had higher explanatory power than any of the environmental variables in explaining community structure at Brownsea strongly contradicts this assertion. It suggests that the community composition is strongly dependent upon the abundance of this taxon. While this does not provide evidence of a mechanism for species interaction, it does strongly suggest that biotic interaction rather than environmental gradients drives species abundance in this habitat at this spatial scale. Other authors have also suggested that interspecies interactions are present, for example between species of hydrobiid snails (Barnes & Gandolfi 1998). However, the extent to which lagoon species distribution is driven by top-down predator action or bottom-up competitive interactions is uncertain (Barnes 1999). Competitive interactions between annelids and gastropods have not previously been reported. The annelid-dominated stations were often stations that had higher organic content; however, this was not universally true and did not account for the generally high A-G ratio observed in November, at which time the organic content was relatively low at Brownsea. Other authors have hypothesised that unsynchronised pulses of certain opportunistic species, including tubificid and capitellid worms, occur due to competition for similar resources – detritus and space (Como & Magni 2009). These fluctuations are thought to be a product of functional redundancy in lagoon systems (Mistri et al. 2001b). The presence of macroalgae has been shown to positively affect epifaunal species while negatively affecting the infauna in lagoons (Arias & Drake 1994). These effects are thought to be mediated by the modification of biological interactions and the sediment (Arias & Drake 1994). However, there was no clear indication that macroalgal presence was driving the observed patterns in annelid-gastropod ratio at Brownsea.

The presence of biotic interactions was not as apparent at Middlebere. It seems in this habitat that the distribution of species was more attributable to the environmental gradients present. The presence of *C. volutator* at the freshwater end of the creek is most likely due lower salinity. While the Gradient Forest analysis did suggest an association of *Corophium* with salinity at Middlebere, this was largely driven by the seasonal, rather than spatial differences.

3.5.4 Detection of non-linear effects by Gradient Forest

As was demonstrated in Chapter 2, different factors were identified as important for determining community structure by the different analytical methods. For example, distance to the sluice at Brownsea was identified as important by Gradient Forest, but not by BIO-ENV. This highlights the ability of Gradient Forest to detect non-linear effects that vary in importance across the environmental gradient. Hence, distance from sluice was important >600 m away from the sluice due to an increase in the abundance of the spionid worm *Pygospio elegans* [Claparede 1863]. However, this association is likely due to a higher proportion of sandy sediments occurring further away from the sluice, as this species was also associated with the median particle size and % gravel gradients, and this species requires fine particles of sand or shell to build its tubes (Bolam & Fernandes 2003).

3.5.5 Seasonal differences in biota

The seasonal variation in invertebrate abundance showed differences between study sites. At both study sites, the abundance of all taxa peaked in November; however, the relative proportions of biomass contributions from each taxa varied between sites – the proportion of biomass contributed by annelids in November was low at Brownsea (~15%) but relatively high at Middlebere (~50%) (Figure 3.4).

The peak in biomass was not aligned with the peak in abundance at Brownsea, although it was at Middlebere. This suggests that differences in size distributions of species occurred between sites (Appendix 5). For example, an increase in <1 cm *H. diversicolor* was observed between August and November suggesting a substantial recruitment of juveniles occurred during this period. However, the lack of larger size classes observed at Brownsea in November suggests that either large worms are heavily selectively predated by the birds on the lagoon, or that reproduction occurs later here compared with the intertidal mudflats. Alternatively, it could occur due to density-dependent lowering of growth rates (Gray & Elliot 2009), as the annelid abundance is so high at Brownsea. The fact that reproduction may occur earlier at the intertidal site is supported by the fact that a large number of <1 cm worms persist in February on the lagoon, but decrease substantially at Middlebere by this time. The suggestion of later spawning times for the *H. diversicolor* in the intertidal mudflat compared with the lagoon has implications for biomass availability between the sites. The numerical abundance of worms at any given time was much higher in abundance at Brownsea, but in terms of biomass, there was not much difference between sites, as there was a higher number of worms in larger size classes at Middlebere. Determining whether this difference is due to earlier spawning in the Creek compared with the lagoon, or reduced growth rates warrants further investigation.

Changes in the timing of peak biomass is one of the key effects of climate change on marine communities (Parmesan 2006). However, the relative consistency in trophic structure throughout the year, in spite of the variation in the abundance of individual species suggests there is a high degree of functional redundancy at both study sites. This might confer a certain amount of resilience to environmental change on the system.

3.5.6 Conclusions

The lagoon habitat was defined by a patchy distribution, driven by biotic interactions rather than environmental gradients. The fauna was dominated by annelids and gastropods that were highly abundant, but with individually low biomass. This faunal distribution may be better suited to generalist foragers. At Middlebere, the fauna was more spatially predictable, related to distance downstream, and biomass was dominated by large bivalves, which may be better suited to specialist foragers hunting by sight.

Chapter 4: A mechanistic model of pied avocet (*Recurvirostra avosetta*) intake rate

4.1 Abstract

The predictive ability of bird population models is improved by incorporating foraging behaviour. Here I examine the foraging behaviour of the pied avocet *Recurvirostra avosetta*, producing a mechanistic model of foraging behaviour which can be used to predict intake rates and relative profitability of foraging strategies based on knowledge of the prey abundance.

I identified three basic foraging strategies: 1) tactile foraging on benthic prey, 2) tactile foraging on pelagic prey, and 3) visual foraging. I determined handling time and search rate associated with each foraging strategy, using field data and anatomical measurements. I predicted the maximum feeding rates using a Type II functional response model and calibrated them using intake rates recorded in the field to determine the value of the unknown variable “capture efficiency”. I then used prey abundances and energy content measured for the study site to determine the intake rates associated with each foraging strategy at the site.

For Brownsea Island Lagoon, energy intake rates were highest for benthic tactile foraging on small worms or *Corophium* (under the assumption that multiple prey types are captured in a single sweep), and for pelagic tactile foraging on prawns (*Palaemonetes varians* [Leach 1814]) or fish (mainly *Pomatoschistus* sp*.),* assuming locally high densities of prey can be identified or created. Foraging on ragworm (*Hediste diversicolor* [Müller 1766]*)* was most profitable for medium size classes of worm. However, since foraging behaviour is complex and dependent on external environmental factors, the most profitable strategies will vary for other sites, and within sites depending on conditions such as weather and ambient light levels.

The key finding of this chapter is that the relationship between prey abundance and intake rates is not simple. However, through mechanistic examination of species foraging strategies it is possible to link the prey abundance to prey availability and efficiency of capture, to accurately determine intake rate.

4.2 Introduction

In this chapter, I aim to link resource availability to intake rates through consideration of different foraging strategies and prey types available to foraging avocets. I predict the conditions under which different foraging strategies are used by the avocet to maximise their energy intake rates. This will advance the understanding of avocet foraging behaviour beyond the concept of "typical" foraging behaviour provide a more complete understanding of the species behaviour than previous studies. In addition, I provide a framework for predicting which foraging strategy will be used in different prey environments, and a tool for predicting energy intake rates that is not site or context specific. The key specialist terms that are used throughout this chapter are defined in Table 4.1.

Table 4.1 Definitions of key shorebird foraging terms as applied to this chapter.

Term	Abbr.	Units	Definition
Approach time	h_a	s	The time taken to move towards visually-located prey, prior to attack.
Attack time	h_p	s	This is time taken to locate prey with a sweep of the bill. For visual foraging attack time also includes the approach time.
Basal metabolic rate	BMR	kJ day^{-1}	The amount of energy expended daily by animals at rest under thermoneutral conditions in a post-absorptive state.
Benthic tactile foraging	a_{bt}	—	Locating prey by sweeping the bill across the sediment by moving the head from side to side whilst moving forwards. Only the tip of the bill contacts the sediment to search for prey.
Capture efficiency	c	—	The probability of successful prey capture when prey is contacted by the bill.
Feeding rate	F	s^{-1}	The number of prey items consumed per second.
Field metabolic rate	FMR	kJ day^{-1}	The total daily energetic cost to an animal living in the wild, including costs of thermoregulation, locomotion, and all other energy expenditure.
Functional response	—	—	The prey intake rate as a function of the prey density.
Handling time	H	s	The total time taken to locate, manipulate and swallow prey. Total handling time includes attack time (h_a) and swallowing time (h_s).
Pelagic tactile foraging	a_{pt}	—	Locating prey by walking or swimming with all or part of the head submerged, using the entire length of its bill to search for prey within the water column.
Prey availability	p	—	The proportion of prey vulnerable to predation.
Prey density	d	m^{-2} or m^{-3}	The number of prey items occurring within 1 m^2 of sediment or 1 m^3 of water.
Searching rate	a	m^2s^{-1} or m^3s^{-1}	Area of sediment (for benthic tactile or visual foraging) or volume of water (for pelagic tactile foraging) searched per second.
Swallowing time	h_s	s	The time taken to manipulate and swallow prey.
Swallowing rate		s^{-1}	Number of times the bird swallows per second.
Sweep rate	s	s^{-1}	Number of times the bird sweeps its bill through the sediment or water per second.
Tactile foraging	—	—	Locating prey by touch.
Visual foraging	a_{vf}	—	Locating prey by sight.

Understanding the decisions made by foragers over when, where and how to forage is key to predicting how changes in the environment will impact population dynamics (Goss-Custard et al. 1995a; Sutherland 2006). Behavioural data inform and strengthen species conservation management practices (Bradbury et al. 2001; Caro 2007). Incorporation of behaviour into population models has created insight into the population dynamics of fish, birds, and other organisms; although in many systems there are inadequate field data to formulate and test these models thoroughly (Van Winkle et al. 1993; Stillman & Goss-Custard 2010; Stephens et al. 2002; Wang & Grimm 2007). Behavioural models of shorebird foraging have successfully predicted population changes in mortality (Stillman & West 2003), and have informed conservation management (Durell et al. 2005; Goss-Custard et al. 2004; Stillman et al. 2010; West et al. 2002; Stillman et al. 2001).

The study of foraging behaviour is often approached by describing the ‘typical foraging behaviour’ of a species, for example, with time-budget data (Ntiamoa-Baidu & Piersma 1998; Ropert-Coudert et al. 2004). However, this approach is flawed because behaviour is flexible and adaptive: it depends on environmental context (Coleman & Wilson 1998; Dill 1983). To develop a better understanding of how changes to the environment will affect a population, we need to understand the drivers of behaviour. One approach is to assume that animals act as ‘optimal foragers’ – which assumes that due to natural selection, animals possess behavioural traits that maximise their fitness (Pyke et al. 1977). The meaning of ‘fitness maximisation’ is ill-defined and variable between species and at different life stages, but can be interpreted as individual lifetime breeding success. Thus, in the case of overwintering shorebirds, it equates to maximising their energy intake rates, so that they can survive the winter in adequate condition to return to their breeding grounds and breed successfully (Goss-Custard et al. 1977).

Here I examined the fitness-maximising foraging behaviour of overwintering pied avocets (*Recurvirosta avosetta*). The basic foraging mechanism has been described previously (Cramp & Simmons 1983), and ‘typical foraging behaviour’ has been described (Gibson 1978; Hötker 1999b; Kostecke & Smith 2003; Moreira 1995a; Moreira 1995b); however, previous studies have not linked intake rates to resource availability, thus are largely context specific so cannot be generalised to all sites and environmental settings. Thus, these studies have limited scope for predicting energy intake rates under changed environmental conditions.

The foraging mechanism of the Recurvirostridae is unique among shorebirds, and involves scything or sweeping the long upturned bill across the surface of the sediment to collect prey (Cramp & Simmons 1983). The avocet is often described as a ‘mainly tactile forager’

(Thomas et al. 2006; Cramp & Simmons 1983); however, visual foraging methods have been recognised (Barbosa 1995; Santos et al. 2010). Avocets exhibited lower stepping rates and higher pecking and sweeping rates in mudflat areas that were illuminated by street lights, suggesting that avocets were using visual foraging in illuminated areas (Santos et al. 2010). Moreira identified 'pecking' as a visual foraging strategy used by avocets (Moreira 1995a). Also, the fact that avocets appear to reduce their foraging effort on very dark, moonless nights, suggests a visual component to foraging (Hötker 1999b); however there are other explanations, such as perception of lowered vulnerability to predation in well-lit situations, leading to a less stressed feeding strategy. However, no studies have examined the relative importance of tactile and visual foraging or the conditions under which either strategy is more profitable. Failure to identify the drivers and mechanisms behind observed foraging behaviour, may have led to inappropriate assertions of certain foraging behaviours being 'typical' when they may in fact be highly context specific (e.g. Moreira's "normal" feeding strategy (Moreira 1995a)). Additionally, 'sweeping rates' alone have been used as a proxy for intake rate (e.g. Santos et al. (2010) found no noticeable change in intake rates when foraging in the dark or under artificial illumination, using sweeping rates as a proxy for intake rate; however, as 'swallowing rate' was not measured in this study, the conclusions may be wrong).

Avocets are known to feed on the common ragworm (*Hediste diversicolor* [Müller 1776]), the mudshrimp (*Corophium volutator* [Pallas 1766]), the prawn *(Palaemonotes varians* [Leach 1814]) and the larvae of chrionomids (*Chironomus salinarius* [Kieffer 1915]) (Cadbury and Olney 1978). Avocets preferentially feed in areas with high percentage of muddy sediments, which may be because fine particulate matter is more suitable for the scything mechanism they use to feed, or that their food items are most abundant in this sediment. Generally predators target prey availability rather than abundance so it is likely that the prey are most easily captured in this type of sediment regardless of their relative abundance (Wolff 1969). However, there is evidence that avocet feeding behaviour varies in different habitats (Drean-Quenec'Hdu et al. 1999; Battley et al. 2003; Ntiamoa-Baidu & Piersma 1998; Hötker 1999b).

4.2.1 Aims and objectives

In this chapter, I aim to link avocet intake rates to prey availability, by providing a mechanistic model of three avocet foraging strategies: benthic tactile foraging (where the bird searches the sediment surface by touch with the bill tip), pelagic tactile (where the bird searches the water column by touch using the entire bill), and visual foraging (where prey is located by sight). In doing so, I aim to provide a framework for predicting energy intake rates that is not site or context specific.

The specific objectives of this chapter are:

- to measure the components of the functional response (i.e. handling time, search rate) for alternative foraging strategies;
- to predict intake rate from a functional response model, and to calibrate the unknown parameter (capture efficiency);
- to use the calibrated functional response model to predict the most profitable foraging strategies, in terms of energy intake rates, under different environmental conditions.

4.3 Methods

4.3.1 Study population and site

I collected observational and video data from the avocet population of Poole Harbour over the winters of 2010–11 and 2011–12. Poole Harbour is one of six UK sites with internationally important numbers of overwintering avocets with 9.6% of the UK overwintering population in 2010–11 (Holt et al. 2012). The location of Poole Harbour within the UK and the location of the main study sites, Brownsea Island Lagoon and Middlebere Creek, are shown in Figure 4.1.

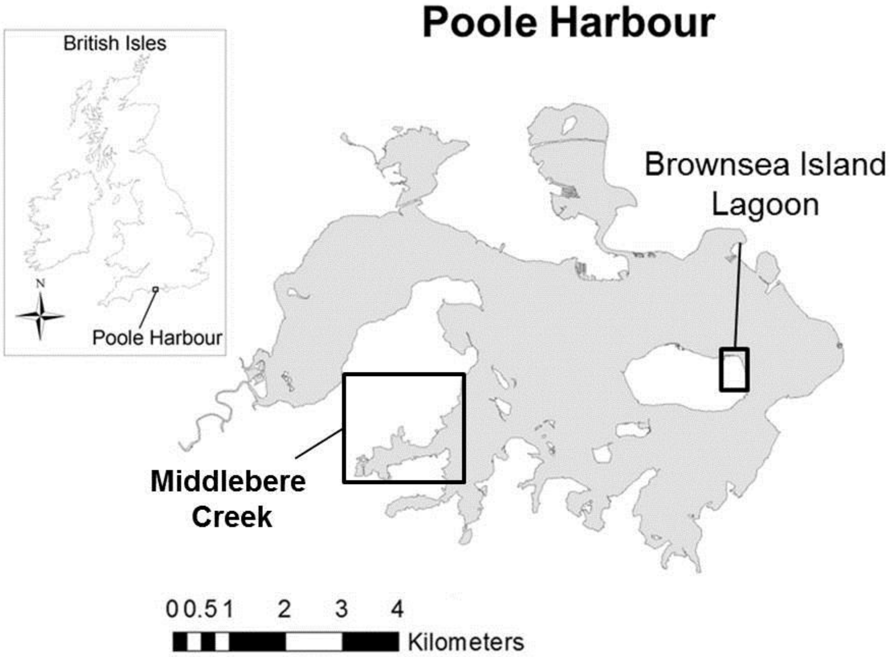


Figure 4.1 Maps showing location of Poole Harbour within the UK and location of study sites – Brownsea Island Lagoon and Middlebere Creek – within Poole Harbour.

4.3.2 Conceptualisation of foraging techniques

Through observation of foraging behaviour, I identified two main classes of foraging behaviour: tactile and visual foraging. Tactile foraging was classified as either benthic or pelagic, according to whether the prey was targeted on the surface of the sediment or in the water column, respectively (Figure 4.2).

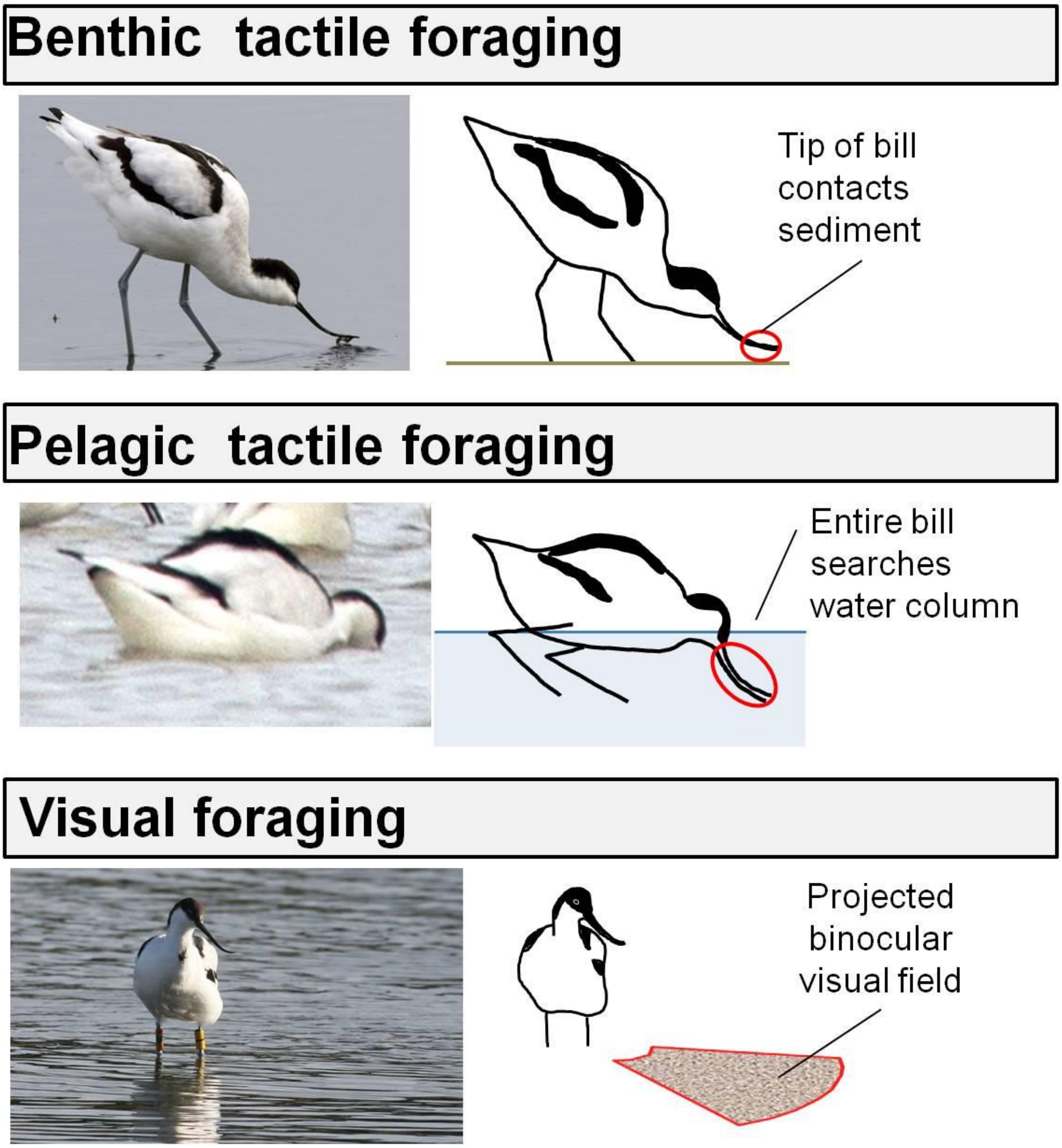


Figure 4.2 Photographs of the three main foraging strategies, and schematic representations of how prey searching occurs for each strategy: (a) tactile foraging on benthic prey; (b) tactile foraging on pelagic prey; (c) visual foraging.

I used video analysis of birds feeding using each of these strategies to determine the mechanistic differences between these feeding strategies, including handling time and search rate. Video analysis was performed in EVENT, an event recording software which displays a video and can record the timings of events occurring within the video (described in Poole et al. (2006)).

4.3.3 Foraging model

To examine the energetic consequences of different foraging strategies and prey types, I used the Type II Functional Response model, described by Holling's disc equation (Holling 1959), which has been shown to be the general shape of functional responses for wading birds (Goss-Custard et al. 2006a):

$$F = \frac{aDpc}{1 + aDpcH} \qquad (1)$$

This equation relates the feeding rate (F), which represents the number of prey items consumed per second, to the searching rate, in m^2 or m^3 searched per second (a), density of the chosen prey, in prey items per m^2 or m^3 (D), and the handling time associated with the chosen prey, in seconds (H). I added the variable 'p' to this standard equation to account for the proportion of prey vulnerable to predation (called "prey availability"), which is applicable here as large burrowing prey such as ragworms (*H. diversicolor*) are able to burrow to depths which are unattainable to the shallow sweep of the avocet bill. Furthermore, the vulnerability of different prey types is determined by how easy they are to catch. I added a capture efficiency term (c), which cannot be measured directly, but will be estimated by comparing the predictions of the model without the capture efficiency term with prey capture rates measured in the field.

4.3.4 Measuring searching rate

I derived formulae to describe searching rate for each type of foraging: benthic tactile foraging, pelagic tactile foraging, and visual foraging, based on observations of behaviour and consideration of how prey is detected in each instance.

(i) Benthic tactile foraging

Benthic tactile foraging involves sweeping the bill across the sediment by moving the head from side to side whilst moving forwards. During this foraging strategy, only the tip of the bill contacts the sediment to search for prey. I measured the bills of 70 preserved adult avocet specimens from the collections at the Natural History Museum at Tring, UK, to determine intraspecific variation in bill tip length (Figure 4.3). I developed a method to measure this length consistently: the shape of the lower mandible was traced onto a piece of paper from the tip of the bill to where feathers start growing on the ventral side of the lower mandible.

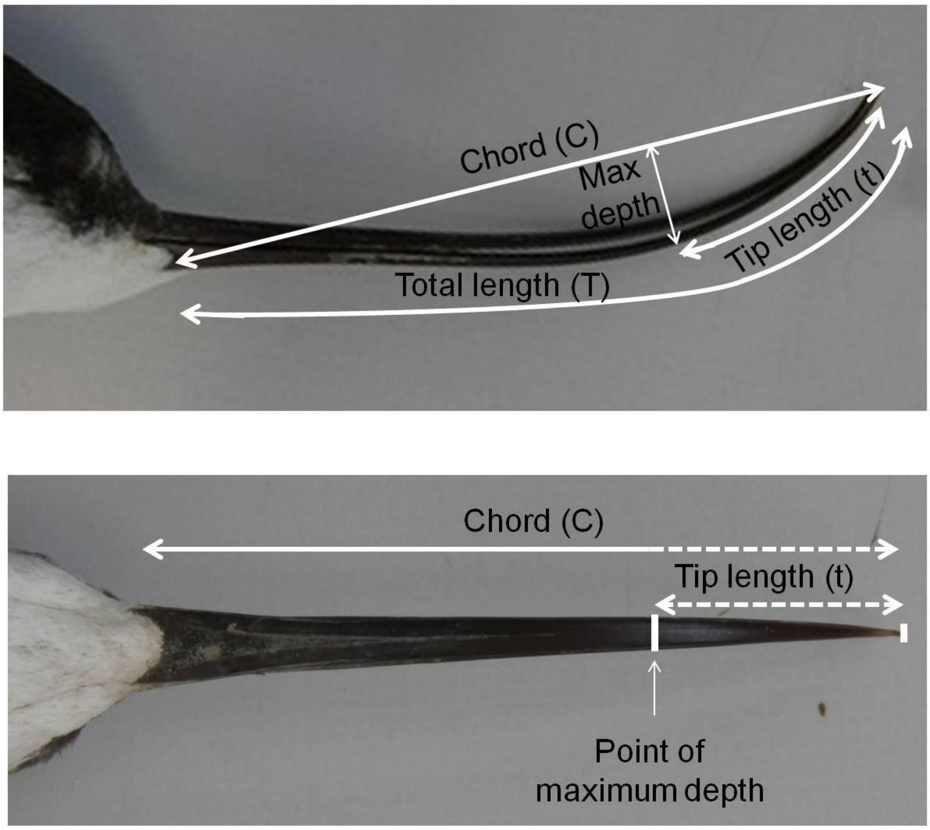


Figure 4.3 Structure of an avocet bill, showing measurements taken in this study.

The shortest distance between these two points was measured as the bill chord (C). The point along the chord that was at maximum distance from the lower mandible (point of maximum depth; h) was determined and I measured the distance from this point to the end of the bill tip (t). Bill tip length was measured using an opsiometer (Gelert Dial Map Measurer), which measures the absolute length of curved lines. However, as the curvature of the bill tip is minimal, the difference between the curved length and flat length was negligible (less than 5% in all cases sampled).

I noted that the marks left behind on the sediment as the bird forages are approximately rectangular (Figure 4.4). Thus search rate for benthic tactile foraging (a_{bt}) was calculated as the area searched per sweep, which is the product of the length of the bill tip (t) and the length of the sweep (x), multiplied by the number of sweeps per second (s_{bt}).

$$a_{bt} = t\ x\ s_{bt} \tag{2}$$

I obtained field-based estimates of sweep rates from 120 second videos of randomly selected birds tactile foraging on benthic prey in Brownsea Island lagoon. Sweep rate is likely to vary according to site, in relation to the sediment properties of the site (Quammen

1982), and is therefore is an important parameter that needs to be measured to ascertain intake rate for a given site.

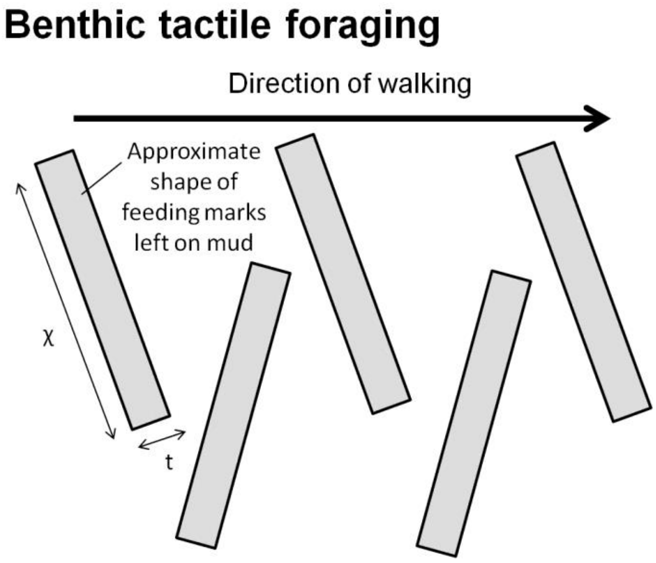


Figure 4.4 Approximation of the shape and orientation of feeding marks left by benthic tactile foraging avocets, and the dimensions used to determine area searched (x, sweep length; t, bill tip length), viewed from above.

(ii) Pelagic tactile foraging

Pelagic tactile foraging is generally performed in water that is at least 10 cm deep (avocet knee height), where the bird walks or swims with all or part of its head submerged, thus using the entire length of its bill to search the water column for prey. Therefore, the area searched is 3-dimensional volume of water, with dimensions dictated by the length of the sweep (x), the total length of the bill (T) and the depth of the bill (h). For simplicity, this volume was approximated to a rectangular cuboid, with dimensions specified by the length (T) and maximum depth (h) of the bill and the length of the sweep (x). The approximated searching pattern for pelagic tactile foraging is shown in Figure 4.5. The searching rate for tactile pelagic foraging is a product of the volume of a single sweep, and the sweep rate (s_{pt}):

$$a_{pt} = T\, h\, x\, s_{pt} \qquad (3)$$

Field estimates of sweep rate were obtained from 120 second videos of randomly selected birds tactile foraging on pelagic prey in Brownsea Island lagoon. As pelagic foraging sweeping occurs underwater and sweeping cannot be visualised directly, the time taken for one sweep was approximated by the movement of the tail which protrudes from the water and moves side-to-side in synchrony with the head motions.

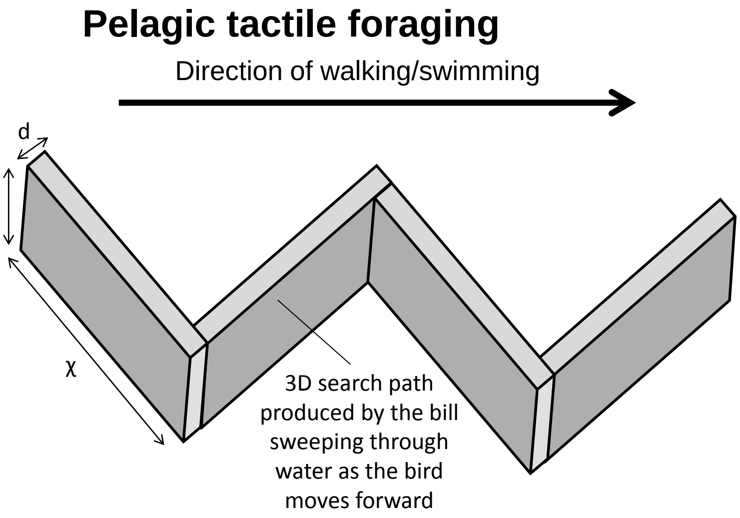


Figure 4.5 A representation of the approximate 3-dimensional area of water searched during pelagic tactile foraging (viewed from above).

(iii) Visual foraging

For visual foraging, the area searched is related to the visual field and acuity of the bird, and is more difficult to estimate in the field. This distance is often estimated as the furthest distance a bird is observed to move towards a prey item (Dias et al. 2009; Pienkowski 1983). I estimated this distance from videos of visually foraging avocets, and validated the estimate from data on the visual field of related shorebird species, the red knot *Calidris canutus* [Linneaus 1758] and golden plover *Pluvialis apricaria* [Linneaus 1758] (Martin & Piersma 2009). The area searched during visual foraging for a moving bird is a product of the width of the visual field and the distance moved per unit time, and for a stationary bird, the area searched approximates to the size of the visual field.

I used field observation of the position of the head during foraging, measured by the angle of the bill angle of the bill from the vertical plane. As shown in Figure 4.6, the angle of the bill from the vertical plane angle (θ_1), and the distance of the avocet eye from the ground (OQ) can be used to determine the approximate distance the birds are looking ahead while they forage. There is a blind spot directly underneath the bird which extends in front of it by a distance determined by how far beneath the bill the visual field extends.

When a bird is actively foraging, the speed of travel will determine the area searched per unit time. Assuming that the bird focusses on the leading edge of the visual field (arc AB in

Figure 4.6), where its visual perception is widest, the search rate for visual foraging (a_{vf}) is defined by the length of arc AB multiplied by the speed the bird is moving (ʋ).

$$a_{vf} = AB \times \upsilon \tag{4}$$

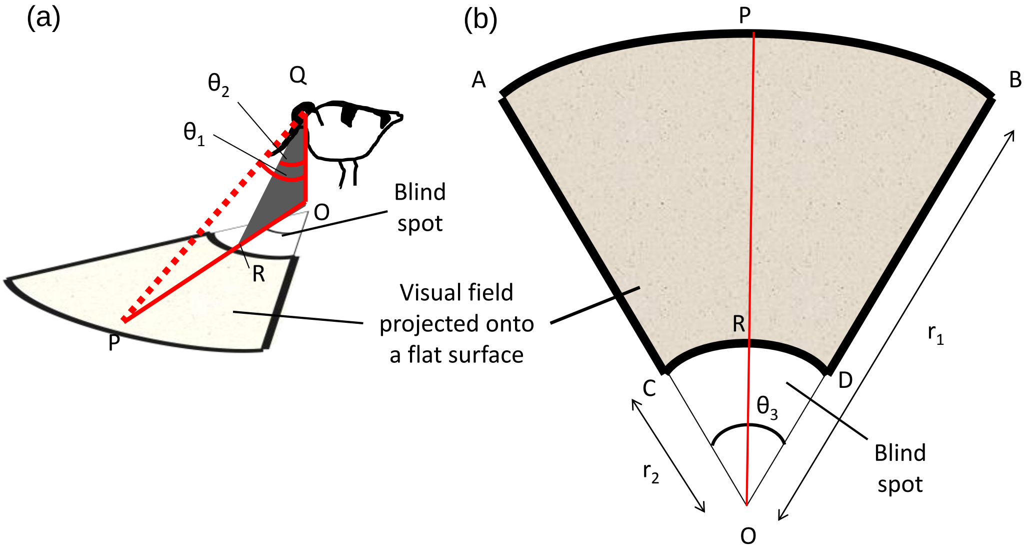


Figure 4.6 The method of estimating the focal point for visually foraging avocets using the angle of the bill from the vertical plane (a). The area of the visual field projected onto a flat surface (sector ABCD, shaded area), and the measurements used to define it (b) (described in the text).

4.3.5 Measuring handling time

I determined handling time by measuring the time taken to catch, manipulate and swallow prey in videos of foraging avocets played at 0.1x normal speed.

For tactile foraging, handling time was measured as the time taken for an average sweep, (through the sediment for benthic tactile foraging, or through the water column for pelagic tactile foraging), the attack time, h_a, plus the time taken to manipulate and swallow prey (h_s). The time taken for an average sweep may vary according to sediment properties (Quammen 1982; Grant 1984), and is therefore site specific. For visual foraging, the attack time consists of the time taken for the avocet to move towards the prey capture it. Thus total handling time for both tactile and visual foraging is defined as:

$$h = h_a + h_s \tag{5}$$

where h_a is attack time and h_s is swallowing time.

To calculate the variation in handling time in relation to prey size, I estimated the size of prey items captured in the field by comparison with the size of the avocet bill, and assigned it to one of the following three size categories: 1) too small to be visible, 2) visible but less than half the bill length, 3) visible and greater than half the bill length.

4.3.6 Determining prey types

The main avocet prey types were determined by observation using a Svarovski STM 80 HD telescope with a 20–60x eyepiece and a Canon Legria HFS10 digital video camera with 10x optical zoom (for larger prey types) and by qualitative analysis of faecal samples. I collected ten faecal samples on 1st October 2011, from avocets captured on an *ad hoc* basis during the hours of darkness, at Brownsea Island lagoon, using mist nets (Gosler 2004). I preserved the samples in 10% formal saline (Fisher Scientific). These samples were examined under a low-power stereo-binocular microscope for identifiable prey fragments. Collection of faecal samples by more standardised methods was not possible, as the avocet population spends virtually all its time feeding and roosting either in shallow water or on mudflats that are not easily accessible.

4.3.7 Prey availability

The vulnerability to predation of *H. diversicolor* (ragworm), a key avocet prey species (Cadbury & Olney 1978), was modelled according to (Esselink & Zwarts 1989). They estimated that ragworm emerged from their burrows and fed at the surface of the mud for roughly 0.1% of the observation period, therefore, I have assumed that the proportion of ragworm vulnerable to visual foraging avocets is 10%. As an avocet sweep penetrates roughly 2 cm into the sediment (Moreira 1995a), I assumed that prey burrowing in the top 2 cm were completely vulnerable to predation. This included all amphipods and worms of <4 cm length. For larger worms, I estimated the vulnerable proportion as the percentage of each size class which burrow in the top 2 cm according to Esselink & Zwarts 1989 (10% of worms length 4–6 cm, 2% of worms length 6–8 cm, 1% of worms length 8–10 cm and 0.1% of worms length >10 cm), plus the 0.1% present on the surface at any given time. I used the size distribution of worms at the study site to determine the vulnerability constant (p). For simplicity, I assumed that all prey in the water column, targeted by pelagic tactile foraging was vulnerable to predation, was perfectly detected, and was non-aggregated.

4.3.8 Model validation

In order to test the model predictions of feeding rate, I collected field data on avocets foraging using benthic tactile, pelagic tactile and visual strategies on Brownsea Island

Lagoon. I recorded individuals foraging for 120 s, noting the number of sweeps and swallows. I calculated the feeding rate as the number of swallows per second, and compared this against model predictions of feeding rate for actual prey densities found at the study site. Benthic prey densities were derived from the mean prey densities of 45 benthic cores taken in August and November 2010 and February and April 2011 (Chapter 3). Pelagic prey densities were determined for Brownsea Lagoon using the mean densities of eight sampling efforts, conducted in March–April and July–August 2012 using an enclosed netting methodology, following Rozas & Minello (1997).

4.3.9 Determining intake rates and time to meet daily energy requirements

I determined the ash-free dry mass (an indicator of prey energy content) of specimens collected from Brownsea Island Lagoon in December 2011. Benthic species were collected by coring, and pelagic species were captured using baited light traps, left overnight in the lagoon. For small species (<1 cm), I measured the average biomass for all individuals collected. For the larger species, I calculated length—biomass relationships (Chapter 3). Final biomass figures were converted to energy availability by accounting for calorific content of different taxa (See Appendix 7a).

I estimated the intake rates, in kJ day^{-1}, achievable for each foraging strategy, based on the prey availability at the study site. I calculated the minimum number of hours required to meet daily energy requirements for each foraging strategy to compare the relative profitability.

To calculate daily energy requirements, I estimated the basal metabolic rate (BMR) of avocets using Kersten & Piersma's metabolic scaling equation for shorebirds (Kersten & Piersma 1987):

$$BMR = 437(BW)^{0.729} \tag{6}$$

where BW is the body weight in kg. Assumption of an average avocet mass of 325 g (Thomas et al. 2006), relates to a BMR of 192.59 kJ day^{-1}. However, to determine daily energetic requirements, it is necessary to estimate of the field metabolic rate (FMR) or the total energetic cost to an animal living in the wild, including costs of thermoregulation, locomotion, and all other energy expenditure (Nagy 1987). FMR can be measured using studies of birds with isotopically-labelled body water, which allows for an estimation of carbon dioxide production (Lifson & McClintock 1966). However, these studies are normally conducted during the breeding season, when birds can be reliably captured, labelled, and recaptured, and energetic requirements may differ significantly in breeding and overwintering birds (Nagy 2005; Kersten 1996; Piersma & Morrison 1994). A small study of FMR in pied avocets during the breeding season in the Wadden Sea found FMR to be 2.3 times the basal metabolic rate (Hötker et al. 1996). However, to take into account the thermoregulatory costs of surviving a British winter, I have used the multiplier of 3.7 X BMR, which was the measured net energy intake for oystercatchers overwintering on the Wash in January (Goss-Custard 1977). This equates to an estimated FMR of 712.58 kJ day^{-1}. Assuming an average assimilation efficiency of 85% (Kersten & Piersma 1987), I estimate the daily energy requirements of an avocet as **838.34 kJ day^{-1}.**

The calculated figure represents an estimate of average daily energy use for an average size bird. Actual requirements will vary according to individual size and metabolism, activity levels, ambient temperature, and time of year (e.g. energy requirements increase prior to migration to build fat stores) (Castro et al. 1992; Kersten & Piersma 1987; Clausen et al. 2012; Daan 1990; Ricklefs et al. 1996; Piersma & Morrison 1994; Dugan et al. 1981; Kvist & Lindström 2003).

4.4 Results

4.4.1 Search rate

Calculated search rates for each of the foraging strategies are presented in Table 4.2, along with the parameters used to calculate them. The search rate for benthic tactile foraging (a_{bt}) was 32.1 cm^{2}s^{-1}, with upper and lower limits, based on the measured variability in bill size and sweep rates, of 140.5 and 2.1 cm^{2}s^{-1}, respectively. The search rate for pelagic tactile foraging (a_{pt}) was 7445 cm^{3}s^{-1}, with upper and lower limits of 74630 and 1020 cm^{3}s^{-1}, respectively. The higher search rate for pelagic tactile foraging was largely due to sweep rates being significantly higher for pelagic tactile (44.0±2.0 sweeps/min) compared with benthic tactile foraging (28.9±0.7 sweeps/min; $t(89)=7.117$, $p<0.001$).The estimate of search rate for visual foraging (a_V) ranged from the most conservative estimate using the golden plover visual field of 1300 cm^{2}s^{-1}, to the highest estimate using the knot visual field of 4470 cm^{2}s^{-1}.

4.4.2 Prey types

Prey types identified by observation were ragworm (*H. diversicolor*) fish (genus *Pomatoschistus*) and crustaceans. I also found *H. diversicolor* mouth parts and chaete and fish bones in faecal samples. In addition, amphipod legs, most likely from one of the two species of *Corophium* present at the study site (*Corophium volutator* and *Monocorophium insidiosum*), were identified in faecal samples.

While I did not find evidence of the prawn *Palomonetes varians* or the isopod *Idotea chelipes* [Fabricius 1798] in faecal samples, both these species were found at high densities at the study site. As only a small number of faecal samples were collected, and these were all collected on the same night, it is unlikely that they provided a complete catalogue of the avocet prey.

Table 4.2 Parameters used to calculate search rate for each foraging strategy.

SEARCHING PARAMETERS FOR EACH FORAGING TYPE	Value	Units	Source
Benthic tactile foraging	Mean (range)		
Length of bill tip (t)	3.3 (2.4–3.9)	cm	Measured from preserved avocet specimens
Length of sweep (x)	19.8 (12.6–32.5)	cm	Moreira, 1995b
Area searched per sweep (tx)	65.3 (30.2–126.8)	cm^2	Calculated from variables above
Sweep rate (s_1)	0.49 (0.13–2.2)	s^{-1}	Estimated from video data
Area searched per second ($\boldsymbol{a_{BT}}$)	**32.1 (2.1–140.5)**	**cm^{2}s^{-1}**	Calculated from variables above
Pelagic tactile foraging	Mean (range)		
Total bill length (T)	8.0 (6.8–9.2)	cm	Measured from preserved avocet specimens
Depth of bill (h)	1.0 (0.7–1.6)	cm	Measured from preserved avocet specimens
Length of sweep (x)	19.8 (12.6–32.5)	cm	Moreira (1995b)
Volume searched per sweep (Thx)	158.4 (60.0–478.4)	cm^{3}s^{-1}	Calculated from variables above
Sweep rate (s_2)	0.78 (0.28–2.6)	s^{-1}	Estimated from video data
Volume searched per second ($\boldsymbol{a_{PT}}$)	**123.6 (16.8–1243.8)**	**cm^{3}s^{-1}**	Calculated from variables above
Visual foraging			
Angle of bill from vertical during foraging	40–50	°	Estimated from field observation
Height above ground level of avocet eye	34–38	cm	Estimated from to-scale drawings of avocets in Hayman et al. (1986)
Distance to focal point (r_1)	28.0–45.3	cm	Calculated from variables above
Length of blind spot (r_2)		cm	Calculated from values in Martin and Piersma (2007)
Plover estimate	0.0–6.7		
Knot estimate	9.7–18.5		
Visual field width (no head rotation)		°	Martin and Piersma (2007)
Plover estimate	15		
Knot estimate	22		
Visual field width (with head rotation)		°	Calculated from variables above
Plover estimate	95		
Knot estimate	202		
Visual field width at focal point (no head rotation)		cm	Calculated from variables above
Plover estimate	7.3–11.8		
Knot estimate	10.8–17.4		
Visual field width at focal point (with head rotation)		cm	Calculated from variables above
Plover estimate	46.4–75.1		
Knot estimate	98.7–159.7		
Area of visual field (stationary bird, no head rotation)		m^2	Calculated from variables above
Plover estimate	0.103–0.263		
Knot estimate	0.132–0.323		
Area of visual field (stationary bird, with head rotation)		m^2	Calculated from variables above
Plover estimate	0.650–1.664		
Knot estimate	1.216–3.014		
Walking speed whilst foraging (υ)	0.28±0.009	ms^{-1}	Dias et al. (2009)
Area searched per second (no head rotation) (a_{VF})		cm^{2}s^{-1}	Calculated from variables above
Plover estimate	200–330		
Knot estimate	300–490		
Area searched per second (**head rotation**) (**$\boldsymbol{a_V}$**)		**cm^{2}s^{-1}**	Calculated from variables above
Plover estimate	**1300–2100**		
Knot estimate	**2760–4470**		

4.4.3 Handling time

The measured values for total handling time, and its constituent components, are shown in Table 4.3. The swallowing component of handling time (h_s) was determined from 218 prey capture events from 27 individual birds, which were foraging by the benthic tactile or visual strategy (as swallowing events were easier to see than with pelagic tactile foraging). h_s was significantly different between the three prey size categories, as determined by a 1-way ANOVA on log-transformed data ($F(2,217) = 72.1$, $p<0.001$). A Tukey *post-hoc* test showed that h_s was significantly different between all three classes ($p<0.001$). Figure 4.7 shows the positive relationship between handling time and prey size. The prey in size category 1 was too small to be identified, but most likely consisted of small worms and crustaceans; prey in category 2 included worms and crustaceans; and all prey in size category 3 were worms. As fish were generally captured by the pelagic tactile strategy, where prey-capture occurs underwater, and is not normally visible, only four instances of fish capture were recorded on video. These data were excluded from Figure 4.7. Swallowing times for fish were 0.68 and 1.32 seconds for fish in size category 2, and 2.4, and 2.72 seconds for fish in size category 3.

The attack component of handling time (h_a) was 0.40, 0.24 and 0.34 s for benthic tactile, pelagic tactile and visual foraging, respectively. While this figure represents only a small fraction of the total handling time, it is worth noting that for benthic tactile foraging it may vary depending on sediment properties, being larger in courser sediments.

Table 4.3 Measured values for handling time.

Foraging strategy	Approach time h_p(s)	Attack time h_a (s) (Median, IQR)	Swallowing time h_s (s) (Median, IQR)	Total handling time H (s)
Benthic tactile foraging	NA	0.40 (0.40), n=199	0.84 (0.56), n=218	1.24
Prey size class 1			0.72 (0.40), n=147	1.12
Prey size class 2			1.28 (0.77), n=48	1.68
Prey size class 3			2.91 (2.76), n=23	3.31
Pelagic tactile foraging	NA	0.24 (0.12) n=44	0.84 (0.56), n=218	1.08
Prey size class 1			0.72 (0.40), n=147	0.96
Prey size class 2			1.00, n=2	1.24
Prey size class 3			2.56, n=2	2.80
Visual foraging*	1.3	0.34 (0.49), n=20	0.84 (0.56), n=218	2.48
Prey size class 2			1.28 (0.77), n=48	2.92
Prey size class 3			2.91 (2.76), n=23	4.55

***** Note, visual foraging for prey size class 1 was not considered, as prey is too small to be hunted visually. IQR=inter-quartile range

For visually foraging avocets, there is an additional handling cost, the ‘approach time’ (h_p). This represents the time taken to move towards visually detected prey, prior to attack. The focal point of the visual forager is generally around 28–43 cm in front of the avocet (see Table 4.2). Dias et al. (2009) have estimated the average length of an avocet pace to be 0.18 ± 0.003 m, thus prey is generally discovered 1.5–2.3 paces in front of the avocet. This is consistent with the field observation that once an avocet detects a prey item, it takes two steps to reach it. Dias et al. (2009) estimated the pace rate of avocets as 93 ± 1.8 paces min^{-1}. This is consistent with the estimate of 0.65 s per pace derived from video data. Thus the time taken to move towards detected prey is approximately 1.30 s.

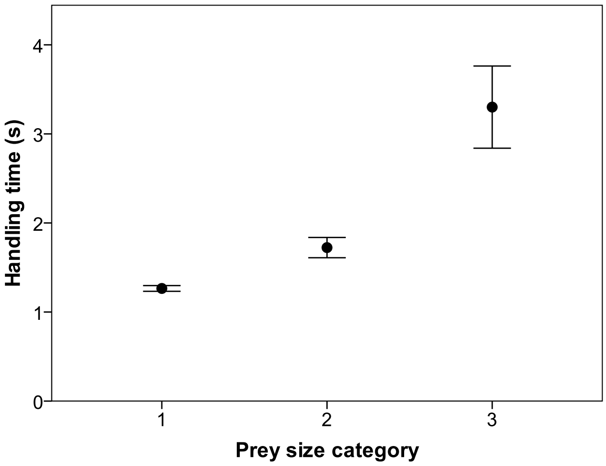


Figure 4.7 The effect of prey size on the swallowing component of handling time (h_s). To calculate total handling time for each foraging type, the approach (h_p) and attack (h_a) components of handling time are added to these values. Prey size classes defined as follows: 1) too small to be visible, 2) visible but less than half the bill length, 3) visible and greater than half the bill length. Error bars represent standard error.

4.4.4 Functional response

I calculated the search rate for each foraging type using mean estimates for each searching parameter (see Table 4.2). I produced a functional response model for benthic tactile (Figure 4.8a), visual (Figure 4.8b), and pelagic tactile (Figure 4.8c) foraging. To take into account the effect of prey size on handling time, I plotted separate curves for each prey size category. The functional response models show that higher feeding rates are achieved by feeding on small prey items, due to the shorter handling time required to swallow small prey. However, very high prey densities are required to achieve similar feeding rates using pelagic tactile foraging compared with the other two strategies (note different scale on x-axis for Figure 4.8c).

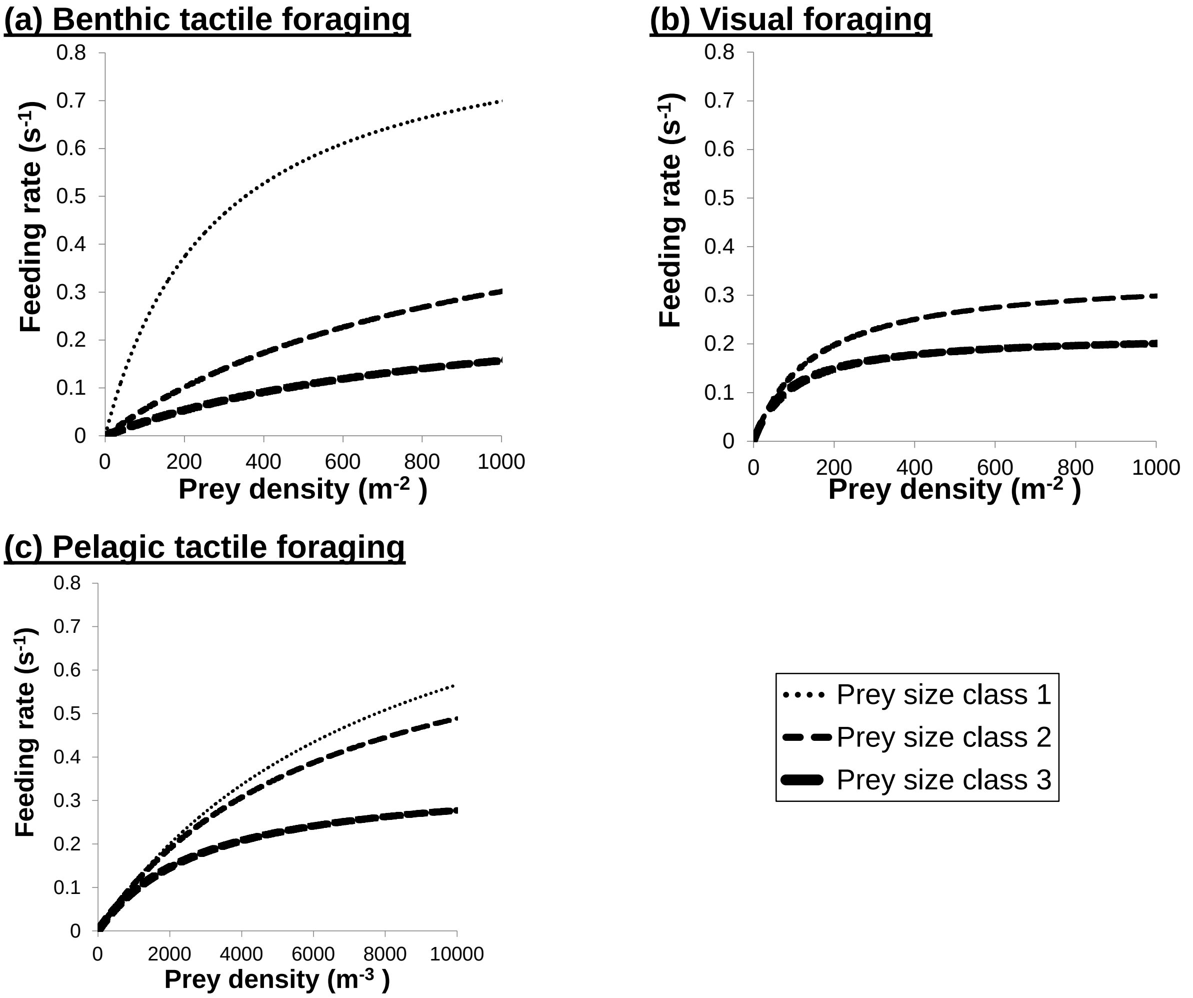


Figure 4.8 Functional responses for (a) benthic tactile foraging, (b) visual foraging, and (c) pelagic tactile foraging. Note the different x-axis scale and units for (c).

