# THE IMPACT OF GREEN MACROALGAL MATS ON BENTHIC INVERTEBRATES AND OVERWINTERING WADING BIRDS

**Ann Thornton**

A thesis submitted in partial fulfilment of the requirements of
Bournemouth University for the degree of Doctor of Philosophy

June 2016

Bournemouth University
in collaboration with
Natural England

# Copyright statement

# The impact of green macroalgal mats on benthic invertebrates and overwintering wading birds

Ann Thornton

## Abstract

A consequence of increased nutrient levels within an estuarine ecosystem is the development of green macroalgal blooms or ‘mats’. These mats can cover extensive areas of estuarine intertidal habitats and have biomass >1 kg $m^{-2}$ (wet weight). One of the key metrics for assessment of the ecological condition status of estuarine features in Europe is the extent and biomass of macroalgal mats.

The aim of this research is to establish whether the development of green macroalgal mats affects feeding relationships between invertebrate assemblages and overwintering migratory wading birds in Poole Harbour - a temperate estuarine ecosystem on the south coast of England. Poole Harbour is designated for its populations of overwintering migratory wading birds. As such, any decline in wading bird numbers as a result of nutrient enrichment affecting their food supply or altering feeding behaviour, would result in sanctions under current legislation.

This field research consisted of three main objectives: 1) Measuring the biomass and extent of the macroalgal mat within Poole Harbour. 2) Analysing any changes to the benthic invertebrate community under varying macroalgal mat densities. 3) Observing and recording the behaviour and feeding success of key wading bird species; in particular how they responded to changes in prey availability and varying levels of macroalgal mat coverage.

Samples of macroalgal mat were taken monthly or bi-monthly on mudflats at four locations around the harbour over two years and wet weight biomass was recorded. Wading bird invertebrate prey availability was measured using benthic core samples taken at upper, mid, and lower shore levels at three key sites. Invertebrate size-classes were recorded and converted into available energy (kJ $m^{-2}$) according to the preferred diet of each of the five wading bird species studied. Observations of wading bird behaviour were recorded over two overwintering periods (September – March). Digital video recordings were taken of different wading bird species’ feeding behaviour and success on varying levels of macroalgal mat coverage.

Coverage by macroalgal mats was high (>50%) with dense patches persisting into autumn. Biomass of algae reached 1 kg m$^{-2}$ at each of the sites during both years with two sites exceeding 2 kg m$^{-2}$ (wet weight) in 2013; although that level was not maintained throughout the summer growth period. The invertebrate community was transformed under increased algal biomass within an increase in abundance (m$^{-2}$) of smaller less energy-dense species when algae reached ~800 g m$^{-2}$ (wet weight). Variation in overall invertebrate community assemblage between benthic samples was best explained by algae biomass; either singularly or in combination with % organic matter. This pattern was repeated with an initial increase in available energy (kJ m$^{-2}$) within each bird species preferred prey under lower macroalgal mat biomass (~800 g m$^{-2}$ wet weight) followed by a decline as algae biomass increased. During autumn, when large areas of macroalgal mat were still visible, foraging behaviour by some wading bird species varied under different levels of algae coverage. Some wading bird species' behaviour also varied in winter on areas which had been covered by algae during the previous growth season.

The current macroalgal mat biomass threshold of concern under SSSI Conditions Assessments is 2 kg m$^{-2}$ (wet weight). Results suggest that the impact from macroalgal mats in Poole Harbour is evident at a biomass lower than 2 kg m$^{-2}$ (wet weight); supporting a lowering of this threshold to 1 kg m$^{-2}$. An increase in abundance of smaller invertebrates has resulted in a decline in energy available for the wading birds' preferred diet. Observations suggest that wading birds may be adapting to these changes with some species appearing to be feeding on smaller, lower-quality prey (i.e. smaller worms/bivalves) and other species feeding on prey found on the surface of the macroalgal mat. Adaptations are site-specific in response to conditions within individual bays but consistent between shore levels within each bay.

# Table of contents

## 6.0 Changes to wading bird feeding rate in response to macroalgal mat coverage ............................................ 125

## List of Figures

# List of Tables

# List of Appendices

# Acknowledgements

Firstly, I would like to thank Bournemouth University and Natural England for providing the funding for this project. A PhD is a journey and, as with any successful journey, travelling companions are essential so I would like to thank my supervisors, Roger Herbert, Richard Stillman, Dan Franklin and, from Natural England, Sue Burton. Their support has been invaluable and I have welcomed our discussions on various aspects of the project from bird behaviour to an experimental design to test the force required for a curlew beak to penetrate dense macroalgal mat. I would also like to thank a number of academics from the Faculty; most notably Christine Maggs for *Ulva* spp. identification, Andy Ford for remote sensing, and Rick Stafford and Duncan Golicher for the mysteries of R.

I have spent the best part of the last four years in mud and water and, remarkably, have not managed to get stuck or drown (excepting the eventful pilot study in Holes Bay). My team of willing volunteer field-assistants have been vital in ensuring I fulfilled the health and safety requirements for this project; Alice Hall, Katharine Bowgen, Catherine Collop, Wayne O'Brien, Daniella Vos, Dean Burnard, Paul Evans, Danny Sheath. I am also grateful for the assistance provided by John Humphreys in the collection of invertebrate core samples. The tides in Poole Harbour are notoriously difficult to navigate particularly when I was keen to obtain samples from north of the railway bridge in Holes Bay; we *almost* ended up stuck on the mud for 6 hours.

My friends, both within the PhD community and outside, and family have been a constant source of support and now know a great deal more about green macroalgal mats, benthic invertebrates and wading bird behaviour.

Finally, most important of all, my wonderful husband Andy. He has remained resolutely cheerful helping me collect samples in all weathers, not complained when having to carry buckets of mud, and even accepted that we have a freezer full of green algae. Without his patience, understanding and support I would not have been able to do this.

This journey has challenged me physically and mentally but I have never found it dull nor have I become disenchanted with the research. Once again, I turn to Douglas Adams to provide the right words:

> *'I may not have gone where I intended to go, but I think I have ended up where I needed to be.'*

# Author's declaration

I confirm that the work presented in this thesis is my own.

Ann Thornton

# 1.0 Introduction

*'…what we are concerned with here is the fundamental interconnectedness of all things...'*

(*Dirk Gently's Holistic Detective Agency*, Douglas Adams, 1987)

It is estimated that 40% of the global population live within 100 km of the coast and almost 1 billion people rely on the marine environment to provide a source of protein (Agardy et al. 2005; Statham 2012). As marine and coastal research catches up with its terrestrial counterparts, there is increasing evidence of the impact of human activity on the estuarine environment (McLusky and Elliott 2004; Elliott and Whitfield 2011; Hawkins 2012; Borja et al. 2012). Threats including climate change, sea-level rise, over-fishing, pollution, habitat loss, and non-native species risk transforming the estuarine ecosystem (Raffaelli 2006; Airoldi and Beck 2007; Elliott et al. 2007; Hawkins 2012). Approximately 1,200 of the world's major estuaries cover an area of c.500,000 km$^2$, with 62% of these located within 50 km of urban populations >100,000 (Agardy et al. 2005). With continued urban development in coastal areas, increased pressure is placed upon estuarine and coastal waters (also known as 'transitional waters') receiving discharges from the surrounding land and rivers (Patrício et al. 2007; WFD-UKTAG 2009; Giordani et al. 2009; Borja et al. 2012; 2013).

Ecosystem services provided by estuarine and coastal waters are myriad with commercial operations including shell-fisheries, bait-digging and cargo transport, and recreational activities including wildlife tourism alongside provisioning services such as flood prevention and effluent disposal (Crooks and Turner 1999; McLusky and Elliot 2004; Agardy et al. 2005; Raffaelli 2006). In order for humans to benefit from these services, estuaries have experienced an unprecedented transformation over the last 50 years with channel-dredging, coastal defence construction, harbour and urban expansion as well as increased artificial light and noise levels (Davidson et al. 1991; Borja et al. 2012; Dwyer et al. 2013). Any suggestion that vital ecosystem services may be threatened raises environmental, economic and social concern amongst local, national, regional and global administrations and governments (Raffaelli 2006).

## 1.1 Consequences of excess nutrient input into an estuarine ecosystem: the development of macroalgal mats.

In June 2008 a large dense macroalgal mat was recorded on beaches off the coast of Qingdao, China. The mat comprised *Ulva prolifera* [O F Müller 1778] (Kong et al. 2010) and covered an area of 12000 km$^2$ making this bloom the largest recorded at that time (Liu et al. 2009; Gao et al. 2010; Shen et al. 2012). Media reports suggested that 20,000 people were involved in clearing the macroalgal mat in time for the city to host the sailing events for the 2008 Olympic Games which commenced 5 weeks later (Yardley 2008; Gao et al. 2010). Satellite images appeared to suggest that the bloom formed further south as a result of coastal eutrophication (Liu, F., et al. 2010). Further research discovered the source to be rafts of *Porphyra yezoensis* [(Ueda) M S Hwang and H G Choi 2011] created as part of an expanded aquaculture 180 km north along the Yellow Sea coast (Liu, D., et al. 2009; 2010).

In contrast to the open sea environment where nutrients can be limited, estuaries are amongst the most naturally nutrient rich systems on Earth (Teichberg et al. 2010). Inputs of allochthonous ('new') nitrogen and phosphorus from land, via rivers and groundwater seepage, combine with tidal input from marine sources and autochthonous ('recycled') nutrients in the sediment to maintain a constant supply; small amounts of which naturally stimulate primary production within an estuarine food-web (Neilson and Cronin 1981; Raffaelli et al. 1999; Bricker et al. 2008; Fox et al. 2009; Day et al. 2013).

Sources of excess nutrients discharged into the estuarine environment as a consequence of anthropogenic activities include the use of fertilisers from farming, land run-off (both agricultural and urban), and discharges from sewage works and storm drains (Nedwell et al. 2002; McLusky and Elliott 2004; Day et al. 2013). In combination, these contribute to an overall increase in the nutrient loading of estuarine waters resulting in a global increase in eutrophication (Costanzo et al. 2001; Gray et al. 2002; Deegan et al. 2012; Hawkins 2012; Day et al. 2013). It can be difficult to determine the early stages of eutrophication due to the natural dynamic variability within the estuarine environment (Raffaelli 1999). In addition, fringe vegetation (e.g. saltmarsh) can mitigate some of the effects of excessive nutrient input through uptake of phosphorus and nitrogen compounds before they reach the water (Deegan et al. 2012). As a system becomes more eutrophic, a visible symptom of excess nutrient enrichment within an estuary can be the development of macroalgal mats (Nedwell et al. 2002;

Scanlan et al. 2007; Teichberg et al. 2010). Dense macroalgal mats are an increasingly common sight within both temperate and tropical estuarine systems (Jones and Pinn 2006; Teichberg et al. 2010). These mats, comprising mainly green alga species (such as *Ulva, Cladophora* and *Chaetomorpha*), are able to uptake nutrients swiftly for rapid growth; Chlorophyta (green algae) can take up nutrients 4-6 times faster than slower-growing, more structurally complex, Phaeophyta (brown algae) (Pedersen and Borum 1997).

Estuaries and beaches in northern France have experienced an increase in macroalgal mats over the last two decades (Ménesguen and Cugier 2006; Perrot et al. 2014). This has been attributed to intensive farming methods used in the surrounding countryside (Ménesguen and Cugier 2006). Macroalgal mats were not reported to be problematic in northern France until the 1990s. However, as nutrient enrichment increased, the development of extensive macroalgal blooms became an environmental issue (Ménesguen and Piriou 1995; Smetacek and Zingone 2013). Chlorophyte *Ulva* spp. are the main component of the macroalgal blooms in this region (Merceron and Morand 2004; Smetacek and Zingone 2013). The decaying algae can release toxic hydrogen-sulphide ($H_2S$) gas; a process that caused the death of a horse and left its rider unconscious in 2008, and resulted in the death of 30 wild boar two years later (Smetacek and Zingone 2013).

However, there is agreement that certain types of estuaries are more susceptible to the effects of eutrophication (Kadiri et al. 2014); particularly those with a limited tidal range and restricted flushing (Scanlan et al. 2007). These micro-tidal estuaries have a range of ~<2 m and reduced water exchange resulting in lower dilution of effluents (McLusky and Elliott 2004), with excess nutrients remaining available within the shallow water and sediment for longer before being flushed out to sea (Monbet 1992). By contrast, on higher energy macro-tidal estuaries, water column mixing ensures excess nutrients do not remain within the system for long periods (Elliott and Whitfield 2011; Kadiri et al. 2014).

## 1.2 The ecological impacts of macroalgal mats on soft-sediment intertidal habitats: a review.

### 1.2.1 Soft-sediment estuarine systems

Sediment washed outward from land run-off and rivers or washed inwards from the sea creates large intertidal mudflats characterised by fine silt and sand (Prater 1981).

These mudflats, formed from sediment predominantly comprising a particle size of <250 µm, support an abundance of specialised invertebrates (Wilson and Fleeger 2013). Although bacterial organisms can live on individual particles and meiofauna in interstitial waters, the larger macrofauna are distributed according to sediment particle size (Leaper et al. 2001). For example, burrowing species such as *Arenicola marina* [Linnaeus 1758] require sand or sandy mud to ensure stability of their burrow (Longbottom 1970).

In addition to particle size affecting invertebrate species and community composition, salinity levels are also important (Whitfield et al. 2012). The salinity of estuarine water is between 0.5 (freshwater) and 35 (marine). The term ‘brackish’ is used to differentiate between estuarine water, freshwater and marine ecosystems (McLusky and Elliott 2004). Due to this variation in salinity levels along the estuarine gradient, species surviving in these conditions tend to be euryhaline – able to survive in fluctuating conditions caused by the changes in salinity levels from marine and freshwater input (Borja et al. 2012). As a consequence of the need for benthic invertebrate species to be able to tolerate varying environmental conditions, the invertebrate community within estuarine environments is less diverse than marine or freshwater systems (McLusky and Elliott 2004).

### 1.2.2 Global context

This review examines the impact of macroalgal mats within northern hemisphere temperate estuarine ecosystems. A study at nine sites comprising both tropical and temperate estuarine systems reported no difference between tropical and temperate sites in the response of green mat-forming alga *Ulva lactuca* [Linnaeus 1753] to the experimental manipulation of nutrient levels. However, the study found seasonal responses in *U. lactuca* growth rate were less apparent in tropical sites with fluctuations in growth possibly triggered by other environmental factors such as increased rainfall during the wet season (Teichberg et al. 2010). Therefore studies in tropical environments will not be considered further.

Studies examining the impact of macroalgal mats as a consequence of enrichment of estuarine and coastal waters have been carried out since the 1960s in temperate regions (Valiela et al. 1997) including Waquoit Bay, Massachusetts (Escartín and Aubrey 1995; Fox et al. 2008), Portugal (Cardoso et al. 2002; Ferreira et al. 2005), and even the harbour wall in Venice (Piazzi and Cinelli 2003). Results have shown that dense macroalgal mats can affect tidal hydrodynamics (Escartín and Aubrey 1995), lead to the decline or disappearance of eel grass (*Zostera* spp.) (Bowen and Valiela 2001) and smother saltmarsh (Boyer and Fong 2005; Newton and Thornber 2012).

### 1.2.3 Impact of macroalgal mats on tidal hydrodynamics

The thickness of macroalgal mats can result in changes to shallow-water estuarine tidal hydrodynamics as the mat can represent >50% of the water depth (Escartín and Aubrey 1995). Flume experiments have recorded increases in friction across the macroalgal mat (Escartín and Aubrey 1995) and a reduced flow rate across dense mats of *U. intestinalis* [Linnaeus 1753] (Venier et al. 2012). It was concluded that this could increase bed stability by reducing sediment transport but also lead to finer sediment particles resulting in increased siltation between the algal layers and a greater organic deposition within the sediment (Venier et al. 2012).

### 1.2.4 Impact of macroalgal mats on intertidal habitats in the UK and Ireland

A number of micro-tidal (tidal range <2 m) and meso-tidal (tidal range 2 m – 4 m) estuaries (McLusky and Elliott 2004) within the UK and Ireland are susceptible to the development of macroalgal mats. Examples include the meso-tidal Ythan Estuary in Scotland (Raffaelli 1999), and micro-tidal Langstone, Chichester and Poole Harbours along the south coast of England (Soulsby et al. 1982; Jones and Pinn 2006). By contrast, the increased turbidity within higher-energy macro-tidal systems (e.g. Severn Estuary) reduces available light thereby preventing the development of macroalgal mats (Painting et al. 2007; Kadiri et al. 2014).

*Ythan Estuary, Scotland*

Research using a long-term (30 year) data set recorded an increase in macroalgal mat biomass and extent during this period particularly during the final decade of the project (1986-1997) (Raffaelli et al. 1999). The study found no significant change in the hydrology or geomorphology of the Ythan Estuary so could not attribute an increase in macroalgal mat development to these factors. It was therefore concluded that a rise in nitrogen loading within the estuary was likely to be the cause of the macroalgal mat development but further research was needed (Raffaelli et al. 1999). A decade later a study examining the effectiveness of using aerial image interpretation technology to measure the spatial extent of the macroalgal mat was carried out in the Ythan Estuary and recorded extensive macroalgal mat coverage although technical limitations prevented an accurate measurement of % coverage (Green 2007). This, and other studies using remote sensing to determine the spatial extent of macroalgal mats, is discussed further in Chapter 2.

*Langstone and Chichester Harbours, Hampshire*

In southern England, macroalgal mat growth usually commences in the spring with densities at their greatest during July and August (Jones and Pinn 2006). Evidence of the development of dense macroalgal mats was first reported in Langstone Harbour in the late 1960s (Soulsby et al. 1982; C. Maggs, pers. comm.) with extensive coverage (>75%) recorded during 1977 and 1978 (Soulsby et al. 1982). During the 1970s macroalgal mat coverage varying from 1% - 100% was recorded on almost 1000ha of Langstone Harbour (representing c. 40% of the intertidal area) (Montgomery and Soulsby 1980). Since that time, macroalgal mats in Langstone Harbour have remained extensive and persistent (Rees-Jones 2004).

### 1.2.5 Impact of macroalgal mats on *Zostera*

From 1938 – 1990, nitrogen input into the Waquoit Bay, Massachusetts doubled resulting in a significant increase in phytoplankton and macroalgal blooms as nutrient levels rose (Bowen and Valiela 2001). The dense macroalgal mats smothered the established seagrass (*Zostera marina* [Linnaeus 1753] - also known as eelgrass) and reduced light availability thereby restricting growth. Aerial images showed a reduction in *Zostera* when nitrogen loading was 20 kg ha$^{-1}$ year$^{-1}$ and, once nitrogen levels reached 100 kg ha$^{-1}$ year$^{-1}$, the *Zostera* beds had almost disappeared (Bowen and Valiela 2001). Experimental manipulation of macroalgal canopies conducted in Waquoit Bay resulted in a decline in new growth of *Z. marina* as densities of macroalgae increased and the study identified a macroalgal canopy height of 9-12 cm as a threshold above which *Z. marina* began to decline (Hauxwell et al. 2001). Results from long-term sampling of nutrient levels and macrophyte community structure in Waquoit Bay (June 1994 – June 2000) also showed a decline in *Zostera* biomass and a corresponding increase in macroalgal biomass under increased nitrogen loading in the estuary (Fox et al. 2008).

A long-term (1993-2005) study at the Mondego Estuary, Portugal, gathered data on nutrient input and the extent of the macroalgal mat development within *Zostera noltii* [Hornemann 1832] beds (Cardoso et al. 2010). The study benefitted from before-and-after-impact analysis due to management intervention in 1998 aimed at reducing nutrient input into the estuary. There was a decline in *Z. noltii* from 1993-1998 as nutrient load increased yet, following the control measures, *Z. noltii* began to recover with levels recorded in 2005 at 100% higher than 1997; although only 50% of the 1993 level (Cardoso et al. 2010). Increases in organic content in low energy estuarine systems can lead to higher turbidity; a consequence being reduced light levels and a decline in *Zostera* (Dolbeth et al. 2003; Fox et al. 2008). After nutrient control measures were implemented in 1998, the estuarine ecosystem was transformed with an increase in the red alga, *Gracilara gracilis* [(Stackhouse) M Steentoft, L M Irvine and W F Farnham 1995], a gradual increase in *Z. noltii,* and a decline in the green macroalgal mats of *Ulva* spp. (Leston et al. 2008).

### 1.2.6 Impact of macroalgal mats on saltmarsh

Saltmarsh communities are also under threat from macroalgal mats (Boyer and Fong 2005; Newton and Thornber 2012). Results from mesocosm and *in situ* experiments carried out in Rhode Island (USA) showed that the growth rate of the dominant saltmarsh species, *Spartina alterniflora,* increased under increased macroalgal biomass within the mesocosm experimental plots. However, growth declined under increased macroalgal biomass in field-based experiments. These results suggest more complex ecological interactions take place within the estuarine system making it less likely that a direct impact from macroalgal mat development can be recorded on saltmarsh plants (Newton and Thornber 2013).

## 1.3 The impact of macroalgal mats on benthic invertebrates

An introduction to the macroalgal mat cycle, and the resultant changes to the sediment chemistry, is provided in Chapter 2. In summary, as the macroalgal mat increases in biomass, lower fronds break down leading to a reduction in oxygen, an increase in anoxic conditions and the aerobic layer being restricted to the sediment surface. This alteration of sediment chemistry affects the benthic macro-invertebrate community within the sediment (Pearson and Rosenberg 1978; Wildsmith et al. 2009; Riedel et al. 2012). Some invertebrate species are able to adapt either by extending siphons, (e.g. the bivalve *Limecola (Macoma) balthica* [Linnaeus 1758] (Thiel et al. 1998) or by moving within the sediment column (e.g. the annelid *Capitella capitata* [Fabricius 1780]) (Rosenberg et al. 2001). However, such behaviour can increase vulnerability to predation from the surface (Grall and Chauvaud 2002; Jones and Pinn 2006). As the macroalgal mat increases in extent, thereby creating a greater area of hypoxic/anoxic sediment, refuges for invertebrates become fewer (Pearson and Rosenberg 1978).

The effect of different species of macroalgae on invertebrates was explored by Cardoso et al. (2004) using field experiments carried out in the Mondego Estuary, Portugal. Measured (0.3 kg $m^{-2}$ wet weight, 1.0 kg $m^{-2}$ wet weight, 3.0 kg $m^{-2}$ wet weight) biomass of green algae *Ulva* (*Enteromorpha*) *intestinalis* and red algae

*Gracilariopsis longissimi (Gracilaria verrucosa)* [(S G Gmelin) M Steentoft, L M Irvine and W F Farnham 1995] were added to caged plots. After four weeks results showed a greater detrimental impact on the invertebrate community from the green algae with populations of *Cyathura carinata* [Krøyer 1847]*, Scrobicularia plana* [da Costa 1778] and *Cerastoderma edule* [Linnaeus 1758] all declining significantly under mats of *Ulva* (*Enteromorpha*) *intestinalis.* This resulted in an increase in more ‘opportunist’ species (e.g. *Peringia* (*Hydrobia*) *ulvae* [Pennant 1777]*, Hediste diversicolor* [O F Müller 1776] and *Capitella capitata*). However, no significant change in the invertebrate community was recorded beneath *G. longissimi* (Cardoso et al. 2004). Experimental studies carried out using laboratory flow tanks found that dense mats of *U. intestinalis* restricted tidal flow and trapped sediment between layers possibly reducing prey availability for filter-feeding bivalves such as cockles (Venier et al. 2012). Similar results were also found following a field experiment conducted in the shallow soft-sediment Bökevik Bay, Sweden (Österling and Pihl 2001). This three week study examined the impact of low (150 g dwt m$^{-2}$) and high (300 g dwt m$^{-2}$) manipulated levels of *Ulva* (*Enteromorpha*) and *Chaetomorpha* on benthic invertebrates. Results showed a decline in abundance of *Corophium volutator* [Pallas 1766] and *C. edule* under low and high levels of macroalgal mat biomass compared to the algae-free control.

The Ythan Estuary, Scotland, supports an abundance of the amphipod *C. volutator* - a vital prey item for a number of overwintering wading bird species, particularly redshank (Goss-Custard and Jones 1976). Two separate studies recorded a decline in *C. volutator* under increasing macroalgal mat biomass whereas the opportunist polychaete, *C. capitata*, increased in abundance (Raffaelli et al. 1991; Leaper et al. 2001). It was suggested that the tubular/filamentous morphology of *U.* (*Enteromorpha*) *intestinalis* restricted the ability of *C. volutator* to feed effectively (Raffaelli et al. 1991).

Field-based experimental studies were carried out in Lowes Cove on the Damariscotta River Estuary, Maine, USA, to examine the response of two species of bivalve, *L. (Macoma) balthica* and *Mya arenaria* [Linnaeus 1758], to the presence of dense macroalgal mats (Thiel et al. 1998). Results showed that *L. (Macoma) balthica*, with its longer siphon, was able to extend further into the macroalgal mat and access food and oxygen above, whereas the shorter, thicker siphon of *M. arenaria* was unable to penetrate the thick mat. A subsequent algae addition/removal experiment found abundance of *M. arenaria* declined significantly beneath macroalgal mat whereas abundance of *L. (Macoma) balthica* remained unchanged (Thiel et al. 1998). By contrast, an experimental field-based study in Poole Harbour recorded a decline in *L. (Macoma) balthica* under increased macroalgal mat density (Jones and Pinn 2006). Algal removal experiments, carried out every two weeks between June – November 1984, and June – November 1986 in Bodega Harbor, California using *Ulva expansa* [(Setchell) Setchell and N L Gardner 1920], recorded a decline in the abundance of large bivalves (particularly *Macoma nasuta* [Conrad 1837]) under increased algal cover. However, there was no significant difference in species richness or total density of small invertebrates under macroalgal mat or cleared plots (Everett 1994).

In the Mondego Estuary, Portugal, a significant decline in abundance of *S. plana* was recorded during the period 1993-1997; mirroring the decline in *Zostera* spp. (Lopes et al. 2000) Following measures to reduce eutrophication and macroalgal mat development in 1998, increases in *S. plana* were recorded indicating a possible recovery of recruitment and survival rates (Verdelhos et al. 2005). By contrast, no decline in *S. plana* was recorded when algae (3 kg wet weight biomass) were experimentally added to 2 $m^2$ treatment plots. Results showed an increased abundance of the opportunist polychaete, *C. capitata*, under algal treatment and an initial increase in abundance of *H. diversicolor* in the first month followed by a decline; other polychaetes (*Streblospio shrubsolii* [Buchanan 1890] and *Amage adspersa* [Grube 1863]) also declined. In contrast to other studies (Hull 1987; Raffaelli et al. 1991) abundance of *P. (Hydrobia) ulvae* remained unchanged in algae and clear plots (Lopes et al. 2000).

Further research carried out in the Mondego Estuary recorded an initial increase in abundance of the isopod *C. carinata* under dense macroalgal mat; benefitting from a higher energy availability supplied by the algae (Ferreira et al. 2004; 2007). However this was a short-term effect as *C. carinata* mortality also increased with 80-90% of individuals dying at 1 year instead of reaching the c. 2 year expected lifespan of the species (Ferreira et al. 2004). Following nutrient reduction in 1998, abundance of *C. carinata* slowly increased with recruitment and mortality returning to expected rates. However, further studies concluded that *C. carinata* were not useful bioindicators of ecosystem health (Ferreira et al. 2007). Research into the diversity and structure of the invertebrate community in the Mondego Estuary continued until 2007 and results showed a shift in the invertebrate community after the 1998 intervention from r-selected to K-selected species with evidence of an increase in the population of slower growing invertebrate macrofauna (e.g. *H. diversicolor, S. plana*) (Dolbeth et al. 2007; 2011).

An increase in overall benthic invertebrate biomass was recorded in Langstone Harbour under increasing macroalgal mat biomass. However, it was acknowledged that this resulted from the increased abundance of *P.* (*Hydrobia*) *ulvae* (Montgomery and Soulsby 1980). These results support findings from a study on estuaries within the Solent European Marine Site and North Kent Marshes Site complex that recorded an increase in abundance of *P.* (*Hydrobia*) *ulvae* under increasing macroalgal mat biomass; particularly when macroalgal mat biomass >4 kg $m^{-2}$ (Rees-Jones 2004). In contrast to other studies (Raffaelli et al. 1998), there was no increase in abundance of other opportunistic species such as *Tubificoides* spp. or *Capitella* spp. recorded as macroalgal mat biomass increased. In addition, contrary to findings from other research (Lopes et al. 2000) there was no variation in abundance of larger polychaete worms (e.g. *H. diversicolor*) or bivalves (e.g. *S. plana*) under increasing macroalgal mat biomass (Rees-Jones 2004).

Herbivores such as *P. ulvae* take advantage of the macroalgal mat as a source of both food and shelter from predators (Cardoso et al. 2004). Other species are also reported to be adapting to increases in macroalgal mats. In Waquoit Bay, stable isotope analysis on invertebrate samples taken from two sub-estuaries (one eutrophic and one oligotrophic) revealed that some omnivorous species (decapod *Palaemonetes* spp. and gastropod *Tritia obsolete* [Say 1822]) switched to a predominantly herbivorous diet in estuarine areas covered by macroalgal mats (Fox et al. 2009). Although so far untested, this could have implications for energy availability to the next trophic level if some prey are lacking in nutrients usually obtained from a carnivorous diet.

## 1.4 The impact of macroalgal mats on overwintering wading birds

A study in the Mondego Estuary, Portugal, carried out between October 1993 and May 1994, reported that the presence of gulls and the presence of macroalgal mats were the two main factors affecting the distribution of wading birds (Cabral et al. 1999). The study focussed on plovers (Charadrii) dunlin (*Calidris alpina* [Linnaeus 1758]), Kentish plover (*Charadrius alexandrines* [Linnaeus 1758]), ringed plover (*Charadrius hiaticula* [Linnaeus 1758]) and grey plover (*Pluvialis squatarola* [Linnaeus 1758]) and found that all species avoided areas covered by macroalgal mat although feeding behaviour was unaffected. It should be noted that the maximum algal coverage recorded in this area was 36% and adjacent areas offered invertebrate-rich bare mud available to the wading birds.  The study concluded that there was a negative impact on Charadrii from gull presence (transient) and macroalgal mats (pernicious) (Cabral et al. 1999).

By contrast, a study carried out during the same time period (October 1993 – May 1994) and in the same area of the Mondego Estuary found no significant variation in abundance of dunlin or grey plover from an increase in macroalgal mat coverage (Múrias et al. 1996).  It was suggested that the birds might be adapting to the presence of the algae by subtle changes to their feeding behaviour.  Dunlin and grey plover both consumed smaller prey items such as *P.* (*Hydrobia*) *ulvae* (abundant in the macroalgal mat) and small polychaetes present in the mud.  The results showed no difference in behaviour of the birds on covered or uncovered areas although this could be due to the limited coverage of the mudflats (<36%) by macroalgal mat.  Although there were no significant differences in feeding between macroalgal mat and bare mud areas during this study, it was acknowledged that longer-term monitoring would be required to test the results (Múrias et al. 1996).

Using a long-term data set (1993-2003) from the Mondego Estuary, Lopes et al. (2006) studied the impact of macroalgal mats on the distribution of dunlin (*C. alpina*) reporting an increase in avoidance of mats by dunlin as the percentage cover increased (>25%). Although this was a long-term study (10 years) the maximum percentage mat cover recorded was 43%.  As a result, conclusions could not be drawn on the impact from extensive (e.g. >75%) macroalgal mat coverage (Lopes et al. 2006).

In the Mugu Estuary, California, visual ‘clues’ indicating the location of preferred prey items were reported to be obscured due to macroalgal mat coverage leading to a decline in feeding by visual foragers (black-bellied plover (grey plover, UK), *Pluvialis squatarola* [Linnaeus 1758]), marbled godwit (*Limosa fedoa* [Linnaeus 1758]) and willet (*Tringa semipalmata* [J F Gmelin 1789]) (Green et al. 2015).  However, species adopting a mixture of both visual and tactile foraging behaviour (e.g. western sandpipers (*Calidris mauri* [Cabanis 1857]) were unaffected by the presence of macroalgal mats.  Although this study was carried out on a highly eutrophic estuary, mean macroalgal mat coverage was only 55% (±0.04% s.e.) (Green et al. 2015).

Results from a short-term study (October 1998-February 1999) in Clonakilty, Ireland, indicated that black-tailed godwits (*Limosa limosa* [Linnaeus 1758]) actively avoided areas covered by macroalgal mats although numbers did not increase once the mat had disappeared (Lewis and Kelly 2001).  The same study reported redshanks (*Tringa* *totanus* [Linnaeus 1758]) were preferentially foraging on areas covered by macroalgal mat and appeared able to adapt to its presence and obtain sufficient prey from either covered or uncovered areas (Lewis and Kelly 2001). Further research in the same area concentrated on the response of black-tailed godwit and redshank to the presence of macroalgal mats (Lewis et al. 2014). Both species foraged in areas covered by macroalgal mat although preferentially selected the bare mud patches. Redshank distribution was negatively impacted by the macroalgal mat and feeding success was 50% lower in these covered areas. Black-tailed godwit foraging rates were lower in the algal-covered patches but feeding success was similar in both areas (Lewis et al. 2014).

The Ythan Estuary, Scotland, has extensive records of wading bird numbers dating back to 1963 providing an ideal opportunity to study the relationship between the early development of macroalgal mats and any fluctuations in coastal bird numbers (Raffaelli et al. 1999). Redshank numbers declined during this period with birds foraging on the upper reaches of the Ythan Estuary where macroalgal mat biomass was lower; the decline in redshank was against the national trend (Raffaelli et al. 1999). Shelduck (*Tadorna tadorna* [Linnaeus 1758]) numbers declined despite a reported increase in *P.* (*Hydrobia) ulvae* (a preferred prey item). It was suggested that the filamentous algae may be inhibiting shelduck feeding success (Raffaelli et al. 1999; Anders et al. 2009).

Numbers of oystercatcher (*Haematopus ostralegus* [Linnaeus 1758]), grey plover (*P. squatarola*), black-tailed godwit (*L. limosa*), bar-tailed godwit (*Limosa lapponica* [Linnaeus 1758]), knot (*Calidris canutus* [Linnaeus 1758]), dunlin (*C. alpina*) and Brent goose (*Branta bernicla* [Linnaeus 1758]) all increased in Langstone Harbour coinciding with an increase in macroalgal mat biomass (Tubbs 1977). Studies were carried out using count data from 1954 – 1975 in conjunction with aerial photos which showed an increase in summer coverage of *Ulva* (*Enteromorpha*) spp. and *Ulva lactuca* with 75% coverage over 20% of the mudflats. Redshank (*T. totanus*), curlew (*Numenius arquata* [Linnaeus 1758]) and shelduck (*T. tadorna*) declined during this period, whereas ringed plover (*C. hiaticula*) numbers fluctuated without showing any apparent trend. This increase in populations of coastal bird species in Langstone Harbour during the 1950s, 1960s and 1970s was reflected in national upward trends. However, although redshank, curlew and shelduck also increased nationally they declined locally suggesting this may have been due to an increase in macroalgal mats within the harbour (Tubbs 1977; Tubbs and Tubbs 1980).

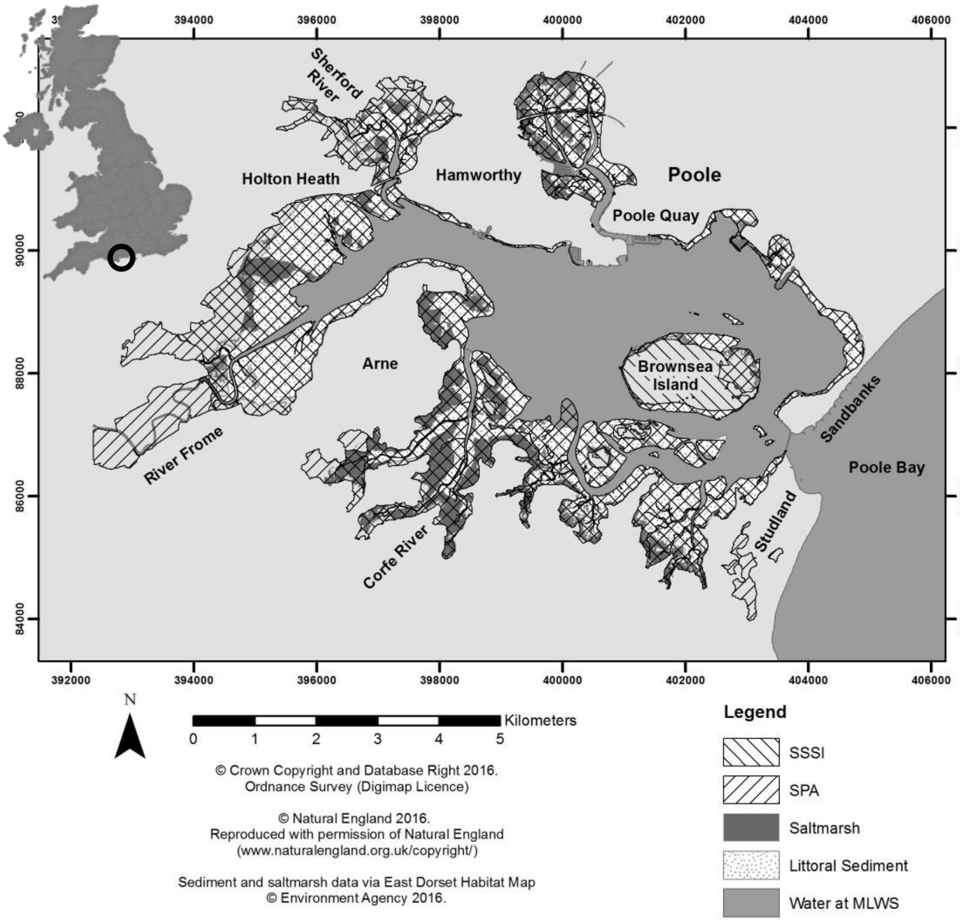
A study on benthic invertebrate response to macroalgal mat coverage in Langstone Harbour also reported observational evidence of a decline in curlew (*N. arquata*) and redshank (*T. totanus*) as macroalgal mat increased. The decline in redshank coincided with an increase in dunlin (*C. alpina*) suggesting increased inter-specific competition for prey resources (Soulsby et al. 1982). An increase in macroalgal mat also coincided with an increase in the numbers of grazing species such as Brent geese (*B. bernicla*) and widgeon (*Anas penelope* [Linnaeus 1758]). It is worth noting that these results are based upon observations rather than sampling analysis as the purpose of the study was not to determine the effect of macroalgal mats on coastal birds (Soulsby et al. 1982).

## 1.5 Study Site: Poole Harbour

Poole Harbour is a 3600 ha bar-built or 'ria' estuary situated on the south coast of England (Fig. 1.1) comprising intertidal mudflats, open water and wetlands (Humphreys and May 2005). Also described as almost 'lagoonal' due to the narrow entrance and limited tidal range (Humphreys 2005), the estuary was formed due to sea level rise at the end of the last ice age and consists of a large central basin with two smaller basins at Holes Bay and Lytchett Bay together with a number of islands, the largest of which is Brownsea Island (Thomas et al. 2004). This topography has resulted in the system being micro-tidal with a tidal-range of <2 m and restricted tidal-flush (McLusky and Elliott 2004; Humphreys 2005). Sediment particle size varies across the harbour with fine silt/clay predominant in the north and coarser sandy/mud near the entrance in the south (Fig. 1.1) (Herbert et al. 2010). Salinity levels range from a mean of 33 at the harbour entrance to 20 10 km away (Kite et al. 2012). However, levels recorded in samples from 1998 – 2008 showed a maximum of >35 and minimum of 25 at the harbour entrance and a maximum of >30 and minimum of 0 10 km away in the Wareham Channel. This was due to tidal input and variations in river flows during the sampling period (Kite et al. 2012).

In addition to the intertidal mudflats, the surrounding terrestrial areas provide a diversity of habitats and land usage within a relatively small area. To the north, the urban conurbation of Bournemouth and Poole supports a commercial port and ferry terminal located at Poole Quay (Bennett 2011). A narrow harbour entrance (370 m) separates some of the world's most desirable real-estate on Sandbanks, from areas of protected heathland and wetland on Studland peninsula to the south (Humphreys and May

2005). Further west, the landscape becomes dominated by agricultural land use including livestock farming (particularly cattle).



© Crown Copyright and Database Right 2016.
Ordnance Survey (Digimap Licence)

© Natural England 2016.
Reproduced with permission of Natural England
(www.naturalengland.org.uk/copyright/)

Sediment and saltmarsh data via East Dorset Habitat Map
© Environment Agency 2016.

**Fig. 1.1:** Location and map of Poole Harbour showing conservation designations.
© Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

Ecologically, Poole Harbour is of national, European and international significance (Underhill-Day et al. 2010). The overwintering bird population uses the invertebrate-rich mud as a valuable resource (Herbert et al. 2010). Protection is afforded to the harbour through a number of statutory designations including the Ramsar Convention for wetlands of international importance and Special Protection Area (SPA) under the European Union Directive on the Conservation of Wild Birds (79/409/EEC) (Fig. 1.1). SPA status is due to the presence of internationally important numbers of avocet (*Recurvirostra avosetta* [Linnaeus 1758]), black-tailed godwit (*L. limosa*) and shelduck (*T. tadorna*) and an internationally important assemblage of over 20,000 waterfowl (Frost et al. 2016). The 2010 condition assessment of Poole Harbour Site of Special Scientific Interest (SSSI) revealed a number of units in ‘unfavourable’ condition due, in part, to the presence of extensive macroalgal mats (Underhill-Day et al. 2010). These factors combine to make the intertidal mudflats present in Poole Harbour an ideal location to study the impact of macroalgal mats on benthic invertebrates and overwintering wading birds.

### 1.5.1 Nutrient input into Poole Harbour

Poole Harbour is failing to achieve ‘good ecological status’ under the European Water Framework Directive (Council Directive 2000/60/EC) due to excess nutrient input (Bryan et al. 2012). Poole Harbour has also previously been designated as a Sensitive Area (eutrophication) and “Polluted Waters” (eutrophication) and the catchment is a Nitrate Vulnerable Zone (NVZ) (Langston et al. 2003; Kite et al. 2012). Nitrogen levels in the harbour were approximately 10000 kg year$^{-1}$ prior to the 1960s and have increased since then (Bryan et al. 2012). As Table 1.1 shows, without mitigation these levels are predicted to be in excess of 2,500,000 kg year$^{-1}$ by 2100 (Kite et al. 2012).

**Table 1.1:** Historical and predicted N and P loading in Poole Harbour (Kite et al. 2012).

| Date | Total N load kg year$^{-1}$ | Total P load kg year$^{-1}$ |
|---|---|---|
| 1980-84 | 1721200 | 177680 |
| c.2004 | 2456720 | 78592 |
| 2006-2010 | 2089800 | 58413 |
| 2100 | 2551400 | 58413 |

Over 50% of nitrogen deposition in Poole Harbour comes from agricultural fertiliser entering the estuarine system either from land run-off or groundwater seepage (Kite et al. 2012). Nitrogen removal was introduced to the Poole Sewage Treatment Works (STW) in 2008 leading to a significant reduction in dissolved inorganic nitrogen (DIN) levels in Holes Bay between 2007 – 2008 (Cascade Consulting 2012). However, this did not lead to a reported reduction in the biomass or extent of macroalgal mats in the immediate vicinity (Kite et al. 2012). Elsewhere around the harbour, although there was a gradient decline in inorganic nitrogen from Wareham Channel to the harbour entrance, there was no reported corresponding decline in the abundance of macroalgal mats (Kite et al. 2012). This supports other studies suggesting a much more complex relationship between high inorganic nitrogen loading within an estuary and the development of macroalgal mats with other environmental interactions also contributing to the increase in macroalgal mats (Cloern 2001; Howarth and Marino 2006).

## 1.6 Rationale

Under legislation within the Birds and Habitats Directives (combined under NATURA 2000), assessments of SSSIs, Special Areas of Conservation (SACs) and SPAs are required to determine the condition status of each area against targets set down within Common Standards Monitoring Guidelines (CSM) (JNCC 2004) for each feature. One of the key metrics for assessment of estuarine features under the CSM is the extent of macroalgal mats (JNCC 2004). Conservation managers also use coastal bird numbers as an indicator of overall estuarine ecosystem health (West et al. 2005).

Poole Harbour is designated for its populations of overwintering migratory wading birds (JNCC 2004). As such, any decline in their numbers as a result of nutrient enrichment affecting their food supply or altering their feeding behaviour, would result in a decline in the feature and sanctions under current legislation (JNCC 2004). A reduction in biodiversity resulting from eutrophication would, therefore, have implications for the UK’s binding agreements under the Birds and Habitats Directives and overall coherence of NATURA 2000 sites (Natural England 2013). Therefore it is important to be able to reliably assess the impact from macroalgal mats on this upper trophic level of the estuarine food-web.

This research will address some of the temporal constraints associated with other studies by beginning sampling at the start of macroalgal mat development and recording changes throughout two complete ecological cycles. In addition, wading bird observations will be related back to the known extent of the macroalgal mat to assess whether that year’s mat growth has impacted or influenced feeding behaviour.

## 1.7 Aims and objectives

The overall aim of this thesis is to determine how the development of green macroalgal mats affects the different trophic levels within an estuarine food-web.

- To determine the extent of the macroalgal mat within a soft-sediment estuarine habitat.
- To assess the benthic invertebrate community structure and determine if this is transformed under macroalgal mats.
- To examine the impact of macroalgal mats on key wading bird species using their preferred prey as an indicator of available resources.

- To determine whether bird foraging behaviour and distribution is affected by the presence of macroalgal mats.
- To assess whether wading birds may be adapting to the presence of macroalgal mats and assess the conservation consequences of any adaptations.

## 1.8 Thesis structure

Fig. 1.2 provides a conceptual diagram highlighting the key themes of this thesis and the chapters in which these are discussed.

### Chapter 1: Introduction

Provides an overview of the importance of estuaries and details of recent global studies into the ecological impact of the development of macroalgal mats. This chapter will introduce the study site, Poole Harbour, and provide an explanation of the conservation importance of the site and why extensive macroalgal mat development might be an issue.

### Chapter 2: The biomass and extent of macroalgal mats in Poole Harbour

Establishes a baseline of the biomass of the macroalgal mat together with an assessment of the extent of the mat in three key areas for overwintering wading birds in Poole Harbour. In addition, the chapter will provide analysis of whether the current threshold of concern for macroalgal mat biomass (2 kg $m^{-2}$) is sufficiently precautionary for Poole Harbour.

### Chapter 3: The effect of macroalgal mats on the benthic invertebrate community

This chapter is split into two parts with the first section analysing the invertebrate community composition in three areas and three shore levels within Poole Harbour. The second part of the chapter will determine the effect of macroalgal mats on the benthic invertebrate community.

### Chapter 4: The effect of macroalgal mats on wading bird prey: implications for individual bird species

Provides an analysis of the impact from macroalgal mats on the preferred prey of five key wading bird species by using the concept of a ‘benthic invertebrate menu’. This is based upon the energy available at each site derived from each wading bird's preferred prey.

### Chapter 5: The relationship between macroalgal mat coverage and wading bird foraging behaviour

Examines how wading bird foraging and distribution might be affected by the presence of varying levels of macroalgal mat coverage. The chapter will assess whether birds are foraging on the macroalgal mat or avoiding areas of mat coverage.

### Chapter 6: Changes to wading bird feeding rate in response to macroalgal mat coverage

Analyses digital video recordings to determine whether macroalgal mat coverage is affecting wading bird feeding rate. This chapter also examines whether wading birds are using different foraging strategies to locate suitable prey or increasing their feeding rate in response to the abundance of smaller, lower quality prey.

### Chapter 7: Conclusions and further research

Brings together the findings from the research and suggests areas for further study.

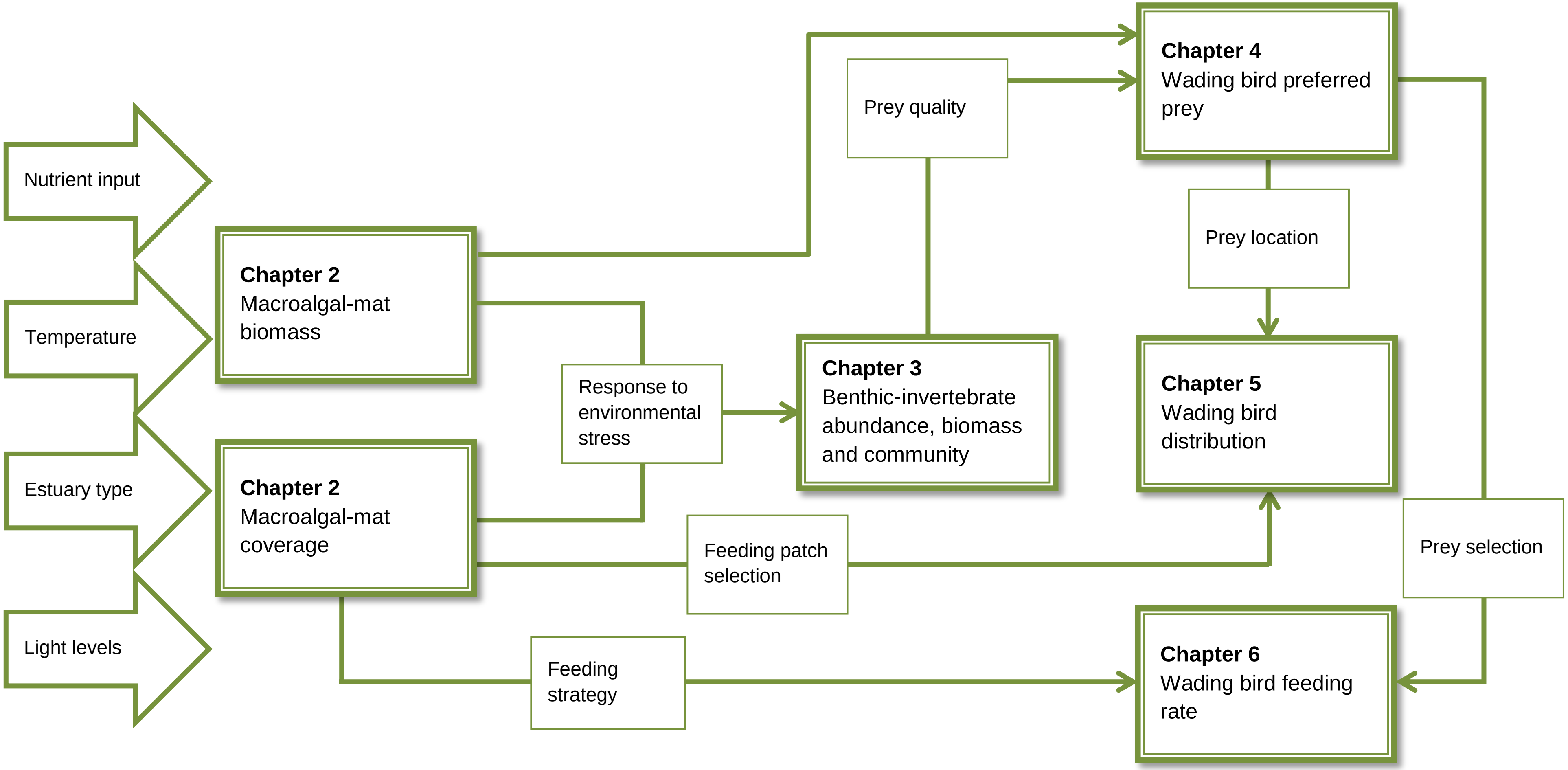


**Fig. 1.2:** Conceptual diagram showing the main drivers of macroalgal-mat development and the main interactions between macroalgal-mats, benthic-invertebrates and overwintering wading birds. Arrows show the direction of the interaction. Hollow boxes indicate the main impact. Solid-frame boxes show the chapter number in which these impacts are analysed.

BLANK

# 2.0 The biomass and extent of macroalgal mats in Poole Harbour

## Abstract

The development of macroalgal mats in estuarine systems is a global conservation concern. Macroalgal mats are largely formed from Chlorophyta (green algae); primarily comprising the genera *Ulva, Chaetomorpha* and *Cladophora.* In the UK, the presence of extensive macroalgal mats in sheltered harbours and on mudflats along the south coast of England has been recorded since the 1960s. Poole Harbour is an example of a micro-tidal estuary on the south coast of England with macroalgal mats recorded on the intertidal mudflats since the 1970s.

Macroalgal mat biomass and extent were measured on a regular basis from March 2013 to February 2015 at four sites around the harbour. Four species of *Ulva* were recorded: sheet-forming *U. rigida*, tubular *U. compressa* and *U. intestinalis*, and filamentous *U. clathrata.* Wet weight biomass exceeded 2 kg $m^{-2}$ on two occasions but this level was not maintained during the growth season; biomass of 1 kg $m^{-2}$ was recorded at all four sites during the survey period. There was no significant variation in macroalgal mat biomass between years. Macroalgal mat coverage was high (>50%) at all sites during the summer growth period each year. Results showed a strong correlation between macroalgal mat coverage within quadrats at the upper shore sampling sites and overall coverage across each of the four bays observed using a telescope.

**BLANK**

## 2.1 Introduction

### 2.1.1 Primary production and macroalgae

Excess nutrient loading within an estuarine system can lead to changes in the community structure of primary producers with consequences for food resources at higher trophic levels. In systems where nitrogen (N) and phosphorus (P) are limited, slower growing, structurally complex species such as *Zostera marina* [Linnaeus 1753] and brown algae are dominant (Flindt et al. 1999; Bowen and Valiela 2001). Although ephemeral green algae are present within non-eutrophied estuarine systems, these faster-growing r-selected species are controlled through grazing and the limited supply of nutrients (Flindt et al. 1999; Fox et al. 2009). Therefore, low levels of green algae are regarded as beneficial and an integral part of primary production within a 'stable' system resulting in an increase in productivity (Raffaelli et al. 1999; Flindt et al. 1999; Scanlan et al. 2007; Fox et al. 2009). As a consequence, symptoms of the initial stages of excess nutrient loading can be difficult to determine as small increases in green algae are often not deemed a 'nuisance' (Fletcher 1996). However, as nutrient loading begins to increase, ephemeral algae respond with ever-larger 'blooms', gradually outcompeting other macroalgal species and plants for nutrients and light and eventually dominating the estuarine habitat (Raven and Taylor 2003; Eriksson and Johansson 2005; Teichberg et al. 2010). This can create a paradox whereby water quality testing for nutrients record 'normal' due to the rapid uptake of nitrates by the macroalgal mats – themselves a symptom of eutrophication (Valiela et al. 1997). By the time the macroalgal mat has become established, the estuary is already exhibiting eutrophic conditions (Morand and Merceron 2005).

### 2.1.2 Mat-forming chlorophytes

Although some species of brown alga (e.g. *Ectocarpus* and *Pilayella*) will form 'blooms', macroalgal mats are largely formed from Chlorophyta (green algae); primarily comprising the genera *Ulva*, *Chaetomorpha* and *Cladophora* (Raffaelli et al. 1998; Raven and Taylor 2003). Studies prior to 2003 refer to species of *Enteromorpha* however it has been shown that *Enteromorpha* and *Ulva* are not two distinct genera (Hayden et al. 2003); both are now classified as *Ulva*. There are a number of morphological traits which ensure the success of these mat-forming species. Green algae are able to assimilate excess nutrients much quicker than slower-growing species of red and brown algae (Taylor et al. 2001; Raven and Taylor 2003). Indeed, Pedersen and Boram (1997) reported that due to the higher growth rates, species of *Chaetomorpha, Ulva* and *Cladophora* were able to take up ammonium and nitrate up to six times faster than *Codium fragile* [Hariot 1889] or *Fucus vesiculosus* [Linnaeus 1753]. However, this was only apparent in nutrient enriched systems, with only marginal increases in uptake reported at low concentrations of ammonium.

The successful and rapid assimilation of nutrients by opportunistic Chlorophyte algae is due to a simple thallus structure (Littler and Littler 1980). A high surface-area:volume ratio created by the sheet, filamentous or tubular forms of thalli ensures maximum exposure to light (Littler and Littler 1980; Hurd et al. 2014). Nutrients are supplied through the water column and taken up through membrane porters on the plant surface; algae are also able to assimilate nutrients from the sediment if necessary (Raven and Taylor 2003). Yet despite their apparent fragility, green algae species of the genus *Ulva* are able to withstand adverse environmental conditions including lower light levels and even anoxic conditions in the sediment (Fletcher 1996). Field experiments carried out in Sweden found that *Ulva intestinalis* [Linnaeus 1753] was highly tolerant of increased sedimentation when compared to *F. vesiculosus* (Eriksson and Johansson 2005). Although this simple morphology enables opportunistic green algae species to take advantage of sudden increases in nutrients, algae are unable to store nutrients for long periods thereby necessitating rapid growth (Fletcher 1996; Day et al. 2013). As energy is concentrated on maximising growth, fragile green algae are also at greater risk from grazing pressure compared to the more structurally complex, slower growing brown algae (Hurd et al. 2014). However, this is compensated by rapid regeneration of new fronds from small fragments of existing vegetation (Raven and Taylor 2003; Brodie et al. 2007).

### 2.1.3 Development cycle of a macroalgal mat

The development of macroalgal mats is a global conservation concern (Borja et al. 2012). In the UK, the presence of extensive macroalgal mats in sheltered harbours and on mudflats along the south coast of England has been recorded since the 1960s (Tubbs 1977). Fig. 2.1 provides an overview of the stages of macroalgal mat development using images taken from Poole Harbour.

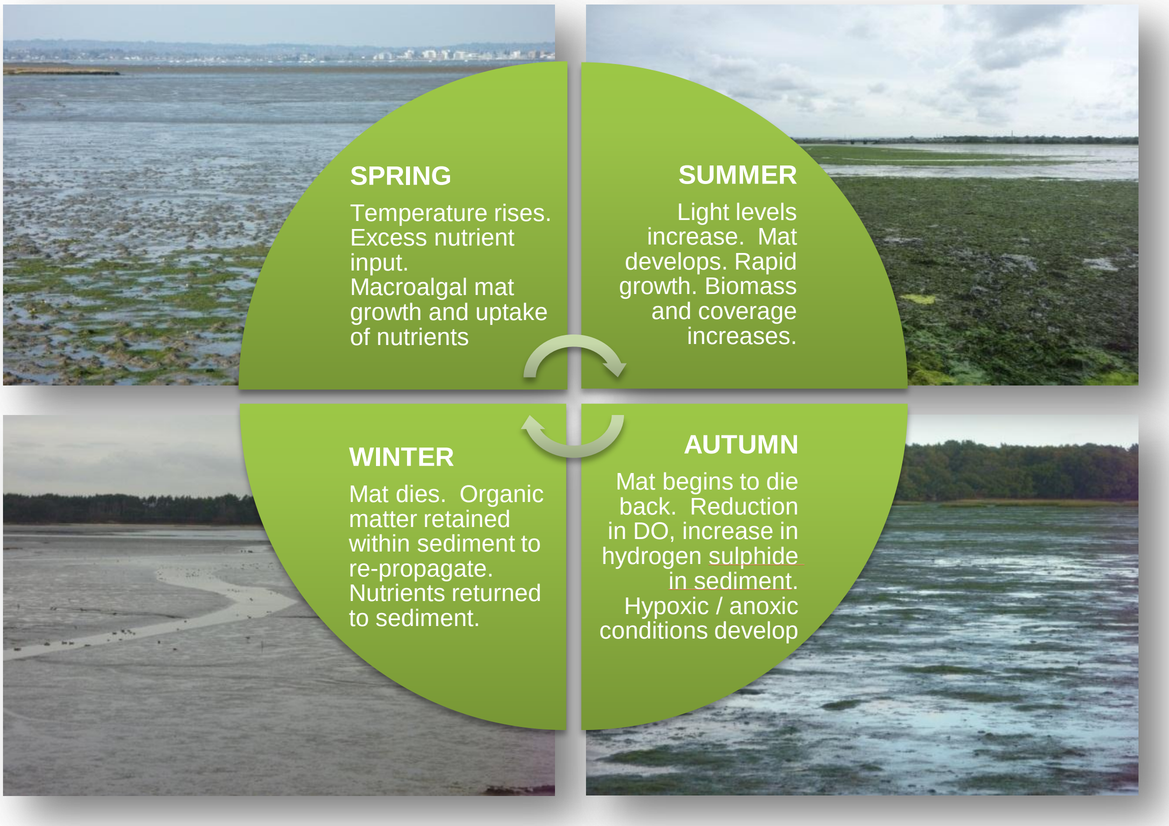


**Fig. 2.1:** The development cycle of macroalgal mats with a summary of the key issues at each stage of growth and decline. Images clockwise from top left: Ower Bay (April 2014), Holes Bay (August 2014), Newton Bay (October 2014), Brands Bay (February 2015). Photographs © A. Thornton.

As discussed in Chapter 1 (Section 1.2) there are a number of similarities between estuaries susceptible to the development of dense macroalgal mats including limited tidal range and reduced tidal flush (Scanlan et al. 2007). Provided conditions are suitable, macroalgal mats in temperate estuaries will begin to develop during spring when mean air temperature reaches c.10 $^{o}$C (Raffaelli et al. 1998). Excess allochthonous nutrient input from anthropogenic sources results in a constant availability of N and P which, in combination with increased light levels during summer, leads to the development of macroalgal mats (Fletcher 1996; Raffaelli et al. 1998;

Anderson et al. 2002; Day et al. 2013). Sheet, filamentous and tubular forms of *Ulva* spp. and filamentous *Chaetomorpha linum* [(O. F. Müller) Kürtzing 1845] all form dense mats with high biomass and extensive coverage. Light penetration is reduced and, as a consequence, the lower fronds become starved of light and begin to deteriorate (Day et al. 2013). These lower fronds get broken down by heterotrophic bacteria and other detritivores; oxygen demand increases resulting in hypoxic and anoxic conditions developing in the sediment (Raffaelli et al. 1989; Anderson et al. 2002; Day et al. 2013). This, in turn, leads to an increase in the naturally occurring production of hydrogen sulphide ($H_2S$) gas which, along with the released dimethyl sulphide (Van Alstyne et al. 2015), contributes to the characteristic pungent aroma on the upper shore (Fletcher 1996; Kaiser et al. 2005). Nutrients released back into the sediment by the breakdown of the algae become an autochthonous supply available to new macroalgal mat development and the cycle continues (Sfriso et al. 1987; Day et al. 2013). Eventually, temperature, wind and wave action, and a reduction in light levels during autumn and winter reduce new growth of algae and the mat disintegrates.

### 2.1.4 Macroalgal mats in Poole Harbour

The micro-tidal, almost lagoonal, environment of Poole Harbour (Humphreys 2005) is particularly vulnerable to the development of macroalgal mats (Jones and Pinn 2006, Fig. 2.1). Macroalgal mats were first reported in Holes Bay in 1971 (Fletcher 1996) and since the 1980s, the area of intertidal mudflats in Poole Harbour affected by macroalgal mat coverage has increased from 100ha to 400ha; with areas of >75% coverage also increasing from 3% to 15% of the total intertidal area (Kite et al. 2012). There have been only a few reported studies investigating the issues and impacts surrounding macroalgal mat development in Poole Harbour (Underhill-Day, 2010; Axelsson et al. 2012; Cascade Consulting 2012; Kite et al. 2012). Jones and Pinn (2006) recorded peak coverage of 91% within a 50 m x 50 m site in Holes Bay. However, no measurement of algal biomass was recorded as the study concentrated on the infaunal community. Monthly sampling was carried out for a single season from July – November 2002.

### 2.1.5 Biomass and extent of macroalgal mats in Poole Harbour

There is considerable discussion regarding the threshold at which algal biomass impacts on the nature conservation interest features of a site (Hull 1987; Raffaelli et al. 1999; Scanlan et al. 2007; Underhill-Day et al. 2010; WFD-UKTAG 2013). Although studies have reported an impact upon invertebrates was apparent when macroalgal wet weight biomass reached 1 kg $m^{-2}$ (Hull 1987; Raffaelli et al. 1999), research carried out along the south coast of England by the UK Environment Agency indicated that a biomass of 1 kg $m^{-2}$ was too ‘precautionary’ and algal biomass of <2 kg $m^{-2}$ caused no adverse effect on macro-invertebrate diversity (Rees-Jones 2004). This level was incorporated into the Site of Special Scientific Interest (SSSI) condition assessment for Poole Harbour (Underhill-Day et al. 2010). Scanlan et al. (2007) argued that the extent of the macroalgal mat should also be considered and suggests that the combined measure of 15-25% coverage with >1 kg – 3 kg $m^{-2}$ is indicative of ‘poor’ quality.

The overall extent and degree of patchiness of the macroalgal mats in Poole Harbour is important to determine as this will affect the scale of impact on areas of bare mud refugia for invertebrates and feeding areas for migratory coastal birds (Lewis et al. 2014). A number of different methods have been used to determine the extent of macroalgal mat coverage within an area including assessment of % coverage using a telescope (Nedwell et al. 2002) or recording % coverage within quadrats to estimate total % coverage within an estuary (Cabral et al. 1999). However, the study site is often too large to enable accurate and total mapping from the upper shore using quadrats (Nedwell et al. 2002) and ideally the measurement of macroalgal mat should also incorporate some form of visual assessment of the coverage across a study site (Alexander et al. 2008). Aerial remote sensing can be costly, particularly for large intertidal areas and requires extensive ground-truthing to validate the results (Raffaelli et al. 1999).

### 2.1.6 Rationale

Macroalgal mat development is dependent upon a number of climate conditions including air temperature, rainfall, and light levels. The first part of the chapter will briefly examine historical data on local climate in order to place the 2013-2014 and 2014-2015 field seasons into context.

Site-specific factors such as sediment temperature and the depth of the anoxic layer within the sediment may also affect the development of the macroalgal mat. The second part of the chapter will address gaps in the knowledge of how the macroalgal mat develops within Poole Harbour in response to site conditions. The primary focus of this part will be to establish whether the biomass of the macroalgal mat exceeds the current higher threshold of concern (2 kg $m^{-2}$) or the more conservative 1 kg $m^{-2}$. As the current level for SSSI condition assessment is 2 kg $m^{-2}$, results from this chapter will contribute to an understanding of whether this is an appropriate threshold in Poole Harbour.

## 2.2 Aims and objectives

| | |
|---|---|
| **Aim 1:** | To establish baseline information on the biomass and extent of macroalgal mats in Poole Harbour. |
| **Aim 2:** | To determine which climatic factors influence the development of macroalgal mats. |
| **Aim 3:** | To determine whether the current threshold of concern for macroalgal mat biomass is effective in Poole Harbour. |
| **Aim 4:** | To determine the extent of macroalgal mat coverage in important feeding areas for migratory overwintering wading bird. |

| | |
|---|---|
| **Objective 1:** | Measure the wet weight biomass of macroalgal mat development over two ecological cycles. |
| **Objective 2:** | Assess the development of the macroalgal mat in relation to climatic variables. |
| **Objective 3:** | Regularly measure the development and extent of the macroalgal mat using terrestrial mapping techniques. |

## 2.3 Methods

### 2.3.1 Climate data

Historical data on air temperature, rainfall and sunshine hours were obtained from the Meteorological Office (Met Office 2016). Data were taken from Bournemouth Airport monitoring station as this is the closest station to Poole Harbour (grid reference: SZ11730 97727).

### 2.3.2: Measurement of the extent and biomass of macroalgal mats at important sites around Poole Harbour

*2.3.2.1 Site selection*

Eight sites were selected: Parkstone Bay, Holes Bay north-east, Upton Park, Holton Heath, Grip Heath (Arne), Ower Bay, Newton Bay and Brands Bay (Fig. 2.2) stratified according to access, surrounding land-use and aspect.

Data collection commenced in March 2013 and continued until February 2015 to include two ecological cycles for macroalgal mat growth (Fletcher 1996). Sampling was carried out each month from March 2013 – March 2014 and every two months from April 2014 – February 2015. Fieldwork was conducted at low-water on a spring tide (<0.9 m above chart datum) (UK Hydrographic Office, 2013-2015). Each site was sampled using a quadrat sampling strategy based upon the Common Standards Monitoring for Littoral Sediment Habitats (JNCC 2004) and Environment Agency monitoring protocol (S. Witt, Environmental Monitoring Officer, Environment Agency, pers. comm.).

In August 2013, due to no extensive macroalgal mat growth, three sites (Parkstone, Holton Heath and Grip Heath) were removed from further sampling during 2013/2014. A visit to each of these sites in October 2013 confirmed that no macroalgal mat had developed. Biomass sampling was not permitted at Upton Park so the area was only assessed for spatial extent of the macroalgal mat from the shore during 2013/2014.

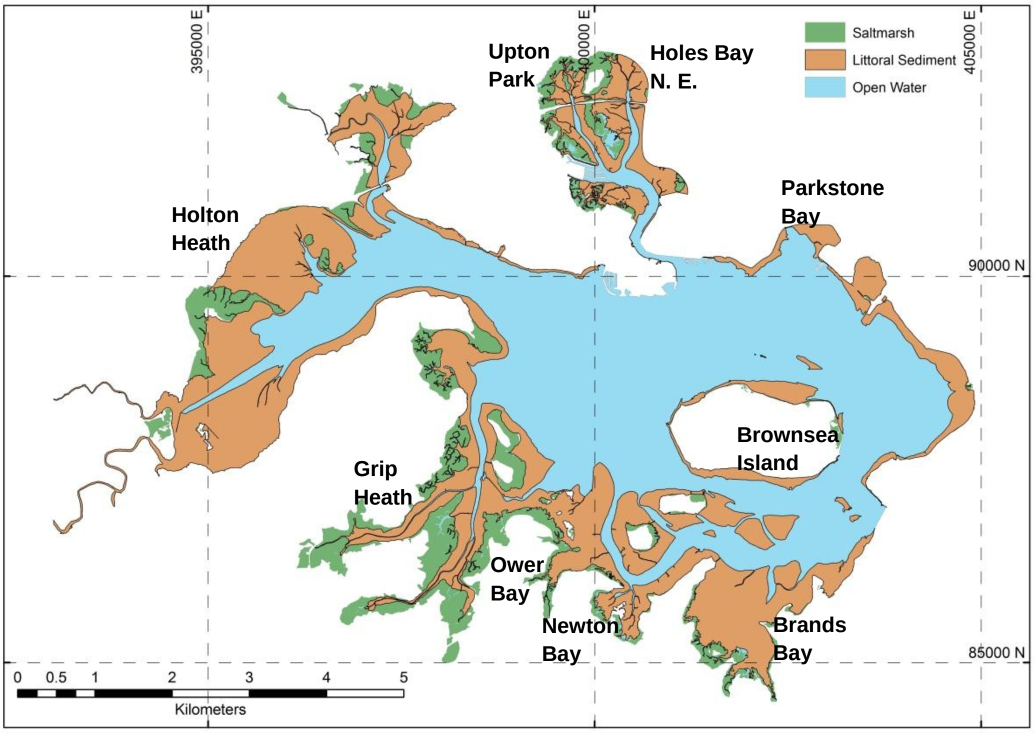


**Fig. 2.2:** Survey sites selected: Parkstone Bay, Holes Bay N.E., Upton Park, Holton Heath, Grip Heath, Ower Bay, Newton Bay, Brands Bay. © Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

Site selection was reviewed in February 2014 prior to the next sampling period. In addition to no macroalgal mat development recorded there were other issues with three sites. The substrate in Parkstone Bay is predominantly sand (Herbert et al. 2010) and therefore not comparable with the muddier, fine silt/clay substrates at other sampling sites around the harbour. Access to Holton Heath had become dangerous due to a collapsing sea wall and asbestos landfill. Grip Heath did not provide suitable conditions for the development of extensive macroalgal mats as the area is formed of extensive salt-marsh fringing a narrow channel rather than an embayment. In 2014/2015 access to the previous year's vantage point was restricted at Upton Park so no further assessment of the extent of macroalgal mat coverage was possible. Therefore, these sites were not sampled during the 2014/2015 season.

#### *2.3.2.2 Macroalgal mat sampling*

The location of the sampling stations was recorded using a Garmin GPS 60CSx with an error of ±3 m. Five quadrats (0.25 $m^2$) were randomly placed on the mudflat between 2 m and 5 m distance from the upper shoreline. Poole Harbour sediment comprises fine silt/clay and the intertidal mudflats are characteristically thixotropic. These spatial limits on placement of quadrats were determined as being far enough from the influence of the upper shore vegetation yet still within safe operating distance.

Algae thickness was measured at five points within the quadrat using a combination square ruler; mean measurement was recorded. A measurement was taken of the depth of the anoxic layer (deemed as the depth at which black mud is visible). Site air temperature was also recorded on each sampling date using a digital thermometer. Sediment temperature was measured from individual quadrats using a Hach HQ30d Portable Meter and a mean value obtained for each survey. Photographs were taken of each quadrat containing algae. Percentage surface cover of algae within the boundaries of each quadrat was determined to the nearest 5% by examining the photographs over a grid on the computer. Algae within each quadrat were cut away and scraped from the surface, placed into a pre-labelled grip-seal bag and removed from site.

#### *2.3.2.3 Macroalgal mat processing*

Samples were processed in the laboratory within 24hours. Algae were rinsed under running tap water over a 500 µm mesh sieve to remove sediment. Any invertebrates were removed and retained. The dominant green algae species was recorded together with other species of Chlorophyta, Rhodophyta*,* and Phaeophyta. Samples were squeezed thoroughly to remove excess water, weighed using an electronic balance to obtain wet weight biomass, bagged and placed in a freezer for storage. Methods were in accordance with sampling guidelines for monitoring under the Water Framework Directive (WFD-UKTAG 2009). Invertebrates found within the algae were fixed in 4% formal saline and then stored in IMS for future identification and measurement.

#### *2.3.2.4 Nutrient data*

Nutrient data were obtained from Environment Agency monitoring carried out within Poole Harbour. However, as samples were collected outside the survey areas, the data were unsuitable for this research.

### 2.3.3 Analysis

All statistical analysis was performed using R version 3.3.0 “Supposedly Educational”, (R Core Team 2016). Assumptions of normality and homogeneity of variance were checked using Shapiro Wilks test within the “stats” package in R Version 3.3.0 “Supposedly Educational” (R Core Team 2016) and Levene test within the “car” package developed for R (Fox and Weisberg 2011) respectively.

Co-linearity between environmental variables (site temperature, air temperature, rainfall, sunshine hours, sediment temperature and depth of anoxic layer) was tested using multiple linear regression within the ‘stats’ package for R (R Core Team 2016); co-linear variables were removed. The relationships between macroalgal mat biomass and remaining environmental variables were tested using Pearson product moment correlation coefficients within the ‘stats’ package for R (R Core Team 2016).

Spatial and temporal variations in macroalgal mat biomass and % coverage did not meet the assumptions of normality and homogeneity of variance required for analysis of variance (ANOVA). Overall and within-site variation in algal biomass between years was determined using Wilcox signed rank test. Between-site variation in algal biomass was determined using Kruskal Wallis test within the ‘stats’ package for R (R Core Team 2016).

Two measures of % coverage were analysed: mean % coverage recorded from the quadrat samples at the upper shore, and % coverage estimated across each survey site. As data did not meet the assumptions of normality or homogeneity of variance required for parametric tests, overall and within-site variation in algae % coverage between years was determined using Wilcox signed rank test. Between-site variation in algae % coverage was determined using Kruskal Wallis test within the ‘stats’ package for R (R Core Team 2016).

The relationship between % coverage of macroalgal mat at the upper shore sampling station and estimated coverage across the bay was assessed using Spearman’s rank correlation within the ‘stats’ package for R (R Core Team 2016).

### 2.3.4 Mapping the extent of macroalgal mat coverage

Two methods were considered in order to map the spatial extent of the macroalgal mat within the study sites: mapping the extent of the macroalgal mat from an upper-shore vantage point using a telescope with laser rangefinder, and using a laser scanner. A pilot study was undertaken to test the effectiveness of using the laser scanner to map 3D images of the surface and extent of the macroalgal mat. This feasibility study revealed the laser scanner to have insufficient range (<100 m) to map the full extent of the macroalgal mat coverage across the larger bays.

The extent of the macroalgal mat was recorded monthly (2013-14) and bimonthly (2014-15) at the same time as the biomass sampling and at the same locations (8 sites in 2013-2014 and 5 sites in 2014-2015 see section 2.3.2). At each site, a visual assessment of coverage of macroalgal mat was made by eye using a mounted telescope (Swarovski HD 20-60x zoom) from a raised vantage point above the shoreline (Ower Bay and Newton Bay 1.0 m, Holes Bay 1.5 m and Brands Bay 10 m). The percentage cover of each patch of algae was estimated and recorded on an Ordnance Survey (OS 1:25000) site map. Each site was visited at low water on a spring tide when predicted low water was <0.9 m above chart datum (UK Hydrographic Office, 2013-2015) thus ensuring the mudflats were exposed.

## 2.4 Results

### 2.4.1 Weather and climate

*2013/2014*

Annual temperature range for 2013 did not vary significantly from the 1981 - 2010 average. However, the UK mean temperature for March 2013 was 3.3 $^{o}$C lower than the 1981-2010 average and the coldest since 1962. Mean temperature for March 2013 at the Bournemouth Airport weather station was 3.4 $^{o}$C (3.5 $^{o}$C lower than the 1981-2010 average). Although July and August were warmer, mean temperatures were only 1.7 $^{o}$C and 0.8 respectively above the 1981-2010 average (Met Office 2016)

*2014/2015*

By contrast, 2014 was the warmest year since 1910 with all months (except August) warmer than 1981 - 2010 average. Rainfall was 113% higher than the 1981 - 2010 average. Severe storms brought damaging winds and heavy rain with flooding during January and February 2014. Spring 2014 was 3.0 $^{o}$C warmer than 2013 and the second warmest spring since 1910 (spring 2011 was warmer) (Met Office 2016).

### 2.4.2 Algae species recorded

Table 2.1 provides details of the four species of *Ulva* recorded within the macroalgal mat samples in Poole Harbour:

**Table 2.1:** Species, location and morphology of four *Ulva* spp. recorded during sampling in Poole Harbour.

| Species | Location | Morphology |
|---|---|---|
| *Ulva rigida* [C. Agardh, 1823] | Holes Bay | Thin sheet-forming thalli |
| *Ulva compressa* [Linnaeus 1753] | Brands Bay | Tubular thalli (similar to *U. intestinalis*) |
| *Ulva intestinalis* [Linnaeus 1753] | Brands Bay | Tubular thalli (similar to *U. compressa*) |
| *Ulva clathrata* [(Roth) C. Agardh 1811] | Ower Bay | Fine, filamentous thalli |

The different species of *Ulva* are notoriously difficult to identify (Hofmann et al. 2010). Identification was supported using Brodie et al. (2007) and Hofmann et al. (2010) and confirmed by Prof. Christine Maggs (pers. comm. May 2016). Fig. 2.3 shows the cell structure of *Ulva clathrata* with multiple pyrenoids and the quadrat from which it was collected in Ower Bay, August 2014. It is possible that other species of *Ulva* or green mat-forming algae were present within the Harbour but identification would require further research outside the scope of this study.

**Fig. 2.3:** Cell structure of *U. clathrata* showing multiple pyrenoids (average 5), one of the identifying features of the species (Brodie et al. 2007, C. Maggs, pers. comm.), and the sample of *U. clathrata* prior to being collected in August 2014 at Ower Bay. Photos © A. Thornton.

### 2.4.3 The effect of air temperature, sunshine hours, rainfall and depth of anoxic layer on macroalgal mat biomass

Climate variables (air temperature, sunshine hours, site temperature and rainfall) were checked for co-linearity and it was found that air temperature, sunshine hours and site temperature were all significantly correlated ($p = <0.05$, $r = >0.85$). Therefore, air temperature and sunshine hours were removed from the analysis. Full details of climate and environmental data are provided in Appendix 1a and 1b.

There was a highly significant correlation between algae biomass and site temperature ($t = 7.297$, $df = 70$, $p = <0.001$, $r^2 = 0.43$, 95% CI = 0.502 – 0.771) and between algae biomass and sediment temperature ($t = 6.183$, $df = 70$, $p = <0.001$, $r^2 = 0.35$, 95% CI = 0.421 – 0.726). Fig. 2.4 shows the correlation between algae biomass and site temperature, and algae biomass and sediment temperature with 95% confidence intervals shaded.

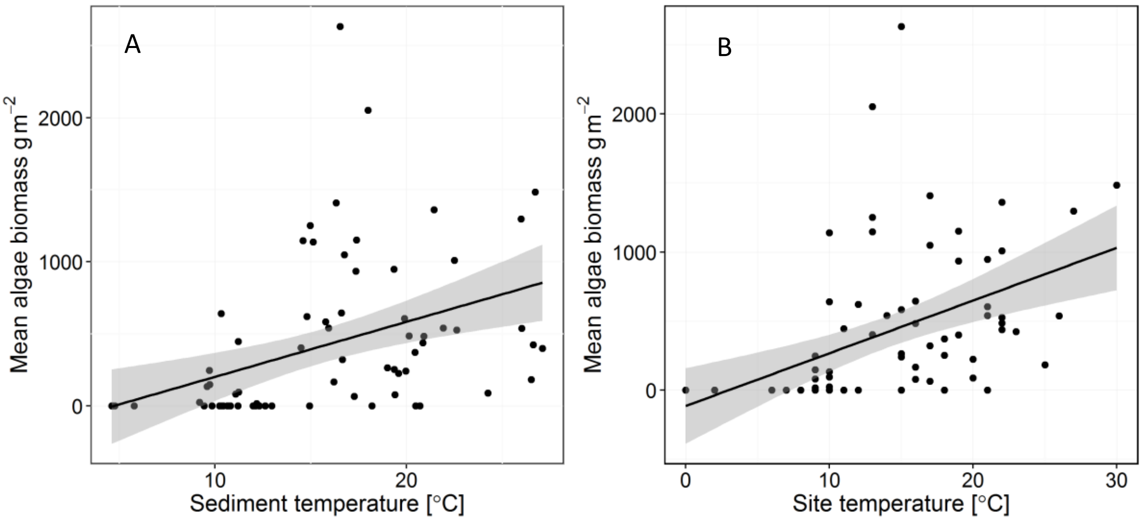


**Fig. 2.4:** Correlation between algae biomass (g (ww) m$^{-2}$) and (A) site temperature ($^{o}$C), (B) sediment temperature ($^{o}$C). Shaded area is 95% confidence interval.

There was no significant correlation between algae biomass and rainfall ($p = >0.05$) or between algae biomass and depth of anoxic layer ($p = >0.05$). Table 2.2 provides details of the anoxic layer depth recorded during sampling.

**Table 2.2:** Mean and range of depths of anoxic layer (visible black mud) recorded during 2013/2014 and 2014/2015 sampling.

| Site | n | Min. depth (mm) | Max. depth (mm) | Mean depth (mm) | 95% C.I. |
|---|---|---|---|---|---|
| Brands Bay 2013/2014 | 12 | 1 | 10 | 4.67 | 1.81 |
| Brands Bay 2014/2015 | 6 | 1 | 15 | 5.17 | 4.42 |
| Holes Bay 2013/2014 | 12 | 1 | 19 | 4.22 | 2.78 |
| Holes Bay 2014/2015 | 6 | 0 | 12 | 5.33 | 4.34 |
| Newton Bay 2013/2014 | 12 | 1 | 20 | 7.18 | 3.67 |
| Newton Bay 2014/2015 | 6 | 1 | 10 | 4.5 | 2.85 |
| Ower Bay 2013/2014 | 12 | 1 | 7 | 3.18 | 1.04 |
| Ower Bay 2014/2015 | 6 | 0 | 10 | 4.83 | 3.10 |

### 2.4.4 Between-year and between-site variation in macroalgal mat biomass

Figure 2.5 shows the mean wet weight biomass (g $m^{-2}$) for algae collected within 0.25 $m^2$ quadrats from the upper shore. There was no significant variation in algal biomass (g $m^{-2}$) between 2013-2014 and 2014-2015 across Poole Harbour (W = 530.5, p = 0.583, n (2013/2014) = 240, n (2014/2015) = 120), yet, as Fig. 2.5 shows, there appeared to be some fluctuations in the development of the macroalgal mat at different sites between years

*2013/2014*

Macroalgal mats began to develop in Brands Bay and Ower Bay in April with biomass increasing rapidly during the early part of the 2013/2014 growth season (Fig. 2.4). By contrast, growth did not appear in Holes Bay and Newton Bay until May 2013. Peak biomass was variable between sites with an early peak in May 2013 (Ower Bay), June 2013 (Brands Bay) and July 2013 (Newton Bay) whereas Holes Bay did not record peak biomass until much later in the season (October 2013). A second, smaller, bloom was recorded in September 2013 (Brands Bay) and October 2013 (Newton Bay) yet this pattern was not recorded in Holes Bay or Ower Bay, although Ower Bay showed a slight increase in biomass in December 2013. The current SSSI Condition Assessment threshold of 2 kg $m^{-2}$ was exceeded early in the 2013/2014 season; occurring in May 2013 in Ower Bay and June 2013 in Brands Bay. In Newton Bay this threshold was within 1 s.e. of the mean biomass in July 2013. No algal growth was recorded during January or February 2014. Although the patterns of macroalgal mat development appeared to vary between sites, these were not significant ($\chi^2$ = 1.5844, df = 3, p = 0.663, n (2013/2014) = 60 per site).

*2014/2015*

Patterns of macroalgal mat biomass development recorded in 2013/2014 were not replicated in 2014/2015 although there was an early season growth recorded in April 2014 at both Brands Bay and Ower Bay (Fig. 2.5). Peak biomass for Holes Bay was earlier in the season than the previous year occurring in June 2014 with Ower Bay also recording peak biomass in that month. By contrast, Brands Bay and Newton Bay both recorded peak biomass for the season in October 2014. Once again a second, smaller bloom was recorded although this only occurred in Holes Bay in December 2014. Peak biomass during 2014 season never reached 2 kg $m^{-2}$, yet remained close to 1 kg $m^{-2}$ at all sites (except Holes Bay) until October 2014. No algal growth was recorded in January or February 2015. Despite the apparent variation in development between sites, these differences were not significant ($\chi^2 = 2.252$, df = 3, $p = 0.522$, n (2014/2015) = 30 per site).

Although there appeared to be fluctuations in the growth and development of macroalgal mat biomass within each site between years, there was no significant variation in algal biomass (g $m^{-2}$) within sites between 2013/2014 and 2014/2015 (Brands Bay, W = 31.5, $p = 0.707$, Holes Bay W = 42.5, $p = 0.557$, Ower Bay W = 26.5, $p = 0.397$, Newton Bay W = 31.5, $p = 0.695$, n (2013/2014) = 60 per site, n (2014/2015) = 30 per site).

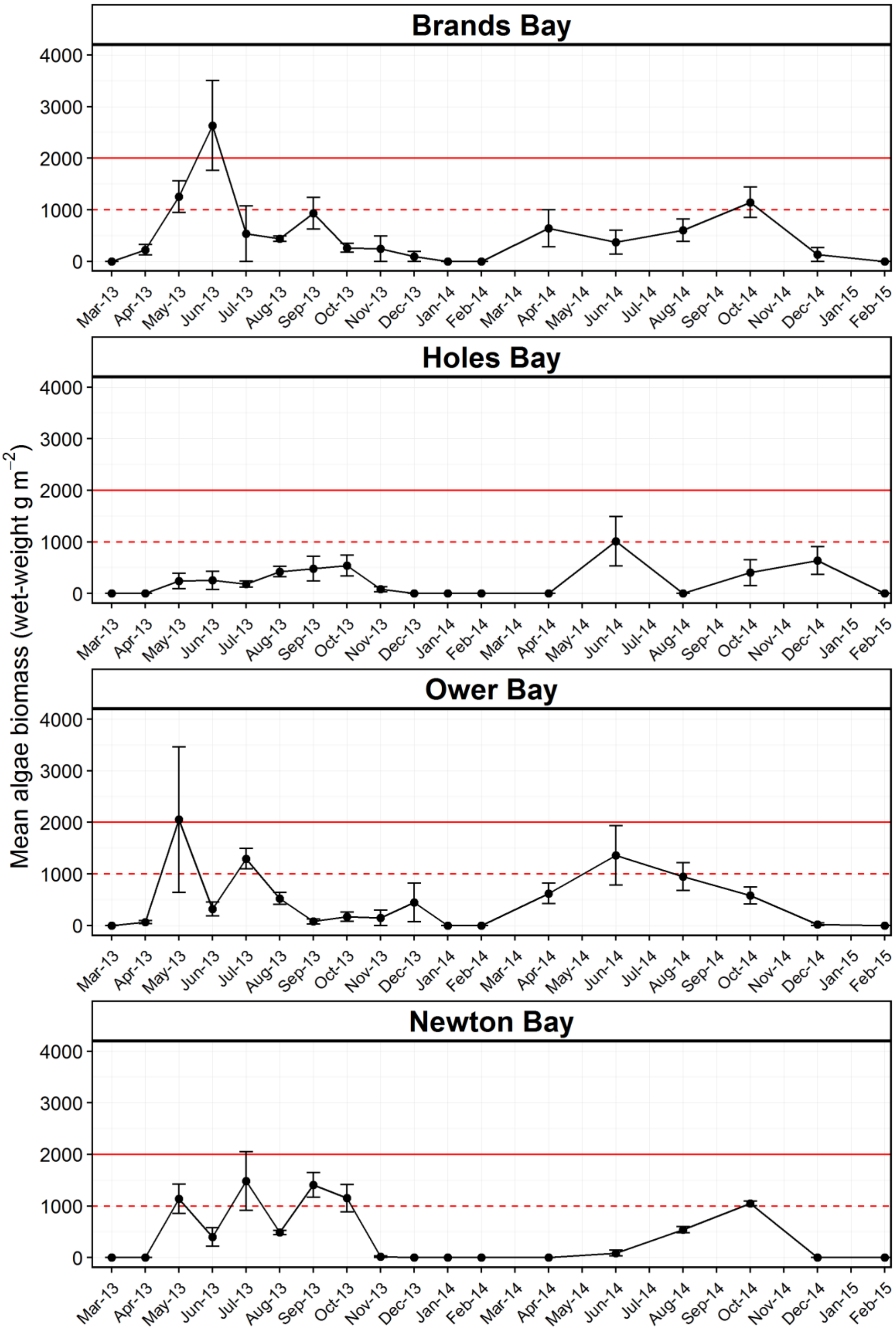


**Fig. 2.5:** Mean wet weight biomass of algae (g (ww) m$^{-2}$) error bars ± 1 s.e.

- - - - - - 1000 g m$^{-2}$ ——— 2000 g m$^{-2}$ (current threshold for SSSI Condition Assessment).

### 2.4.5 Mapping macroalgal mat coverage

Figure 2.6 shows the estimated percentage cover across each bay together with the mean percentage cover within that month's upper shore quadrat samples. With the exception of Newton Bay, in 2013/2014 there was an apparent difference between percentage cover of algae recorded in the quadrats and percentage cover recorded across the whole bay early in the season. By August the quadrat percentage cover is similar to the percentage cover across the bay. Newton Bay was the only area where both quadrat coverage and bay coverage were similar across the season. By contrast, in 2014/2015, development of macroalgal mat biomass more closely matched coverage recorded during 2014/2015. Results from August 2014 in Newton Bay show zero percentage cover for the quadrat samples as the macroalgal mat did not extend to the upper shore. Although the coverage within quadrats was higher in Ower Bay, the trend was similar with corresponding increases in coverage at the upper shore and across the bay. Each season the rate of decline was similar for coverage measured within quadrats and coverage estimated across each site.