4.4.5 Prey availability and abundance at study site

I calculated the relative proportion of worms vulnerable to predation by benthic tactile foraging (present in the top 2 cm of sediment) or visual foraging (present at the surface), based on Esselink & L. Zwarts (1989) (see methods).The figures for benthic tactile foraging were based on the size distributions of worms at the study site: 4–6.0 cm (90%), 6.1–8.0 cm (8%), 8.1–10.0 cm (2%). The proportion of prey vulnerable to predation is given in Table 4.4.

Table 4.4 The proportion of vulnerable prey for each foraging strategy and prey size class.

Foraging strategy	**Proportion of prey vulnerable to predation (p)** Brownsea	 Middlebere
Benthic tactile foraging		
Prey size class 1	1.0000	1.0000
Prey size class 2	0.6841	0.5838
Prey size class 3	0.1036	0.1883
Visual foraging*		
Prey size class 2	0.1000	0.1000
Prey size class 3	0.1000	0.1000
Pelagic tactile foraging		
Prey size class 1	1.0000	1.0000
Prey size class 2	1.0000	1.0000
Prey size class 3	1.0000	1.0000

*prey size class 1 omitted as it is not targeted by visual foraging; prey size class 1: <5 mm; prey size class 2: 6–39 mm; prey size class 3: >40 mm. Proportion of prey vulnerable to predation was calculated based on *H. diversicolor* burrow depths from Esselink & L. Zwarts (1989), and the proportion of worms in each size class at the study sites (see text for details).

The abundance of the main avocet prey types, estimated from benthic coring and pelagic light traps are presented in Table 4.5.

Table 4.5 Average abundances and availability for each foraging strategy of main prey types found within the mud and in the water column at Brownsea Island Lagoon and Middlebere Creek.

Benthic prey	***Corophium sp***	**Small worms (<5 mm)**	**Medium worms (6–39 mm)**	**Large worms (>40 mm)**
Total abundance (m^{-2})				
Brownsea	3533.04	4707.55	2171.93	363.83
Middlebere	364.79	501.38	738.11	189.73
Availability for benthic tactile foraging (m^{-2})				
Brownsea	3533.04	4707.55	1485.82	37.69
Middlebere	364.79	0	0	0
Availability for visual foraging (m^{-2})				
Brownsea	0	0	217.19	36.38
Middlebere	0	0	0	0
Pelagic prey	***Corophium sp***	***Idotea chelipes***	***Palamonetes varians***	***Pomatoschistus sp***
Total abundance (m^{-3})				
Brownsea	3.97	0.19	3	1.69

Small, medium and large worms represent prey size categories 1, 2 and 3, respectively.

4.4.6 Energy content of prey types

To determine the energy intake rate for each foraging strategy from the feeding rates, I determined the relative energy content of each prey type. Table 4.6 shows the mean energy content of prey items collected from Brownsea Island Lagoon. Biomass was calculated for each prey type by the loss of mass of dry specimens on ignition method (described in Chapter 3). Length—biomass regressions for 2 additional species, which were not reported in Chapter 3 as they were sampled by pelagic netting rather than benthic coring, are given in Appendix 7a. Biomass in mg ash-free dry mass (AFDM) was converted into available energy in kJ using the conversion factors listed in Appendix 7b.

Table 4.6 Biomass in ash-free dry mass (AFDM) and energy content of prey items.

Prey	Biomass per organism (mg AFDM)*	Energy content per organism (kJ)
Corophium sp	0.1133	0.00235
Small worms (<5 mm)	0.2300	0.00491
Medium worms (6–39 mm)	1.8239	0.03589
Large worms (>40 mm)	7.6521	0.15059
Idotea chelipes	1.9729	0.04892
Palaemonetes varians	80.5352	1.99727
Pomatoschistus sp	152.1835	3.49413

*The biomass for ‘small worms’ was based on the average biomass determined for 30 small annelids <5 mm length; biomass for ‘medium worms’ and ‘large worms’ was based on the length—biomass relationships in Chapter 3 (Table 3.2), based on *H. diversicolor* of lengths 20 mm and 60 mm, respectively. Biomass of the remaining species were calculated using the length—biomass relationships in Chapter 3 (Table 3.2) and Appendix 7a, based on the average length of organisms sampled at Brownsea Island Lagoon, which were *Corophium sp*: 3.4 mm; *I. chelipes*: 10 mm; *P. varians*: 40.5 mm; and *Pomatoschistus sp*: 44.5 mm.

4.4.7 Model calibration using observed feeding rates to determine the capture efficiency

I calculated feeding rates using the functional response model for benthic tactile foraging based on the average abundance of prey at Brownsea Island Lagoon, using data from from benthic surveys described in Chapter 3. I compared predicted feeding rates with feeding rates I measured in the field. Figure 4.9 shows the difference between predicted and observed feeding rates, for Brownsea Island Lagoon. For benthic tactile foraging, the median value of observed feeding rate was 36.0% that of the predicted feeding rate. For visual foraging, median observed feeding rate was 19.8% that of the predicted feeding rate. For pelagic tactile foraging, median observed feeding rate was 120.5% that of the predicted feeding rate. Calibrating the functional response models such that the output matches observed feeding produces gives a capture efficiency figure ('c' from Equation 1) of 0.01095 for benthic tactile foraging, and 0.01237 for visual foraging. Calculating 'c' for pelagic tactile foraging yields a value of 153.

I also compared predicted and observed feeding rates for benthic tactile foraging at a second site, Middlebere Creek (visual foraging was not observed at this site, and pelagic tactile foraging could not be calculated as I did not have data on abundance of pelagic prey at this site). Here predicted intake rates were for benthic tactile foraging were similar to the predicted values.

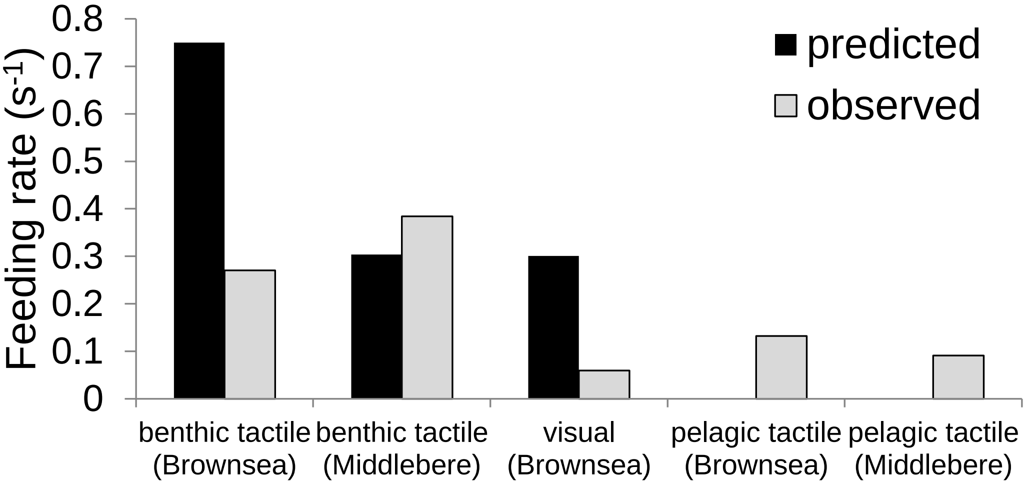


Figure 4.9 Comparison of predicted and observed feeding rates (used to calibrate functional response model.

4.4.8 Energetic profitability of foraging strategies

I used the prey energy content, and observed intake rates derived from the calibrated functional response model, including the capture efficiency parameter (c), to determine the time taken to meet the daily energy requirement (DER) of **838.34 kJ day^{-1}** using each foraging strategy, assuming that one prey item is collected per sweep (Figure 4.10).

The model output indicates that the greatest energy intake rates can be achieved by pelagic tactile foraging on energy dense prey items such as gobies (*Pomatoschistus* sp.) or ditch shrimp (*P. varians*). However, this strategy is only feasible if locally high abundance of prey is identified. To achieve the energy intake rates represented in Figure 4.10, the effective prey abundance needs to be roughly 150 times greater than the actual densities recorded by the sampling methods. It is extremely unlikely that the density of *Corophium* found in the water column would ever be high enough to make their capture by pelagic tactile foraging energetically feasible.

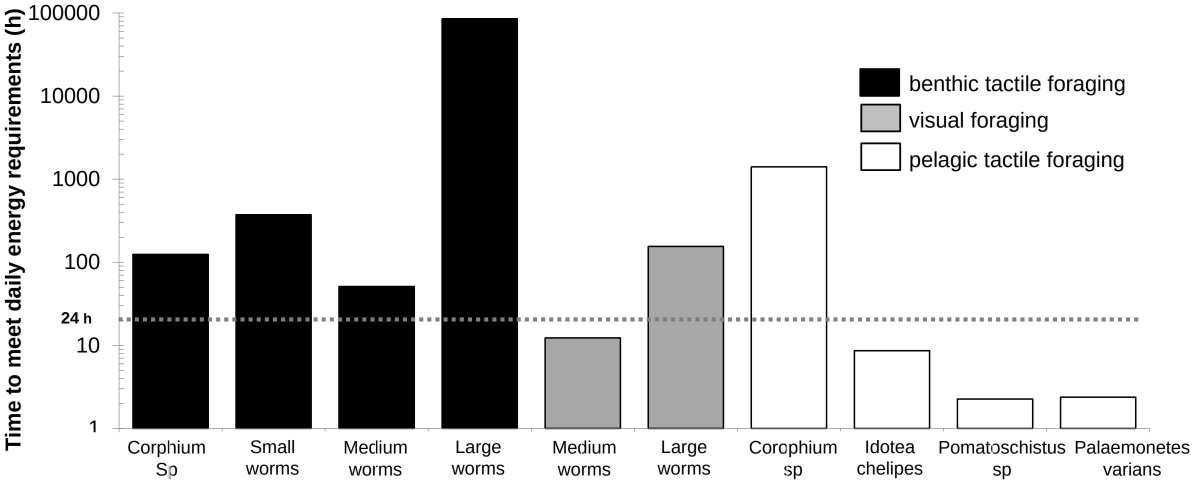


Figure 4.10 Time taken to reach daily energy requirements (DER), for different prey types and foraging strategies for the prey abundances found at Brownsea Island Lagoon, assuming one prey item is collected per sweep.

The relatively low availability of large worms, due to their tendency to burrow to unattainable depths in the sediment, results in very low intake rates achievable by benthic tactile foraging. However, much greater intake rates are obtainable by targeting this prey type visually. Although, with the densities of large worms present at the study site, the encounter rate is so low that a bird could never meet its DER just searching for very large worms. The increased availability of medium-sized worms makes them a much more profitable prey type. Intake rates were 24.1% higher if medium-sized worms were targeted by visual rather than benthic tactile foraging at the study site.

According to Figure 4.10, benthic tactile foraging on the smallest prey types (small worms and *Corophium*) does not yield high enough intake rates to meet DER. However, it should be noted that the model has assumed that a maximum of 1 prey item is taken per sweep. This is a valid assumption for the larger prey types; however, according to a quantitative study of avocet faecal contents and prey swallowing rates, the author concluded that multiple small worms were captured and ingested in a single sweep (Moreira 1995b). The estimated number of worms ingested per swallow ranged from 2 to 24. If I take the upper limit of this estimate, and apply it to benthic tactile foraging on small worms and *Corophium*, the number of hours needed to meet DER drops to 13.3 hours and 4.6 hours, respectively.

4.5 Discussion

This chapter demonstrates that avocets are able to achieve the highest intake rates by targeting energy-dense pelagic prey, but only when these prey are present at high densities. The relative profitability of foraging by sight or touch on benthic prey depends on the prey composition found at the site. If prey consists of few large individuals, then visual foraging is more profitable; although this strategy is only possible under certain environmental conditions, such as good visibility and calm conditions. Benthic tactile foraging represents a 'safe' strategy, which will usually provide sufficient intake rates to meet daily energy requirements, as long as the density of small prey is not unusually low, or the sediment too grainy, as this may interfere with prey capture (Quammen 1982).

These results show that prey availability is more important to avocet survival than prey abundance. This means that great care is required when drawing inference from benthic sampling as to the likely survival of avian predators. Avocets employ a range of feeding strategies based on local prey availability and by explicitly parameterising each strategy the results show that pelagic tactile foraging on large prey items was the most profitable strategy, followed by benthic tactile predation on *Corophium* and small worms, assuming that multiple prey items are collected in a single sweep. This study provides strong evidence for the assertion that multiple small prey items are collected in a single sweep of the bill, as benthic tactile foraging on very small prey was commonly observed at the study site, so under optimal foraging theory we must assume that it is an energetically profitable strategy.

Pelagic tactile foraging on *Pomatoschistus* and *Palaemonetes* was predicted to meet energetic requirements within 2.3 and 2.4 hours, respectively. For pelagic tactile foraging, the fact that observed intake rate was higher than predicted for this type of foraging has two possible interpretations. Firstly, that the actual density of pelagic prey is higher than that which I estimated from the sampling methods used. Secondly, that the distribution of the highly mobile pelagic prey is not homogeneous, but patchy, and pelagic tactile foraging is a response to a bird encountering a locally high abundance of prey. The abundances I recorded are unlikely to be reflective of the biologically relevant, high densities which transiently occur as the pelagic prey moves around. In the absence of these prey clusters, predicted intake rates for this foraging method are extremely low, suggesting that pelagic tactile foraging is a very inefficient means of prey capture at low prey densities. Thus, pelagic tactile foraging is likely to be an opportunistic strategy, which is profitable when locally high densities of large prey items are encountered. The idea that locally high abundance of prey may be created by the birds as they form social foraging flocks, will be explored further in Chapter 5.

I found that at Brownsea Lagoon, foraging on larger worms was less profitable than foraging on medium-sized worms, despite the extra energy associated with individual prey items. This was due to the longer handling times limiting the maximum feeding rate, but also the very low availability of large worms. Even though the abundance of large worms estimated by core sampling was 363.83 worms m^{-2}, due to decreased probability of worms being found in the top 2 cm of sediment (i.e. available for benthic tactile foraging), or at the surface (i.e. available for visual foraging), the effective abundance of these worms was nearly ten times lower. As the abundance of medium-sized worms was roughly six times higher than the abundance of large worms, medium-sized worms were associated with higher intake rates. Indeed there may be a threshold worm size which affords them some immunity from predation by avocets by virtue of their deeper burrowing depths (Esselink & Zwarts 1989). Thus there is likely to be a complex set of feedback interactions between secondary production and avocet survival. However, the key point here is that predators target areas of high prey *availability* or “catchability” over abundance, which has been demonstrated in other predator-prey systems (Balme et al. 2007). As surveys of prey available to shorebirds generally focus on *abundance*, this highlights the importance of models such as the one I have developed here, to provide the link between abundance and intake rates.

In addition, the model indicated that for larger benthic prey, it was more efficient to hunt by vision than touch. While visual foraging had higher handling time associated with the approach time, in a prey landscape where very large, energy rich prey are present, even at low density, visual foraging may be a more efficient foraging strategy.

Comparing the predictions of the un-calibrated foraging model to observed feeding rates in the field (Figure 4.9), I derived a figure for an unknown component of the species’ foraging ecology – the efficiency of prey capture (‘c’). However, the ecological meaning of this variable differs between the 3 foraging types. Also, by comparing predicted and observed intake rates for a second study site (Middlebere Creek), I showed that capture efficiency is site specific. For benthic tactile foraging the interpretation of c is simply that only a small percentage of the prey that is contacted by a scything bill will be captured and ingested. For visual foraging, the capture efficiency is a measure of the percentage of prey within the visual field which is perceived and attacked. Both of these estimates are likely to be affected by environmental conditions – scything efficiency may be lower in sandier sediments (Quammen 1982), and visual foraging is only possible in non-turbulent water or on exposed mud, and the presence of wind may also decrease prey detection (Velásquez & Navarro

1993; Goss-Custard 1984). On the other hand, water movement may increase the tendency of larger worms to migrate to the surface in search of food, which increases their availability to predators (Esselink & Zwarts 1989). The most likely reason for the lower capture efficiency at Brownsea compared with Middlebere is that the sediment at the latter site is much finer (Chapter 3) and less likely to interfere with the delicate foraging apparatus of the bill. In addition, the high density of hydrobiid snails at Brownsea (Chapter 3) could also interfere with the prey-detecting sensitivity of the bill, in a similar way to grainy sediment. In pelagic tactile foraging, the capture efficiency actually provides a means of estimating the effective prey abundance for highly mobile prey.

4.5.1 Sources of uncertainty

A great deal of uncertainty surrounds estimates of daily energy requirements of birds. The use of allometric scaling of BMR has been criticised by some authors, as data are often collected from small sample sizes, under artificial experimental conditions and confounded by phenotypic plasticity (McKechnie & Wolf 2004; McKechnie et al. 2006). However, in the absence of species-specific data, there is little alternative. It has been proposed that waders have a higher metabolic rate than non-waders of similar size (Kersten & Piersma 1987), although other authors have argued that BMR does not differ between passerines and non-passerines if phylogeny is taken into account (McKechnie & Wolf 2004). There is still much uncertainty in accounting for the metabolic costs of thermoregulation and different foraging regimes (Birt-Friesen & Montevecchi 1989). Metabolic parameters exhibit strong phylogenetic dependence, therefore, closely related species should exhibit similar metabolism (Freckleton et al. 2002). Furthermore, the correlation between BMR and FMR has been shown to be variable, and is most likely subject to behavioural adaptation (McKechnie & Swanson 2010).

The estimate of the relative profitability of each feeding strategy does not take into account the likelihood that the different feeding strategies will have different rates of energy expenditure associated with them. Based on the locomotive properties of each strategy alone, it is likely that visual foraging expends the least amount of energy, as it represents a ‘saltatory’ foraging strategy, by which the forager pauses to search for prey (O’Brien et al. 1989). Tactile foraging, on the other hand requires constant motion of the head and neck as the bill scythes the surface of the mud or through the water column, and can be considered a form of ‘cruise’ foraging (O’Brien et al. 1990). The relative profitability of each type of foraging depends on the prey environment. Unlike cruise foraging, saltatory searching can be modified to suit the environment (O’Brien et al. 1990), thus represents a more flexible and adaptive foraging behaviour. This was exemplified at Brownsea, when visual foraging was used more frequently on still days when water turbulence was minimal and prey visibility was maximal.

Based on sweeping rates, which were approximately 37% higher for pelagic tactile foraging compared with benthic tactile foraging, it is likely that pelagic foraging is the most energetically costly strategy. The relative energetic costs may also depend on the consistency of the substrate (it requires more effort to sweep the bill across a surface of uneven, sandy sediment) and depth of water (if the water is at a depth that the entire head must be submerged, this must require more energy than if the bill alone is submerged). The relative profitability of each strategy may also be temperature dependent. For example, a study of red knots has shown that the heat generated by vigorous activity may offset the cost of thermoregulation if the temperature is lower than that required for thermoneutrality (Bruinzeel & Piersma 1998). Thermoneutrality is roughly 10ºC for the oystercatcher (Kersten & Piersma 1987), which is similar in size to an avocet, therefore overwintering avocets in the UK will be expending considerable amounts of energy to stay warm. All points considered, it is likely that pelagic foraging is a more energetically costly strategy, and thus will only be employed when extremely high densities of prey are encountered.

4.5.2 The importance of visual foraging in avocets

There is much debate as to the extent to which nocturnal foraging is important in avocet ecology. While it is likely that tactile foraging may be able to occur at night, it is very unlikely that avocets are able to forage visually at night, or in low light levels. In fact, night-time feeding activities may be limited to moonlit nights or areas where there is light from anthropogenic sources. This has consequences for resource acquisition, as it means avocets are restricted to tactile foraging at night, and are not able to visually select larger more profitable prey. This may negatively impact their intake rate, particularly if they are feeding in sediments which contain high number of low energy prey, such as the mud snail *Ecrobia ventrosa*.

4.5.3 Conclusions

The key finding of this chapter is that the relationship between prey abundance and intake rates is not simple. This is perhaps why some studies fail to find clear relationships between invertebrate prey abundances and bird foraging densities (Thomas et al. 2004b). Thus, models such as the one developed here are required to accurately determine intake rates by detailed examination of the species foraging strategies, the prey abundance, and crucially the prey availability and efficiency of capture.

Chapter 5: A comparison of pied avocet (*Recurvirostra avosetta*) foraging behaviour in a tidal and non-tidal habitat

5.1 Abstract

To predict the impacts of future environmental changes and inform conservation management of non-breeding shorebird populations, it is essential to understand the behaviour and ecological requirements of each species. Shorebird foraging behaviour can differ substantially between tidal and non-tidal habitats. There is an increasing interest in evaluating the utility of artificial non-tidal habitats in supporting overwintering bird populations, as intertidal habitats are increasingly under threat from anthropogenic changes.

In this chapter I examine the winter foraging behaviour of an internationally important overwintering population of pied avocets (*Recurvirostra avosetta*). This population uses both an intertidal mudflat and a non-tidal saline lagoon during the winter, and the relative use and behaviour of the birds in these two habitats is compared. I recorded the proportion of birds foraging, and feeding rates at both sites, and these behaviours were examined in relation to a number of factors, including season, tidal factors, weather, water depth, sediment properties, prey availability and number of conspecifics and heterospecifics foraging in close proximity. In addition, I recorded the occurrence and feeding rates of avocets in social foraging aggregations to assess the relative contribution of this foraging mechanism to the population's energy acquisition.

The proportion of time avocets spent foraging varied in response to seasonal and tidal effects, and the precise relationship was different between the tidal and non-tidal study sites. In addition, avocet feeding rates varied in accordance with seasonal and tidal factors, and local invertebrate abundance. Social foraging showed seasonal, tidal and diurnal variation, and differed in timing and frequency between the tidal and non-tidal sites. Furthermore, the minimum threshold for number of birds necessary for social foraging to occur was higher at the non-tidal site.

5.2 Introduction

It is essential to understand the behaviour and ecological requirements of non-breeding shorebird populations to predict the impacts of future environmental changes to these species and inform conservation management practices (Caro 2007; Stillman & Goss-Custard 2010). The foraging behaviour of non-breeding shorebirds is affected by a number of environmental factors. Studies have shown an effect of season (Hötker 1999b; Goss-Custard & Jenyon 1977), tides (Granadeiro et al. 2006; Burger et al. 1977), temperature (Moreira 1996; Kelly et al. 2002; Pienkowski 1983), wind (Taylor & Taylor 2005; Verkuil et al. 1993), day length (Dodd & Colwell 1998), substrate type (Quammen 1982; Finn et al. 2008), moonlight (Dodd & Colwell 1998; Evans & Harris 1994) and human disturbance (Burton et al. 1996; Gill et al. 2001b) on foraging behaviour. Prey density and distribution are also important, and many of the other factors affect behaviour indirectly by altering prey availability, or the efficiency of prey capture (Bryant 1979; Backwell et al. 1998; Cardoso et al. 2008; Santos et al. 2009; Quammen 1982).

Shorebird foraging behaviour can differ substantially between tidal and non-tidal habitats (Masero 2003; Smart & Gill 2003). There are many studies outlining shorebird foraging behaviour in a variety of non-tidal habitats, including lagoons (Kelly et al. 2002; Holm & Clausen 2006; Robertson 1993; Battley et al. 2003; Verkuil et al. 1993), artificial saltpans (Velasquez 1992; Masero et al. 2001; Dias 2009; Perez-Hurtado et al. 1997) and other man-made water bodies (Evans & Harris 1994; Erwin et al. 1994; Breininger & Smith 1990). However, there are few studies which directly compare the behaviour and choice of foraging habitat in a landscape containing tidal and non-tidal habitats. Examining the behaviour of birds in all habitats within an overwintering site is essential for developing valid conservation management plans (Burger et al. 1997). As intertidal habitats are currently undergoing unprecedented rates of environmental change, in the form of habitat loss, pollution and resource exploitation (Nicholls et al. 2007; Jackson 2008), there is an increasing interest in evaluating the utility of artificial non-tidal habitats in supporting overwintering bird populations (Gomez-Sapiens 2013).

The pied avocet (*Recurvirostra avosetta*) is a shorebird species which is overwintering in increasing numbers in the UK. Currently, around 7200 pied avocets overwinter at coastal sites in the UK, of which roughly 20% are found in Poole Harbour (Holt et al. 2012). To date, the majority of studies on pied avocets have been conducted during the breeding season (Hötker et al. 1996; Hötker & Segebade 2000; Hötker 2002; Hötker 1999b; Hötker 1999a; Cuervo 2005; Goutner 1985; Lengyel 2006; Cadbury & Olney 1978; Hill & Carter 1991; Olsen & Schmidt 2004). Winter feeding ecology of avocets has been described previously on the Tagus Estuary in Portugal (Moreira 1995a, 1995b); however, this study was based on a small proportion of the overwintering population (<100 individuals). Another previous study of non-breeding pied avocets focussed on proportion of time spent foraging, but did not describe the feeding rate of the birds (Hötker 1999b). With the exception of a small study on the Tamar estuary in Cornwall (Reay 1988), there are no studies of overwintering avocets in the UK.

In this chapter, I compare observed behaviour of a population of overwintering avocets in an intertidal mudflat and a non-tidal saline lagoon, and link the differences in observed behaviours to environmental variables, through consideration of the unique foraging mechanism of the avocet (see Chapter 4). To fully understand the differences in habitat use between the sites, I consider several aspects of behaviour: the proportion of time spent foraging, and the searching and feeding rates in each habitat. I also distinguish between solitary foraging, which targets the relatively sessile benthic invertebrate prey, and 'social foraging', which targets faster moving, nektonic prey such as small fish and prawns.

Social foraging has been extensively studied in Ciconiiformes (the order including herons and egrets) (Kersten et al. 1991; Kushlan 1976; Stolen et al. 2012; Krebs 1974; Smith 1995), and to a lesser extent in wildfowl (Drent & Swierstra 1977) and various species of seabird, including gulls (Gotmark et al. 1986), cormorants (Glanville 1992), albatrosses (Grünbaum & Veit 2003) and mixed-species aggregations (Duffy 1989). However, there are relatively few studies of the phenomenon within the Charadriiformes (Battley et al. 2003; Ntiamoa-Baidu & Piersma 1998; Boettcher et al. 1994). In shorebirds, attention has focussed more on the negative impacts of foraging in close proximity to other birds, i.e. interference (Goss-Custard 1980; Ens et al. 1990; Rutten et al. 2010; Stillman et al. 2000a; van der Meer & Ens 1997). Social foraging behaviour has been described in American Avocets (*Recurvirostra americana*) as a mechanism for herding nektonic invertebrates (Boettcher et al. 1994). The phenomenon has also been described in pied avocets (Ntiamoa-Baidu & Piersma 1998; Battley et al. 2003; Hötker 1999b), but the conditions under which it occurs and its relative importance in energy acquisition in comparison with other feeding mechanisms have not been investigated.

5.2.1 Aims

The aims of this chapter are:

- to compare foraging behaviour between a tidal and non-tidal habitat in terms of:
    - the proportions and absolute numbers of birds solitary and socially feeding and roosting under a variety of environmental conditions;
    - the observed feeding rates for solitary and socially feeding avocets under a variety of environmental conditions;
- to investigate the relationship between observed behaviour and differences in local environmental factors (i.e. sediment characteristics, water depth, local invertebrate densities, number of conspecific and heterospecific birds within 5 m of the focal individual and weather conditions).

5.3 Methods

5.3.1 Study sites

The main foraging habitat of the avocet population within Poole Harbour included a non-tidal brackish lagoon (Brownsea Island Lagoon) and a tidal soft sediment creek (Middlebere Creek).

5.3.2 Measuring foraging behaviour

For the duration of the avocet overwintering period (September–March), in 2010–11 and 2011–12, I conducted systematic counts, one day a week at each study site, on the spring tide with the greatest tidal range and the neap tide with the smallest tidal range. The survey dates are listed in Appendix 8. I conducted hourly counts between sunrise and sunset, using the scanning method (Altmann 1974), recording the number, location, and behaviour (feeding or roosting) of avocets present at the study sites. Feeding was characterised as solitary or social. Social foraging was defined as birds showing "directionally synchronised movements" (Battley et al. 2003). Solitary foraging included all non-socially foraging birds. Roosting included all non-feeding behaviours such as preening, bathing or loafing. If no avocets were present at the site, I ceased observation after 2 hours.

5.3.3 Measuring feeding rates

During the winter of 2010–11, I collected video data of randomly selected solitary and socially foraging avocets. In total, 501 videos were analysed, including 415 of solitary foraging behaviour (289 from Brownsea, 126 from Middlebere) and 86 of social foraging behaviour (73 from Brownsea, 13 from Middlebere). I counted the number of times the bird scythed the sediment with its bill to collect prey (henceforth "sweeping") and the number of times it swallowed prey in 120 s. In instances that the focal bird was interrupted during the two minutes and ceased feeding, the timer was stopped and restarted when the bird recommenced feeding. In cases where the focal bird stopped feeding and did not recommence, the record was discounted, unless the bird had been feeding for ≥90 s, in which case the observed number of sweeps and swallows was increased by a third to adjust for the missing time. This method was adopted, as the alternative of discounting any record in which the focal individual ceased foraging before 120 s completed, could conceivably have introduced a sampling bias if birds were more likely to cease foraging when feeding in an "unfavourable" patch. As feeding rates were generally fairly uniform throughout the 120 s observation, the adjusted sweep and swallow rates should be similar to the real sweep and swallow rates. Feeding rates were calculated for solitary and socially foraging birds separately.

5.3.4 Recording local environmental conditions

At the time of video data collection, local environmental conditions, including water depth, number of avocets feeding within 5 m of the focal birds, number of birds of other species feeding within 5 m of the focal bird, air temperature, wind speed and cloud cover, were recorded for each observation. Details of the measurement of these factors are presented in Table 5.1. The time and location of each foraging event was recorded on a map and subsequently entered into a Geographical Information System (GIS) (ESRI, 2010). Foraging events were separated into three temporal categories. Period 1 included all observations from September; period 2 included all observations in October, November and December; and period 3 included observations from January, February and March. These periods were chosen such that a benthic survey occurred in the mid-point of each period (Figure 5.1). For each period, I used data from the benthic surveys described in Chapter 3, to determine the spatial distribution of sediment properties and invertebrate abundance. This included the proportion of coarse (>500 µm) and fine (<63 µm) sediments, and the numerical densities of the most abundant invertebrate groups (small (≤1 cm), medium (>1–4 cm) and large (>4 cm) worms, *Corophium* spp. and Hydrobiidae). The absolute abundance of medium and large worms was modified according to a 'worm availability constant' (see Chapter 4), which takes into account the burrow depths of differently sized worms (Esselink & Zwarts 1989). The worm availability constants used for each study site during each period are presented in Appendix 9. I used inverse distance weighting (IDW) interpolation to calculate the values for all unsampled points, which calculates the value of unsampled points as the distance-weighted average of neighbouring sampled points (Lu & Wong 2008). The resultant maps are presented in Appendix 10 (a–h).

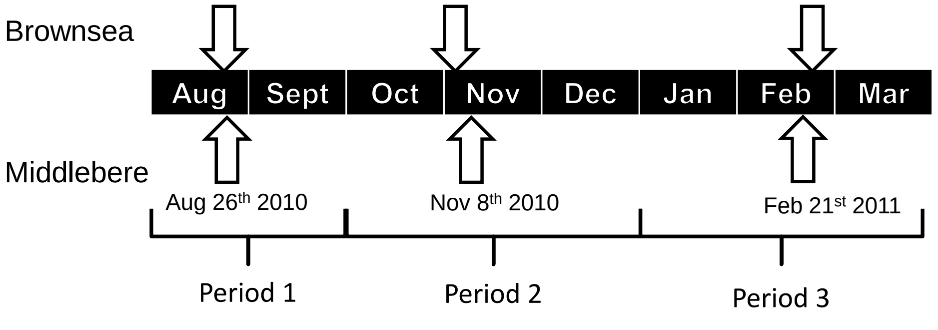


Figure 5.1 Timeline for invertebrate and sediment sampling.

Table 5.1 Details of recording methodology for environmental variables.

Factor	Scale	Details
Air Temperature	°C	Measured with a handheld mercury thermometer
Cloud cover	% cover	Estimated by eye
Precipitation	0–2	0=no precipitation 1=light precipitation 2=heavy precipitation
Wind	0–4	0=no wind 1=light breeze (≈1 or 2 on Beaufort scale) 2=moderate breeze (≈3 or 4 on Beaufort scale) 3=strong breeze (≈5 or 6 on Beaufort scale) 4=very strong wind (≈7+ on Beaufort scale)
Time after sunrise	Hours:mins	(to the nearest 15 min)
Time before sunset	Hours:mins	(to the nearest 15 min)
Time after high tide	Hours:mins	(to the nearest 15 min)
Tidal state	Spring/neap	
Tidal phase	1–5	1=high 2=high2[1] 3=ebb 4=low 5=flow
Tide height		Estimated from Poole Harbour tidal prediction timetables[2]
Water depth	0–4	0=exposed mudflat 1=up to avocet ankle 2=up to avocet knee 3=up to avocet belly 4=avocet swimming
No of conspecifics feeding within 5 m		A 5 m radius was estimated visually as 10 avocet body lengths
No of heterospecifics feeding within 5 m		

[1] high2 represents observations taken during the second peak of the double high water phenomenon (described in Humphreys & May 2005).

[2] (Proudman Oceanographic Laboratory 2010; Proudman Oceanographic Laboratory 2011)

5.3.5 Statistics

I used univariate tests to determine the differences in the proportion of birds feeding by site, month, tidal state and phase, and time after sunrise (Mann-Whitney U tests for bifactorial parameters and Kruskal-Wallis tests for multifactorial parameters). I used a linear mixed-effects model with binomial error structure, using the R package lme4 (Bates et al. 2013), to incorporate the random effect of observation day and test the significance of interactions between site and other factors. To test the significance of individual fixed effects, I compared a full model against a reduced model without the fixed effect in question, using a likelihood ratio test (Bolker et al. 2009).

Differences in sweep and swallow rates were tested using univariate tests (Mann-Whitney U tests and Kruskal-Wallis tests, as above). To determine the influence of local environmental conditions on sweeping and swallowing rates I used a generalised linear model (GLM) with Poisson error structure. As there were a large number of potential covariates, I used a multi-model inference approach (Burnham et al. 2010), using the MuMIn R package (Barton 2013), to determine model coefficients by averaging over all possible models.

The mixed-effects and GLM model assumptions were tested by visually assessing residual plots to ensure no deviation from linearity or homoscedasticity. Histograms of residuals were visually examined for signs of non-normality. DFBeta values were examined to ensure none of the data points had excessive influence on model outputs.

5. 4 Results

5.4.1 Differences in bird behaviour between Brownsea and Middlebere

(i) by site

I recorded the total number of birds that were feeding and roosting at each site during the observation period. Figure 5.2 compares Brownsea and Middlebere in terms of the proportion of birds that were feeding or roosting (a,b,c) and the total cumulative number of birds feeding or roosting at each site (d,e,f). Roosting included all non-feeding behaviours such as preening, sleeping and loafing). At Middlebere, a higher proportion of the birds present at the site were feeding, compared with Brownsea (Mann-Whitney U=7919.000 (df 238,113), Z=-6.365, p<0.001). The median proportion of birds feeding was 0.24 at Brownsea and 0.76 at Middlebere. This finding and was consistent for both winters studied (Figure 5.2b and c). The majority of feeding birds were solitary feeding. At Middlebere, a larger proportion of the birds fed socially, compared with Brownsea (Mann-Whitney U=13046.000 (df 237, 119), p=0.036); however, in terms of absolute numbers, there was no difference between sites (Mann-Whitney U=13108.500 (df 234, 119), p=0.090).

In terms of cumulative numbers of birds using each site, there was a much greater number of bird roosting hours at Brownsea compared with Middlebere (Mann-Whitney U=7300.000 (df 239,119), Z=-7.505, P<0.001); however, the number of bird feeding hours was not significantly different between sites (Mann-Whitney U=12583.500 (df 239,119), Z=-1.775, p=0.076; Figure 5.2c). This pattern was approximately similar for both winters studied, except during 2011–12 the number of foraging hours was significantly higher at Middlebere, compared with Brownsea (Mann-Whitney U=3167.500 (df 120,65), Z=-2.107, p=0.035; Figure 5.2f).

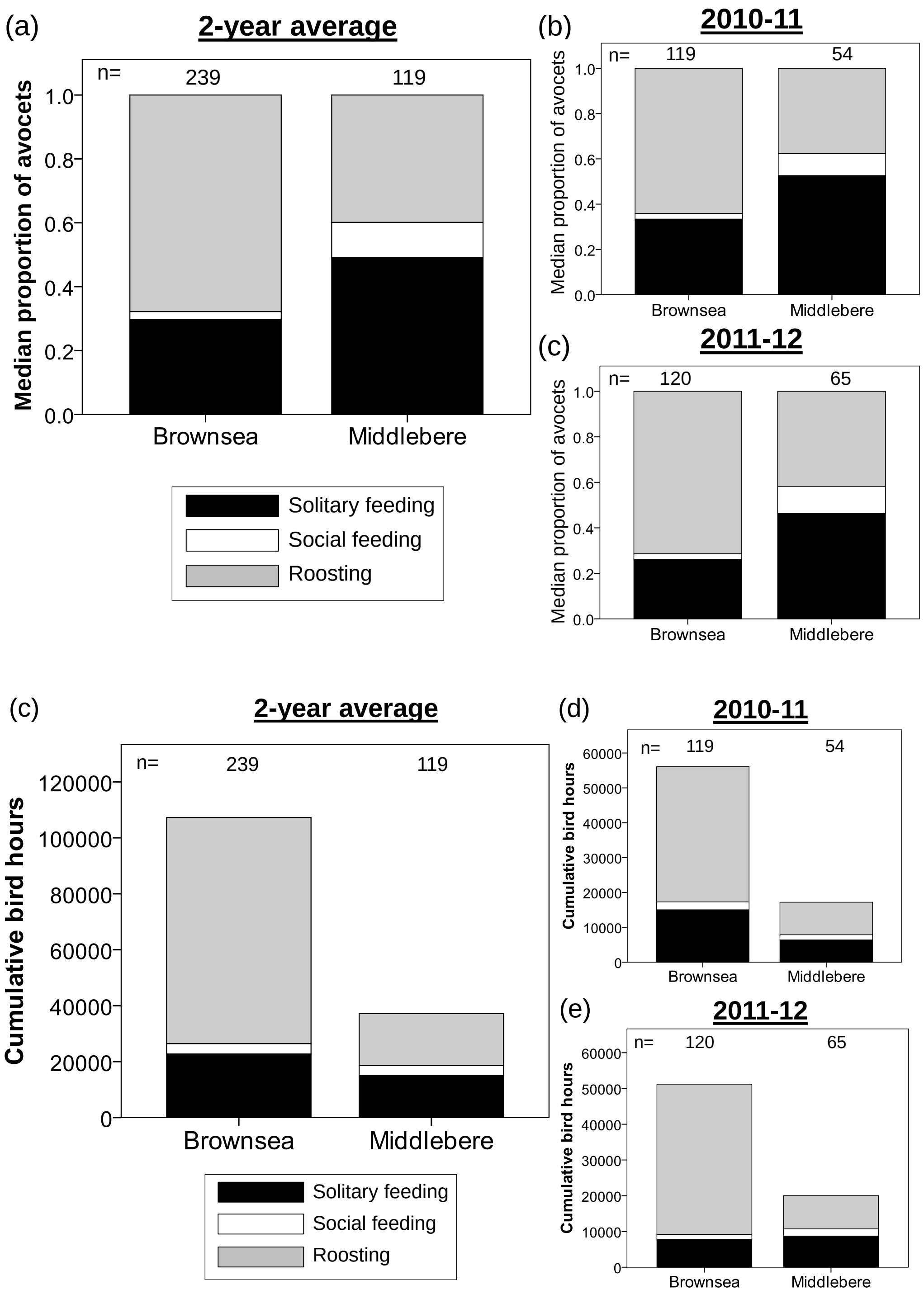


Figure 5.2 The median proportion of avocets feeding (solitary and socially) and roosting at Brownsea Island Lagoon compared with Middlebere Creek (a) averaged over 2 winters of observation, (b) during the 2010–11 winter, (c) during the 2011–12 winter. The cumulative number of feeding and roosting bird hours at Brownsea and Middlebere (d) over two years of observation, (e) during the 2010–11 winter, (f) during the 2011–12 winter. Numbers above columns represent the observation hours.

(ii) by month

There were significant differences in the proportion of birds feeding during each month (Figure 5.3a,b), both at Brownsea (Kruskal-Wallis H=64.085 (df 6), p=<0.001) and Middlebere (Kruskal-Wallis H=13.734 (df 4), p=0.008). At Brownsea, the proportion of birds feeding was low initially (4% in September) and generally increased until January, where it remained constant at around 60% for the remaining winter months. When the birds began using Middlebere in late October, initially it was solely for feeding, but as the winter progressed, the proportion of birds feeding decreased to 0.55 in December and remained roughly constant for the remaining winter months.

In terms of cumulative bird numbers, at Brownsea there were significant differences in the number of bird foraging hours each month (Kruskal-Wallis H=22.549 (df 6), p=0.001) and the number of bird roosting hours (Kruskal-Wallis H=121.204 (df 6), p<0.0001) (Figure 5.3c). At Middlebere, there was a significant difference in the number of avocets feeding each month (Kruskal-Wallis H=32.313 (df 4), p<0.0001), but not in the number roosting (Kruskal-Wallis H=7.482 (df 4), p=0.113) (Figure 5.3d).

The higher total number of birds observed in October and November was in part due to a higher number of observation hours (as the number of hours of daylight was greater). However, if the effect of observation hours was removed by examining the average number of avocets feeding and roosting for each observation hour, the number of foraging hours and roosting hours are still highest at Brownsea during October and November (data not shown).

At Brownsea, social foraging occurred exclusively in the first four months, with the highest proportion and cumulative numbers occurring in October. At Middlebere, initially a high proportion of the birds fed socially, and a small proportion of birds socially foraged in all subsequent months.

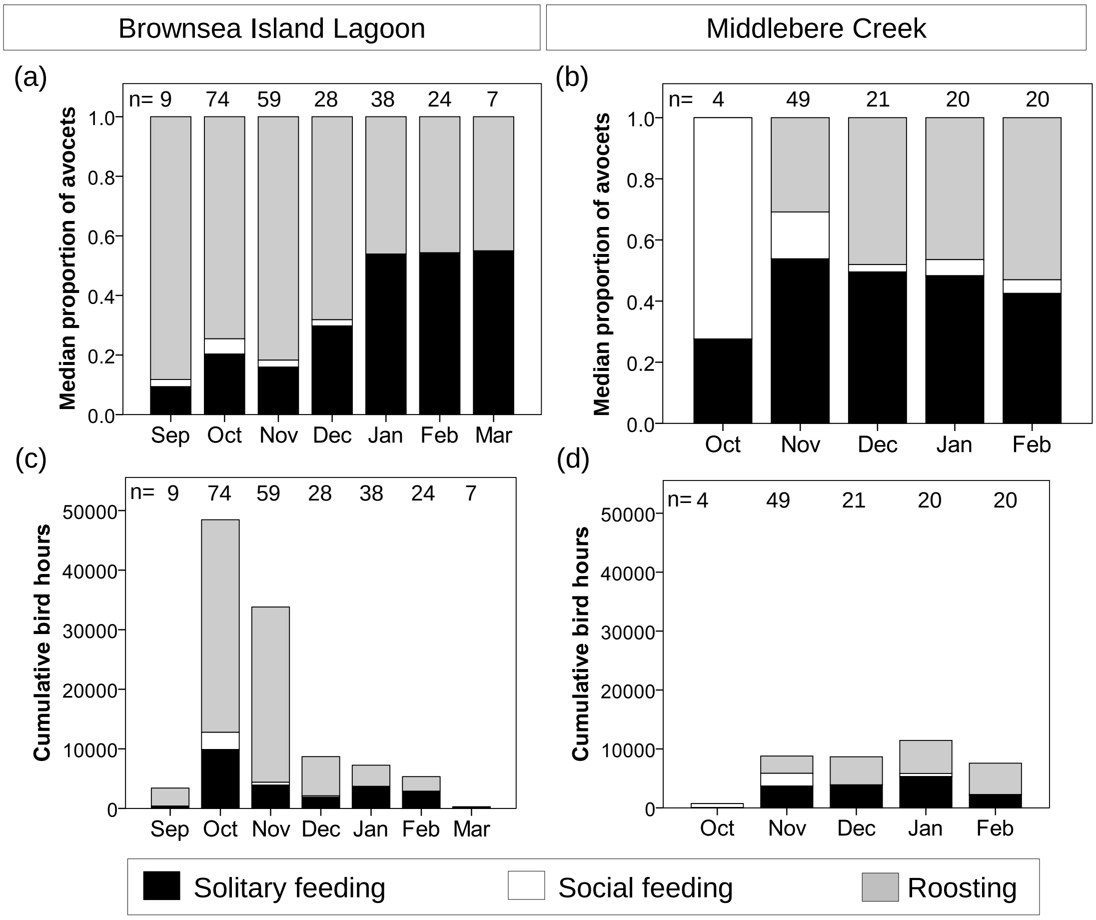


Figure 5.3 The median proportion of avocets feeding (solitary and socially) and roosting in each month at Brownsea Island Lagoon (a) and Middlebere Creek (b), over two years of observation. The cumulative number of feeding and roosting bird hours each month at Brownsea (c) and Middlebere (d) over two years of observation. Numbers above columns represent the observation hours.

(iii) by tidal factors

I examined the behaviour of avocets feeding at each site in relation to tidal factors. At Brownsea, the proportion of birds feeding during neap tides was marginally higher than for spring tides (U=5216.500 (df 116,121), Z=-3.594, p<0.001; Figure 5.4a). However, there was no difference at Middlebere (U=1620.500 (df 56,56), Z=-0.23, p=0.982; Figure 5.4b).

Figure 5.4c shows that at Brownsea, there were higher numbers of avocets present during spring tides compared with neap tides (Mann-Whitney U=5745.500 (df 117,122), Z=-2.604, p=0.009). Furthermore, at Brownsea, comparing between spring and neap tides, there was a significant difference in the numbers of birds feeding (Mann-Whitney U=5965.000 (df 117,122), Z=-2.194, p=0.028), and roosting (Mann-Whitney U=5164.500 (df 117,122), Z=-3.692, p<0.0001). However, the numbers of birds at Middlebere did not vary significantly between spring and neap tides (Mann-Whitney U=5745.500 (df 59,60), Z=-2.604, p=0.102) (Figure 5.4d).

There were no significant differences in the proportion or absolute numbers of avocets social foraging during spring tides and neap tides at Brownsea or Middlebere.

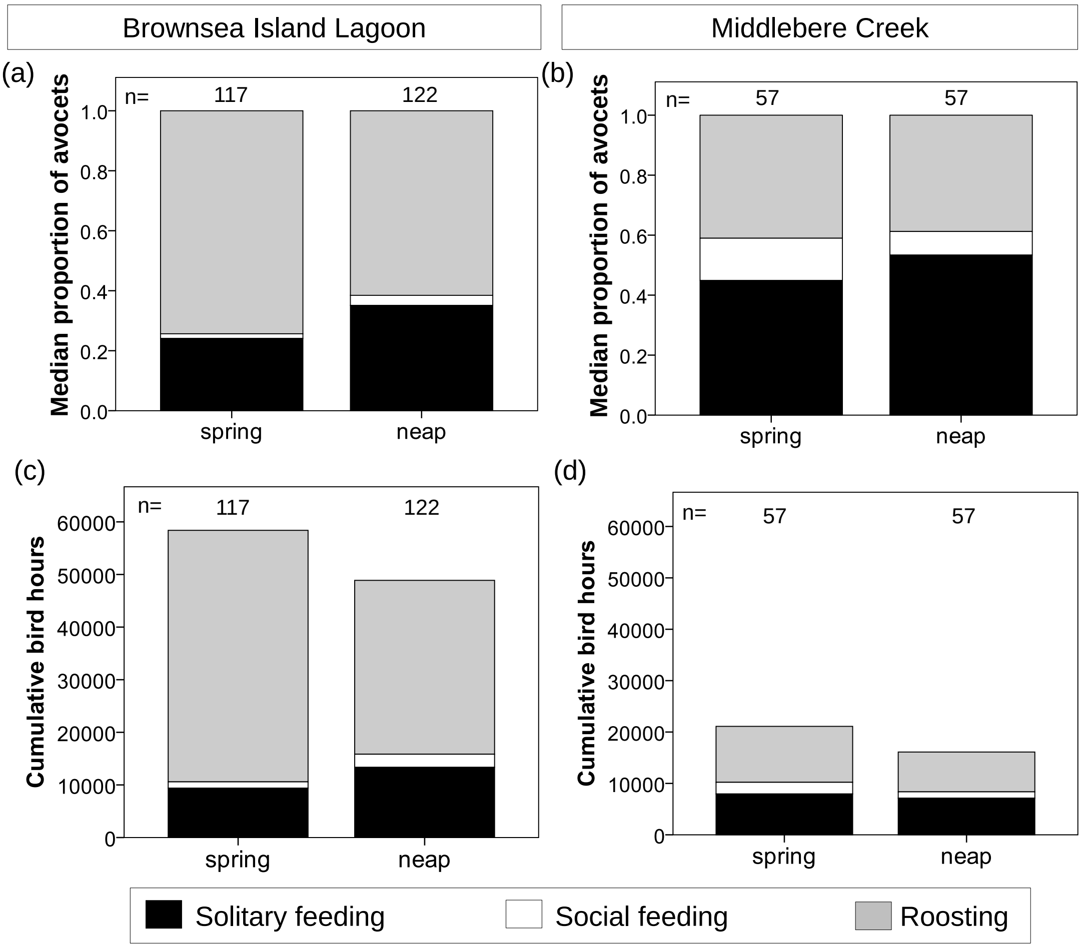


Figure 5.4 The median proportion of avocets feeding (solitary and socially) and roosting during spring or neap tides, for Brownsea (a) and Middlebere (b). The cumulative number of feeding and roosting bird hours during spring or neap tides at Brownsea (c) and Middlebere (d) over two years of observation. Numbers above columns represent the observation hours.

Comparing proportion of avocets feeding throughout the different phases of the tidal cycle (high water, second high water, ebb tide, low tide and flow tide), showed a statistically significant difference between phases at Middlebere (H=22.365 (df 4), p<0.001; Figure 5.5b), but no significant difference at Brownsea (H=4.99 (df 4), p=0.287; Figure 5.5a). At Middlebere, very few avocets fed at high tide and most avocets fed at low tide. During second high water (which is a result of the double high tide phenomenon in Poole Harbour (Humphreys & May 2005)), the proportion of avocets foraging was 0.50. During ebbing and flowing tides the proportion of avocets feeding was 0.76 and 0.72, respectively.

As there were an uneven number of observations for each phase of the tidal cycle, I have presented average, rather than cumulative, bird hours in Figure 5.5c and 5.5d. Figure 5.5c indicates that at Brownsea, the total number of birds present was higher at high tide and lower at low tide, but relatively constant throughout the other tidal phases. The data for Middlebere also indicated a lower number of birds during low tide.

At Middlebere, social foraging occurred only during ebb, flow and low tides, and was most common at low tide. Conversely, at Brownsea, the highest proportion and absolute number of avocets social foraging occurred at high tide.

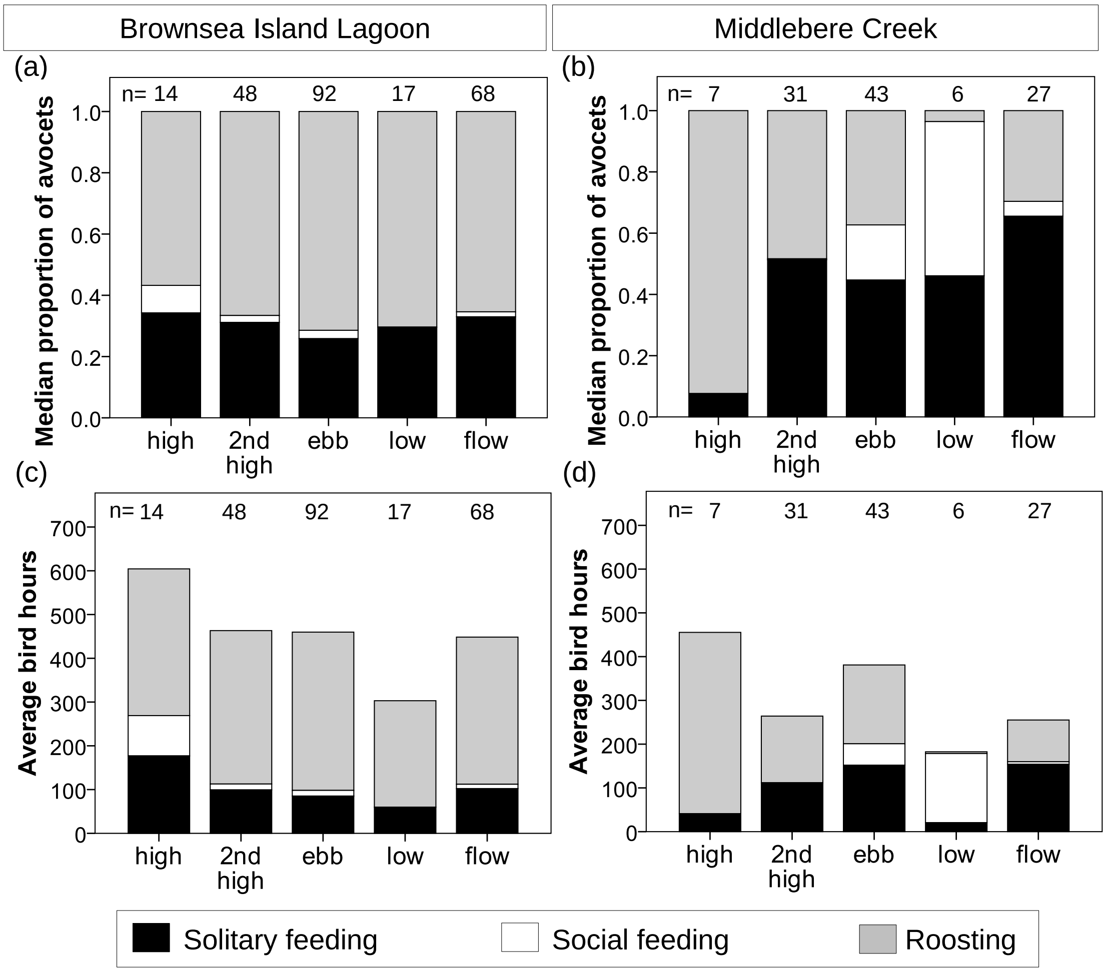


Figure 5.5 The median proportion of avocets feeding (solitary and socially) and roosting during the different phases of the tidal cycle (high, 2nd high, ebb, flow and low) for Brownsea (a) and Middlebere (b) over 2 years of observation. The average number of birds recorded in each observation hour, for each tidal phase, at Brownsea (c) and Middlebere (d). Numbers above columns represent the observation hours. 2nd high refers to the second high water in Poole Harbour, which lags behind the first high water by 3–4 h, and is less high.

The proportion of avocets feeding in relation to each hour in the tidal cycle is shown in Figure 5.6a and 5.6b. Again, there was no significant difference in the proportion of birds feeding by hour at Brownsea (H=6.186 (df 11), p=0.861) but there was a significant difference at Middlebere (H=28.126 (df 11), p=0.003). At Middlebere, the proportion of birds feeding increased steadily, peaking roughly 8 hrs after high tide; however, this pattern was driven by a decrease in the absolute number of birds roosting at low tide, rather than an increase in the number of birds feeding. The absolute numbers of birds solitary feeding was roughly constant throughout the tidal cycle at both sites.

At Brownsea, the proportion of avocets feeding socially peaked around high tide. However, at Middlebere there was no social foraging at high tide, but social foraging occurred during ebb, low and flow tides.

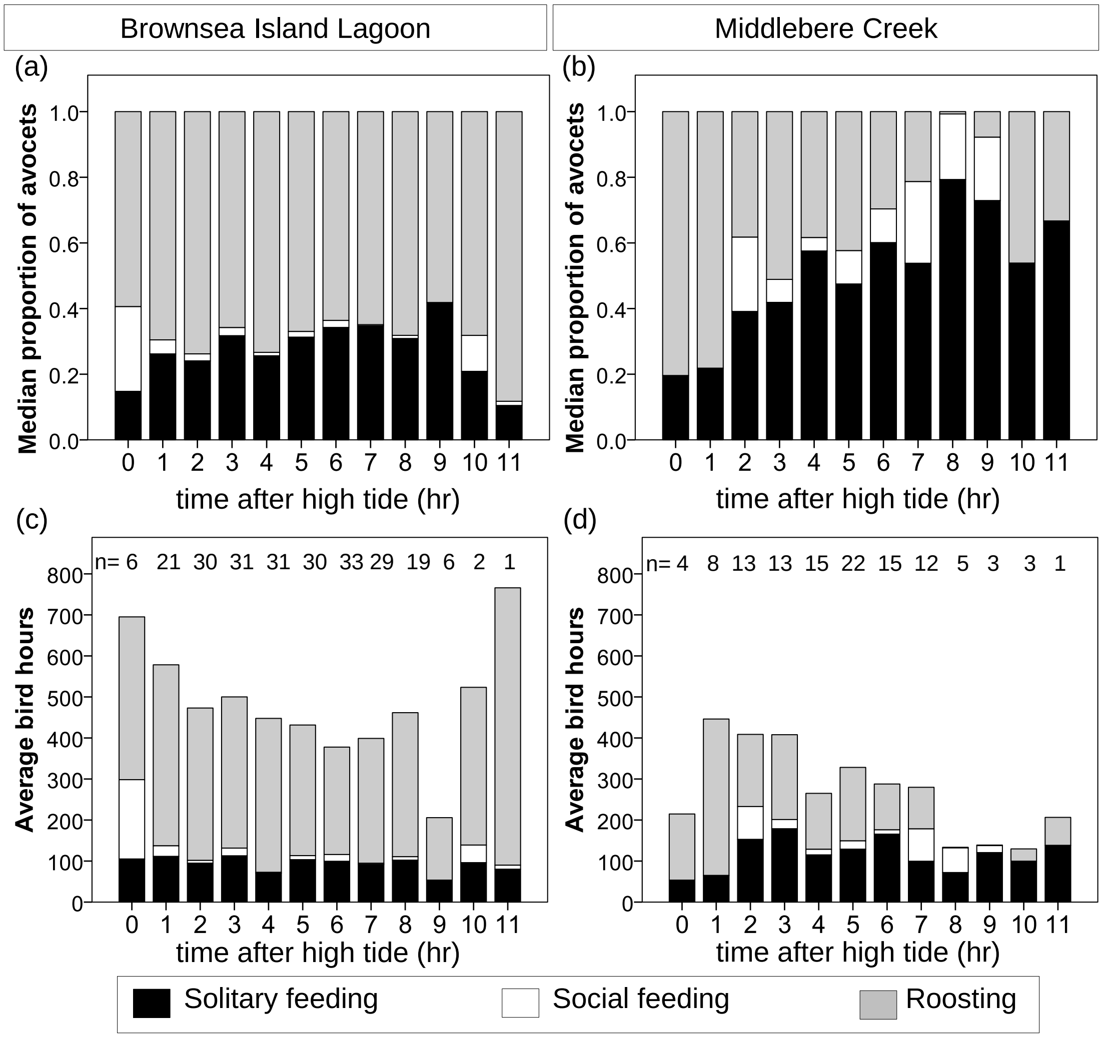


Figure 5.6 The median proportion of avocets feeding (solitary and socially) and roosting each hour after high tide for Brownsea (a) and Middlebere (b) over two years of observation. The average number of birds feeding and roosting per observation hour, for every hour after high tide at Brownsea (c) and Middlebere (d). Numbers above columns represent the observation hours.

(iv) by time of day

Figure 5.7 shows the proportion of feeding avocets each hour after sunrise, which showed a significant difference between hours for Brownsea (H=23.157 (df 13), p=0.040) and for Middlebere (H=32.526 (df 10), p<0.0001). At Brownsea, two daily peaks of feeding activity occurred, just after sunrise and approximately 6 hours after sunrise. The pattern at Middlebere was less clear, as the diurnal variation in foraging behaviour was partly obscured by the influence of the tide at this site, but generally, the proportion of bird feeding was lowest in the morning and steadily increased, peaking at 8 hours after sunrise.

At Brownsea, there was a peak in the proportion of socially foraging birds just after sunrise. At Middlebere, social foraging occurred more commonly in the late afternoon and evening.

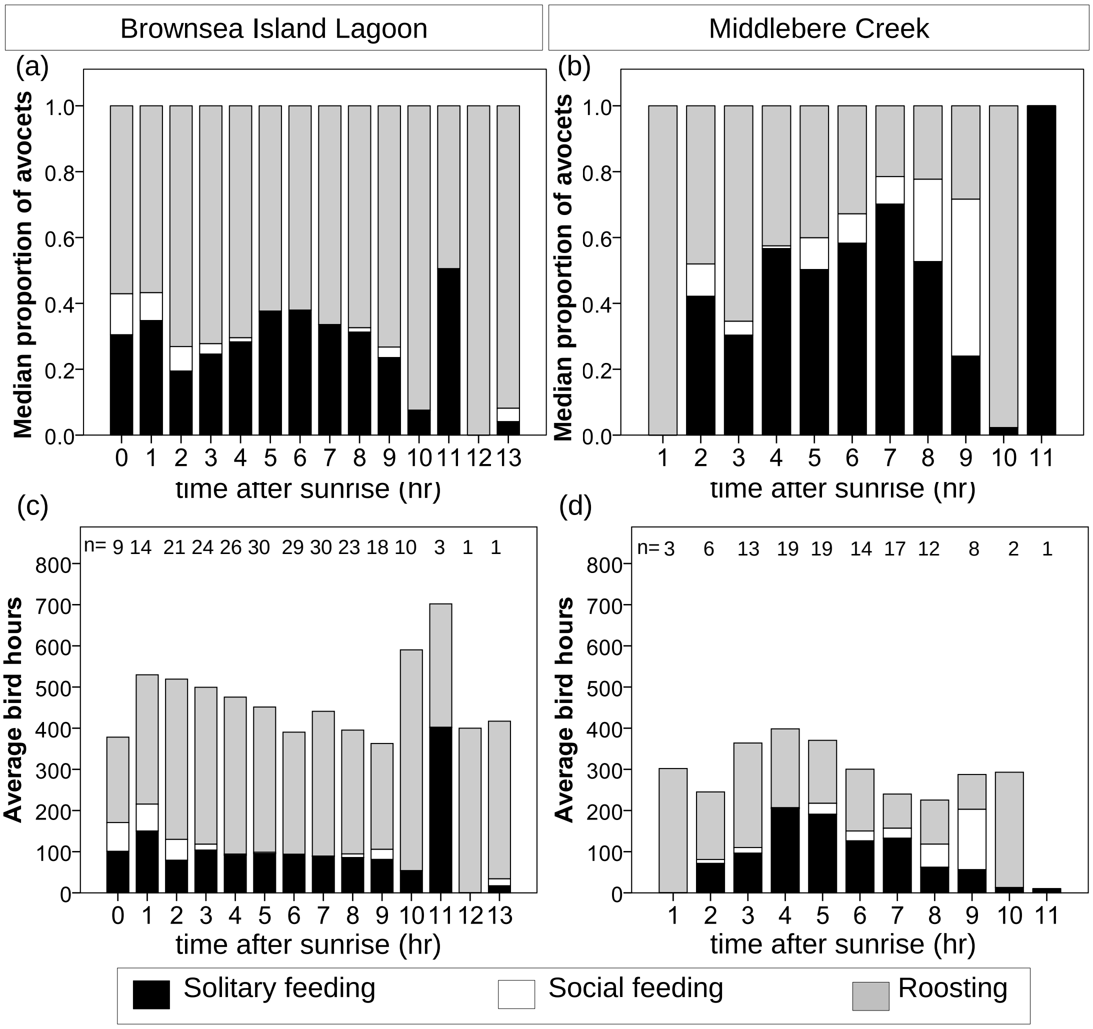


Figure 5.7 The median proportion of avocets feeding (solitary and socially) and roosting each hour after sunrise, at Brownsea (a) and Middlebere (b), over two years of observation. The average number of birds feeding and roosting per observation hour, for each hour after sunrise at Brownsea (c) and Middlebere (d). Numbers above columns represent the observation hours.

(v) Relative importance of factors in explaining bird behaviour

I used the lme4 package (Bates et al. 2013) in R (R Core Development Team 2012) to produce a mixed-effects model to examine the relative effects of the environmental factors on the proportion of birds feeding (Table 5.2). As fixed effects, I used site, year, month, tidal state, tidal phase, hours after sunrise and hours after high tide, plus interaction terms of site:month, site:tidal phase, site:hours after high tide and site:hours after sunrise, to account for the factors behaving differently at each site. I specified observation day as a random effect, to account for potential differences due to observing the population on a different day, and used a random intercept model. To determine if fixed effects were significant, I compared the likelihood value of the model with or without the term (Bolker et al. 2009).

Table 5.2 Output of mixed-effects model of factors affecting proportion of avocets feeding, with random intercept.

Fixed effects	**Effect size**	**Standard error**	**Z value**	**P value**
Site	8.02	1.419	5.65	<0.0001*
Month	0.40	0.126	3.19	0.0014*
Year	-0.04	0.314	-0.13	0.8949
Tidal state (spring/neap)	0.67	0.410	1.66	0.0973
Tidal phase	-0.13	0.006	-20.01	<0.0001*
Hours after high tide	0.08	0.004	20.86	<0.0001*
Hours after sunrise	-0.13	0.003	-39.11	<0.0001*
Site:month	-1.43	0.231	-6.22	<0.0001*
Site:tidal state	-2.08	0.633	-3.29	0.0009*
Site:tidal phase	0.40	0.016	25.28	<0.0001*
Site:Hours after high tide	0.02	0.009	2.29	0.0218*
Site:Hours after sunrise	0.21	0.010	20.66	<0.0001*

This model showed the proportion feeding was generally 8.02% higher at Middlebere. The fixed effects of year (p=0.8949) and tidal state (p=0.0973) were not significant; however, month was significant (p=0.0014) the interaction terms for site:month (p<0.0001) and site:tidal state (p=0.0009) were significant, indicating month and tidal state affect the proportion of birds feeding differently at each site. There was a significant effect of hours after high tide on proportion of birds feeding (p<0.0001); however, the effect size was so small it is unlikely to be biologically relevant, and the non-significant interaction term indicates the effect of this factor was similar at both sites. Hours after sunrise had a small but significant effect on proportion of birds feeding (p<0.0001). And finally, the interaction term for site:tidal phase was significant (p<0.0001).

The numbers of birds socially foraging at each site was strongly related to the total number of birds present (Figure 5.8). However, at Brownsea there was a threshold of roughly 500 birds, below which social foraging was not observed. Conversely, at Middlebere, social foraging occurred even at low numbers.

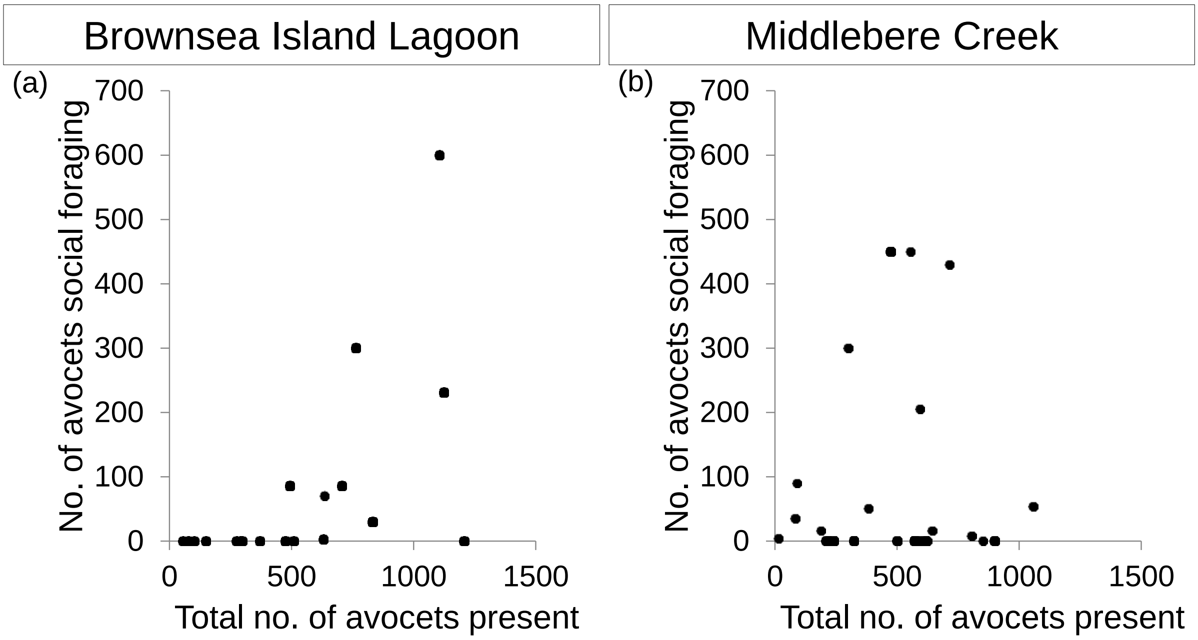


Figure 5.8 The relationship between total number of avocets present and number of avocets social foraging at Brownsea (a) and Middlebere (b). Counts represent the maximum numbers recorded per observation day.

5.4.2 Differences in feeding rates

Video data on feeding rates were collected from solitary foraging birds and analysed for 501 foraging events, 363 at Brownsea and 139 at Middlebere. The spatial distribution of foraging events is presented in Figure 5.9.

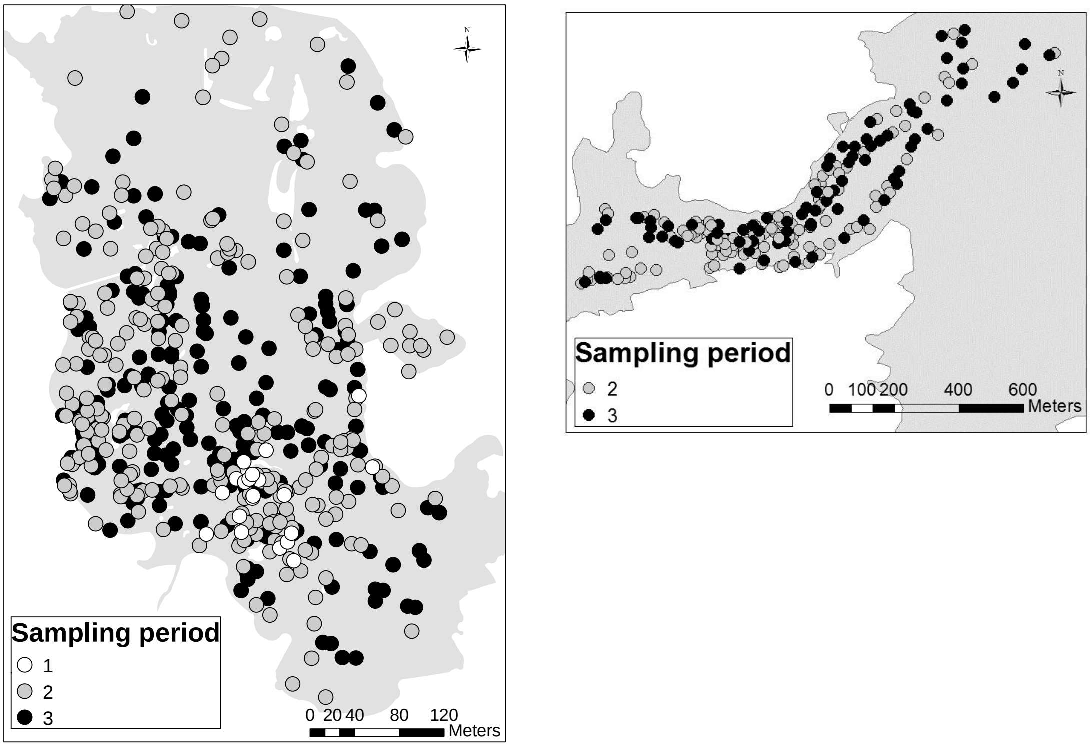


Figure 5.9 Spatial distribution of foraging events recorded at (a) Brownsea Island Lagoon, (b) Middlebere Creek, during period 1 (September; white circles), period 2 (October–December; grey circles) and period 3 (January–March; black circles). No data were collected for Middlebere during Period 1, as birds were not present at the site for this period.

(i) by site

Comparing all observations at each study site, median sweep rates were significantly higher at Middlebere compared with Brownsea (Mann-Whitney U=11014.500 (df 272,126), p<0.001; Figure 5.10a). A similar pattern was observed for swallow rate (Mann-Whitney U=8785.000 (df 272,126), Z=-7.824, p<0.0001).

For comparison, sweep and swallow rates for socially foraging birds are also included in Figure 5.10. Sweep rates for socially foraging birds were higher than for solitary feeding birds, and swallow rates were lower, at both sites. However, there was no clear difference between sites. Swallow rates were lower in social foraging birds compared with solitary foraging birds at both sites.

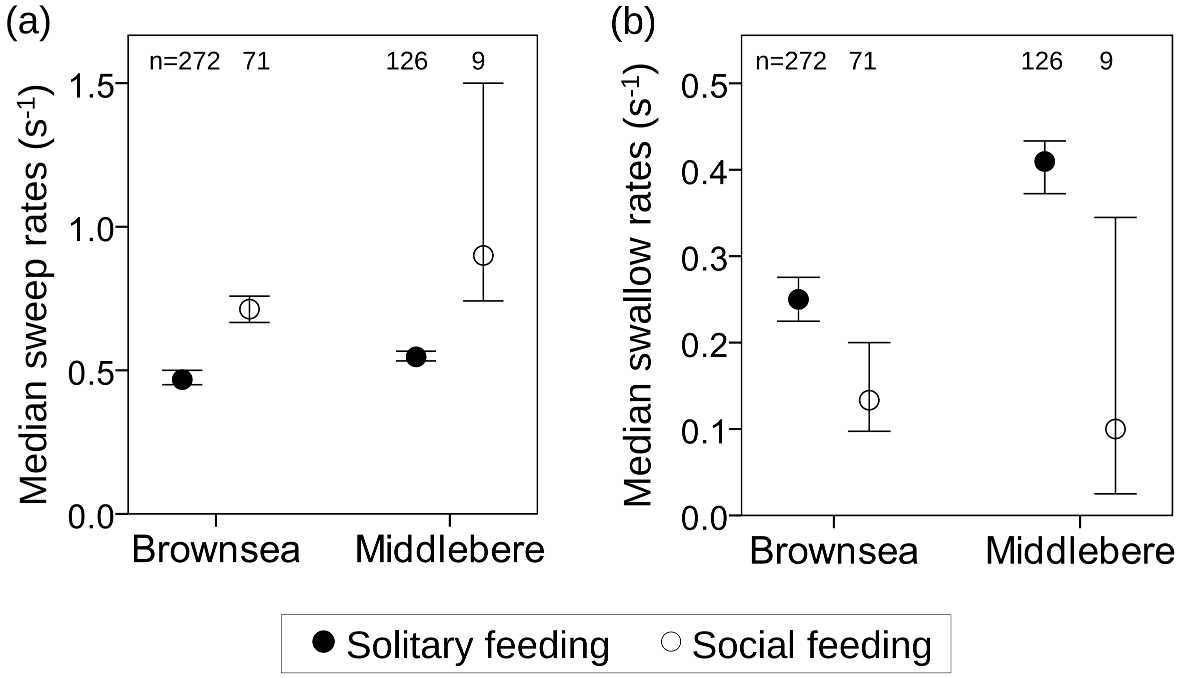


Figure 5.10 Median sweep rates (a) and swallow rates (b) observed at Brownsea Island Lagoon and Middlebere Creek for solitary (solid circles) and socially (open circles) foraging avocets. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category.

(ii) by month

Sweep rate differed by month at Brownsea (H=75.404 (df 6), $p<0.001$; Figure 5.11a), as did swallow rates (Kruskal-Wallis H=132.103 (df 6), $p<0.0001$; Figure 5.11c). However, at Middlebere, there was a difference in swallow rate by month (Kruskal-Wallis H=34.893 (df 5), $p<0.0001$; Figure 5.11d), but not sweep rate (H=4.910 (df 5), $p=0.427$; Figure 5.11b). Sweep rates generally increased at Brownsea throughout the winter, plateauing in January.

There was no clear seasonal pattern in sweep or swallow rates for social foraging (data not shown).

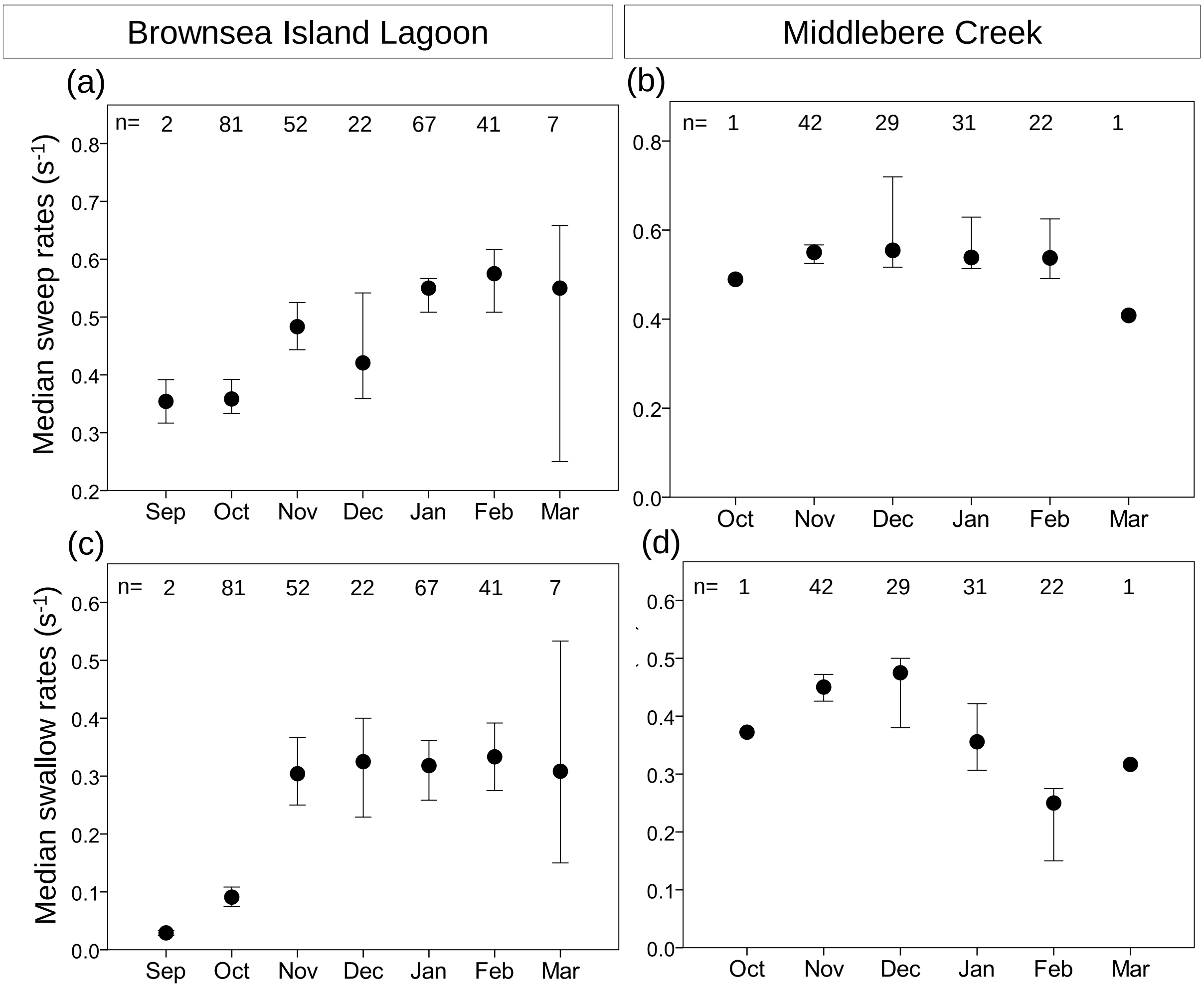


Figure 5.11 Median sweep rates (a,b) and swallow rates (c,d) observed each month, at Brownsea Island Lagoon and Middlebere Creek. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events analysed each month.

(iii) by tidal factors

Comparing sweep rates during different tidal stages, showed sweep rates were slightly higher during neap tides, both at Brownsea (U=7855.5 (df 130,142), Z=-2.121, p=0.034; Figure 5.12a) and Middlebere (U=1515.5 (df 69,57), Z=-2.211, p=0.027; Figure 5.12b). However, the difference was so small it is unlikely to be biologically significant. Swallowing rates were similar during springs and neaps at Brownsea, but there was a difference at Middlebere (Mann-Whitney U=1515.500 (df 69,57), Z=-2.211, p=0.027; Figure 5.12d), with median swallow rates being higher during neap tides.

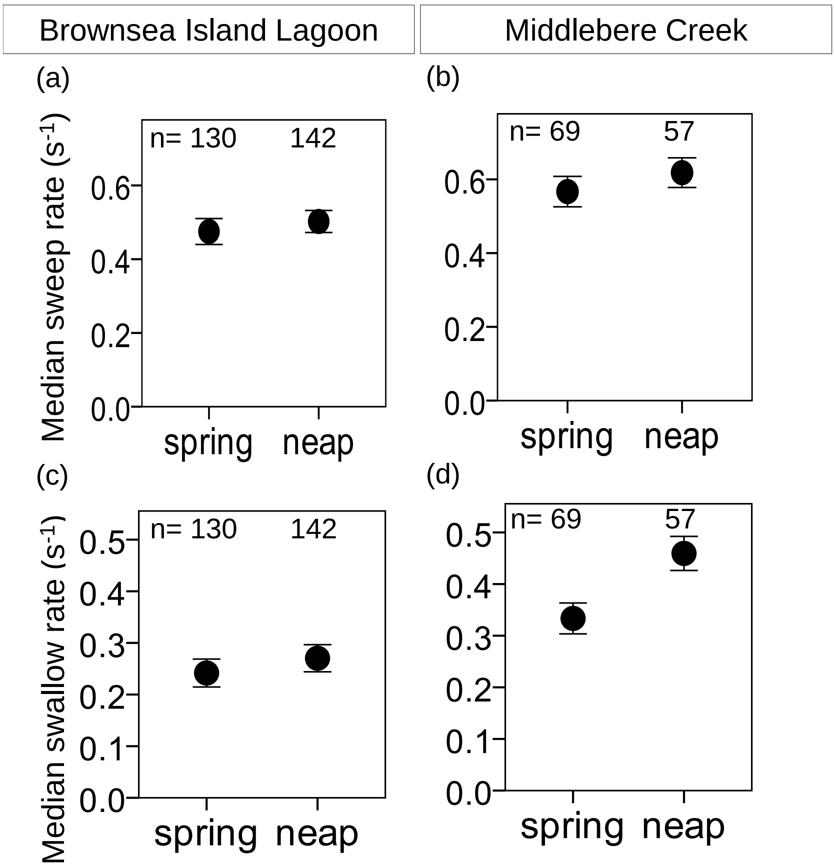


Figure 5.12 Median sweep rates (a,b) and swallow rates (c,d) observed during spring and neap tides, at Brownsea Island Lagoon and Middlebere Creek. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category.

There was no significant difference in sweeping rates according to different tidal phases, either at Brownsea, the non-tidal lagoon, or at Middlebere, the tidal mudflat (Figure 5.13). However, there was a detectable difference in swallow rates at Brownsea (H=18.291 (df 6), p=0.001; Figure 5.13c), with median swallow rates being lowest during high tide and low tide. There was a suggestion of lower swallow rates during high tide and low, compared with ebb and flow tides, however, as there were only a small number of observations recorded at high and low tide, these differences were not statistically significant.

There was no detectable difference in sweep or swallow rates for socially foraging avocets according to tidal stage, phase or hours after high tide (data not shown).

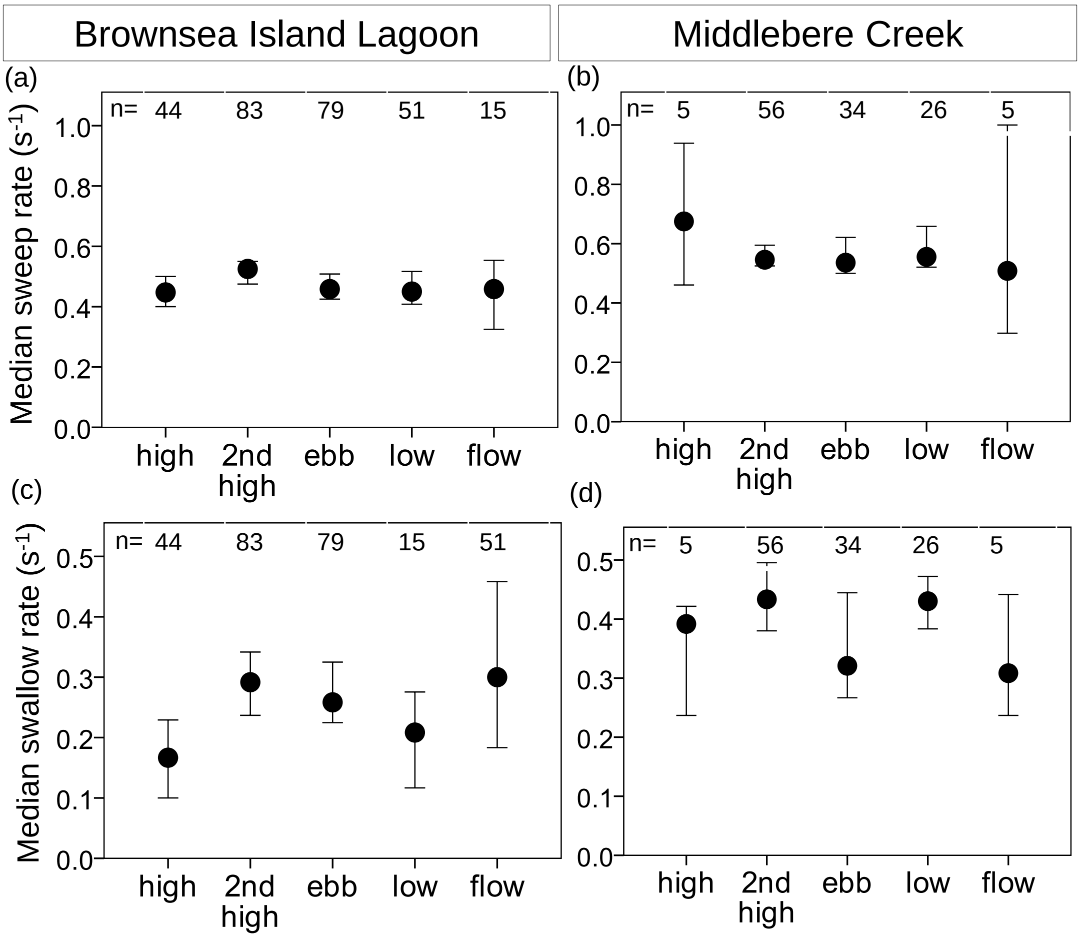


Figure 5.13 Median sweep rates (a,b) and swallow rates (c,d) observed during each phase of the tidal cycle (high, 2nd high, ebb, low and flow), at Brownsea Island Lagoon and Middlebere Creek. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category. 2nd high refers to the second high water in Poole Harbour, which lags behind the first high water by 3–4 h, and is less high.

(iv) by depth

The depth at which the avocets foraged had a significant effect on sweep rates at Brownsea (Kruskal-Wallis H=32.457 (df 4), p<0.0001; Figure 5.14a) and Middlebere (Kruskal-Wallis H=21.557 (df 4), p<0.0001; Figure 5.14b) and swallow rates at Brownsea (Kruskal-Wallis H=24.915 (df 4), p<0.0001; Figure 5.14c) and Middlebere (Kruskal-Wallis H=12.040 (df 4), p=0.017; Figure 5.14d).

Sweep rates for socially foraging birds followed a similar trend to solitary foraging birds, in relation to depth (Kruskal-Wallis H=40.966 (df 3), p<0.0001; Figure 5.14a); however, the effect on swallow rates was less clear (Kruskal-Wallis H=8.301 (df 3), p=0.04; Figure 5.14c).

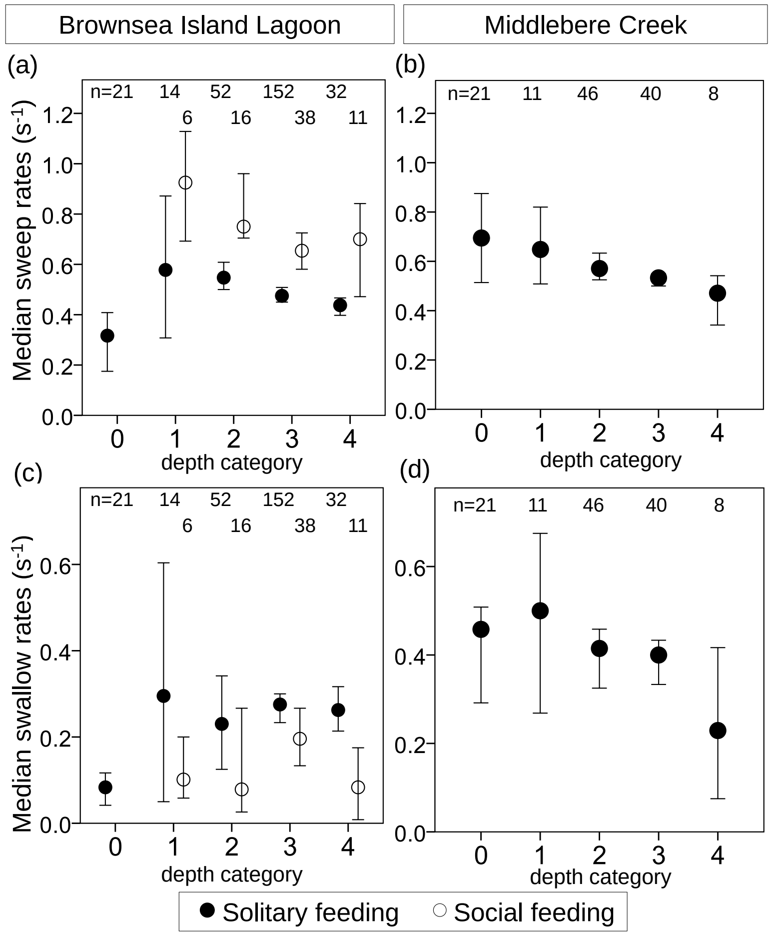


Figure 5.14 Median sweep rates (a,b) and swallow rates (c,d) observed for avocets foraging at different water depths, at Brownsea Island Lagoon and Middlebere Creek. Depth categories were defined as follows: 0=exposed mudflat, 1=water below avocet ankle, 2=water below avocet knee, 3=water below avocet belly, 4=avocet swimming. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category.

(v) by number of foraging conspecifics or heterospecifics

There was no clear relationship between sweep rates or swallow rates and the number of avocets (conspecifics; Figure 5.15) foraging within 5 m of the focal individual. Similar results were observed for the number of heterospecifics within 5 m of the focal individual (data not shown). However, when sweep and swallow rates were examined in relation to the total number of avocets foraging on that day, there was a significant effect at Brownsea but not at Middlebere (Figure 5.16).

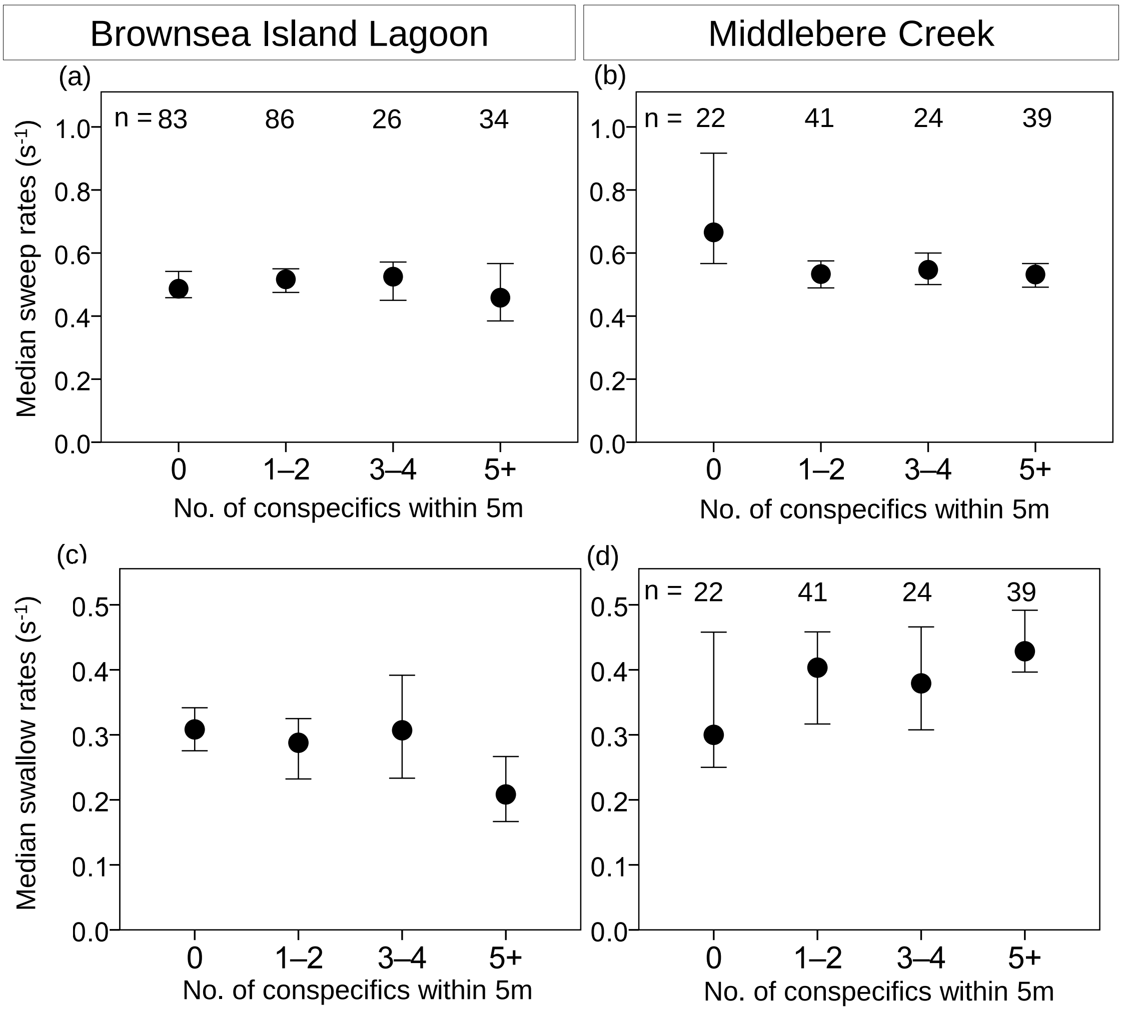


Figure 5.15 Median sweep rates (a,b) and swallow rates (c,d) for avocets foraging with different numbers of conspecifics foraging within 5 m of the focal individual, at Brownsea Island Lagoon and Middlebere Creek. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category.

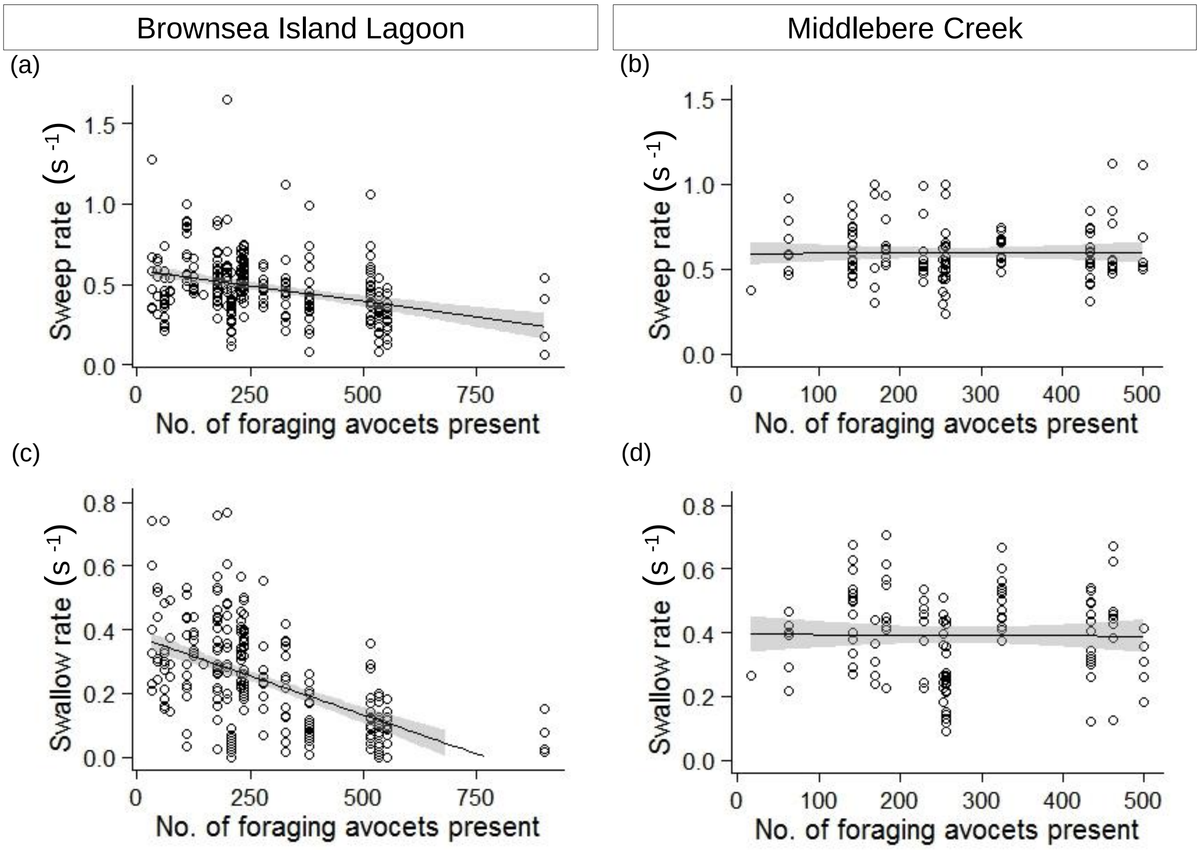


Figure 5.16 The effect of number of foraging avocets present on the day of observation on sweep rates (a,b) and swallow rates (c,d) at Brownsea Island Lagoon and Middlebere Creek. Counts represent the maximum number of avocets foraging on the day of observation. Grey shading represents 95% confidence intervals.

At Brownsea, there was a significant negative correlation between sweep rates and number of foraging avocets present (r^2=0.123, df 266, p<0.0001), and between swallow rates and number of avocets present (r^2=0.287 df 266, p<0.0001). However, at Middlebere there was no significant correlation between sweep rates and number of foraging avocets (r^2=0.00006, df 122, p=0.932) or swallow rates and number of foraging avocets (r^2=0.0001, df 122, p=0.900).

(vi) by other factors

Temperature appeared to have an effect at Brownsea on sweep rates (Kruskal-Wallis H=27.945 (df 3), p<0.001; Figure 5.17a) and swallow rates (Kruskal-Wallis H=39.460 (df 3), p<0.001; Figure 5.17c), as both sweep and swallow rates were significantly lower when temperature was >15ºC. A comparable pattern was not observed at Middlebere, as the avocets did not forage at this site during the warmer months of the year.

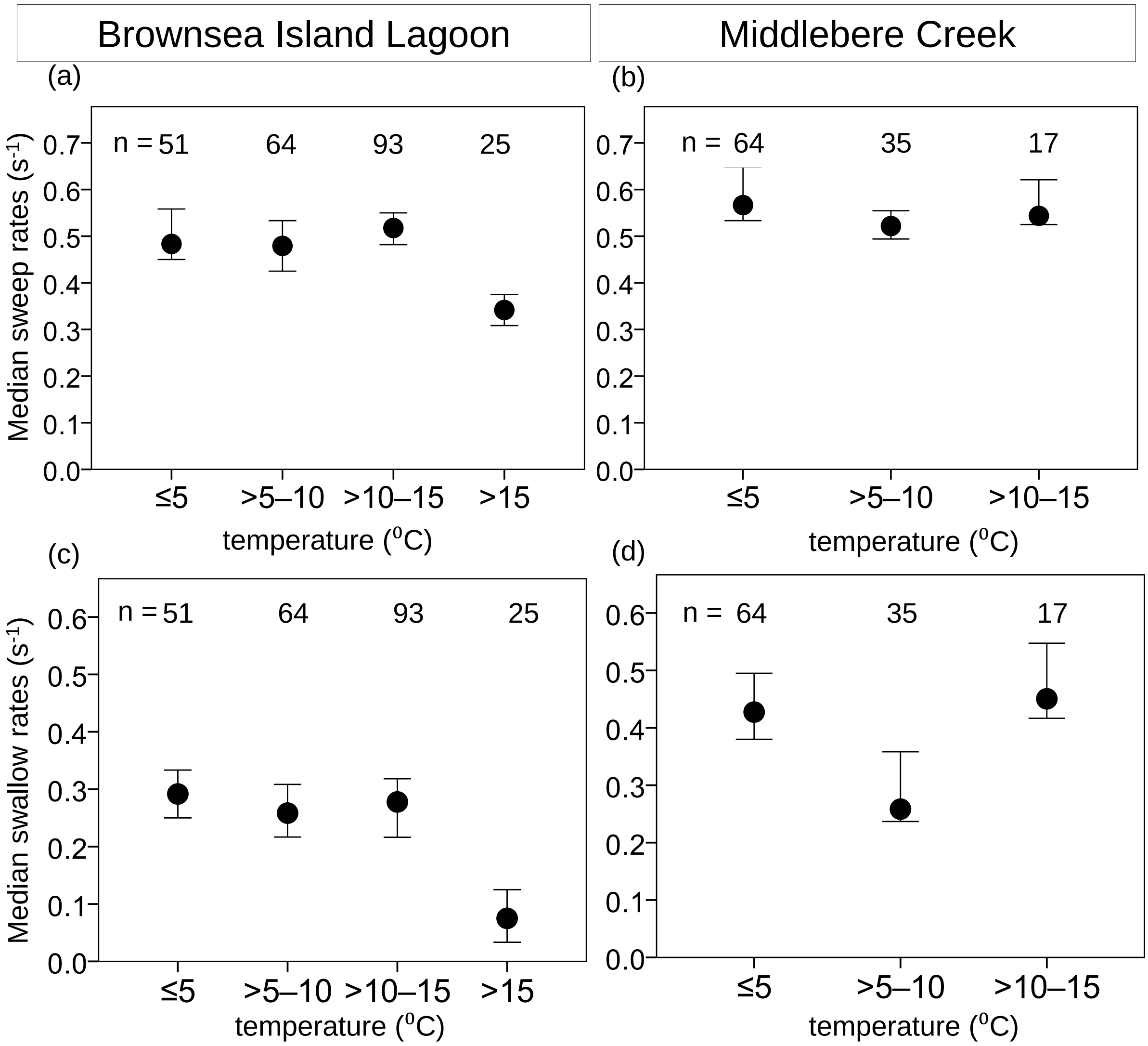


Figure 5.17 Median sweep rates (a,b) and swallow rates (c,d) for avocets foraging at different air temperatures, at Brownsea Island Lagoon and Middlebere Creek. Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category.

There was no effect of wind on sweep rates at Brownsea (Kruskal-Wallis H=5.970 (df 4), p=0.201; Figure 5.18a) or Middlebere (Kruskal-Wallis H=6.068 (df 4), p=0.194; Figure 5.18b). However, there was a significant effect of wind on swallow rates at Middlebere (Kruskal-Wallis H=10.471 (df 4), p=0.033; Figure 5.18d), with lower swallow rates observed at higher wind speeds.

There was no clear relationship between sweep or swallow rates and precipitation or cloud cover for solitary or socially foraging avocets (data not shown).