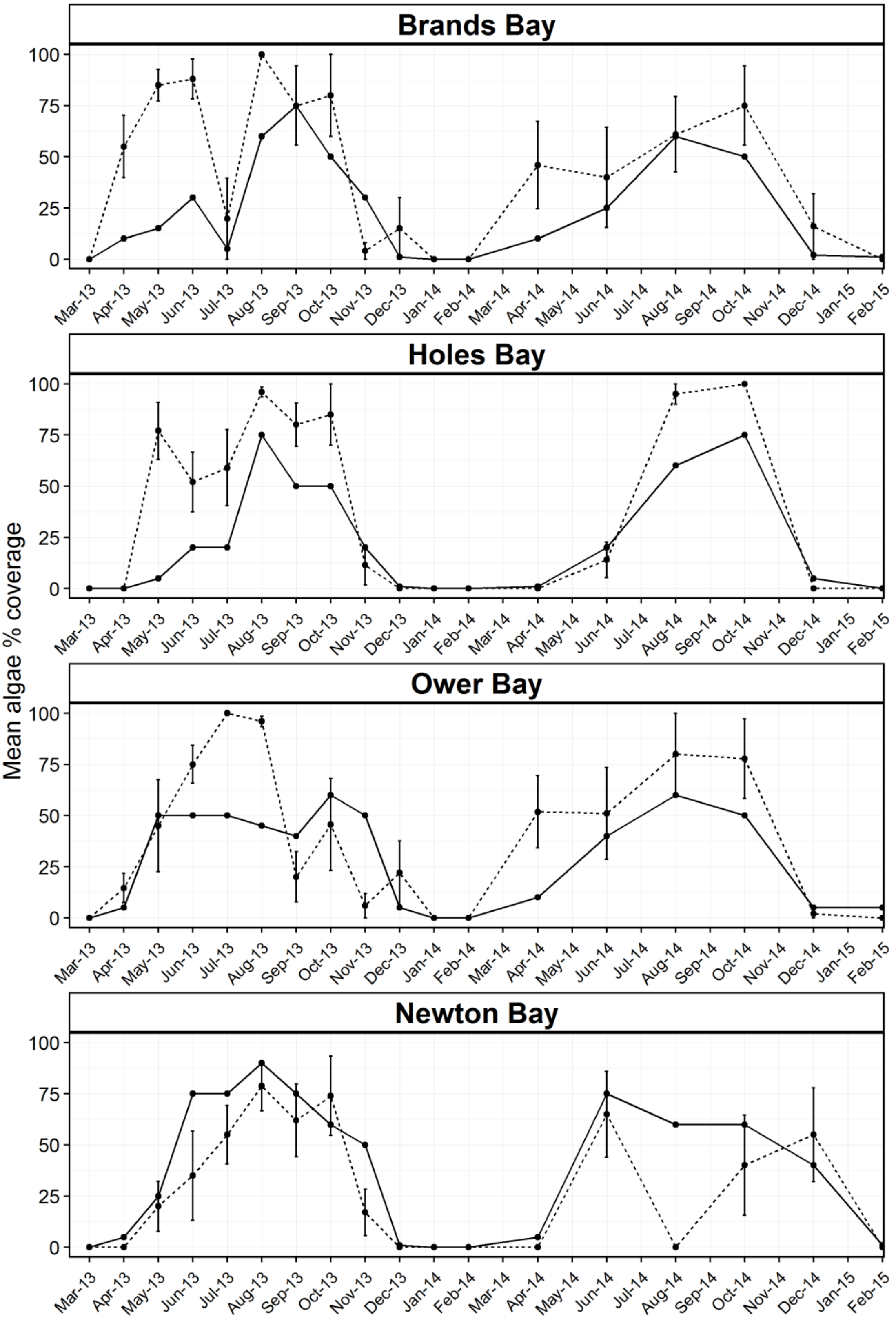


**Fig. 2.6:** Algae % coverage measured in quadrats and estimated across each bay.

---------- = quadrat coverage ——— = bay coverage. Error bars (for quadrat coverage) ±1s.e.

### 2.4.6 Between-year variation in % algae coverage

#### *2.4.6.1 Upper shore quadrat samples*

There was no significant variation in overall % algae coverage at the upper shore between years (W = 588, p = 0.889). There was no significant within-site variation in % algae coverage at the upper shore between years (Brands Bay: W = 39, p = 0.814; Holes Bay: W = 35.5, p = 0.999; Ower Bay: W = 29.5, p = 0.572; Newton Bay: W = 38, p = 0.883)

#### *2.4.6.2 Estimated overall % coverage across each bay*

There was no significant variation in overall % algae coverage across sites between years (W = 488.5, p = 0.295). There was no significant within-site variation in % algae coverage between years (Brands Bay: W = 32, p = 0.742; Holes Bay: W = 30, p = 0.6; Ower Bay: W = 33, p = 0.811; Newton Bay: W = 33.5, p = 0.850).

### 2.4.7 Between-site variation in % algae coverage

#### *2.4.7.1 Upper shore quadrat samples*

There was no significant variation between sites for % algae coverage in upper shore quadrat samples for 2013/2014 ($\chi^2$ = 1.218, df = 3, p = 0.749) or for 2014/2015 ($\chi^2$ = 1.282, df = 3, p = 0.733)

#### *2.4.7.2 Estimated overall % coverage across each bay*

There was no significant variation between sites for % coverage across each bay for 2013/2014 ($\chi^2$ = 1.218, df = 3, p = 0.749) or for 2014/2015 ($\chi^2$ = 1.01, df = 3, p = 0.799).

### 2.4.8 Relationship between upper shore and bay-wide % algae coverage

There was a highly significant correlation between % coverage measured using upper shore quadrat samples and estimated coverage across each bay over both survey years (S = 15252, p = <0.001, rho = 0.755). There was also a highly significant correlation between % coverage at the upper shore and across the bay each year: 2013/2014 (S = 3816.3, p = <0.001, rho = 0.793) 2014/2015 (S = 517.75, p = <0.001, rho = 0.775).

## 2.5 Discussion

### 2.5.1 Climate

It is apparent from the results that temperature (as the main co-linear variable) is an important environmental driver of macroalgal mat growth with 43% of the variance in algal biomass being accounted for by air temperature. Sediment temperature was also significant accounting for 35% of the variance in algal biomass. There are other, untested environmental variables which will account for the remaining variance yet Figs. 2.5 and 2.6 clearly show that when mean air and sediment temperatures began to rise, there was an almost immediate corresponding rise in macroalgal mat development. This is likely due to the opportunistic nature of the ephemeral green algae being able to rapidly respond to changes in temperature. Macroalgal mat growth is inhibited by extremes of temperature (Raffaelli et al. 1998), therefore, it had been expected that, with the extremely low temperatures in spring 2013, the algal bloom may have been reduced or delayed. In fact the reverse was apparent with a high algal biomass recorded at some sites in May 2013 (Fig. 2.5).

It was surprising that rainfall was not a significant factor in algal growth. Winter 2013/2014 was the ‘wettest since 1766’ (Met Office 2016) and it was predicted that the bloom during summer 2014/2015 season would be extensive as the rain may have washed additional nutrients straight off the land; although an increased flow may have rapidly flushed the nutrients out of the estuary. However, there was no significant difference in overall biomass between years. It is also possible that the flooding washed excessive amounts of sediment into the harbour thereby increasing turbidity levels and reducing light penetration; although *U. intestinalis* has been shown to be highly tolerant of increased sedimentation in field experiments carried out in Sweden (Eriksson and Johansson 2005).

### 2.5.2 Algal growth

In general, macroalgal mat development in Poole Harbour was typical of other temperate estuarine systems (Raffaelli et al. 1998; Nedwell et al. 2002; Anderson et al. 2002). However, the ‘peak’ biomass recorded each year did not occur between June-August as anticipated (Jones and Pinn 2006; WFD-UKTAG 2009). It is noteworthy that in 2013/2014 the ‘peak’ biomass was not particularly high so it is possible that further growth during July-August was inhibited due to the high temperatures recorded during those months; surface fronds of macroalgal mat in August 2013 were visibly yellowing possibly indicating stress.

It was surprising that there was no significant variation in algae biomass between sites as it had been expected that Holes Bay would record a lower biomass than the other sites. This is due to the sheet-forming morphology of the dominant *Ulva* species in Holes Bay; the thin sheet-like thalli covered up to 75% of the intertidal area in Holes Bay yet recorded lower biomass and density. By contrast the tubular or filamentous fronds of the *Ulva* species dominant in the southern part of the harbour form dense, impenetrable mats. Under the WFD a biomass of 2 kg $m^{-2}$ is the threshold at which the Environment Agency suggests further investigation (Rees-Jones 2004). This level was reached during 2013 in May (Ower Bay) and June (Brands Bay) but not maintained. The lower threshold of wet weight biomass of 1 kg $m^{-2}$ was reached in May in Brands Bay, July in Ower Bay and July, September and October in Newton Bay. The maintenance of this level at Newton Bay is possibly due to the surrounding land-use. The site is fringed by arable farmland and access to the sampling area is across a patch of wet woodland. There was evidence of cattle poaching in this area which may have resulted in localised nutrient input into the bay.

Macroalgal mat development during 2014/2015 showed surprising results. There appeared to be a ‘double-bloom’ with early peak biomass recorded in April (Brands Bay) and June (Holes Bay and Ower Bay). A second peak of macroalgal mat development with a biomass >500 g $m^{-2}$ was recorded at all sites in October 2014 and was recorded in Newton Bay at this level in December 2014. The persistence of the macroalgal mat into autumn and even December may have implications for the overwintering birds and their invertebrate prey. It is worth pointing out that the biomass samples were taken from the upper shore area and, as such, are likely to be higher than mid and lower shore areas. However, all shore levels are used by overwintering wading birds and the implications of increased biomass at the upper-shore level are discussed in later chapters.

### 2.5.3 Extent

Terrestrial methods for mapping algal coverage have been trialled albeit on a smaller scale than Poole Harbour (Nedwell et al. 2002). It was possible to estimate the coverage across each bay using a mounted telescope from elevated positions. The vantage point at the largest site, Brands Bay, was a bird hide situated approximately 10 m above the shore, Holes Bay vantage point was on a raised footpath approximately 1.5 m above the shore and the smallest site, Ower Bay, vantage point was on a bank approximately 1.0 m above the shore. However, due to the tidal system in Poole Harbour, low water spring tides occur in late afternoon which presented some difficulties in estimating coverage particularly during autumn when the sun was lower and reflecting off the wet algae. The laser range-finder proved ineffective in determining distance of the algal patches from the upper shore vantage points. The macroalgal mat is relatively flat on the surface of the mud so the laser could not secure a sufficiently raised point to establish a distance.

Coverage of algae in the upper shore quadrats was higher at the start of the survey season compared to coverage across each bay. This supports observations in the field suggesting growth of macroalgal mat generally begins at the upper shore (except at Newton) and extends down the shore gradient as the season progresses (March – July). Therefore simply extrapolating the extent of coverage across a bay from the percentage cover recorded in quadrats at the upper shore level is not a reliable measure whilst macroalgal mats are developing. Yet once the peak extent has been reached it appears that the mats deteriorate at a similar rate across shore-levels. Even so, relying solely upon coverage in quadrats to estimate coverage across a bay is unreliable. Some form of remote sensing (either terrestrial or aerial or both) is vital to determine the extent of the macroalgal mats in a given area (Alexander et al. 2008).

Although peak coverage recorded across each bay reached 75% at Brands Bay, Holes Bay and Newton Bay for both 2013/2014 and 2014/2015 and 60% in Ower Bay, there were areas within each site that remained ‘algae-free’. High levels (>50%) of macroalgal mat coverage remained at all sites in September and October 2013 and 2014; coinciding with the arrival of the overwintering wading bird population. The implications of high levels of macroalgal mat coverage on the wading bird population are discussed in Chapters 4, 5 and 6. Although a peak coverage of >75% was recorded at all sites, this was expected during the summer months (Nedwell et al. 2002) when increased light and temperature levels stimulate macroalgal mat development (Raffaelli et al. 1998). The high levels of coverage are consistent with an earlier study in the harbour where peak coverage of 91% was recorded in August 2002 within a 50 m x 50 m study site in Holes Bay (Jones and Pinn 2006). Coverage of ~50% recorded at all sites during September – December is consistent with other studies examining the impact of macroalgal mats on overwintering wading birds. Results from work on the Mondego Estuary, Portugal, recorded peak macroalgal mat coverage of 36% between October 1993 and May 1994 (Múrias et al. 1996). Maximum coverage of 55% was recorded in winter 2000/2001 in the Clonakilty Estuary, Ireland, (Lewis et al. 2014). High coverage (>75%) of algae was recorded in winter 1977 –

1978 at sheltered sites in Langstone Harbour, UK (Soulsby 1982); an area where macroalgal mat persists throughout the year (Rees-Jones 2004).

### 2.5.4 Conclusion

Temperature is an important factor in macroalgal growth and persistence (Raffaelli et al. 1998). Therefore any rise in air or sediment temperature due to climate change may result in areas of the harbour being permanently covered by macroalgal mats.

Although the macroalgal mat biomass was only recorded above the 2 kg $m^{-2}$ threshold on a few occasions, levels were consistently around 1 kg $m^{-2}$ throughout each season. It could be argued that these biomass values were obtained at the upper shore and, therefore, not representative of the rest of the intertidal area. However, coverage is also an important metric within the Water Framework Directive (Scanlan et al. 2007). Coverage was maintained at over 50% at all sites during 2013/2014 and 2014/2015 at both the upper shore level and across each bay. These results support earlier studies indicating a wet weight algal biomass of 1 kg $m^{-2}$ should be the target threshold (Hull 1987; Raffaelli et al. 1999). Natural England is currently reviewing the 2 kg $m^{-2}$ target used for SSSI condition assessments and it is likely that this threshold will be reduced to 1 kg $m^{-2}$ (D. Kite pers. comm.).

# 3.0 The effect of macroalgal mats on the benthic invertebrate community

## Abstract

Benthic macro-fauna represent the pivotal trophic level within an estuarine ecosystem by providing both top-down control of primary production, through herbivorous species such as hydrobid snails, and bottom-up food supply for secondary/tertiary consumers such as carnivorous polychaete worms (e.g. *Nephtys hombergii*) and top predators (e.g. overwintering wading birds).

This chapter investigates the impact of macroalgal mats on the benthic invertebrate community within a temperate estuarine ecosystem on the south coast of the UK. Benthic core samples were obtained in September 2013, December 2013 and September 2014 at upper, mid and lower shore levels at three sites around Poole Harbour (Holes Bay, Brands Bay and Ower Bay) which showed varying levels of macroalgal mat growth. These sites also provide important feeding areas for the overwintering wading bird population for which Poole Harbour is a designated Special Protection Area (SPA).

Abundance/Biomass Comparison curves were used to provide an initial indication of areas under environmental stress. Variation in community structure was significantly different between Holes Bay and Brands Bay, and Holes Bay and Ower Bay. This variation was mainly due to the polychaete *Hediste diversicolor* and smaller r-selected opportunists such as *Tubificoides* spp. and Hydrobidae.

Algae biomass, either singularly or in combination with % organic content within the sediment, provided the best explanatory model for variance in the overall community assemblage; annelid worm assemblage; crustacean assemblage; and five of the six individual species contributing over 60% of the variation in invertebrate assemblage. *Tubificoides* spp. variance was best explained by % organic content. Results showed that overall abundance of invertebrates increased under low levels macroalgal mat biomass (~800 g $m^{-2}$ wet weight) then began to decline. The transformation of the benthic invertebrate community has implications for available prey items for the overwintering bird population.

BLANK

## 3.1 Introduction

### 3.1.1 Benthic invertebrate response to environmental change

Benthic macro-fauna represent the pivotal trophic level within an estuarine ecosystem by providing both top-down control of primary production, through herbivorous species such as hydrobid snails, and bottom-up food supply for secondary/tertiary consumers such as carnivorous polychaete worms (e.g. *Hediste diversicolor* [O. F. Müller 1776]) and top predators (e.g. overwintering wading birds) (McLusky and Elliott 2004; Wildsmith et al. 2009; Fox et al. 2012).

Under increasing hypoxic and anoxic conditions within the sediment resulting from the breakdown of the macroalgal mat, the invertebrate community could become dominated by species tolerant of low oxygen levels, such as oligochaetes and capitellid polychaete worms; highly abundant but with low biomass. Species less able to tolerate increased stress within the system will either move or perish; leading to a further reduction in diversity (Pearson and Rosenberg 1978; Fox et al. 2009). However, the increase in abundance of one or two taxa should not be used as the only indicator of environmental stress (Gray and Mirza 1979; Warwick 1986). Eutrophication is a chronic stressor within an estuarine system with symptoms such as macroalgal mats developing over a number of years (Kite et al. 2012). Capitellids, for example, are opportunists and will take advantage of sudden stress events (Pearson and Rosenberg 1978). These species are normally out-competed within a short period of time as the system either returns to normal or other stress-adapted species take over (e.g. *Peringia ulvae* [Pennant 1777], *Hediste diversicolor*) (Warwick 1986).

Differences between overall abundance and biomass of an invertebrate community could indicate chronic environmental stress caused by macroalgal mats (Warwick 1986). Although estuarine environments are naturally stressed due to fluctuations in salinity and exposure, these systems should contain a greater biomass of invertebrates in relation to their abundance; suggesting a community dominated by larger, slower growing K-selected species rather than those smaller, faster growing opportunistic r-selected species (Warwick 1986).

### 3.1.2 Benthic invertebrate response to macroalgal mats

Determining the effect of algae on benthic invertebrates has previously proved difficult. Much of the current understanding of impacts has been developed through manipulation experiments in controlled situations with algae either removed (Everett

1994; Lewis et al. 2003) or added (Raffaelli et al. 1991; Österling and Pihl 2001; Cardoso et al. 2004) in measured amounts. Whilst these experiments have led to an increased understanding of the impacts of algae on invertebrates, many of the interactions found during experimental work have not been confirmed in the field. For example Yarrington et al. (2013) reported that, under experimental conditions, gastropods were facilitating the growth of macroalgae. This was due, in part, to the sudden availability of a food source and nutrient deposition from pseudofaeces. However, similar results were not recorded in subsequent field manipulation experiments. A study in the Waquoit Bay, Massachusetts, found a lower abundance of benthic invertebrates in the eutrophic estuary with high macroalgal mat biomass compared to the non-eutrophic site (Fox et al. 2009). In addition, the study suggested increases in macroalgal mat biomass could provoke a regime shift resulting in a more herbivorous dominated invertebrate community (Fox et al. 2009). As the survival of the overwintering bird population depends upon gaining sufficient energy from invertebrates, any reduction in prey size and quality could have significant implications at higher trophic levels (Raffaelli et al. 1991).

### 3.1.3 Benthic invertebrates and macroalgal mats in Poole Harbour

The extensive, intertidal mudflats in Poole Harbour contain an abundance of benthic macrofauna (Thomas et al. 2004; Herbert et al. 2010). These, in turn, support the large populations of overwintering birds for which Poole is nationally and internationally designated. If the macroalgal mat is affecting the functional ecology or diversity of the invertebrate community this could impact upon the survival of the estuary's upper trophic levels, in this case, wading birds (Raffaelli et al. 1999).

Yet, in spite of the importance of the invertebrate community to Poole Harbour, there has only been one peer-reviewed article examining changes in invertebrate diversity and species-richness under macroalgal mats (Jones and Pinn 2006). This study looked at invertebrates inhabiting the sediment and within the macroalgal mat itself. Research was carried out from June – November 2002 within a 50 m x 50 m area of Holes Bay approximately 900 m south-west from a tertiary treated sewage outflow and approximately 500 m north-east from a marina complex. Although no algae biomass measurements were taken, maximum coverage of 91.3% and thickness of 90 mm were recorded within the study site. As the macroalgal mat developed, invertebrate diversity and species richness initially increased reaching a peak in June and July. Once the macroalgal mat reached its maximum coverage (August 2002), invertebrate species richness and biomass were at their lowest. The macroalgal mat was found to have a negative impact upon infaunal species-richness although the epifaunal species abundance and diversity increased (Jones and Pinn 2006). However, as the study was carried out during summer and autumn months, it is possible that fluctuations in invertebrate abundance and diversity were due to seasonal trends.

A harbour-wide survey for English Nature (Natural England) using 80 sampling stations was carried out in September and October 2002 (Thomas et al. 2004). This study aimed to establish baseline data on the invertebrate community within Poole Harbour; primarily to ensure sufficient food resources for the wading bird population within the harbour. A total of 61 species were recorded comprising 23 Annelida, 20 Arthropoda, 15 Mollusca and 3 other (Thomas et al. 2004). Although not specifically addressing the relationship between invertebrate community and macroalgal mats, algae coverage ranging from 0% - 100% was recorded at the sample sites. No relationship was found between coverage and tidal-height. Sediment particle size (% fine silt and % coarse sand) was found to be the best explanatory environmental variable for the variation in invertebrate distribution (Thomas et al. 2004). This study was repeated in September and October 2009 (Herbert et al. 2010). Despite not being the primary objective of the study, Herbert et al. (2010) did investigate the relationship between macroalgal biomass, % algal cover, % organic content and % sand; finding weak yet significant relationships between invertebrate assemblage and % organic content and % sand. Weak, significant associations were also recorded between the algae variables and % organic content and % sand. However, there was no significant relationship between the invertebrate community or diversity and either algal biomass or algal % coverage. Caldow et al. (2005) provides an overview of other invertebrate surveys carried out in Poole Harbour dating back to 1971. None of these studies examined the relationship between invertebrate assemblage and macroalgal mats; nor did many obtain size classes for the invertebrates recorded. Further details, analysis and discussion of these reports are presented in Caldow et al. (2005).

### 3.1.4 Rationale

Although recent reports and analysis of invertebrates within Poole Harbour have recorded levels of macroalgal mat coverage (Thomas et al. 2004; Herbert et al. 2010), there are no data showing the benthic invertebrate community assemblage *before* the macroalgal mat developed. Therefore, in order to determine the impact of macroalgal mats on wading birds, it is necessary to determine the prey resources available at the start of the overwintering season (September) and also the resources available when the extent of the macroalgal mat has declined (December).

This chapter will investigate how macroalgal mats are spatially and temporally affecting the invertebrate community of Poole Harbour. As discussed in Chapter 2, macroalgal mats have been present on the intertidal mudflats in Poole Harbour for over 40 years (Fletcher 1996). These data will also provide the basis for analysis of the availability and quality of prey items for the overwintering wading birds discussed in Chapter 4. Results will also determine whether the current threshold of concern for macroalgal mat biomass (2 kg $m^{-2}$) is appropriate for Poole Harbour.

## 3.2 Aims and objectives

| | |
|---|---|
| **Aim 1:** | To investigate the spatial and temporal variability in benthic invertebrate species diversity and assemblage at three sites in Poole Harbour under varying levels of macroalgal mat coverage and biomass. |
| **Aim 2:** | To determine whether macroalgal mats are transforming the invertebrate community. |
| **Aim 3:** | Provide data on abundance of invertebrate species to inform availability of suitable prey items for the overwintering wading birds. |

| | |
|---|---|
| **Objective 1:** | Sample the benthic macro-invertebrate community under varying levels of macroalgal mat biomass and coverage. |
| **Objective 2:** | Assess the impact of macroalgal mats on the invertebrate assemblage. |

## 3.3 Methods

### 3.3.1 Site selection

The assessment of macroalgal mat extent carried out between March and August 2013 was used to inform the selection of sampling sites for the invertebrate surveys (see Section 2.3.2.1). Macroalgal mat coverage and biomass recorded at each of the selected sites varied during that period. In addition, as these sites were also to be used for observation of bird feeding behaviour, it was necessary to ensure good visual coverage of each bay from a single vantage point. Three sites were deemed suitable: Holes Bay, Ower Bay and Brands Bay (Chapter 2, Fig. 2.2). Macroalgal mat extent in 2013 and 2014 varied within each site with patches ranging from 0% - 100% coverage (Chapter 2, Fig. 2.6) and correspondingly varying levels of algal biomass (Chapter 2, Fig. 2.5).

Due to the variation in environmental conditions around Poole Harbour, it was not possible to select a suitable control site. There were uncontrollable environmental conditions present in the ‘algae-free’ bays proposed as potential control sites and, as a result, differences in invertebrate community structure which would have been impossible to attribute solely to the lack of macroalgal mat. One particular site, Holton Heath, was proposed as this area remained algae-free throughout the summer of 2013. However, access was dangerous due to its proximity to a former weapons factory and land-fill site used for asbestos waste. Wareham Channel was considered as this area also remained algae-free during summer 2013. This site, however, was not comparable due to it being a long-thin channel rather than a sheltered bay and, therefore, not susceptible to the development of macroalgal mats. Parkstone Bay to the east of the harbour was too sandy and likely to contain a different benthic invertebrate community.

### 3.3.2 Sampling design

As one of the aims is to determine whether macroalgal mats have an impact on invertebrate prey for the wading bird population, benthic core samples were taken at the start of two overwintering seasons (September 2013 and September 2014) and the mid-point of a season (December 2013).

Each site was stratified according to shore gradient and classified as either upper, mid or lower shore. Poole Harbour’s unique ‘double high-water’ can result in some lower shore levels remaining under water (water level above mean tide level) for 16 out of 24 hours (Humphreys 2005). Mid-shore stations aimed to represent the low water level for a neap tide. In addition, as wading birds tend to follow the receding tide (Goss-Custard et al. 1977), sampling at different shore levels enabled assessment of bird prey availability during a complete tidal-cycle.

The sampling design was applied to each of the three sites (Brand’s Bay, Holes Bay and Ower Bay) (Fig. 3.1). Within each shore-level, two sampling stations were chosen using random point selection; S1, S2 (lower shore), S3, S4 (mid-shore), S5, S6 (upper-shore). At least 50 m separated stations within the same shore level and >150 m separated stations on different shore-levels. Six replicate core samples were taken at each station. A map showing locations of the sampling stations is provided in Appendix 2.

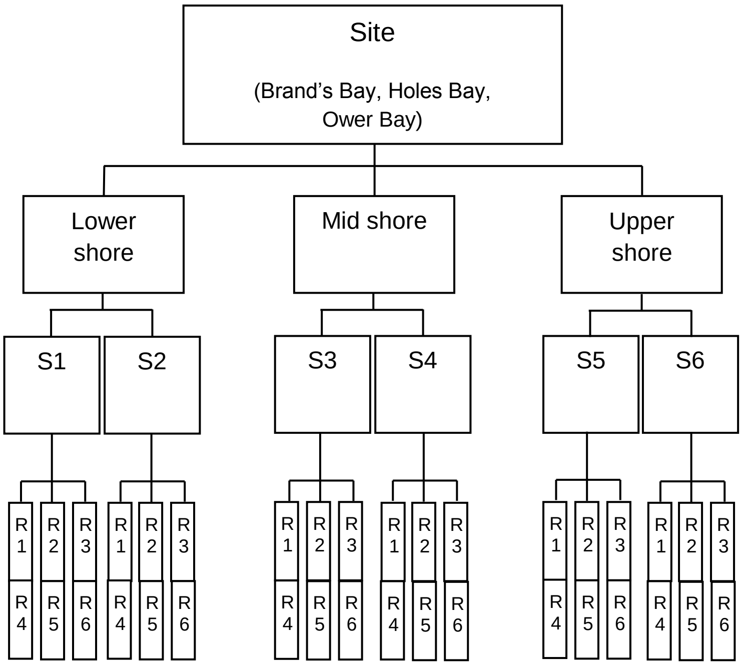


**Fig. 3.1:** Nested hierarchical sampling design for benthic invertebrate core sampling.

### 3.3.3 Core sampling and processing

Upper shore core samples were obtained at low tide from the shore using a hand corer 10 cm diameter to a measured depth of 15 cm (Ausden and Drake 2006). Mid and lower shore stations were sampled from a boat using a cylindrical suction corer 10 cm diameter 15 cm deep (Fig. 3.2). In addition, a single core was taken at each station for sediment and organic content analysis. Samples were immediately placed into labelled bags. A total of 324 individual invertebrate core samples were collected during the three sampling periods. Samples were stored for a maximum of 24 hours prior to being sieved in running water over a 0.5 mm mesh sieve. Invertebrates and any organic matter within the core samples were fixed in 4% formal saline for at least 72 hours before identification and analysis. Sediment core samples were frozen for storage within 24 hours to prevent organic matter decomposition.

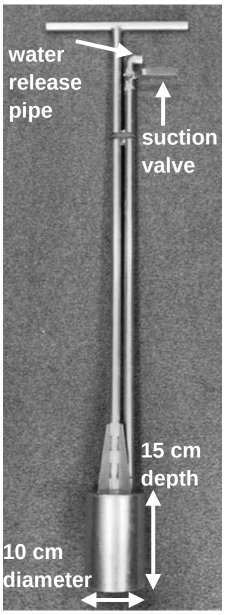


**Fig. 3.2:** Annotated diagram of suction corer used for mid and lower shore benthic invertebrate sampling.

### 3.3.4 Identification and measurement of invertebrates

In the laboratory, each sample was rinsed over a 0.5 mm mesh sieve to remove residual formalin. Samples were then examined using a Nikon stereo zoom microscope (0.8 – 8 x zoom) with x10 eyepiece. Invertebrates were removed and placed in 70% industrial methylated spirit (IMS).

Individual invertebrates were counted, identified and measured using a Brunel BMS stereo zoom microscope (0.7 – 4.5 x zoom) with x10 graticule eyepiece. Callipers (0.1 mm) were used when individuals were >10 mm. Samples were identified to the lowest possible taxonomic level (at least genus) with species identified where possible using Hayward and Ryland (1998), Crothers (1997), and taxonomy confirmed using the World Register of Marine Species (WoRMS) (www.marinespecies.org).

Head widths (across peristomium) were taken of all larger worms (e.g. *Hediste diversicolor*) together with lengths of complete specimens and a regression equation calculated to provide lengths of incomplete specimens. Lengths of Crustacea (from tip of rostrum to end of telson) were recorded and shell lengths of gastropoda and bivalves were measured. When in high abundance, *Peringia* (*Hydrobia*) *ulvae* were sub-sampled, with the mean of 10 measurements taken. It is often difficult to ascertain whether hydrobid shells contain tissue therefore, once measured, 10% were opened and the percentage of empty shells noted; a corresponding percentage of *Peringia ulvae* were removed from the total count. Length to ash-free dry-mass (AFDM) (mg) calculations were based upon existing equations for species recorded in Poole Harbour (Thomas et al. 2004; Herbert et al. 2010). Full details of all equations used are provided in Appendix 3.

### 3.3.5 Algae from benthic-cores

Algae was removed from the sieved core sample and processed according to methodology detailed in Section 2.3.2.3. Wet weight of algae samples was recorded using an electronic balance and samples were placed into labelled bags prior to being frozen for storage. Wet weight (ww) (g) of algae obtained from each core was converted to g $m^{-2}$.

### 3.3.6 Sediment particle size and organic content

Once sediment samples were defrosted, each sample was mixed by hand to ensure homogeneity of particle distribution. As some of the sediment samples contained a high water-content, samples were dried at 105 $^{o}$C for 18 hours. Dried samples were weighed using an electronic balance then placed in a muffle furnace at 450 °C for 12 hours. Each sample was re-weighed to determine organic % loss on ignition.

Particle size distribution was determined using a Mastersizer 3000 particle characterisation system (Malvern Instruments). Output provided percentages of the sediment within pre-defined particle size categories using the soil characteristic measurements contained in ISO14688-1:2002. As the instrument cannot measure particles >2 mm, samples were first sieved over a 2 mm mesh and particles >2 mm removed and weighed with the representative percentage added to the final output.

### 3.3.7 Statistical analysis

#### *3.3.7.1 Between-site and between-date variation in algae biomass from core samples*

Spatial and temporal variations in macroalgal mat biomass collected from core samples did not meet the assumptions of normality and homogeneity of variance required for ANOVA so were tested using non-parametric Kruskal-Wallis test in R Version 3.0.3 “Supposedly Educational” (R Core Team 2016).

#### *3.3.7.2 Spatial and temporal variation in invertebrate abundance and biomass*

Invertebrate abundance and biomass values from individual replicate cores were combined and abundance values converted to individuals $m^{-2}$; combined biomass values were converted to mg $m^{-2}$.

Assumptions of normality and homogeneity of variance were checked using Shapiro Wilks test within the “stats” package in R (R Core Team 2016) and Levene test within the “car” package developed for R (Fox and Weisberg 2011) respectively. Variations in total abundance and total biomass of invertebrates were tested using Analysis of Variance (ANOVA) with subsequent pair-wise analysis conducted using Tukey post-hoc test in R Version 3.0.3 “Supposedly Educational” (R Core Team 2016).

#### *3.3.7.3 Diversity indices*

Univariate indices were calculated using Plymouth Routines In Multivariate Ecological Research (PRIMER) v.6 (Clarke and Gorley 2006). Diversity indices measured were number of species $(S)$; numerical abundance $(N)$; Margalef’s index of richness $(d)$ whereby $d = (S-1)/log(N)$; Shannon-Weiner diversity $(H'(log_e)\ H' = -\Sigma i\ p_i\ log(p_i)$ where $p_i$ is the proportion of the total count arising from the $i$th species; Pielou’s evenness index ($J$) where $J = H'/H'_{max} = H'/logS$, and Simpson’s diversity ($1-\lambda$) $1-\lambda = 1-\{\Sigma_i N_i(N_i-1)\}/\{N(N-1)\}$ where $N_i$ is the number of individuals of species $i$, (Clarke and Warwick

2001). Variation between sites was analysed using ANOVA with a Tukey post-hoc test in R (Version 3.0.3 “Supposedly Educational”, R Core Team 2016) or Kruskal-Wallis test if assumptions required for ANOVA were not met.

### 3.3.7.4 Invertebrates as indicators of nutrient pollution

Abundance/Biomass Comparison (ABC) curves for each site were plotted using PRIMER v.6 (Clarke and Gorley 2006). Differences are highlighted by a W value with a positive W value indicating biomass greater than abundance and, therefore, a less stressed environment. A negative W value would suggest a stressed system (Warwick 1986). As the differentiations between stress levels are not indicated by Warwick (1986), W values were determined as:

W = >0.00 ‘less stressed’
W = ≤ 0.00 - ≤ -0.05 ‘moderately stressed’
W = >-0.05 ‘highly stressed’

### 3.3.7.5 Multivariate analysis of invertebrate community assemblage

PRIMER (v.6) was used to analyse spatial and temporal variation in invertebrate assemblage (Clarke and Gorley 2006). The community assemblage was determined using abundance $m^{-2}$ of each species recorded from the combined species totals of the six replicate core samples per station. Abundances were transformed as necessary and converted into a distance based matrix using Bray Curtis Index of Dissimilarity (Clarke et al. 2006).

Data were plotted on a non-metric multi-dimensional scaling (nMDS) plot and any obvious separation between samples noted. Analysis of Similarity (ANOSIM) was carried out on the assemblage data to determine any significant spatial or temporal variation in community structure. Once significant variation had been determined, ‘similarity percentages’ (SIMPER) was used to determine which species were the main drivers of variation between sites or dates (Clarke and Gorley 2006).

### 3.3.7.6 The influence of algae, organic content and sediment particle size on macrobenthic community assemblage

A distance-based linear model (DISTLM) was used to determine the influence of four environmental factors on invertebrate community assemblage. DISTLM within the PERMANOVA add-on to PRIMER (v.6) provides a method for analysing multiple dependent variables within an assemblage against one or more associated predictor variables (Anderson et al. 2008). Transformed assemblage abundance data are placed into a distance matrix (in this case Bray Curtis Index of Dissimilarity). Where sub-sets of data were tested, a zero-adjusted Bray-Curtis coefficient was used and a 'dummy sample' of value 1 was added. This enabled the index to reflect actual dissimilarity between denuded samples (i.e. those which contain no species within the sub-set group) rather than inferring similarity between samples due to absence of species (Clarke et al. 2006). The four environmental variables used; algae biomass, algae % coverage, % organic content and % sand, were normalised using Euclidean distance measure to enable comparison between different metrics (Clarke et al. 2006).

#### *3.3.7.7 The effect of macroalgal mat biomass on invertebrate abundance ($m^{-2}$)*

Total abundance ($m^{-2}$) of invertebrates plotted against algae biomass appeared to show a non-monotonic curved relationship. A generalised additive model (GAM) was plotted with a loess smoothing curve applied using ggplot2 package in R (version 3.3.0 "Supposedly Educational", R Core Team 2016) (Wickham 2009).

## 3.4 Results

Section 3.4.1 provides analysis of any variation in algae biomass collected from benthic cores. Sections 3.4.2 – 3.4.6 analyse spatial and temporal variation in the benthic invertebrate community during autumn and winter periods at the three sampling sites. Sections 3.4.7 to 3.4.9 focus on the impact of macroalgal mats on the benthic invertebrate community.

### 3.4.1 Algae biomass from core samples

Fig. 3.3 shows the mean wet weight algal biomass (ww g $m^{-2}$) for samples collected using either hand or suction corer from upper, mid and lower shore-levels in September 2013, December 2013 and September 2014. It is apparent that biomass at the different shore levels within each site mirrored the results from the upper shore quadrat samples whereby Holes Bay recorded a much lower biomass than either Brands Bay or Ower Bay. Both Ower Bay and Brands Bay recorded upper shore, mid shore and even some lower shore macroalgal mat biomass >1000 g (ww) $m^{-2}$, and some mid shore and upper shore samples >2000 g (ww) $m^{-2}$. Mid-shore and upper-shore biomass in Ower Bay was high and there was a large variation in September 2014 upper shore samples in Brands Bay. Despite this, there was no significant variation in macroalgal mat biomass from core samples between sites (p = >0.05) or between dates (p = >0.05).

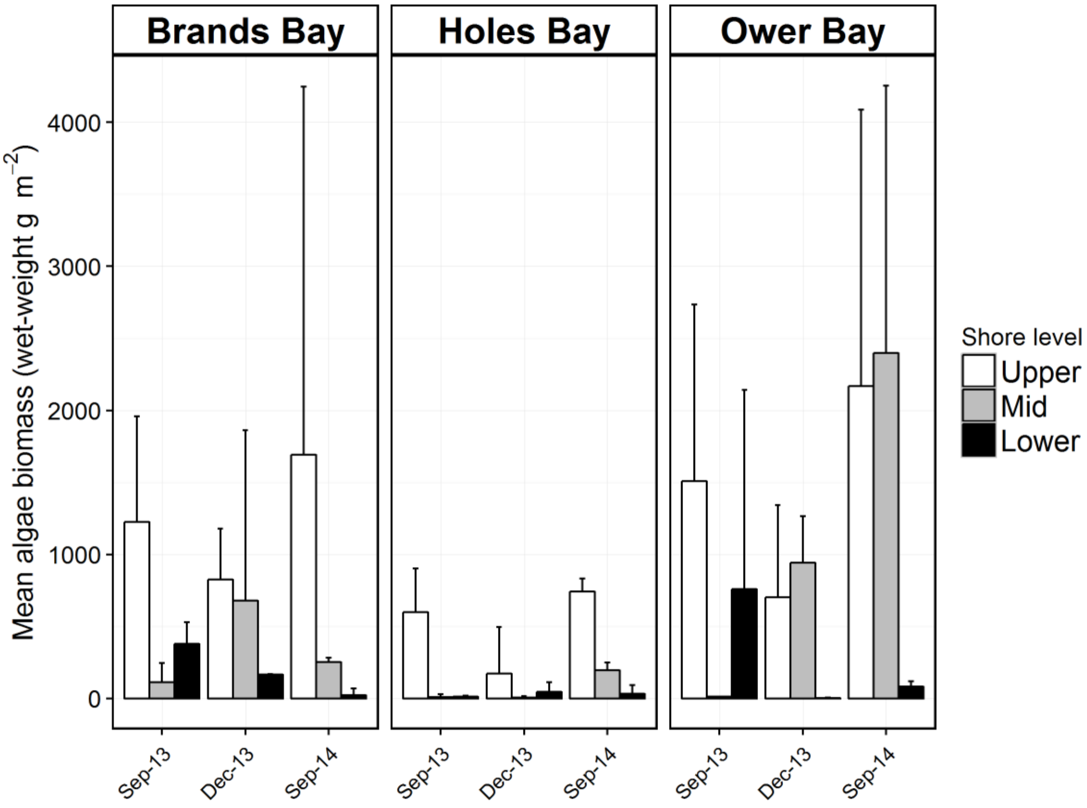


**Fig. 3.3:** Mean wet weight biomass of algae (g m$^{-2}$) recorded in core samples taken at upper, mid and lower shore levels in September 2013, December 2013 and September 2014. Error bars + 1 s.e. There was no significant variation (p = >0.05) in macroalgal mat biomass between sites or between dates.

### 3.4.2 Benthic invertebrate community

A total of 42 invertebrate species were recorded during the study – 18 annelids (17 polychaetes, 1 oligochaete), 10 crustaceans, 10 molluscs (5 bivalves, 4 gastropods and 1 chiton), 2 larval insects (Chironomidae and Dolichopodidae), 1 nemertea and 1 actinaria. These included common benthic invertebrates such as *Corophium volutator* [Pallas 1766], *Tubificoides* spp. *Hediste diversicolor,* and *Peringia* (*Hydrobia*) *ulvae,* together with non-native species (*Desdemona ornata* [Banse 1957], and *Ruditapes philippinarum* [Adams & Reeve 1850]). A full list of species recorded is presented in Appendix 4.

### 3.4.3 Spatial variation in species diversity

Table 3.1 shows diversity indices (number of species (S), numerical abundance (N), Margalef's index of richness (d), Pielou's evenness index (J), Shannon-Weiner diversity (H'(log$_e$), and Simpson's diversity (1-λ) calculated for each site irrespective of date and shore level. Table 3.2 provides details of significant variations between sites for diversity indices. Although there were only two significant differences between sites, these were both between Brands Bay and Holes Bay.

**Table 3.1:** Diversity indices (number of species *(S)*, numerical abundance *(N)*, Margalef's index of richness *(d)*, Shannon-Weiner diversity $(H'(\log_e)$, Pielou's evenness index ($J'$) and Simpson's diversity ($1\text{-}\lambda$) on square-root transformed abundance for all samples per site (±95% confidence interval in parentheses).

| | ***S*** | ***N*** | ***d*** | $J'$ | $H'(\log_e)$ | $1\text{-}\lambda$ |
|---|---|---|---|---|---|---|
| Brands Bay | 12.611 (±1.80) | 209.66 (±27.52) | 2.18 (±0.32) | 0.82 (±0.03) | 2.05 (±0.17) | 0.82 (±0.03) |
| Holes Bay | 10.00 (±1.14) | 186.91 (±29.86) | 1.73 (±0.18) | 0.87 (±0.02) | 1.96 (±0.09) | 0.83 (±0.02) |
| Ower Bay | 11.61 (±1.29) | 173.84 (±27.64) | 2.07 (±0.22) | 0.84 (±0.03) | 2.04 (±0.12) | 0.83 (±0.02) |

**Table 3.2:** ANOVA and Tukey post-hoc analysis between sites for diversity indices (Margalef's index of richness *(d)*, Shannon-Weiner diversity $(H'(\log_e)$, Pielou's evenness index ($J'$) and Simpson's diversity ($1\text{-}\lambda$) for the benthic invertebrate community. BB: Brands Bay HB: Holes Bay OB: Ower Bay. Significance codes: *** <0.001 ** <0.01 * <0.05 NS = not significant (p = >0.05).

| **Diversity index** | **F** | **Df** | **Sig.** | **Tukey post-hoc** |
|---|---|---|---|---|
| Margalef's richness *(d)* | 3.649 | 2,51 | p = 0.033* | BB>HB p = 0.033* |
| Pielou's evenness ($J'$) | 3.435 | 2,51 | p = 0.040* | HB>BB p = 0.031* |
| Shannon-Weiner diversity $(H'(\log_e)$ | | 2,51 | NS<br>p = 0.506 | - |
| Simpson's diversity ($1\text{-}\lambda$) | | 2,51 | NS<br>p = 0.823 | - |

### 3.4.4 Spatial variation in overall abundance and overall biomass of invertebrates

#### *3.4.4.1 Abundance*

Figure 3.4 shows mean abundance (individuals $m^{-2}$) and mean biomass (mg $m^{-2}$) by site for species recorded. There was significant variation in the abundance of molluscs between sites ($F_{2,51} = 3.291$, $p = 0.045$) with a significantly greater abundance in Brands Bay than Ower Bay ($p = 0.036$). There was also a significant variation in larval insect abundance between sites ($F_{2,51} = 4.773$, $p = 0.013$) with a significantly greater abundance recorded in Brands Bay than Holes Bay ($p = 0.014$). There was no significant variation in abundance of annelid worms, crustaceans or Hydrobidae between sites ($p = >0.05$).

### *3.4.4.2 Biomass*

Biomass of annelid worms varied significantly between sites ($F_{2,51} = 5.832$, $p = 0.005$) with significantly higher annelid biomass recorded in Holes Bay than Brands Bay ($p = 0.011$) and in Holes Bay than Ower Bay ($p = 0.016$). There was significant variation in mollusc biomass between sites ($F_{2,51} = 5.368$, $p = 0.008$) with greater biomass recorded in Holes Bay than Brands Bay ($p = 0.012$) and Holes Bay than Ower Bay ($p = 0.028$). Larval insect biomass varied significantly between sites ($F_{2,51} = 4.773$, $p = 0.013$) with greater biomass in Brands Bay than Holes Bay ($p = 0.014$). There was no variation in crustacean or Hydrobidae biomass between sites ($p = >0.05$).