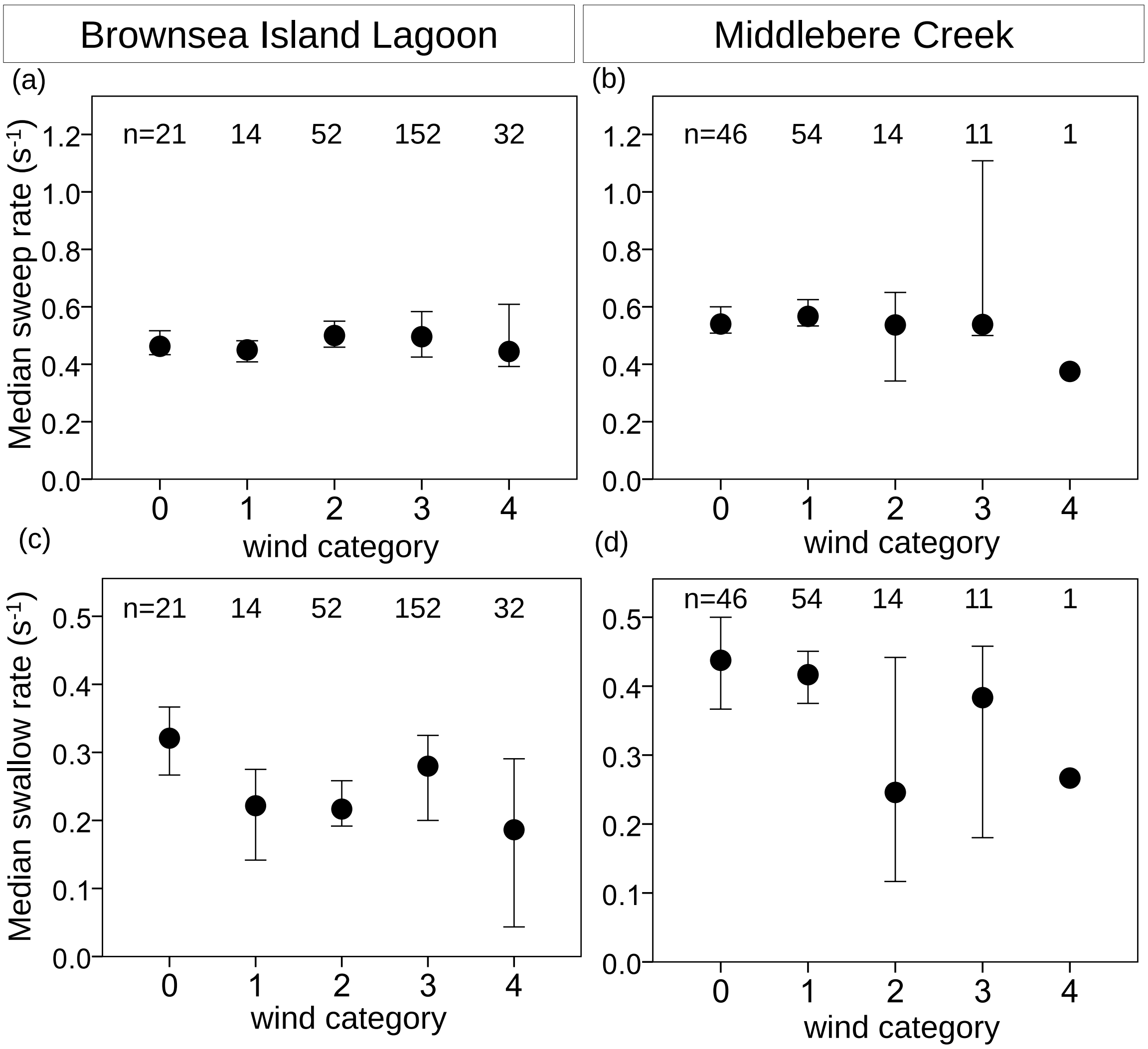


Figure 5.18 Median sweep rates (a,b) and swallow rates (c,d) for avocets foraging at different wind intensities, at Brownsea Island Lagoon and Middlebere Creek. Wind categories were defined as follows: 0=no wind, 1=light breeze (≈1 or 2 on Beaufort scale), 2=moderate breeze (≈3 or 4 on Beaufort scale), 3=strong breeze (≈5 or 6 on Beaufort scale), 4=very strong wind (≈7+ on Beaufort scale). Error bars represent 95% confidence intervals. Numbers above columns represent the number of foraging events in each category.

5.4.3 Explaining the differences in sweep and swallow rate

I tested the hypothesis of whether observed differences in sweep and swallow rate could be explained using a selection of variables related to the sediment. The explanatory variables tested were: abundance of *Corophium spp;* Worms (small, medium and large), small bivalves and Hydrobiidae, temperature, % fine sediment and % coarse sediment, depth, number of conspecifics and number of heterospecifics.

Table 5.3 shows the parameter estimates for the generalised linear model (GLM) to show the effect of environmental covariates on sweep rate. The abundance of medium-sized worms had a positive effect on sweep rate (p<0.0001), and depth (p<0.0001), Hydrobiidae abundance (<0.0001), large-worm abundance (p=0.02) and temperature (p<0.0001) had a significant negative effect.

Table 5.3 Generalised linear model (GLM) showing the effect of environmental covariates on sweep rates. Variables exhibiting significant effects are in bold.

Fixed effects	**Full model-averaged coefficients**	**Standard error**	**Z value**	**P value**
Intercept	3.942	0.262	14.977	<0.0001*
$\log_{10}$ (Fine sediment)	**0.510**	**0.110**	**4.605**	**<0.0001***
$\log_{10}$ (Corophium)	**0.103**	**0.016**	**6.533**	**<0.0001***
$\log_{10}$ (Coarse sediment)	**0.102**	**0.018**	**5.511**	**<0.0001***
$\log_{10}$ (Large worms)	0.027	0.019	1.378	0.168
$\log_{10}$ (Small worms)	0.008	0.020	0.388	0.698
$\log_{10}$ (Medium worms)	0.003	0.036	0.090	0.929
No. heterospecifics within 5 m	-0.001	0.000	2.789	0.005*
temperature	-0.002	0.002	1.288	0.198
No. conspecifics within 5 m	-0.003	0.002	1.626	0.104
$\log_{10}$ (Bivalves)	-0.031	0.020	1.582	0.114
depth	**-0.106**	**0.007**	**14.383**	**<0.0001***
$\log_{10}$ (Hydrobidae)	**-0.217**	**0.026**	**8.430**	**<0.0001***

Table 5.4 shows the parameter estimates for the GLM to show the effect of environmental covariates on swallow rate. The abundance of worms of all size classes had a positive effect on swallow rates ($p<0.0001$), whereas the abundance of Hydrobiidae ($p<0.0001$) and the % of coarse sediment ($p<0.0001$) had a negative effect on swallow rates.

Table 5.4 Generalised linear model (GLM) showing the effect of environmental covariates on swallow rates. Variables exhibiting significant effects are in bold.

Fixed effects	**Full model-averaged coefficients**	**Standard error**	**Z value**	**P value**
Intercept	3.232	0.313	10.313	<0.0001*
log$_{10}$ (Medium worms)	**0.365**	**0.049**	**7.355**	**<0.0001***
log$_{10}$ (Small worms)	**0.201**	**0.029**	**7.008**	**<0.0001***
log$_{10}$ (Fine sediment)	0.159	0.154	1.029	0.304
log$_{10}$ (Large worms)	**0.114**	**0.028**	**4.077**	**<0.0001***
log$_{10}$ (Bivalves)	0.045	0.027	1.638	0.101
No. of conspecifics within 5 m	0.005	0.002	2.393	0.017*
No. of heterospecifics within 5 m	-0.002	0.001	2.792	0.005*
temperature	-0.018	0.002	8.108	<0.0001*
depth	-0.042	0.009	4.407	<0.0001*
log$_{10}$ (Corophium)	-0.085	0.021	4.103	<0.0001*
log$_{10}$ (Coarse sediment)	-0.088	0.023	3.810	<0.0001*
log$_{10}$ (Hydrobidae)	**-0.324**	**0.043**	**7.604**	**<0.0001***

5.5 Discussion

In this chapter, I examined how avocet foraging behaviour differed between a tidal and non-tidal site, and in relation to local environment conditions. The proportion of time avocets spent foraging varied in response to seasonal and tidal effects, and the precise relationship was different between the tidal and non-tidal study sites. In addition, avocet feeding rates varied in accordance with seasonal and tidal factors, and local invertebrate abundance. I examined sweep rates and swallow rates separately, which has not always been done in previous studies of avocet feeding ecology. Sweep rates are an indication of the speed at which an avocet is searching for food, whereas swallow rates are a measure of the success of prey capture. Therefore, both are essential for understanding energy intake rates. The fact that sweep rates were sensitive to the sediment composition and water depth, but swallow rates were not could indicate the avocets modify their search rate under different conditions in order to maintain relatively constant intake rates. The way in which the environment impacts the ability of birds to feed at or close to their maximum intake rate affects how changes to the environment will impact the overall status of the birds.

5.5.1 Comparison of habitat use and behaviour at Brownsea and Middlebere

The use of non-tidal habitat by shorebirds can be considered an indication of a lack of adequate resources in intertidal habitat (Smart & Gill 2003). This is not the case for the avocets of Poole Harbour. In both study years, when the avocets arrived in Poole Harbour at the start of the winter, they fed exclusively at Brownsea Island Lagoon for roughly 60 days, even though adequate resources were present in the intertidal mudflats. The number of birds at Brownsea Island Lagoon steadily increased from the end of August until the end of October (see Figure 6.5 in Chapter 6), and when the numbers reached roughly 1100, some of the birds began to use Middlebere as a foraging ground. Based on the numbers of birds foraging at Brownsea during September and October, Brownsea Lagoon was able to provide approximately 7200 “avocet days” before prey depletion forces some of the birds to seek alternative prey resources at Middlebere. The maximum observed density of avocet on the lagoon, prior to the efflux to Middlebere was 62 birds ha^{-1}, which is lower than the threshold for interference observed in redshank (Stillman 2000). No evidence for direct interference between individuals was observed (i.e. sweep and swallow rates were unaffected by other avocets or birds of other species feeding in close proximity. However, there was a significant relationship between swallowing rates and the total number of birds present at the site foraging, which could indicate indirect interference through depletion of prey resources; and this was observed at Brownsea but not at Middlebere (Figure 5.16).

The proportion of time spent foraging in this study is compared with other studies of avocet foraging in Table 5.5. Studies on American avocets are included, but no studies for red-necked avocets (*R. novaehollandiae*) or Andean avocet (*R. andina*) were found. The average proportion of birds foraging at Brownsea was 30% (solitary foraging) and 2.5% (social foraging). The average proportion of birds foraging at Middlebere was 49% (solitary) and 11% (social). The higher average proportion of birds feeding at Middlebere was related to the relatively large proportion of time birds spend roosting at Brownsea (birds foraging at Middlebere left the site to roost at Brownsea), whereas in terms of absolute numbers, similar numbers of hours were spent foraging at Brownsea and Middlebere (Figure 5.2). The higher average proportion of birds socially foraging at Middlebere was partly due to the fact that birds only foraged socially at Brownsea for a restricted time period, from September to December.

The proportion of time spent foraging at Middlebere was similar to that observed for American avocets on intertidal mudflats in Humboldt Bay, California (Evans & Harris 1994). Here the birds also fed on a combination of benthic and nektonic prey. Overall, the proportion of time foraging appears to be strongly related to the prey targeted. In studies where the main prey was fish, birds foraged for roughly 20% of the time (Hötker 1999b; Ntiamoa-Baidu & Piersma 1998). However, in studies where the diet comprised small prey items, such as Daphnia or Chrionomid larvae, foraging time was much higher (>60%) (Hötker 1999b). The time spent foraging at Brownsea was intermediate between studies where fish is the main prey source, and those in which benthic invertebrates are the main prey source. The exceptionally high proportion of birds foraging on the Tagus Estuary is thought to be due to the fact that the birds leave the mudflat to roost elsewhere (Moreira 1995a; Lourenço et al. 2008). This is similar to the behaviour at Middlebere, although it appears to occur to a greater extent on the Tagus.

Table 5.5 Proportion of time spent feeding in studies of non-breeding pied avocet (*Recurvirostra avosetta*) and American avocet (*Recurvirostra americana*).

Location & habitat	Species	Prey type	Study months	Proportion of time feeding (%)	Refs
Poole Harbour UK, intertidal mudflat	*R. avosetta*	Benthic invertebrates and nektonic prey	Oct–Feb	49 (solitary)† 11 (social) †	1
Poole Harbour UK, saline lagoon	*R. avosetta*	Benthic invertebrates and nektonic prey	Sep–Mar	30 (solitary)† 2.5 (social) †	1
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	Benthic invertebrates	Aug–Apr	86†	2
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	Benthic invertebrates	Jan–Apr	82 (day) † 94 (night) †	3
Guembeul, Senegal, hypersaline lagoons	*R. avosetta*	Chironomid larvae	Nov–Jan	>60	4
Beltringharder Koog, Northern Germany, non-tidal brackish lake	*R. avosetta*	Common gobies (*Pomatoschistus microps*)	Sep–Oct	20	4
Songor and Keta lagoons, Southeast Ghana	*R. avosetta*	Juvenile tilapiine cichlid fish (mainly *Saratherodon melanotheron*)	Oct–Nov	20	5
Lake Turkana, Kenya	*R. avosetta*	Not specified	Apr–May	55	6
Tamar Estuary, Cornwall UK, intertidal mudflat	*R. avosetta*	Benthic invertebrates and nektonic prey	Oct–Apr	54†	7
Playa Wetlands, Southern Texas, USA	*R. americana*	Not specified	Apr–May	46 (day) 62 (night)	8
South Island, North Carolina, USA, intertidal mudflats	*R. americana*	Benthic invertebrates and nektonic prey	Jan–May	44 (benthic) 14 (nektonic)	9
Humboldt Bay, California, USA, sewage oxidation ponds	*R. americana*	*Daphnia magna*	Oct–May	78†	10
Humboldt Bay, California, USA, intertidal mudflat	*R. americana*	Benthic invertebrates	Oct–May	61†	10

References:[1]This study, [2]Moreira (1995a), [3]Lourenço et al. (2008), [4] Hötker (1999b), [5]Ntiamoa-Baidu & Piersma (1998), [6]Fasola & Canova (1993), [7]Reay (1988); [8]Kostecke & Smith (2003), [9]Boettcher et al. (1994), [10]Evans & Harris (1994); †data represent proportion of birds foraging.

The average sweep rate for solitary foraging avocets was 28.7 min^{-1} at Brownsea and 35.6 min^{-1} at Middlebere. The most likely reason for this difference was the sediment compositional differences between sites, with Middlebere generally containing a higher percentage of fine grain sediment and Brownsea containing coarser sediments. The observed reduction in sweep rates in coarser sediment could be due to increased resistance of movement of the bill through the sediment (Tjallingii 1972), or a tendency to peck (i.e. forage visually) rather than sweep in sandy sediments (Quammen 1982).

In Table 5.6, the average sweep and swallow rates observed in this study are compared with other studies of non-breeding pied and American avocets. Sweep rates of pied avocets observed in studies on the Tagus Estuary varied between 20.5 and 51.5 min^{-1} (Moreira 1995a; Lourenço et al. 2005; Lourenço et al. 2008; Dias et al. 2009; Granadeiro et al. 2006). Observed differences in sweep rate on the Tagus Estuary were due to foraging method and prey type (Moreira 1995a), proximity to channels (Lourenço et al. 2005), and location on upper or lower reaches of the mudflat (Dias et al. 2006). While these studies did not distinguish between solitary and social foraging when examining sweep rates, the study by Granadeiro et al. (2006), focussed on “tide following” birds, and the high sweep rates observed in this study were similar to those observed in Poole Harbour for socially foraging avocets. Swallow rates were higher at Middlebere, compared with Brownsea, which is also likely to be related to sediment properties. Quammen (1982) suggested that sandy sediments similar in diameter to the target prey interfere with prey detection or capture in American avocets. Only one other study (Moreira 1995a) recorded swallowing rates as well as sweeping rates, which makes comparison of expected intake rates between studies problematic. However, other studies have concluded that fine sediments are preferred by avocets (Moreira 1999; Goss-Custard & Verboven 1993), which suggests there is some fundamental benefit to foraging in finer sediments.

Table 5.6 Sweep and swallow rates reported in studies of non-breeding pied avocet (*Recurvirostra avosetta*) and American avocet (*Recurvirostra americana*).

Location, habitat	Species	Sweep rates (min^{-1})	Swallow rates (min^{-1})	Refs
Poole Harbour UK, intertidal mudflat	*R. avosetta*	35.6 (solitary) 62.3 (social)	23.5 (solitary) 9.4 (social)	1
Poole Harbour UK, saline lagoon	*R. avosetta*	28.7 (solitary) 44.1 (social)	14.2 (solitary) 9.9 (social)	1
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	28 (normal feeding strategy) 46 (worm feeding strategy) 13 (*Scrobicularia* feeding strategy) 20.5 (mixed feeding strategy)	25 (normal feeding strategy) 3 (worm feeding strategy) 13 (*Scrobicularia* feeding strategy) 10.25 (mixed feeding strategy)	2
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	29 (diurnal) 30 (nocturnal)	Not recorded	3
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	24.8 (close to channels) 35.3 (far from channels)	Not recorded	4
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	24.1	Not recorded	5
Tagus Estuary, Portugal, intertidal mudflat	*R. avosetta*	42.0 (lower creek) 51.5 (upper creek)	Not recorded	6
Tamar Estuary, Cornwall UK, intertidal mudflat	*R. avosetta*	22–31 (exposed mud) 35–42 (shallow water)	Not recorded	7
Upper Newport Bay, California, USA, intertidal mudflat with sand artificially added to plots	*R. americana*	8.8 (plots with sand) 11.4 (plots without sand)	Not recorded	8

References: [1]This study, [2]Moreira (1995a), [3]Lourenço et al. (2008), [4]Lourenço et al. (2005), [5]Dias et al. (2009), [6]Granadeiro et al. (2006), [7]Reay (1988), [8]Quammen (1982).

5.5.2 Seasonal effects

The proportion of birds feeding each month showed different trends at each site (Figure 5.3). This is likely due to varying availability of food resource. However, seasonal differences in energy requirements due to temperature or the need for pre-migratory loading, may also affect the proportion of birds foraging (Castro et al. 1992; Kersten & Piersma 1987; Zwarts & Wanink 1993; Ricklefs et al. 1996). During the initial period of the winter when the birds feed solely at Brownsea, the proportion of time spent foraging was very low (~4%). This indicated that the birds arrived from their breeding grounds in a well-fed state, and were able to meet their daily energy requirements with minimal effort. It also indicated the availability of an energy-dense food supply, from which they could meet their daily energy requirements in a short space of time. The birds at Middlebere showed the opposite trend – the proportion of birds feeding decreased as the winter progressed (Figure 5.3b). However, this was due to an increase in the numbers roosting at Middlebere, rather than a decrease in the numbers foraging (Figure 5.3d). Earlier in the year, the majority of avocets left Middlebere after feeding, returning to roost at Brownsea. The increased use of Middlebere as a roost site later in the year could signify an attempt to minimise energetic costs of returning to Brownsea to roost. In addition, it may have been due to reduced competition for space with other species of waders and wildfowl at Middlebere in the latter months of the winter.

There were clear seasonal differences in the sweep and swallow rates. The lower sweeping rates observed in September and October at Brownsea (Figure 5.11), could similarly be indicative of lower energetic requirements upon arrival in the harbour, and thus, a less vigorous hunting strategy.

5.5.3 Tidal effects

In general, a greater number of birds were present at Brownsea during spring tides, compared with neap tides (Figure 5.4c). However, as the number of birds present at Middlebere during neap tides was not significantly greater than at Brownsea, this suggests that other parts of the harbour, such as Holes Bay, may be being used by the population during neap tides. The increased proportion of birds feeding at Brownsea during neap tides may be a compensatory effect due to the decreased exposure times of the intertidal mudflats during neap tides (see Appendix 11).

The “tide following” behaviour of avocets is well documented in other studies (Granadeiro et al. 2006; Moreira 1995b). In this study the absolute number of birds feeding during each phase of the tidal cycle did not differ much at Middlebere (Figure 5.5d); however, the behaviour of foraging birds switched from solitary to social during ebbing and low tide in particular. Due to the relatively shallow bathymetric gradient at Middlebere, the creek drains very quickly so there is limited time to feed on the incoming and outgoing tides. This could explain why low tide is relatively more important for the avocets at Poole Harbour, compared with other estuaries (Granadeiro et al. 2006).

The lower number of birds recorded during low tide (Figure 5.5) was likely to be an observation artefact, as the avocets moved downstream at Middlebere at low tide, they were less visible from the hide, which likely resulted in under-recording of the numbers. As I can be much more certain that the numbers recorded at Brownsea were accurate, it is likely that the ‘missing’ birds were present at Middlebere during low tide, foraging on areas of mudflat not visible from the hide. A small proportion of birds could also have been feeding at other minor feeding sites within the harbour, such as Holes Bay and Arne Bay.

There was little variation in sweep and swallow rates during spring and neap tides, except that swallow rates appeared to be higher at Middlebere during neap tides. This may have been due to increased activity and availability of invertebrate prey on the upper mudflats during the increased exposure time associated with neap tides. The ragworm (*Hediste diversicolor)*, a key avocet prey species, is known to be more active on mudflats in the later phases of exposure, and thus more likely to be captured (Rosa et al. 2007). There was no evidence to support differences in sweep rates during different phases of the tide (high, low, etc.).

5.5.4 Water depth

The water depth in which the avocets foraged had a clear effect on sweep rates. Generally, sweep rates were lower in deeper water, probably due to frictional forces. However, notably, when the birds foraged on exposed mudflat at Brownsea, they had exceptionally low sweep rates. There are two possible interpretations for this result. Firstly, due to the higher proportion of coarse grain sediment at Brownsea, when the sediment was not covered in water, there were particularly high frictional forces that prevented efficient sweeping. Secondly, the birds were more likely to forage visually on exposed sediment at Brownsea, due to higher densities of medium- and large-sized worms, and this strategy is associated with lower sweeping rates. The effect of depth on swallow rates was less clear, but there appeared to be a decrease in swallowing rates on exposed sediment at Brownsea. Again, this could signify that the birds were targeting less common, larger prey species by visual foraging, or that prey capture efficiency was lower in the absence of water.

5.5.5 Number of conspecifics

There was no clear relationship between the numbers of avocets or birds of other species in close proximity to the focal bird, and sweep or swallow rates. This contrasts the findings of Moreira (1995a) on avocets feeding on the Tagus estuary, in which sweep rates were found to correlate with avocet density around the focal bird. However, on the Tagus Estuary, aggressive encounters between individuals were frequently recorded (Moreira 1995a). Aggressive encounters were never observed at Middlebere, and were only rarely observed at Brownsea. However, the fact that there was a relationship between the total number of birds present on Brownsea Lagoon and feeding rates suggests that there was an indirect interference effect, most likely due to depletion of food resources (Figure 5.16). This effect was not observed at Middlebere, probably due to the larger available area. This suggests that while Brownsea is close to its carrying capacity in terms of the number of avocets it can support, Middlebere is not.

5.5.6 Prey abundance

The abundance of certain invertebrate species was important in explaining sweep and swallow rates. The abundance of small and medium-sized worms had a strong positive effect on swallow rates. As worms are a key prey type for the avocet, this result is unsurprising. The abundance of hydrobiid snails had a strong negative effect on both sweep rates and swallow rates. The effect on sweep rates could be due to the Hydrobiidae behaving like coarse sediment, increasing the friction associated with sweeping. As this is thought to be a non-preferred prey type (see Chapter 6), reduced swallowing rates could also signify active avoidance of this prey by the foraging birds. Furthermore, hydrobiid-rich areas tended to be lower in annelid worm abundance (see Chapter 3). Sweep rates were lower in the presence of high abundances of large worms, which are often targeted by visual foraging, and higher in the presence of high abundance of medium-sized worms, which are captured by benthic tactile foraging. Thus the findings of this study support the importance of prey type and foraging mechanism in determining sweep rates, as suggested by Moreira (1995a).

5.5.7 Weather factors

Sweep rates and swallow rates appeared to be lower when temperature was >15ºC. However, as the lowest rates were observed in the warmer months of September and October, this result is most likely due to seasonal variation in invertebrate abundance, rather than a direct effect of temperature. High winds appeared to reduce swallow rates – which could be due to a reduction in prey availability or capture efficiency in high winds (Verkuil et al. 1993). The wind effect was observed only at the exposed mudflat at Middlebere, as

Brownsea Island largely shelters the lagoon from the effects of southwesterly winds. As the degree of shelter can have a large effect on energy expenditure in overwintering waders (Wiersma & Piersma 1994)**,** this may be an important factor in determining the preference of the avocets for Brownsea as a roost site. Wind speed was found to negatively correlate with the number of American avocets (*Recurvirostra americana*) foraging on mudflats in Humboldt Bay, California (Dodd & Colwell 1998).

5.5.8 Social foraging

Social foraging occurs in many species of birds, and it can involve groups of varying sizes and one or more species (Stolen et al. 2012; Beauchamp 1998). Social foraging may benefit individuals by several mechanisms, including anti-predator defence (Kenward 1978; Sridhar et al. 2009; Hamilton 1971; Morse 1970), increasing foraging success ("social facilitation") (Drent & Swierstra 1977; Kushlan 1978), or signalling the presence of profitable foraging patches ("local enhancement") (Kushlan 1978; Krebs 1974; Beauchamp 1998) or a combination of factors (Sridhar et al. 2009). However, social foraging strategies are generally most effective at targeting prey resources which are ephemeral or vary in availability either temporally or spatially (Kushlan 1981; Pöysä 1992).

According to the social facilitation hypothesis, the presence of a group of foragers disturbs prey and makes it more susceptible to predation, and thus the intake rate of individual foragers is enhanced (Stolen et al. 2012). However, in this study, the apparent feeding rate was lower in birds feeding in social groups compared with solitary foragers (Figure 5.10b), even though the searching rate, and presumably the energy expenditure associated with this feeding strategy were higher (Figure 5.10a). Thus, in this case, social foraging may be enabling a prey switch, from low energy, readily available benthic resource, to the highly mobile energy rich nektonic prey.

Avocet social foraging also showed signs of local enhancement, as initially small groups of socially foraging individuals were joined by additional foragers, attracted to the site by visual or aural cues. It is thought that the plumage of certain bird species, such as snowy egrets (*Egretta thula*) or seabirds with striking white upper parts, may act as a visual cue to attract other birds (Kushlan 1977; Gotmark et al. 1986; Smith 1995). The initial formation of the flock may be due to a locally high prey density, and thus represents a form of scramble competition which is not social *per se*; however, the maintenance of the flock may have a social element, as the prey become disorientated in the presence of large number of foragers (Nicholson 1954; Battley et al. 2003).

In Poole Harbour, the avocets spent relatively little time socially foraging compared with solitary foraging. However, socially foraging avocets consumed an estimated 85 kJ h^{-1}, which is greater than the maximum energy obtained with any other foraging strategy (see Chapter 4). This begs the question, why is social foraging not observed more frequently? There are examples of sites at which high abundances of fish are present but avocets feed only on small prey items such as crustaceans and chironomids (Fasola & Canova 1993). It has been suggested that foraging on fish is an opportunistic strategy, which is only possible under certain conditions (Hötker 1999b). For example, in a shallow lagoon in Northern Germany, the construction of a sea wall caused high densities of Common gobies (*Pomatoschistus microps*) to be confined to a small area (Hötker 1999b). Similarly it was suggested that nektonic prey entering managed brackish water impoundments through structures that control the water levels result in local high densities that provide increased opportunity for location and capture by American avocets feeding at the site (Boettcher et al. 1994). The creeks in the intertidal mudflat may perform a similar function in channelling prey into a smaller area.

Social foraging had a distinct seasonal pattern – this could suggest a change in the availability of the nektonic prey resource throughout the winter. Social foraging occurred most frequently during October and November at both sites. Studies on seasonal variation in fish biomass in shallow soft bottom waters in Northern Europe showed peak biomass occured between August and November (Nellbring 1985; Pihl & Rosenberg 1982). This peak in abundance generally coincided with the recruitment of young fish in the late summer and autumn (Ehrenberg et al. 2005).

At Brownsea, social foraging occurrence peaked around high tide, and sunrise. A peak of activity at sunrise could be related to prey increased availability of fish in the lagoon at this time. For example, early morning aggregations of Little egrets (*Egretta garzetta*) feeding on fish in small pools in the Camargue, southern France, have been attributed to macrophytes depleting the oxygen concentration overnight; this causes the fish to aggregate in open areas and come to the surface to respire (Kersten et al. 1991). The occurrence of social foraging at high tide could be due to the slightly higher numbers of birds present on the lagoon during high tide, increasing the chance of social aggregations forming, as there was a clear relationship between the number of birds present on the lagoon, and the number of birds socially foraging (Figure 5.8a). Conversely, social foraging at Middlebere was more constrained by the tidal cycle. Social foraging did not occur at high tide, and occurred most commonly at low tide, when the avocets were able to feed only in the narrow channels which retain water even at low tide. The fact that social foraging occurred at Middlebere when fewer individuals were present was likely due to the fact that the channels funnelled the nektonic prey into a smaller area, so the maintenance of social foraging aggregations was less reliant on the presence of large numbers of birds to disorient the prey, as was apparently necessary on the lagoon. The potential for Allee effects to occur with social foraging has been proposed (Berec 2010). Social foraging was not observed at Brownsea lagoon when the total number of avocets present was less than 500 (Figure 5.8a). This relatively high threshold implies the possibility of an Allee effect for social foraging where there are no natural prey-concentrating mechanisms, such as the presence of creeks or tides, for naturally herding the prey into small patches.

A further social element to the avocet foraging ecology may exist in the preferential use of Brownsea Island Lagoon at the beginning of the winter. The congregation of birds at a single site may indicate the importance of this roost site as an “information exchange centre” (Ward & Zahavi 1973). In addition, communally roosting at a single site may facilitate the formation of foraging groups (Buckley 1996). This may be important in a mosaic habitat such as Poole Harbour, particularly as groups of birds begin to ‘sample’ new feeding habitats when depletion of prey on the lagoon draws them out to other foraging grounds in the intertidal mudflats.

5.5.9 Conclusions

This chapter has identified several key differences in pied avocet behaviour between a tidal and non-tidal habitat. The proportion of time avocets spent foraging varied in response to seasonal and tidal effects, and the precise relationship was different between the tidal and non-tidal study sites. In addition, avocet feeding rates varied in accordance with seasonal and tidal factors, and local invertebrate abundance. Social foraging showed seasonal, tidal and diurnal variation, and differed in timing and frequency between the tidal and non-tidal sites. Furthermore, the minimum threshold in number of birds necessary for social foraging to occur was higher at the non-tidal site.

Chapter 6: Predicting the effects of sea-level rise and habitat loss on the overwintering avocet population of Poole Harbour

6.1 Abstract

Coastal habitats such as lagoons and estuaries are under threat from the effects of climate change, including sea-level rise (SLR) and habitat loss. The ecological effects of such changes are difficult to predict in advance; however, policy makers and land managers require accurate predictions for the purposes of land-use planning, development, conservation and developing appropriate mitigation measures. Poole Harbour is one of the UK's most important overwintering grounds for the pied avocet (*Recurvirostra avosetta*), and supports internationally important numbers of this species over the winter.

Individual-based modelling (IBM) is a simulation modelling technique in which systems are represented as a collection of autonomous agents that act to maximise their own fitness. The technique has been widely applied to ecological systems, including behaviour-based models of shorebirds, to generate accurate predictions under novel environmental conditions.

Here I develop an IBM for the pied avocet, a shorebird with a unique foraging mechanism, which has not previously been studied using this approach. The model was validated using field data collected over two winters. The model is used to test assumptions about the requirement for a non-benthic food resource, and to test the effect of the loss of tidal and non-tidal foraging habitat due to SLR on the mortality and behaviour of the birds.

I found that the present day population is dependent on a nektonic food resource (most likely small fish captured by social foraging) to survive the winter. The mortality of the birds was affected by SLR ≥22.4 cm, and the presence of the non-tidal Brownsea Lagoon reduced the observed mortality in these scenarios. A sensitivity analysis showed that the model was most sensitive to gross energetic parameters, but parameters relating to the foraging behaviour, such as capture efficiency and search area were also important.

6.2 Introduction

6.2.1 Threats to coastal ecosystems

Many coastal habitats such as estuaries and lagoons are under threat from the effects of climate change, including sea-level rise (SLR) and habitat loss (Nicholls et al. 2007). The south of England is particularly at risk due to the combinatorial effects of rising sea levels and isostatic tilt (Lowe et al. 2009). Furthermore, the natural landward migration of intertidal habitats in response to SLR is often prevented as the coastline is highly populated and often reinforced with man-made infrastructure, leading to "coastal squeeze" (Hughes 2004).

The ecological effects of these climate-related changes are uncertain, although significant effects on species phenology and physiology are predicted (Harley et al. 2006b; Hughes 2000). Predicting the consequences of long-term changes, such as SLR, is notoriously difficult, as ecological systems are inherently complex, stochastic, and exhibit multiple levels of organisation (Anand et al. 2010). However, it is essential to understand precisely how populations will respond to environmental changes before they occur, to design future coastal management strategies (Evans et al. 2012).

Since many estuaries are designated as Special Protection Areas (SPAs) under Article 4 of the European Commission Directive on the Conservation of Wild Birds (79/409/EEC), there is a statutory requirement to ensure future changes to a site will not lead to deterioration in site quality for the species for which the site is designated, and to put suitable mitigation measures in place. For many of the UK's estuaries, the species of concern are migratory bird populations, which use the habitats for overwintering or as migratory staging posts.

6.2.2 Individual-based modelling of coastal bird populations

Individual-based models (IBMs) are useful to ecologists as they can address applied management issues and forecast impacts of environmental change or proposed mitigation schemes, in a reproducible way that is not possible in the real world (Goss-Custard et al. 2004; Durell et al. 2005; Goss-Custard et al. 2006b; Kaiser 2006). In addition, the models can be used to identify priorities for management or monitoring purposes (West et al. 2007; Stillman et al. 2001; Goss-Custard & Stillman 2008; West et al. 2005; Toral et al. 2012).

Coastal bird species are ideally suited to the IBM approach as they forage in a 2-dimensional habitat which is easy to visualise, many individuals aggregate in a relatively small area, and a large body of field data on the foraging ecology of some shorebird species is available, therefore it has been possible to parameterise and test a number of models

(Stillman et al. 2000b; Goss-Custard et al. 2006; Goss-Custard et al. 1995). Much of the early theoretical work was based on oystercatchers (*Haematopus ostralegus*) foraging on mussel beds, but subsequent models have been applied to other shorebird species including redshank (*Tringa totanus*), black-tailed godwit (*Limosa limosa*), curlew (*Numenius arquata*) and dunlin (*Calidris alpina*) (Durell et al. 2005; Durell et al. 2006; Goss-Custard et al. 1995; Goss-Custard et al. 1995). Models have addressed a range of management issues including habitat loss (Goss-Custard et al. 1995), sea-level rise (Durell et al. 2006), wind farm development (Kaiser 2006), shell-fishing (Stillman et al. 2001), and human disturbance (West et al. 2002).

6.2.3 The rationale for IBMs

The use of IBMs to determine site quality has shifted the focus away from the traditional use of count data to determine key demographic parameters – mortality rates, emigration and immigration rates (Stillman et al. 2010). Such parameters are difficult to measure in the field, particularly for migratory populations, whose numbers may be affected by environmental change at multiple sites (Sandercock 2003). Furthermore, long-term estimates of mortality rate are often confounded by seasonal compensation effects, whereby a change in population size leads to a change in density-dependent limits to population growth, or carry-over effects, by which some aspect of an organism’s fitness is affected by conditions in the previous season (Duriez et al. 2012; Harrison et al. 2011). Most importantly, even when a long time-series of demographic data are available, it is extremely difficult to predict future trends if there is no mechanistic link between mortality rates and site quality.

Individual-based models (IBMs) provide this mechanistic link, by focussing on the processes executed by individual agents, and the interactions between them. System-level properties, such as mortality rates, emerge from the adaptive behaviour of the interacting individual agents (Grimm & Railsback 2005). As the models are linked to the adaptive behaviour of individuals, they are able to capture temporal correlations and non-linear, threshold-dependent behaviour which is difficult to reproduce with models based on simple differential equations (Bonabeau 2002). Individuals in the model behave as optimal foragers, acting to maximise their own fitness. Currently observed behaviour is assumed to be the result of fitness-maximising behaviour (birds deciding where and when to forage) to maximise their intake rate. The precise meaning of ‘fitness maximisation’ varies from system to system, but in the case of overwintering shorebirds, it involves maximising the short-term intake of energy from prey ingestion, with the ultimate aim of surviving the winter in adequate condition to return to the breeding grounds and reproduce successfully (Stillman & Goss-Custard, 2010). As survival and reproduction are the basic aims of all species, as stated in the theory of evolution by natural selection (Darwin 1859), it is fair to assume that even when environmental changes occur in the landscape, this fitness maximisation rule will always govern the behaviour of individual foragers (Grimm & Railsback 2005). Hence IBMs offer a robust tool for predicting behaviour under future conditions. If a model can demonstrate that birds will maintain their present levels of fat accumulation under future scenarios, it shows the habitat will not have 'deteriorated' from the birds' perspective.

6.2.4 The Poole Harbour avocet population

Poole Harbour is one of the largest lowland harbours in Europe, and is designated as a SPA on account of its overwintering birds (Humphreys & May 2005; Natural England 2010). Pied avocet is one of three species found in internationally and nationally important numbers (i.e. >1% of the international and national populations) (Natural England 2010). Since the 1990s, the avocet population in Poole Harbour has increased from a few individuals to the 3rd most important overwintering sites for avocet in the UK (Holt et al. 2012; Pickess 2007). However, Poole Harbour faces long-term environmental changes due to predicted SLR and loss of saline lagoon habitat at Brownsea Island Lagoon, which is currently protected by a sea wall – yet the long-term management strategy for the site is unclear (Drake & Bennett 2011).

Here I describe the parameterisation of an IBM of a non-breeding population of pied avocets in Poole Harbour. The species has not previously been studied using an IBM approach, and detailed data on their foraging mechanisms, including the functional response, were not previously available. The model includes foraging parameter estimates derived from data collected from individual bird behaviour, but the model was tested using emergent population-level patterns, such as the distribution of foraging birds and the time spent feeding throughout the winter. As such, the data that were used to test the model predictions were not directly derived from those used to parameterise the model.

6.2.5 Aim and objectives

In this chapter I outline the parameterisation of an IBM to predict the effect of SLR and lagoon habitat loss on the avocet population of Poole Harbour. The model incorporates the findings of previous chapters, including the invertebrate prey resource (Chapters 2 and 3), and aspects of the foraging behaviour (Chapter 4, 5, and 6). The key quantitative prediction of the model is the number of birds that survive the winter and their body condition (in terms of energy reserves) at the end of the winter.

The specific objectives were:

- to determine the extent to which existing benthic food resources met the overwinter energy demands of avocets;
- to simulate future environmental change scenarios within Poole Harbour, including the loss of a key foraging area (Brownsea Island Lagoon) and decreased intertidal mudflat exposure time due to SLR, and to determine the effect on the mortality and fitness of the avocet population;
- to test the model predictions using field data on avocet distribution and proportion of time spent foraging;
- to conduct a sensitivity analysis to determine which parameters had the strongest effect on model predictions.

6.3 Methods

6.3.1 Study site

The study site was Poole Harbour, on the south coast of Dorset, UK, 50.6958° N, 1.9886° W. The two key avocet foraging areas were identified using the Wetland Birds Survey (WeBS), records from the Dorset Environmental Records Centre (DERC) and local knowledge: 1) Brownsea Island Lagoon and 2) Middlebere Creek and the connected Wych Lake in the southwest corner of the harbour (henceforth referred to as Middlebere).

6.3.2 Model description

In this chapter I used the MORPH IBM (described fully in Stillman 2008), which follows the decisions of foragers as they attempt to meet their daily energy requirements. The model predicts the number of birds that survive the winter, and the energy reserves each bird possesses throughout the winter. In addition, the model predicts the patches in which the birds feed and the prey diets upon which they feed. I included two main types of foraging habitat in the model – an intertidal mudflat and a non-tidal saline lagoon. Saltmarsh roosting habitat was also included in the model.

6.3.3 Global parameters

(i) Time period

The model simulation runs from 00:00 on September 1st to 11:59 on March 31st, and progresses in 1 hour time-steps. This period encompassed the arrival and emigration dates of the vast majority of avocets in Poole Harbour. During each time-step, the environment remains constant, and the model birds forage in a single patch on a single diet. The model explicitly represented the day/night cycle, to allow visual foraging behaviour to occur during daylight hours only. Times of sunrise and sunset for Poole Harbour were obtained from the US Naval Observatory website (aa.usno.navy.mil).

6.3.4 Patch parameters

(i) Spatial extent

Spatial extent of the model is shown in Figure 6.1. The model contained eleven foraging patches, 10 intertidal mudflat patches and a single non-tidal lagoon. There were 5 saltmarsh patches at Middlebere, and a single sand spit roost within the lagoon. These roost patches contained no food resource, but could be accessed when high quality foraging patches were unavailable.

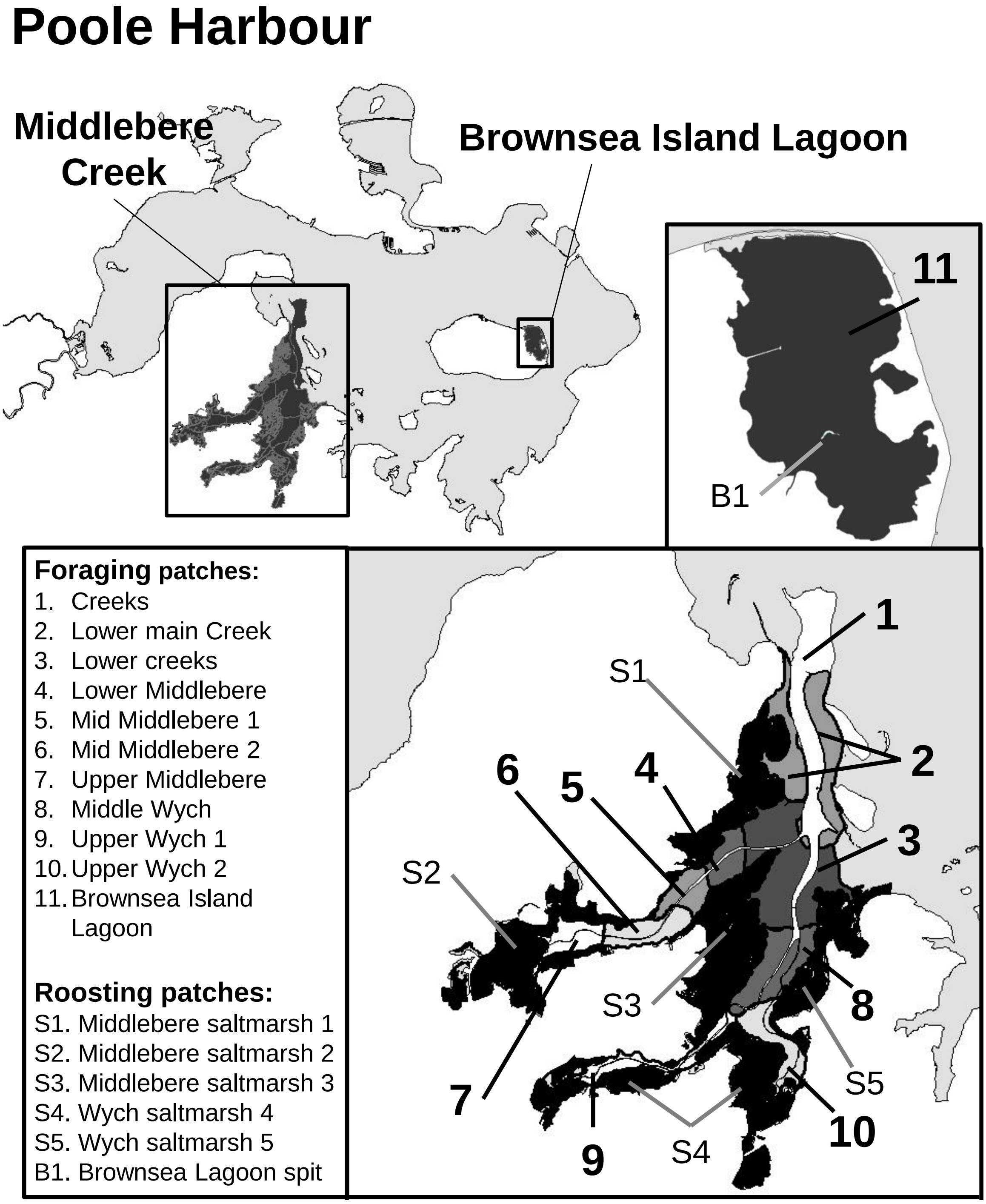


Figure 6.1 Spatial extent of model and location of patches.

(ii) Tidal model

The tides were based on a 2-dimensional depth averaged hydrodynamic model of Poole Harbour, developed by HR Wallingford (HR Wallingford 2004). The tidal model produces two spring/neap tidal cycles, which were looped to produce continuous tidal flows for the 212 model days. To produce realistic exposure periods, I used the tidal curve for the deepest part of Middlebere Creek (Patch 1), and adjusted the position of the curve on the y-axis according to the bathymetry of each patch. Figure 6.2 shows a section of the tidal curve for patches 1 and 7, the deepest and shallowest patches, respectively. The dotted line represents the maximum depth at which avocets forage, thus patch 1 is never accessible to foragers as the water is too deep. Average patch bathymetry was calculated from HR Wallingford's model of existing bathymetric conditions in Poole Harbour (HR Wallingford 2004).This model combined data from depth soundings of Poole Harbour, provided by the Poole Harbour Commissioners, and the Poole Bay Admiralty charts 2611, 2175 and 2172. Brownsea Island Lagoon is non-tidal, and as the average water depth is ~15cm, this patch was always available to the birds. Water levels in the lagoon are managed by the Dorset Wildlife Trust using a system of sluices to minimise seasonal variation. The relative size and exposure time of each patch are included in Appendix 11. The sequence of patch exposure during a single tidal cycle of the model is presented in Figure 6.3.

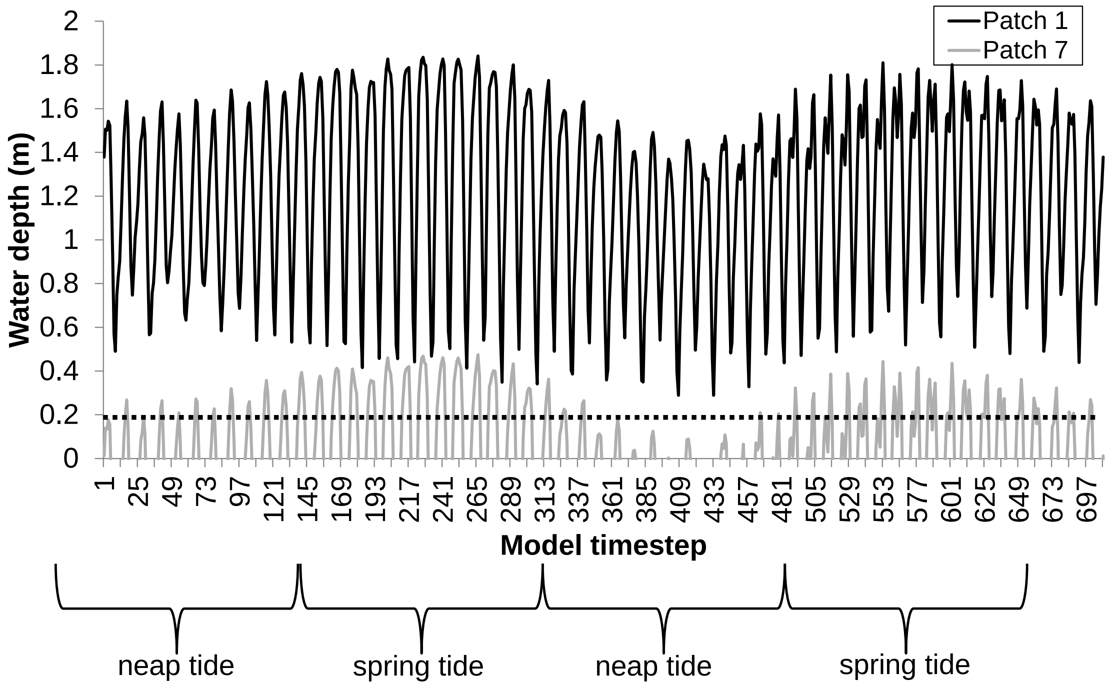


Figure 6.2 A section of the tidal curve for patches 1 and 7 (the deepest and shallowest patches, respectively). The dotted line represents the maximum depth in which avocets are able to forage.

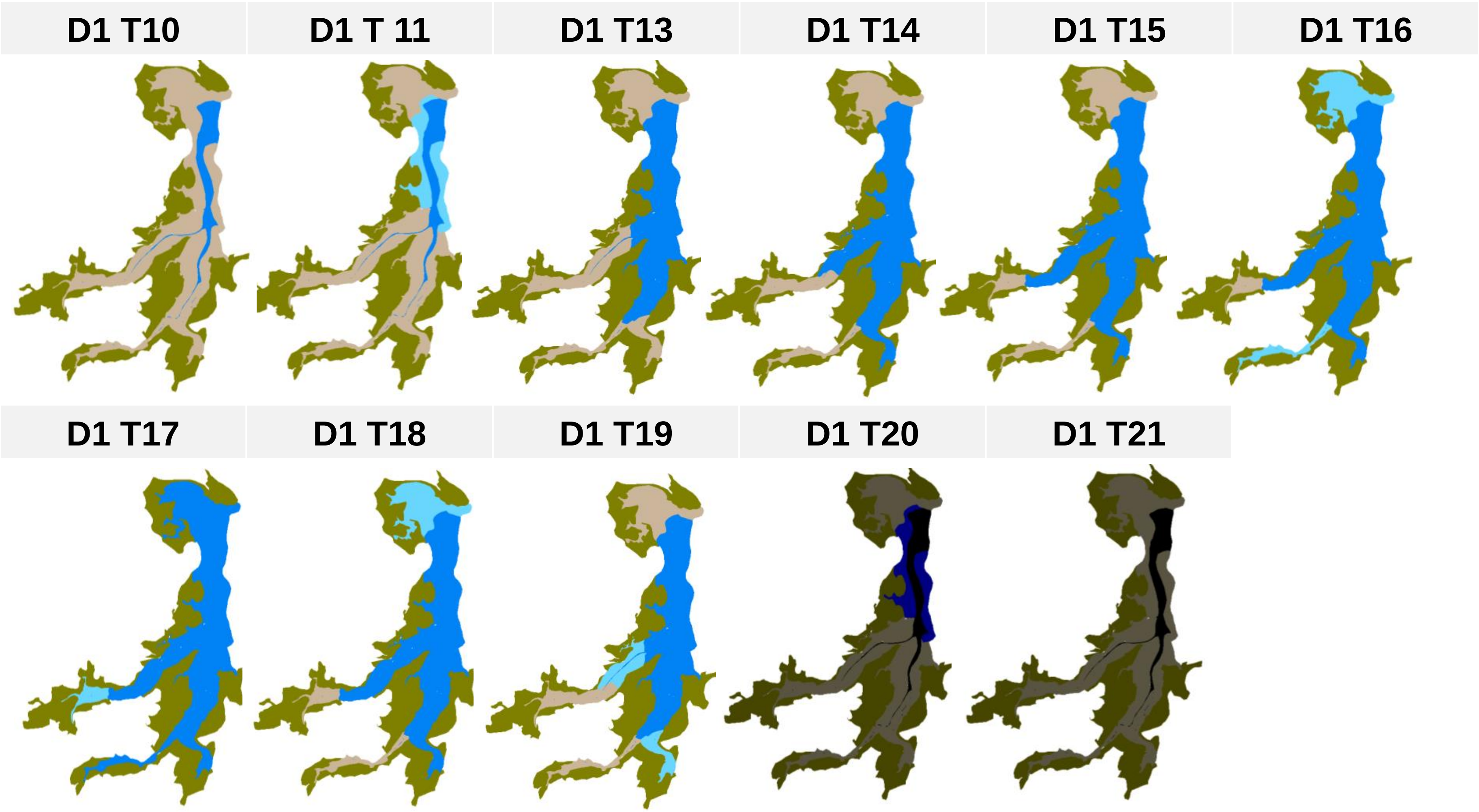


Figure 6.3 Sequence of tide covering and exposing intertidal mudflat, as represented in the model. Sequence shown is day (D) 1, time-steps (T) 10–21. During the day, dark blue represents water deeper than 25 cm; light blue is water 10–25 cm; beige is exposed mudflat, and green is saltmarsh. Note change of colour scheme after dark (time-step 20), where black represents water deeper than 25 cm; dark blue is water 10 –25 cm; dark beige is exposed mudflat, and dark green is saltmarsh.

(iii) Prey abundance and energy content

The invertebrate prey within the model was based on surveys detailed in Chapter 3. The density of prey within each patch was taken as the average value of sampling points occurring within each patch. Thus, each patch represents the average of at least 2 sampling points. The survey dates for Brownsea and Middlebere are shown in Figure 6.4. The initial invertebrate density at the start of the model simulation (Sept 1) was based on the results of invertebrate surveys conducted at the end of August. The resources were updated twice in the model, on day 66 (Nov 5th) and day 175 (Feb 22nd), to account for factors other than the predation pressure of avocets affecting prey density throughout the winter (e.g. species-specific reproduction and recruitment rates, and predation from other species). The initial invertebrate abundances in each patch, for each survey, are presented in Appendix 12.

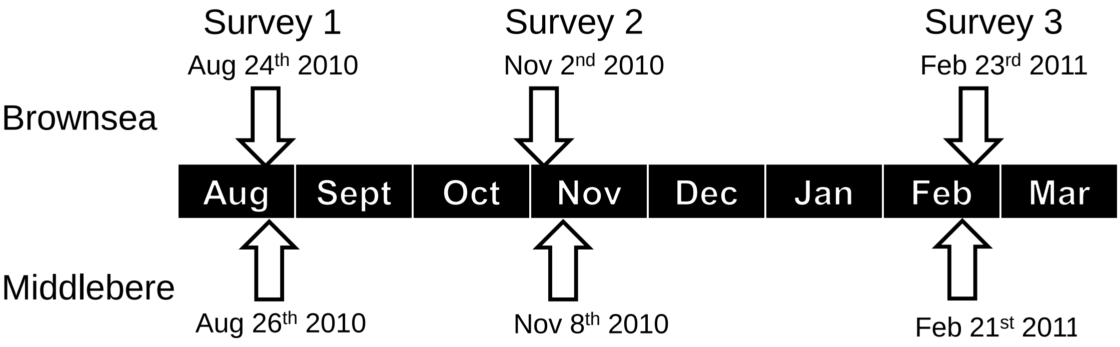


Figure 6.4 Invertebrate sampling dates.

Patches occurring within Wych Lake were not surveyed, so I applied the invertebrate density in patch 7 (Upper Middlebere) to patch 9 and 10 (Upper Wych 1 and 2), and from patch 6 (Mid Middlebere 2), to patch 8 (Mid Wych), based on the relative distance of the patches from the freshwater end of the creeks. A previous survey indicated the species abundance in Wych Lake and Middlebere Creek were comparable (Herbert et al. 2010).

The quantification of prey biomass in mg ash-free dry mass (AFDM) for each prey type is outlined in Chapter 3.

(iv) Prey availability

Availability of polychaete worms ≥4 cm in length, was calculated for each patch based on size-dependent burrow depth of ragworm *Hediste diversicolor* (Esselink & Zwarts 1989). Prey was available for visual foraging if it was present at the surface, and available for benthic tactile foraging if it was present in the top 2 cm of sediment. Small prey, such as

Corophium spp. and worms <4 cm in length were assumed to be constantly available, as they occur in the top 2 cm of the sediment, and thus available to an avocet sweep (Moreira 1995b). Availability of worms to visual foraging was based on the observation that 10% of worms are found at the surface (Esselink & Zwarts 1989). Availability of worms for benthic tactile foraging included this 10%, plus the likelihood of worms in each size class to be present in the top 2 cm of sediment (see Chapter 4 for details). As the size-class structure of worms varied in each patch, this value was patch-specific. Availability constants for each patch are listed in Appendix 13.

6.3.5 Forager parameters

(i) Population size

The number of avocets in the model was 1200, based on a peak count of 1207 birds on Brownsea on Nov 16th 2010 and 1119 birds on Nov 18th 2011. The immigration of birds into the model was based on a uniform distribution of arrival between day 1 (September 1st) and 61 (November 1st), based on arrival of avocets in Poole Harbour over two winters (see Figure 6.5).

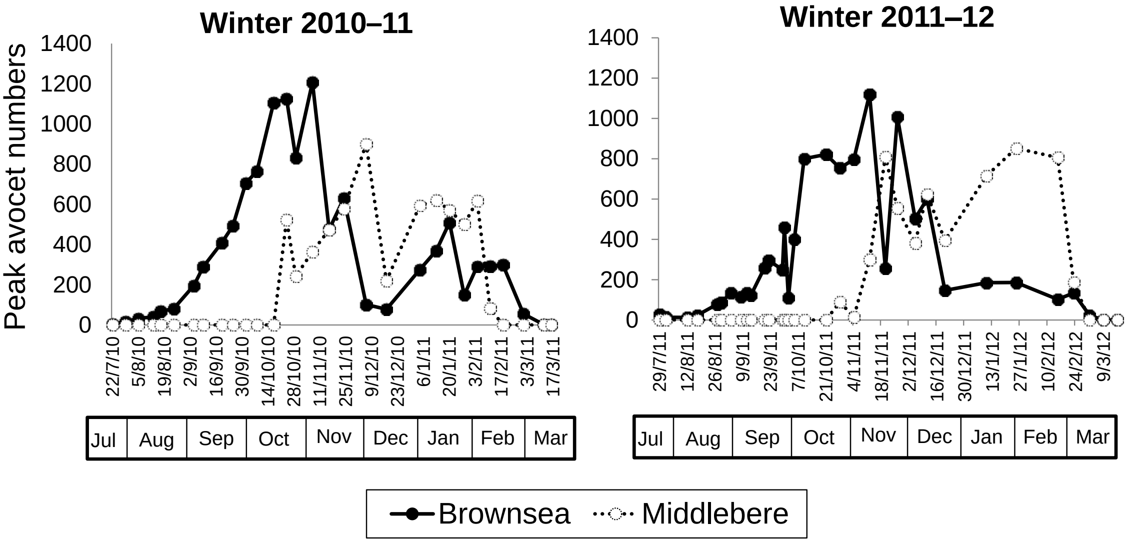


Figure 6.5 The number of avocets present at Brownsea Island Lagoon (solid line) and Middlebere Creek (dotted line) over two winters of observation.

(ii) Target body mass and starvation body mass

I used the figure of 325 g as the target body mass for an avocet (Thomas et al. 2006), which was consistent with the weights of adult avocets ringed on Brownsea Island Lagoon by the Stour Ringing Group (see Results Table 6.2). As no data were available on the starvation body mass of adult avocets, I estimated this using the starvation masses of a range of shorebird species, collated by Goss-Custard (unpublished data, included in Appendix 14), which relates bird starving mass (M_s) to the body mass (M_b) by the equation:

$$M_s = 6.2078 + 0.5624\, M_b$$

Thus the starvation mass of an avocet was estimated as 189 g.

Birds enter the model at target body mass, and die of starvation if their body mass falls below their starvation body mass. Birds attempt to maintain their target body mass, and reduce the amount of time spent feeding if they achieve it.

(iii) Metabolism and bioenergetics

The energy density of shorebird body reserves (fat and protein) has been estimated, for oystercatchers, as 34.3 kJ g^{-1} (Kersten & Piersma 1987). The conversion of prey biomass (in mg ash-free dry mass; AFDM) to usable energy in kJ varies according to prey type. The AFDM values for each prey size class, and the conversion factors to calculate energy availability in kJ are provided in Appendix 15.

The energy expenditure during each time-step was estimated from the metabolic scaling equation of field metabolic rate (FMR) for non-passerine birds with body mass (Nagy 1987):

$${M_b}^{0.681} \times 10.5$$

This estimates FMR for avocets as 539.2 kJ day^{-1} or 22.5 kJ hr^{-1}.

I included an energetic cost of moving between patches, as Brownsea is roughly 5 km away from the intertidal feeding grounds. I estimated avocet flight speed as 33.7 ms^{-1} using the following equation that relates body mass to flight speed (U_e; ms^{-1}) (Alerstam et al. 2007):

$$U_e = 15.9 \times (M_b)^{0.13}$$

I estimated flight costs of avocets as 0.02 kJ s^{-1}, assuming flight costs to be roughly 9 times BMR (Piersma 2011), and using the equation which calculates BMR from body weight in kg (BW) for waders (Kersten & Piersma 1987):

$$BMR = 437(BW)^{0.729}$$

(iv) Avocet diet

Prey included in the model was based on observation of foraging behaviour, and analysis of avocet faecal samples (see Chapter 4). These included small oligochaete worms, polychaete worms in 5 mm size classes (from 1–5 mm to 121–125 mm), small crustaceans, *Corophium* sp, in 5 mm size classes, and small fish, likely to be *Pomatoschistus* sp as these were the most common species in the lagoon. As the avocet foraging mechanism is assumed to be 'non-specific', several other potential prey items which are found in high densities at the study sites (hydrobiid snails, *Ecrobia ventrosa* and *Peringia ulvae,* bivalve spat and isopods *Cyathura carinata* in 5 mm size classes), were also included initially. There was no direct evidence of avocets foraging on these prey types, as they were too small to be observed, and no discernible fragments of these prey were found in the faecal samples. However, as they are present in high abundance at the study site, I tested the energetic consequences of including them in the diet to determine whether they were a likely prey source.

During each time-step, the model birds forage on one of four possible diets: small prey by benthic tactile foraging, small crustaceans by visual foraging, large worms by benthic tactile foraging or large worms by visual foraging, as it is known from field observation and published data that avocets feed on these species (Moreira 1995a; Hötker 1999b). The patch and diet that provide the highest possible energy intake rate for that time-step is selected by foragers. The prey types and functional response equations associated with each diet are listed in Table 6.1. For details on the functional response models, see Chapter 4. Visual foraging methods were constrained within the model to only occur during the hours of daylight. Visual foraging was also susceptible to interference through prey depression (see below). For benthic tactile foraging on small prey, I assumed the birds were able to capture 10.9 prey items per sweep, based on "sweeping experiments" with an avocet bill (Moreira 1995b).

A fish diet was not included explicitly in the model due to lack of data on the density of fish in each patch and the functional response. Therefore, this diet was represented in model simulations by decreasing the metabolic costs by the amount of energy the birds would gain from feeding on fish (or another nektonic food resource).

The proportion of energy from the prey that is assimilated by the predator (assimilation efficiency) was assumed to be 85%, based on an experimental determination of assimilation efficiency in oystercatchers (Kersten & Piersma 1987).

Table 6.1 Prey types and functional response equations used for each diet (more detail on functional responses provided in Chapter 4).

Diet	Prey types	Functional response equation Feeding rate (F) in items captured hr^{-1}
Benthic tactile (small prey)	Small crustaceans (*Corophium* sp, and *Cyathura carinata*), small oligochaete worms, small polychaete worms (≤10mm), Hydrobiidae[†], small bivalves[†]	$F = \frac{EnDcA}{1+DcAH} * 3600$ A = 0.003213 $m^{-2}s^{-1}$ H = 1.12 s
Benthic tactile (large worm)	Polychaete worms 11–125 mm	$F = \frac{EDacA}{1+DacAH} * 3600$ A = 0.003213 $m^{-2}s^{-1}$ H = 1.68 s
Visual (crustaceans)	Small crustaceans (*Corphium* sp, and *Cyathura carinata*[†])	$F = \frac{EIDacA}{1+DacAH} * 3600$ A = 0.2 m^{-2} s^{-1} H = 2.48 s
Visual (worms)	Polychaete worms 11–125 mm	$F = \frac{EIDacA}{1+DacAH} * 3600$ A = 0.2 m^{-2} s^{-1} H = 2.92 s

E=forager efficiency; I=interference susceptibility; n=number of prey items collected per sweep; D=numerical density of prey (m^{-2}); c=capture efficiency; A=search area ($m^{-2}s^{-1}$); a=prey availability; H=handling time (s); [†]prey were not included in all simulations

v. Interference by prey depression

The negative effect of high densities of visual foraging conspecifics was represented in the model with a standard interference function (Stillman & Goss-Custard 1996):

$$F_i = F\left(\frac{gD+1}{D_0+1}\right)^{-m} \qquad if\ D > D_0$$

$$F_i = F \qquad if\ D \le D_0$$

If the perceived density of avocets within a patch (gD) is higher than the threshold (D_0), then the feeding rate (F) is decreased by the value of the interference constant (m). Perceived density is the actual density of birds (D) multiplied by a spatial aggregation factor (g). The aggregation factor represents the extent to which birds cluster together while feeding. This was calculated as the average proportion of Brownsea Island Lagoon occupied by foraging avocets from September–December 2010: ~20.3%. The threshold density (D_0) was assumed to be 100 birds ha^{-1}, the threshold for redshank interference from prey depression (Stillman et al. 2000a), and the interference constant (m) was also obtained from the redshank-*Corophium* system (Yates et al. 2000).

(vi) Individual variation

Individuals in the model varied in their feeding rates by a normal distribution with a standard deviation of 0.09. This figure was based on the coefficient of variation in bill tip length of 70 adult avocets specimens at the Natural History Museum, Tring (mean=3.32 cm; standard deviation=0.31 cm). Length of bill tip was expected to impact foraging efficiency by enhancing the area searched during benthic tactile foraging.

6.3.6 Initial parameterisation

In reality, upon arrival in Poole Harbour, the avocets congregated on Brownsea Island Lagoon. For roughly the first 60 days (until Nov 1st in 2010 and Oct 29th in 2011), Brownsea was the sole foraging habitat. This provided an opportunity to test foraging hypotheses in a simplified, single patch habitat, as the birds must derive enough nutrition from prey in the lagoon to sustain them. Thus I ran the model for a reduced number of time-steps (61 days) to determine 1) that the balance of intake rate and energy expenditure had been realistically represented in the model, 2) the extent to which the avocets rely on nektonic food resources (assumed to be the small fish and prawns present in the lagoon), and 3) whether or not the hydrobiid snails and small bivalves are a likely food source.

6.3.7 Model validation

To determine whether the model birds behaved like real birds, I compared model outputs with field data collected over 2 winters: firstly, the relative amount of time birds spent in each patch; secondly, the proportion of time the birds spent feeding during each month at Brownsea and Middlebere; thirdly, the overwinter mortality; and fourthly, the body mass of birds. The first pattern was tested by comparing the predicted relative number of birds present in each patch, with the actual cumulative number of birds present in each patch throughout the winter. The latter was produced by systematically recording the number and location of birds foraging each hour, for 8 hours a day, approximately once a week throughout the winter of 2010–11 and 2011–12. The observations were converted into foraging densities and summed over the entire observation period using ArcGIS (ESRI 2010). I compared simulation outputs where the birds were constrained to forage at Brownsea for the first 61 days of the model ("constrained model"), with an output where they were free to choose where to forage for the entire simulation ("unconstrained model").

The second pattern I tested was the proportion of time birds spent feeding during each month at Brownsea and Middlebere. The model predicts the proportion of time each bird spent foraging during each model time-step. As it was not possible to obtain exactly the same data from the real birds, the proportion of birds feeding each hour, at each site, was used as a proxy.

Thirdly, I compared the predicted and observed overwinter mortality. And finally, I compared predicted body mass with the mass of birds caught on Brownsea Lagoon at the beginning of the winter.

6.3.8 Environmental change scenarios

To test the specific effects of potential environmental changes in Poole Harbour, I modelled 8 future sea-level rise (SLR) scenarios:

1) Brownsea Island Lagoon present, SLR 15.9 cm
2) Brownsea Island Lagoon absent, SLR 15.9 cm
3) Brownsea Island Lagoon present, SLR 18.8 cm
4) Brownsea Island Lagoon absent, SLR 18.8 cm
5) Brownsea Island Lagoon present, SLR 22.4 cm
6) Brownsea Island Lagoon absent, SLR 22.4 cm
7) Brownsea Island Lagoon present, SLR 41.4 cm
8) Brownsea Island Lagoon present, SLR 41.4 cm

The SLR predictions were based on the low, medium and high CO_2 emissions scenario projections for SLR estimates for the south of England by 2050, and the medium emissions projection for 2095. Projections were relative to 2000 levels, and took into account the effects of vertical land movement (Lowe et al. 2009).

I also tested the effect of variation in a nektonic food supply on each of the predictions. Simulations in which Brownsea Island Lagoon were included were run once with the assumption that a nektonic food supply was available for the first 61 days, when the birds fed exclusively at Brownsea, and once with the assumption that they were able to achieve the same level of nektonic food throughout the whole winter. The simulations where Brownsea was not included were run once with the assumption that no nektonic food was available at Middlebere, and once with the assumption that the birds were able to achieve similar levels of nektonic resource consumption at Middlebere.

6.3.9 Sensitivity analysis

I conducted a sensitivity analysis on 22 individual model variables, to test the effect on two model outputs: overwinter mortality and proportion of time feeding. All parameters were increased or decreased by 25% from the standard simulation values. The baseline simulation, against which all other values were compared, was run 10 times. The individual parameter sensitivity simulations were run 3 times each. I used the 41.4 cm SLR scenario as the baseline simulation, as it had a low level of mortality, compared with the other simulations in which mortality rate was zero, so it would not have been possible to assess the effect of parameters in reducing the mortality rate. I used 2-tailed T-tests assuming homogenous variance to determine if the changes in mortality and proportion of time feeding were significant ($\alpha=0.05$).

6.4 Results

6.4.1 Initial parameterisation

From the initial model runs, it was evident that the benthic invertebrate resource present in the model was insufficient to sustain the model birds over the course of the winter. The model birds were able to feed initially at a sufficiently high rate to sustain their energy reserves, but the invertebrate resources were quickly depleted leading to mass mortality. This level of prey depletion was not consistent with observed changes in prey biomass, which depleted somewhat between avocet arrival and November 1st, but not to the extent predicted by the model. Therefore, a nektonic food source, such as the small fish captured by socially foraging birds, was essential in the model for sustaining the population under present conditions. When hydrobiid snails and small bivalves were included in the benthic tactile diet, the predicted departure date from Brownsea was long after the observed departure date of November 1st. Furthermore, this led to depletion of Hydrobiidae and bivalves between arrival and Nov 1st in the model, but in reality these prey increased in abundance during this period. As there was also no evidence of shell fragments in the faecal samples, I concluded that Hydrobiidae and small bivalves were unlikely to feature in the avocet diet, and did not include them in subsequent model runs.

6.4.2 Inclusion of a nektonic food resource

To determine the extent to which the birds relied on nektonic prey as an energy resource, I used the initial 61 days, during which the birds were only present at Brownsea, as a calibration period. I varied the nektonic food resource availability, to determine the amount of extra energy necessary to allow the birds to survive for at least 61 days at Brownsea alone, but also caused their energy reserves to begin depleting by this date. Assuming that the birds leave the lagoon and forage in the intertidal mudflat when they can no longer maintain their energy reserves above 90% of their initial energy (which represents a non-critical state of emaciation (Shimmel & White 1983)), I predicted departure date from Brownsea for a range of nektonic energy values (Figure 6.6). The nektonic energy value which corresponded to the departure date of the real birds (day 61) was **6.1 kJ h^{-1}**. The variability in predicted departure day at each level of nektonic food resource was dependent upon the average arrival date of the birds in the model run (which was represented as a stochastic process). When the average arrival date was earlier, resources depleted sooner and the predicted departure date was therefore earlier.

I also determined the predicted mortality rate for various levels of nektonic food resource. Figure 6.7 shows the mortality at day 85, to take into account the lag between resource depletion and bird mortality. No bird mortality was observed at nektonic food resource levels of ≥8 kJ h^{-1}. Therefore, I predict that on average, each avocet requires roughly 6–8 kJ h^{-1} from a non-benthic food resource during this period.

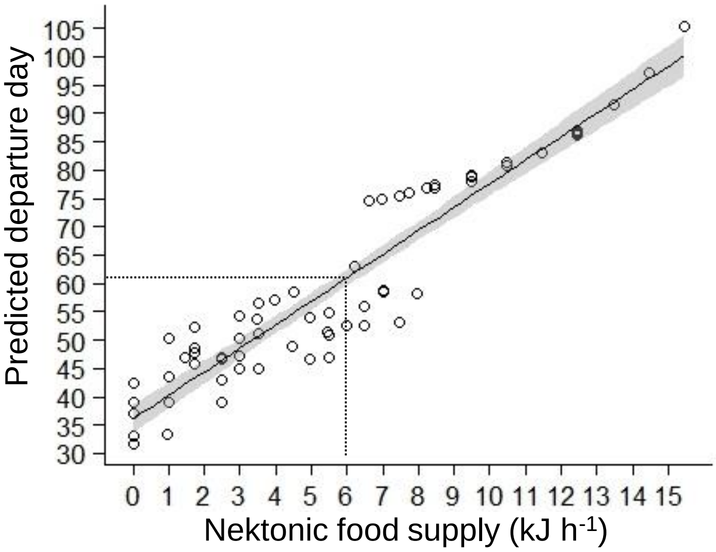


Figure 6.6 Variation in predicted departure day from Brownsea Island Lagoon with amount of nektonic food resource. The grey shaded area represents 95% confidence intervals. The dashed line represents the observed departure day.

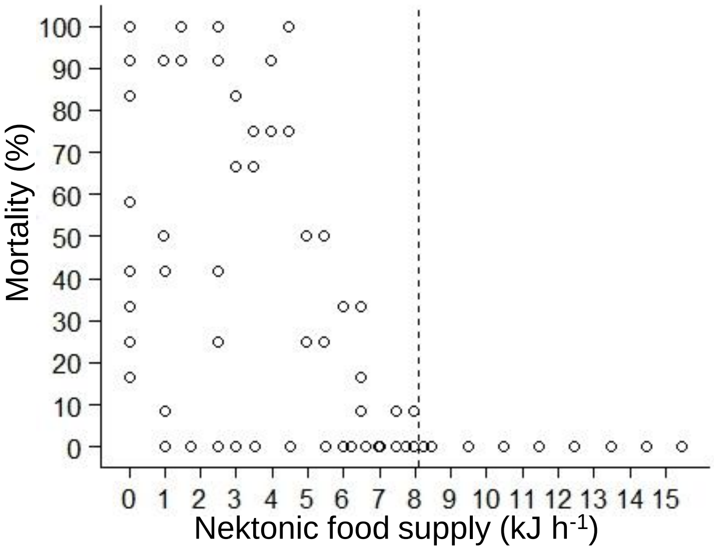


Figure 6.7 The effect of nektonic food availability on mortality at day 85. Dotted line represents the threshold for mortality (~8.1 kJ h^{-1}).

6.4.3 Model validation: do the model birds behave like the real birds?

To validate the model, I compared predictions of key model outputs with field data: the distribution of birds, the time spent feeding, mortality rate, and forager body mass.

(i) Bird distribution

Broadly speaking, the distribution of birds within the model was similar to the behaviour of real avocets: at high tide, birds fed at Brownsea or roosted in the saltmarsh at Middlebere. As the tide uncovered upper Middlebere and Wych, the birds fed here, then moved to downstream patches as the tide ebbed. For illustrative purposes, a sequence of ebbing tide, with model foragers represented as white dots, is shown in Figure 6.8.

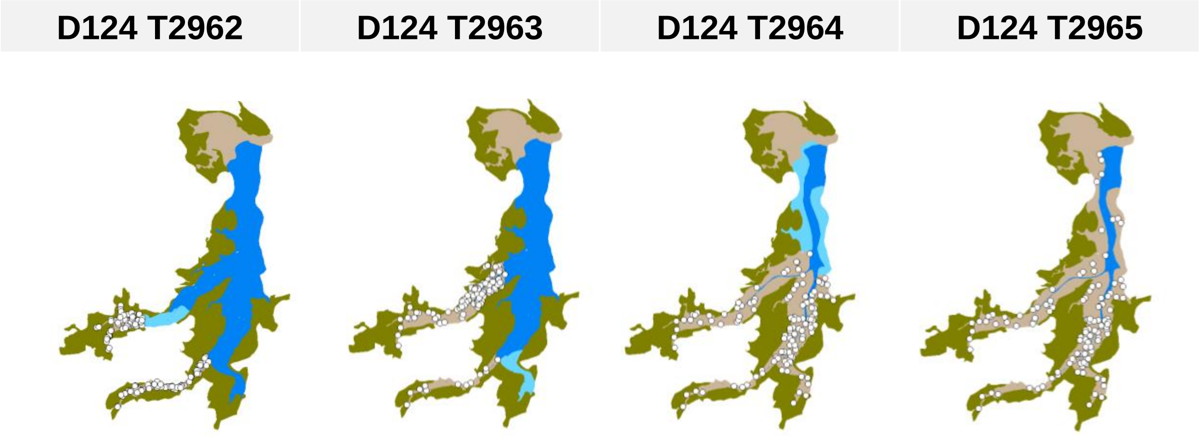


Figure 6.8 A sequence of four consecutive time-steps (T2962–2965) on an ebbing tide on model day (D) 124, illustrating the dispersion of avocet model foragers on the intertidal mudflats. Each white dot represents 10 foragers.

Figure 6.9 shows the relative cumulative bird numbers in each patch, for the unconstrained model (a), in which birds chose where to forage throughout the simulation, and for the constrained model (b), in which the birds were constrained to Brownsea for the first 61 days. The birds in the unconstrained model spent more time foraging in the lower and mid-creek patches and less time at Brownsea, compared with the constrained model. Figure 6.9c shows the observed cumulative density of foragers over the study area, over two winters. While the resultant map is finer scale than the model outputs, it allows for comparison of relative patch usage. Both constrained and unconstrained models replicated the relative importance of the patches: Brownsea had the highest cumulative bird numbers, followed by the upper reaches of the creeks. However, in the constrained model, the predicted pattern resembles the observed pattern more closely, with higher numbers in patch 3 and lower numbers in the mid-creek patches.

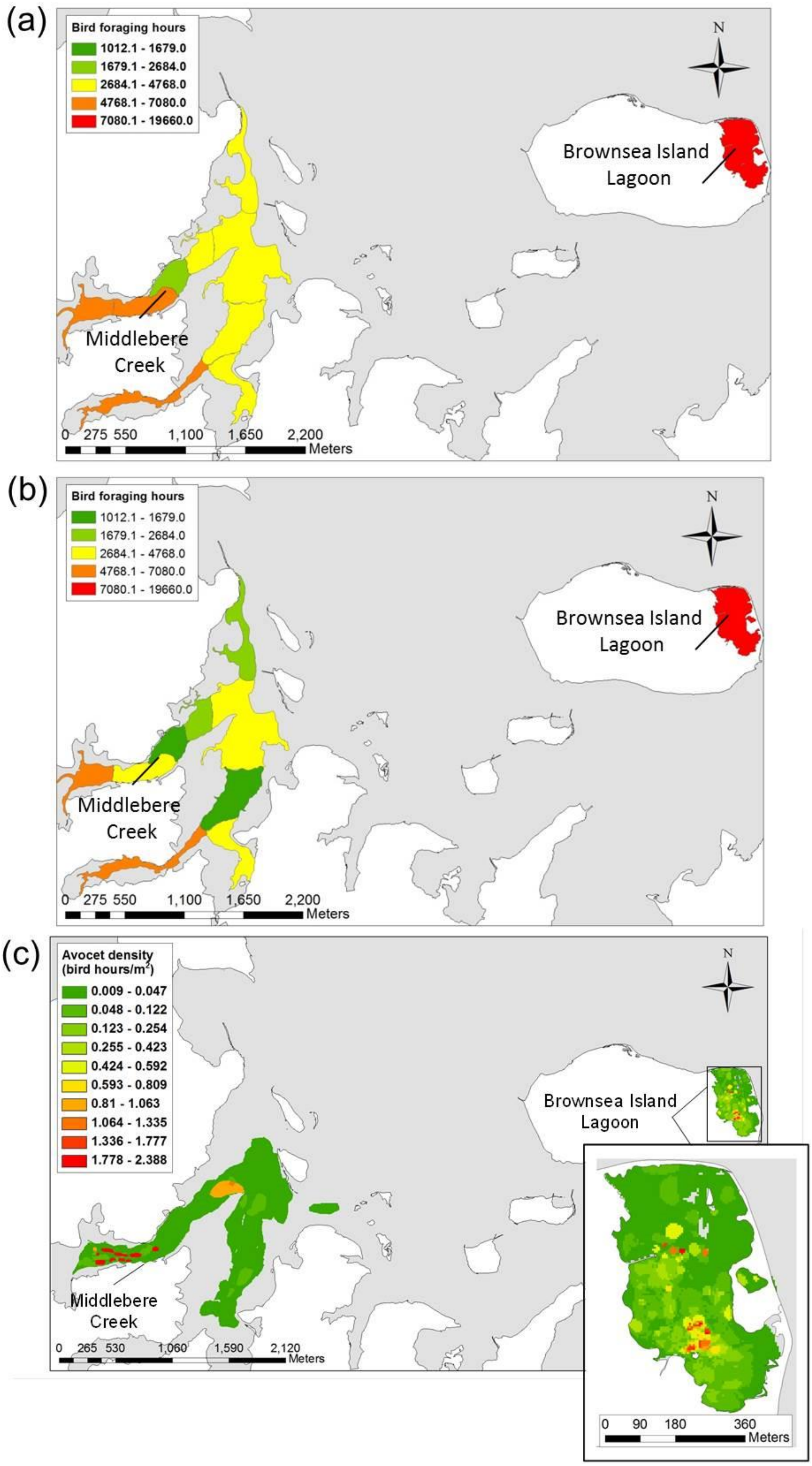


Figure 6.9 Comparison of model outputs of cumulative bird hours in each patch for (a) an unconstrained model in which birds chose where to forage throughout the simulation (b) a constrained model in which birds only occur at Brownsea for the first 61 days, and (c) field data of bird foraging density during two winters.

The relative patch usage is shown in graphical format in Figure 6.10. The cumulative bird numbers predicted for each patch for the constrained and unconstrained models are compared with the cumulative number of foraging birds observed over 2 winters. The observed numbers were based on 241 hours of observation at Brownsea and 193 hours of observation at Middlebere, so were adjusted to be comparable with model predictions (which represent 5088 hours). Generally the observed bird numbers in each patch were lower than model predictions for either simulation. This was due to the fact that in the real system, a small proportion of birds emigrate from the harbour in January and February. However, the model predicted the relative distribution between Brownsea (patch 11) and Middlebere (all other patches) well. Observed numbers in patches 2, 9 and 10 were lower than predicted by the model; however, this is most likely due to observer bias as these patches were the furthest from the observer vantage points, so the number of birds present in these patches was likely to have been under-recorded.

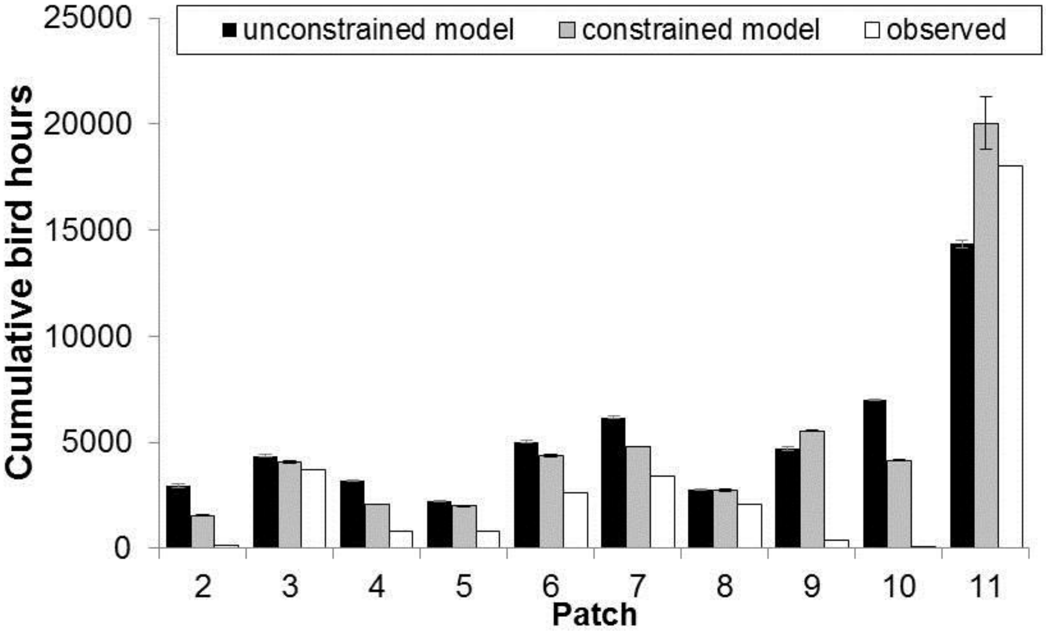


Figure 6.10 Predicted cumulative bird numbers in each patch for the unconstrained (black bars), and constrained (grey bars) model simulations, and the cumulative observed numbers of foraging birds (white bars). Error bars represent standard deviation of results of four model runs.

(ii) Proportion of time feeding

Figure 6.11 compares the predicted proportion of time birds spent feeding in the unconstrained (a) and constrained (b) models, with the observed proportion of birds feeding each month (c). Both the constrained and unconstrained models predicted that birds at

Brownsea spend <50% of their time feeding in September and October, increasing to >75% for the rest of the winter. A similar pattern (low proportion of birds feeding early in the year and higher proportion feeding later in the year) was observed in the real birds (Figure 6.10c), although the increase occurs in December rather than November. Generally the proportion of time spent feeding while the birds were at Brownsea was higher in the model birds compared with the real birds, and the proportion of time spent feeding while the birds were at Middlebere was higher in the real birds compared with the model birds.

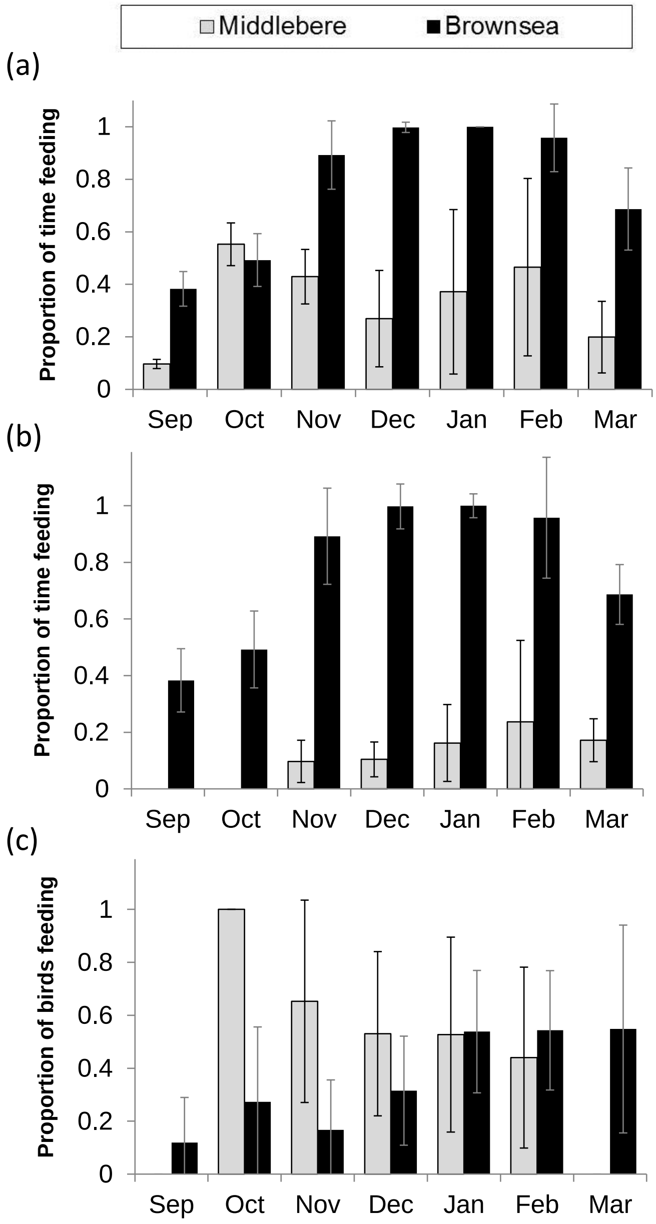


Figure 6.11 The proportion of time birds spent feeding each month in (a) the unconstrained model in which the birds chose where to forage throughout the year and (b) the constrained model in which birds can forage only at Brownsea for the first 61 days; and (c) the observed proportion of birds feeding each month, at Brownsea and Middlebere.

(iii) Mortality

The model predicted no mortality in the avocet population under present day conditions.

(iv) Body mass

The body masses of avocets that were sporadically captured for ringing at Brownsea Island Lagoon are presented in Table 6.2. Most of these masses were ≥ to the average mass of an adult avocet (325 g), indicating that these birds were in good condition. There was no indication that birds caught in October had a lower body condition than birds caught in September. Although based on a small sample size (n=7), these body mass data support the model predictions that the avocets are initially easily able to fulfil their energy requirements during the first few months of the winter.

Table 6.2 Body mass of adult avocets captured for ringing on Brownsea Island Lagoon (data courtesy of Stour Ringing Group).

Capture date	**Body mass (g)**
18/10/2008	335
4/9/2011	335
4/9/2011	325
4/9/2011	285
1/10/2011	292
1/10/2011	350
1/10/2011	362
	$\bar{x}$ = 326.3

6.4.4 Forecasting the effects of environmental change

I ran each of the 8 future scenarios three times: SLR of 15.9, 18.8, 24.4 and 41.4 cm, with and without Brownsea present. For the simulations in which Brownsea was present, I included a nektonic food resource of 7 kJ h^{-1}, and forced the birds to feed at Brownsea for the first 61 days. For the simulations in which Brownsea was not present, I did not include a nektonic food resource. Figure 6.12 showed that mortality was only seen at the two highest SLR scenarios of 24.4 and 41.4 cm. The predicted mortality rate at 41.4 cm SLR was much higher if Brownsea Island Lagoon was not present, and mortality only occurred at 24.4 cm SLR when Brownsea was not present. In terms of the body condition of birds at the end of the winter, a reduction in final energy store was observed in SLR scenarios of 18.8 cm and above, when Brownsea was not present. However, a reduction in energy store was not observed for the 41.4 cm scenario, as bird mortality provided more favourable foraging conditions for the surviving foragers.

If a nektonic food resource of 3.5 kJ h^{-1} or greater was available to the foragers in the SLR 41.4 cm scenario, then mortality was reduced to zero. However, the nektonic food resource did not prevent mortality if it was only available for the first 61 days.

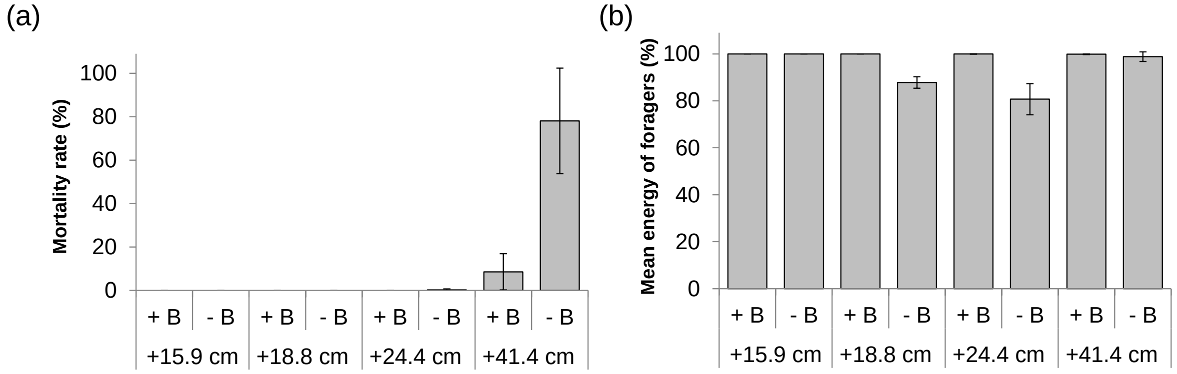


Figure 6.12 Predicting the effects of future environmental change – presence/absence of Brownsea Island Lagoon, ±B, and various sea-level rise scenarios – on (a) the mortality rate and (b) the average final energy store of the avocet population, expressed as a percentage of the energy at the start of the simulation. Scenarios in which Brownsea was present, assumed that feeding on fish occurred only at Brownsea and only during the first 61 days. Bars represent the average of three simulations, and error bars represent the standard deviation.

6.4.5 Sensitivity analysis

I tested the effects of altering 22 model variables by ±25% on the model outputs overwinter mortality (Figure 6.12) and proportion of time feeding (Figure 6.13). The latter was used to demonstrate that changes in certain variables (such as energy from fish) did not cause large changes in the overall mortality, but did lead to large changes in the behaviour of the birds over the winter, which could indicate a reduction in fitness. All parameters tested had a statistically significant effect on mortality ($p<0.05$) for either an increase or decrease in the parameter value, and most parameters had a significant effect for both the increase and decrease. A decrease in prey abundance, prey energy density and assimilation efficiency caused a large negative effect on mortality, as did an increase in metabolic rate. The factors which had the greatest effect on mortality were gross energetic parameters which related directly to the avocet energy requirements.

Parameters relating to the feeding behaviour had a lesser effect on mortality than the gross energetic parameters, but still had significant effects. In particular, a decrease in capture efficiency and search area increased mortality by ~30%. Decreasing the number of prey items captured per sweep and increasing the handling time both increased mortality, but were not as important as capture efficiency and search area. The factors relating to interference (spatial aggregation factor and interference threshold) had very little effect on mortality.

The factors which had the strongest effect on mortality rate were also tested using the present-day sea level simulation, to test whether the model was sensitive to changes in the parameters. For this scenario, 25% increase or decrease in any individual parameter did not affect morality rate, apart from a decrease prey energy density, which marginally increased mortality rate to 5%.

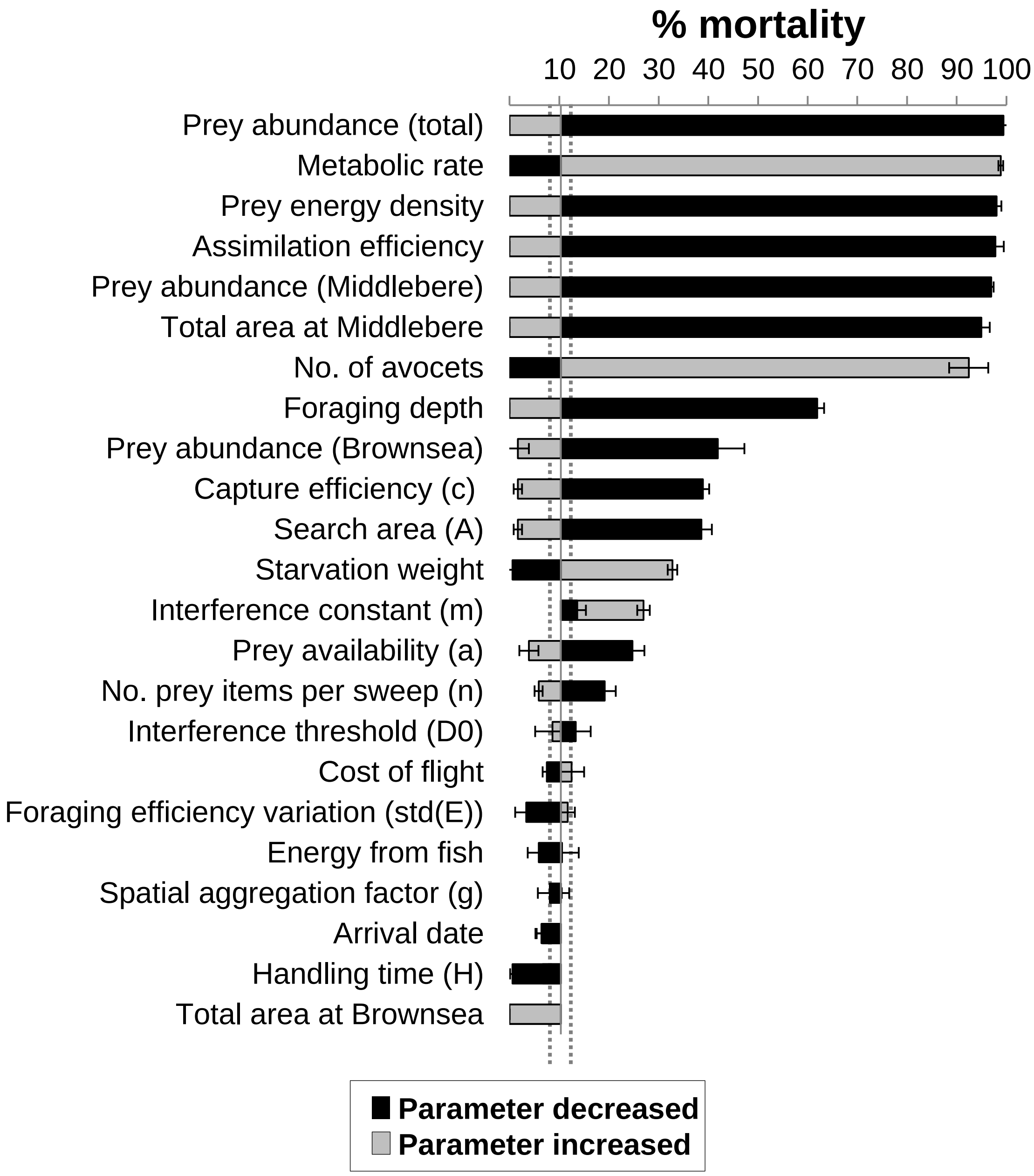


Figure 6.13 Sensitivity of predicted overwinter mortality to changes in parameter values. Solid vertical line indicates the mean % mortality for the baseline scenario (SLR 41.4 cm) and the dotted line represents the standard deviation of ten model runs. The bars show predicted mortality when parameters were increased (grey bar) or decreased (black bar) by 25%. Each bar represents the mean of 3 model runs, and error bars represent the standard deviation.

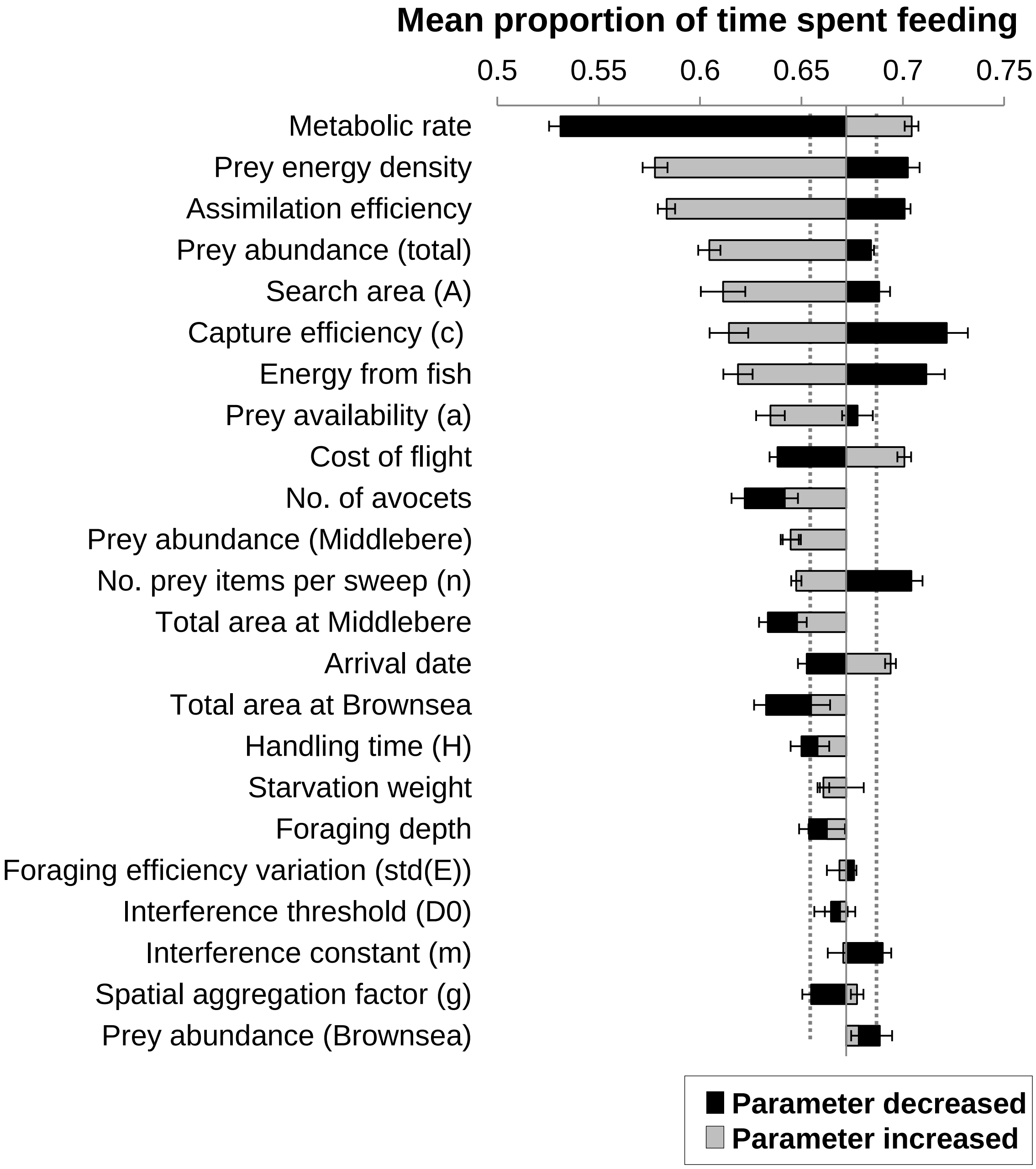


Figure 6.14 Sensitivity of predicted proportion of time foragers spent feeding to changes in parameter values. Solid vertical line indicates the mean proportion of time feeding for the baseline scenario (SLR 41.4 cm) and the dotted line represents the standard deviation of ten model runs. The bars show predicted proportion of time feeding when parameters were increased (grey bar) or decreased (black bar) by 25%. Each bar represents the mean of 3 model runs, and error bars represent the standard deviation.

6.5 Discussion

In this study, I developed an individual-based model (IBM) of avocets overwintering in Poole Harbour, to predict the potential impacts of future environmental changes to the site. The key finding was that maintenance of the present day avocet population depends on an energy source in addition to the benthic invertebrate resource in their current preferred feeding areas, Brownsea Island Lagoon and Middlebere Creek. This energy is most likely provided by small fish, as there were significant numbers of small fish bones found in the faecal samples of birds captured at Brownsea in October 2011. Furthermore, small fish are found in reasonably high densities in the Lagoon, at least during the summer (Wheeler 2012). Based on my estimate of the intake rate for socially foraging avocets (Chapter 4) as 0.0075 prey items s^{-1}, the required energy deficit of 6–8 kJ h^{-1} could be achieved by feeding on small fish at Brownsea for roughly 2 hours per day. However, we know very little about the spatial and seasonal variation in density of fish at Middlebere. Data from other European estuaries indicate small fish densities slightly higher than those found at Brownsea, with seasonal abundance being lowest during the winter months (Wheeler 2012; Cattrijsse et al. 1994; Drake et al. 2002). It is possible that creeks in the intertidal zone operate as a funnel to create locally high densities of nektonic prey (Cattrijsse et al. 1994). This is supported by the fact that social foraging at Middlebere commonly occurred in the creeks (*pers. obs*). Therefore, the extent to which the population will be affected by habitat loss in the future will be strongly dependent upon the availability of the nektonic food resource in the intertidal areas of the harbour.

If the birds are able to obtain a supply of fish that is available throughout the winter at similar densities to those which they currently obtain at Brownsea, then that even at the 2095 SLR projection of 41.4 cm, the birds will still be able to obtain sufficient energy to maintain their reserves throughout the winter.

6.5.1 Sea-level rise – and why predicted mortality rates are a ‘worst case scenario’

I used a simple method for modelling the effects of SLR, by shifting the baseline for the present day tidal curve for each patch. The result was a reduction in exposure time of the patches. However, this method does not take into account future changes in estuary morphology, such as dieback of the *Spartina* saltmarsh (Raybould 2005) and landward migration or vertical accretion of intertidal mudflats through sediment deposition (Mcleod et al. 2010). The precise changes that will occur will also be sensitive to changes in the hydrological regime and wind, so are difficult to predict (Allen & Duffy 1998). However, as the land surrounding Middlebere is an RSPB reserve, with no man-made infrastructure to restrict the flow, coastal squeeze is not an issue. Furthermore, the flat topography around the upper reaches of the creek will be amenable to horizontal inland migration. Therefore, the degree of intertidal habitat loss due to SLR in the model represents a “worst-case scenario”.

Poole Harbour is subject to a double high tide effect, which reduces the mudflat exposure time, relative to other UK estuaries (Humphreys & May 2005). However, the model showed that with the current prey densities found in Poole Harbour, avocets are able to meet their energy requirements with relatively short periods of exposure. Furthermore, due to their longer legs and bills, and ability to feed through the water column, avocets are able to forage in deeper water compared with other shorebird species. Hence, while SLR of 40 cm was predicted to cause 100% mortality in dunlin, redshank, black-tailed godwit, oystercatcher and curlew (Durell et al. 2005), some avocets would survive at this level of SLR.

It is also worth noting, that while the model was designed to predict mortality as a consequence of insufficient resources in the harbour, in reality it is an unlikely outcome. A reduction in the quality of a single site for the birds is likely to lead to dispersive behaviour, including dispersion to lower quality sites, as has been observed in black-tailed godwits (Gill et al. 2001b). A certain amount of dispersion is expected to occur within the harbour itself, including to lesser used sites, such as Holes Bay, which has already seen an increase in avocet numbers in recent winters (Pickess 2007), particularly in response to extreme cold weather, as it tends to be a few degrees warmer there (*pers. obs*).

6.5.2 Sensitivity analysis

I tested the effect of an increase or decrease of 25% in each parameter on mortality rate and proportion of time spent feeding. The latter was important because mortality rates were quite low, so factors which reduced mortality rate significantly were not discernible from factors which only reduced it slightly. Furthermore, certain factors, such as energy obtained from fish and arrival date were important in determining the behaviour of the birds in the early stages of the winter, and therefore could be important for predicting the response of the birds to future changes, but had little impact on the overall mortality. This indicates that the model birds were able to adapt their behaviour (e.g. by increasing the proportion of time spent feeding) to keep mortality low, so sensitivity of the parameters are not necessarily reflected in the mortality rates. Furthermore, some variables, such as energy obtained by fish, did not have a significant effect on mortality when varied by 25%, but if this variable is completely removed from the model, then predicted mortality was much higher (44%).