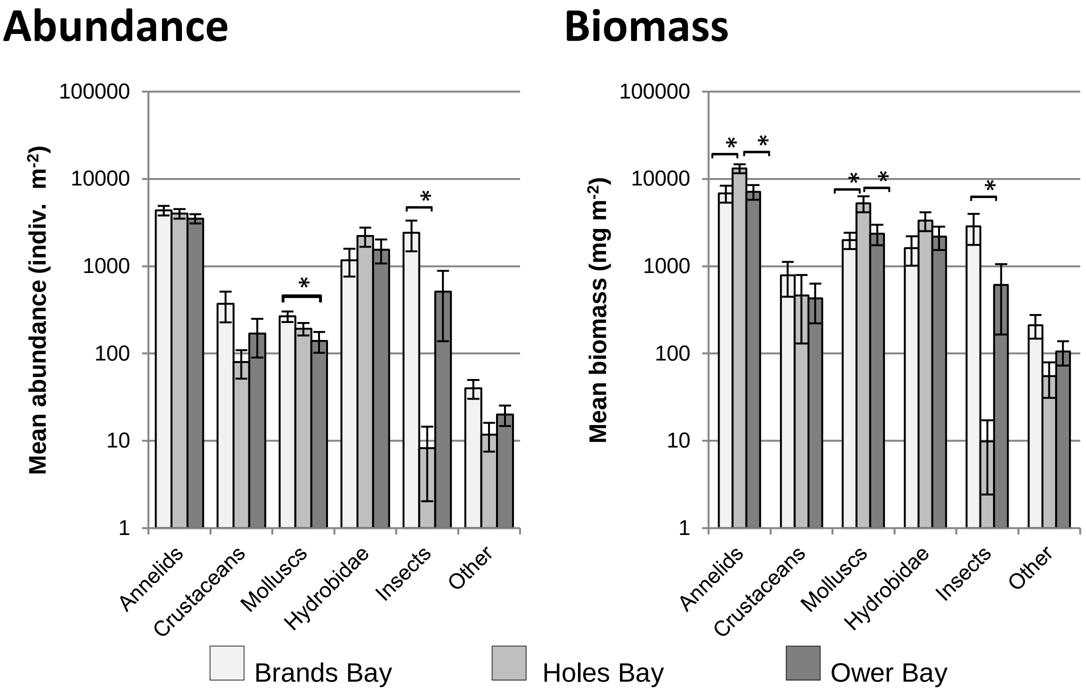


**Fig. 3.4:** Mean abundance (individuals $m^{-2}$) and mean biomass (mg $m^{-2}$) for key invertebrate groups by site with significant pairs ($p = <0.05$) shown (*). Annelid worms, Crustaceans, Molluscs (excluding Hydrobidae), Hydrobidae and Insects (comprising larval Chironomidae and Dolichopodidae). Error bars ± 1 s.e. Data are shown on a $\log_{10}$ scale for clarity.

### 3.4.5 Temporal variation in overall abundance and overall biomass of invertebrates

Figure 3.5 shows mean abundance (individuals $m^{-2}$) and mean biomass (mg $m^{-2}$) by date for species recorded. There was a significant variation in annelid worm abundance between dates ($F_{2,51} = 4.369$ , $p = 0.042$), with a significantly ($p = <0.05$) greater abundance recorded in December 2013 compared to September 2013 ($p = 0.042$) and December 2013 compared to September 2014 ($p = 0.03$). There were no other significant variations between dates ($p = >0.05$).

There was no statistically significant variation in biomass (mg $m^{-2}$) between dates.

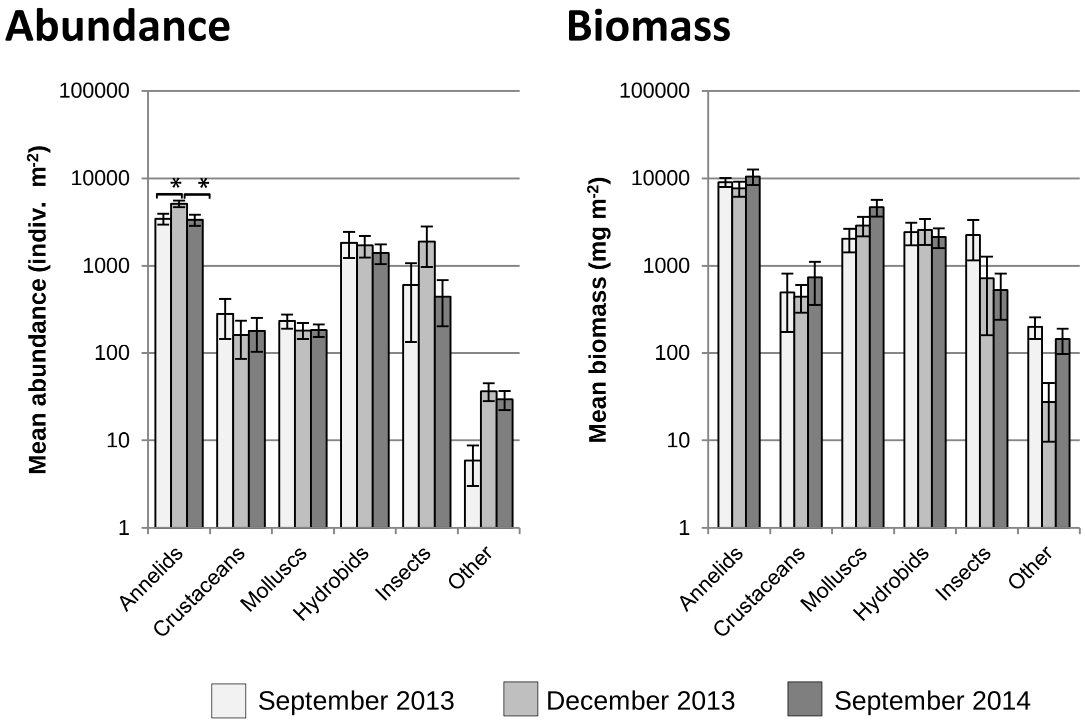


**Fig. 3.5:** Mean abundance (individuals $m^{-2}$) and mean biomass (mg $m^{-2}$) for key invertebrate groups by date with significant pairs ($p = <0.05$) shown (*). Annelid worms, Crustaceans, Molluscs (excluding Hydrobidae), Hydrobidae and Insects (comprising larval Chironomidae and Dolichopodidae). Error bars ± 1 s.e. Data are shown on a $\log_{10}$ scale for clarity.

### 3.4.6 Using benthic invertebrates as indicators of environmental stress

Figure 3.6 shows the Abundance/Biomass comparison (ABC) curves for each site and date. All sites were showing either moderate ($W = \leq 0.00 - \leq -0.05$) or high ($W = >0.05$) levels of stress with the exception of Holes Bay in September 2014 which showed a low positive W measurement. These values indicate a higher abundance of opportunistic r-selected species over K-selected species (Warwick 1986).

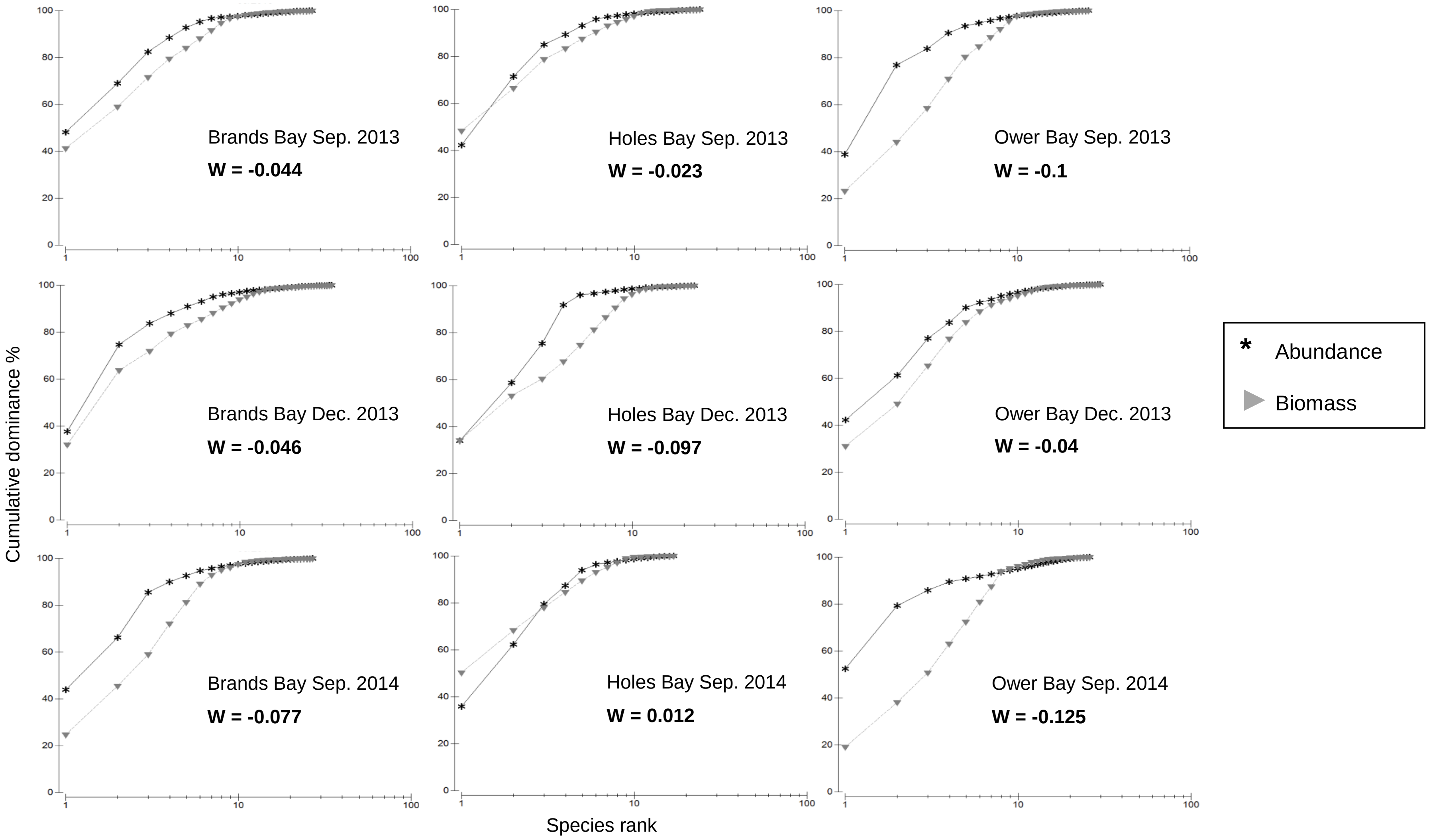


**Fig. 3.6:** Abundance/Biomass Comparison curves plotted for each site by date using square-root transformed values within a Bray Curtis index of dissimilarity. W values: >0.00 ‘less stressed’, ≤ 0.00 - ≤ -0.05 ‘moderately stressed’, >-0.05 ‘highly stressed’.

### 3.4.7 Spatial and temporal variation in benthic invertebrate community assemblage

It is apparent from the spatial separation in the non-metric multi-dimensional scaling (nMDS) plot shown in Fig. 3.7 that the community structure in Holes Bay is less similar to that in Brands Bay or Ower Bay.

A one-way ANOSIM test showed significant variation in community assemblage between sites (R = 0.446, p = 0.01) with significant variation between Brands Bay and Holes Bay (R = 0.716, p = 0.01) and between Holes Bay and Ower Bay (R = 0.473, p = 0.01) no variation was found between Ower Bay and Brands Bay (p = 0.09). There was no significant variation in community assemblage between dates (p = >0.05).

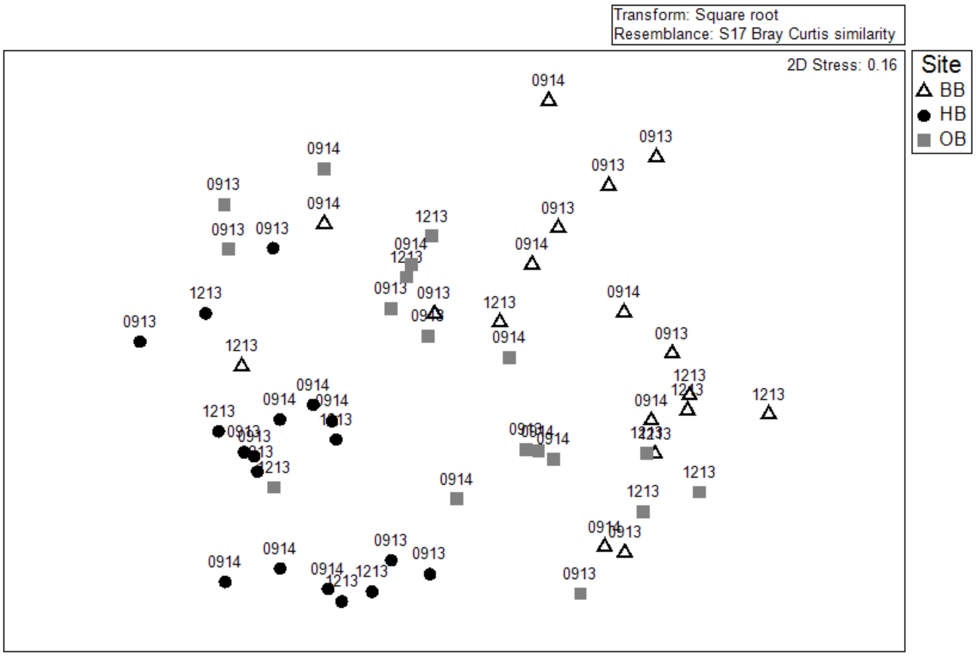


**Fig. 3.7:** Non-metric multidimensional scaling (nMDS) plot of Bray Curtis similarity on square-root transformed community abundance ($m^{-2}$). Samples from September 2013 (0913), December 2013 (1213) and September 2014 (0914) at Brands Bay (BB), Holes Bay (HB) and Ower Bay (OB). Each point represents the mean value ($m^{-2}$) of six replicate benthic cores.

SIMPER analysis of the significant differences identified by ANOSIM revealed that the main species contributing to variance in community structure between Holes Bay and Brands Bay, and Holes Bay and Ower Bay was *H. diversicolor.* This species contributed 15% and 16% respectively of the variation between the sites. Overall dissimilarity between communities on different sites was largely driven by six species. These species (*H. diversicolor,* Chironomidae, *Tubificoides* spp., *P. ulvae, Streblospio shrubsolii* [Buchanan 1890] and *Aphelochaeta marioni* [Saint-Joseph 1894]) contributed 67% of the variation between Holes Bay and Brands Bay, and 65% of the variation between Holes Bay and Ower Bay. Table 3.3 provides details of the individual % contribution from these six species. Of the 42 species recorded, 19 were responsible for 90% of the variation in community structure between Holes Bay and Brands Bay and 18 responsible for 90% of the variation between Holes Bay and Ower Bay. A table showing all species contributing up to 90% of the cumulative variation between sites is provided in Appendix 4.

**Table 3.3:** Results from SIMPER showing the main contributors to variation in the invertebrate community structure between sites. Pairs of sites with significant variation were identified from ANOSIM results (BB: Brands Bay. HB: Holes Bay. OB: Ower Bay). Comparisons between BB and OB were not significant so are not given. Data show average abundance for species within the two groups, individual species % contribution and the cumulative % contribution. Data are square-root transformed abundance within Bray-Curtis index of dissimilarity.

| **Brands Bay and Holes Bay**<br>Average dissimilarity = 62.27 | | | | |
|---|---|---|---|---|
| | **BB** | **HB** | | |
| Species | Average Abundance (indiv. m$^{-2}$) | Average Abundance (indiv. m$^{-2}$) | Contributory % | Cumulative % |
| *H. diversicolor* | 6.06 | 42.1 | 15.11 | 15.11 |
| Chironomidae | 36.37 | 0.93 | 13.79 | 28.9 |
| *Tubificoides* spp. | 57.47 | 29.04 | 13.03 | 41.93 |
| *P. ulvae* | 25.95 | 40.97 | 11.43 | 53.36 |
| *S. shrubsolii* | 3.41 | 21.9 | 7.78 | 61.14 |
| *A. marioni* | 10.11 | 13.74 | 5.73 | 66.87 |
| **Ower Bay and Holes Bay**<br>Average dissimilarity = 53.33 | | | | |
| | **OB** | **HB** | | |
| Species | Average Abundance (indiv. m$^{-2}$) | Average Abundance (indiv. m$^{-2}$) | Contributory % | Cumulative % |
| *H. diversicolor* | 14.3 | 42.1 | 15.76 | 15.76 |
| *P. ulvae* | 32.92 | 40.97 | 13.3 | 29.06 |
| *Tubificoides* spp. | 48 | 29.04 | 12.97 | 42.03 |
| *S. shrubsolii* | 2.38 | 21.9 | 10.6 | 52.63 |
| *A. marioni* | 9.98 | 13.74 | 6.79 | 59.42 |
| Chironomidae | 12.78 | 0.93 | 6.02 | 65.44 |

### 3.4.8 The impact of algae biomass on benthic invertebrate species richness, evenness and diversity

Analysis was carried out on the effect of algae biomass on Pielou's evenness, Shannon diversity and Margalef richness between sites and within sites. Algal biomass had a significant negative effect on Pielou's evenness across all sites ($F_{1,52} = 9.43$, $p = 0.003$, adj. $R^2 = 0.14$). Algae biomass did have a statistically significant positive effect upon Margalef richness in Holes Bay ($F_{1,16} = 6.538$, $p = 0.021$, adj. $R^2 = 0.246$). However, the $R^2$ values indicate other, untested, biotic and abiotic factors are affecting species' evenness and richness. No other significant effects were found between algae biomass and biological indices.

### 3.4.9 The impact of algae, sediment organic content, and sediment type on benthic invertebrate community assemblage

Table 3.4 provides details of the DISTLM routine with algae biomass (g $m^{-2}$), algae % coverage, % organic, and % sand, against Bray-Curtis dissimilarity index for abundance of invertebrates. Separate DISTLM routines were run for the six species which were the main drivers of community assemblage variation between sites as identified by the ANOSIM (Section 3.5.7). Significant variation was found for all groups except mollusc abundance excluding *P. ulvae* ($p = 0.096$). Strength of correlations using Pearson (r) coefficient are shown for individual species' abundance against the individual contributory environmental variables in the best explanatory model. All the models shown, except *P. ulvae* variance, recorded a $R^2$ of >15% with some models explaining >25% of the variation in community structure.

Algae biomass, either singularly or in combination with % organic, provided the best explanatory model for variance in the overall community assemblage; annelid worm assemblage; crustacean assemblage and five of the six species identified by ANOSIM. *Tubificoides* spp. variance was best explained by % organic content. Full details of the algae biomass, % algae cover, % organic content and % sand for each sample are provided in Appendix 5.

The correlations for individual species show negative (r) values for algae biomass and abundance for each individual polychaete worm species whereas there was a positive correlation for algae biomass on both Chironomidae and *P. ulvae* abundance. Organic content was negatively correlated with *Tubificoides* spp. abundance and Chironomidae abundance; although the spionid polychaete, *S. shrubsolii,* abundance showed a positive correlation with organic content.

**Table 3.4:** DISTLM results for log(x+1) transformed benthic invertebrate community abundance m$^{-2}$ within a Bray Curtis Index of Dissimilarity. Environmental variables tested: algae biomass (g m$^{-2}$); algae % coverage; % organic; % sand. Pearson (r) values given for individual species' correlations.

| **Abundance (groups)** | **Explanatory category** | **Pseudo F (res. df)** | **Adj. R$^2$** | **P value** |
|---|---|---|---|---|
| All abundance | Algae biomass+ % organic | 4.325 (51) | 0.16 | 0.001 |
| Annelida | Algae biomass+ % organic | 5.250 (51) | 0.22 | 0.001 |
| Crustacea | Algae biomass+ % organic | 3.420 (51) | 0.12 | 0.015 |
| Mollusca | - | - | - | 0.096 |

| **Abundance (species)** | **Explanatory category** | **Pseudo F (res. df)** | **Adj. R$^2$** | **P value** | **Pearson r** |
|---|---|---|---|---|---|
| *A. marioni* | Algae biomass | 15.946 (52) | 0.22 | 0.001 | -0.51 |
| *H. diversicolor* | Algae biomass | 11.013 (52) | 0.16 | 0.001 | -0.44 |
| *S. shrubsolii* | Algae biomass+ % organic | 8.830 (51) | 0.30 | 0.006 | -0.41<br>0.46 |
| Chironomidae | Algae biomass+ % organic | 6.814 (51) | 0.28 | 0.008 | 0.40<br>-0.45 |
| *Tubificoides* spp. | % organic | 10.861 (52) | 0.17 | 0.001 | -0.43 |
| *P. ulvae* | Algae biomass | 4.977 (52) | 0.09 | 0.02 | 0.41 |

### 3.4.10 The impact of algae biomass on overall benthic invertebrate abundance

Results from the DISTLM models show both negative and positive correlations for abundances of the top six species. By plotting overall abundance of invertebrates against algae biomass irrespective of site or date it became clear that the relationship was more complex. Scatter plots were visually examined and appeared to show a non-monotonic curve. A generalised additive model (GAM) was fitted with loess smoothing curve and 95% confidence intervals plotted. Figure 3.8 shows this applied to abundance of invertebrates (individuals m$^{-2}$) against algal biomass (g m$^{-2}$)

irrespective of date or site. It shows an initial increase in overall invertebrate abundance up to an algal biomass ~800 g (ww) m$^{-2}$ before abundance begins to decline.

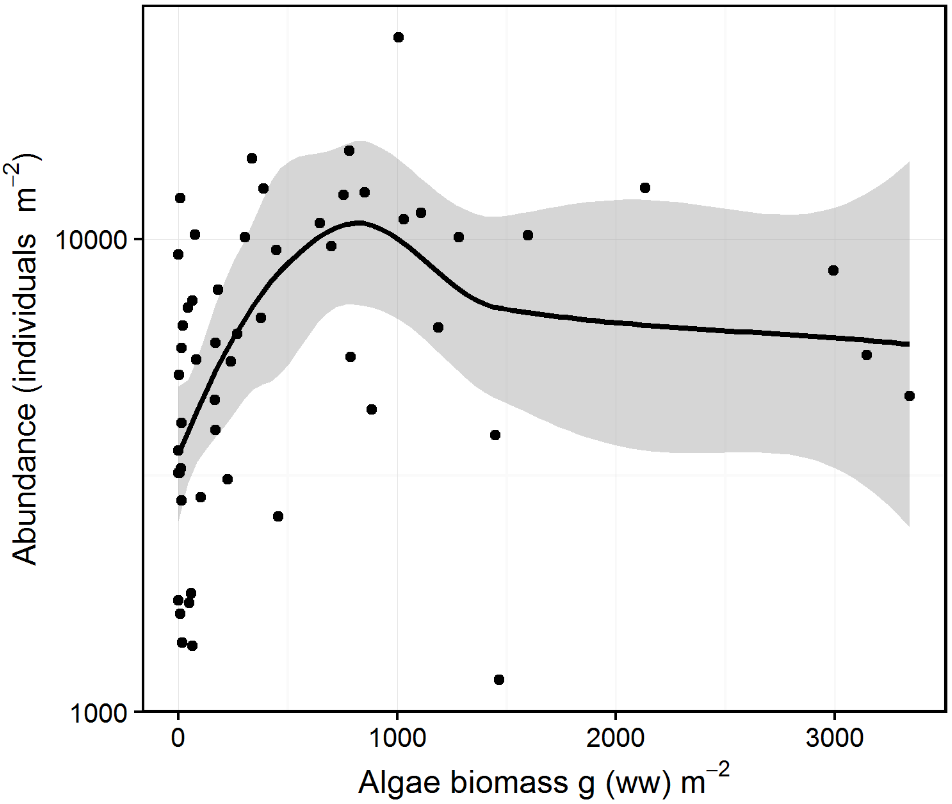


**Fig. 3.8:** GAM plot with loess smoothing curve showing the relationship between invertebrate abundance (individuals m$^{-2}$) against algae biomass (g (ww) m$^{-2}$). Shaded area shows 95% confidence interval. Data are plotted on a $\log_{10}$ scale for clarity.

## 3.5 Discussion

The aims of this chapter were, firstly, to investigate the invertebrate community within Poole Harbour under varying levels of macroalgal mat coverage, and secondly to determine whether the macroalgal mat is transforming that community.

### 3.5.1 Benthic invertebrate community

There were fewer species recorded during this survey than have previously been found in Poole Harbour using a similar sampling methodology (Thomas et al. 2004; Herbert et al. 2010). This is not surprising as those earlier surveys were specifically designed to record invertebrate species' diversity across the whole harbour; thus requiring a greater number and spatial distribution of sampling sites. The aim of this research was to determine invertebrate prey availability and diversity within three selected sites and under varying macroalgal mat conditions. The community structure remained consistent with previous studies, showing a greater abundance of annelid worm species (n = 20) compared to molluscs (n = 10) and crustaceans (n = 10). These results support a possible regime shift of macro-invertebrates from one dominated by bivalve molluscs to a more ‘worm-dominated’ system reported during the 1990s (Caldow et al. 2005). This change in community structure has been attributed to sediment contamination of bivalves from high levels of tributyltin (TBT) (Langston et al. 2015). However, this would require further investigation which falls beyond the scope of this research.

### 3.5.2 Using benthic invertebrates as indicators of environmental stress

The ABC curves were established in order to test levels of pollution within an estuarine environment (Warwick 1986). However, the relationship between abundance and biomass of individual invertebrates can be used to determine other potential environmental stress such as macroalgal mats. The ABC curves shown in Fig. 3.6 indicate that all three sites were showing either moderate (W≤ 0.00 - ≤ -0.05) or high (W>0.05) levels of stress, with the exception of Holes Bay in September 2014. Even this site, however, still only showed a low positive W measurement. These values suggest a higher proportion of fast growing r-species are present within the bays. These species are likely to be opportunists or pollution tolerant and able to take advantage of a fluctuating environment. Estuaries are by nature stressed environments (McLusky and Elliott 2004) so it could be argued that the ABC values are only indicating stress inherent within the system. However these models do not require baseline data as the curves are plotted using abundance and biomass data from fieldwork (Warwick and Clarke 1994). Analysis is bounded by the site limits and cannot be used to infer environmental stress in other areas. As it is widely agreed that using individual species as indicators of environmental stress is an unreliable method (Warwick 1986; Gray and Elliot 2010), ABC curves can provide a useful initial overview of the levels of stress within a system and whether further investigations are required.

The ABC curves showed that each area contained a greater abundance of smaller species or opportunists rather than slower-growing and larger fauna. Once the subsequent ANOSIM and SIMPER analyses were completed the results confirmed the output from the ABC curves. The top six most abundant species for each survey site comprised small worms, opportunistic gastropods, Chironomidae larvae and the highly adaptable *H. diversicolor;* all small r-selected species with the exception of *H. diversicolor.* However, although slower-growing, *H. diversicolor* is an adaptable feeder able to alter its feeding strategy in response to available food supply; *H. diversicolor* will switch from a carnivorous to a detritivorous or herbivorous diet (Barnes 1994).

### 3.5.3 The impact of algae, sediment organic content, and sediment type on benthic invertebrate community assemblage

The results revealed that each site contained a greater abundance of smaller r-selected species than K-selected thereby suggesting a stressed system (Warwick 1986; Gray and Elliot 2010). The second part of this chapter aimed to determine whether algae biomass, algae coverage, sediment organic content or sediment type were contributory factors to this stress.

The negative impact on species evenness from algal biomass recorded is possibly a consequence of the increased numbers of the opportunist species. An increase in richness in Holes Bay is consistent with results recorded during an earlier study at a nearby site described in Jones and Pinn (2006). Although this work found the increase in richness occurred during the peak algae growth period (June – August) and was followed, in November, by a decline. Other studies in locations away from Poole Harbour have found macroalgal mats have negatively impacted some biological indices. For example, in a study in two sub-estuaries of the Waquoit Bay, Massachusetts, Fox et al. (2009) recorded a significant decline in invertebrate species abundance in the eutrophicated area with macroalgal mat compared to the non-algae area. By contrast Everett (1994) found no relationship between invertebrate diversity, richness, or evenness between algae plots and cleared plots in an experimental design.

Based on results from Herbert et al. (2010), it had been expected that sediment type and organic content would be the main contributory environmental factors to the distribution of the invertebrate assemblage. However, given that the main species contributing to the variation in assemblage were all highly adaptable or opportunists, it was not surprising that sediment type was unimportant. The combination of algae biomass and organic content suggests that the organic matter within the sediment comprises decaying or fragments of green macroalgae. More detailed analysis of the organic matter within the sediment would be required to confirm this.

There is clearly a relationship between annelid worm assemblage and algae biomass with organic content. Whilst the negative effect of algae biomass on important polychaete species (*H. diversicolor, S. shrubsolii, A. marioni*) supports work carried out in other temperate estuaries (Bolam et al. 2000; Raffaelli et al. 2000), other studies recorded an increase in abundance of *H. diversicolor* under increased algal biomass (Cardoso et al. 2004). Indeed experimental work carried out in the Mondego Estuary, Portugal, recorded an initial increase in abundance of *H. diversicolor* followed a month later by a decline (Lopes et al. 2000).

Capitellid species were not recorded in large numbers in either Brands Bay or Holes Bay and were only the 5th most abundant species in Ower Bay. It had been expected that these pollution tolerant species would be highly abundant under the macroalgal mat as previous studies have recorded similar results (Raffaelli et al. 2000). An abundance of capitellids can be a reliable indicator of nutrient enrichment (Pearson and Rosenberg 1978) and have been regarded as a 'universal indicator of organic pollution (Gray and Elliott 2010). However, *Capitella* spp. are highly opportunistic; taking advantage of a sudden disturbance in the functioning ecosystem and increasing their reproduction rate in response (Gray and Elliot 2010). As the estuarine system responds to disturbance, *Capitella* spp. are rapidly outcompeted by other benthic invertebrates and return to their normal population levels. It is reasonable to suppose that the *Capitella* spp. population in Poole developed rapidly during the peak growth period of the algae (June – August) and then declined once the more stress tolerant species colonised the area. It is possible that the timing of the invertebrate surveys carried out in this research resulted in the early population growth of capitellids being missed. Given that one of the aims of this research was to determine prey availability for the overwintering bird population, mid-summer surveys would not have been appropriate.

However, it could equally be argued that the experimental manipulation of algal biomass carried out in previous studies might be regarded as a sudden 'acute' stress event and therefore encourage the rapid population growth of capitellids which is not repeated in the field. Given that the natural development of macroalgal mats takes place over a period of months, it could be interpreted as 'chronic' rather than 'acute' stress (Gray and Elliott 2010). As macroalgal mats have been a feature of many estuarine systems for decades it is possible that the continued long-term impact may have resulted in capitellids being outcompeted by other opportunist species.

There were fewer crustaceans recorded during this survey than previously within the harbour (Thomas et al. 2004; Herbert et al. 2010); no crustaceans were in the top six species recorded at any site. Nonetheless, the effect of algae biomass on crustacea is widely acknowledged. A decline in abundance of *C. volutator* under increased algal biomass was recorded in the Ythan Estuary (Raffaelli et al. 2000); a decline in abundance of *Cyathura carinata* [Krøyer 1847] was found under long-term macroalgal mat development in the Mondego Estuary (Ferreira et al 2004; Cardoso et al 2004). By contrast Bolam et al. (2000) reported an increase in abundance of *Gammarus* spp. after 6 weeks of a 20 week experimental manipulation of algae biomass on the Firth of Forth, Scotland. It is worth noting that this experiment was conducted on sandflats rather than intertidal mudflats although it was acknowledged that results were similar to those found in muddier sediment.

It was expected that abundance of the herbivore *P. ulvae* would increase in response to an increase in available resources obtained from the macroalgal mat biomass; previous studies have also reported an increase in *P. (Hydrobia) ulvae* (Soulsby et al. 1982; Cardoso et al. 2004). It is possible that the dense macroalgal mat is providing an ideal habitat for the gastropod with an abundant food supply and shelter from predators.

One notable feature of the estuarine community in Poole Harbour is the abundance of larval Chironomidae; particularly in Brands Bay and, to a lesser extent, in Ower Bay. Chironomidae response to an increase in algal biomass has not been reported in previous studies. However studies have shown that an increase in hydrogen sulphide ($H_2S$) can lead to an increase in chironomid larvae (Fletcher 1996) therefore it had been anticipated that chironomid larvae abundance would increase as macroalgal mat biomass increased. Indeed it is reported that the larvae utilise the tubular thallus of *U. intestinalis* both for shelter and as a food source (McAllen 1999). It was expected that chironomid abundance would be higher in December due to the reported seasonal fluctuation of this species (Como and Magni 2009). However, although there were a greater number of insect larvae recorded in December 2013, there was no significant variation in abundance or biomass of insects between September 2013, December 2013 or September 2014. Given that, with two individual exceptions, the abundance of insects comprised entirely of chironomids, seasonal variation does not account for the fluctuation in abundance.

The negative correlation between *Tubificoides* spp. and % organic content is noteworthy as oligochaetes will consume organic matter within the sediment and facilitate bacterial decomposition of organic matter by breaking down larger particles

(Giere 2006). It is possible that the quantity or size of the organic matter fragments were too large to be effectively broken down (Giere 2006).

### 3.5.4 The impact of algae biomass on overall invertebrate abundance; a threshold for macroalgal mat biomass in Poole Harbour

A certain amount of algae (as primary production) is essential to stimulate growth and consumption within an estuarine system (Raffaelli et al. 1999; Fox et al. 2009). What remains unclear is at what point the algal biomass becomes too great, leading to a detrimental impact upon benthic invertebrate abundance (Rees-Jones 2004). Despite almost all being opportunists, the ‘top six’ species recorded in Poole Harbour responded very differently to increases in algal biomass. Given the complexity of the relationship between just six species, it was not surprising to find the response of the overall population of invertebrates was variable. Fig. 3.8 shows an initial increase in invertebrate abundance up to an algal biomass of ~800 g (ww) $m^{-2}$ thereby supporting the suggestion that an algal biomass >1000 g (ww) $m^{-2}$ could be regarded as the ‘tipping point’ beyond which invertebrates in the Poole Harbour estuarine system may be detrimentally impacted. These data also support previous studies where a detrimental impact upon invertebrate species was recorded when algae biomass was >1000 g (ww) $m^{-2}$ (Hull 1987; Raffaelli et al. 1998).

However, it is acknowledged that there were fewer invertebrate samples taken under macroalgal mat biomass >2000 g (ww) $m^{-2}$, as reflected in the wider confidence intervals shown in Fig. 3.8. Therefore it is recommended that further research be undertaken, particularly during the peak growth period of the algae (June – August), in order to determine whether 1000 g (ww) $m^{-2}$ is an appropriate ‘tipping point’.

### 3.5.5 Conclusion

There is no doubt that interactions between algae and benthic macro-invertebrates are complex. What remains clear is that there are no predictable general effects and each system has a unique set of environmental and algae variables contributing to assemblage characterisation and species diversity. In addition there appears to be some scope for further research using a combined experimental and survey approach to determine the impact on invertebrates from macroalgal mats.

BLANK

# 4.0 The effect of macroalgal mats on wading bird prey: implications for individual bird species

## Abstract

It is estimated that UK estuaries support 1.5 million overwintering wading birds making these areas a priority habitat for conservation in Europe. In temperate coastal areas, wading birds begin to arrive in September to take advantage of the rich supply of invertebrates available within the estuarine sediment. Macroalgal mat coverage in Poole remained extensive during September – November and algal biomass >1 kg $m^{-2}$ was recorded in benthic core samples from September 2013 and September 2014.

This chapter examines how the macroalgal mats affect the preferred benthic invertebrate prey of migratory wading birds in Poole Harbour. Five species of wading bird; Eurasian curlew (*Numenius arquata*); black-tailed godwit (*Limosa limosa*); oystercatcher (*Haematopus ostralegus*); redshank (*Tringa totanus*) and dunlin (*Calidris alpina*) were selected for study. Not all prey items are available to all birds nor will all prey items provide sufficient energy for different wading bird species. Each wading bird species was allocated a 'benthic invertebrate menu' (BIM) based upon energy values contained within the preferred prey species/sizes available at each study site (Holes Bay, Brands Bay, Ower Bay).

Results showed the highest energy available for each wading bird species was in Holes Bay. There was also an initial increase in each species' BIM under lower macroalgal mat biomass (<~800 g (ww) $m^{-2}$) in Holes Bay and Ower Bay followed by a decline in BIM at higher macroalgal mat biomass; a pattern not as apparent in Brands Bay. A reduction in available energy within each bird's preferred prey could have implications for the overwintering wading bird's ability to maintain sufficient energy to ensure winter survival.

BLANK

## 4.1 Introduction

It is estimated that UK estuaries support 1.5 million overwintering wading birds (RSPB accessed 03/2016) making these areas a priority habitat for conservation in Europe (Durell et al. 2006). Large populations of wading birds (comprising Charadriidae, Recurvirostridae, Scolopacidae, Haematopodidae) are supported by the rich invertebrate prey resources provided by temperate intertidal mudflats; an essential overwintering habitat for the birds (Stillman et al. 2010). The British Trust for Ornithology (BTO) reported that, following long-term declines, ringed plover (*Charadrius hiaticula* [Linnaeus, 1758]), oystercatcher (*Haematopus ostralegus* [Linnaeus, 1758]) and dunlin (*Calidris alpina* [Linnaeus, 1758]) all recorded a small increase, redshank (*Tringa totanus* [Linnaeus, 1758]) numbers may be stabilising, and populations of black-tailed godwit (*Limosa limosa* [Linnaeus, 1758]) remained high (Frost et al. 2016). Numbers of other species (including turnstone (*Arenaria interpres* [Linnaeus, 1758]), grey plover (*Pluvialis squatarola* [Linnaeus, 1758]) and curlew (*Numenius arquata* [Linnaeus, 1758]) declined resulting in curlew being included on the Birds of Conservation Concern 4 Red List (Eaton et al. 2015). The trend appears to be a decline in the overall population of wading birds in the UK from 1974 – 2013 as shown in Fig. 4.1 (Holt et al. 2015).

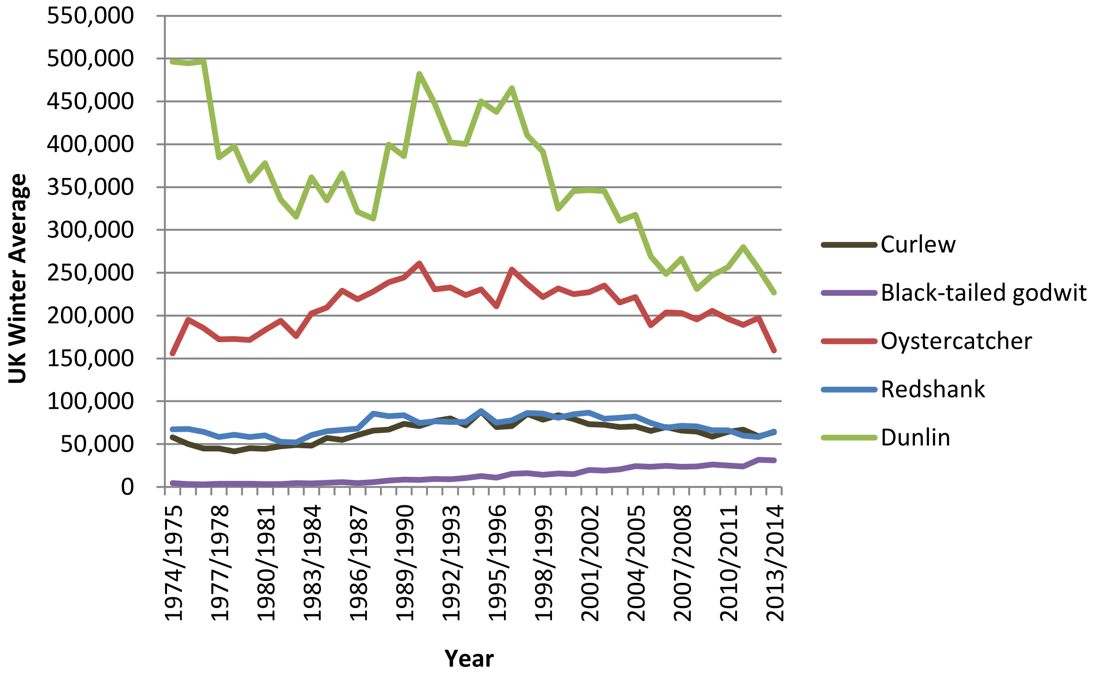


**Fig. 4.1:** UK winter average 1974 – 2013 for 5 key species of wading bird: Curlew (*Numenius arquata*), black-tailed godwit (*Limosa limosa*), oystercatcher (*Haematopus ostralegus*), redshank (*Tringa totanus*), and dunlin (*Calidris alpina*). Data from British Trust for Ornithology (BTO) Wetland Bird Survey (WeBS) Report 2013/2014 (Holt et al. 2015).

In temperate coastal areas, wading birds begin to arrive in September from their breeding grounds further north to take advantage of warmer conditions and the rich supply of invertebrates available within the sediment (Ferns 1992). Each individual bird's behaviour is governed by a need to maximise its chances of survival and maintain sufficient energy stores to be fit enough to return to breed the following spring (Prater 1981). Wading birds are one of the top predators within an estuarine food-web and their survival largely depends upon the availability during winter of sufficient prey within the mudflats (Raffaelli and Milne 1987). Overall numerical abundance of invertebrates within a system is, therefore, an important factor when assessing the quality and diversity of the intertidal mudflats (West et al. 2005). However, abundance alone cannot provide an indicator of suitable resources for wading birds; prey quality (measured as size), and the energy contained within the prey, is key to the success of the overwintering bird population (West et al. 2007).

Larger wading birds have a greater daily energy requirement (DER) due to their size and will therefore consume larger size prey to obtain that energy (Goss-Custard et al. 1977; Zwarts and Wanink 1993). Each bird will select prey based upon ensuring maximum energy intake with minimum energy cost (Goss-Custard 1977; Durell 2000); energy cost in obtaining prey includes time spent locating and handling the prey item (Zwarts and Wanink 1993). An item which is too small will result in a greater energy cost than the prey contains; too large and the bird is unable to consume the item (Goss-Custard et al. 1977; Durell 2000; Gill et al. 2001a). As a result, each wading bird species has a preferred diet comprising an optimum range of size classes of prey which will return maximum energy for minimum effort (Zwarts and Wanink 1993; Santos et al. 2005).

There are two important reasons why temperate intertidal mudflats are able to support such large and diverse populations of overwintering wading birds. Firstly, as discussed in Chapter 3, the sediment supports an abundance and diversity of invertebrates thereby providing sufficient resources (in conjunction with terrestrial habitats) for overwintering wading birds. Secondly an assemblage comprising a variety of wading bird species can be supported due to variations in birds' body size, bill length/shape, and intestinal morphology resulting in birds requiring different sizes and species of invertebrate prey (Alves et al. 2010).

The Eurasian curlew, (*N. arquata*), Europe's largest wading bird, has an average bill length of 12 cm (male) and 14 cm (female) enabling the species to access prey items located at depths of up to 15 cm (Evans et al. 1976; van de Kam et al. 2004). Larger size classes of invertebrate prey such as annelid worms, burrow deeper into the sediment with some species (e.g. *Hediste diversicolor* [O. F. Müller 1776] and *Nephtys hombergii* [Savigny in Lamarck 1818]) recorded at sediment depths of 30 cm (Zwarts and Wanink 1993). In addition it has been shown that the curlew's curved bill enables the bird to successfully access prey from deep in the sediment (Ferns and Siman 1994), with a greater proportion of prey remaining intact (Davidson et al. 1986). Black-tailed godwits will take prey from depths around 10 cm and the smaller birds, (e.g. redshank and dunlin) will take smaller prey items from the top 3-4 cm of mud (Dierschke et al. 1999). Although oystercatcher's bill length is between 6.5 cm – 9 cm and they can probe up to 10 cm into the sediment, this rarely occurs; oystercatchers tend to probe to depths of ~4 cm (Zwarts 1996). This niche separation enables large and diverse populations of wading birds to feed on the same area of intertidal soft-sediment habitat with each species selecting prey according to size and availability (Sutherland et al. 2005).

### 4.1.1 Impact of macroalgal mats on wading bird benthic invertebrate prey

Macroalgal mats have been shown to alter the sediment chemistry resulting in invertebrate species having to adapt to increasingly anoxic or hypoxic conditions (Lyons et al. 2014). It is possible that, as a consequence, invertebrates are adapting to the conditions either by moving within the sediment column or extending siphons upwards to feed in oxygenated sediment closer to the surface (Thiel et al. 1998; Raffaelli 1999; Österling and Pihl 2001). This behavioural change could increase inter-specific competition between wading birds as larger prey sizes (previously only accessible to the larger birds) become available to smaller wading birds at shallower sediment depths. In addition, as discussed in Chapter 3 (Section 3.5.7), there is a greater abundance of lower-quality smaller invertebrate species under increasing macroalgal mat biomass. This could lead to a reduction in energy provision from invertebrates with implications for all wading bird species but in particular the larger birds which require greater energy intake (Zwarts and Wanink 1993).

The effect of macroalgal mats on overwintering birds' prey resources has been the focus of a number of studies. Research carried out in the Ythan Estuary, Scotland, recorded a decline in the abundance of *Corophium volutator* [Pallas, 1766] under increased macroalgal mat biomass (Raffaelli et al. 1991); *C. volutator* is an important prey item for wading birds (particularly redshank) on that site (Goss-Custard 1970). A similar decline in the abundance of important bivalve species, such as *Scrobicularia* *plana* [da Costa, 1778], was recorded under increasing macroalgal mat biomass in the Mondego Estuary, Portugal (Cardoso et al. 2004). Bivalves of family scrobicularidae form a significant part of the diet of black-tailed godwits on the Tagus Estuary, Portugal (Moreira 1994). These studies experimentally manipulated levels of algal biomass and presented analysis of the change in abundance of individual invertebrate species under varying measured algae densities.

### 4.1.2 Wading bird diet

Studies examining the diet of overwintering wading birds have been produced since the 1960s although wading bird diets can be difficult to determine as the digestive process can result in soft-bodied prey items being under-recorded in analysis of pellets or droppings (Goss-Custard and Jones 1976; Sutherland et al. 2005). A comprehensive review of research into wading bird diet composition was carried out by Goss-Custard et al. (2006b) resulting in a list of preferred prey taxa and sizes for nine wading bird species. Full details of the methodology and studies used are presented in Goss-Custard et al. (2006b) and Durell et al. (2006). Wolff (1969) suggested that wading bird distribution was determined by prey distribution. However, as shown in Goss-Custard et al. (2006b) wading birds have preferred prey comprising a variety of taxa in sizes which will deliver the required amount of energy.

### 4.1.3 Rationale

Not all prey items are available to all birds (Sutherland et al. 2005) nor will all prey items provide sufficient energy for different wading bird species. Therefore examining overall abundance or biomass of invertebrates could result in an overestimation of the availability of suitable prey items for birds. This could also lead to an underestimation of the impact from macroalgal mats on the overwintering wading birds (for example from an increase in smaller, less energy-dense prey). In addition, the invertebrate community varies between estuaries; the Ythan Estuary, for example, supports a very high abundance of *C. volutator* (Raffaelli et al. 1991). By contrast, the invertebrate community recorded in Poole Harbour in recent years found fewer crustaceans but a greater abundance of annelid worms (Thomas et al. 2004; Herbert et al. 2010). Therefore, although it is important to ascertain the impact of macroalgal mats on single invertebrate prey species, this must be within the context of the preferred prey according to each wading bird's diet; and the availability of a diversity of invertebrates at a chosen site.