As with previous shorebird IBMs, the model was highly sensitive to gross energetic parameters, such as metabolic rate and assimilation efficiency (Stillman et al. 2000b). The model was also highly sensitive to prey abundance. The prey abundance at Middlebere was more important than that at Brownsea, presumably due to the larger size of Middlebere. Prey availability was less important. As this parameter applied only to the larger prey types, which were eaten less regularly than smaller prey items, prey availability was not as important as overall prey abundance. In addition, the model was sensitive to prey energy density, suggesting that harsh winters that affect the relative energy content of prey such as *H. diversicolor* (Zwarts & Wanink 1993), could affect the population. Increasing the total area available for foraging at Middlebere and Brownsea led to a reduction in mortality. Conversely, decreasing the total area available at Brownsea had no effect, whereas decreasing the total area available at Middlebere had a strong effect on mortality. This indicates that the birds were able to compensate for the reduced feeding area at Brownsea by increasing their feeding effort at Middlebere, even under SLR. In fact, if the model birds were not constrained to forage on Brownsea for the first 61 days, the area available at Brownsea was even less important.

Two behavioural parameters had a reasonably large effect on mortality rates: capture efficiency and search area. Number of items captured per sweep and handling time were less important, but still had an effect. A decrease in handling time reduced mortality, but increasing handling time did not increase mortality.

Increasing the number of birds present in the model increased mortality, suggesting that Poole Harbour is probably quite close to capacity in terms of the number of avocets it can support. This is supported by the fact that while numbers have steadily increased since the 1990s, they appear to have plateaued in recent years (Pickess 2007; Holt et al. 2012).

Factors relating to interference had very little impact on model predictions. This contrasts with IBMs of redshank and oystercatchers, in which interference has been shown to be important (Stillman et al. 2000a; Yates et al. 2000). Two key mechanisms of interference competition in shorebirds are kleptoparasitism and prey depression (Triplet et al. 1999; Stillman et al. 2000a). Kleptoparasitism is profitable when large prey and long handling times are involved (Ens et al. 1990); however, as the avocets mainly feed on relatively small prey with short handling time, it does not commonly occur. Interference by prey depression could feasibly impact birds visually foraging on large polychaetes that burrow to depths inaccessible to the bill sweep depth. However, depression of small prey such as *Corophium* by nearby foragers, which is known to affect redshank (Yates et al. 2000; Stillman et al. 2000a), would not affect avocet because these prey are not hunted visually, and are vulnerable to predation even when retreated into burrows. In the avocet model, interference only affected visually foraging birds when the density was >100 birds ha^{-1}, and as visual foraging was a less common feeding strategy in the model birds than benthic tactile foraging, interference had only a minor effect on model outputs.

The model also showed that the rate of depletion of invertebrate resources at Brownsea Island Lagoon at the beginning of the winter was quite sensitive to the arrival date of the birds. Arrival date was modelled as a uniform distribution, so there was inherent variability in the average arrival date of the birds. This led to a variability of ~15 days in the predicted departure date from Brownsea (see spread of simulation results in Figure 6.6). This has important implications for the real birds, because it is uncertain how climate change will affect the timing of autumnal migrations (Anthes 2004; Adamík & Pietruszková 2008). If the arrival of avocets in Poole Harbour is much earlier, prey depletion will make it more difficult to meet their energetic requirements throughout the winter.

6.5.3 Model evaluation: how well did the model predict observed patterns?

The comparison of model predictions with observed overwinter foraging behaviour of the Poole Harbour avocet population revealed that the model predicted some aspects of the foraging behaviour well. The spatial distribution of the birds throughout the winter, in terms of the relative usage of each patch was similar to the observed patterns. In particular the relatively higher proportion of time spent at Brownsea was close to the observed pattern, even when the population was not constrained to foraging at Brownsea alone for the first 61 days. However, the model did not reproduce the tendency for some of the birds to remain at Brownsea at all times, even when higher intake rates could be achieved on the intertidal mudflats. This indicates that the real birds are not necessarily following a short term optimal foraging strategy: they have an inherent preference to stay on the non-tidal lagoon. This is also evidenced by the fact that the model did not predict the tendency for the avocets to stay on Brownsea for the first 61 days until local resource depletion triggers their search for alternative foraging grounds (i.e. Middlebere). To reproduce this pattern it had to be ‘hardwired’ into the model.

Fish abundance at Brownsea may hold the key to this inherent preference; however, this is difficult to show definitively, as there are currently no comparable data on fish abundance at Middlebere. Furthermore, if there is a seasonal variability in this nektonic resource at Brownsea, this could be a trigger for the departure for Middlebere around November 1st, in addition to the depletion in invertebrate resource that is observed between September and November. Also, as the preference for Brownsea continues into January–March, when fish foraging at Brownsea was rarely observed, it seems that the preference may instead be due to the suitability of roosting habitat at Brownsea. Here birds are not constantly moving to avoid incoming tides, there is shelter from strong winds, and there is less competition for space with larger wildfowl species, such as brent geese (*Branta bernicla* [Linneaus 1758]), which occured in high densities around the creek edges at Middlebere.

There was a clear spatial pattern in the observed foraging densities at Brownsea (Figure 8c), that was not captured in the model, as Brownsea was represented as a single patch, as there were no consistent spatial patterns in invertebrate densities within the lagoon throughout the winter. The spatial foraging patterns at Brownsea showed no clear correlation with invertebrate abundance; however, foraging was most intense in close proximity to the favoured roost site. The inherent preference for Brownsea over Middlebere may be a similar phenomenon operating at a larger scale: an inherent preference to forage close to the roost site. A study of American avocets (*Recurvirostra americana*) in Humboldt Bay, California, reported that avocets rarely foraged >3 km away from their roost site (Evans & Harris 1994).

The aspect of behaviour that was least well predicted by the model was the proportion of time spent feeding. Compared with model predictions, the real birds spent relatively less time feeding at Brownsea and relatively more time feeding at Middlebere. This is also likely to be related to the inherent preference to use Brownsea as a roost site – the proportion of birds feeding at Brownsea is lower for the real birds, because a proportion of birds always remain on the lagoon not feeding. Conversely, when the real birds go to Middlebere, they do so to feed. Hence, the proportion of birds foraging while at Middlebere was higher in the real birds than in the model birds. As the birds were able to achieve their energy requirements fairly easily at Middlebere, they only spent a low proportion of time feeding. Once the real birds have obtained their energy requirements, they leave Middlebere, and return to Brownsea, whereas the model birds generally stayed at Middlebere until they were forced to leave by the incoming tide.

Another possible reason for the disparateness in proportion of time spent feeding in real and model birds, is that the foraging data were collected during daylight hours. If the real birds spent proportionally more time feeding at night at Brownsea, this would account for the observed proportion of time feeding being lower than the model predictions. It is quite feasible that birds foraged at night on the lagoon as ambient light levels from the harbour ensure that the lagoon is never completely dark even on moonless nights. The degree to which night feeding is important to avocets varies between studies and appears to be context specific (Hötker 1999b; Lourenço et al. 2008; Zwarts et al. 1990).

Another pattern that the model reproduced accurately was for the birds at Brownsea to spend an increasing proportion of time feeding as the winter progressed, which was consistent with the observed pattern of decreasing prey abundance at Brownsea as the winter progressed, necessitating a greater feeding effort required to fulfil energy demands.

The model predicted that at current environmental conditions, the overwinter mortality of the population is zero. It is difficult to be certain about mortality rates of migratory shorebird populations as, with the exception of oystercatchers, there is a dearth of information on their mortality rates in the south of the UK (Durell et al. 2006; Durell 2000; Goss-Custard & Durell 1984). However, the numbers arriving in the harbour each year have risen steadily since 1990s (Holt et al. 2012), which indicates that the model prediction of low mortality rate in the present population is likely to be realistic. Furthermore, the population in the harbour is more than likely a composite of several breeding populations, as colour ring sightings have identified birds that were ringed as chicks in France, Holland and Cambridgeshire, thus the numbers arriving in the harbour each year will be dependent on conditions at multiple sites and may be subject to seasonal compensation effects (Harrison et al. 2011). Furthermore, the body mass data collected from avocets ringed in the harbour in September and October were in the upper estimates for the masses of adult avocets, indicating that the birds were in good condition, at least at the beginning of the winter.

While the current combination of parameters seems to reproduce the behaviour of the real birds reasonably well, it is feasible that other parameter combinations could reproduce the observed patterns equally well. Where possible in the model, I have used data from the real birds to derive parameter estimates (e.g. variation in bill length to determine differences in forager efficiency, estimates of swallow rates to determine capture efficiency, and data on real foraging behaviour to determine the functional response).

6.5.4 Importance of other food resources

I tested the consequences of including hydrobiid snails and small bivalves in the avocet diet, as these prey types are found in high densities at Brownsea. However, if these prey types were included, the avocets had sufficient energy to sustain them at Brownsea beyond November 1st, and the model predicted that the abundance of these prey type would deplete between September and November. However, observed abundance of this prey type increased dramatically over this time period. In addition, there were no traces of hard shell material found in the avocet faecal samples. Therefore I concluded that these prey types were not commonly included in the avocet diet. It may be that these prey were avoided due to the high shell:flesh ratio. In Chapter 3, I showed that the spatial distribution of Hydrobiidae was patchy in the lagoon, and samples tended to be either worm dominated or snail dominated. Therefore, it is plausible that this spatial patchiness enables the avocets to avoid snail dominated areas, so they are able to avoid eating high numbers of this prey type, even though their sweeping mechanism is “non-specific”. The increase in abundance of Hydrobiidae between September and November also provides another possible trigger for the departure of avocets from Brownsea Lagoon – as the proportion of ‘unfavourable’ prey at the site increases, it becomes increasingly difficult to avoid the snail-dominated patches.

6.5.5 Recommendations for further work

Possible extensions of this work include identification of thresholds for invertebrate prey abundance that would lead to a reduction in avocet survival, and how likely the natural annual fluctuations in prey abundance would be to decrease prey availability below these thresholds at the various SLR scenarios. To make the model more generalizable to other study sites, a mechanistic linkage between the environment and the avocet capture efficiency, which was estimated separately for the Brownsea and Middlebere based on swallowing rates at each site, needs to be determined. It is likely that this factor is related to sediment grain size (Quammen 1982; Tjallingii 1972) – larger sediment grain sizes such as those found at Brownsea, interfere with the sweeping mechanism, possibly by making prey detection more difficult. A study of capture efficiency at a number of sites with different sediment properties would be necessary to demonstrate this mechanistic link. This may also improve the accuracy of future predictions, as it is likely that SLR will change the distribution of the sediments within avocet feeding areas.

As the importance of fish in the avocet diet is not widely recognised in the literature, it was not until the discovery of fish bones in the avocet faecal samples that it became apparent how potentially important this food resource was for the birds. For this reason it was not possible to apply the same level of sampling effort to the nektonic prey resource as was expended on the benthic invertebrate resource. Hence there are currently no data on how the abundance of fish varies seasonally and spatially, between patches. While a reliable method has been developed for determining the density of nektonic prey in the non-tidal lagoon (Wheeler 2012), it is difficult to conceive of a sampling methodology that would accurately estimate the density of fish in the tidal patches, during the periods that the water is shallow enough for foraging avocets, particularly considering the difficulty in accessing the mudflat at any time other than the highest spring tide. Although sampling in the drainage channels of the intertidal patches may provide some insight (Drake et al. 2002). However, establishing the functional response for avocets feeding on fish in shallow water would allow a more accurate representation of foraging on this prey type in the model. This could be achieved using a captive population in a tank seeded with known densities of fish. If more was known about the efficiency of fish capture by avocets, it would be possible to obtain estimates of fish densities in the different patches by observing foraging behaviour.

Finally, there is a lack of species-specific data on energetics of foraging, and many of the parameters included in this model were determined using allometric equations. Further work into this area would substantially improve the predictive accuracy of the models.

6.5.6 Management implications

According to the Poole Harbour SPA designation, there is a requirement to maintain or restore “the extent and distribution of the habitats of the qualifying feature” and “the structure and function of the habitats of the qualifying features” (Natural England 2012). As such, if Brownsea Island Lagoon is to succumb to rising sea levels in the long term, there is a requirement to create alternative habitat to offset this loss, which is suitable for the avocet population.

In considering the priorities for creation of new saline lagoon, to ensure the site is suitable for avocets it may be most important to include suitable roosting space, such as the narrow sand spit ‘banana island’ in Brownsea Island Lagoon. Furthermore, monitoring the nektonic species in the new lagoon may be just as important, or more important, than monitoring the benthic invertebrate abundances in ensuring the character of the lagoon is suitable for the avocet population. It will also be essential to ensure that the water depth in the lagoon will permit foraging on fish (roughly 10–25 cm). Furthermore, lagoons should be located in close proximity to the sea, with designs that allow sufficient water exchange to ensure colonisation and persistence of fish populations.

Chapter 7: Overall discussion and conclusions

7.1 Introduction

In the context of quickening rates of environmental changes in coastal ecosystems, there is a need for process-based models that provide quantitative predictions on the ecological effects of change. Such models provide evidence for strategic planning by coastal managers and policy makers. The overall aim of this thesis was to develop an individual-based model (IBM) to assess the effect of sea-level rise on the overwintering avocet population of Poole Harbour. This population represents a nationally and internationally important overwintering colony, for which the site is designated a Special Protection Area (SPA). Thus there is significant interest, from both a conservation and statutory standpoint, in ensuring this population will not suffer from the effects of anthropogenically-induced changes to the site.

The benthic invertebrate landscape is a key component of an IBM; however, in soft sediment habitats it is both expensive and time-consuming to collect these data, and there is limited understanding of the factors which regulate the seasonal and annual variation in biomass availability. Therefore, I investigated the extent to which soft sediment benthic faunal abundance can be explained by physical and biological factors (Chapter 2) and the degree of annual and seasonal variation in the biota in the main avocet feeding grounds within Poole Harbour (Chapter 3).

Previous shorebird IBMs have focussed on species with a similar foraging ecology ("probers"). The avocet has a unique foraging mechanism (a "sweeper") and I developed a mechanistic model of its foraging strategies that I used to determine intake rates (Chapter 4). In addition, I investigated the effects of a range of physical and biological drivers on foraging behaviour, including social foraging (Chapter 5). Finally, I used the benthic invertebrate data and the avocet behavioural data to parameterise the IBM, which I validated with data I collected on the distribution and time-budget data of avocets in Poole Harbour.

In this final chapter, I synthesise the key findings of my study, outline management implications of the work, and comment on the limitations of the study and the potential extensions of the research.

7.2 Synthesis of findings

7.2.1 Benthic invertebrate modelling

In Chapter 2 I tested the degree of association between environmental parameters and soft sediment intertidal benthic fauna. There is a paucity of such studies due to the lack of well-resolved, fine-scale hydrodynamic models for soft sediment habitats. Therefore, this study represents a valuable contribution to the understanding of drivers of marine community compositional change along environmental gradients. I compared the outputs of two modelling approaches: Gradient Forest, a new technique based on machine learning (Ellis et al. 2012), and BIO-ENV, a routine within PRIMER that has been widely used by both researchers and practitioners for many years (Clarke 1993). To my knowledge, these two methods have not been directly compared. I showed that additional information is extracted from the data using the machine learning method, including the identification of thresholds in environmental variables above which considerable change in benthic community structure occurred (e.g. wave height of ≥8 cm and organic content of ≥2%). These thresholds have potential implications for marine spatial planning and site monitoring and management. Furthermore, I demonstrated that fine-scale hydrodynamic models can be used to generate improved predictions of intertidal invertebrate distributions. Crucially, this study also highlighted the occurrence of temporal fluctuations in the associations between the environment and the biota, which highlights the danger of applying surveys from one year to other years.

In Chapter 3, I showed that the factors driving the spatial distribution of invertebrates differed between a tidal and non-tidal habitat. In general, non-tidal saline lagoon fauna was characterised by patchy distributions and a tendency for smaller individuals in higher numbers, whereas the communities on the intertidal mudflat were more uniform, with a predictable spatial gradient in invertebrate communities down the length of the creek. This demonstrated that there are measurable differences in the fauna of artificial non-tidal habitats and intertidal mudflats, which need to be taken into account when considering the utility of artificial habitats in offsetting the effects of sea-level rise on bird populations. There were seasonal fluctuations in the biomass, as well as the contributions of various taxa, and the abiotic factors driving these patterns varied in importance seasonally. This highlighted the necessity of including data from several time periods throughout the year to inform the IBM (Chapter 6).

7.2.2 Avocet foraging ecology

The foraging ecology of pied avocets had not previously been studied to the level of mechanistic detail required to explicitly model this species in an IBM. In Chapter 4 I developed functional response models for avocet feeding strategies to link avocet intake rates to prey availability. By comparing the predictions of the functional response model to intake rates measured in the field, I was able to determine the efficiency of prey capture at each of my study sites, and calibrate the functional response model. Crucially, this highlighted the importance of prey “catchability” (which incorporated prey availability and the efficiency of capture) to accurately determine intake rates. The predictions of the IBM were shown to be sensitive to these parameters in Chapter 6. The potential for large energetic rewards from feeding on pelagic prey, assuming a mechanism for creating locally high prey densities is available, was also highlighted by this study. This concept was explored further in Chapter 5, which examined when and how social foraging was used in the avocet population of Poole Harbour. The implications of the observed feeding and roosting habitat preferences determined in Chapter 5 are discussed below, but in general, the study highlighted the importance of considering net energy intake rates and time-budget data in assessing habitat quality, as bird numbers alone can be misleading.

This thesis has also highlighted some important points about the trophic niche of the avocet. Unlike some shorebird species that are confined to probing or pecking at benthic prey such as ragworm and *Corophium* due to the morphology of their bills, the avocet has the capacity to switch to feeding at higher trophic levels, allowing them to fill their energetic requirements in less time. This capacity may offer some resilience to avocets in areas that future sea-level rise threatens to reduce the amount of time available for shorebirds to feed on intertidal mudflat. While some other shorebird species are known to occasionally feed on fish, such as the greenshank, and one other species, the spotted redshank is known to exhibit a foraging mechanism similar to the pelagic tactile method described in Chapter 4, neither of these species are known to form large social foraging flocks as the avocets do, and thus, are not able to capture pelagic prey as efficiently as the avocet. The avocet trophic niche may depend on site-specific factors: for example high reliance on pelagic prey may only be possible if a physical mechanism for locally enhancing prey densities is available, such as the combined effects of tidal action and the creeks at Middlebere, or if locally high prey densities can be created by the birds themselves, which may require a minimum number of birds (social foraging did not occur at Brownsea Island Lagoon when there were fewer than 500 avocet present).

7.2.3 Avocet individual-based model (IBM)

The key quantitative output of the IBM was that sea-level rise did not affect the mortality rates of the avocet population in SLR scenarios up to and including 24.4 cm. The fitness of the population was affected by SLR scenarios of 18.8 cm and above. However, the reduction in fitness due to SLR was offset by the presence of Brownsea Island Lagoon at scenarios of 18.8 cm and 24.4 cm SLR. Furthermore, the mortality rates at 41.4 cm SLR were significantly reduced by the presence of Brownsea Lagoon. This is a significant finding as according to current projections, Brownsea Lagoon will revert back to intertidal habitat in the next 40–50 years without considerable investment to fortify the present sea wall. Thus, if site managers decide not to preserve this site, this study provides strong evidence that additional non-tidal habitat will need to be created in order to sustain the avocet population at present-day numbers.

Another key finding was that in order for artificial non-tidal habitats to be effective providing feeding habitat to offset the effects of SLR for avocet populations they must contain an adequate density of pelagic prey. More generally, as avocets are quite large shorebirds, and their prey is quite small, for any site to provide adequate food for a large population, the benthic prey alone is unlikely to provide sufficient energy to sustain the population.

7.3 Recommendations for management

One of the key findings of this study was that the presence of a non-tidal artificial foraging habitat will offset the effects of SLR on the Poole Harbour avocet population. The same is likely to be true for other similar sites. Therefore, there is strong justification for the creation of such habitat. However, based on the findings of this study, habitat should conform to the following design criteria to create maximum benefit for overwintering pied avocets:

- *Sediment composition* – the upper 2 cm of sediments in feeding habitat should contain **minimal amounts of sediment with particles >63 µm** as this lowers feeding rate by decreasing the capture efficiency (evidenced by a significant negative effect of coarse sediment on intake rates in Chapter 5).
- *Water depth* – to ensure that avocets can feed efficiently by both benthic and pelagic tactile foraging methods, the water should be **between 10 and 20 cm**. Pelagic tactile foraging was never observed in this study in water shallower than 1 cm, and it was most commonly observed in water above avocet knee-depth. However, there was a reduction in intake rates in water deep enough for the avocets to swim. Other studies have shown this depth range to support the greatest diversity of wildfowl and waders (Colwell & Taft 2000; Ma et al. 2009), so this measure is likely to be beneficial to species other than avocet.
- Seawater exchange – recruitment of benthic and pelagic prey resources may be enhanced by ensuring effective exchange with sea water using a **system of floodgates or sluices**. This was supported by the casual observation in this study that pelagic prey occurred in the highest densities in close proximity to the sluice gate at the south end of Brownsea Lagoon. Other studies have drawn similar conclusions (Brusati et al. 2001; Collazo et al. 2002; Ma et al. 2009). Effective exchange will ensure also **salinity** does not fall below optimum levels for maintenance of high biomass of key prey types (**18–24 ppt**) (Bamber et al. 2001).
- *Roosting habitat* – as avocets appear to have a preference to forage close to their roosting habitat, roosting habitat should be provided in close proximity to the feeding habitat. The preferred roosting habitat at Brownsea consisted of a **vegetation-free sandy spit**, no more than a few cm above the water level However, care must be taken to not contaminate the foraging habitat with excessive amounts of sand. This study showed that the sandy spit at Brownsea had by far the highest number of bird-roosting hours than any other roost site within Poole Harbour.
- *Shelter* – a degree of **shelter from the prevailing winds** is likely to be beneficial, as intake rates were found to be lower in moderate and strong breezes at the exposed

study site (Middlebere). Particularly in light of the fact that two of the key predicted effects of climate change to coastal ecosystems in Europe are increased storminess and windiness (Watt et al. 2005), and the degree of shelter can have a large effect on energy expenditure in overwintering shorebirds (Wiersma & Piersma 1994)**.** Furthermore, wind speed has been reported to negatively correlate with the number of American avocets (*Recurvirostra americana*) foraging on mudflats in Humboldt Bay, California (Dodd & Colwell 1998).

Furthermore, as the IBM demonstrated the critical importance of nektonic prey in sustaining large populations of overwintering avocets, **increased nektonic monitoring effort** is recommended for sites which are designated or being managed for avocets.

7.4 Study limitations and suggestions for further research

One of the fundamental limitations of this study is that it is essentially a case study of a single site. This particularly applies to the invertebrate modelling work: for example, to determine whether the threshold for changes in community structure environments with wave heights of >8 cm is a universally occurring pattern or a unique characteristic of Poole Harbour, studies at other sites are required. Therefore, the generality and wider applicability of some of the conclusions could be demonstrated by conducting similar studies at other sites, and through carefully controlled experimental design. The effects of wave height in particular warrant further investigations as increases in storminess and windiness are forecasted for the UK (Watt et al. 2005), and changes in prevailing wind direction and strength could have impacts on the fetch and degree of sheltering in many UK harbours and estuaries.

In sampling only the intertidal zone in Poole Harbour, I may have underexploited the true utility of fine-scale hydrodynamic models in predicting benthic community composition. While Poole Harbour intertidal zone contains a mosaic of habitat types including mudflat, sandflat and saltmarsh, the range of hydrodynamic conditions occurring in these habitats was fairly restricted. By extending the boundaries of the study site to include the sub-tidal channels, a much stronger environmental-biota association might be revealed.

In general, the approach I have taken to modelling invertebrate species abundance is *correlative* in nature (rather than process-based as in the IBM). As such there is difficulty in determining whether the associations identified are causally linked. To overcome this problem, I critically examined the biology of the species that showed significant relationships with environmental gradients to determine whether the associations were likely to be due to the effect of the gradient (e.g. species requiring sandy substrates to build their burrow showed associations with median particle size).

In calculation of biomass availability, I used a single length—biomass relationship, based on worms that were collected from Brownsea Island Lagoon in November 2010. Therefore, the study assumed the length—biomass relationship did not change throughout the winter, and was similar at Brownsea and Middlebere. There is evidence that body weights of similarly sized prey can vary 30–60% in summer and winter; however, as the reference worms were collected in the middle of the winter, and the model only considered winter months, the variation is likely to be smaller than this. As reference worms were collected in a particularly cold month the biomass estimate was likely to be conservative.

Due to the inability to accurately estimate the densities of nektonic prey found at the study sites, it was not possible to calibrate a functional response model for pelagic tactile foraging (i.e. I could not determine the efficiency of capture). Therefore, I was limited in the amount of mechanistic detail I could include in the IBM for feeding on fish. This included a detailed representation of the effects of social foraging on local prey enhancement and the potential impact on intake rates. To increase understanding of the functional response of avocets feeding on fish, experiments could be designed based on pools stocked with known densities of fish. Similar experiments have been conducted for Ciconiiformes in the Florida Everglades – although they examined the density of birds feeding, rather than feeding rates (Gawlik 2002). This would make it possible to explicitly test the effects of social foraging aggregations in more detail using an IBM.

Sea-level rise in the IBM was modelled in a basic fashion. I simply modelled an increase in sea levels, assuming the present-day harbour morphology, not allowing for landward migration of intertidal habitat. As the extent of landward migration of habitat in Poole Harbour is unknown, this assumption was precautionary. The model also assumed the present-day invertebrate distribution remained constant under SLR scenarios. It is expected under SLR that many estuaries will become wider and more energetic, and thus have an increased sediment particle size (Austin et al. 2001). However, the extent to which it will be true for Poole Harbour is uncertain, due to its sheltered nature, particularly in the mudflats in the southwest of the harbour, which are used by the avocet population. As the northern shores of the harbour are more heavily defended, intertidal habitat in this region of the harbour is more vulnerable to coastal squeeze, but this is unlikely to affect the avocet population.

As with other shorebird IBMs that have been developed (e.g. Stillman et al. 2000b), the avocet model was particularly sensitive to gross energetic parameters. Uncertainty surrounds these parameters, which are usually determined using allometric relationships. Further research into the bioenergetics of avocets would be valuable, particularly as this is a species that tends to feed mostly on prey that are small relative to its body size (e.g. worms and *Corophium*), compared with other large waders such as curlew (*Numenius arquata* [Linneaus 1758]) and oystercatchers (*Haematopus ostralegus* [1758]) that feed on shellfish and larger worms.

As IBM design, implementation and analysis is an iterative process (Railsback & Grimm 2011), there is scope for building upon the current model as new data become available – detailed data on avocet bioenergetics, the seasonal abundance of nektonic prey in the harbour, mechanistic detail on the functional response for feeding on fish, and future changes to harbour morphology or sediment composition could all be included at a later stage if and when the data are available. There is also scope for applying the IBM in its current form to a range of other research questions. As Chapters 2 and 3 provided evidence of significant inter-annual variation in invertebrate availability, it would be worthwhile to identify thresholds of various invertebrate taxa that could lead to adverse impacts on the avocet population, and determine whether these thresholds occur within the range of ‘natural’ variability. The IBM could also be used to test the effects of a range of future management proposals on the avocet population.

7.5 Closing remarks

This thesis has detailed the development of an individual-based model to predict the effects of sea-level rise on the avocet population of Poole Harbour. The completion of this thesis coincides with the publication of the International Panel for Climate Change (IPCC) 5th Assessment Report, stating that we can be highly confident that the rate of sea-level rise in the past 150 years has been greater than the mean rate of the previous two millennia (IPCC, 2013), thus the need for studies to predict the ecological effects of climate change is greater than ever. This study has supplied a quantitative prediction as to the level of sea-level rise that is likely to cause a decrease in fitness to the population and demonstrated the benefit of a non-tidal artificial habitat in offsetting these effects. I have produced specific management recommendations which apply to Poole Harbour, and more widely to similar habitats seeking to offset the effects of habitat loss due to SLR on avocet populations. This study has furthered the understanding of avocet foraging ecology, and the factors that determine the spatial and seasonal availability of benthic invertebrates in soft sediment habitats, and in doing so contributes to the evidence base for managing the effects of environmental change in coastal habitats.

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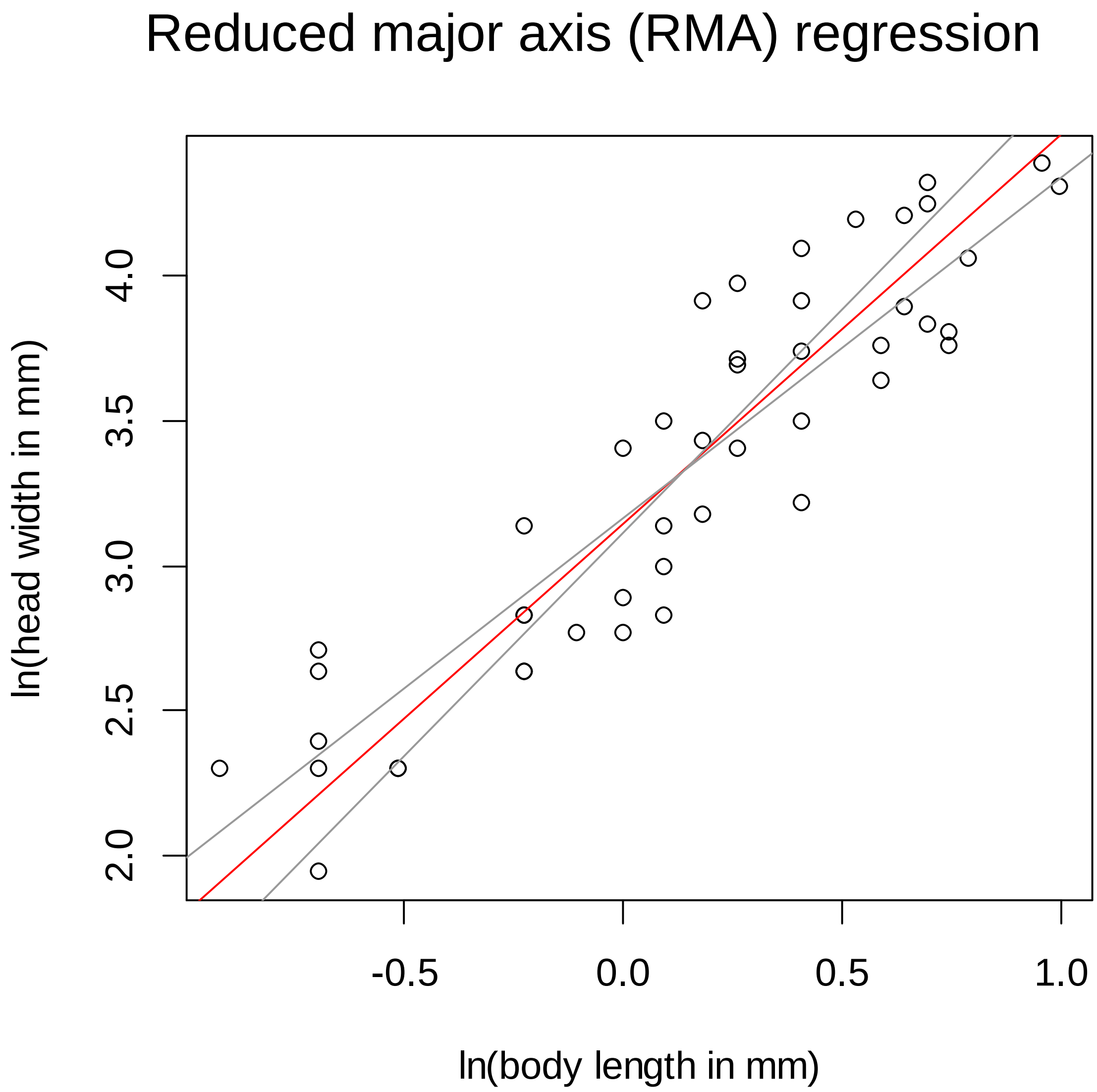
Appendix 1. The relationship between *Hediste diversicolor* head width and body length.



RMA linear regression output

Slope	**intercept**	**n**	**r**	**R^2**	**P (2-tailed)**
1.344008	3.140542	46	0.915	0.837	<0.0001

Appendix 2(a). Species list for Brownsea Island Lagoon.

ACTINIARIA
*Nematostella vectensis***

PHYLUM NEMATODA
Nematoda indet.

PHYLUM ANNELIDA
Aphelochaeta marioni
Capitella capitata
Caulleriella zetlandica
Desdemona ornata
Enchytraeidae indet
Hediste diversicolor
Polydora cornuta
Pygospio elegans
Streblospio shrubsolii
Tubificoides benedi
Tubificoides pseudogaster

SUBPHYLUM CRUSTACEA
Ostracoda sp.
Praunus inermis

Amphipoda
Corophium volutator
Melita palmata
Monocorophium insidiosum

Isopoda
*Idotea chelipes**
Lekanesphaera rugicauda

Decapopda
Palaemonetes varians

PHYLUM MOLLUSCA
Abra tennuis
*Cerastoderma glaucum**
*Ecrobia ventrosa**
Peringia ulvae

PHYLUM INSECTA
Chironomidae
Dolichopodidae

*lagoon specialist species

**lagoon specialist protected under Schedule 5 of the Wildlife and Countryside Act (1981)

Appendix 2(b). Species list for Middlebere Creek.

ACTINIARIA
Actinaria indet.

PHYLUM NEMATODA
Nematoda indet.

PHYLUM NEMERTEA
Nemertea indet.

PHYLUM ANNELIDA
Aphelochaeta marioni
Capitella capitata
Desdemona ornata
Eteone longa
Hediste diversicolor
Melinna palmate
Nephtys hombergii
Polydora cornuta
Pygospio elegans
Streblospio shrubsolii
Tubificoides benedi
Tubificoides pseudogaster

SUBPHYLUM CRUSTACEA
Ostracoda sp.

Amphipoda
Corophium volutator

Isopoda
Cyathura carinata

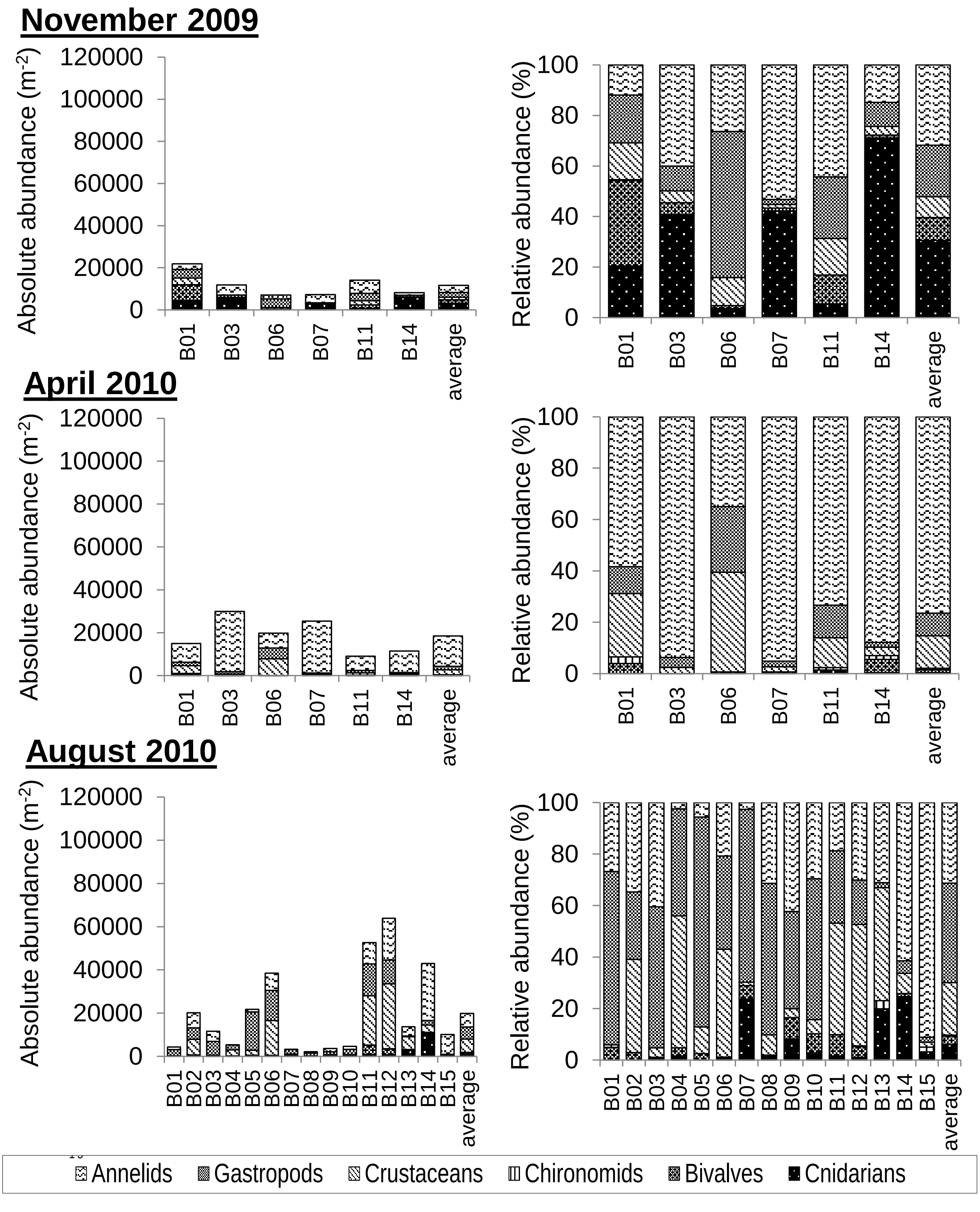
Decapopda
Palaemonetes varians

PHYLUM MOLLUSCA
Abra tennuis
Cerastoderma glaucum
Cerastoderma edule
Macoma balthica
Mya arenaria
Peringia ulvae
Retusa obtusa
Scrobicularia plana
Venerupis philippinarum

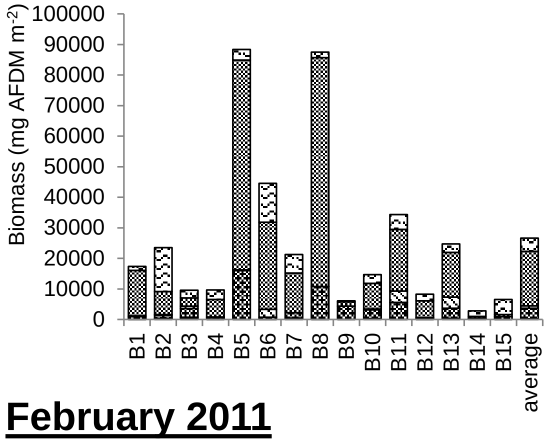
PHYLUM INSECTA
Chironomidae

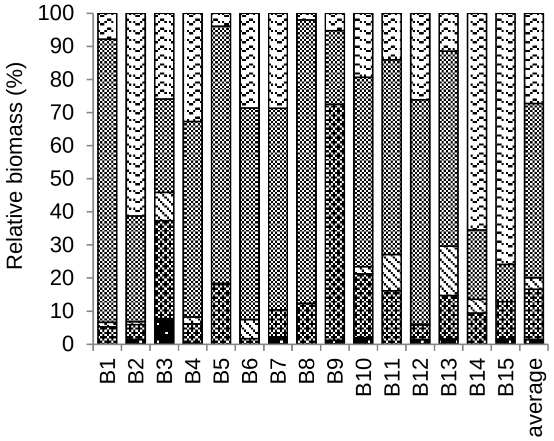
Chironomidae

Appendix 3(a). Seasonal variation in invertebrate abundance in Brownsea Island Lagoon.

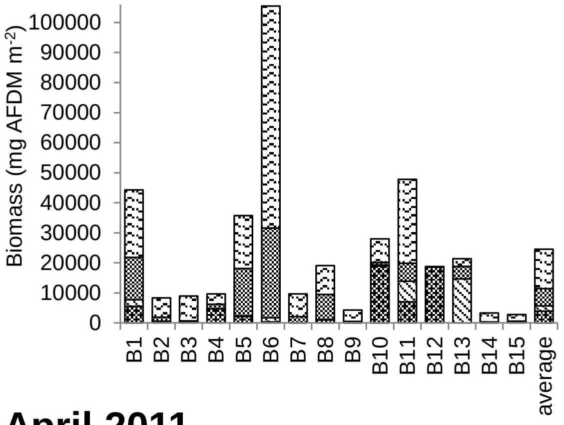


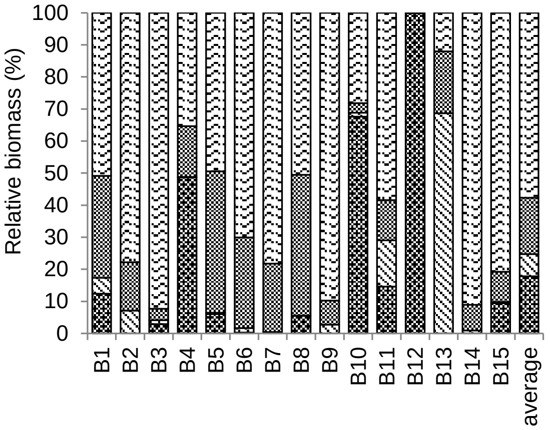
November 2010



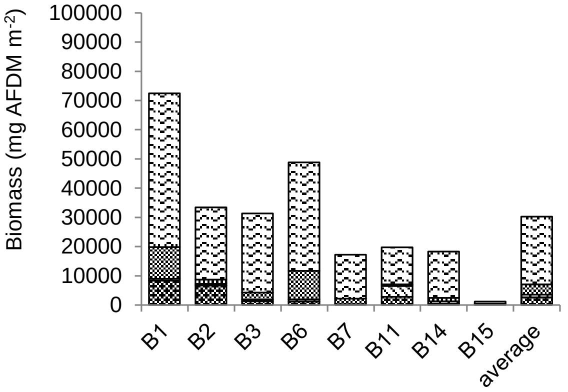


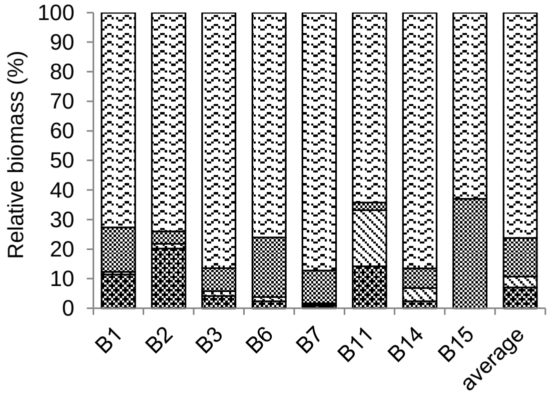
February 2011





April 2011

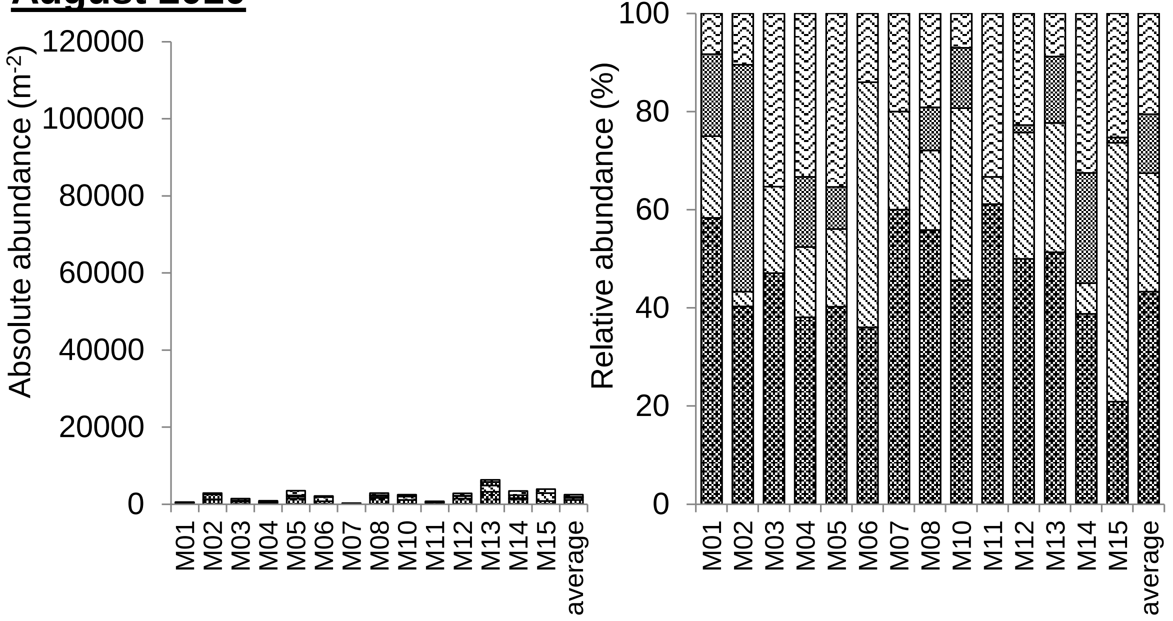




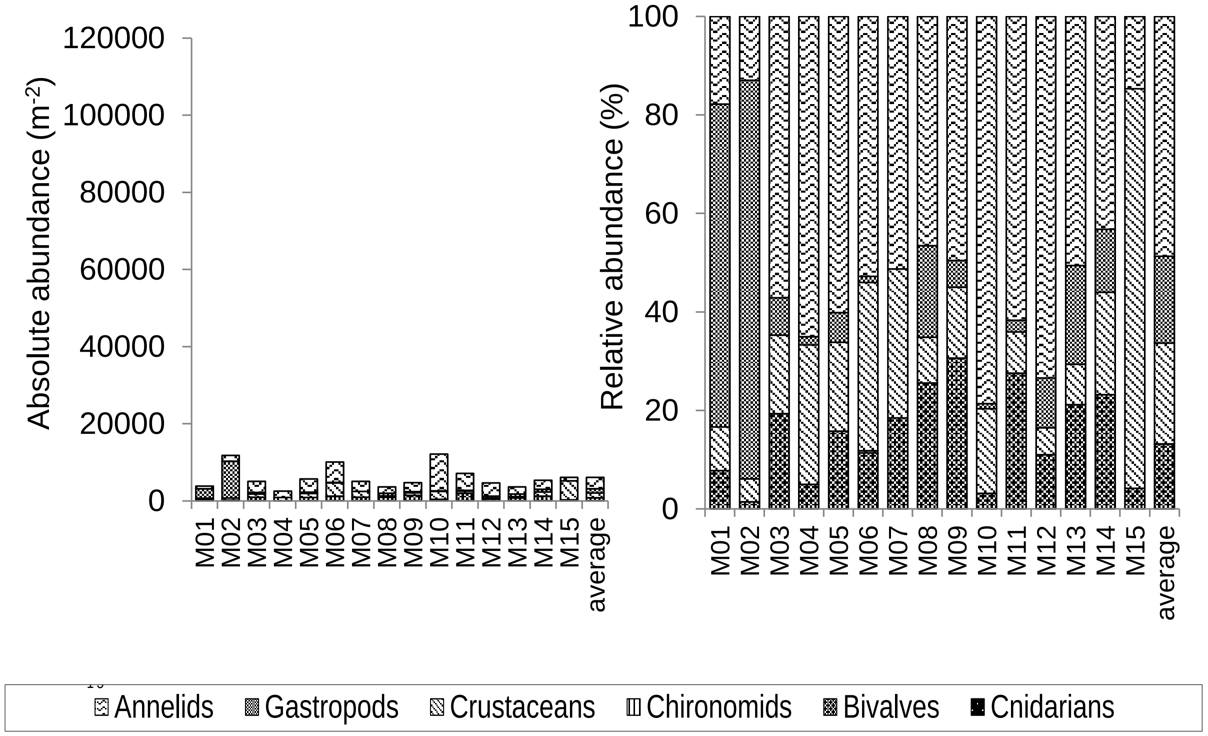
■ Nematostella ▩ Bivalves ◫ Chironomid ▧ Crustaceans ▩ Gastropods ▨ Annelids

Appendix 3(b). Seasonal variation in invertebrate abundance in Middlebere Creek.

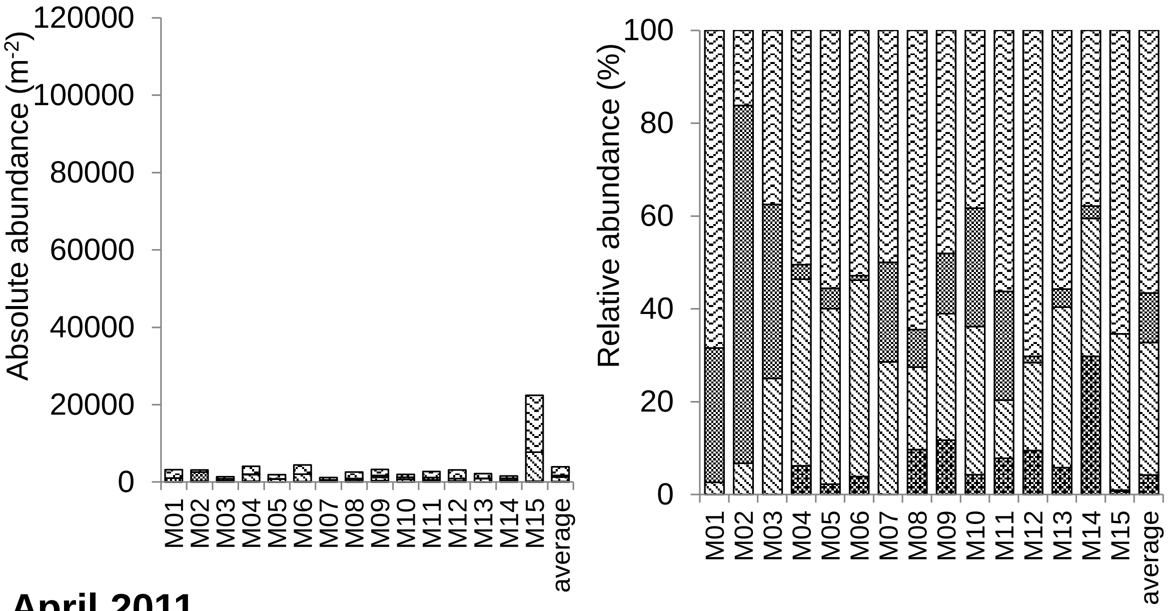
August 2010



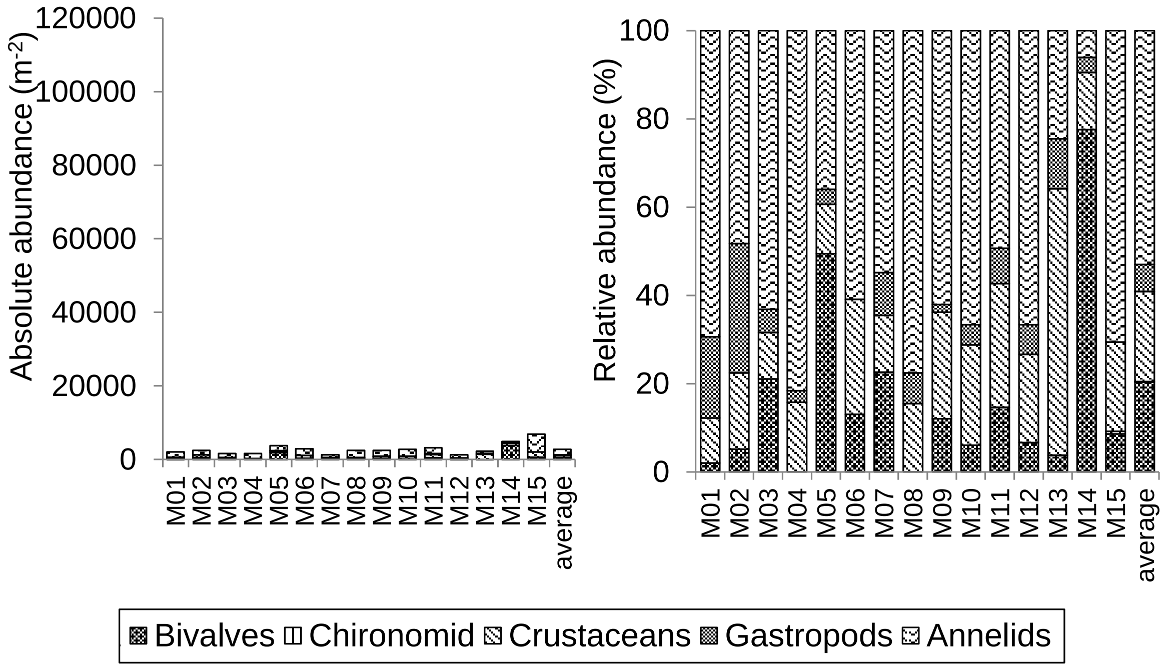
November 2010



February 2011



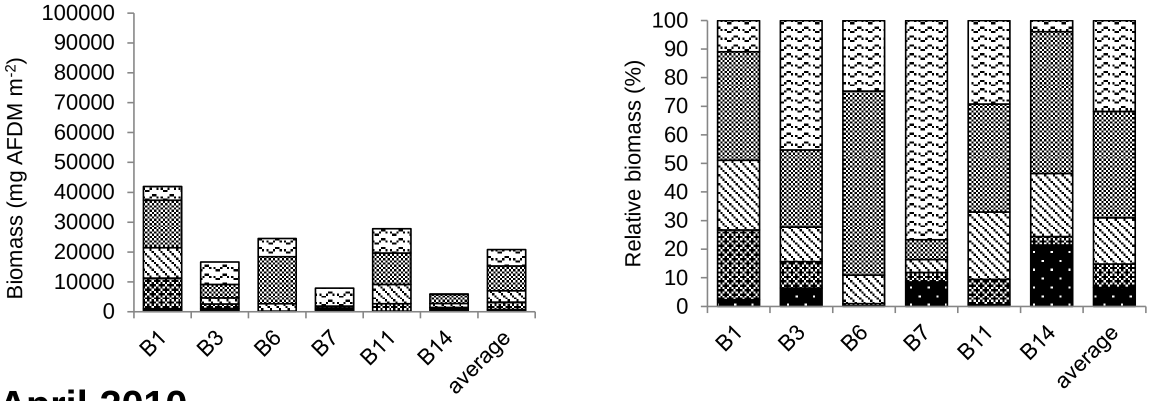
April 2011



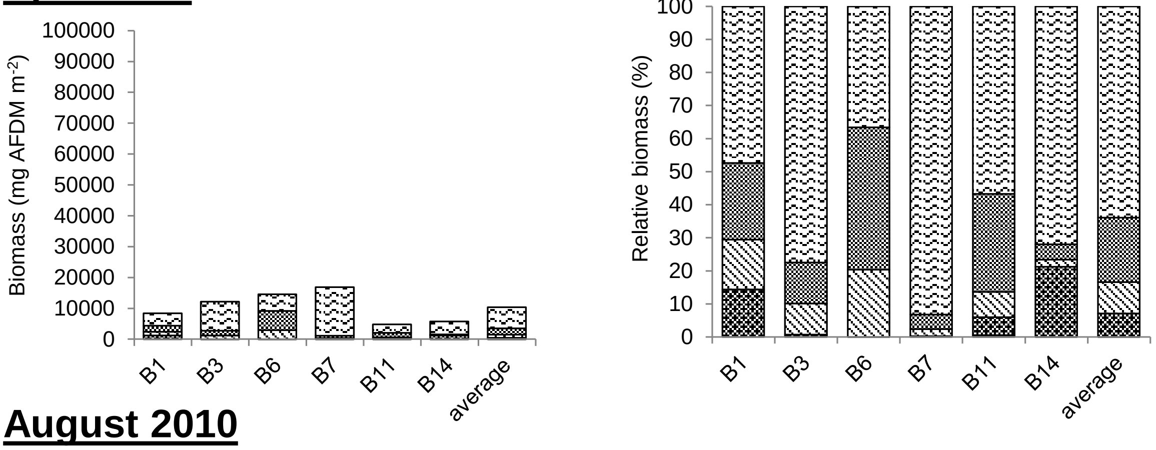
Appendix 4(a). Seasonal variation in invertebrate biomass in Brownsea Island Lagoon.

AFDM = ash-free dry mass

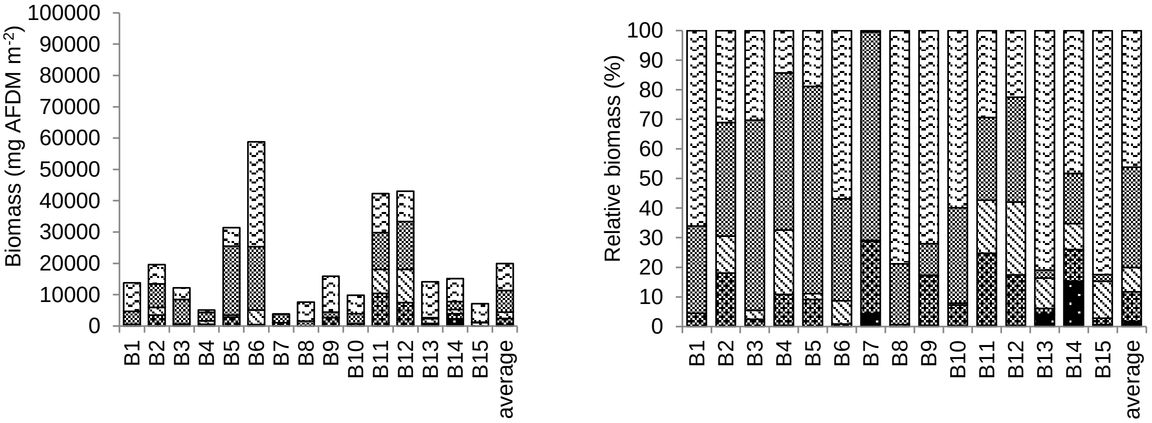
November 2009



April 2010



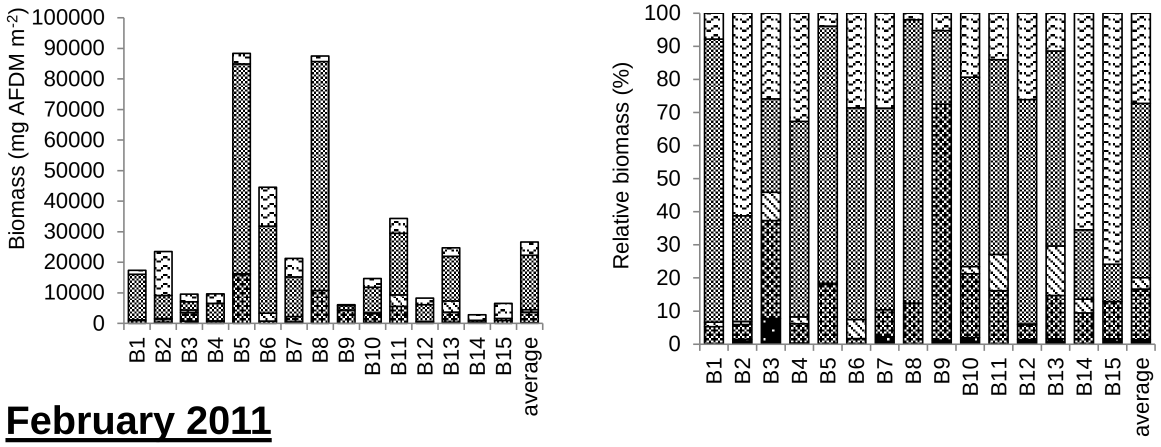
August 2010



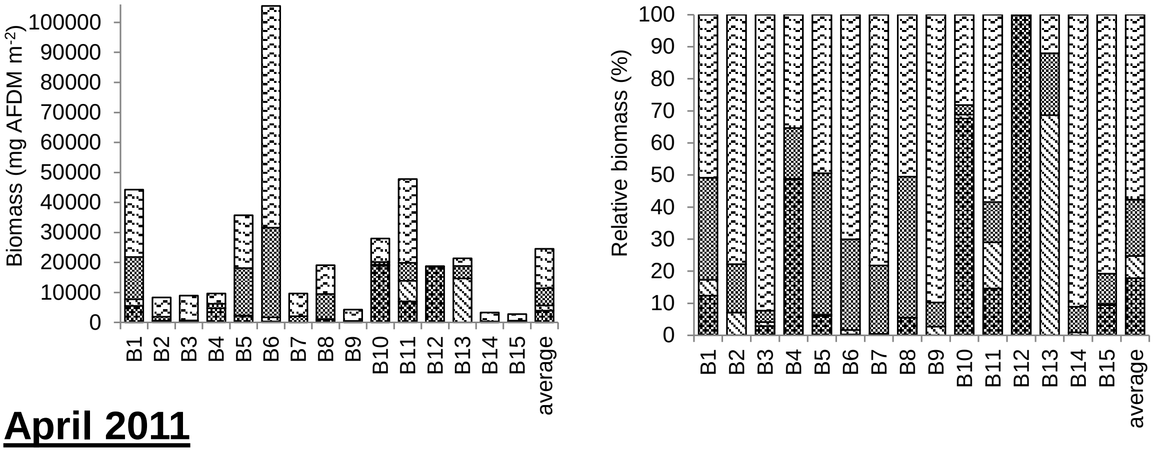
■ Nematostella ▩ Bivalves ▥ Chironomid ▧ Crustaceans ▦ Gastropods ▤ Annelids

AFDM = ash-free dry mass

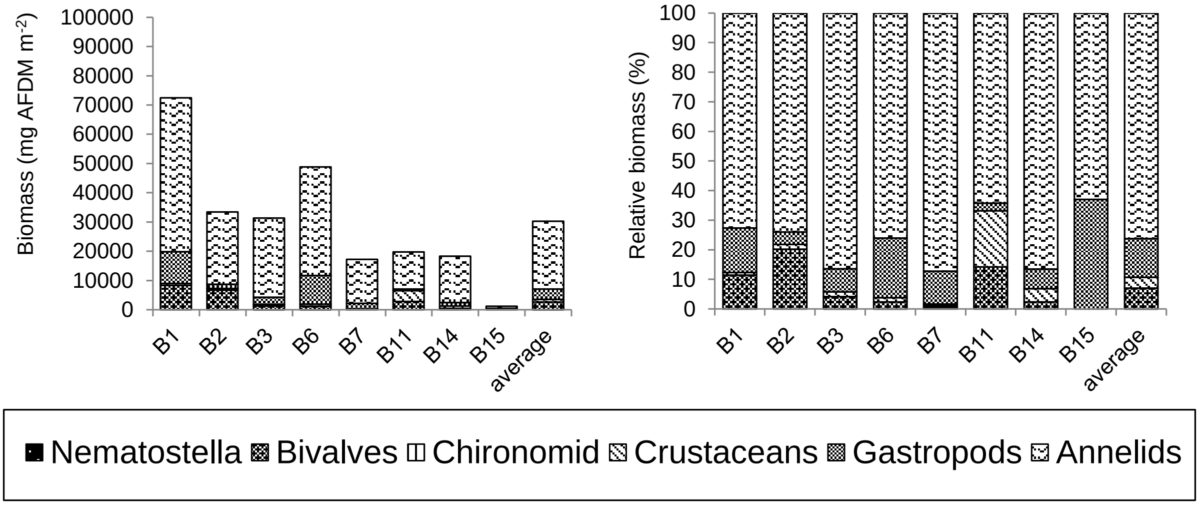
November 2010



February 2011



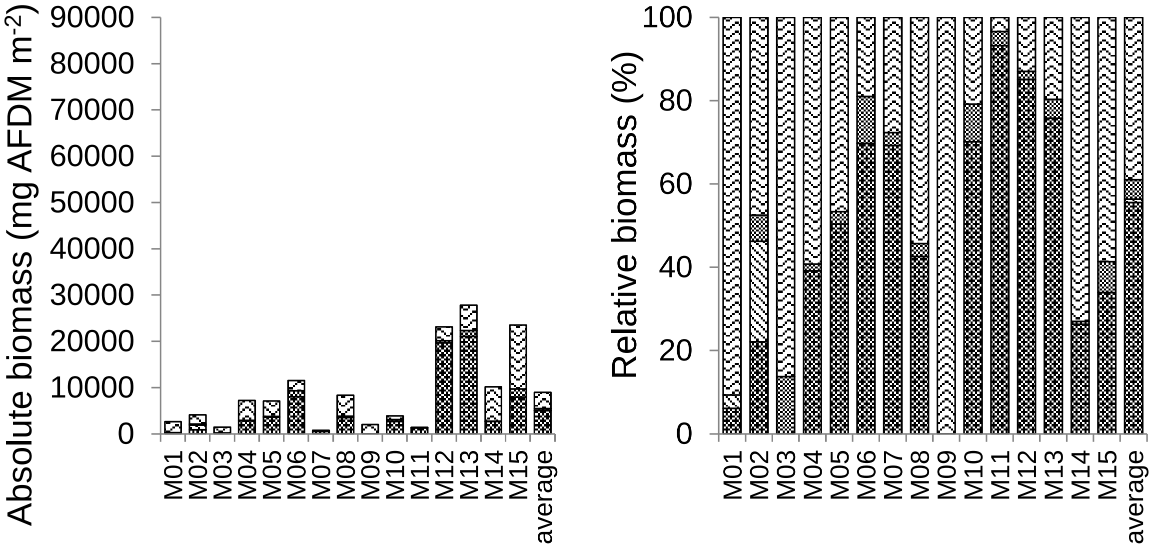
April 2011



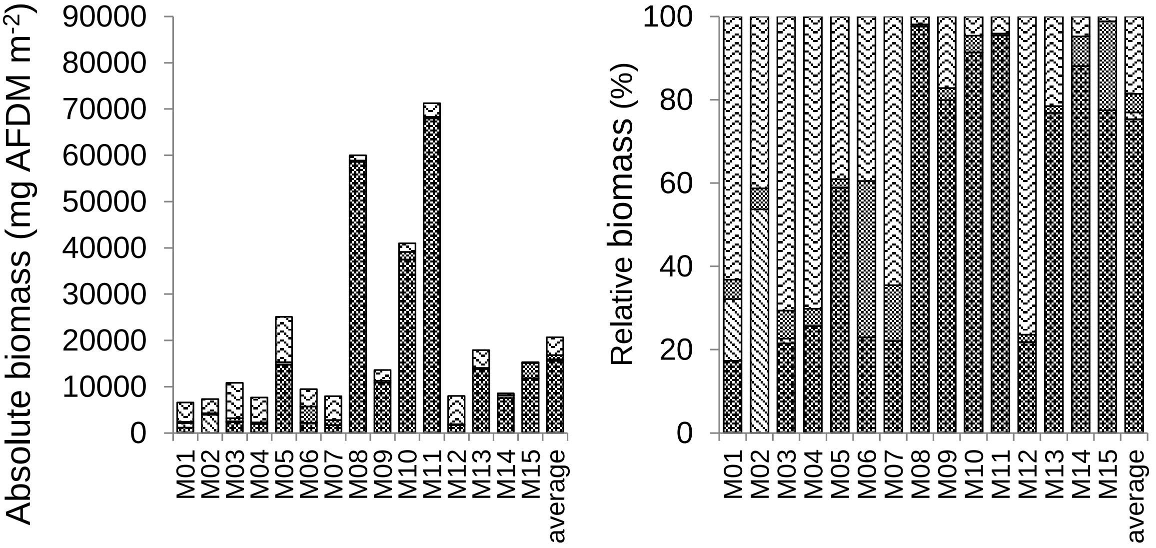
Appendix 4(b). Seasonal variation in invertebrate biomass in Middlebere Creek.

AFDM = ash-free dry mass

August 2010



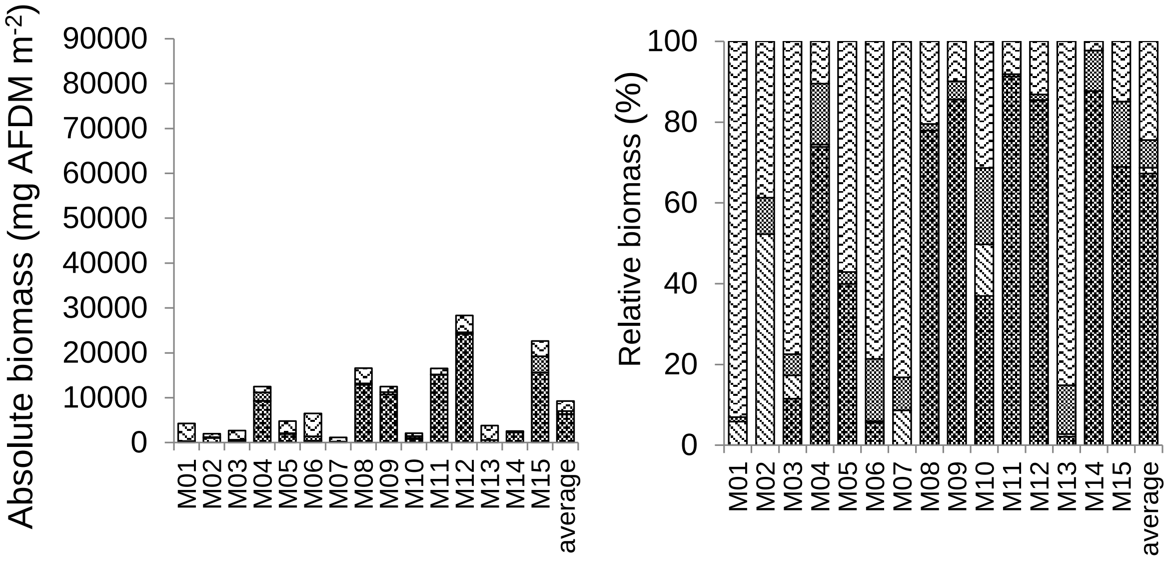
November 2010



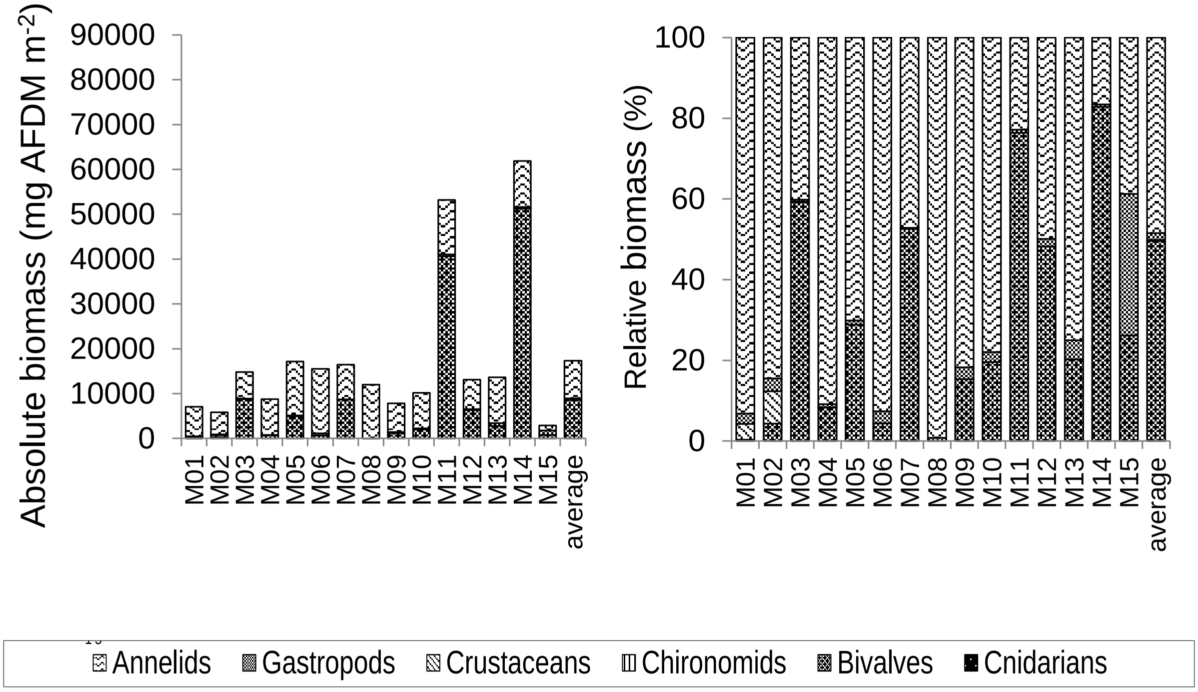
▨ Annelids ▨ Gastropods ▨ Crustaceans ▥ Chironomids ▨ Bivalves ■ Cnidarians

AFDM = ash-free dry mass

February 2011



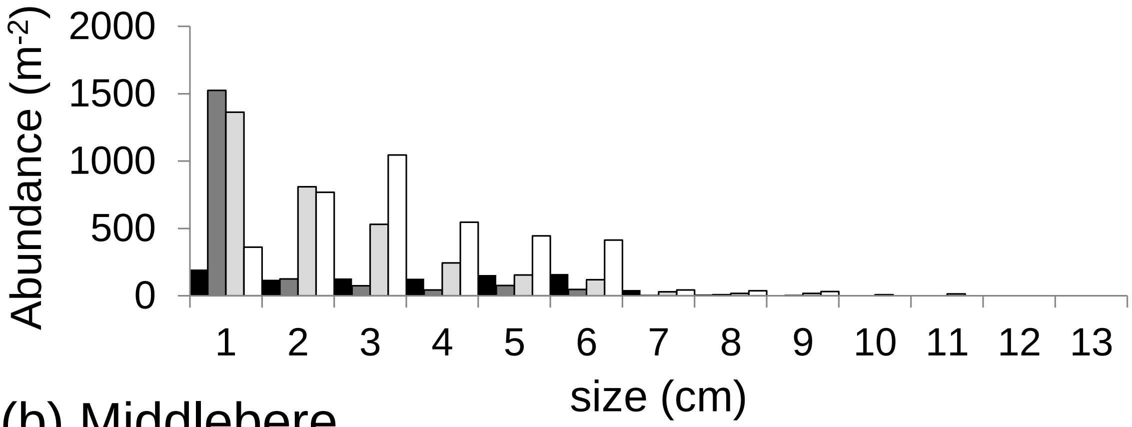
April 2011



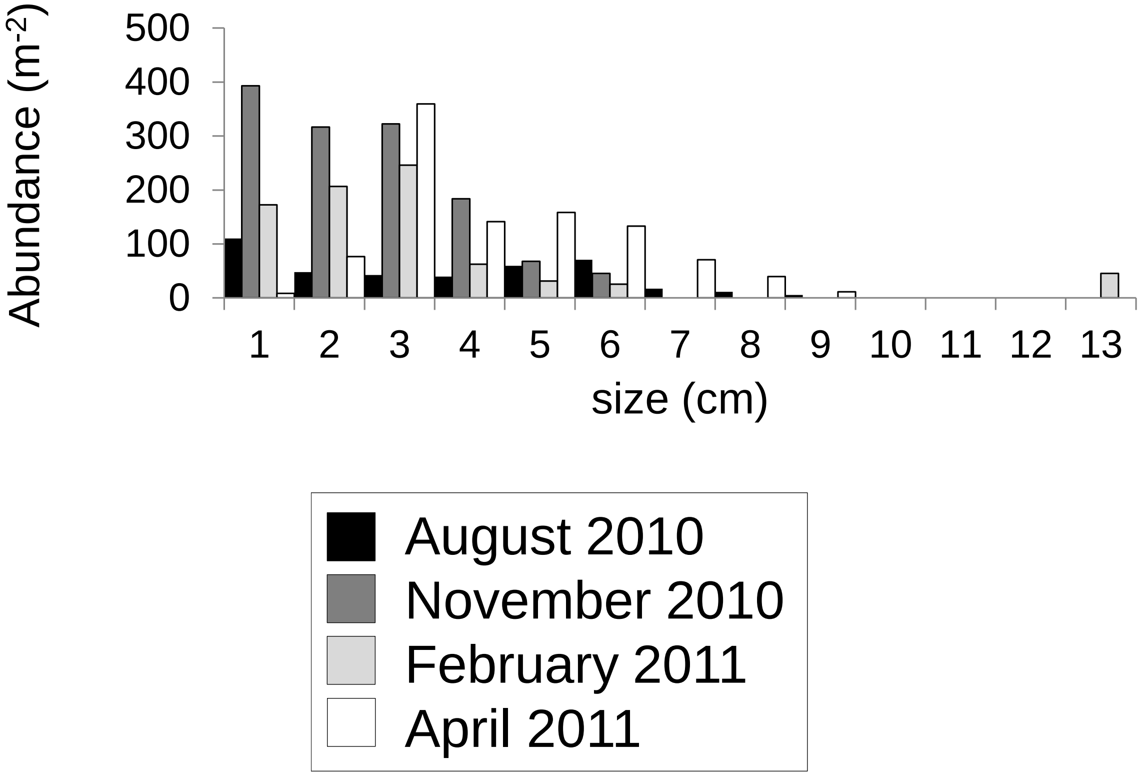
Appendix 5. Size-class distributions for invertebrate taxa.

Hediste diversicolor

(a) Brownsea

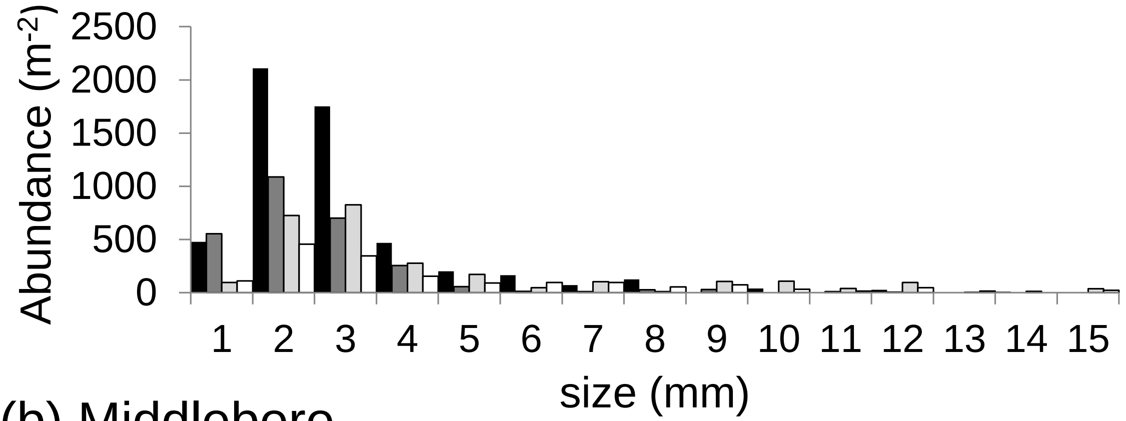


(b) Middlebere

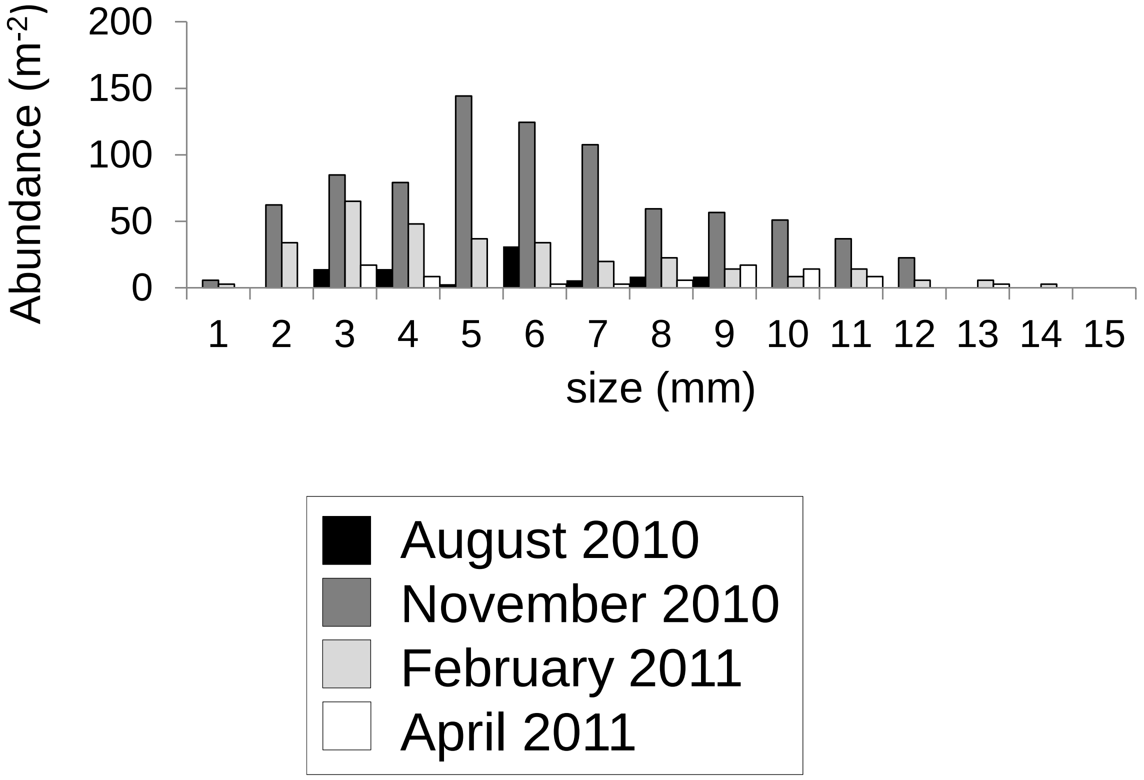


Corophium spp.

(a) Brownsea

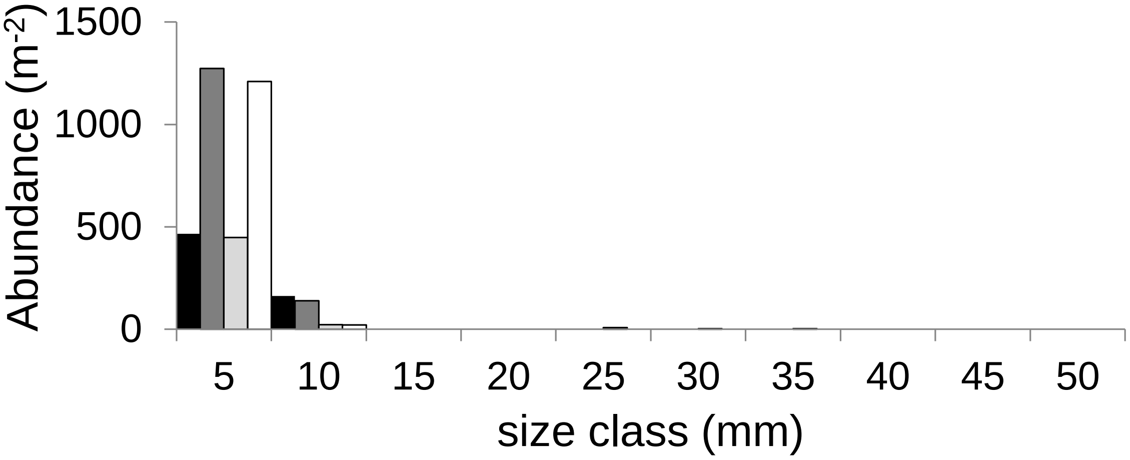


(b) Middlebere

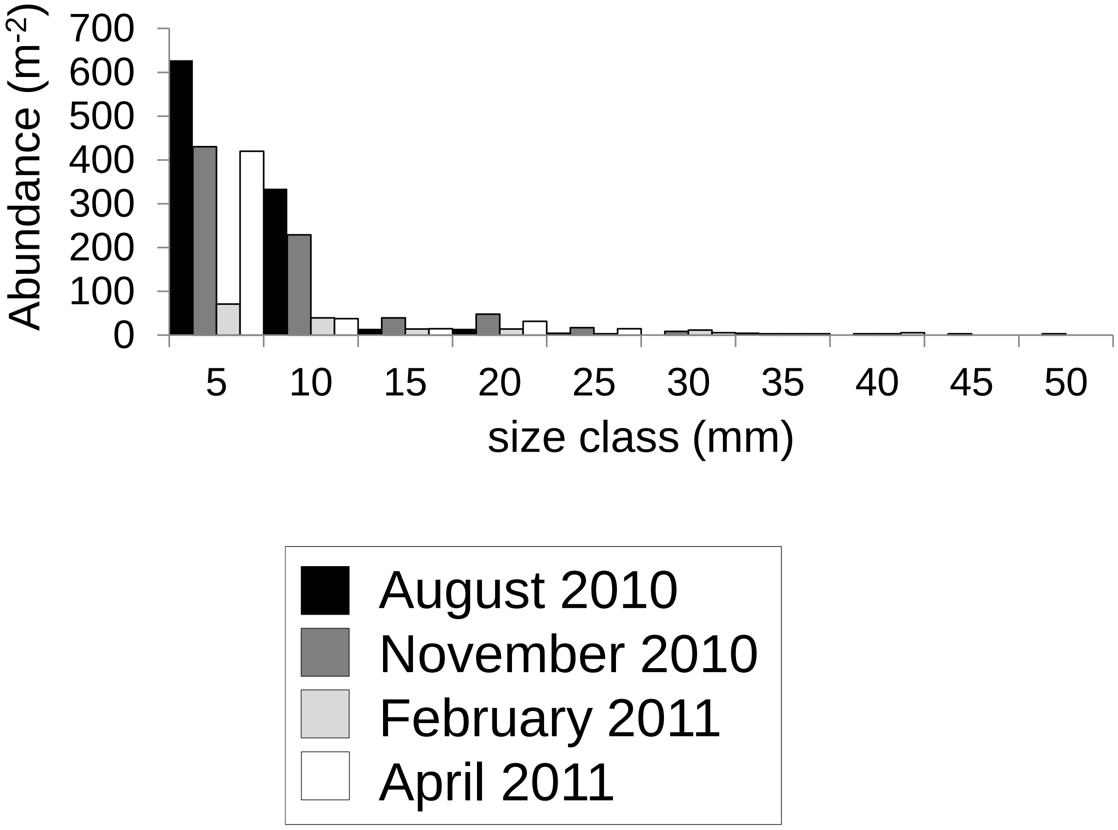


Bivalvia

(a) Brownsea

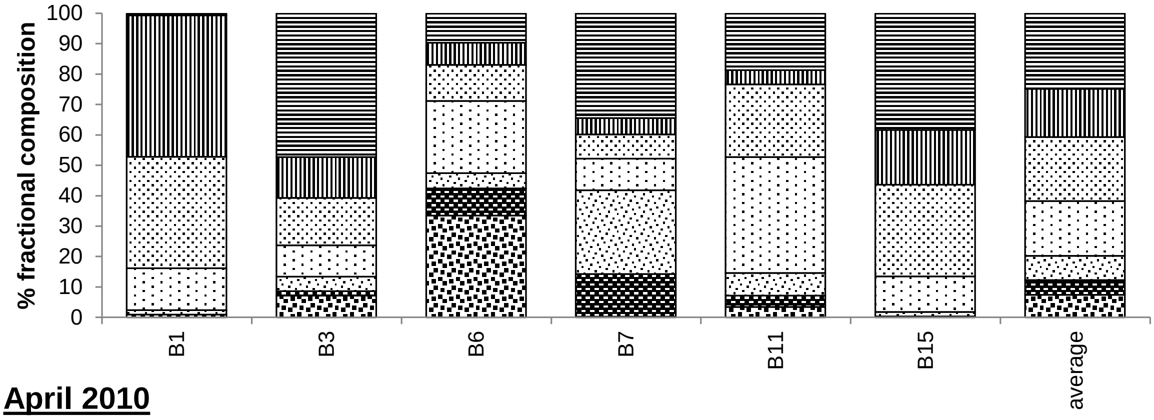


(b) Middlebere

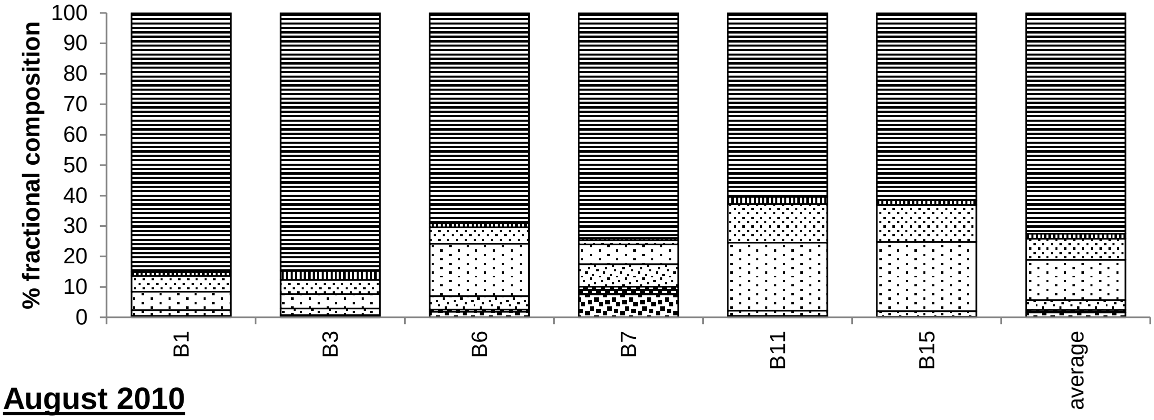


Appendix 6(a). Spatial variation in sediment composition at Brownsea Island Lagoon.

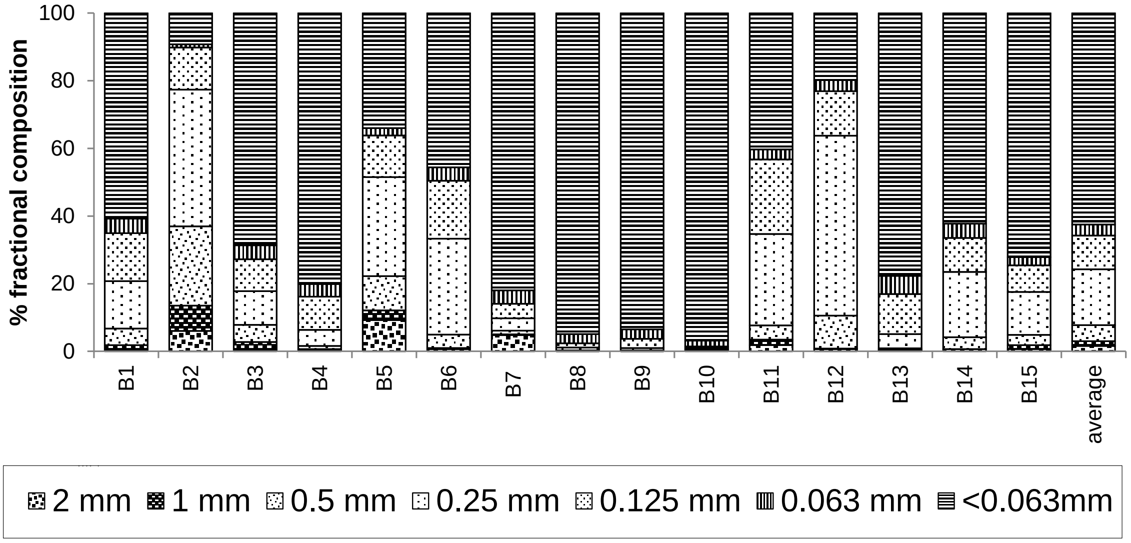
November 2009



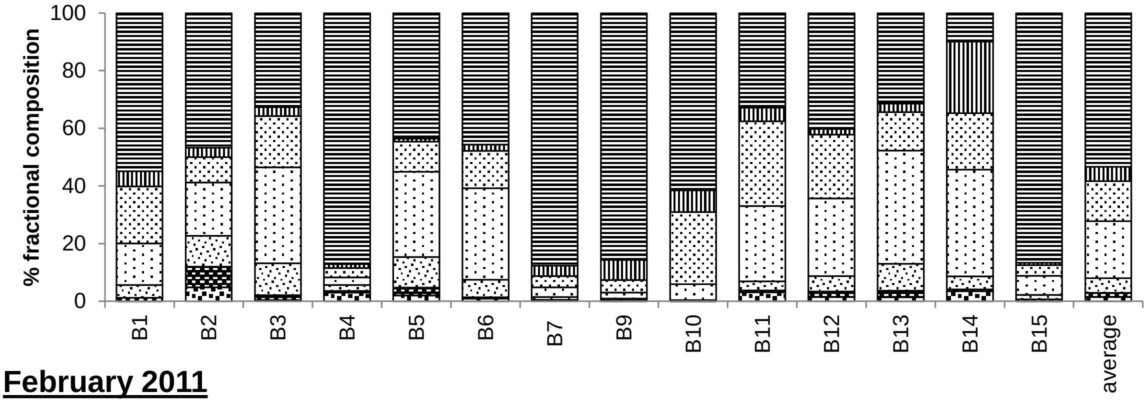
April 2010



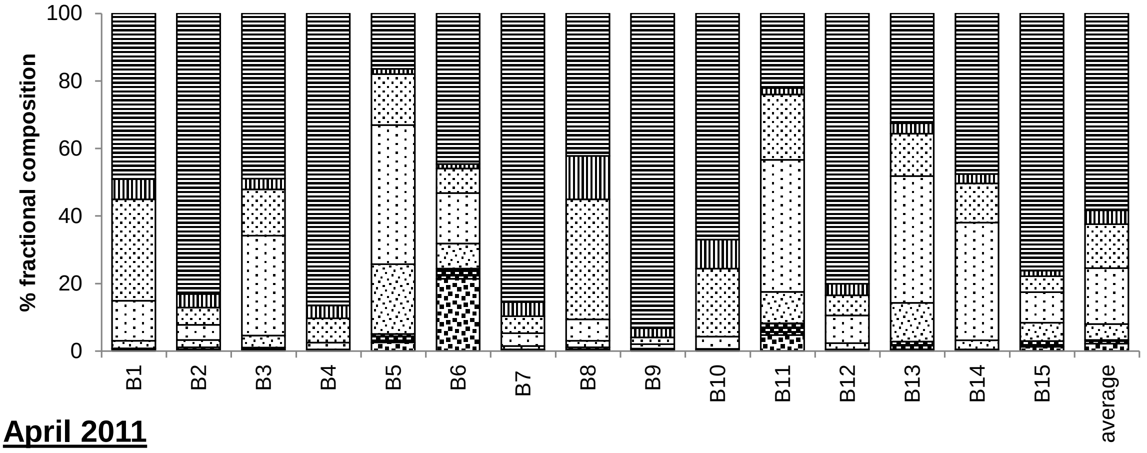
August 2010



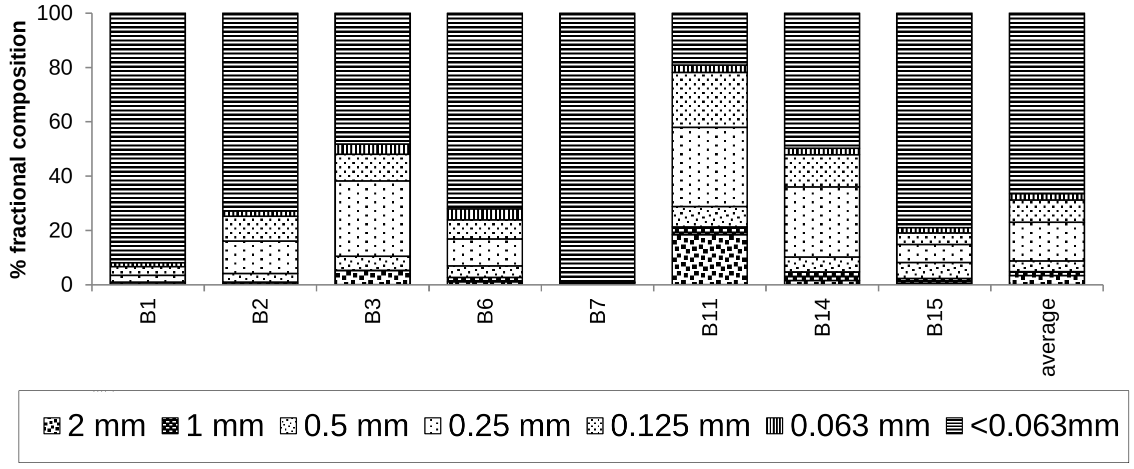
November 2010



February 2011

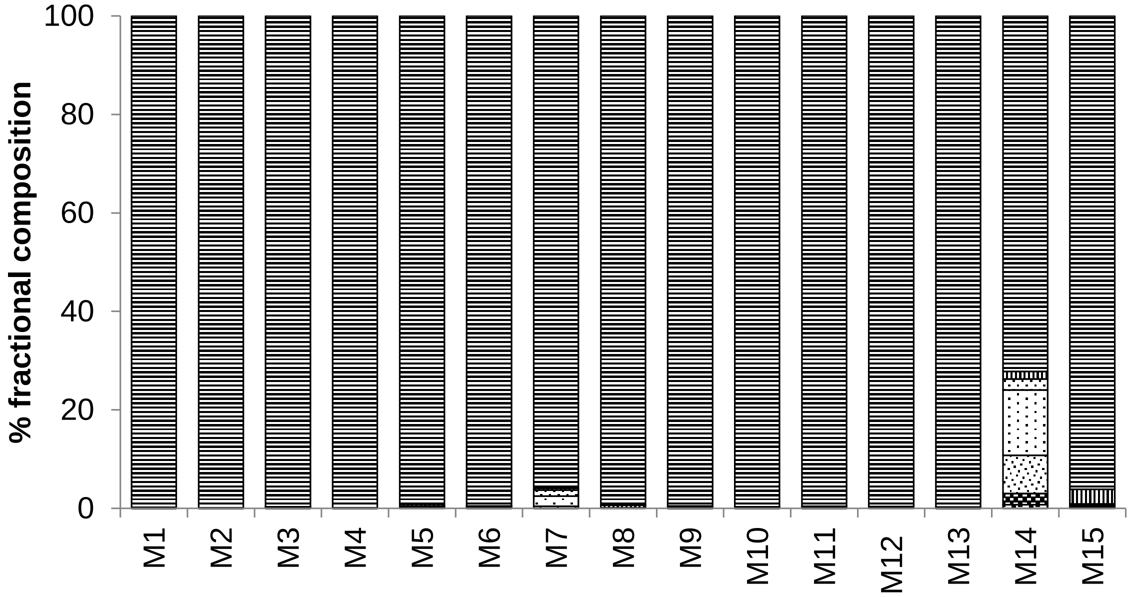


April 2011

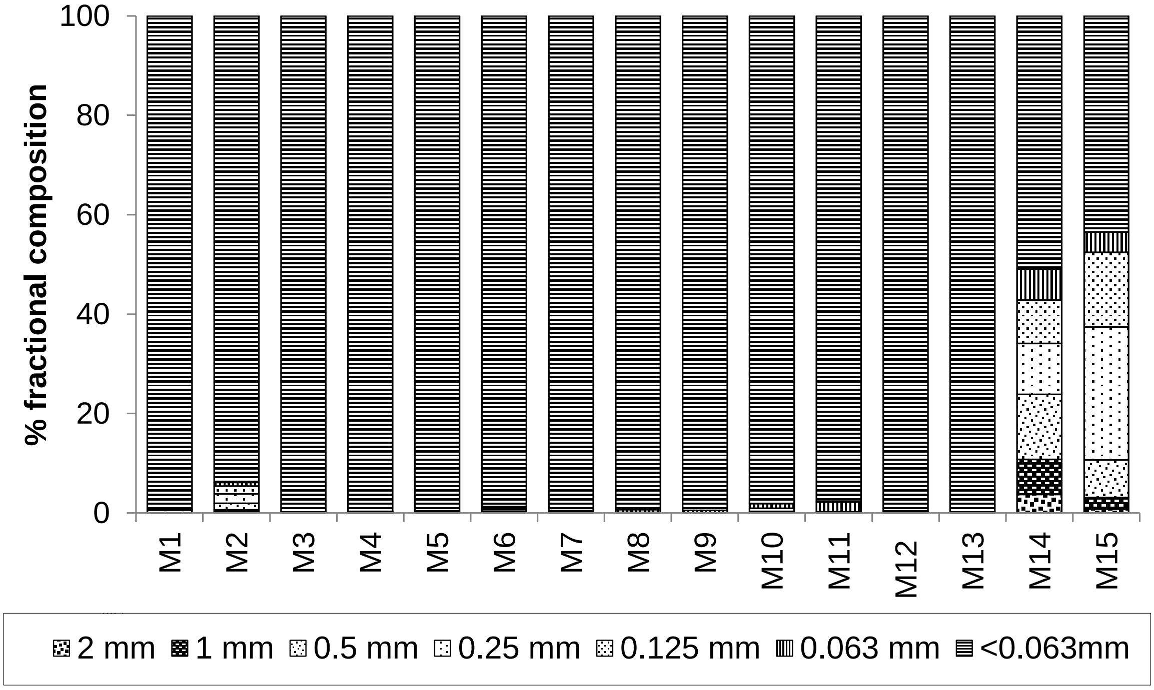


Appendix 6(b). Spatial variation in sediment composition at Middlebere Creek.

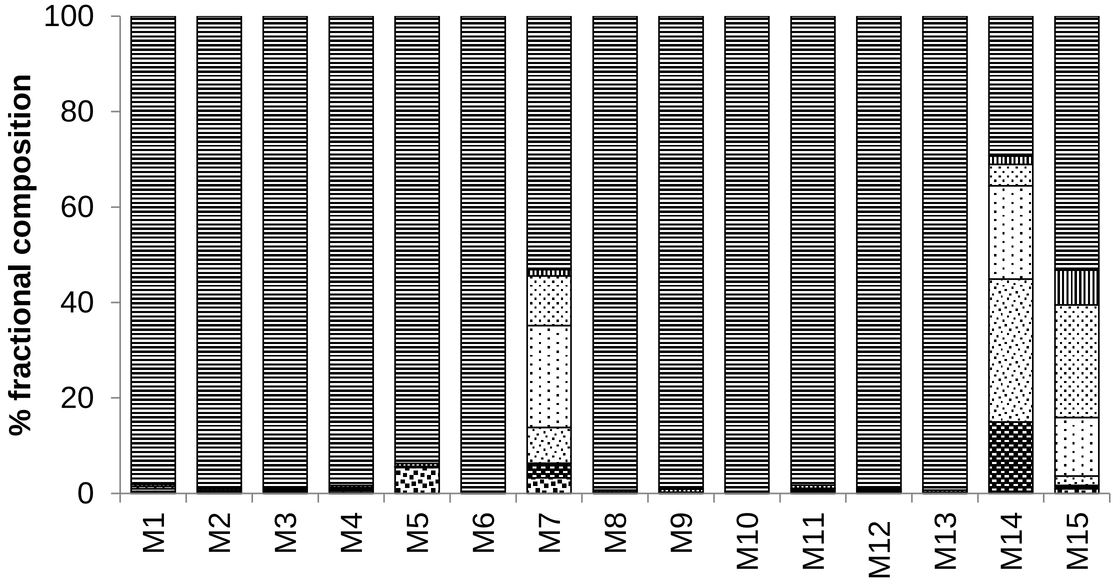
August 2010



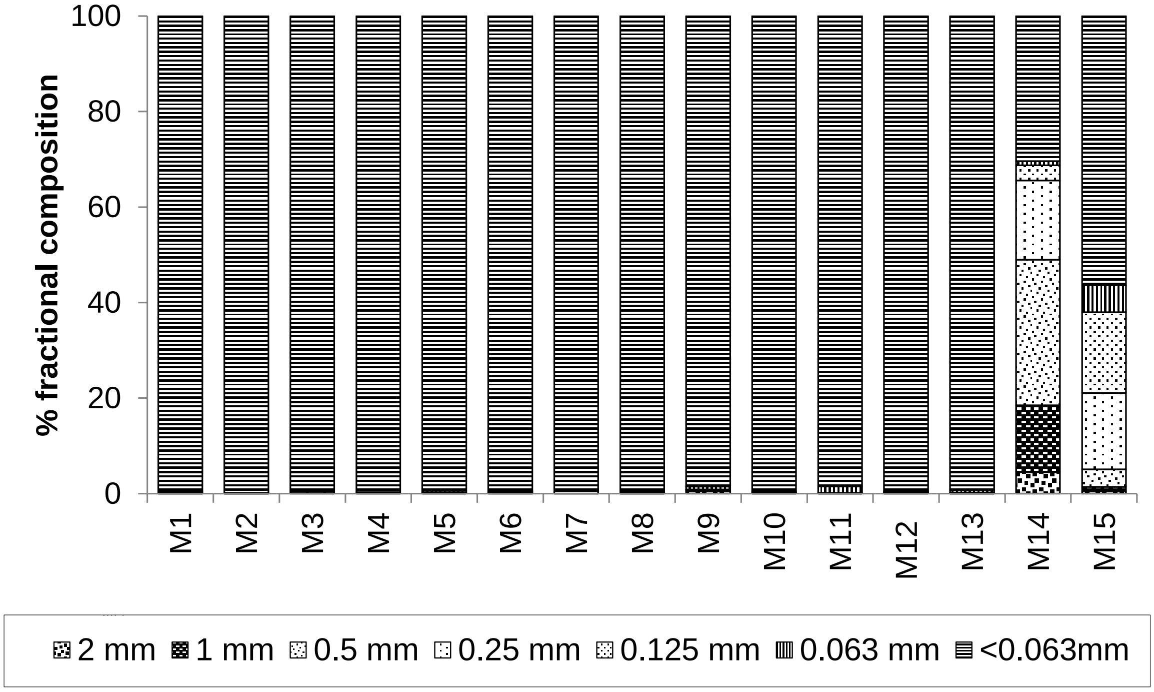
November 2010



February 2011



April 2011



Appendix 7(a). Allometric equations used to relate ash-free dry mass (AFDM) in mg (A), to total length in mm (TL) for large pelagic species from Brownsea Island Lagoon.

Species	n	Allometric equation	Pearson's R	R^2	P (2-tailed)
Pomatoschistus sp	30	$lnA = 4.230797 \times ln(TL) - 11.032857)$	0.924	0.854	<0.000001
Palaemonetes varians	29	$lnA = 3.069473 \times ln(TL) - 6.972352)$	0.939	0.882	<0.000001

Appendix 7(b). Conversion factors for prey items in this study, from biomass in mg ash-free dry mass (AFDM) to energy in kJ.

Species (or group)	kJ/g AFDM	Reference
Small worms	21.3537	Thomas et al. (2004b)
Medium and large worms	19.6789	Thomas et al. (2004b)
Corophium sp	20.74	Steimle & Terranova 1985
Idotea chelipes	24.80	Steimle & Terranova 1985
Palaemonetes varians	24.80	Steimle & Terranova 1985
Pomatoschistus sp	22.96	Steimle & Terranova 1985

Appendix 8(a). Survey dates and times for Brownsea Island Lagoon.