This chapter will build upon the findings discussed in Chapter 3 by examining the invertebrate prey community from the birds' perspective. Using existing data on preferred prey species and prey size for different wading birds (Goss-Custard et al. 2006b) each species will be allocated a 'benthic invertebrate menu' (BIM) based upon energy values contained within the preferred prey species/sizes. The study will assess the impact of macroalgal mats on the overall energy available (determined as a function of size of invertebrate) from all the preferred prey constituting the BIM of different wading bird species. The BIM is based on the principle that a wading bird will search for prey items of a certain size that will deliver sufficient energy (Zwarts and Wanink 1993). Given that overwintering wading birds generally return to the same region each year populations adapt to certain location-specific conditions; in particular the resources available at each site (Martins et al. 2013). Examining the impact of macroalgal mats on individual wading bird's BIM will enable a more accurate assessment of the effect of these mats on the energy resources vital for each bird's survival.

## 4.2 Aims and objectives

**Aim 1:** Determine the availability of different size classes of invertebrate species within Poole Harbour.

**Aim 2:** Establish the preferred prey sizes and taxa available for each studied wading bird species.

**Aim 3:** Provide each wading bird species with a species-specific benthic invertebrate menu (BIM).

**Aim 4:** Assess the impact from macroalgal mats on wading bird's BIM.

**Objective 1:** Measure the sizes of invertebrates collected during sampling at three different sites and on three different dates in Poole Harbour.

**Objective 2:** Allocate each wading bird species a diet comprising the preferred prey sizes (as determined by Goss-Custard et al. 2006b) recorded in samples from Poole Harbour.

**Objective 3:** Using field samples, measure the energy content of each wading bird species preferred prey. Allocate a specific benthic invertebrate menu to each wading bird species based upon energy contained within the preferred prey sizes and within samples collected.

**Objective 4:** Measure the impact on BIM under varying levels of macroalgal mat biomass. Assess whether there is a 'tipping point' above which there is a significant detrimental effect on wading bird BIM.

## 4.3 Methods

### 4.3.1 Selection of wading bird species

Five species of wading bird; Eurasian curlew (*Numenius arquata* [Linnaeus 1758]); black-tailed godwit (*Limosa limosa* [Linnaeus 1758]); oystercatcher (*Haematopus ostralegus* [Linnaeus 1758]); redshank (*Tringa totanus* [Linnaeus 1758]); and dunlin (*Calidris alpina* [Linnaeus 1758]), were selected for study. These species were chosen as important representatives of the overall assemblage of >20,000 overwintering birds for which Poole Harbour is a designated Special Protection Area (SPA). Individual species are also of conservation importance as the harbour is designated for internationally important populations of black-tailed godwits (Frost et al. 2016). A decline in the population of all five wading bird species has been reported over the last 10 years (Frost et al. 2016) with the decline in curlew population resulting in its inclusion on the UK Red List of Birds of Conservation Concern (Eaton et al. 2015). According to the most recent Wetland Bird Survey (WeBS), all five selected bird species were recorded at each of the study sites (Brands Bay, Holes Bay and Ower Bay) (Frost et al. 2016).

### 4.3.2 Wading bird species' preferred prey

Table 4.1 provides information on the preferred size classes of invertebrate prey for each of the five wading bird species studied (Goss-Custard et al. 2006b).

**Table 4.1:** Size range for preferred invertebrate prey within the diet of each studied wading bird species (adapted from Goss-Custard et al. 2006b).

| **Prey** | **Curlew** | **Black-tailed godwit** | **Oystercatcher** | **Redshank** | **Dunlin** |
|---|---|---|---|---|---|
| Annelid worm | ≥50 mm | ≥25 mm | ≥50 mm | 15 mm – 80 mm | 10 mm – 60 mm |
| Bivalve (excl. *Cerastoderma edule*) | ≥5 mm | 5 mm – 20 mm | ≥10 mm | 5 mm – 15 mm | <5 mm – 10 mm |
| *C. edule* | 5 mm – 20 mm | No | ≥15 mm | No | No |
| Crustacean (incl. *Carcinus maenas*) | ≥10 mm | ≥3 mm | ≥10 mm | ≥3 mm | ≥3 mm |
| Hydrobidae | No | No | No | <5 mm | <5 mm |

### 4.3.3 Calculating the energy value within invertebrate prey items

Invertebrate prey samples were collected and processed using the methodology described in Chapter 3, Section 3.3.3. Lengths of invertebrate species were measured using the methodology described in Chapter Section 3.3.4. Invertebrates were allocated a size class as shown in Table 4.2.

**Table 4.2:** Size classes of benthic invertebrates. The 'small worms' category includes polychaetes, *Tubificoides* spp. and Chironomidae larvae.

| **Invertebrate category** | **Size range** |
|---|---|
| Small worms | <5 mm |
| Annelid worms | 5 mm - >105 mm<br>In 5 mm bands |
| Crustaceans (including *Carcinus maenas*) | <3 mm, 3-<10 mm, then in 5 mm bands to >40 mm |
| Bivalves (excl. *Cerastoderma edule*) | <5 mm – 55 mm in 5 mm bands |
| *C. edule* | <5 mm – 55 mm in 5 mm bands |
| Molluscs (excl. bivalve and Hydrobidae | <5 mm – 55 mm in 5 mm bands |
| Hydrobidae | <5 mm ≥5 mm |

Numerical abundance (individuals m$^{-2}$) recorded within each size class shown in Table 4.2 was converted into ash-free dry mass (AFDM mg m$^{-2}$) according to species-specific equations provided in Appendix 3 (Thomas et al. 2004; Herbert et al. 2010). Values for length within the equation were calculated using the median value for each size class (e.g. AFDM calculated for annelid worm size class 70- <75 mm was based upon a worm length of 72.5 mm). The AFDM values for the largest size categories (e.g. Annelid worm >105 mm) were calculated by adding 2.5 mm to the maximum length value (e.g. AFDM for annelid worm >105 mm was calculated using length of 107.5 mm). Zwarts and Wanink (1993) proposed an energy conversion value of 21-23 kJ for each gram of AFDM. A conversion value of 22 kJ was used for this study whereby

$$Energy\ (kJ) = AFDM\ g * 22$$

### 4.3.4 Defining the wading birds' benthic invertebrate menu (BIM)

The energy values were calculated for the preferred prey size per taxa for each of the studied wading bird species. Energy values per taxa were combined to produce a benthic invertebrate menu (BIM) for each species of wading bird. Each bird's BIM will vary according to prey availability at different sites and/or different dates. For example the curlew BIM in Holes Bay would be calculated as:

$$BIM = \Sigma(a_1 \dots a_n), (b_1 \dots b_n), (c_1 \dots c_n), (n_1 \dots n_n)$$

Where $a_1$ = energy (kJ) value of the smallest size and $a_n$ = energy (kJ) value of the largest size class of annelid worm, $b_1$ = energy (kJ) value of the smallest size and $b_n$ = energy (kJ) value of the largest size class of bivalve, $c_1$ =energy (kJ) value of the smallest size and $c_n$= energy (kJ) value of the largest size class of *C. edule*, $n_1$ = energy (kJ) value of the smallest size and $n_n$= energy (kJ) value of the largest size class of $n^{th}$ taxa within curlew preferred prey recorded in Holes Bay.

### 4.3.5 Analysis

#### *4.3.5.1 Between-site and between-date variation in BIM*

Variation in mean energy between sites and stations were analysed using analysis of variance (ANOVA) with pairwise Tukey post-hoc tests in R Version 3.3.0 "Supposedly Educational" (R Core Team 2016). Assumptions of normality and homogeneity of variance were checked using Shapiro Wilks test within the "stats" package in R Version 3.3.0 "Supposedly Educational" (R Core Team 2016) and Levene test within the "car" package developed for R (Fox and Weisberg 2011) respectively.

#### *4.3.5.2 Determining a 'tipping point' for macroalgal mat biomass impact on wading bird BIM*

Mean energy (kJ m$^{-2}$) of invertebrate prey for each wading bird species BIM were plotted against algae biomass; each showed a non-monotonic relationship. A generalised additive model (GAM) was plotted with a loess smoothing curve applied using "ggplot2" developed for R (Wickham 2009).

## 4.4 Results

### 4.4.1 Spatial and temporal variation in invertebrate size-class distribution

Fig. 4.2a-c shows variation in abundance m$^{-2}$ for size-classes of important prey items for overwintering birds. Sizes of annelid worms <5 mm include oligochaetes and

Chironomidae larvae as these were classified as ‘small worms’ due to their low energy value.

The annelid worm populations in both Holes Bay and Ower Bay show a range of sizes with polychaete worms recorded in all size-classes, although fewer recorded in Ower Bay than Holes Bay. Fewer larger worms (>35 mm) were recorded in Brands Bay with none recorded in categories 75-105 mm.  Larger bivalves and *Cerastoderma edule* [Linnaeus 1758] were recorded at all sites.  There were fewer crustaceans >10 mm recorded with only two individuals >20 mm recorded at Brands Bay and Holes Bay and none of that size-class recorded in Ower Bay.

# Brands Bay

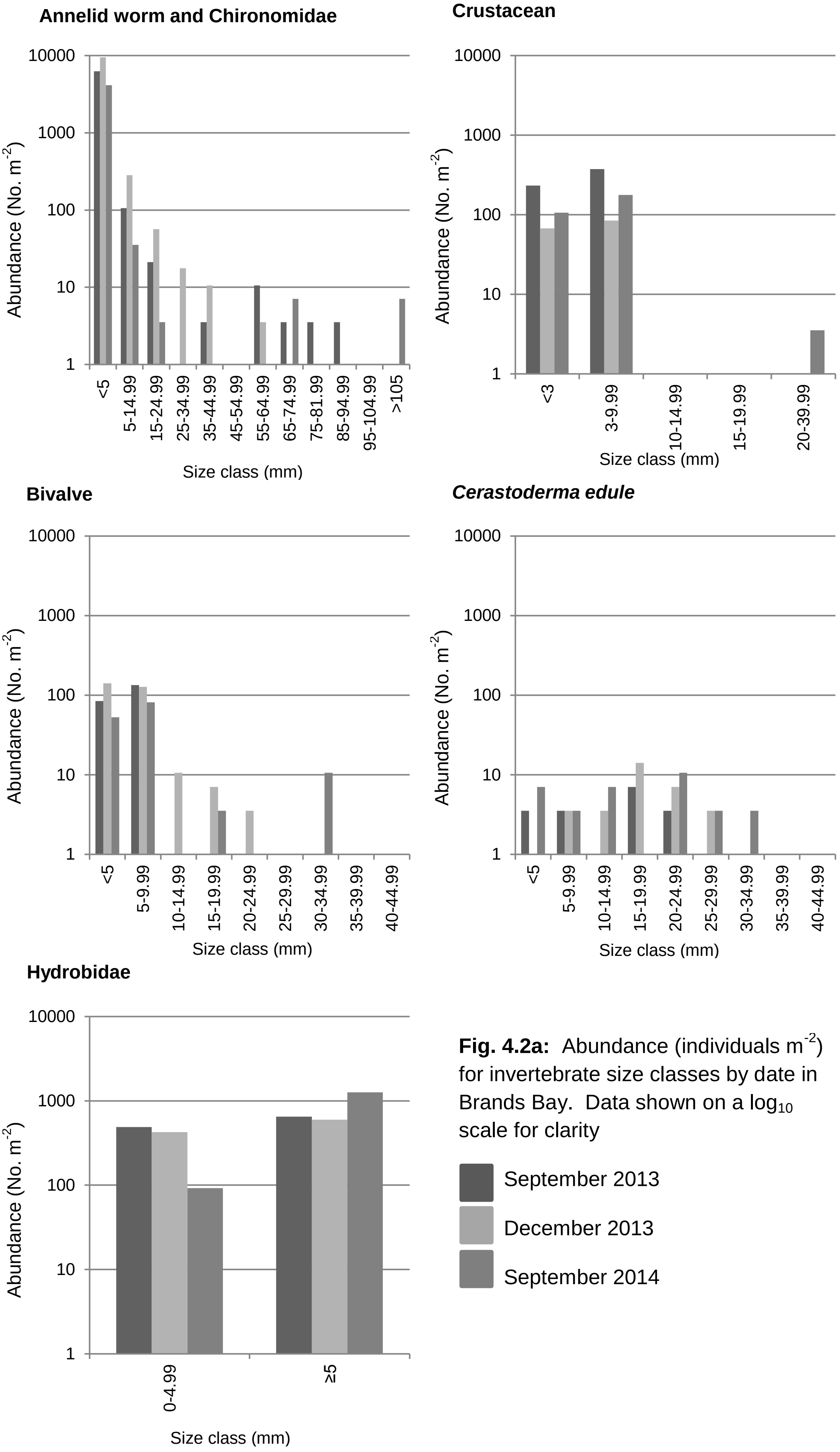
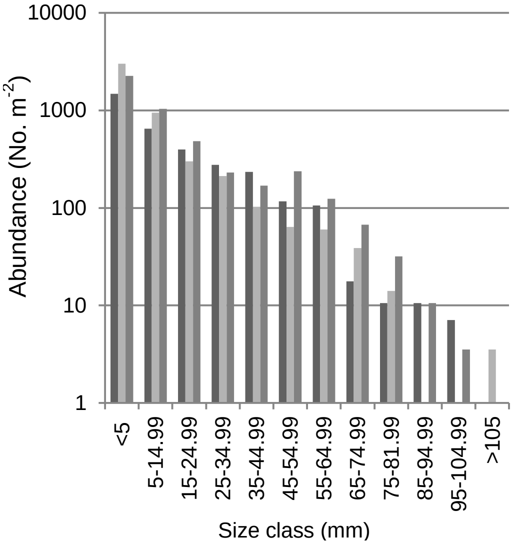


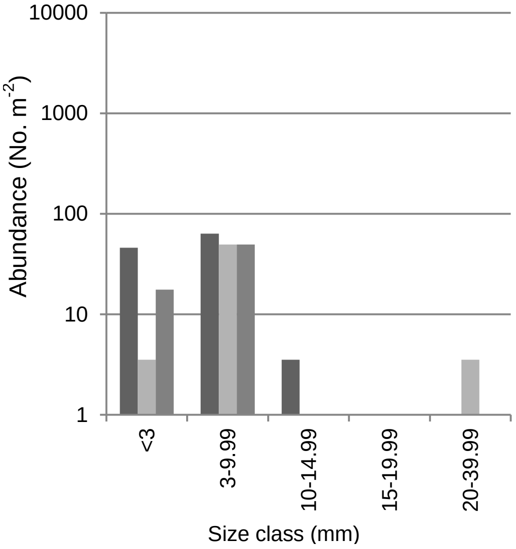
**Fig. 4.2a:** Abundance (individuals $m^{-2}$) for invertebrate size classes by date in Brands Bay. Data shown on a $\log_{10}$ scale for clarity

# Holes Bay

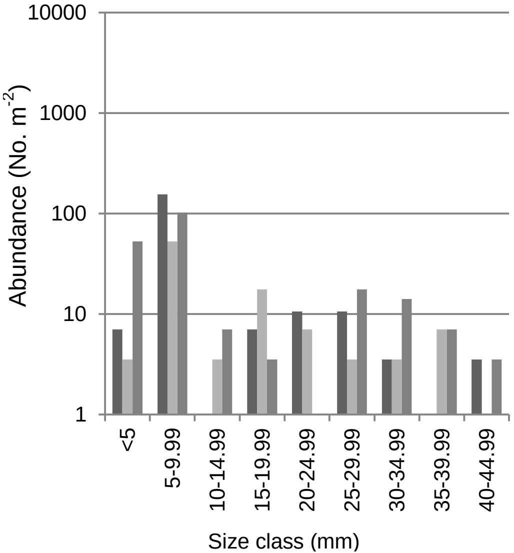
**Annelid worm and Chironomidae**



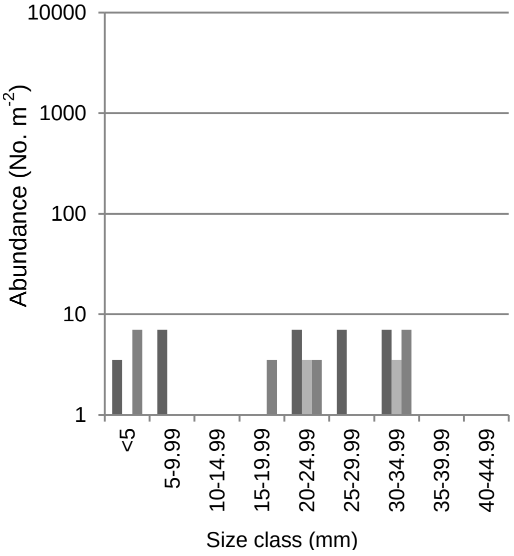
**Crustacean**



**Bivalve**



***Cerastoderma edule***



**Hydrobidae**

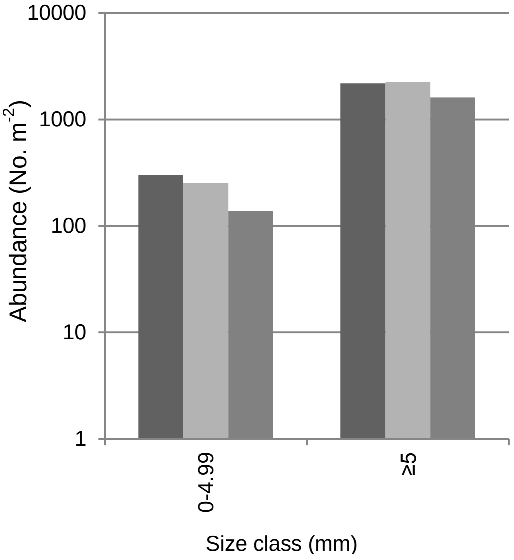


**Fig. 4.2b:** Abundance (individuals m$^{-2}$) for invertebrate size classes by date in Holes Bay. Data shown on a $\log_{10}$ scale for clarity

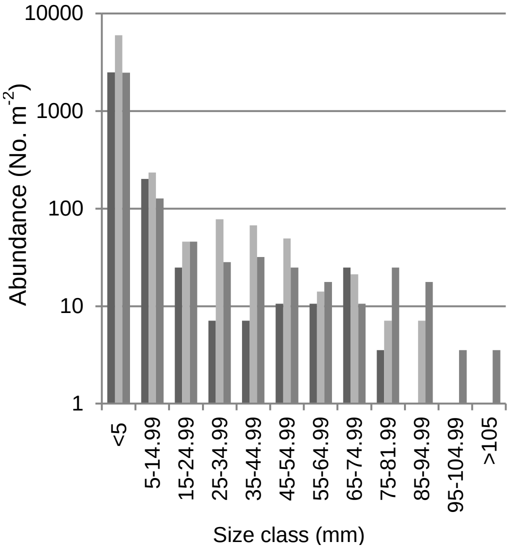
▇ September 2013

▒ December 2013

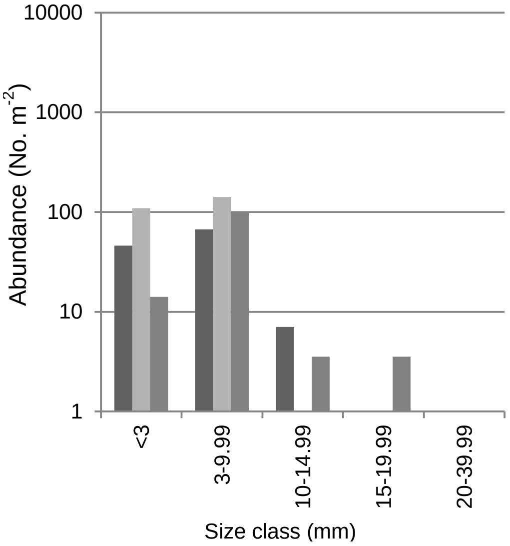
▓ September 2014

# Ower Bay

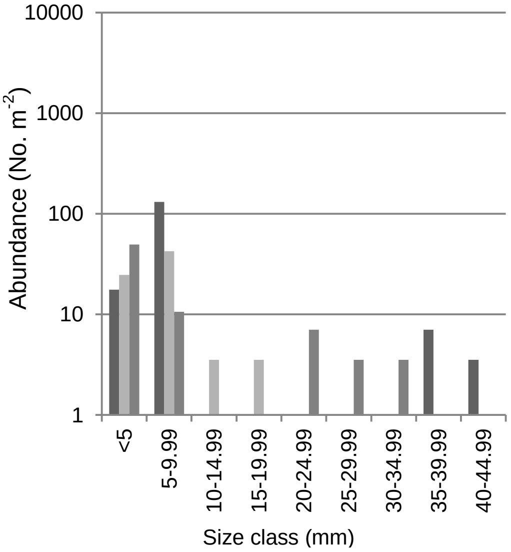
**Annelid worm and Chironomidae**



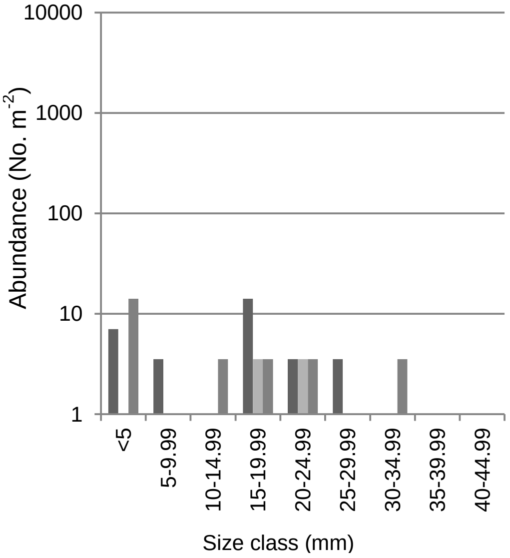
**Crustacean**



**Bivalve**



***Cerastoderma edule***



**Hydrobidae**

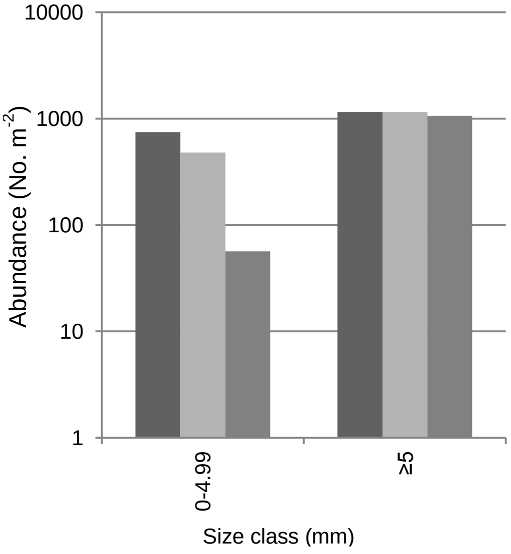


**Fig. 4.2c:** Abundance (individuals $m^{-2}$) for invertebrate size classes by date in Ower Bay. Shown on a $\log_{10}$ scale for clarity

■ September 2013

■ December 2013

■ September 2014

### 4.4.2 Between-site and between-date distribution of energy by taxa

Fig. 4.3 shows the energy distribution and diversity of the preferred prey for each of the five studied wading bird species across all three sites. Energy (kJ $m^{-2}$) is shown for recorded taxa within each bird species' preferred prey: annelid worms, bivalves (excluding *C. edule*), *C. edule,* crustaceans and Hydrobidae.

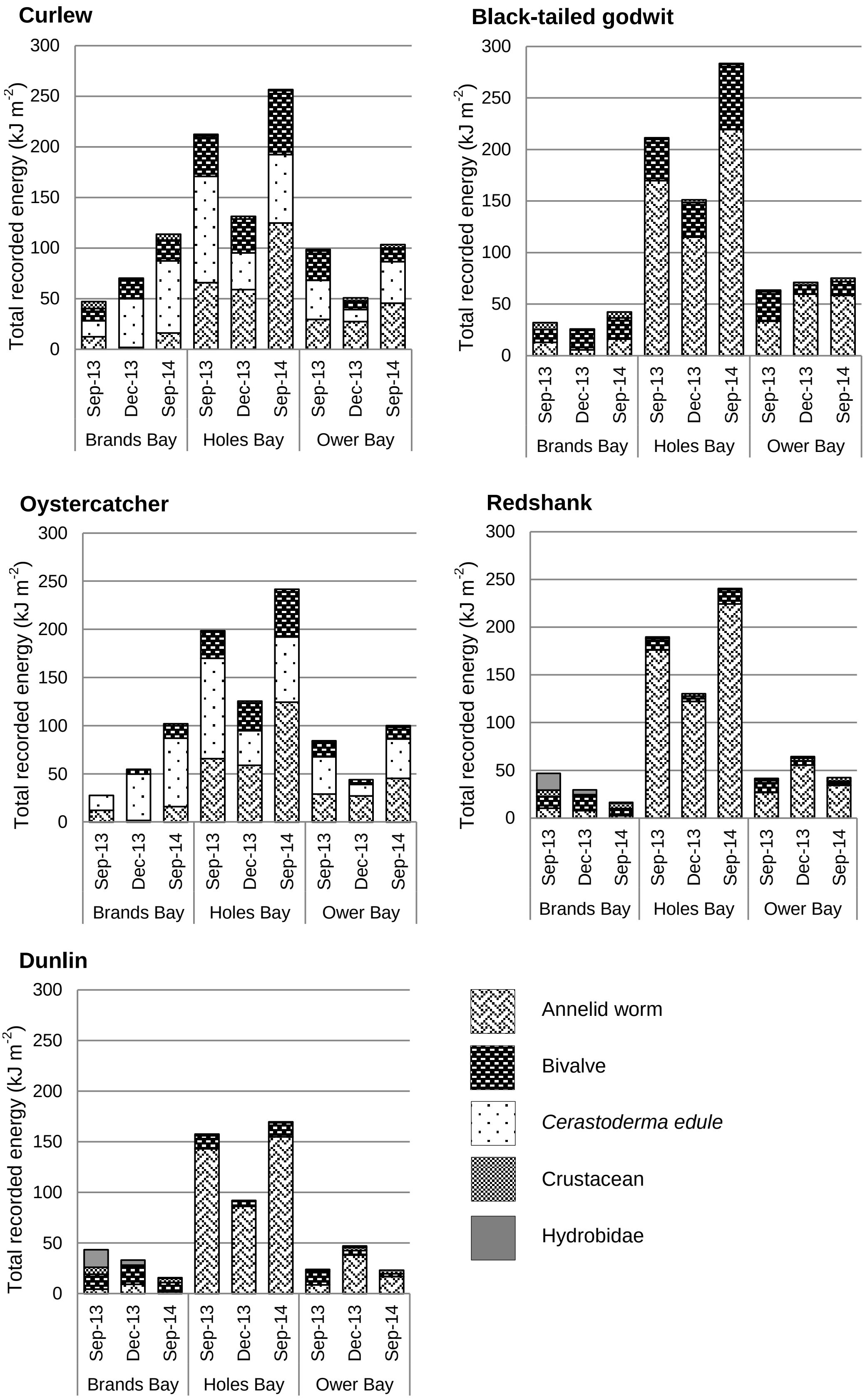


**Fig. 4.3:** Total energy (kJ m$^{-2}$) recorded in core samples for each wading bird species' BIM by taxa. Samples taken in September 2013, December 2013, September 2014.

Within Poole Harbour black-tailed godwit, redshank and dunlin BIM comprises mainly annelid worms. Both curlew and oystercatcher BIM is composed of almost equal amounts of annelid worms and *C. edule*. A greater abundance of *C. edule* was recorded in Brands Bay whereas Holes Bay recorded a greater abundance of annelid worms within the birds' BIM size categories.

### 4.4.3 Spatial variation in wading bird species' BIM

Figure 4.4 provides details of spatial distribution of mean energy (kJ m$^{-2}$) for each bird species' BIM. Holes Bay provides the highest mean energy for each of the wading bird species.

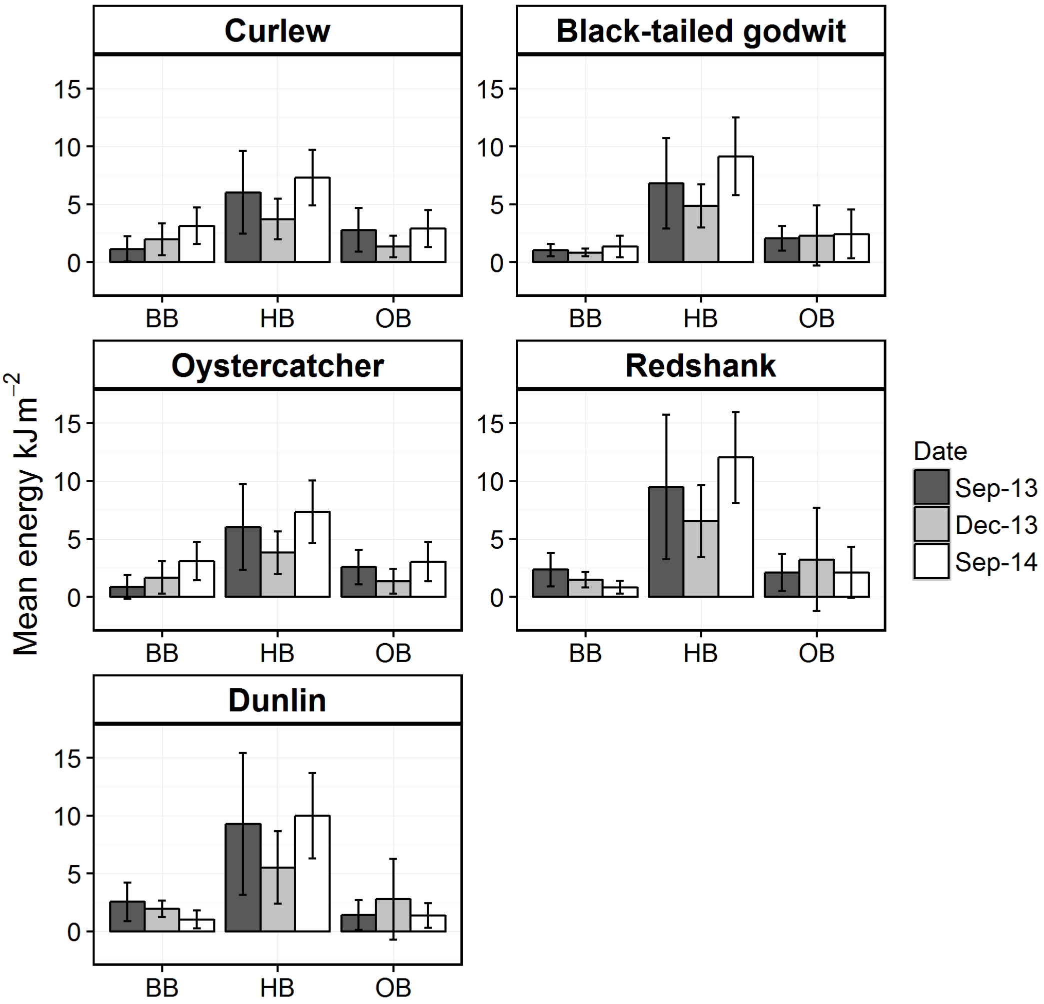


**Fig. 4.4:** Mean energy (kJ m$^{-2}$) available by site for individual wading bird species. Values taken from combined core samples for September 2013, December 2013 and September 2014. Error bars 95% confidence intervals. BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

### 4.4.4 Between-site variation in wading bird BIM

Table 4.3 provides details of the results of ANOVA between sites for each wading bird species' BIM. Energy available for all species' BIMs was greater in Holes Bay than either Brands Bay or Ower Bay suggesting that this site provides a potentially more profitable feeding area than the two southern sites. There was no significant variation between Brands Bay and Ower Bay for the BIM for any wading bird.

**Table 4.3:** ANOVA between sites for energy (kJ $m^{-2}$) available for each wading bird species' BIM with pairwise Tukey post-hoc test for significant ($p = <0.05$) sites.
BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.
Significance codes: *** <0.001, ** <0.01, * <0.05

| Wader Species BIM | F | Df | Sig. | Tukey post-hoc |
|---|---|---|---|---|
| Curlew | 10.76 | 2,51 | p = <0.001 *** | HB>BB p = <0.001 ***<br>HB>OB p = 0.002 ** |
| Black-tailed godwit | 29.74 | 2,51 | p = <0.001 *** | HB>BB p = <0.001 ***<br>HB>OB p = <0.001 *** |
| Oystercatcher | 11.99 | 2,51 | p = <0.001 *** | HB>BB p = <0.001 ***<br>HB>OB p = <0.001 *** |
| Redshank | 25.86 | 2,51 | p = <0.001 *** | HB>BB p = <0.001 ***<br>HB>OB p = <0.001 *** |
| Dunlin | 21.72 | 2,51 | p = <0.001 *** | HB>BB p = <0.001 ***<br>HB>OB p = <0.001 *** |

### 4.4.5 Between-date variation in wading bird species' BIM

*4.5.5.1 Variation between dates*

There was no statistically significant ($p = <0.05$) difference in energy (kJ $m^{-2}$) availability for any wading bird BIM between dates (irrespective of site). Curlew (p = 0.087); black-tailed godwit (p = 0.42); oystercatcher (p = 0.068); redshank (p = 0.832); or dunlin (p = 0.816).

### 4.4.6 The impact of algae biomass on wading bird BIM

Figure 4.5 provides results from the non-linear GAM output for mean energy available for each individual bird's BIM (kJ $m^{-2}$) against algae biomass (g (ww) $m^{-2}$). It is apparent that there is an initial increase in energy availability under low algae biomass followed by a decline when algae biomass reaches ~800 g (ww) $m^{-2}$. Wider 95% confidence intervals reflect fewer samples where algae biomass >2000 g (ww) $m^{-2}$. The individual site plots shown in Fig. 4.6 indicate that this initial increase in wading bird BIM at algae biomass <800 g (ww) $m^{-2}$, is replicated in Holes Bay and Ower Bay. There appears to be a more obvious decline for all wading bird species BIM at algae biomass >1000 g (ww) $m^{-2}$ in Ower Bay although this levels out at much higher algae biomass. This is due to fewer samples containing invertebrate species in the larger size classes required for wading bird BIM under higher algae biomass. In Brands Bay there was an initial increase in black-tailed godwit, redshank, and dunlin BIM under lower algae biomass yet a decline in curlew and oystercatcher BIM at the same algae biomass levels. Once again, fewer samples containing larger prey sizes were recorded in Brands Bay at higher algae biomass. It was not possible to extrapolate beyond the data in Holes Bay to suggest whether a decline in energy would be apparent at higher algal biomass. However, Holes Bay is the site which contains the highest BIM for all studied wading bird species.

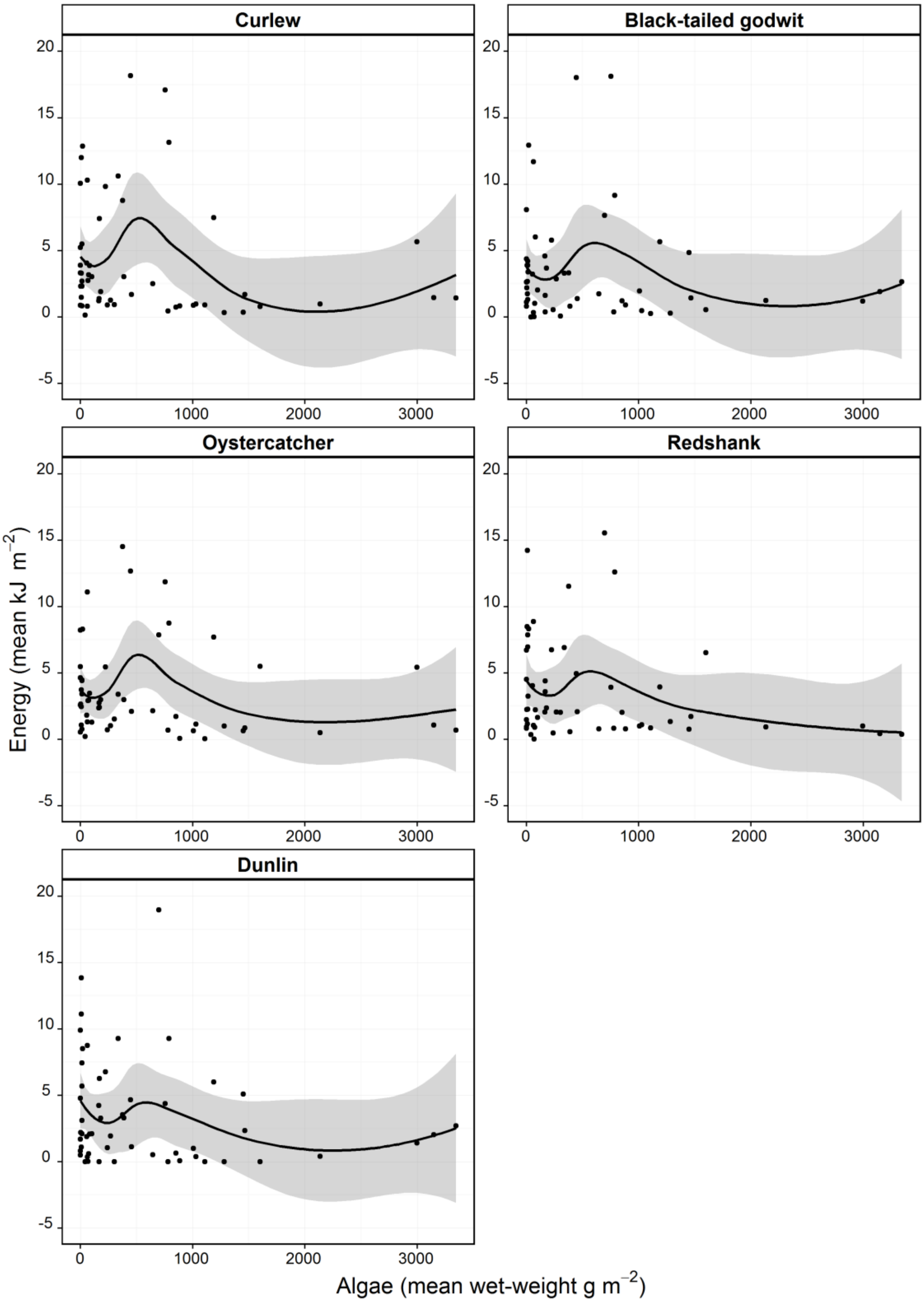


**Fig. 4.5:** GAM chart with loess smoothing curve showing the relationship between mean energy available within each bird species' BIM (kJ m$^{-2}$) and algae biomass (mean wet weight g m$^{-2}$) for all values recorded irrespective of site and date. Shaded areas are 95% confidence intervals.

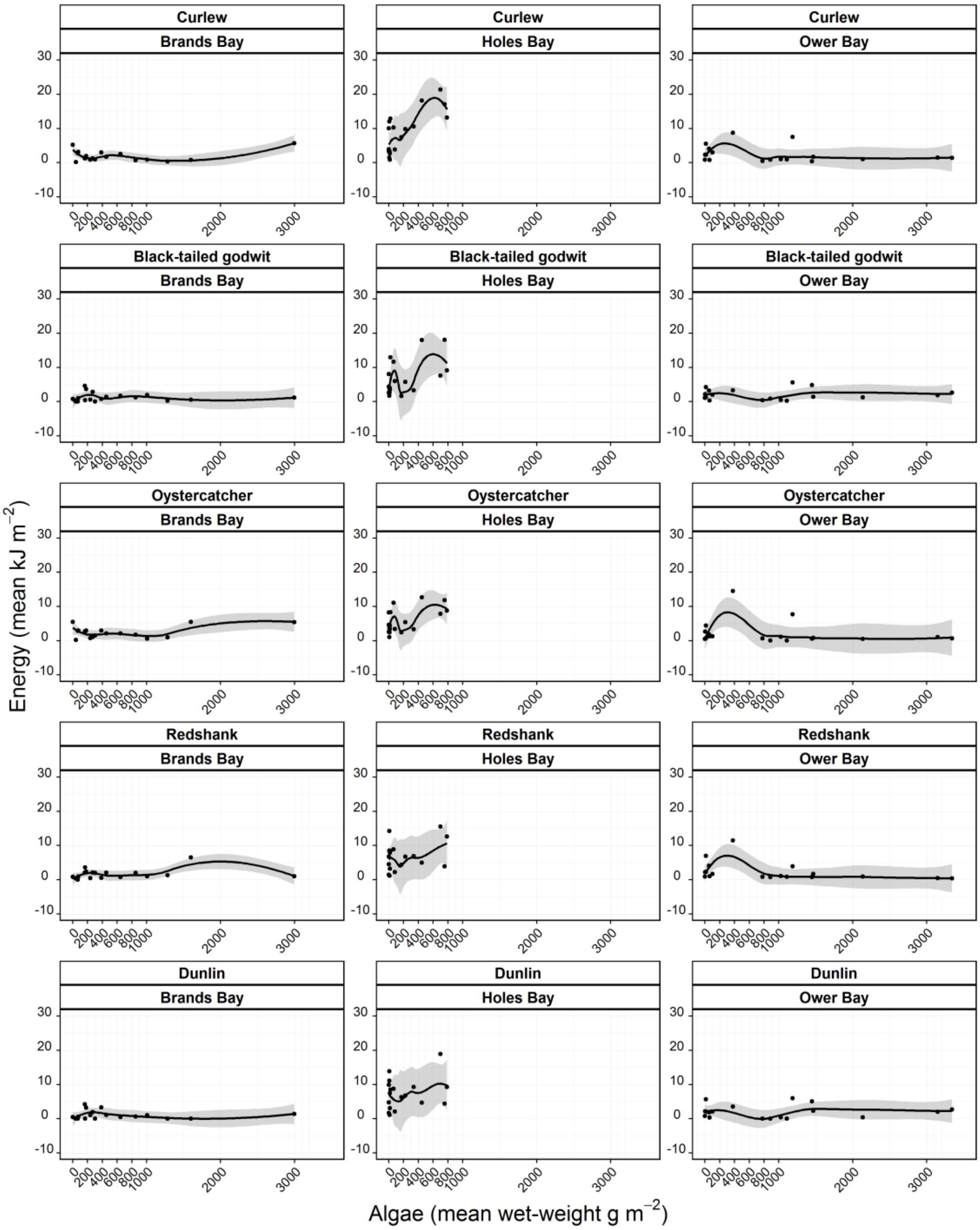


**Fig. 4.6:** GAM charts with loess smoothing curve showing the relationship between mean energy available within each bird species' BIM (kJ m$^{-2}$) and algae biomass (mean wet weight g m$^{-2}$) recorded at each site irrespective of date. Shaded areas are 95% confidence intervals. Highest mean algae biomass recorded in core samples taken in Holes Bay was <1000 g (ww) m$^{-2}$.

## 4.5 Discussion

### 4.5.1 Invertebrate size-class distribution

It was not surprising that there were a greater number of annelid worms in all size classes in Holes Bay. As has been discussed in Chapter 3, this site contained a significantly greater abundance of *H. diversicolor* than either Brands Bay or Ower Bay. Indeed, this species was the main driver behind variation in community assemblage between the sites (Chapter 3, Table 3.3). Although there were a greater number of 'small worms' (<5 mm) recorded in Brands Bay, this figure comprised a significant number of *Tubificoides* spp. and Chironomidae; the implications of which were discussed in Chapter 3 (section 3.6.3). There was a paucity of larger invertebrates in Brands Bay; particularly annelid worms >55 mm and bivalves >10 mm. It is noteworthy that there were few individuals in the larger crustacean size classes (>10 mm). This is of particular concern as the category also included *Carcinus maenas* [Linnaeus 1758] and *Crangon crangon* [Linnaeus 1758]. It is possible that *C. crangon* were not present in the sampling sites due to their preference for much sandier sediment (Barnes 1994). However, it is more likely that this species was able to avoid the suction corer and was therefore under-recorded rather than absent. Smaller *C. maenas* were recorded however a lack of larger sizes present has implications for larger wading birds' BIM.

### 4.5.2 Spatial and temporal variation in wading bird species' BIM

Combining these taxa into a BIM for wading bird species provided a more direct comparison between sites to determine which might be the most profitable for the birds. Energy from species recorded for each wading bird BIM was significantly higher in Holes Bay than either Brands Bay or Ower Bay; in particular redshank and dunlin BIM. As the BIM energy values are derived from sizes of invertebrates, these results support the size class distribution shown in Fig. 4.3. Redshank and dunlin also consume *Peringia ulvae* [Pennant 1777] (<5 mm) which contributed to the BIM available for these birds at all sites. The lower abundance of larger invertebrates could impact upon the larger wading bird species (such as curlew, oystercatcher and black-tailed godwit) (Goss-Custard et al. 1977; Zwarts and Wanink 1993).

An initial inspection of the overall size-class distribution shown in Fig. 4.2a-c would indicate that there was a greater abundance of invertebrates in December 2013; suggesting there was prey available for the wading birds. However, analysis revealed there was no significant variation in wading bird BIM between dates (irrespective of site). This was surprising as it had been expected that invertebrate abundance would vary significantly between both September 2013 and September 2014 compared to December 2013 as the macroalgal mat coverage was greatly reduced (Chapter 2, Fig. 2.4). However, although there was no extensive surface coverage of algae (maximum coverage 40% in Ower Bay mid and upper shores) the biomass values recorded in the core samples remained high suggesting a large amount of entrained algae was still present. This, together with the recorded anoxic layer being <10 mm below the surface of the mud during December (see Chapter 2, Table 2.2), might have resulted in a greater number of invertebrates being prevented from burrowing deeper into the sediment. There are myriad environmental factors such as mild winter temperatures which might contribute to the spatial and temporal distribution of invertebrates (Barnes 1994). These would require further research beyond the scope of this study.