Date	Observation hours	Times
25/9/2010	10	09:00–18:00
2/10/2010	8	11:00–18:00
8/10/2010	11	07:00–16:30
17/10/2010	11	08:30–18:00
24/10/2010	10	8:30–17:00
29/10/2010	5	13:00-17:00
7/11/2010	8	9:00–16:00
16–17/11/2010	8	10:00–16:30; 7:30–8:30
24–25/11/2010	6	15:00–16:00; 8:00–11:00
6/12/2010*	2	10:00–11:00
17/12/2010*	2	11:00–13:30
4/1/2011*	2	12:00–14:00
13/1/2011	5	8:00–13:00
20/01/2011	5	12:00–15:30
28/1/2011	6	10:00–15:00
4/2/2011	3	11:00–13:00
11/2/2011	7	9:30–15:00
18/2/2011	6	11:00–16:00
1/3/2011	5	12:00–16:00
5–6/10/2011	12	18:00–19:00; 7:00–16:00
21/10/2011	9	7:30–15:00
28/10/2011	9	9:30–17:00
4/11/2011	10	8:00–17:00
12/11/2011	10	8:00–17:30
20/11/2011	8	9:00–16:00
26/11/2011	8	9:00–16:00
5/12/2011	7	10:00–16:00
11/12/2011	9	9:00–16:30
20/12/2011	8	8:30–15:30
10/1/2012	4	13:00–16:00
18/1/2012	9	8:00–16:00
25/1/2012	6	12:00–17:00
15/2/2012	3	12:00–14:00
23/2/2012	5	13:00–17:00
2/3/2012	2	10:00–11:00
TOTAL	**241 hrs**	

*lagoon frozen

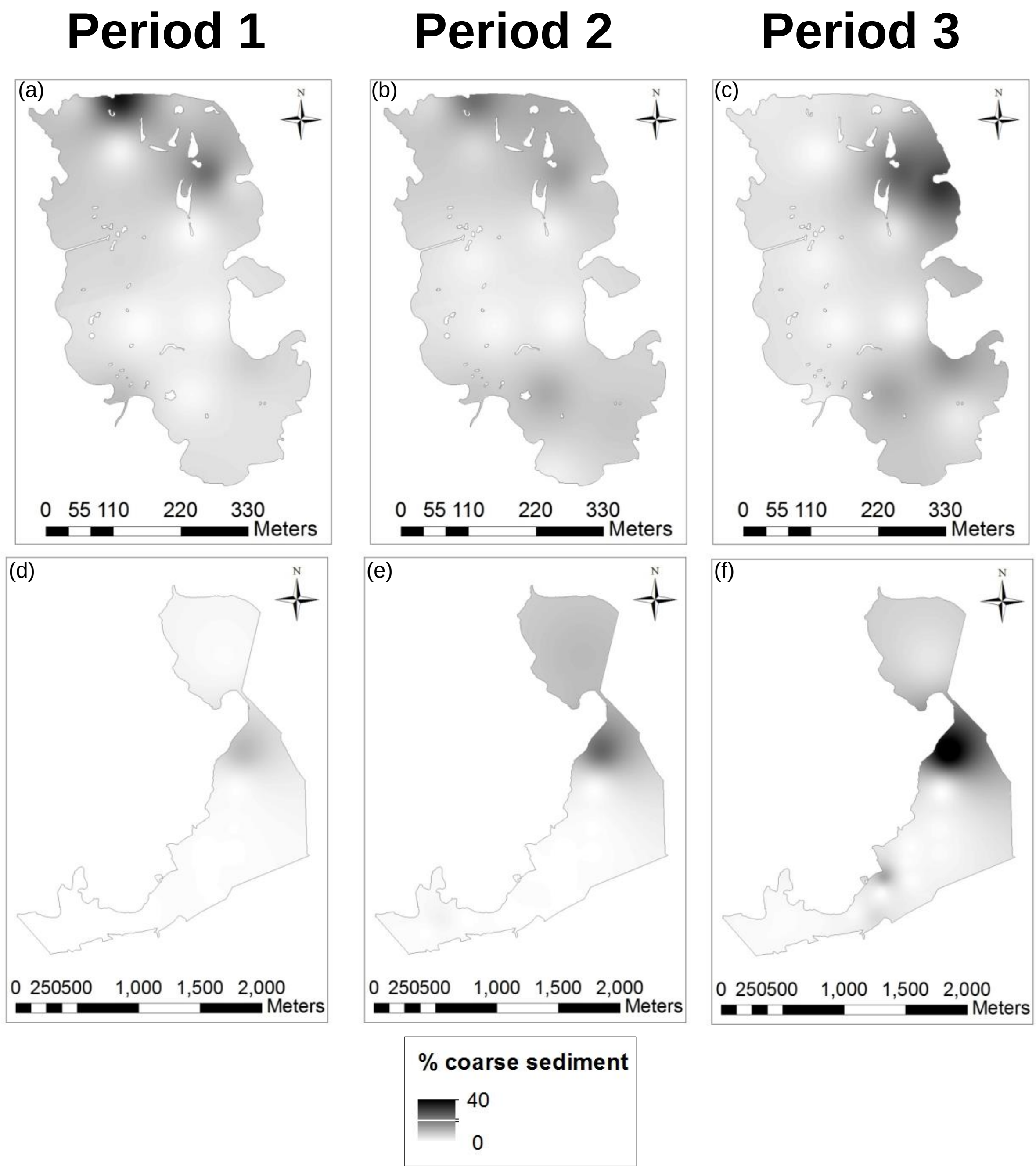
Appendix 8(b). Survey dates and times for Middlebere Creek.

Date	Observation hours	Observation hours (avocets present)	Times
1/11/10	4	4	11:00–15:00
6/11/10	8	2	10:00–16:00
17–18/11/10	4	4	11:30–15:30
23/11/10	4	4	12:00–15:30
30/11/10	4	4	12:00–15:00
6–7/12/10	3	3	11:00–15:00
15–16/12/10	4	4	10:30–15:30
3/1/11	5	5	11:00–15:00
15/1/11	3	2	8:30–10:30
21/1/11	5	5	11:30–15:00
27/1/11	3	3	11:30–13:30
3/2/11	5	5	10:00–15:00
12/2/11	4	4	10:00–13:30
19/2/11	3	0	11:00–13:00
15/10/11	7	0	10:00–16:00
23/10/11	9	3	10:00–18:00
29/10/11	4	2	15:00–18:00
4/11/11	10	9	8:00–17:00
12/11/11	9	9	9:00–17:00
18–19/11/11	8	8	9:30–16:30
27/11/11	7	3	10:30–17:00
1/12/11	8	8	9:00–16:00
11/12/11	9	8	8:30–16:00
20/12/11	10	10	9:00–16:00
9/1/12	5	5	11:00–15:00
19/1/12	3	3	10:30–12:30
24/1/12	3	3	11:30–13:30
4/12/12	6	0	8:30–13:30
11/2/12	9	4	8:00–16:30
17/2/12	2	2	13:00–14:00
22/2/12	6	4	9:00–14:00
TOTAL	**193 hrs**	**149 hrs**	

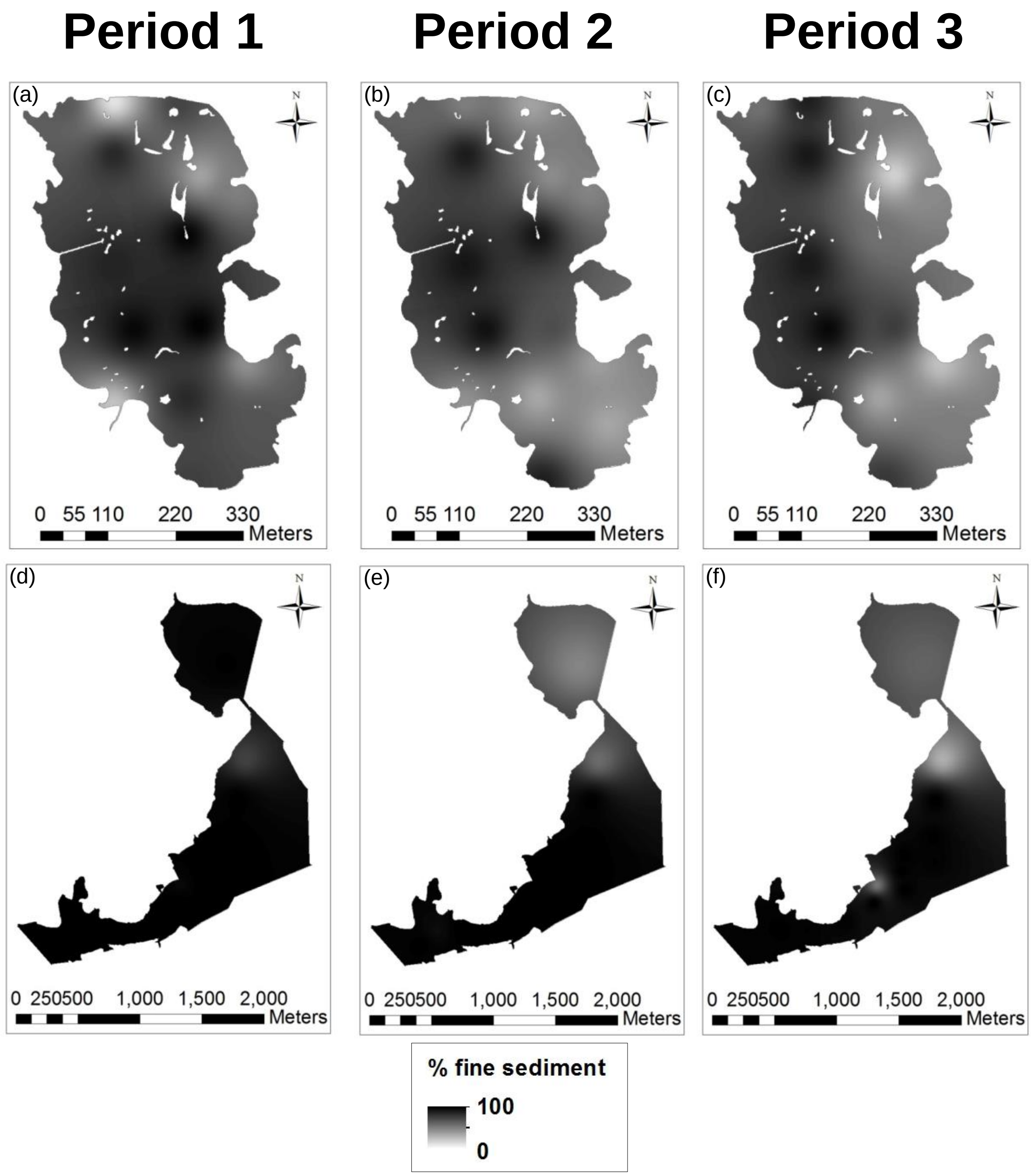
Appendix 9. Worm availability constants for Brownsea and Middlebere during each foraging period.

	Brownsea			**Middlebere**		
	Small worms	Medium worms	Large worms	Small worms	Medium worms	Large worms
Period 1	1.0000	0.5774	0.1041	1.0000	0.6683	0.1769
Period 2	1.0000	0.8597	0.1013	1.0000	0.6490	0.2000
Period 3	1.0000	0.7520	0.1035	1.0000	0.6112	0.2000

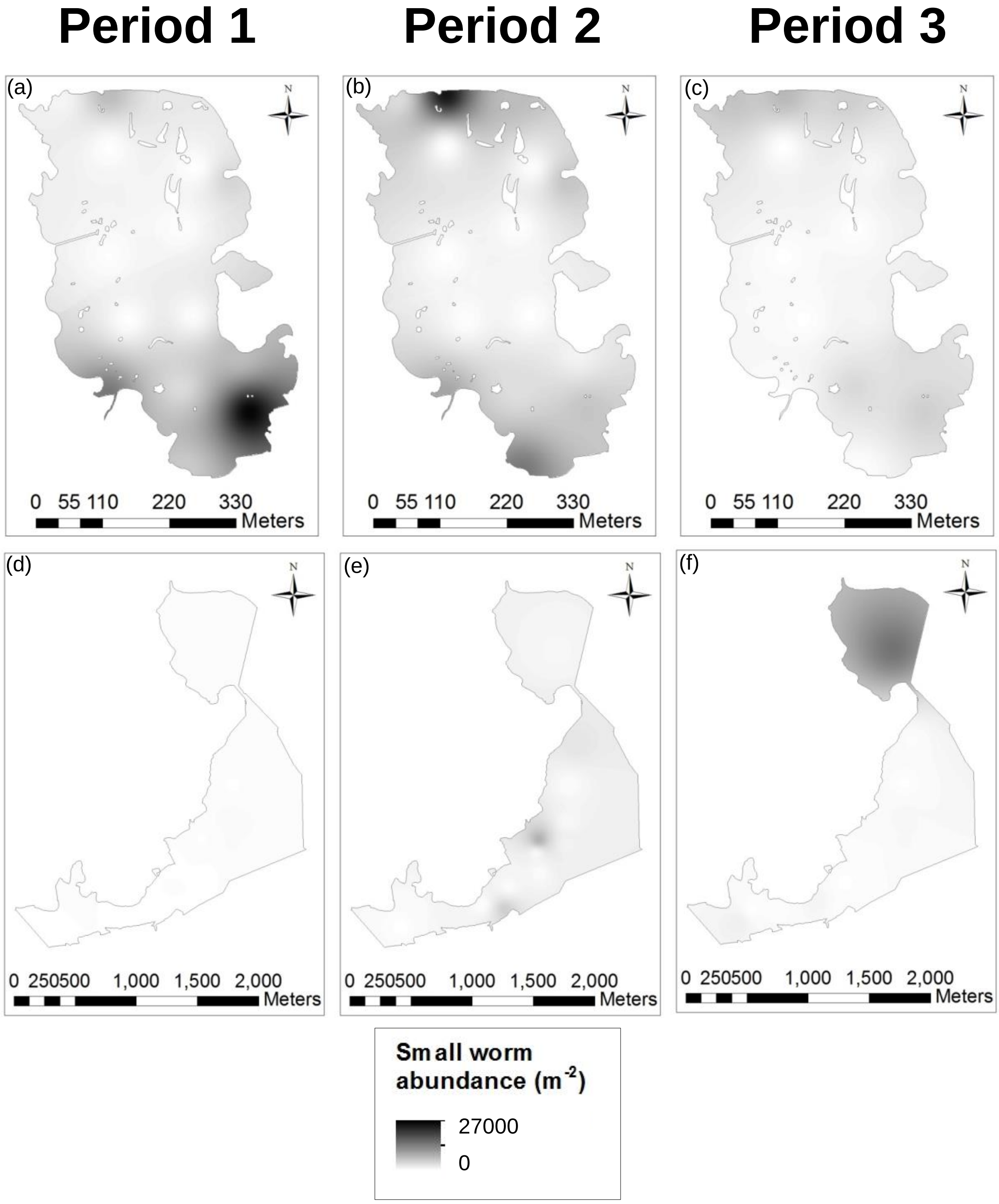
Appendix 10(a). Spatial distribution of coarse sediment in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



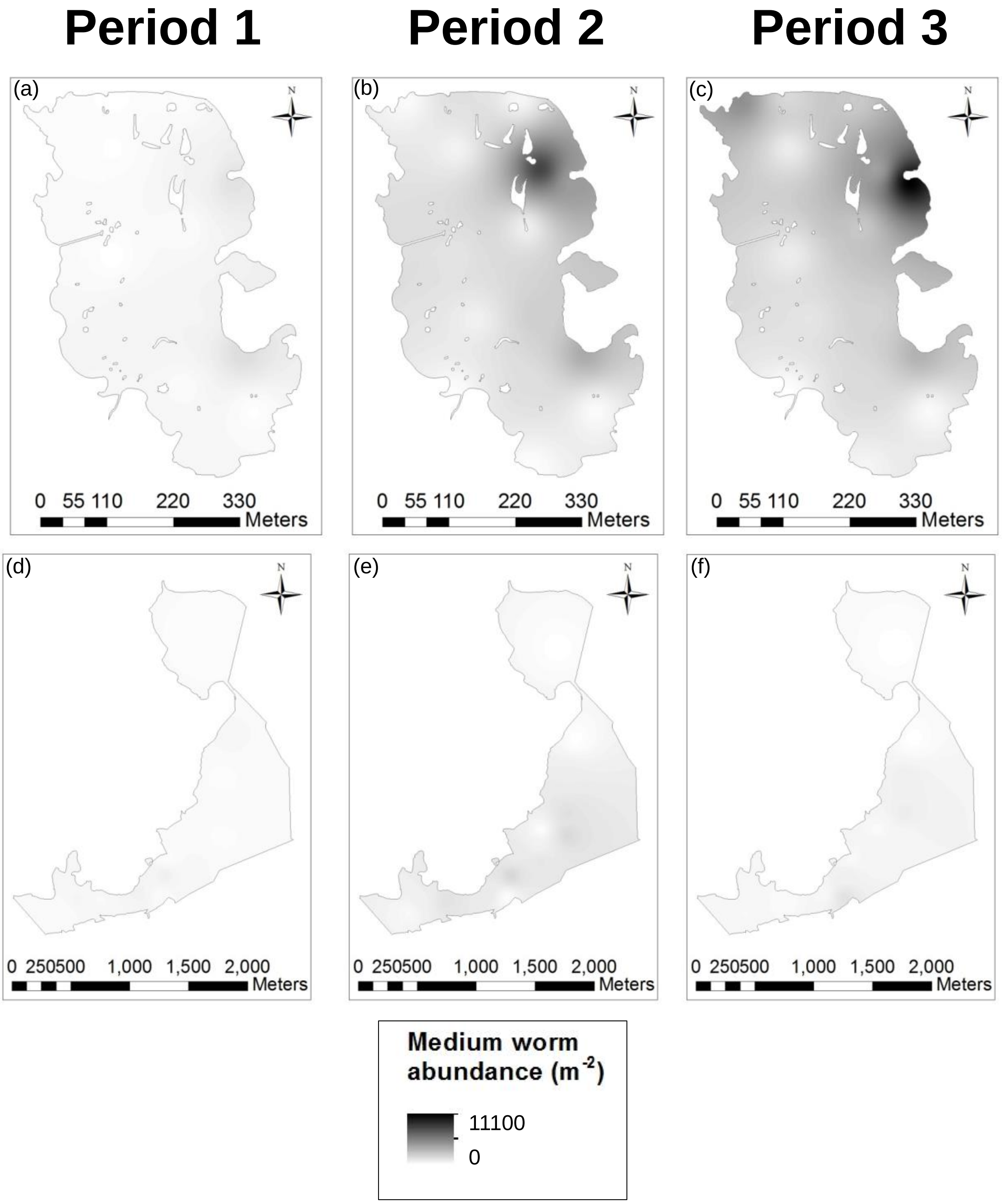
Appendix 10(b). Spatial distribution of fine sediment in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



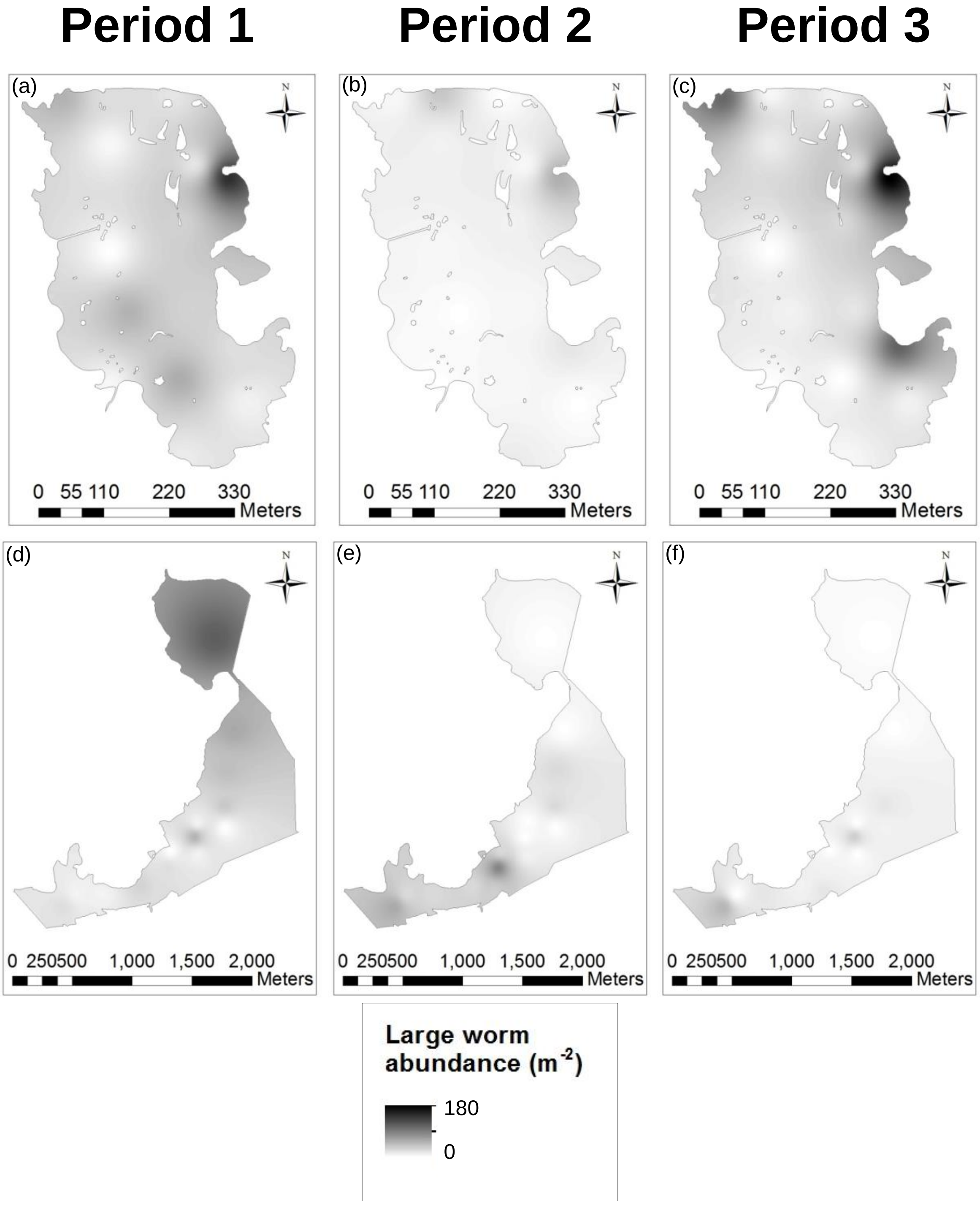
Appendix 10(c). Spatial distribution of small worms (≤1 cm) in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



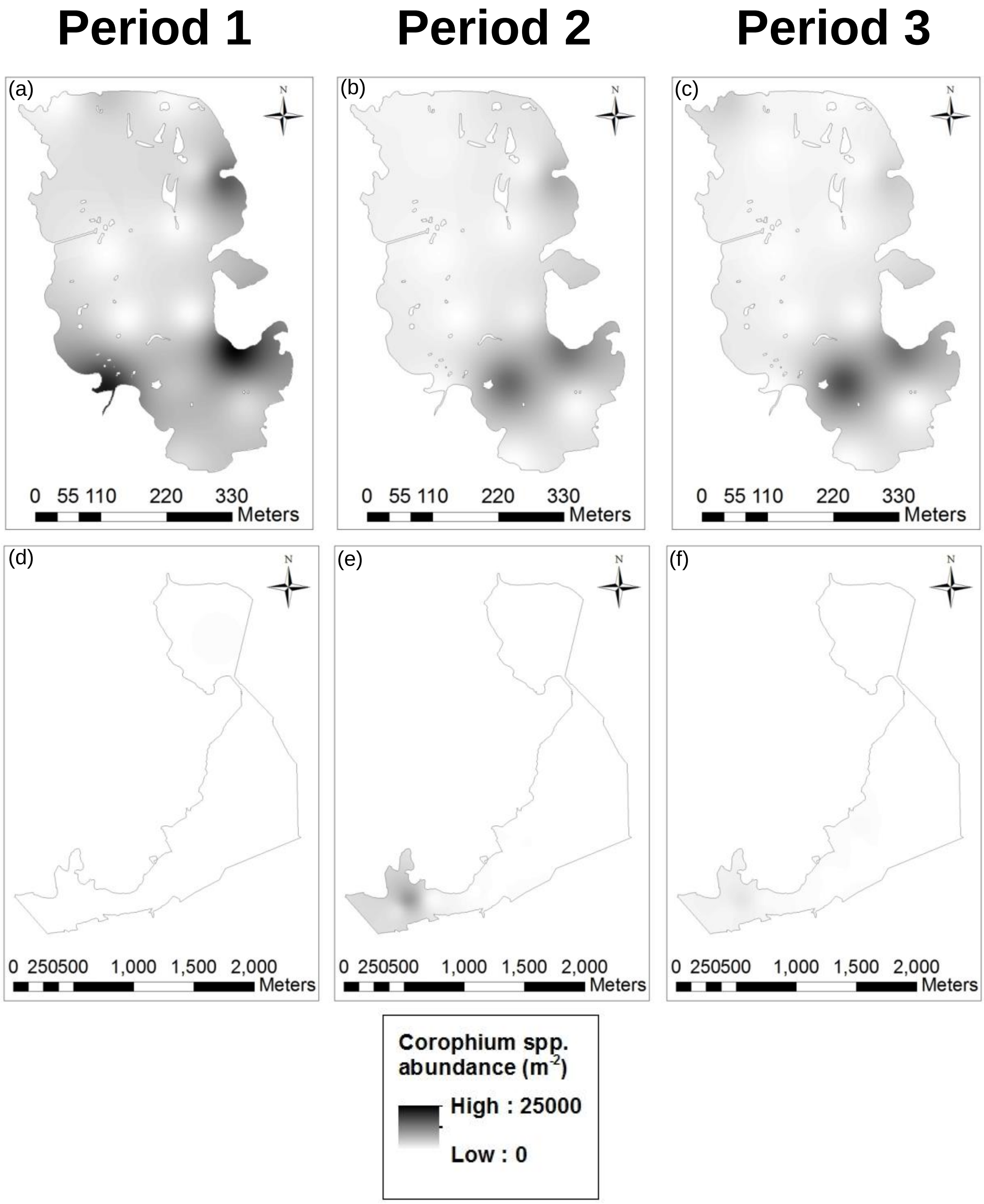
Appendix 10(d). Spatial distribution of medium worms (>1–4 cm) in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



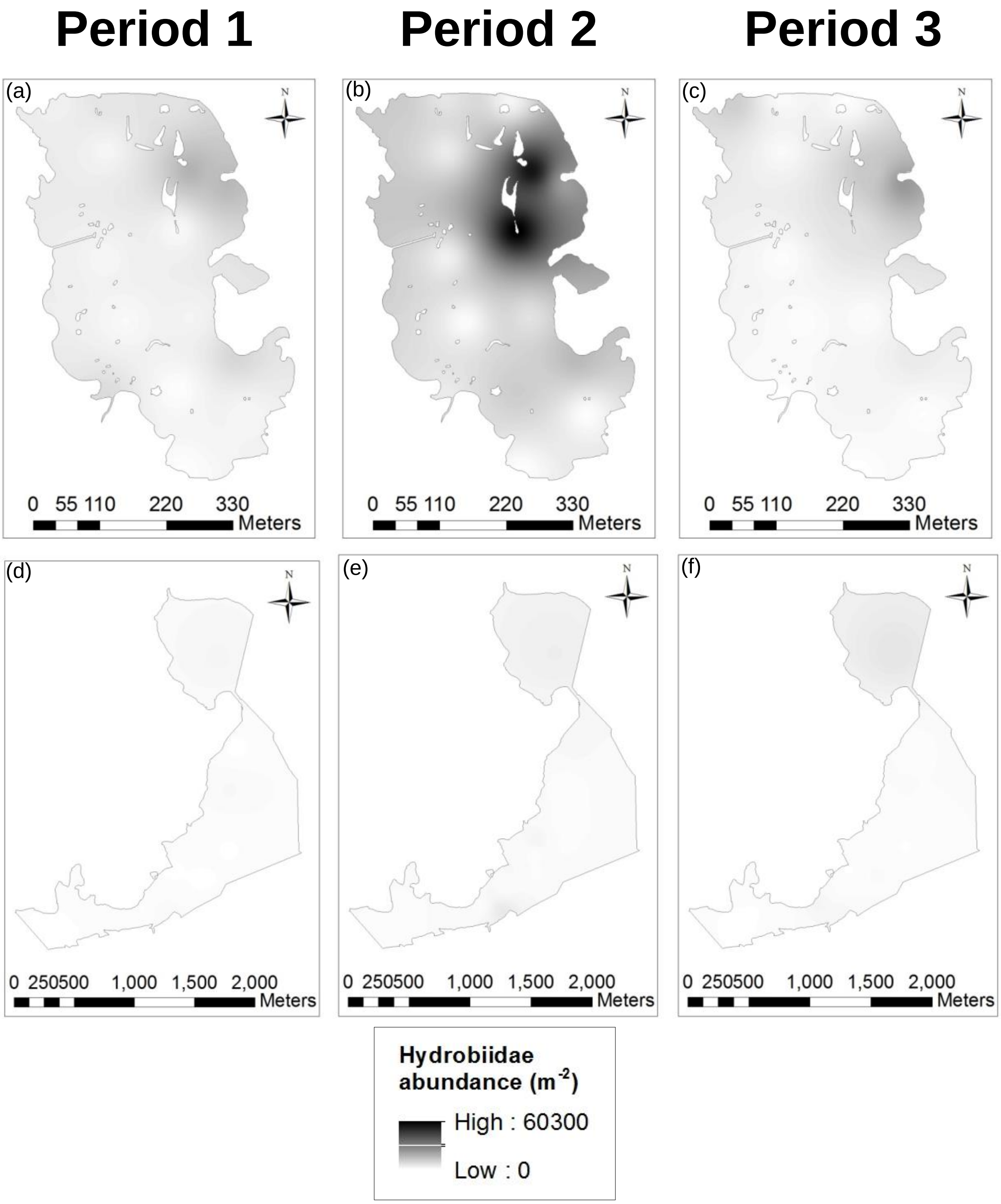
Appendix 10(e). Spatial distribution of large worms (>4 cm) in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



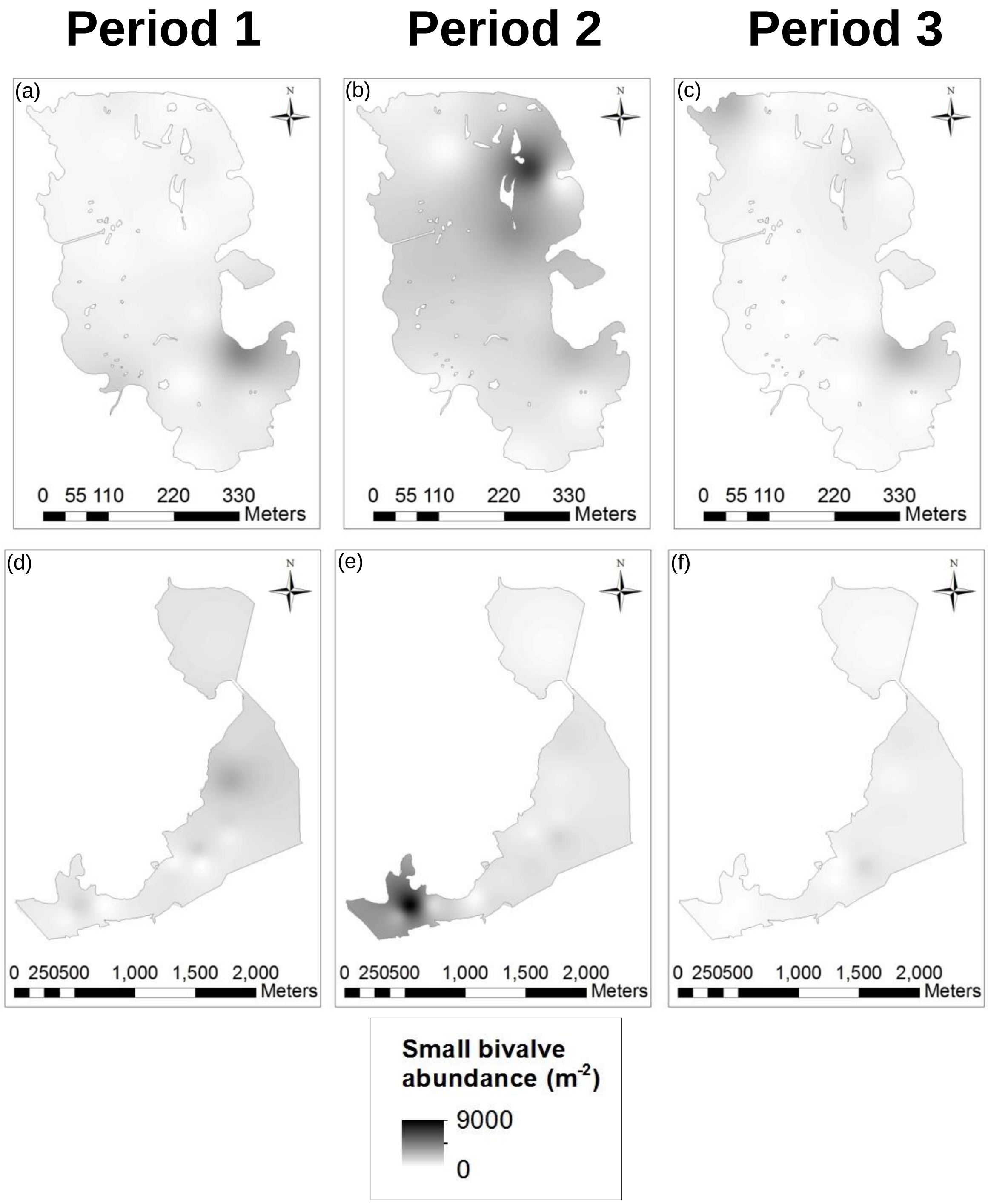
Appendix 10(f). Spatial distribution of *Corophium* spp. in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



Appendix 10(g). Spatial distribution of Hydrobiidae in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



Appendix 10(h). Spatial distribution of small bivalves in Period 1, 2 and 3 at Brownsea (a,b,c) and Middlebere (d,e,f).



Appendix 11. Relative size and exposure time of each patch during spring and neap tides, for present day and sea-level rise scenarios.

		Duration of exposure (h tide^{-1})									
		Present		SLR + 15.9 cm		SLR + 18.8 cm		SLR + 22.4 cm		SLR + 41.4 cm	
Patch	Patch area	Spring	Neap	Spring	Neap	Spring	Neap	Spring	Neap	Spring	Neap
Foraging habitat											
Intertidal mudflat											
Creeks	445179	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lower main creek	113702	2.07	2.74	1.3	1.33	1.23	1.26	1.05	1.19	0.07	0.25
Lower creeks	347797	2.81	3.79	1.75	2.25	1.61	1.89	1.47	1.61	0.46	0.67
Lower Middlebere	160607	4.46	6.21	3.51	4.84	3.37	4.46	3.12	4.21	1.79	2.28
Middle Middlebere 1	97398.5	4.46	6.21	3.51	4.84	3.37	4.46	3.12	4.21	1.79	2.28
Middle Middlebere 2	94983.5	5.58	8.21	4.63	6.46	4.28	6.11	4.07	5.61	3.05	4.07
Upper Middlebere	74787.7	8.04	11.19	6.14	8.77	5.93	8.56	5.54	8.14	4.18	5.96
Middle Wych	69687.7	2.74	3.79	1.75	2.11	1.54	1.82	1.44	1.51	0.42	0.63
Upper Wych 1	88403.6	3.89	5.4	3.09	4.07	2.74	3.79	2.6	3.47	1.44	1.51
Upper Wych 2	82305	7.37	10.74	5.79	8.42	5.44	8.11	5.19	7.44	4	5.58
Lagoon											
Brownsea Island Lagoon	178024	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.
Roosting habitat											
Saltmarsh 1	230061	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.
Saltmarsh 2	317421	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.
Saltmarsh 3	314567	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.
Saltmarsh 4	380105	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.
Saltmarsh 5	202517	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.
Brownsea Island sand spit	157.87	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.	A.E.

A.E. = always exposed

Appendix 12(a). Initial prey abundance (m^{-2}) on model day 1.

Prey type (sizeclass in mm)	**Patches**									
	2	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
SmallWorms	127.32	106.10	56.59	0.00	42.44	84.88	42.44	84.88	84.88	4873.04
Worms1to5	42.44	318.31	56.59	0.00	84.88	21.22	84.88	21.22	21.22	98.39
Worms6to10	106.10	106.10	99.03	15.92	297.09	21.22	297.09	21.22	21.22	115.75
Worms11to15	42.44	42.44	14.15	15.92	84.88	42.44	84.88	42.44	42.44	49.19
Worms16to20	84.88	0.00	70.74	159.16	84.88	84.88	84.88	84.88	84.88	101.28
Worms21to25	21.22	0.00	42.44	95.49	21.22	84.88	21.22	84.88	84.88	98.39
Worms26to30	42.44	0.00	70.74	47.75	84.88	84.88	84.88	84.88	84.88	136.01
Worms31to35	0.00	42.44	14.15	0.00	84.88	21.22	84.88	21.22	21.22	20.26
Worms36to40	0.00	0.00	14.15	79.58	0.00	42.44	0.00	42.44	42.44	92.60
Worms41to45	0.00	0.00	14.15	31.83	0.00	0.00	0.00	0.00	0.00	17.36
Worms46to50	42.44	63.66	28.29	31.83	0.00	21.22	0.00	21.22	21.22	11.57
Worms51to55	84.88	42.44	28.29	15.92	21.22	42.44	21.22	42.44	42.44	98.39
Worms56to60	42.44	0.00	28.29	15.92	63.66	21.22	63.66	21.22	21.22	95.49
Worms61to65	0.00	0.00	14.15	15.92	0.00	0.00	0.00	0.00	0.00	34.72
Worms66to70	21.22	0.00	14.15	0.00	0.00	0.00	0.00	0.00	0.00	26.04
Worms71to75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.26
Worms76to80	42.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.57
Worms81to85	42.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms86to90	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms91to95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms96to100	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms101to105	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms106to110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms111to115	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms116to120	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms121to125	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corophium1to5	0.00	0.00	0.00	0.00	0.00	1252.02	0.00	1252.02	1252.02	5495.19
Corophium5to10	0.00	0.00	0.00	0.00	0.00	827.61	0.00	827.61	827.61	436.95
Corophium10to15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	43.41
Corophium15to20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SoftBivalves1to5	1718.87	275.87	650.77	222.82	63.66	848.83	63.66	848.83	848.83	465.89
SoftBivalves6to10	318.31	551.74	198.06	429.72	275.87	0.00	275.87	0.00	0.00	156.26
SoftBivalves11to15	42.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SoftBivalves16to20	21.22	0.00	14.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves1to5	21.22	21.22	14.15	15.92	21.22	0.00	21.22	0.00	0.00	0.00
HardBivalves6to10	0.00	84.88	28.29	0.00	84.88	0.00	84.88	0.00	0.00	5.79
HardBivalves11to15	21.22	0.00	28.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves16to20	21.22	0.00	0.00	15.92	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves21to25	0.00	0.00	0.00	15.92	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves26to30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves31to35	21.22	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves36to40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves41to45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves46to50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrobia1to5	679.06	297.09	367.82	461.55	297.09	233.43	297.09	233.43	233.43	5408.38
Hydrobia6to10	148.54	42.44	0.00	143.24	21.22	0.00	21.22	0.00	0.00	5.79
Cyathura1to5	721.50	21.22	113.18	47.75	148.54	0.00	148.54	0.00	0.00	0.00
Cyathura6to10	106.10	0.00	42.44	63.66	0.00	0.00	0.00	0.00	0.00	0.00
Cyathura11to15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 12(b). Initial prey abundance (m^{-2}) on model day 66.

Prey type (size class in mm)	Patches									
	2	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
SmallWorms	1222.31	721.50	2843.57	2037.18	424.41	169.77	424.41	169.77	169.77	5189.84
Worms1to5	50.93	212.21	155.62	14.15	169.77	21.22	169.77	21.22	21.22	1220.65
Worms6to10	203.72	806.39	339.53	99.03	360.75	254.65	360.75	254.65	254.65	370.90
Worms11to15	101.86	466.85	254.65	113.18	424.41	127.32	424.41	127.32	127.32	85.81
Worms16to20	76.39	212.21	56.59	42.44	169.77	127.32	169.77	127.32	127.32	74.73
Worms21to25	101.86	254.65	84.88	240.50	339.53	63.66	339.53	63.66	63.66	33.21
Worms26to30	76.39	169.77	56.59	212.21	509.30	42.44	509.30	42.44	42.44	27.68
Worms31to35	127.32	169.77	56.59	127.32	297.09	84.88	297.09	84.88	84.88	24.91
Worms36to40	25.46	127.32	0.00	99.03	148.54	0.00	148.54	0.00	0.00	38.75
Worms41to45	25.46	21.22	14.15	56.59	106.10	21.22	106.10	21.22	21.22	19.38
Worms46to50	50.93	21.22	0.00	14.15	63.66	84.88	63.66	84.88	84.88	11.07
Worms51to55	0.00	21.22	0.00	70.74	84.88	84.88	84.88	84.88	84.88	41.52
Worms56to60	0.00	0.00	0.00	0.00	21.22	21.22	21.22	21.22	21.22	19.38
Worms61to65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.54
Worms66to70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.77
Worms71to75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms76to80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.77
Worms81to85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.77
Worms86to90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.77
Worms91to95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms96to100	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms101to105	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.77
Worms106to110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms111to115	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms116to120	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms121to125	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corophium1to5	0.00	0.00	28.29	0.00	42.44	2737.47	42.44	2737.47	2737.47	2767.91
Corophium5to10	0.00	0.00	14.15	0.00	106.10	2864.79	106.10	2864.79	2864.79	83.04
Corophium10to15	0.00	0.00	0.00	0.00	0.00	445.63	0.00	445.63	445.63	16.61
Corophium15to20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Soft.bivalves1to5	560.23	700.28	367.82	466.85	572.96	190.99	572.96	190.99	190.99	1256.63
SoftBivalves6to10	203.72	254.65	339.53	254.65	254.65	21.22	254.65	21.22	21.22	130.09
SoftBivalves11to15	0.00	84.88	42.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SoftBivalves16to20	0.00	21.22	0.00	0.00	21.22	21.22	21.22	21.22	21.22	0.00
HardBivalves1to5	25.46	0.00	14.15	0.00	0.00	0.00	0.00	0.00	0.00	16.61
HardBivalves6to10	0.00	0.00	14.15	0.00	42.44	0.00	42.44	0.00	0.00	8.30
HardBivalves11to15	25.46	21.22	56.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves16to20	76.39	127.32	42.44	14.15	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves21to25	25.46	0.00	28.29	0.00	21.22	0.00	21.22	0.00	0.00	0.00
HardBivalves26to30	25.46	0.00	14.15	0.00	21.22	0.00	21.22	0.00	0.00	0.00
HardBivalves31to35	0.00	0.00	14.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves36to40	0.00	0.00	14.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves41to45	0.00	0.00	14.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves46to50	0.00	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrobia1to5	789.41	424.41	933.71	2122.07	679.06	381.97	679.06	381.97	381.97	13969.66
Hydrobia6to10	50.93	0.00	127.32	240.50	127.32	63.66	127.32	63.66	63.66	16.61
Cyathura1to5	152.79	106.10	141.47	42.44	21.22	0.00	21.22	0.00	0.00	0.00
Cyathura6to10	432.90	169.77	155.62	14.15	169.77	0.00	169.77	0.00	0.00	0.00
Cyathura11to15	127.32	42.44	28.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 12(c). Initial prey abundance (m^{-2}) on model day 175.

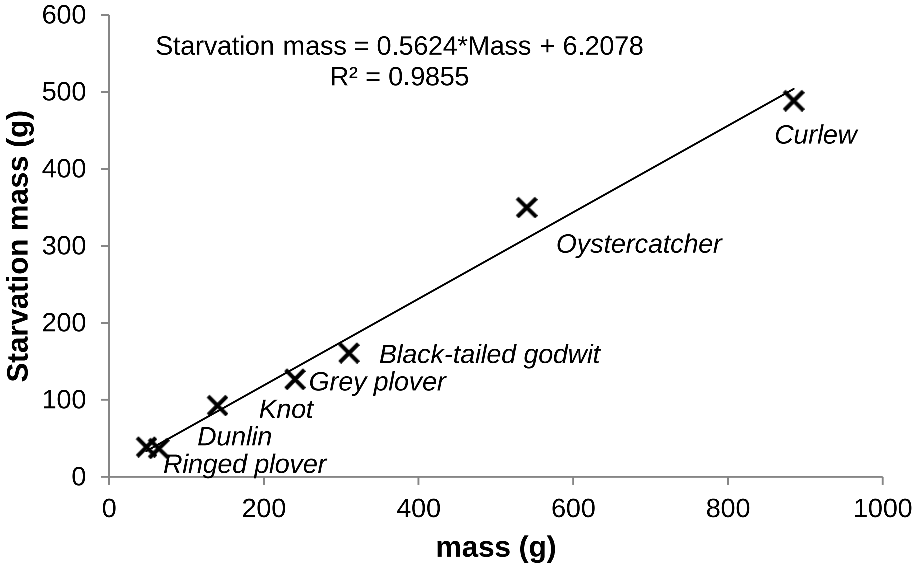
	Patches									
Prey type (size class in mm)	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
SmallWorms	148.54	615.40	240.50	438.56	63.66	827.61	63.66	827.61	827.61	3191.59
Worms1to5	0.00	148.54	56.59	42.44	21.22	21.22	21.22	21.22	21.22	540.42
Worms6to10	0.00	318.31	127.32	141.47	148.54	84.88	148.54	84.88	84.88	919.56
Worms11to15	127.32	106.10	141.47	212.21	106.10	212.21	106.10	212.21	212.21	611.16
Worms16to20	84.88	127.32	56.59	70.74	0.00	63.66	0.00	63.66	63.66	466.85
Worms21to25	63.66	254.65	70.74	169.77	84.88	0.00	84.88	0.00	0.00	237.67
Worms26to30	190.99	84.88	113.18	254.65	190.99	63.66	190.99	63.66	63.66	246.16
Worms31to35	63.66	63.66	28.29	42.44	42.44	0.00	42.44	0.00	0.00	110.35
Worms36to40	0.00	21.22	28.29	28.29	63.66	21.22	63.66	21.22	21.22	62.25
Worms41to45	0.00	21.22	28.29	28.29	21.22	0.00	21.22	0.00	0.00	36.78
Worms46to50	0.00	21.22	14.15	14.15	0.00	42.44	0.00	42.44	42.44	56.59
Worms51to55	21.22	0.00	0.00	0.00	21.22	84.88	21.22	84.88	84.88	39.61
Worms56to60	0.00	21.22	14.15	0.00	21.22	0.00	21.22	0.00	0.00	84.88
Worms61to65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.29
Worms66to70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.81
Worms71to75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.32
Worms76to80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.83
Worms81to85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.83
Worms86to90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.15
Worms91to95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.98
Worms96to100	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.83
Worms101to105	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms106to110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.49
Worms111to115	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms116to120	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Worms121to125	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.15
Corophium1to5	0.00	21.22	42.44	28.29	106.10	1167.14	106.10	1167.14	1167.14	2232.41
Corophium5to10	21.22	0.00	113.18	113.18	127.32	254.65	127.32	254.65	254.65	401.78
Corophium10to15	0.00	0.00	14.15	0.00	0.00	190.99	0.00	190.99	190.99	200.89
Corophium15to20	0.00	0.00	0.00	0.00	0.00	42.44	0.00	42.44	42.44	14.15
Soft.bivalves1to5	190.99	127.32	42.44	70.74	0.00	0.00	0.00	0.00	0.00	458.37
SoftBivalves6to10	21.22	42.44	84.88	14.15	0.00	0.00	0.00	0.00	0.00	22.64
SoftBivalves11to15	0.00	0.00	14.15	14.15	0.00	0.00	0.00	0.00	0.00	0.00
SoftBivalves16to20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves1to5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves6to10	0.00	0.00	28.29	14.15	21.22	0.00	21.22	0.00	0.00	0.00
HardBivalves11to15	0.00	0.00	28.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves16to20	21.22	21.22	28.29	0.00	21.22	0.00	21.22	0.00	0.00	0.00
HardBivalves21to25	0.00	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.49
HardBivalves26to30	0.00	21.22	28.29	14.15	0.00	0.00	0.00	0.00	0.00	2.83
HardBivalves31to35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.83
HardBivalves36to40	0.00	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves41to45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HardBivalves46to50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrobia1to5	572.96	360.75	537.59	1131.77	254.65	127.32	254.65	127.32	127.32	4521.42
Hydrobia6to10	21.22	21.22	56.59	183.91	0.00	21.22	0.00	21.22	21.22	0.00
Cyathura1to5	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cyathura6to10	21.22	21.22	183.91	0.00	63.66	0.00	63.66	0.00	0.00	0.00
Cyathura11to15	0.00	21.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 13. Patch-specific worm availability constants.

Patch		Prey availability	
		Benthic tactile	Visual
2	Lower main creek	0.239344059	0.1
3	Lower creeks	0.224572079	0.1
4	Lower Middlebere	0.27356726	0.1
5	Middle Middlebere 1	0.256507858	0.1
6	Middle Middlebere 2	0.20829904	0.1
7	Upper Middlebere	0.307276771	0.1
8	Middle Wych	0.20829904	0.1
9	Upper Wych 1	0.307276771	0.1
10	Upper Wych 2	0.307276771	0.1
11	Brownsea Island Lagoon	0.306735091	0.1

Appendix 14. The predicted relationship between body mass and starvation mass.

Estimates of body mass for each species were obtained from British Trust for Ornithology (BTO) data (Robinson 2005), and starvation masses were compiled by John Goss-Custard (unpublished data).



Appendix 15. Ash-free dry mass (AFDM) values and energy conversion factors.

	Biomass per item (mg AFDM)	Energy density per item (kJ mg^{-1})*	Energy per item (kJ)
SmallWorms	0.2300	0.0214	0.0049
Worms1to5	0.0266	0.0197	0.0005
Worms6to10	0.2485	0.0197	0.0049
Worms11to15	0.7017	0.0197	0.0138
Worms16to20	1.3904	0.0197	0.0274
Worms21to25	2.3172	0.0197	0.0456
Worms26to30	3.4841	0.0197	0.0686
Worms31to35	4.8926	0.0197	0.0963
Worms36to40	6.5441	0.0197	0.1288
Worms41to45	8.4397	0.0197	0.1661
Worms46to50	10.5804	0.0197	0.2082
Worms51to55	12.9671	0.0197	0.2552
Worms56to60	15.6006	0.0197	0.3070
Worms61to65	18.4815	0.0197	0.3637
Worms66to70	21.6107	0.0197	0.4253
Worms71to75	24.9887	0.0197	0.4917
Worms76to80	28.6160	0.0197	0.5631
Worms81to85	32.4933	0.0197	0.6394
Worms86to90	36.6210	0.0197	0.7207
Worms91to95	40.9996	0.0197	0.8068
Worms96to100	45.6296	0.0197	0.8979
Worms101to105	50.5113	0.0197	0.9940
Worms106to110	55.6453	0.0197	1.0950
Worms111to115	61.0318	0.0197	1.2010
Worms116to120	66.6713	0.0197	1.3120
Worms121to125	72.5641	0.0197	1.4280
Corophium1to5	0.0611	0.0207	0.0013
Corophium5to10	0.5558	0.0207	0.0115
Corophium10to15	1.5518	0.0207	0.0322
Corophium15to20	3.0519	0.0207	0.0633
SoftBivalves1to5	0.6262	0.0217	0.0136
SoftBivalves6to10	4.0669	0.0217	0.0882
SoftBivalves11to15	9.7072	0.0217	0.2105
SoftBivalves16to20	17.2173	0.0217	0.3734
HardBivalves1to5	0.7249	0.0217	0.0157
HardBivalves6to10	7.2143	0.0217	0.1565
HardBivalves11to15	14.7631	0.0217	0.3202
HardBivalves16to20	45.0349	0.0217	0.9768
HardBivalves21to25	103.5929	0.0217	2.2469
HardBivalves26to30	201.4684	0.0217	4.3698
HardBivalves31to35	350.5020	0.0217	7.6024
HardBivalves36to40	563.2383	0.0217	12.2166
HardBivalves41to45	852.8478	0.0217	18.4983
HardBivalves46to50	1233.0682	0.0217	26.7452
Hydrobia1to5	0.5495	0.0212	0.0116
Hydrobia6to10	1.9975	0.0212	0.0423
Cyathura1to5	0.1043	0.0248	0.0026
Cyathura6to10	1.0719	0.0248	0.0266
Cyathura11to15	3.1668	0.0248	0.0785
Pomatoschistus	159.5503	0.0230	3.6633
Palaemonetes	77.5222	0.0248	1.9225

*references provided in Appendix 7(b).