### 4.5.3 The effect of increased macroalgal mat biomass on wading bird BIM

What is apparent from the charts shown in Fig. 4.5 and Fig. 4.6 is a similar relationship between wading bird BIM and algae biomass as that found when examining the overall invertebrate community (Chapter 3, Fig. 3.8). There is an initial increase in energy (kJm$^{-2}$) up to ~800 g (ww) m$^{-2}$ algae and then a decline for each wading bird BIM. These results support other studies which recorded a detrimental effect on invertebrates under algae biomass >1000 g (ww) m$^{-2}$ (Hull 1987; Raffaelli et al. 1999). Therefore it could be argued that algae biomass of 1000 g m$^{-2}$ represents a ‘tipping point’ in Poole Harbour indicating detrimental effect on wading birds through a decline in BIM. Although it is acknowledged that determining sizes of invertebrate samples would increase research costs, it is clearly necessary in order to more accurately determine the effect of macroalgal mats on different wading bird species.

One area which has yet to be explored within the context of wading bird BIM is the impact on preferred prey from different species of *Ulva* recorded at the sites. The dominant species and differences in morphology have already been discussed in Chapter 2 (Section 2.4.2). However, the differences between algae species may also explain the between-site variance in wading bird BIM. Holes Bay recorded the highest % coverage of algae yet the lowest algae biomass (see Chapter 2, Figs. 2.5 and 2.6); the site is dominated by less dense, sheet forming, *Ulva.* By contrast, Ower Bay and Brands Bay were dominated by denser tubular or filamentous *Ulva*. It has been suggested that the filamentous algae may prevent certain invertebrate species from feeding successfully (Raffaelli et al. 1991). It is possible that other invertebrate species may be prevented from obtaining food either from beneath the denser, tubular/filamentous form of *Ulva* or by being unable to penetrate the algae (Thiel et al.

1998). Filter feeders, for example, may be restricted due to the increased sediment trapped within the macroalgal mat layers (Bolam and Fernandes 2002; Green et al. 2015). This may, in turn, restrict growth of the invertebrates resulting in a reduction in size classes and a consequential reduction in wading bird BIM. This hypothesis would require further research and testing using manipulation experiments beyond the scope of this study.

### 4.5.4 Conclusion

Ensuring the conservation of nationally and internationally important populations of overwintering wading birds is one of the main conservation priorities under the SPA legislation for Poole Harbour (Durell et al. 2006). The intertidal mudflats provide an important food resource for these birds and therefore the protection of the food source within their key feeding areas is vital to maintain these populations. Numbers of wading birds *per se* cannot provide a reliable indicator of the health of an estuarine ecosystem (Durell et al. 2006). Bird survival not only depends upon there being sufficient prey resources within the intertidal mudflats but also that the food is of suitable quality (i.e. provides sufficient energy) (Bowgen et al. 2015). It has been suggested that wading birds' 'starvation threshold' (<90% survival) is reached when biomass of invertebrates falls below 4 g AFDM $m^{-2}$ (West et al 2007). Converted to energy this level represents 88kJ $m^{-2}$ (after Zwarts and Wanink 1993).

An initial inspection of the results would suggest that the most profitable site for each wading bird species studied would be Holes Bay. This site had the highest BIM for each species of bird largely due to the greater abundance of larger sizes of *H. diversicolor* recorded. These results might indicate that there is sufficient energy available from annelid worms to support a greater number of birds in Holes Bay. However, it is worth noting that these results only show the BIM *potentially* available to wading birds. It has been suggested that wading birds may not always feed in the most profitable areas (Stillman et al. 2005), possibly due to a combination of external factors including competition and density (Stillman 2008). In addition, this study concentrates on energy availability only and does not incorporate digestion time, prey handling or even inter-specific or intra-specific competition.

As demonstrated by the ABC curves shown in Fig. 3.3 and supported by the charts shown in Fig. 3.4, each intertidal system has its own site-specific invertebrate community that is able to support the overwintering bird population. The decline in one invertebrate species within a system can be compensated by an increase in another;

wading birds will select from their BIM based upon the availability at each site (West et al. 2007). Therefore, those wading bird species that include a diversity of prey types within their BIMs could be more resilient to changes in environmental conditions (Bowgen et al. 2015). Curlew and oystercatcher, for example, will feed on *C. edule* as well as annelid worms; both of which are abundant within Poole Harbour (Thomas et al. 2004; Herbert et al. 2010). In addition, as shown in Chapter 3, Table 3.4, overall mollusc community distribution was not significantly affected by algae biomass, algae cover, % organic or % sand. It is also worth noting that these curlew and oystercatcher are ‘site faithful’ and will utilise different food supplies when their preferred prey is unavailable (van de Kam et al. 2004); redshank, dunlin and black-tailed godwit will travel between sites if their preferred prey is unavailable. However, species which rely on the larger annelid worms (e.g. black-tailed godwit) without abundant alternative prey taxa are likely to be more vulnerable to population fluctuations in prey species potentially caused by increases in macroalgal mat biomass.

BLANK

# 5.0 The relationship between macroalgal mat coverage and wading bird foraging behaviour

## Abstract

The intertidal mudflats within Poole Harbour provide an ideal range of conditions for supporting large assemblages of overwintering wading birds including internationally important populations of black-tailed godwit (*Limosa limosa*) and nationally important populations of redshank (*Tringa totanus*) and dunlin (*Calidris alpina*). Within each chosen overwintering region, wading birds will select feeding sites based upon certain criteria; one of the most important is a sufficient supply of suitable invertebrate prey.

This chapter examines the impact of macroalgal mats on wading bird foraging behaviour. Five species of wading bird; Eurasian curlew (*Numenius arquata*); black-tailed godwit (*Limosa limosa*); oystercatcher (*Haematopus ostralegus*); redshank (*Tringa totanus*) and dunlin (*Calidris alpina*) were selected for study. Bird foraging behaviour was observed from vantage points in Poole Harbour within three survey sites (Holes Bay, Brands Bay, Ower Bay) each month from September 2013 – March 2014 and September 2014 – March 2015. Wading bird activity and the level of visible macroalgal mat coverage was recorded. Surveys were split by season (autumn and winter) in order to assess bird behaviour on areas of the mudflat where macroalgal mat remained on the surface (autumn observations) and areas which had recorded levels of macroalgal mat coverage during the previous growth period (winter observations).

Foraging behaviour by curlew, black-tailed godwit, oystercatcher and dunlin was affected by macroalgal mat coverage (either visible or previous peak) during the overwintering period. Results showed that curlew and dunlin were affected by the presence of macroalgal mat coverage in autumn – curlew density (number ha$^{-1}$) was greater on high macroalgal mat coverage than low coverage in Holes Bay. Densities of curlew and oystercatcher were greater on areas of zero previous algae coverage compared to areas of either low or high previous coverage. Black-tailed godwit density was higher on areas of high previous algae coverage compared to low in Brands Bay. Redshank density was not affected by macroalgal mat coverage. Variations in foraging behaviour on different levels of macroalgal mat coverage could suggest wading birds may be adapting to the presence of macroalgal mats with implications for their ability to feed efficiently.

**BLANK**

## 5.1 Introduction

In northern-European estuarine systems, overwintering migratory wading birds mainly arrive in September and remain until March (Stillman et al. 2010). During these months, outside the breeding season, a bird's primary objective is to obtain sufficient energy in order to survive and ensure a successful return to the breeding site the following spring (Kersten and Piersma 1987; Stillman and Goss-Custard 2010). Therefore it is a reasonable assumption that an individual bird's behaviour is focused upon feeding and maximising its chances of gaining food with minimal effort (Finn et al. 2008; Kuawe et al. 2010; Martins et al. 2013). How the macroalgal mats affect the abundance and distribution of key invertebrate prey items has been explored in Chapters 3 and 4. These chapters highlighted a transformation of the invertebrate community (Chapter 3) and a shift in each key bird species' benthic invertebrate menu (BIM) due to the presence of dense macroalgal mats (Chapter 4). It has been suggested that macroalgal mats affect birds' ability to access prey; either by obscuring visual clues to prey location (Green et al. 2015) or by preventing birds from penetrating the thick mat in order to obtain prey from the sediment (Kuwae et al. 2010).

### 5.1.1 Site choice and use by overwintering migratory wading birds

Populations of overwintering migratory wading birds have a 'wintering range' and will return to the same region each year (Evans 1976). Black-tailed godwits (*Limosa limosa* [Linnaeus, 1758]), for example, are highly philopatric in their choice of winter feeding site (Gill et al. 2001a; Gunnarsson et al. 2005a; 2006). Within each location, birds will utilise a number of key areas (e.g. Poole Harbour) in order to ensure their survival by maximising their energy intake in the areas with the highest potential food resource (Goss-Custard and Charman 1976). Therefore, overwintering wading birds will be familiar with each area within their preferred region and will adapt to local environmental conditions and even site-specific variation in their preferred prey (Bryant 1979; van de Kam et al. 2004; West et al. 2005; Gunnarsson et al. 2005c). It is worth noting that juvenile black-tailed godwits do not migrate with their parents and will, therefore, make the important choice of winter feeding ground on their first migration (Gunnarsson et al. 2005c).

Observing bird behaviour can provide a useful insight into how different wading birds use a particular site under varying macroalgal mat conditions (Lewis and Kelly 2001). As discussed in Chapter 1, there have been several behavioural studies carried out on wading bird species in relation to macroalgal mats in temperate estuaries in the UK

(Raffaelli et al. 1998, Lewis et al. 2014), Europe (Cabral et al. 1999) and north-America (Green et al. 2015). Experimental studies were carried out in the Clonakilty Estuary, Ireland, by Lewis et al. (2003). Yet, although the study reported changes in the invertebrate community under manipulated levels of algae coverage, too few wading birds were recorded on the experimental plots (10 m x10 m) for analysis. By contrast, results from a later study on the same estuary found that black-tailed godwits were avoiding areas of high algae cover whereas redshanks were observed foraging on algae (Lewis et al. 2014). This study also reported that black-tailed godwits were utilising algae-free patches which were revealed as the macroalgal mat began to break down.

What has not been fully explored is the residual impact from the algae. During the winter months (December – February) most areas of macroalgal mat in Poole Harbour have declined significantly or disappeared altogether. However, those areas will still contain decaying or fragments of algae within the sediment (Raffaelli et al, 1998). Although these areas appear to be ‘bare mud’ the sediment composition and organic content could be different from those areas which never showed any algal growth (Hardison et al. 2010).

An additional consideration is the delay between the surface algae disappearing and the anoxic layer depth lowering. The depth of the layer of black mud (a visible indicator of anoxic/hypoxic conditions within the sediment) measured during sampling remained close to the surface throughout the winter months at all sites monitored for algae biomass (Chapter 2, Table 2.1). Indeed the lowest recorded depth at which black mud was visible was in March 2013 at Newton Bay (20 mm) at the end of the overwintering season for wading birds. Therefore, although the surface algae had virtually disappeared, the invertebrate response to chronic residual impacts would remain unchanged (Pearson and Rosenberg 1978; Wildsmith et al. 2009). As discussed in Chapters 3 and 4, the invertebrate community has become dominated by smaller r-selected species under macroalgal mats.

### 5.1.2 Bird behaviour in Poole Harbour

The intertidal mudflats within Poole Harbour provide conditions for supporting large assemblages of overwintering wading birds including internationally important populations of black-tailed godwit together with nationally important populations of redshank and dunlin (Frost et al. 2016). The importance of the area to these birds has already been discussed in Chapter 1. Understanding the impact of macroalgal mats on the overwintering bird population is important as the extent and biomass of the macroalgal mats provides a measure of the quality and condition of a Site of Special Scientific Interest (SSSI) feature and, as such, its ability to support the coastal bird community (Underhill-Day et al. 2010). Any decline in this feature will impact on the overall quality of the Special Protection Area (SPA) designation for Poole Harbour (Durell et al. 2006).

As discussed in Chapter 1, Poole Harbour is susceptible to the development of macroalgal mats. Yet, despite the national and international importance of the harbour for overwintering migratory wading birds, there has only been one study specifically examining the impact from macroalgal mats on birds (Axelsson et al. 2012). The small-scale study, commissioned by Natural England, was carried out between November 2011 and February 2012 and recorded bird activity at four points around Brands Bay. These points comprised adjacent patches of macroalgal mat (c. 20 m x 20 m) and clear mud. The study concluded that curlew and oystercatcher were deterred from feeding on the macroalgal mat and displayed a preference for clear mud. Other species of wading bird were not significantly affected by the presence of macroalgal mats. However this study was restricted in scale and lasted only three months.

In addition, due to the unique double high-water, some areas of the intertidal mudflats can remain under water (water level above mean tide level) for up to 16 hours each day (Humphreys 2005). This significantly reduces the available feeding time for the overwintering birds. If access to prey is further restricted due to the macroalgal mats (whether visible on the surface or residual within the sediment) the birds may simply not have time within each day to ensure sufficient prey is consumed.

### 5.1.3 Rationale

Chapters 5 and 6 have been developed within a behavioural ecology framework using key concepts within that framework to support the investigation into the impact of macroalgal mats on overwintering wading birds. Elements of species' behavioural adaptation and optimal-foraging theory will be explored with the aim of informing conservation objectives and indicating threshold levels of concern in macroalgal mat development. A link between animal behaviour and conservation was established during the 1990s however collaboration between an essentially academic discipline and a practical industry has not been without problems (Caro et al. 2007). At a fundamental level, however, both disciplines utilise elements of the other; behavioural ecologists are keen to conserve species being studied and conservation ecologists use known animal behaviour to ensure appropriate timing for surveys of species of conservation concern (Sutherland 2006).

### *Optimal -Foraging Theory*

First proposed in the 1960s (MacArthur and Pianka, 1966; Emlen 1966), optimal-foraging theory uses observational studies and models to determine feeding behaviour based on the principal that each predator makes a series of ‘choices’ in order to maximise energy intake with minimum effort (Townsend et al. 2008). These decisions are summarised below (Townsend et al. 2008):

- Feeding patch selection: Which patch, within a chosen feeding site, offers the best chance of finding prey.
- Predator avoidance: Maximising energy input whilst avoiding predation
- Length of time at a patch: How long to remain in one profitable patch with depleting resources before moving to an alternative patch where prey-quality and availability are unknown.
- Competitor density: Whether to remain in a profitable patch with increased competition or move to a lesser quality patch with fewer competitors.
- Prey choice: Whether to use energy feeding on lower quality prey or continue searching for better quality items.

The remaining two chapters will examine how varying levels of macroalgal mat coverage disrupt two of these choices: foraging patch selection (Chapter 5) and prey choice/availability (Chapter 6).

Within each chosen overwintering region, wading birds will select feeding sites based upon certain criteria; one of the most important is a sufficient supply of suitable invertebrate prey (Durell et al. 2006). This chapter will build upon findings reported in earlier chapters and examine how the birds respond to the presence of macroalgal mats within the context of three different bays within Poole Harbour. This study examines whether foraging birds display an aversion to or a preference for areas affected by macroalgal mats. The criteria by which wading birds select their feeding location within the harbour for a particular tidal-cycle has been extensively studied and, as such, falls outside the scope of this research (Durell et al. 2006; Stillman and Goss-Custard 2010).

Although previous studies have been few, it has been reported that the presence of large areas of macroalgal mats can affect wading bird behaviour (Cabral et al. 1999; Lewis and Kelly 2001; Lewis et al. 2014). All these investigations have quantified activity levels of birds on areas of differing algae coverage and bare mud. Yet, to date, studies have concentrated primarily on recording avoidance of surface algae coverage. There is a gap in the knowledge that this chapter aims to address, namely whether there is any change in behaviour in areas that were previously covered by algae as opposed to those areas which remained ‘bare mud’ due to no algal growth. As demonstrated in Chapter 3 (Section 3.5.1) there is a notable difference in the visual recording of algae coverage, particularly in Holes Bay, and the biomass recorded in the core samples taken the same month. Core samples taken in areas which had been recorded as ‘bare mud’ (i.e. no visible surface algae) did, in fact, contain a quantity of algae within the sediment. It is important to determine whether there is any residual impact from algal growth during the winter months as this could result in birds still being affected by macroalgal mats despite the surface coverage having disappeared. This has implications as the winter months are the most stressful for overwintering birds due to a number of factors including prey availability, reduced temperature and limited daylight (Zwarts 1996; Dwyer et al. 2013).

## 5.2 Aims and objectives

**Aim 1:** To determine whether macroalgal mats are affecting wading bird distribution around Poole Harbour.

**Aim 2:** To examine different species’ response to present or previous coverage of macroalgal mat and whether this behaviour is site-specific or can be applied more generally.

**Objective 1:** The aims will be addressed by observing and recording active foraging behaviour of a number of key wading bird species on varying levels of algae % coverage.

## 5.3 Methods

### 5.3.1 Site selection

Sites for bird observations were selected from the four sites used for algae biomass monitoring. Newton Bay was rejected as there was no single vantage point from which to observe a large enough area of the whole bay. Therefore Holes Bay, Ower Bay and

Brands Bay were chosen.  Full details of the site selection methodology can be found in section 2.3.2.1.

### 5.3.2 Species selection

Coastal birds can be observed with relative ease from a single vantage point on the shore (Bibby et al. 2005).  Five wading bird species; Eurasian curlew (*Numenius arquata* [Linnaeus 1758]); black-tailed godwit (*Limosa limosa* [Linnaeus 1758]); oystercatcher (*Haematopus ostralegus* [Linnaeus 1758]); redshank (*Tringa totanus* [Linnaeus 1758]); and dunlin (*Calidris alpina* [Linnaeus 1758]), were selected for study. Details of the selection criteria can be found in section 4.3.1.

### 5.3.3 Timing of surveys

Surveys were carried out each month from September 2013 – March 2014 (hereafter termed Y1) and September 2014 – March 2015 (hereafter termed Y2).  Over both years, a total of 22 surveys were undertaken (12 on neap tides and 10 on spring tides) at each of the three sites.  Neap and spring tides were determined by predicted low water depth (UKHO Admiralty Easy Tide), with neap tide low water depth ≥1.0 m Chart Datum (CD) and spring tide low water depth <1.0 m CD.  Year 1 and Year 2 counts were combined then divided by season.  Autumn (September – November) when algae was visible on the surface, and winter (December – March) the macroalgal mat had disintegrated and was no longer visible.  March observations were included in winter analysis as there was no visible algal growth in March 2013 or March 2014 (Chapter 2, Fig. 2.5). In addition, average air temperature for the month did not remain above the 10 $^{o}$C (Met Office 2016) required to stimulate macroalgal mat growth (Raffaelli et al. 1998).

### 5.3.4 Bird counts

#### *5.3.4.1 Determining bird location within each site*

Using an Ordnance Survey 1:25,000 map, each site was divided into a number of discrete patches.  Boundaries for these patches were determined visually using landscape features such as channels in the mud, protruding saltmarsh and prominent terrestrial markers (e.g. buildings and trees).  Patch boundaries were checked using aerial photographs in conjunction with Ordnance Survey maps then each patch was plotted as a spatially referenced polygon in ArcGIS (version 10.1).  Once mapped, patch areas were measured (ha) and then amalgamated into three shore levels using tidal curves to determine upper, mid and lower shore levels for each of the sites (www.ukho.gov.uk).  Sizes of each shore level patch are provided in Table 5.1.

**Table 5.1:** Area (ha) of each shore level within visible range for observations of bird behaviour.

| Site | Shore level | Area (ha) |
|---|---|---|
| Brands Bay | Lower | 6.67 |
| | Mid | 22.76 |
| | Upper | 12.36 |
| | **Total** | **41.79** |
| Holes Bay | Lower | 7.2 |
| | Mid | 11.76 |
| | Upper | 6.85 |
| | **Total** | **25.81** |
| Ower Bay | Lower | 8.74 |
| | Mid | 4.57 |
| | Upper | 2.94 |
| | **Total** | **16.25** |

#### *5.3.4.2 Bird observations*

Wading bird identification was confirmed using Svensson et al. (2010). Bird behaviour was observed using timed scans counting bird numbers, recording the location and activity on each patch (Altman 1974). Observations were carried out every half-hour from 1 hour before low water to 1 hour after low water (n = 5 observations per survey) and took approximately 10 minutes to complete. Low water time was based on data supplied by UK Hydrographic Office (UKHO) (www.ukho.gov.uk). Scans were carried out using a Swarowski 20-60 zoom telescope and were conducted from left to right across each bay to avoid 'double counting' of birds. Birds which moved between patches were noted and only counted once. Birds which flew away before their patch was scanned were not counted. Given that Poole Harbour supports an assemblage of over 20,000 wading birds, it is highly unlikely that an identical flock was counted on two separate occasions. Number and species of wading birds present were recorded on field maps showing the different patches. The behaviour of each bird or flock of birds on a patch was recorded as either active or passive. Passive bird numbers were counted but did not form part of the study. Table 5.2 provides details of the behaviour within each category. In order to avoid temporal autocorrelation, bird numbers recorded during each survey were totalled and a mean value obtained. Mean bird numbers per patch were converted into density (individuals ha$^{-1}$).

**Table 5.2:** Behavioural categories observed during bird observations.

| Behaviour | Description |
|---|---|
| **Active** | |
| Foraging | Bird observed searching for prey.<br>No prey obtained. |
| Feeding | Swallowing motion and/or prey observed. |
| Walking | Moving between feeding patches.<br>Not searching for prey. |
| **Passive** | |
| Resting or preening | Not actively searching for prey or moving |

### 5.3.5 Algae coverage

#### *5.3.5.1 Autumn visible coverage of algae*

Percentage cover of algae within individual patches was recorded during each survey using the methods described in Section 2.3.4.1. For the autumn observations, algae coverage was categorised as 0 (<5% coverage), Low (5%-50% coverage) and High (51%-100% coverage). Where algal coverage was not visible at the start of the survey, values were ascribed when the intertidal area was exposed. Occasionally some individual patches remained water covered throughout a neap-tide survey. When this occurred, algae coverage was determined using other sampling or surveys carried out in the same month.

#### *5.3.5.2 Winter algae from previous peak coverage.*

Previous algae cover was determined by taking values from algal growth recorded during the preceding summer. Previous algae coverage was also categorised as 0 (<5%), Low (5%-50% coverage), High (51%-100% coverage) with data taken from each area's peak coverage recorded during the previous season's growth period. Peak algae was used as opposed to mean algae coverage for the whole season as this is the maximum area of each bay which would likely contain decaying or fragments of macroalgal mat.

### 5.3.6 Statistical analysis

All statistical tests were carried out using R version 3.3.0 “Supposedly Educational” (R Core Team 2016). Assumptions of normality and homogeneity of variance were checked using Shapiro Wilk’s test within the “stats” package in R (R Core Team 2016) and Levene’s test within the “car” package developed for R (Fox and Weisberg 2011) respectively. Paired t-tests were used to determine variation in mean bird density (individuals $ha^{-1}$) between years. Kruskal-Wallis tests were used to analyse temporal and spatial variation in bird density and analyse variation in bird density between varying macroalgal mat coverage with post-hoc Nemenyi test for pairwise multiple comparisons carried out using “PMCMR” package developed for R (Pohlert 2016). Effect size, using Pearson’s r correlation coefficient, was determined for significant pairs using exact Wilcoxon-Mann-Whitney Test to obtain z scores then the equation r = z/sqrt(N) with N being the number of samples (Barto and Rillig 2012; Field 2012). Effect sizes are defined as small (r = <0.3), medium (r = <0.5), large (r = >0.5) (Cohen 1994).

## 5.4 Results

### 5.4.1 Spatial and temporal variation in wading bird density (individuals $ha^{-1}$)

#### *5.4.1.1 Between-year variation in wading bird density*

Fig. 5.1 shows variation in mean density for all studied species of wading bird at each site between years. The only significant variation in bird density between years was black-tailed godwit density in Brands Bay, which was higher in year 2 than year 1 (t = -2.142, df = 43.054, p = 0.038). No significant variation in density between years was found for curlew, oystercatcher, redshank or dunlin for any site (p = >0.05).

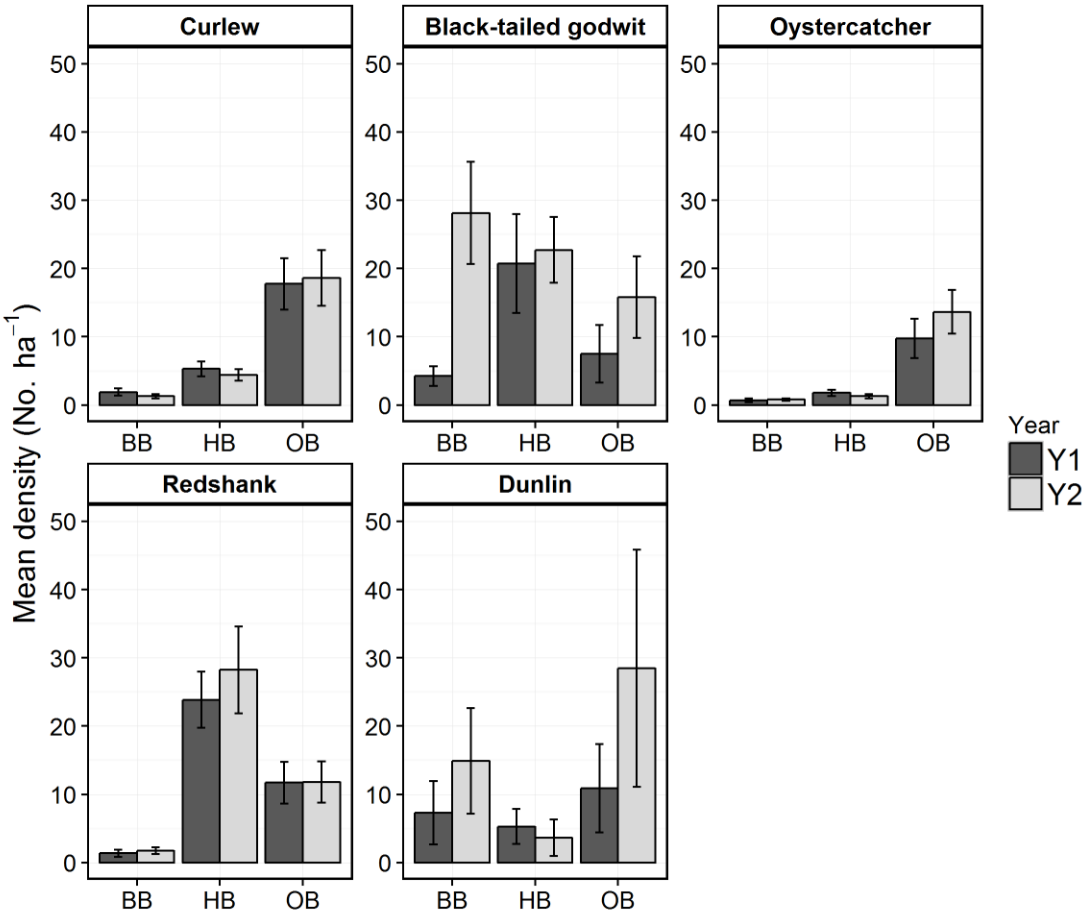


**Fig. 5.1:** Mean density (number ha$^{-1}$) per year of five wading bird species recorded at each site. Error bars 95% confidence intervals. Y1 = year 1 (2013/2014), Y2 = year 2 (2014/2015). BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

#### *5.4.1.2 Seasonal variation in wading bird density between sites*

Table 5.3 provides details of the Kruskal-Wallis and post-hoc Nemenyi tests on wading bird density between sites for autumn and winter. Individual species density varied significantly (p = <0.05) between sites with data from both years combined. Curlew density was highest in Ower Bay in autumn. Winter density of curlew was higher in Holes Bay than Brands Bay and higher in Ower Bay than Brands Bay. Holes Bay also recorded higher autumn density of black-tailed godwit than Ower Bay and a higher winter density than both Brands Bay and Ower Bay. Ower Bay recorded the highest density of oystercatchers in autumn and a higher density in winter than Brands Bay. Autumn and winter densities for redshank were higher in Holes Bay and Ower Bay than Brands Bay. Overall, Brands Bay did not record higher densities for any wading bird species in either autumn or winter.

**Table 5.3:** Kruskal-Wallis test for seasonal variation in wading bird densities between sites with Nemenyi post-hoc test for pairwise significance. Data are combined for both years. Significance codes: *** = <0.001, ** = <0.01, * = <0.05. NS = not significant
BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

| Species | Season | $\chi^2$ (df) | P | Post-hoc Nemenyi |
|---|---|---|---|---|
| Curlew | Autumn | 30.725 (2) | <0.001*** | OB>BB p = <0.001***<br>OB>HB p = <0.001*** |
| Curlew | Winter | 16.528 (2) | <0.001*** | HB>BB p = 0.002**<br>OB>BB p = <0.001*** |
| Black-tailed godwit | Autumn | 8.472 (2) | 0.015* | HB>OB p = 0.016* |
| Black-tailed godwit | Winter | 11.84 (2) | 0.003** | HB>BB p = 0.027*<br>HB>OB p = 0.011* |
| Oystercatcher | Autumn | 19.427 (2) | <0.001*** | OB>HB p = <0.001***<br>OB>BB p = 0.008 ** |
| Oystercatcher | Winter | 8.373 (2) | 0.015* | OB>BB p = 0.015* |
| Redshank | Autumn | 10.586 (2) | 0.005** | HB>BB p = 0.006**<br>OB>BB p = 0.049** |
| Redshank | Winter | 25.231 (2) | <0.001 *** | HB>BB p = <0.001***<br>OB>BB p = 0.004** |
| Dunlin | Autumn | 3.370 (2) | 0.186 | NS |
| Dunlin | Winter | 5.143 (2) | 0.076 | NS |

### *5.4.1.2 Shore-level variation in wading bird density*

*Autumn*

Shore-level only had a significant (p = <0.05) impact on black-tailed godwit density in Brands Bay in autumn ($\chi^2$ =7.304, df = 2, p = 0.026*, mid-shore>upper-shore p = 0.005**, z = 2.747, r = 0.43) and redshank density in Brands Bay in autumn ($\chi^2$ =12.661, df = 2, p = 0.002**, mid-shore>upper-shore p = 0.004**, z = 2.794, r = 0.44, mid>lower p = 0.003**, z = 2.865, r = 0.45). No other significant (p = <0.05) effects for shore level on wading bird density for autumn were recorded.

*Winter*

Shore-level only had a significant impact on redshank density in Ower Bay in winter ($\chi^2$ =7.551, df = 2, p = 0.229*, mid-shore>lower-shore p = 0.009**, z = 2.597, r = 0.41). No other significant (p = <0.05) effects for shore level on wading bird density for winter were recorded.

### 5.4.2 The effect of autumn macroalgal mat coverage on wading bird density

Fig. 5.2 shows numbers of active birds at each of the three sites under different levels of macroalgal mat coverage in autumn (September, October, November).

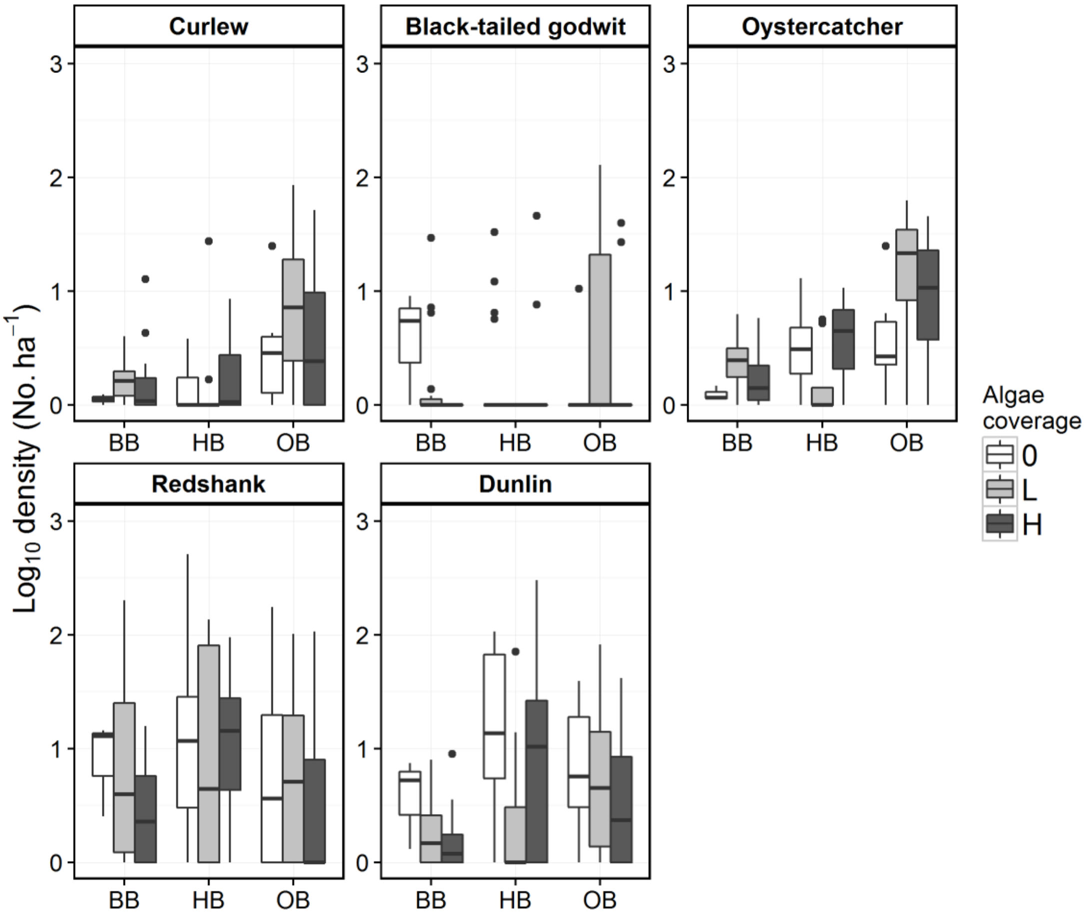


**Fig. 5.2:** Box plots showing median bird density (number ha$^{-1}$) recorded at each site for varying levels of algae coverage in autumn (September, October, November) shown on $\log_{10}$ scale for clarity. BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.
Algae coverage 0 = <5%, L = 5%-50%, H = 51%-100%.

Table 5.4 provides results from the Kruskal-Wallis test on wading bird species numbers on varying levels of algae coverage during autumn.

**Table 5.4:** Kruskal-Wallis analysis between median bird density and algae coverage present at each site recorded in autumn with post-hoc Nemenyi test for pairwise comparisons. Effect size (r) small (r = <0.3), medium (r = <0.5), large (r = >0.5). Year 1 and Year 2 data are combined. BB: Brands Bay. HB: Holes Bay. OB: Ower Bay. Algae coverage 0 = <5%, L = 5%-50%, H = 51%-100%. Significance codes: *** = <0.001 ** = <0.01 * = <0.05 NS = not significant (p = >0.05).

| Species | Site | $\chi^2$ (df) | P | Post-hoc Nemenyi | Z | r |
|---|---|---|---|---|---|---|
| Curlew | BB | 7.929 (2) | 0.019** | No significant pairs | N/A | N/A |
| | HB | 7.233 (2) | 0.027 * | H>L p = 0.016* | 2.390 | 0.35 |
| | OB | 4.426 (2) | 0.109 | NS | | |
| Black-tailed godwit | BB | 2.292 (2) | 0.318 | NS | | |
| | HB | 0.346 (2) | 0.841 | NS | | |
| | OB | 1.563 (2) | 0.458 | NS | | |
| Oystercatcher | BB | 2.300 (2) | 0.223 | NS | | |
| | HB | 2.582 (2) | 0.275 | NS | | |
| | OB | 2.659 (2) | 0.265 | NS | | |
| Redshank | BB | 3.275 (2) | 0.194 | NS | | |
| | HB | 4.660 (2) | 0.097 | NS | | |
| | OB | 1.363 (2) | 0.506 | NS | | |
| Dunlin | BB | 9.024 (2) | 0.011 * | No significant pairs | N/A | N/A |
| | HB | 2.993 (2) | 0.224 | NS | | |
| | OB | 5.878 (2) | 0.053 | NS | | |

Results from the autumn surveys indicate that algae coverage had a significant impact upon curlew activity (i.e. foraging, feeding or walking) with a greater density of active birds recorded on high algae coverage compared to low in Holes Bay with a ‘medium’ effect size (r>0.30). Curlew and dunlin activity were affected by autumn algae coverage in Brands Bay but no pairwise significance was found. Black-tailed godwit, oystercatcher and redshank were unaffected by algae coverage. No significant effect was found for any species in Ower Bay.

### 5.4.3 The effect of previous macroalgal mat coverage on wading bird density

Figure 5.3 shows the median bird numbers on a $\log_{10}$ scale on levels of previous algae coverage.

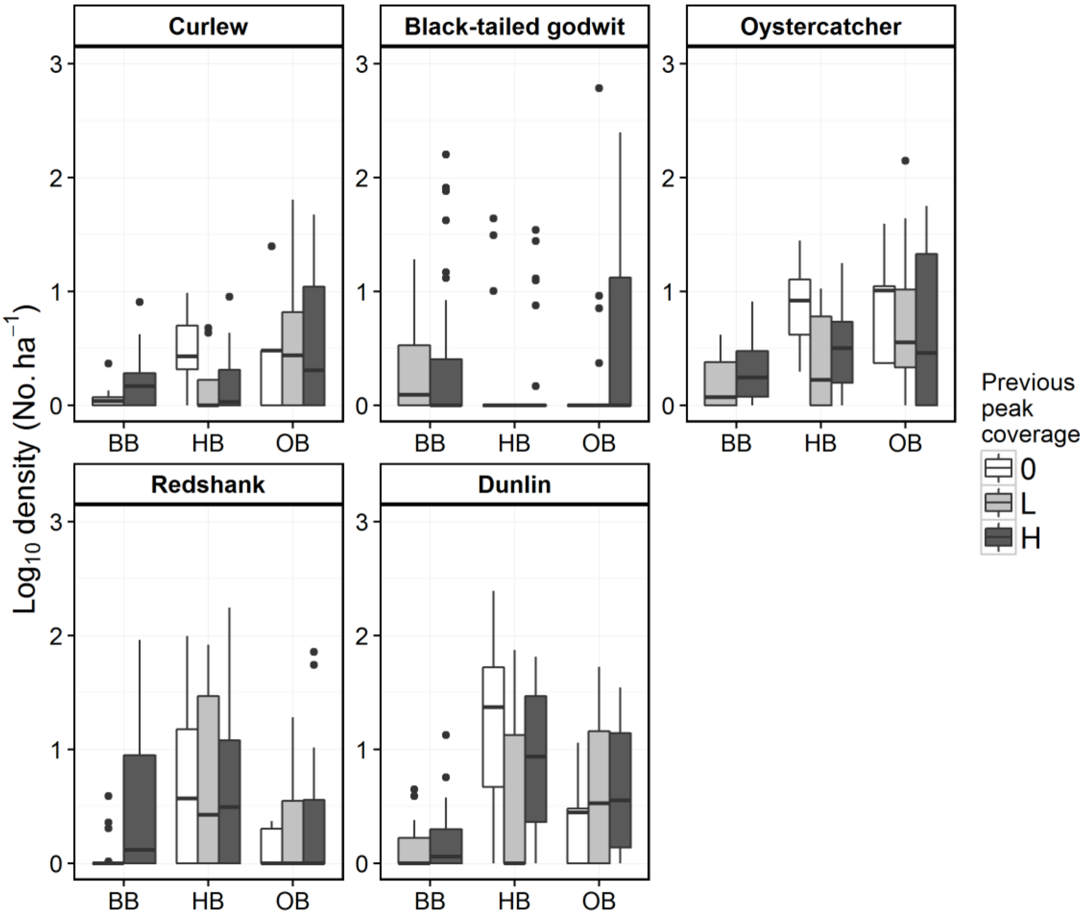


**Fig. 5.3:** Box plots showing median bird density (number ha$^{-1}$) recorded in winter at each site for varying levels of previous macroalgal mat coverage on a $\log_{10}$ scale for clarity. Previous macroalgal mat coverage is maximum coverage recorded during the preceding summer's macroalgal mat growth. BB: Brands Bay HB: Holes Bay OB: Ower Bay.
Algae coverage 0 = <5%, L = 5%-50%, H = 51%-100%.

Table 5.5 provides results from the Kruskal-Wallis test on wading bird species density on varying levels of previous algae coverage during winter. There was no '0' level of previous macroalgal mat coverage in Brands Bay.

**Table 5.5:** Kruskal-Wallis analysis between median bird density and previous macroalgal mat coverage at each site recorded in winter with post-hoc Nemenyi test for pairwise comparisons. Effect size (r) small (r = <0.3), medium (r = <0.5), large (r = >0.5). Year 1 and Year 2 data are combined. BB: Brands Bay HB: Holes Bay OB: Ower Bay. Algae coverage 0 = <5%, L = 5%-50%, H = 51%-100%. Significance codes: *** = <0.001 ** = <0.01 * = <0.05 NS = not significant (p = >0.05).

| **Species** | **Site** | **$\chi^2$ (df)** | **P** | **Post-hoc Nemenyi** | **Z** | **r** |
|---|---|---|---|---|---|---|
| Curlew | BB | 2.466 (1) | 0.116 | NS | | |
| | HB | 11.772 (2) | 0.003** | 0>L p = 0.012*<br>0>H p = <0.001*** | 2.48<br>3.241 | 0.33<br>0.43 |
| | OB | 1.354 (2) | 0.508 | NS | | |
| Black-tailed godwit | BB | 6.315 (1) | 0.012* | H>L p = 0.011* | 2.513 | 0.36 |
| | HB | 0.110 (2) | 0.946 | NS | | |
| | OB | 0.106 (2) | 0.948 | NS | | |
| Oystercatcher | BB | 5.793 (1) | 0.016* | H>L p = 0.015* | 2.407 | 0.35 |
| | HB | 14.696 (2) | <0.001*** | 0>H p = <0.001***<br>0>L p = 0.011* | 3.697<br>2.505 | 0.49<br>0.33 |
| | OB | 0.139 | 0.933 | NS | | |
| Redshank | BB | 0.915 (1) | 0.339 | NS | | |
| | HB | 4.405 (2) | 0.111 | NS | | |
| | OB | 0.814 (2) | 0.666 | NS | | |
| Dunlin | BB | 1.043 (1) | 0.307 | NS | | |
| | HB | 2.026 (2) | 0.363 | NS | | |
| | OB | 4.080 (2) | 0.130 | NS | | |

There were significant effects from previous macroalgal mat coverage on species densities in winter. Curlew density was greater on bare mud than either low or high levels of previous macroalgal mat coverage in Holes Bay. The density of black-tailed godwits was greater on high levels of previous macroalgal mat coverage than low levels in Brands Bay. Oystercatcher density was greater on high levels of previous macroalgal mat coverage compared to low levels in Brands Bay, and greater on '0' levels compared to both high and low levels of previous macroalgal mat coverage in Holes Bay whereas they were unaffected by the surface coverage of algae in autumn. For each of the significant results in winter, the effect size was medium (r>0.30). Redshank and dunlin were unaffected by the previous algae coverage.

In summary, mean density of black-tailed godwits was significantly higher in Brands Bay in Y2 than Y1; mean density at other sites did not vary between years. There was seasonal variation in wading bird density between the sites although, where significant differences were recorded, densities in Brands Bay were always lower than either Holes Bay or Ower Bay. Curlew density at Holes Bay varied significantly under autumn macroalgal mat coverage; the effect size in was medium (r = 0.35). Curlew and dunlin densities also varied significantly in autumn at Brands Bay although the post-hoc test was not significant. Curlew and oystercatcher densities at Holes Bay varied significantly in winter on areas of previous peak macroalgal mat coverage; densities were higher on ‘0’ than either low or high previous coverage with a medium effect size (r>0.3). Densities of black-tailed godwits and oystercatchers were higher in winter at Brands Bay on high levels of previous coverage compared to low; again, the effect size was medium (r>0.3).

## 5.5 Discussion

### 5.5.1 Spatial and temporal variation in bird numbers

With the exception of black-tailed godwit, bird numbers were similar between years. Winter 2013/2014 was one of the wettest on record with areas along the south coast experiencing flooding (www.metoffice.gov.uk). It is possible that large numbers of black-tailed godwits re-located to flooded meadows further inland in order to take advantage of the sudden abundance of available prey (Gill et al. 2007). Black-tailed godwit numbers were higher in Poole Harbour in 2014/2015 (average count 2,636) than 2013/2014 (average count 2,070) (Frost et al. 2016).

It had been expected that Holes Bay would record the highest densities of all studied wading bird species given that this site contained the greatest amount of energy for each bird species’ BIM (Chapter 4, Section 4.5.3). Although densities of individual wading bird species did vary between sites, this variation was not consistent with differences in available BIM (discussed in Chapter 4, section 4.6.3). Ower Bay recorded a significantly higher density of curlews than either Brands Bay or Holes Bay and a significantly higher density of oystercatchers than Holes Bay. This is despite Ower Bay being the smallest of the three study sites.

### 5.5.2 Shore-level and bird distribution

It was not surprising that redshank density was affected by shore-level as this species will follow the receding tide to forage (Goss-Custard 1970). However, density was highest on mid-shore levels in Brands Bay in autumn rather than the upper or lower shore areas. Redshank will also forage alongside channels (Goss-Custard et al. 1977) which, in Brands Bay, were a feature of mid-shore areas. This foraging behaviour is likely to account for the impact of shore level in winter in the smallest study area, Ower Bay.

Black-tailed godwit density was affected by shore-level in Brands Bay with fewer birds recorded on the upper shore than the mid-shore. Brands Bay is the largest of the three study sites with an extensive mid-shore area. During the autumn months, the majority of black-tailed godwits were recorded feeding on the lower and mid shore areas in the south-west of the study site. However, there was an observed change in behaviour during the winter months as large numbers of black-tailed godwits were recorded within the north-eastern patches; shore-level was not significant for black-tailed godwit abundance during winter.

It is possible that birds avoided some upper shore patches, not as a result of higher macroalgal mat coverage but because these areas were subject to human disturbance (Burton et al. 2002). However, although quantifying bird response to disturbance was outside the scope of this study, some personal observations were made. Holes Bay was most prone to disturbance from walkers, runners and cyclists using the footpath around the northern and eastern edge of the bay (see Appendix 2). Observations of feeding behaviour on areas of upper shore adjacent to the path showed that birds appeared undisturbed by the human traffic or even the vehicle noise from the main road <20 m away. Bird surveys in Brands Bay were carried out from a hide located approximately 10 m above the mudflats with birds seen foraging on the upper shore area immediately below the hide. Ower Bay is very secluded and not accessible by car and there were only a few occasions when other people were present at the vantage point. Wading birds were observed foraging in areas of upper shore adjacent to the vantage point although birds appeared to prefer upper shore areas on the opposite bank (see Appendix 2 for location of vantage point at each bay).

### 5.5.3 The impact of surface coverage (autumn) and previously recorded peak coverage (winter) of macroalgal mats on wading bird densities

Of the five wading bird species studied, only variation in densities of curlew and dunlin were significantly affected by autumn coverage of macroalgal mats. By contrast, areas likely to contain residual algae following the summer 'peak' coverage had a significant effect on densities of curlew, black-tailed godwit and oystercatcher. It is worth noting that there were no areas in Brands Bay which remained free from macroalgal mat coverage during the preceding summer growth and therefore it is assumed that no areas in Brands Bay were without some level of residual algae.

_Curlew_

To date there have been no studies specifically examining the impact of macroalgal mats on curlew. It had been expected that the larger wading birds (particularly curlew) would be most susceptible to the impact of macroalgal mats in Poole Harbour. This could be due, in part, to increased interspecific competition as larger prey items move upwards in the sediment column, due to the development of anoxic/hypoxic conditions, thereby becoming available to smaller wading bird species (Lewis and Kelly 2001). This has been discussed in Chapter 3. Given the shape and length of its bill, it had been expected that curlews would be able to penetrate the algae to access prey. However Finn et al. (2008) reported a negative correlation between density of substrate and density of Eastern curlew (*Numenius madagascariensis* [Linnaeus, 1766]) which could suggest that curlews may find penetrating dense macroalgal mat difficult. In addition a curlew bill is not as robust as some other wading bird species due to the curved design and is therefore restricted to feeding on softer sediment (Davidson et al. 1986).

It is possible that variation in wading bird distribution may be due to morphological differences in the different *Ulva* species recorded at each site. The *Ulva* spp. recorded at Brands Bay comprised dense, tubular/filamentous morphology. It is possible that the overall variation in density of curlews on the site was due, in part, to the dense algae preventing access to suitable prey. Yet, although the pair-wise analysis was not significant there was a greater median density of curlew on low algae compared to either '0' or high algae coverage in Brands Bay. In addition, there was no significant difference in curlew density on different algae coverage at Ower Bay; the site where the greatest density of curlews was recorded. The dominant algae species at Ower Bay was also the tubular/filamentous *Ulva* spp. and coverage remained high at the upper shore throughout autumn. In addition, *U. clathrata* [(Roth) C. Agardh, 1811] was also recorded at Ower Bay; comprising very fine filamentous fronds also forming dense mats (Brodie et al. 2007). Curlews were observed in Ower Bay actively foraging on all shore levels and all algae coverage. By contrast, there were higher densities of curlews on high algae coverage than low algae coverage in Holes Bay. The macroalgal mat at Holes Bay is formed of less dense, sheet-forming *Ulva* spp.; curlews should be able to penetrate thin sheet-form thalli easier than the tubular/filamentous mats. Curlews were also recorded foraging on patches of high algae coverage in preference to adjacent large patches of bare mud which might indicate a change in feeding strategy at Holes Bay. This site-specific feeding adaptation theory will be explored further in Chapter 6.

It is also worth considering the structure of the mat itself. Although Holes Bay contained the highest curlew BIM, prey items may not be available to the birds (Sutherland 2005). Curlews are the heaviest wading bird overwintering in the UK (male = 716.0 g ±67.97 g, female = 851.8 g ±89.04 g, www.bto.org) and, as such, require a harder substrate upon which to stand (van de Kam et al. 2004). Although % sand was not found to be a determining factor in the variation in curlew BIM, it is worth noting that mean particle size in Holes Bay results in the sediment being classified as ‘fine silt/clay’ whereas Brands Bay is classified as ‘mixed mud/sand’ (Herbert et al. 2010). It is possible that the reason that curlew density was higher on high than low algae coverage in Holes Bay is due to the algae providing the birds with a firmer surface and an alternative food supply. This could be tested in future research using full-size models of curlews and measured density of algae and sediment.

The fact that curlew densities were higher on areas of ‘0’ previous algae compared to both low and high levels supports the findings discussed in Chapter 3. Some invertebrate species (e.g. annelid worms) were affected by % organic in conjunction with algae biomass and it is suggested (although as yet untested) that a significant proportion of the organic content within the sediment comprises fragmented or decaying macroalgal mat. What is of particular note is the implication that algae biomass is still having an effect on curlew distribution despite the surface coverage having disappeared.

*Black-tailed godwit*

As black-tailed godwits are tactile feeders (Granadeiro et al. 2006; Dias et al. 2009), it had been expected that this species would be unable to access prey through the dense macroalgal mats. Yet there was no significant difference between densities of black-tailed godwits on varying levels of macroalgal mat coverage. Indeed, flocks of black-tailed godwits were observed foraging and feeding on adjacent patches of 0% and >50% algae coverage in Holes Bay. This behaviour supports findings from Lewis et al. (2014) indicating that black-tailed godwits were unaffected by increased macroalgal mat coverage. By contrast, Green (et al. 2015) reported that marbled godwits (*L. fedoa*) avoided foraging on areas of higher algae coverage in the Mugu Lagoon, California. However, it is worth noting that the mean coverage of macroalgal mat recorded by Green et al. (2015) was 55% (±0.04%) and the results only compared bird feeding activity on algae or bare mud.

Black-tailed godwit density was higher on high levels of previous algae coverage in Brands Bay. This suggests that the birds are able to obtain a greater amount of energy from areas of Brands Bay that were previously covered by high levels of algae; the implications of this behaviour are explored fully in Chapter 6.

### *Oystercatcher*

It had been expected that oystercatchers would be unaffected by the presence of macroalgal mats as their bill strength would enable them to penetrate the algae successfully (Hulscher 1996). Although the results showed no significant variation in density between varying levels of macroalgal mat coverage, there were fewer oystercatchers recorded during the study than any other species. Therefore, further observations are needed before concluding that macroalgal mat coverage does not affect oystercatcher activity.

By contrast, oystercatchers were significantly affected by previous macroalgal mat coverage in both Brands Bay and Holes Bay. Similar to black-tailed godwits in Brands Bay, it was areas with previously high levels of algae coverage which supported a greater density of oystercatchers. As oystercatcher BIM is very similar to curlew BIM in terms of sizes of invertebrates preferred (although oystercatchers are able to consume larger bivalves), it is not surprising that a similar response was found between the two species in terms of preference for areas of 0 previous algae coverage in Holes Bay. Both oystercatcher and curlew are large wading birds with higher energy requirements necessitating accessing larger prey (Goss-Custard et al. 2006b). Yet oystercatcher BIM was highest in Holes Bay suggesting that there were prey resources available, although these would be predominantly annelid worms. If the macroalgal mats are preventing oystercatchers accessing this prey the birds may have to adopt different feeding strategies in order to ensure their overwinter survival.

*Redshank*

Redshanks adopt a visual feeding strategy during daylight (Dwyer et al. 2013). Therefore it was surprising that redshank distribution was unaffected by macroalgal mat coverage in all three sites. However, this supports the findings from an earlier study in Poole Harbour (Alexesson 2012) which found no significant preference by redshank for algae patches or bare mud in Brands Bay. By contrast, Lewis et al. (2014) found redshanks were negatively affected by the presence of dense macroalgal mats at the Clonakilty Estuary, Ireland. The species was observed altering its feeding strategy and probing through sparse algae coverage but unable to penetrate denser mats. It is worth noting that maximum coverage recorded during the study was 55% at one site (Lewis et al. 2014). In an earlier, experimental study at the same site, Lewis and Kelly (2001) found redshank feeding in greater numbers on algae than on bare mud. However, the study used relatively small experimental plots of 50 m x100 m and 100 m x100 m.

Redshank abundance was unaffected by levels of previous algae coverage. It is probable that the birds were able to visually search the surface of the mud for *Peringia ulvae* [Pennant, 1777], an important alternate prey, which remained abundant throughout the winter months. Variation in feeding strategy in response to macroalgal mat coverage is explored in Chapter 6.

*Dunlin*

There was overall variation in dunlin density on different levels of algae coverage. However, there were no dunlins recorded on high algae coverage in Brands Bay during the study period. The average length of a dunlin bill is 3 cm (van de Kam et al. 2004) therefore it is possible that macroalgal mat formed of dense tubular/filamentous *Ulva* in Brands Bay presented a thick barrier to the dunlin preventing the birds penetrating beneath the mat to access their prey. The results support studies carried out on the Tagus Estuary (Cabral et al. 1999) which reported a significant negative effect on dunlin distribution on macroalgal mats. However, it is worth noting that macroalgal mat coverage never exceeded 36% during that study. Dunlins were recorded foraging on high algae coverage in Holes Bay, although the variation in dunlin density and macroalgal mat coverage was not significant.

Dunlin distribution was unaffected by previous algae coverage. This could be due, in part, to the high numbers of an important item (*P. ulvae*) still being present and accessible to the dunlin during the winter (Chapter 4, Fig. 4.2a – 4.2c).

### 5.5.4 Summary

Earlier studies indicated that birds would be unlikely to be impacted by macroalgal mats particularly as these tended to break up during autumn (Lambeck et al. 1996). What this study has shown is that, with the exception of redshank, all species are affected by macroalgal mats at some point during the overwintering season. Of the five wading bird species studied, it is the curlew that is most affected by macroalgal mats (either visible coverage or previous coverage).

What is also apparent from the results is that using prey availability alone cannot predict the distribution of wading bird species. By virtue of the area containing the highest BIM, Holes Bay should have supported the highest density of all wading birds studied. Yet this was not the case with Ower Bay supporting higher autumn densities of curlews and oystercatchers and a higher density of redshank than Brands Bay. It is important to consider the accessibility of prey items as it has been shown that macroalgal mats are potentially impacting wading bird ability to access suitable prey items which could have consequences for the bird’s ability to maintain required energy levels (Goss-Custard et al. 2002; Sutherland et al 2005). However, not all wading bird species respond in the same way to fluctuations in prey availability. Oystercatchers and curlews, for example, are site faithful with populations remaining similar in size despite fluctuations in resources (van de Kam et al. 2004). By contrast, it has been suggested that redshanks will only return to an overwintering site where there is an abundance of preferred prey (van de Kam et al. 2004). Given that wading birds will return to the same overwintering area each year, it is likely that they will be adapted to variation in conditions at each site (Gill et al. 2001b; Gunnarsson et al. 2005b). The appearance of dense macroalgal mats was first reported in Holes Bay (Poole Harbour) in 1972 (Fletcher 1996; Langston et al. 2003). Table 5.6 shows the typical and maximum recorded lifespan for each of the five studied wading birds.

**Table 5.6:** Typical lifespan and maximum-recorded lifespan for the five studied wading bird species. Data taken from British Trust for Ornithology (www.bto.org).

| Species | Typical lifespan | Maximum recorded (year of record) |
|---|---|---|
| Curlew | 5 years | 32 years (2011) |
| Black-tailed godwit | 18 years | 23 years (2001) |
| Oystercatcher | 12 years | 40 years (2010) |
| Redshank | 4 years | 20 years (2007) |
| Dunlin | 5 years | 19 years (2010) |

With typical lifespans ranging from 4 years to 18 years it is reasonable to suppose that the birds have become adapted to the site conditions. Indeed, even if each individual bird reached the maximum recorded life-span they would be unaware of pre-macroalgal mat conditions in Poole Harbour.

The contradictory studies highlighted in this chapter demonstrate a clear indication that a species-specific response to macroalgal mats in one area cannot predict the response in another; one behavioural response does not ‘fit all’. Within the harbour itself this study has shown that birds appear to be adapting to the conditions prevalent in individual bays, although behaviour remains consistent within each bay. Longer-lived species may remain ‘faithful’ to a site even as the quality of this site deteriorates resulting in a ‘lag’ between environmental conditions worsening and a noticeable decline in bird numbers (West et al. 2007). There is a trade-off between travelling further from their preferred breeding ground and finding a site with sufficient prey to sustain their winter feeding (Gill et al. 2001b). In addition, suitable sites along the south coast (including Langstone and Chichester Harbours) are also susceptible to dense areas of macroalgal mat coverage (Hull 1987); thereby reducing the choice of overwintering site still further. This has implications for the wading bird population in terms of the overall conservation of the SPA feature and may affect breeding success the following season (Gill et al. 2001b). This is particularly important if bird numbers remain the main indicator of estuarine ecosystem health (Durell et al. 2006).

BLANK

# 6.0 Changes to wading bird feeding rate in response to macroalgal mat coverage

## Abstract

Wading birds will feed in areas where they can optimise their energy intake; although these may not always be the most profitable areas due to a wide range of disturbances. An important research theme is whether the macroalgal mat is causing changes to a wading bird's feeding rate (defined as the number of times a bird swallows per minute). Birds may display an aversion to, or preference for, areas covered by macroalgal mat, yet there could be subtle differences in feeding rate that might indicate a reduction in energy intake. These changes, albeit small, could have a cumulative effect resulting in birds not reaching the required weight in order to ensure successful breeding.

This chapter examines feeding rate of wading birds under varying levels of macroalgal mat coverage. Five species of wading bird; Eurasian curlew (*Numenius arquata*); black-tailed godwit (*Limosa limosa*); oystercatcher (*Haematopus ostralegus*); redshank (*Tringa totanus*) and dunlin (*Calidris alpina*) were selected for study. A total of 535 digital video recordings were taken of bird feeding behaviour on areas of intertidal mudflats and on varying levels of macroalgal mat coverage. Recordings were taken during the period 1hr before to 1hr after low water on both neap and spring tides between September 2013 – March 2014 and September 2014 – March 2015. Feeding rate (number of swallows $min^{-1}$) was determined for curlew, black-tailed godwit, oystercatcher and redshank, and a peck rate (number $min^{-1}$) determined for dunlin. Analysis showed apparent behavioural adaptations to the presence of macroalgal mats including a higher feeding rate by black-tailed godwits on high levels of macroalgal mat coverage in Brands Bay; where they appeared to be consuming smaller prey items. Curlews were recorded foraging for prey on the surface of the macroalgal mat and shaking sheets of *Ulva* spp. to dislodge prey, notably shore crabs. These behavioural changes may have implications for each individual wading bird's ability to meet its daily energy requirement and maintain fitness in order to be able to return to the breeding ground in spring.

BLANK

## 6.1 Introduction

Determining whether an overwintering bird population is able to obtain sufficient prey in order to return to their spring breeding ground is a key conservation objective associated with a Special Protection Area (SPA) designated for populations of overwintering migratory wading birds (West et al. 2005; Durell et al. 2006; Stillman et al. 2010; JNCC 2013). Any indication that these birds are unable to feed effectively or efficiently could result in a decline in the individual species numbers or the overall assemblage of wading birds (West et al. 2007). An important research theme when assessing the overall impact of macroalgal mats on wading birds is the question of whether the macroalgal mat is causing changes to a wading bird’s feeding rate (defined as the number of times a bird swallows per minute). To date, there have been few studies specifically examining feeding rate under varying levels of macroalgal mat cover. Lewis et al. (2014) studied feeding rate for black-tailed godwit and redshank on varying macroalgal mat coverage in the Clonakilty Estuary, Ireland. Black-tailed godwits made fewer foraging attempts on areas of macroalgal mat coverage whereas redshanks made a similar number of foraging attempts on bare mud and algae covered patches but with a reduced feeding rate on algae areas. The maximum macroalgal mat coverage recorded during that study was 55%.

Wading birds require a large amount of energy in order to survive to return to the breeding areas in spring (Kersten and Piersma 1987) and each species has an optimal ‘diet’ based upon the energy intake requirements together with the need to ensure maximum intake with minimum effort (Goss-Custard et al. 2006b). As discussed in previous chapters, the presence of dense macroalgal mats is transforming the invertebrate community and affecting the energy available to wading birds through their benthic invertebrate menu (BIM). Using the sizes of prey recorded to determine energy availability, it was shown in Chapter 4 that the most profitable of the three study sites in terms of bird BIM was Holes Bay. However, the distribution of wading birds recorded and discussed in Chapter 5 suggested that birds were not always foraging in the most profitable areas. In Chapter 5 it was reported that density of curlews (*Numenius arquata* [Linnaeus, 1758]) was affected in certain areas by the presence of macroalgal mats. In addition, densities of curlews, oystercatchers (*Haematopus ostralegus* [Linnaeus 1758]) and black-tailed godwits (*Limosa limosa* [Linnaeus, 1758]) were affected by the previous algae coverage in Brands Bay and Holes Bay. Birds may display an aversion to, or preference for, areas covered by macroalgal mat yet there could be subtle differences in feeding rate that might indicate a reduction in energy intake. These changes, albeit small, could have a cumulative effect resulting in birds not reaching the required weight in order to ensure successful breeding (Goss-Custard et al. 2006a).

There are two techniques adopted by overwintering wading bird species when foraging for benthic invertebrates in soft sediment habitats; tactile or visual (Davidson et al. 1986; Dias et al 2009). Curlews will adopt both tactile and visual foraging strategies (Davidson et al. 1986) although it is not fully understood how prey are located within the sediment but it has been suggested that the length and curvature of a curlew's bill enables the bird to access larger prey from deeper burrows (Ferns and Siman 1994). By contrast, black-tailed godwits are reported to adopt a tactile foraging strategy with a series of several quick probes into the sediment often described as a 'sewing machine' technique (Dias et al. 2009). Oystercatchers will utilise both tactile and visual feeding techniques; probing in the sediment to obtain large worms and buried bivalves by touch and also visually searching the surface for bivalves and crabs (van de Pol et al. 2009). Redshank (*Tringa totanus* [Linnaeus, 1758]) adopt a characteristic 'run stop peck' visual feeding strategy searching for evidence of invertebrates in the sediment or prey on the surface (Little 2000) and will adopt a tactile feeding strategy at night (Dwyer et al. 2013). Dunlin (*Calidris alpina* [Linnaeus, 1758]) visually search and peck the surface of the sediment for small hydrobid snails and crustaceans and probe the sediment to 'crop' bivalve siphons (Martins et al. 2013). Birds will switch between strategies and, during night feeding, those birds which rely on a visual foraging strategy during the day will switch to a tactile approach (Mouritsen 1994; Dwyer et al. 2013).

### 6.1.1 Methods for recording feeding success and prey selection

Given that most feeding on intertidal areas takes place at low water when the mudflats are exposed, wading bird feeding behaviour can be observed and analysed with relative ease from a suitable shoreline vantage point (Goss-Custard et al. 1991; Dias 2009). However, observing and recording feeding success and size of prey taken is more difficult.

*Field observations*

Most wading birds display a very distinctive 'swallowing' motion when a prey item is taken and this can be easily recorded during observations of birds at low water (Dias et al. 2009). Figure 6.1 shows a sequence of feeding success for a black-tailed godwit from prey acquisition, moving the item up the bill and finally swallowing. The video sequence (Chapter 6 Fig 6,1 black-tailed godwits feeding in Brands Bay) is provided in the attached cd.  This motion can be differentiated from a bird lifting its head in order to check for predators by the upward tilting and rapid head movement indicating swallowing (Fitzpatrick and Bouchez 1998).

**Fig. 6.1:** Black-tailed godwit feeding sequence taken from video recording on 4th November 2014 in Brands Bay on low (5%-50%) algae coverage at the mid-shore level.  A:  prey located, B: prey in bill, C: prey swallowed.  Photos: © A. Thornton.  The full video sequence (Chapter 6 Fig 6,1 black-tailed godwits feeding in Brands Bay) is provided in the attached cd.

Although, as Fig. 6.1 shows, it is clear when a bird has swallowed prey, accurate determination of prey species taken can be problematic using field observations alone (Goss-Custard and Jones 1976).  Variation in bill size, light conditions, distance from the bird, and speed of prey handling were all reported to contribute to both underestimation and overestimation of energy intake from a prey item (Lee and Hockey 2001).  A study on the intertidal mudflats of the Ria de Huelva, Spain, recording feeding behaviour and prey selection by black-tailed godwits found difficulty in determining prey items taken; analysis could only sort prey items into two categories, ‘worm’ and ‘unidentified prey’ which, it was reported, could also include small worms (Dominguez 2002).

*Video recordings*

Digital video recording of bird behaviour provides a more reliable method for determining feeding success (Lee and Hockey 2001; Sutherland et al. 2005).  Analysis can be carried out using computer video technology enabling recordings to be slowed down and played back repeatedly ensuring more accurate counts of swallowing and, in many cases, determination of prey taken.  This reduces the observer error reported in other studies (Lee and Hockey 2001).  Using digital video recordings Martins et al. (2013) determined changes in foraging and feeding strategies adopted by migrating dunlin on intertidal areas of the Tagus Estuary, Portugal. From recordings taken at a short distance it was possible to determine the proportion of the dunlin diet derived from *Hediste diversicolor* [O. F. Müller 1776] and *Scrobicularia plana* [da Costa, 1778] (Martins et al. 2013). Variation in predator avoidance and flocking behaviour was analysed using video recordings of dunlin flocks adopting visual or tactile feeding behaviour (Barbosa 1997).

*Droppings*

An additional method used to support the video analysis is the collection of droppings (Sutherland et al. 2005). Analysis of droppings collected at a suitable interval following the video recording can be used to corroborate the determination of prey items taken (Goss-Custard and Jones 1976; Rippe and Dierscheke 1977; Sutherland et al. 2005). Success using this method relies upon the researcher's ability to locate and collect droppings without causing unnecessary disturbance to the birds or the dropping itself being washed away. The collection of droppings on a rising tide or at a roost site can prevent birds being disturbed whilst feeding and this method was adopted by Santos et al. (2005) when examining the diet of overwintering dunlin on the Tagus Estuary. Cabral et al. (1991) used experimental plots of 1ha and was able to collect droppings by observing the species location and following the bird footprints. Martins et al. (2013) observed dunlin feeding in the study area for 1 hour before collecting droppings to ensure they contained prey from the survey location. However, there is danger that prey items or identifiable fragments may not survive the digestion process (Goss-Custard and Jones 1976).

### 6.1.2 Bird feeding in Poole Harbour

*Feeding rate*

There remains some confusion around the terms 'feeding rate' and 'intake rate' (Goss-Custard et al. 2006b). For the purposes of this research, feeding rate is the number of times an individual bird is observed swallowing per unit time (Goss-Custard et al. 2002). Intake rate refers to the amount of energy consumed by an individual wading bird and requires an accurate determination of the size and species of prey item consumed (Goss-Custard et al. 2006b). Feeding rate is a wading bird's functional response to the abundance and availability of suitable invertebrate prey (Goss-Custard et al. 2006b).

Holes Bay contained significantly greater energy than either Brands Bay or Ower Bay for each of the studied wading bird species' BIM; although there was no difference in energy available between Brands Bay and Ower Bay for any of the wading bird's BIM. This led to the expectation that there would be correspondingly fewer birds feeding in Ower Bay and Brands Bay than in Holes Bay (Pickess and Underhill-Day 2002). As shown in Chapter 5 this was not evident from the observations; there was no variation between sites for the total numbers of the five key wading bird species. Indeed, both curlew and oystercatcher numbers were significantly higher in Ower Bay than either Brands Bay or Holes Bay.

Droppings were not collected for this research as the consistency of the sediment in Poole Harbour prevented easy and timely access. In addition, the surface water film on the mud would have led to the breakdown of the dropping before it could be collected.

### 6.1.3 Rationale

This chapter will address a gap in the knowledge by assessing whether wading bird feeding rate is affected by the presence of macroalgal mats. It has already been suggested that macroalgal mats are transforming the invertebrate community and, as a consequence, impacting upon the wading bird's BIM. Yet wading birds will feed in areas where they can optimise their energy intake (Dias et al. 2009); although these may not always be the most profitable areas (Stillman and Goss-Custard 2010). It is not possible for birds to take prey items which are larger than their gullet (Davidson et al. 1986). However, there is also a maximum feeding rate even if a bird is consuming prey within their BIM; feeding rate will be limited by the time needed for the gut to process prey (Goss-Custard et al. 2006a).

Digital video recordings were made of bird feeding rate under different algae coverage to compare the effect of macroalgal mat coverage at different sites. Research also examined whether birds are adapting to the presence of macroalgal mats and modifying their feeding behaviour to compensate by exploiting new or alternative food sources. In addition, the analysis should determine whether species-specific foraging behaviour on levels of macroalgal mat coverage is site-specific or consistent between sites.

## 6.2 Aims and objectives

| | |
|---|---|
| **Aim 1:** | To establish whether the macroalgal mat is contributing to variations in feeding rate of predatory wading birds. |
| **Aim 2:** | To determine whether there are behavioural adaptations apparent on varying levels of macroalgal mat coverage. |
| **Aim 3:** | To predict the time required for wading birds to reach their daily energy requirement (DER) at each site if consuming preferred-size prey or smallest-size prey. |

| | |
|---|---|
| **Objective 1:** | Observe and record the behaviour of key wading bird species over the course of two winter seasons (September – March 2013/2014, and September – March 2014/2015). |
| **Objective 2:** | Use video recordings of bird feeding behaviour to establish a feeding rate for each wading bird species on varying levels of macroalgal mat coverage. |
| **Objective 3:** | Establish wading bird DER and plot predicted intake rate for two prey sizes using feeding rate recorded. |

## 6.3 Methods

### 6.3.1 Digital video recording

Five species of wading bird; Eurasian curlew (*Numenius arquata* [Linnaeus 1758]); black-tailed godwit (*Limosa limosa* [Linnaeus 1758]); oystercatcher (*Haematopus ostralegus* [Linnaeus 1758]); redshank (*Tringa totanus* [Linnaeus 1758]); and dunlin (*Calidris alpina* [Linnaeus 1758]), were selected for study. Digital video recordings were made in daylight and in suitable weather conditions during the period 1hr before to 1hr after low water on both neap and spring tides between September 2013 – March 2014 and September 2014 – March 2015 in conjunction with observation surveys detailed in Section 5.4.3. Species were recorded at all three sites and all shore-levels (where possible) during the two survey seasons and on varying levels of macroalgal mat coverage. Each recording was two minutes in length and made using a Swarowski 20-60 zoom telescope with a Swarowski digiscope attachment on a Pentax K30 digital camera recording in HD 1087p. The same individual was not recorded more than once in the same area of the bay. Given the number of overwintering birds present in Poole Harbour, it is unlikely that the same individual would be recorded on more than one occasion in any year. Videos were replayed on computer in slower motion and the length of the recording for each individual was noted; recordings of <30seconds were rejected.  Where more than five birds were recorded, five individuals were randomly selected for analysis.  Videos were also assessed for quality and recordings were rejected if the bird's swallowing motion was not clearly visible.  The maximum distance for a successful recording varied according to the size of species, the size of the site, and weather conditions at the time of recording.

### 6.3.2 Feeding rate

Feeding rate was determined by counting the number of swallowing motions by individual birds per minute.  This was possible for curlew, black-tailed godwit, oystercatcher and redshank as these species display clear swallowing motion when taking prey, even if the prey item is not visible.  It was not possible to determine a distinct swallowing motion by dunlin as the species adopts a pecking foraging strategy and will take up prey without lifting its head (Santos et al. 2005).  Therefore, for the purposes of this study, peck rate (number of pecks per minute) was recorded for dunlin.

### 6.3.3 Algae coverage

Recordings of each species were made on varying levels of algae coverage which were confirmed during video analysis.  Algae coverage was recorded on three levels 0 (<5% cover), low (L) (5%-50% cover), high (H) (51%-100% cover).  The level of coverage was determined by the location of the recorded bird within the frame of the video not the overall coverage of the patch.  This provided an indication of behaviour in adjacent patches of algae and bare mud.

#### *6.3.3.1 Determining feeding strategy*

Recordings were also analysed to determine whether wading birds could be observed alternating between visual and tactile feeding strategies whilst foraging.  Birds using visual techniques were observed looking for prey items or evidence of buried prey by tilting their head, pecking from the macroalgal mat or sediment surface or changing direction suddenly to peck or probe for prey.  Tactile feeding techniques involved rapid probing into the macroalgal mat or sediment, rapid surface pecking, or random probing of the sediment.

#### *6.3.3.2 Calculation of daily energy requirements using basal metabolic rate*

The difference in number of hours required for each bird to obtain its daily energy requirement (DER) were calculated for each wading bird species consuming preferred prey size within its BIM, and the smallest prey size. Preferred prey size was calculated as the mean size of prey within each invertebrate group for each wading bird BIM that was available at each of the three sites. An example is shown in Table 6.1 with details of values for all size classes used provided in Appendix 7 and AFDM equations provided in Appendix 3. An energy value was calculated from the AFDM of an individual of the mean preferred size and smallest size using the formula based on calculations by Zwarts and Wanink (1993):

$$Energy\ (kJ) = AFDM\ g * 22$$

**Table 6.1:** Example showing how the mean size value was calculated for curlew's preferred size of *C. edule* available from samples taken in Holes Bay.

| Wading bird | Preferred prey size within BIM | Size range available at Holes Bay | Mean size for determining DER |
|---|---|---|---|
| Curlew | *C. edule* 5 - 20 mm | 5 mm - 20 mm | 12.5 mm |

Basal metabolic rate (BMR) is calculated using formula in Kersten and Piersma (1987):

$$BMR = 437 * (body\ weight\ kg)^{0.729}$$

Body weight for each species of wading bird was taken from BTO Bird Facts website (BTO 2016) with average weight used where males and females differ. Full details are provided in Appendix 7.

The DER for a foraging / resting wading bird was determined using formula in Kersten and Piersma (1987). The value of 2.1 is calculated from the energy expenditure for cage existence metabolism (2*BMR) plus an additional 10% estimated energy required for periods of flight taken as the mid-point of 10-30 minutes (Zwarts et al. 1996).

$$DER = 2.1 * (BMR)$$

### 6.3.4 Analysis

#### *6.3.4.3 Spatial and temporal variation in feeding rate*

All analysis was carried out using R version 3.0.3 “Supposedly Educational”, (R Core Team 2016).

Counts of successful swallowing were converted to feeding rate. Assumptions of normality and homogeneity of variance were checked using Shapiro Wilks test within the “stats” package in R (R Core Team 2016) and Levene test within the “car” package developed for R (Fox and Weisberg 2011) respectively. Variation in feeding rate between sites was analysed using ANOVA with post-hoc Tukey test within the “stats” package in R (R Core Team 2016). Variation in dunlin peck rate between sites was carried out using Welch’s one-way ANOVA (not assuming equal variance) with post-hoc Games-Howell test carried out using the “userfriendlyscience” package developed for R (Peters 2016). Seasonal variation in feeding rate for each species was tested using ANOVA. Effect size, using Pearson’s r correlation coefficient, was determined for significant pairs using exact Wilcoxon-Mann-Whitney Test to obtain z scores then the equation r = z/sqrt(N) with N being the number of samples (Barto and Rillig 2012; Field 2012). Effect sizes are defined as small (r = <0.3), medium (r = <0.5), large (r = >0.5) (Cohen 1994).

#### *6.3.4.4 Variation in feeding rate under macroalgal mat coverage*

Within-site variation in feeding rate under macroalgal mat coverage was analysed using ANOVA with Tukey post-hoc tests within the “stats package” for R (R Core Team 2016) or non-parametric Kruskall-Wallis test (R Core Team 2016) with post-hoc Nemenyi tests carried out using “PMCMR” package developed for R (Pohlert 2014). Between-site variation in feeding rate on levels of macroalgal mat coverage was determined using ANOVA with Tukey post-hoc tests within the ‘stats’ package for R (R Core Team 2016). Effect size (r) was calculated using exact Wilcoxon-Mann-Whitney Test as detailed above.

## 6.4 Results

### 6.4.1 Number of recordings per species

Table 6.2 provides details of the number of recordings taken for each wading bird species and the level of macroalgal mat coverage visible in the recording. Site conditions and the rapid fragmentation of the macroalgal mat in Holes Bay resulted in some wading birds not being recorded on low levels of macroalgal mat coverage at this site.

**Table 6.2:** Number of individual birds recorded per site and on each level of macroalgal mat coverage. Levels of coverage 0 (<5%), Low (5% - 50%), High (51% - 100%).

| Species | Site | Total recordings | 0 algae coverage | Low algae coverage | High algae coverage |
|---|---|---|---|---|---|
| Curlew | Brands Bay | 15 | 7 | 5 | 3 |
| | Holes Bay | 18 | 12 | 0 | 6 |
| | Ower Bay | 32 | 15 | 9 | 8 |
| Black-tailed godwit | Brands Bay | 92 | 11 | 56 | 25 |
| | Holes Bay | 68 | 39 | 14 | 15 |
| | Ower Bay | 44 | 9 | 29 | 6 |
| Oystercatcher | Brands Bay | 15 | 5 | 8 | 2 |
| | Holes Bay | 9 | 8 | 0 | 1 |
| | Ower Bay | 29 | 15 | 7 | 7 |
| Redshank | Brands Bay | 20 | 13 | 4 | 7 |
| | Holes Bay | 31 | 26 | 0 | 5 |
| | Ower Bay | 34 | 15 | 15 | 4 |
| Dunlin | Brands Bay | 56 | 44 | 12 | 0 |
| | Holes Bay | 8 | 8 | 0 | 0 |
| | Ower Bay | 64 | 32 | 27 | 5 |

### 6.4.2 Spatial and temporal variation in feeding rate

#### *6.4.2.1 Between-site variation in feeding rate*

Table 6.3 provides details on variations in wading bird feeding rate between sites irrespective of date.

**Table 6.3:** Variation in mean feeding rate (No. $min^{-1}$) between sites for curlew, black-tailed godwit, oystercatcher and redshank, and variation in mean peck rate (No. $min^{-1}$) for dunlin. Significance codes: *** = <0.001 ** = <0.01 * = <0.05. NS = not significant (p = >0.05). BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

| Species | F (df) | P | Post-hoc Tukey |
|---|---|---|---|
| Curlew | 2.159 (2, 62) | 0.124 | NS |
| Black-tailed godwit | 96.704 (2, 62) | <0.001*** | BB>HB p = <0.001***<br>BB>OB p = <0.001***<br>OB>HB p = <0.001*** |
| Oystercatcher | 3.42 (2, 62) | 0.041* | OB>BB p = 0.036* |
| Redshank | 0.219 (2, 62) | 0.804 | NS |
| Dunlin | 7.866 (2, 19.696) | 0.003** | BB>OB p = 0.009** |

Mean black-tailed godwit feeding rate varied significantly between all sites with the highest mean feeding rate recorded in Brands Bay. Oystercatcher mean feeding rate was higher in Ower Bay than Brands Bay. Dunlin mean peck rate was higher in Brands Bay than Ower Bay.

#### *6.4.2.2 Within-site variation in feeding rate between seasons*

Although there was some variation in feeding rate between seasons, there was no pattern. Curlew feeding rate was higher in winter whereas black-tailed godwit, oystercatcher and redshank recorded a higher mean feeding rate in autumn. By contrast, winter feeding rate for oystercatcher was higher in winter than autumn in Holes Bay. Table 6.4 provides details of the analysis and post-hoc tests on wading bird feeding rate between seasons per site; autumn (September-November), winter (December- March).

**Table 6.4:** Variation in mean feeding rate (No. min$^{-1}$) within sites for curlew, black-tailed godwit, oystercatcher and redshank, and variation in mean peck rate (No. min$^{-1}$) for dunlin between seasons; autumn (September-November), winter (December- March).
Significance codes: *** = <0.001 ** = <0.01 * = <0.05. NS = not significant (p = >0.05).
BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

| Species | Site | F (df) | P |
|---|---|---|---|
| Curlew | BB | 5.894 (1,13) | Winter > autumn p = 0.031* |
| | HB | 3.031 (1,16) | NS p = 0.101 |
| | OB | 1.878 (1,30) | NS p = 0.181 |
| Black-tailed godwit | BB | 9.506 (1,90) | Autumn > winter p = 0.003** |
| | HB | 2.168 (1,66) | NS p = 0.146 |
| | OB | 0.051 (1,42) | NS p = 0.823 |
| Oystercatcher | BB | 6.998 (1,13) | Autumn > winter p = 0.020* |
| | HB | 7.687 (1,7) | Winter > autumn p = 0.028* |
| | OB | 0.152 (1,27) | NS p = 0.7 |
| Redshank | BB | 15.2 (1,13) | Autumn > winter p = 0.001** |
| | HB | 1.369 (1,29) | NS p = 0.251 |
| | OB | 1.366 (1,32) | NS p = 0.251 |
| Dunlin | BB | 1.357 (1,54) | NS p = 0.249 |
| | HB | NA | NA |
| | OB | 2.901 (1,62) | NS p = 0.094 |

### 6.4.3 The impact of macroalgal mat coverage on feeding rate

*6.4.3.1 Within-site variation in feeding rate under macroalgal mat coverage*

Recording data for both years were combined irrespective of season.

Figure 6.2 shows the feeding rate for curlew, black-tailed godwit, oystercatcher and redshank, and peck rate for dunlin, under varying levels of macroalgal mat coverage within each site.

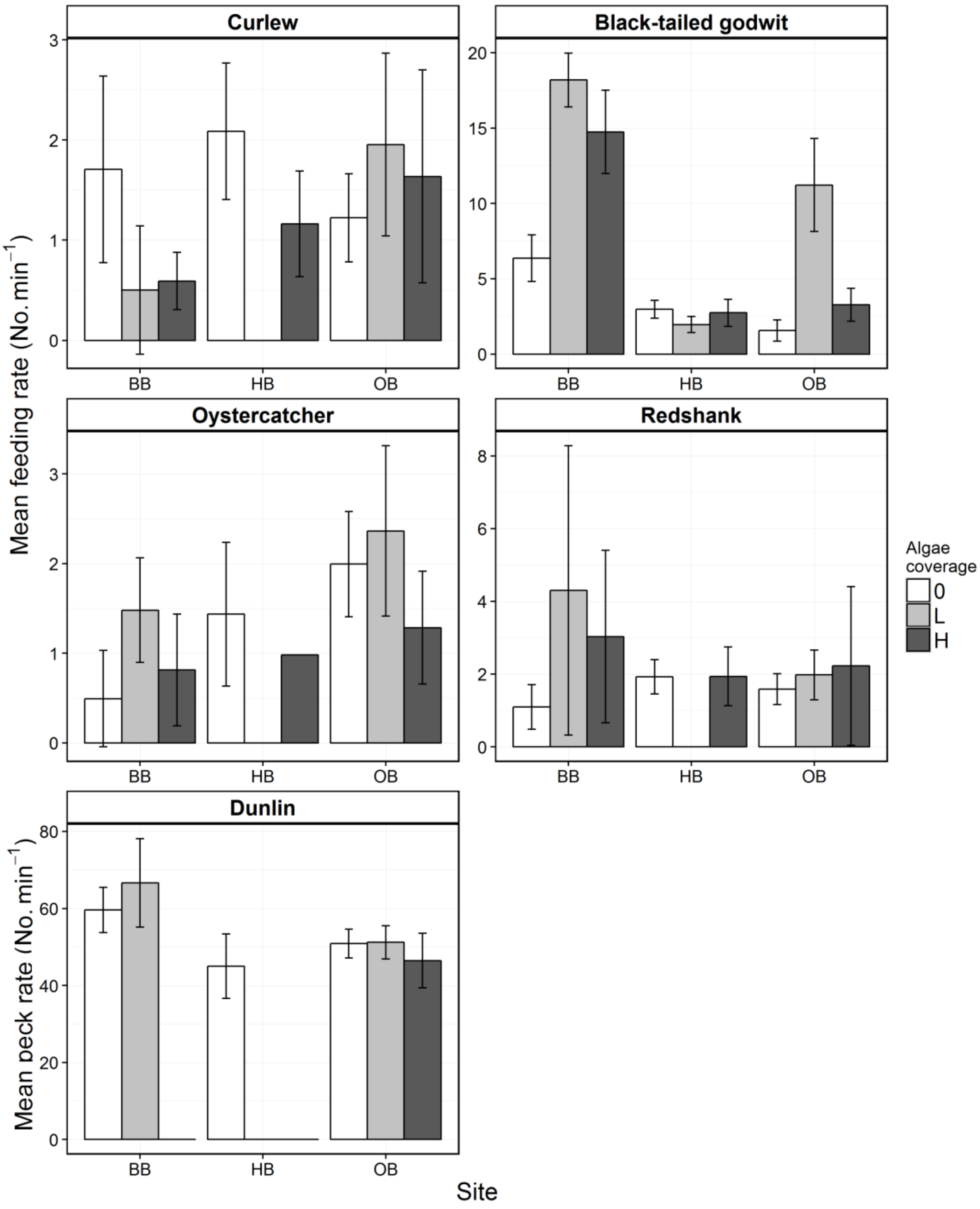


**Fig. 6.2:** Mean feeding rate (No. min$^{-1}$) recorded against levels of macroalgal mat coverage for curlew, black-tailed godwit, oystercatcher, redshank, and peck rate (No. min$^{-1}$) against macroalgal mat coverage for dunlin. Error bars 95% confidence intervals. Macroalgal mat coverage 0 = 0 (<5% cover), L = low (5%-50% cover), H = high (>50% cover).
Data are combined for both years and both seasons.
Site BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

*Black-tailed godwit*

There was very highly significant variation in black-tailed godwit feeding rate between macroalgal mat coverage in Brands Bay ($F_{2,89}$ = 10.32, p = <0.001) with a higher rate on low algae compared to '0' algae (z = 3.8334, p = <0.001, r = 0.40), and a higher feeding rate on high algae compared to '0' algae (z = 3.2883, p = <0.001, r = 0.34). There was very highly significant variation in black-tailed godwit feeding rate between macroalgal mat coverage in Ower Bay ($\chi^2$=25.628, df = 2, p = <0.001) with a higher feeding rate on low algae compared to '0' algae (z = 4.4832, p = <0.001, r = 0.68), and a higher feeding rate on low algae compared to high algae (z = 2.9773, p = <0.01, r = 0.45). There was no significant variation in feeding rate for black-tailed godwits on different macroalgal mat coverage in Holes Bay.

*Redshank*

Redshank feeding rate varied significantly under different macroalgal mat coverage in Brands Bay ($F_{2, 17}$ = 4.073, p = 0.036) but no pair-wise significance was found. There was no significant variation in feeding rate under varying macroalgal mat coverage in Holes Bay or Ower Bay.

*Curlew, oystercatcher and dunlin*

Curlew and oystercatcher feeding rate did not vary significantly between macroalgal mat coverage levels at any site. Dunlin peck rate did not vary significantly between macroalgal mat coverage at Brands Bay or Ower Bay. There were insufficient samples in Holes Bay to provide analysis.

#### *6.4.3.2 Between-site variation in feeding rate on varying macroalgal mat coverage.*

Figure 6.3 shows the feeding rate for curlew, black-tailed godwit, oystercatcher and redshank, and peck rate for dunlin, under similar levels of algae coverage between sites.

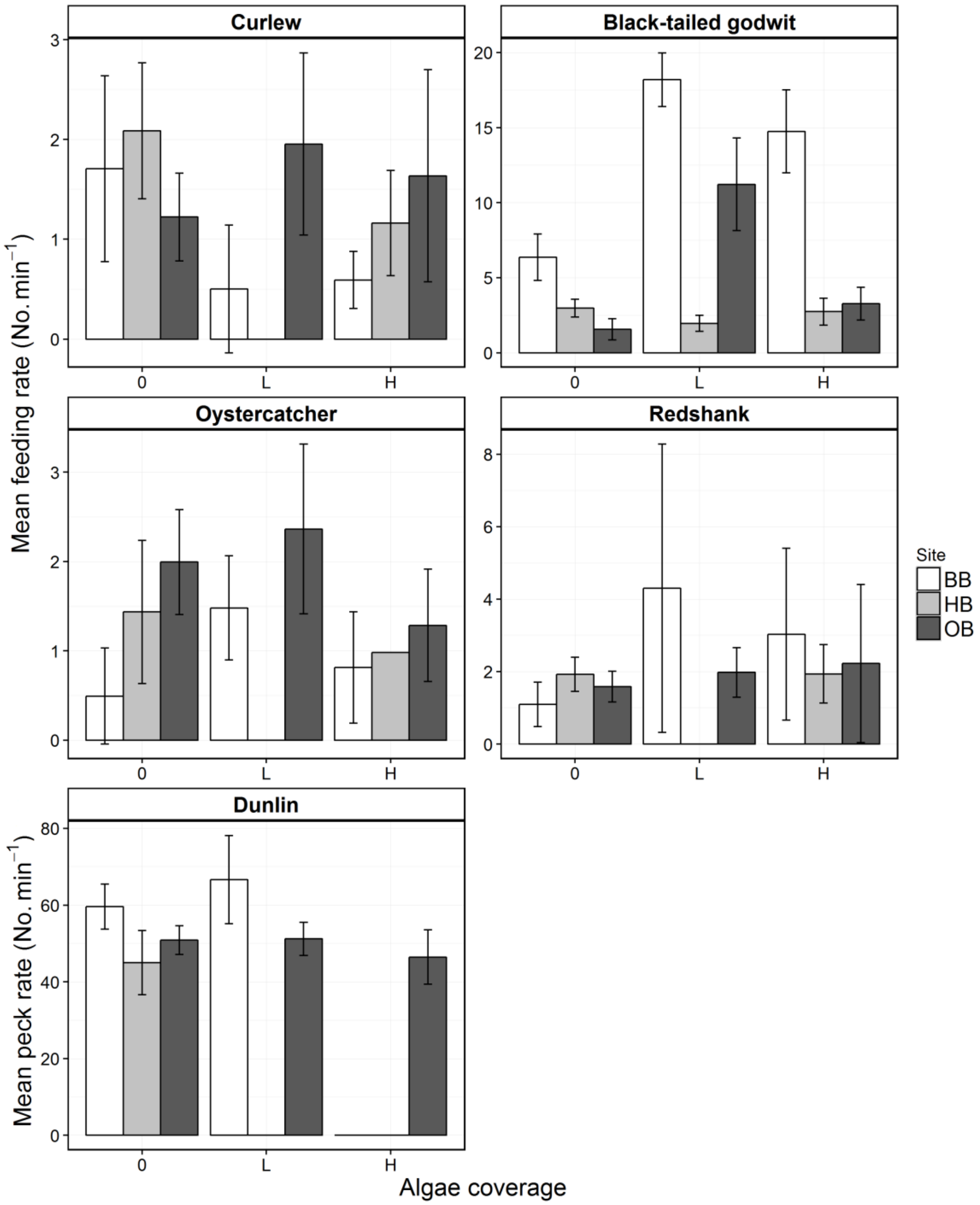


**Fig. 6.3:** Mean feeding rate (No. min$^{-1}$) recorded against equivalent levels of macroalgal mat coverage between sites for curlew, black-tailed godwit, oystercatcher, redshank, and peck rate (No. min$^{-1}$) against equivalent levels of macroalgal mat coverage between sites for dunlin. Error bars 95% confidence intervals. Macroalgal mat coverage 0 = 0 (<5% cover), L = low (5%-50% cover), H = high (>50% cover). Data are combined for both years and both seasons.
Site BB: Brands Bay. HB: Holes Bay. OB: Ower Bay.

*Black-tailed godwit*

There was very highly significant variation in feeding rate for black-tailed godwits on 0 algae between sites ($F_{2,52}$ = 14.63, p = <0.001) with a higher rate on ‘0’ algae in Brands Bay than Holes Bay (z = 3.136, p = <0.001, r = 0.42) and a higher rate on ‘0’ algae in Brands Bay than Ower Bay (z = 3.240, p = <0.001, r = 0.44).

There was very highly significant variation in feeding rate for black-tailed godwit on low algae between sites (F $_{2, 53.40}$ = 195, p = <0.001) with a higher rate on low algae in Brands Bay than Holes Bay (z = 5.783, p = <0.001, r = 0.57), a higher rate on low algae in Brands Bay than Ower Bay (z = 3.716, p = <0.001, r = 0.37), and a higher rate on low algae in Ower Bay than Holes Bay (z = 4.939, p = <0.001, r = 0.49).

There was very highly significant variation in feeding rate for black-tailed godwit on high algae between sites ($F_{2, 43}$ = 50.08, p = <0.001) with a higher rate on high algae in Brands Bay than Holes Bay (z = 5.1005, p = <0.001, r = 0.75) and a higher rate on high algae in Brands Bay than Ower Bay (z = 3.652, p = <0.001, r = 0.54). There was no significant variation in feeding rate on high algae between Holes Bay and Ower Bay.

*Oystercatcher*

Oystercatcher feeding rate varied significantly between sites on ‘0’ algae ($F_{2,25}$ = 5.392, p = <0.05) with a higher rate in Ower Bay than Brands Bay (z = 2.708, p = <0.01, r = 0.51). Oystercatcher feeding rate did not vary significantly between sites on low or high algae coverage.

*Dunlin*

Dunlin peck rate varied significantly on ‘0’ algae between sites ($F_{2,76}$ = 4.611, p = <0.05) with a higher rate in Brands Bay than Holes Bay (z = 2.194, p = <0.05, r = 0.25) and a higher rate in Brands Bay than Ower Bay (z = 1.925, p = <0.05, r = 0.23). There was no significant variation in peck rate on ‘0’ algae between Holes Bay and Ower Bay.

Dunlin peck rate varied significantly on low algae between sites with a higher rate in Brands Bay than Ower Bay (z = 2.1815, p = <0.05, r = 0.33). There were insufficient recordings of dunlin on low algae in Holes Bay to enable analysis.

*Curlew and redshank*

There was no variation in curlew or redshank feeding rate on any level of macroalgal mat coverage between sites.

### 6.4.4 Variation in feeding strategy on different levels of macroalgal mat coverage

Figs. 6.4a and 6.4b show the observed variation in percentage of the recording where birds used tactile and visual feeding strategies. Only curlews and redshank were observed using different feeding strategies. Apart from one occasion where an oystercatcher caught and consumed a fish, both black-tailed godwit and oystercatchers used tactile feeding only. It was not possible to determine whether dunlin used tactile or visual feeding strategies as only peck rate was recorded.

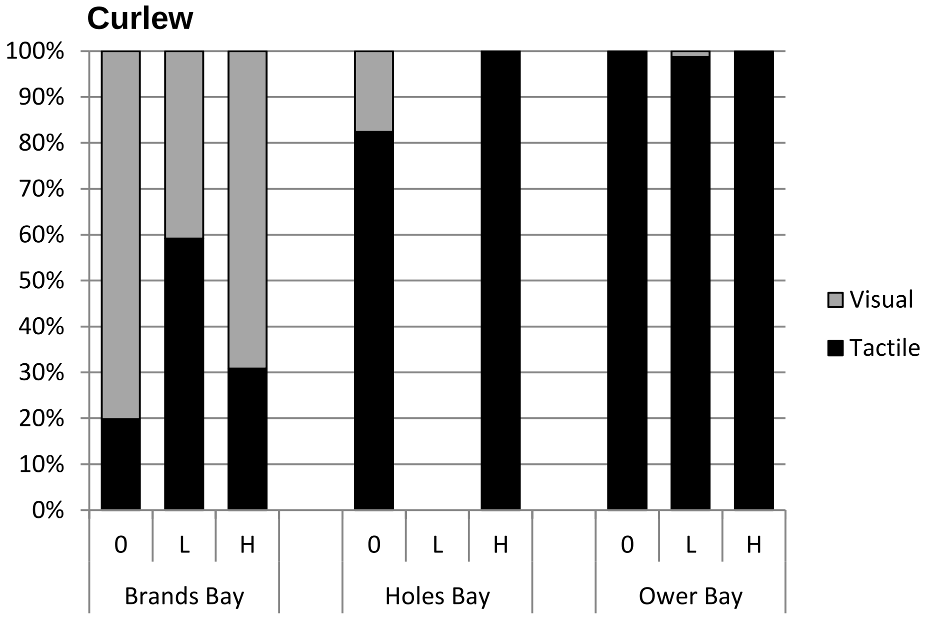


**Fig. 6.4a:** Proportion of time curlews were recorded using a visual or tactile foraging technique on varying levels of macroalgal mat coverage.

Macroalgal mat coverage 0 = 0 (<5% cover), L = low (5%-50% cover), H = high (>50% cover).

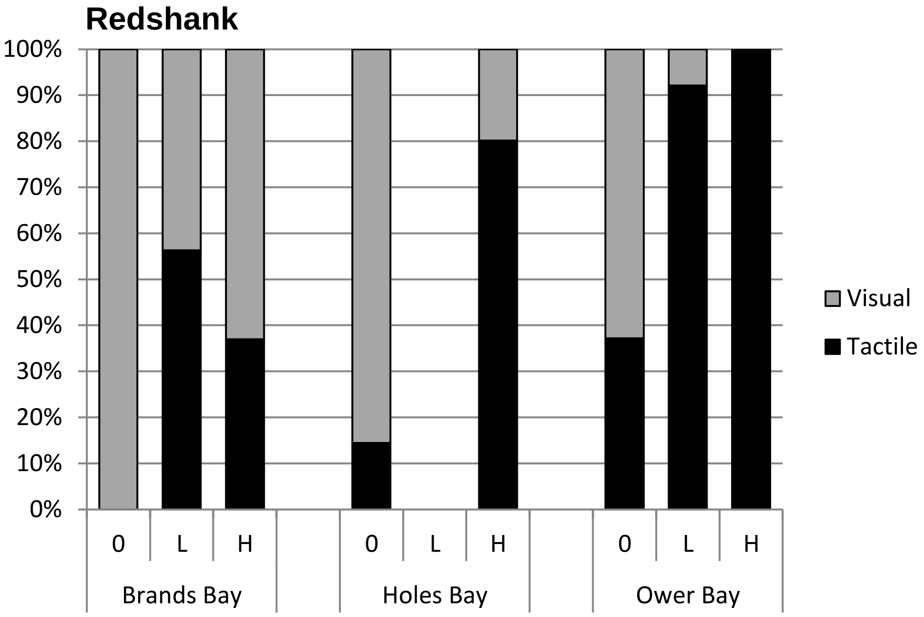


**Fig. 6.4b:** Proportion of time redshanks were recorded using a visual or tactile foraging technique on varying levels of macroalgal mat coverage. Macroalgal mat coverage 0 = 0 (<5% cover), L = low (5%-50% cover), H = high (>50% cover).

### 6.4.5 Observations of curlew foraging behaviour

As figure 6.4a indicates, curlews switched from visual to tactile foraging in response to all levels of macroalgal coverage; yet in Ower Bay in particular they used tactile foraging almost exclusively. However, in Ower Bay, curlews were recorded rapidly pecking the surface of the algae when coverage was high; although their feeding rate did not vary.

Curlews were also observed using a different feeding technique by searching for prey beneath the algae by picking up and shaking sheets or sections of the macroalgal mat to dislodge invertebrates. Holes Bay was covered by the sheet-forming *Ulva* spp. which is less dense and easier to move. Figure 6.5 provides a still image taken from a video recording showing a curlew picking up a piece of algae and shaking it. The full video sequence (Chapter 6 Fig 6,5 curlew shaking algae sheet in Holes Bay) is provided in the attached cd. Although on that occasion there was no prey underneath, the foraging behaviour was observed (but not recorded) on two other occasions; both of which resulted in the curlew finding and consuming a large shore crab. Curlews are known to throw larger prey items (particularly crabs) onto the sediment in order to break the body of the prey into more manageable pieces (van de Kam et al. 2004). It is stressed that these are observations and any significant behavioural change would require further study.

**Fig. 6.5:** Image taken from a video recording showing a curlew foraging on high algae in Holes Bay. The full video sequence (Chapter 6 Fig 6,5 curlew shaking algae sheet in Holes Bay) is provided in the attached cd. The curlew is recorded picking up a piece of algae and shaking it suggesting it hoped to dislodge prey from the algae. Photo © A Thornton

### 6.4.6 Impact on feeding rate if smallest-size prey taken

Fig. 6.6a-c provides an overview of the difference in feeding time required should birds have to rely solely on the smallest-size prey for their daily energy requirement (DER) on different levels of algae coverage.

It is apparent from these data that all studied wading bird species would be unable to fulfil their (DER) during a 12hour available feeding period if only the smallest prey size were available. However, it is possible for black-tailed godwits in Brands Bay to achieve their DER within 24hours by only taking the smallest prey. This is using feeding rate recorded on those levels of macroalgal mat. However, these figures also show that even a slight decrease in mean prey size resulting from changes in environmental conditions under macroalgal mats could have significant impacts upon a bird’s ability to meet its DER.

**Brands Bay**

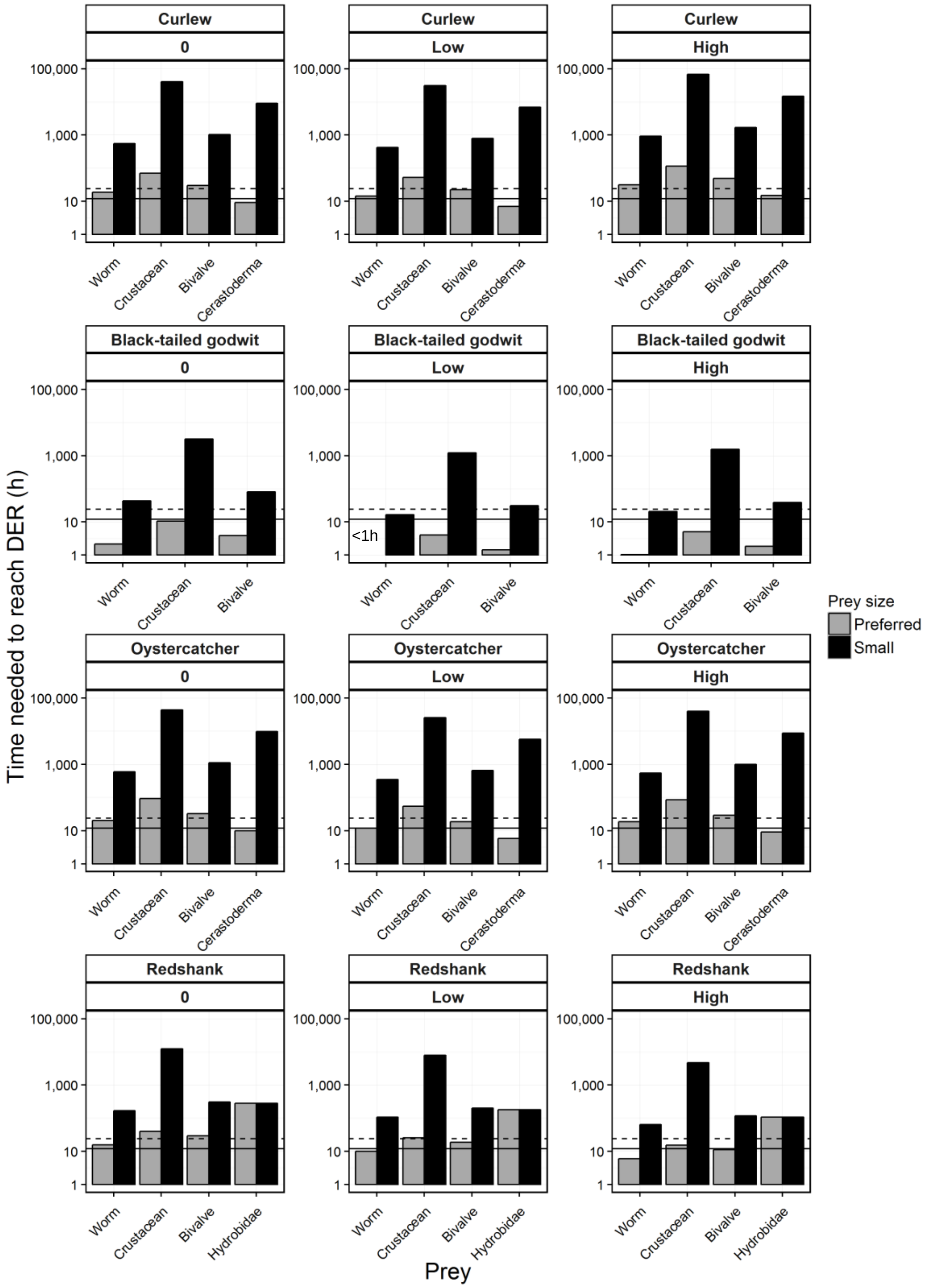


**Fig. 6.6a:** Time needed (h) for birds to reach DER in Brands Bay consuming one individual item of preferred size available (according to their BIM) or smallest-size prey. Data are based on recorded feeding rate for each bid species on varying macroalgal mat coverage 0 (<5%), low (5%-50%), high (51%-100%). ——— 12hr - - - - 24hr thresholds. Data are presented on a $\log_{10}$ scale for clarity.

**Holes Bay**

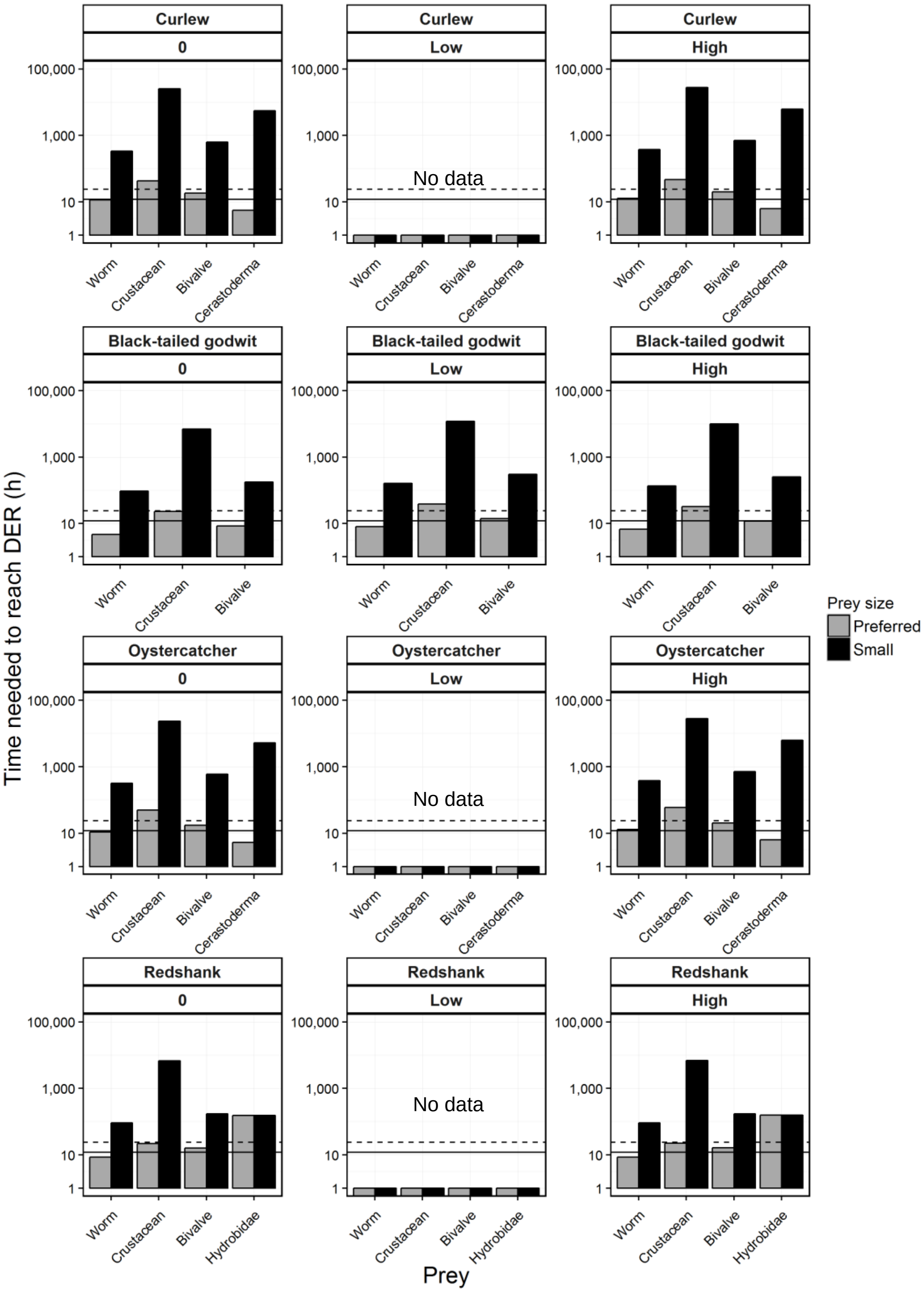


**Fig. 6.6b:** Time needed (h) for birds to reach DER in Holes Bay consuming one individual item of preferred size available (according to their BIM) or smallest-size prey. Data are based on recorded feeding rate for each bid species on varying macroalgal mat coverage 0 (<5%), low (5%-50%), high (51%-100%). ——— 12hr - - - - 24hr thresholds. Data are presented on a $\log_{10}$ scale for clarity. No data = no recordings of curlew, oystercatcher or redshank on low algae.

**Ower Bay**

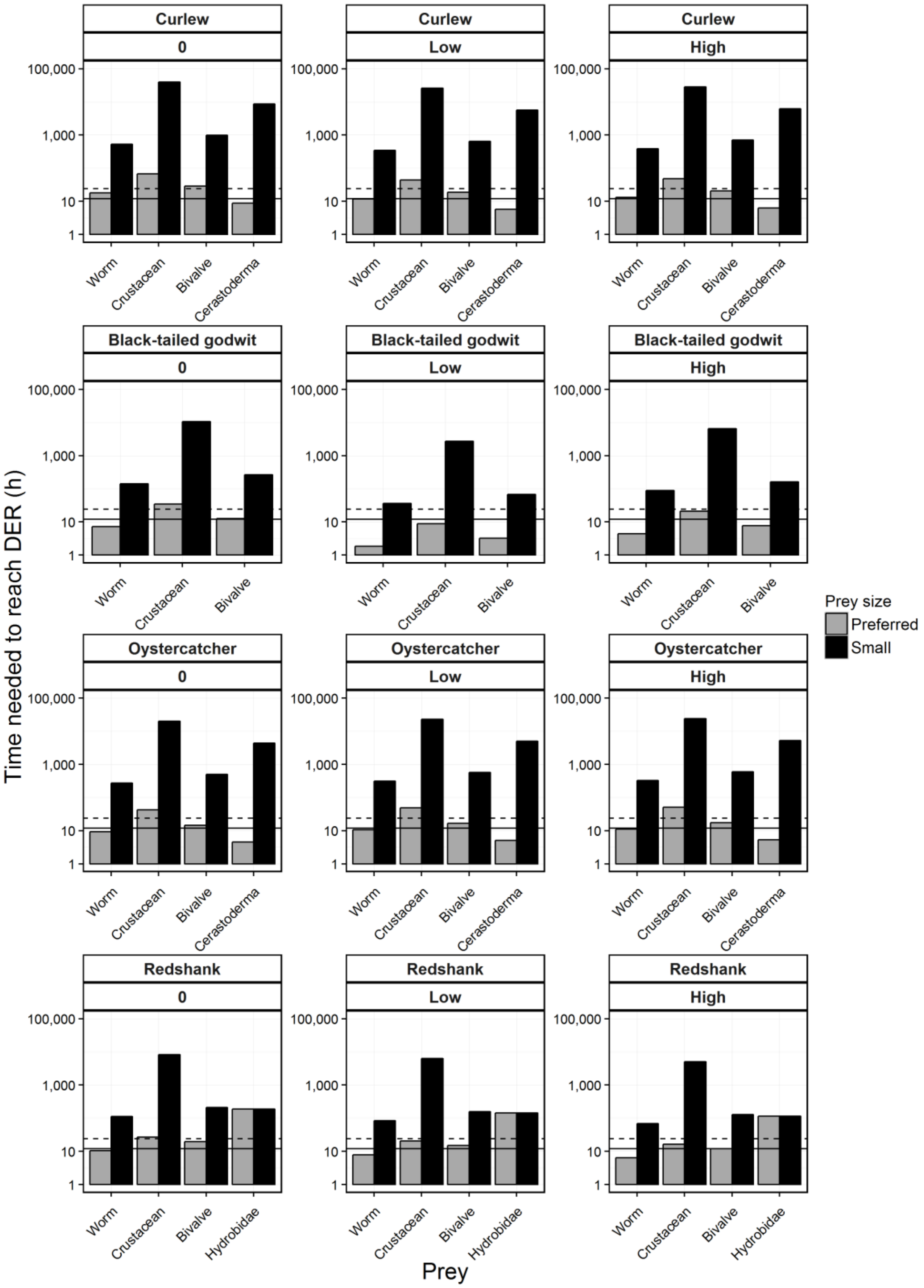


**Fig. 6.6c:** Time needed (h) for birds to reach DER in Ower Bay consuming one individual item of preferred size available (according to their BIM) or smallest-size prey. Data are based on recorded feeding rate for each bid species on varying macroalgal mat coverage 0 (<5%), low (5%-50%), high (51%-100%). ——— 12hr - - - - 24hr thresholds. Data are presented on a $\log_{10}$ scale for clarity.

## 6.5 Discussion

### 6.5.1 The impact of macroalgal mat on feeding rate

Macroalgal mats are transforming the invertebrate community with consequential transformations evident for bird's BIM and subsequent foraging behaviour. Given that the algae has been a feature of the intertidal mudflats in Poole Harbour for over 40 years (Fletcher 1996) it would be reasonable to suppose that birds have made some adaptations to their feeding behaviour in response to these transformations. Results have shown site-specific and species-specific responses by wading birds to the presence of macroalgal mats. The five species of wading bird studied responded differently to varying levels of macroalgal mat coverage. Feeding rate varied significantly for some species whereas others appeared unaffected by macroalgal mats. Yet, despite the lack of variation in feeding rate by some species, there were still apparent behavioural adaptations to the presence of macroalgal mats.

#### *Curlew*

Although distribution did vary in response to levels of macroalgal mat coverage in Holes Bay (see Chapter 5, Sections 5.5.2 and 5.5.3), curlew feeding rate did not vary. This suggests that the curlews were able to find suitable prey irrespective of the level of macroalgal mat coverage.

Curlews will remain faithful to a site provided there are sufficient prey resources available and accessible (van de Kam et al. 2004). As Fig. 6.6a-c shows, curlews would need hundreds or even thousands of hours per day to acquire their DER from the smallest prey-size. It is unlikely that they could increase their feeding rate to such a level. In addition, due to the curlew bill length and structure (Davidson et al. 1986), it is not possible for the bird to obtain sufficient energy from smaller prey items as handling time would be lengthy (van de Kam et al. 2004). Given that, as suggested in Chapter 4 (Section 4.1), it is curlews that are most at risk from high macroalgal biomass, an alternative feeding adaptation may be necessary. Their long bills enable large prey to be obtained from deeper in the sediment in areas unreachable by all the other wading bird species (Ferns and Siman 1994). Yet, if these invertebrates move upwards in response to changes in the sediment chemistry, interspecific competition may have increased. Curlews, however, are still able to consume much larger prey items than black-tailed godwit, redshank and dunlin (Goss-Custard et al. 2006b); only oystercatchers could present additional competition for the largest invertebrates (Goss-Custard et al. 2006b). The observations of curlews shaking sections of the macroalgal mat and dislodging prey could indicate that they may have switched their preferred prey to larger shore crabs on the macroalgal mat or *C. edule* which may have moved upwards into the macroalgal mat (Österling and Pihl 2001).

*Black-tailed godwit*

Levels of macroalgal mat coverage had a significant effect on the feeding rate of black-tailed godwits. It had been expected that birds would avoid areas with macroalgal coverage in favour of areas where there was '0' algae however, the opposite was found with feeding rate higher on both low and high algae when compared to '0' algae in both Brands Bay and Ower Bay. This contradicts findings by Lewis and Kelly (2001) where black-tailed godwits were shown to prefer areas of bare mud to algae covered patches. Given that black-tailed godwits will forage in patches where there is a greater abundance of prey (Dias et al. 2009) this behaviour suggests that the birds may be able to obtain a greater amount of energy when algae is present (either at a low or high level of coverage). Although there was no difference in the distribution of black-tailed godwits in autumn (see Chapter 5, Section 5.5.2), there were a greater number recorded on areas of Brands Bay where there were high levels of previous algae coverage (see Chapter 5, Section 5.5.3). Therefore it is suggested that the change in feeding rate may be a response to conditions created by the presence of algae. Black-tailed godwit feeding rate was highest in Brands Bay on all three levels of macroalgal mat coverage. The results contrast with the study carried out by Lewis et al. (2014), in the Clonakilty Estuary, Ireland, where black-tailed godwits made fewer foraging attempts on areas of macroalgal mat coverage than areas of bare mud.

There was a greater abundance of smaller prey sizes under high algae coverage in Brands Bay (Chapter 4, Section 4.5.1). This could indicate a change in feeding strategy with birds taking smaller, less profitable prey at an increased feeding rate. This scenario was similar in Ower Bay with black-tailed godwits' feeding rate higher on areas where macroalgal mats were present. As reported in Chapter 4 (Section 4.5.1), both these sites contained an abundance of smaller worms and other less energy-dense prey. In addition, the composition of the macroalgal mat at both sites was the tubular/filamentous forms of *Ulva* spp. with a higher biomass already shown to have altered the invertebrate community (see Chapter 3, Section 3.5.8). The BIM for black-tailed godwits was lower in Brands Bay and Ower Bay than Holes Bay - the site where there was no variation in black-tailed godwit feeding rate between algae coverage.

When looking at the potential implications of energy intake for black-tailed godwits consuming preferred prey or less profitable prey, the only site where the bird's DER is achievable within a 24 hour period when consuming the smallest-size prey is Brands Bay (Fig. 6.6a). Although it is acknowledged that birds are not physically able to feed constantly for 24 hours, the feeding rate recorded at this site would result in a mathematically possible DER being achieved per day if the birds were consuming small worms. Indeed, if the birds were consuming their preferred size of annelid worms at the feeding rate recorded, each individual would reach its DER in less than an hour. It could also be argued that if black-tailed godwits were feeding on their preferred size of prey there would be an increase in handling time (Goss-Custard et al. 2006b); this was not apparent from the recordings. As discussed in Chapter 3, higher macroalgal mat biomass resulted in an increased abundance of smaller opportunistic species including Chironomidae larvae (categorised as small worms for the purposes of this study) - a highly abundant species in Brands Bay. Black-tailed godwits have been recorded feeding on Chironomidae larvae (Santiago-Quesada et al. 2014) therefore it is possible that the birds are taking advantage of this abundance and feeding at a greater rate on smaller species available on high levels of macroalgal mat coverage.

Black-tailed godwits will move within their preferred overwintering region and will respond to changes in local prey availability (Gill et al. 2001b); populations are known to move to poorer quality sites if density becomes too great at a higher quality site (Gunnarsson et al. 2005b). In addition, although this falls outside the scope of this study, black-tailed godwits will use terrestrial areas to support their feeding requirements (Durell et al. 2006; Navedo et al. 2013). Indeed, there is anecdotal evidence that the black-tailed godwits overwintering in Poole Harbour have been recorded feeding on flooded fields ~10 miles away in Christchurch.

### *Oystercatcher*

It was not surprising that oystercatcher's feeding success was unaffected by varying macroalgal mat coverage. The species is highly adaptable and the strength of their bill would not present a problem accessing prey from within the sediment (Hulscher 1996). Oystercatchers used tactile methods for locating prey at each of the sites studied with the exception of one incidence where an oystercatcher caught a fish in shallow water in Brands Bay. However, fish are not regarded as important prey items for oystercatchers (Goss-Custard et al. 2006b). Although it is reported that oystercatchers locate their benthic invertebrate prey by touch alone, the prey will reveal clues on the surface from breathing holes which the oystercatcher will see (Hulscher 1996). Figure 6.7 shows two oystercatchers foraging in close proximity on high levels of macroalgal mat coverage in Ower Bay.

**Fig. 6.7:** Two oystercatchers (and a redshank) foraging at Ower Bay on high macroalgal mat coverage in autumn 2014. Photo © A Thornton.

Oystercatchers do appear to be able to reach their DER within 24 hours if their preferred prey size is available yet, as shown in figure 6.6c, would struggle if prey size were reduced to the smallest size category as a result of increase in macroalgal mat coverage. Oystercatchers avoid smaller prey items (Zwarts 1996) and were not observed actively foraging beneath the algae sheets in a similar fashion to curlews. This strongly suggests that the species do not forage for prey on the surface of the algae. Oystercatchers will remain faithful to a particular overwintering site even if there is a decline in their preferred prey (Stillman and Goss-Custard 2010). Given that the macroalgal mat development could have led to an increase in smaller species, this could have implications for the oystercatcher population in Poole Harbour if they remain in an increasingly poor quality site. It is worth noting that oystercatchers' BIM is not restricted to bivalves – the birds will consume larger worms (Goss-Custard et al. 2006b). This may prove vital in the 'worm-dominated' Poole Harbour as larger sizes of *H. diversicolor* remained abundant in Holes Bay under increasing macroalgal mat biomass and coverage.

*Redshank*

It was not surprising that redshank were unaffected either in distribution or feeding success by the presence of macroalgal mats. Individuals were able to switch between visual and tactile strategies in response to the presence of algae (see Fig. 6.6b) and were recorded probing the sediment and also pecking from the surface of the macroalgal mat (Fig. 6.8). However, the findings contrast those by Lewis et al. (2014) where a decline in redshank foraging success was recorded on higher levels of macroalgal mat coverage. Maximum macroalgal mat coverage reported during that study was 55% whereas the maximum coverage recorded in Brands Bay was 100%.

**Fig. 6.8:** Redshanks foraging on low algae at Ower Bay in autumn 2013. Photo © A Thornton.

Redshank appear less susceptible to the impact from a decline in preferred prey size as their DER is lower and generally made up of smaller-sized prey (Goss-Custard et al. 2006b). However it is still apparent that they would struggle to obtain sufficient energy per day should this only be available from small gastropods (e.g. *Peringia ulvae*) Redshank will select alternative prey items to their preferred prey (e.g. *Corophium*) but do not 'downsize' by selecting smaller worms to compensate (Goss Custard 1977). If prey sizes are reduced as a consequence of increased macroalgal mat biomass, redshanks may struggle to reach their DER in Poole Harbour. However, as discussed in Chapter 5, redshanks will move to different sites in search of prey (van de Kam et al. 2004).

### *Dunlin*

Dunlin avoided areas of high algae coverage in Brands Bay and Holes Bay yet there was no variation in dunlin peck rate between algae coverage within sites. It had been expected that dunlin would avoid areas with even low macroalgal mat coverage as these small birds were unable to probe beneath the mat (Mouritsen and Jensen 1992). Other studies have shown an increase in peck rate in areas of algae coverage (Múrias et al. 1996) although maximum coverage recorded in that study was 36%.

Due to the lack of availability of dunlin recordings on all levels of macroalgal mat coverage it was not possible to accurately determine any behavioural changes in relation to the macroalgal mat.

### 6.5.2 Conclusion

There is evidence that macroalgal mats are transforming the behaviour of the studied wading bird species with the exception of redshanks. However, responses to macroalgal mats are site-specific with birds appearing to adapt their feeding behaviour dependent upon the macroalgal mat conditions and coverage at a particular site. It also appears that the macroalgal mat itself is providing some habitat structure that can be utilised by some wading bird species. The thickness of the mat may benefit curlews as, even if the larger prey items are moving upwards in the sediment column, the macroalgal mat adds a surface layer that could prevent smaller birds with shorter bills from accessing the prey. However, there is a lag between a decline in algae and the sediment anoxic layer returning to a lower level that could result in larger prey items remaining in the upper layer of the sediment without protection afforded by the macroalgal mat. This could lead to increased predation by the wading birds.

These results have shown that it is likely to be the larger wading birds (curlew, oystercatcher and black-tailed godwit) that will be most affected by the macroalgal mats. The greatest impact will be due to the increase in smaller opportunist species such as *Tubificoides* spp. as a result of increased macroalgal biomass. Curlews and oystercatchers do have an advantage over black-tailed godwits as these species' BIMs include larger *C. edule* as an additional food source. By contrast, black-tailed godwits appear to have adapted to an increased abundance of smaller prey sizes and increased their feeding rate accordingly. Moreover this species will move to more profitable feeding areas should the quality of their preferred site deteriorate (Gill et al. 2001b). Black-tailed godwits were not recorded adopting visual feeding strategies nor were birds observed taking prey from the surface of the macroalgal mat.

It appears that black-tailed godwit's feeding rate is significantly affected by the transformation of the invertebrate community under dense macroalgal mats and the increase in smaller prey items that are less profitable for the birds. This has implications for the population under the SPA given that currently Poole Harbour supports 2.6% of the overwintering Icelandic population of black-tailed godwits (*Limosa limosa islandica*) (Natural England 2016). Although all the wading bird species appear to be adapting to the continued presence of macroalgal mats this should not lead to complacency.  The cumulative impacts of increasing coverage and biomass of macroalgal mats, and reduction in prey size could have serious implications for wading bird’s ability to meet their DER with consequences for their winter survival and fitness to return to the spring breeding grounds.

BLANK

# 7.0 Discussion and conclusion

*'…The connections between causes and effects are often much more subtle and complex than we ... might naturally suppose…'*

(*Dirk Gently's Holistic Detective Agency*, Douglas Adams, 1987)

## 7.1 Introduction

Increasing nutrient enrichment and the development of macroalgal-mats are global conservation concerns. The overall aim of this research has been to demonstrate the impact of the development of green macroalgal-mats on the overwintering wading bird population for which Poole Harbour is a designated SPA. This aim was addressed using extensive fieldwork data to analyse the interactions between macroalgal-mats and different trophic levels within a temperate estuarine food-web; impacts from the primary production macroalgal-mat on primary/secondary consumers (the benthic invertebrate community) upwards to the tertiary consumers/top predators (overwintering wading birds). Previous studies have focused on interactions between these trophic levels but there has been a tendency for studies to investigate impact only between macroalgal-mats and either benthic invertebrates or wading birds (e.g. Jones and Pinn 2006; Lewis et al. 2014).

Studies examining the impacts of green macroalgal-mats on the ecology of soft-sediment estuarine habitats have been carried out since the 1970s (Fletcher 1996). Yet, despite a general consensus that the macroalgal-mats are transforming these intertidal habitats (Fletcher 1996; Raffaelli et al. 1998; McLusky and Elliott 2004; Borja et al. 2012), there is little agreement on any single, measurable impact resulting from macroalgal-mat development. Indeed, even studies within the same geographical region (e.g. the south coast of England) are unable to provide a reliable 'threshold' for macroalgal-mat biomass above which there is a definite detrimental impact on the benthic invertebrate community or wading bird population (Soulsby 1982; Hull 1987; Rees-Jones 2004). Intertidal estuarine habitats are dynamic ecosystems with each example subject to a range of environmental conditions (McLusky and Elliott 2004) making each site a unique study.

## 7.2 The biomass and extent of macroalgal-mats in Poole Harbour

Results from this chapter demonstrated that the macroalgal-mat develops in response to air temperature and sediment temperature and is not affected by heavy rainfall. Although the influence of temperature was expected (Raffaelli et al. 1998), it was surprising that the heavy rainfall and flooding which occurred during January and February 2014 did not result in any change in the overall biomass of the macroalgal-mat.

Macroalgal-mat biomass did not vary significantly between the two survey seasons although peak biomass was recorded at different times of year. Given that dense macroalgal-mats have been a feature of sheltered areas of Poole Harbour for over 40 years it is perhaps not surprising that no significant variation was found in a relatively short survey period. It is possible that macroalgal-mat development/growth has reached a zenith given current environmental conditions. However, a more likely cause is the morphology of the *Ulva* species within the macroalgal-mat itself with sheet-forming *Ulva* developing into less dense mats with lower biomass but greater coverage; possibly limiting light availability to the lower frond development.

From a conservation perspective, consideration needs to be given to the current threshold of concern for macroalgal-mat development for the SSSI Condition Assessment in Poole Harbour (currently set at 2 kg $m^{-2}$ wet-weight algal biomass) (Underhill-Day et al. 2010). This biomass was reached in some areas of the harbour but the level was not maintained throughout the season and not reached in Holes Bay or Newton Bay. Results demonstrated that the lower threshold of 1 kg $m^{-2}$ being consistently maintained across the study sites may be a more appropriate threshold for Poole Harbour.

Although determining the extent of the macroalgal-mat across the whole harbour would have provided a measure of the % coverage at a single point during the growth season, it was more important to be able to monitor the development on a monthly basis and use those data to assess the impact on overwintering wading birds. As discussed in Chapter 2, regular monitoring of macroalgal-mat growth patterns and extent within each bay provided records of levels of coverage present during the first four months of the overwintering bird season. In addition, results demonstrated a clear correlation between the algae % coverage present in quadrats at the upper shore level and the overall coverage across each survey site. This provided evidence suggesting the macroalgal-mat develops from the upper shore then follows the shore gradient yet deteriorates at a similar rate across each bay. This is important when considering the impact from coverage persisting into the wading bird overwintering season. Terrestrial methods are useful to provide an overview of the condition of an area in terms of macroalgal-mat development. In addition, when looking at amenity ecosystem services provided by the harbour (e.g. wildlife watching, dog walking, cycling), public perception of the problem caused by macroalgal-mats will be based upon the coverage in accessible bays. Anecdotal evidence gathered during fieldwork and bird observations support the view that Holes Bay and Brand's Bay in particular are 'very green and smelly' during the summer.

## 7.3 The impact of macroalgal-mats on the benthic invertebrate community

As there was no possibility of using before/after experimental methodology to determine the impact of macroalgal-mats on the benthic invertebrate community due to a paucity of records for benthic invertebrates in Poole Harbour prior to the development of the macroalgal-mat, ABC curves were plotted to establish whether there were any areas experiencing environmental stress. This proved a very useful first phase in establishing the status of the invertebrate population at key wading bird overwintering sites. The results showed Poole Harbour is an environmentally 'stressed' system with species indicative of organically enriched estuarine environments recorded in high abundance. These curves also provided the first indication that there was variation in the invertebrate response to environmental stress between sites.

The distance-based linear-models (DISTLM), provided evidence that the intertidal mudflats in Poole Harbour support an abundance of opportunistic r-selected rather than the slower growing K-selected species. The exception to this was the presence of the highly adaptable *Hediste diversicolor*. This was further supported by demonstrating that algae biomass and/or % organic content within the sediment were the main environmental drivers of dissimilarities between benthic invertebrate community structure and distribution. This is important to consider as previously it was found that sediment particle size and/or organic content were the best explanatory variables for species distribution. It is likely that the organic content within the sediment in the areas studied comprises decaying macroalgal mat.

## 7.4 The effect of macroalgal-mats on wading bird prey: implications for individual bird species

This chapter tested a novel approach to determining the impact of macroalgal-mats on wading birds by assessing individual bird species' preferred prey rather than an overall abundance / biomass of invertebrates. In doing so, it was demonstrated that, although there was an overall abundance of invertebrates, once the smaller species were removed as being below the preferred prey size for key overwintering wading birds, the effect from macroalgal-mats was more apparent. The work was based upon the theory that non-breeding overwintering wading birds are focussed on obtaining maximum energy intake for minimum effort. Therefore, by establishing site-specific and species-specific BIM it was possible to determine the impact of macroalgal-mats on each bird species at each site. This enabled a more accurate analysis of the available energy under site-specific macroalgal-mat biomass development.

Using a measure of energy required for each wading bird species demonstrated the need to record sizes classes of invertebrates in order to obtain these energy values. Simply recording abundance of invertebrate taxa is not sufficient to predict impact on wading birds from macroalgal-mats. In addition, it was demonstrated that the BIM for each wading bird species increases under low levels of macroalgal-mat biomass then begins to decline; further supporting the lowering of the current threshold of concern for macroalgal-mat biomass from 2 kg $m^{-2}$ to 1 kg $m^{-2}$ for Poole Harbour. By removing those size classes of invertebrates which are of insufficient quality for wading bird's BIM, it became apparent that the abundance of suitable sized annelid worms comprised mainly *H. diversicolor.* Whilst this prey item is an abundant food source in Holes Bay, it was not as abundant in either Brands Bay or Ower Bay. Despite estuarine sediments being relatively species-poor compared to terrestrial or fully marine systems (McLusky and Elliott 2004), the possibility that energy from larger worms is derived from a single species raises concern. Biodiversity is vital to ecosystem resilience (Borja et al. 2012); particularly a worm-dominated system such as Poole Harbour. *H. diversicolor* was one of the top six most abundant species recorded under macroalgal-mats and appears to be adapting to the current levels of macroalgal-mat biomass. However, there remains the potential for a sudden population decline which would have consequences for the overwintering birds' ability to reach their daily energy requirements.

## 7.5 The relationship between macroalgal-mat coverage and wading bird foraging behaviour

This chapter demonstrated that birds may avoid areas of current macroalgal-mat coverage and those areas where previous algae coverage was low or high. This particularly affected curlews; a species recently added to the BTO Red List for Birds of Conservation Concern (Eaton et al. 2015). As Europe's largest wading bird it is the species most likely to be affected by the transformation of the invertebrate community and presence of macroalgal-mats yet this has not previously been investigated. Curlews are positively and negatively impacted by macroalgal-mats with birds in Holes Bay appearing to use the dense algae coverage as a structure upon which to stand yet avoiding areas where there was previous coverage of algae.

Evidence from analysis of the distribution of wading bird BIM suggested that, despite the high BIM in Holes Bay, this area was not used exclusively by wading birds; supporting the optimal foraging theory that other factors, apart from availability of prey, will determine the location of foraging birds (Sutherland et al. 2005). Results also showed that the macroalgal-mat is having an impact on the distribution of all the studied wading bird species (with the exception of redshank) at some point during their overwintering period.

## 7.6 Changes to wading bird feeding rate in response to macroalgal-mat coverage

The success of the video recordings used in this chapter enabled a detailed analysis of the feeding rate for four out of the five wading bird species studied. Observations of bird feeding behaviour suggested that the birds are adapting to the presence of the macroalgal-mats in different ways and at different sites. This was supported by evidence of curlew actively foraging on the algae and even moving sheets of *Ulva* in Holes Bay to search for prey. Both curlews and redshanks switched between tactile and visual feeding strategies on varying levels of macroalgal-mat coverage. However, it was the behaviour of the black-tailed godwits which has proved noteworthy as their feeding rate increased on low and high levels of macroalgal-mat coverage in Brands Bay. This may indicate that birds are feeding at a much higher rate on smaller, less energy dense species such as the abundant Chironomidae larvae or *Tubificoides* spp. This behaviour has not previously been recorded.

## 7.7 Limitations to the study

*Control site*

Results from this study demonstrated that a control site would not have been an effective experimental methodology given the intrinsic variation in site conditions even with macroalgal-mat coverage. Basing a control site on a lack of macroalgal-mat development would be meaningless unless other variables could be controlled. The most suitable control site in terms of size and morphology was Holton Heath. However, although this site did not show macroalgal-mat development during 2013, there are numerous other factors which may have affected this including possible chemical leeching from landfill on the site and residual groundwater leeching of chemicals from the former ammunition factory on site. In addition, extensive reed-beds which fringe the site may have mitigated some of the nutrient input thereby rendering the site less enriched than others around the bay.

*Spatial and temporal limitations*

These results are based upon two ecological cycles of macroalgal-mat development; a timescale longer than previous studies in the harbour yet too short to predict the impact of macroalgal-mats which have been a feature of the intertidal mudflats for 40 years. In addition, it is acknowledged that this study concentrates on a single site, Poole Harbour. However, there is variation in responses of invertebrates and wading bird species to macroalgal-mat development between the study areas within the harbour suggesting this site-specific approach is appropriate.

Despite every effort to ensure all five bird species were recorded on each level of macroalgal-mat coverage at each site, this was not possible. Some patches, particularly the lower shore where macroalgal-mat coverage was generally ‘0’, were further away from the raised vantage point in Brands Bay and Holes Bay. Indeed, Holes Bay proved the most challenging as the macroalgal-mat was predominantly sheet-forming *Ulva* spp. which broke down rapidly during the autumn months resulting in a lack of patches with low macroalgal-mat coverage. In addition, the wide bay presented problems recording birds’ feeding behaviour. Although the birds could be counted accurately, they were often foraging >500 m from the vantage point. This resulted in a number of recordings being discarded as it was not possible to determine feeding rate even when the telescope was on maximum zoom; further compounded by the low winter light levels at the low-tide spring observations when the maximum area of mudflat was exposed and birds were feeding along the water line. It had been anticipated that variation in feeding rate according to shore-level could be analysed. However, there were insufficient recordings of birds on the different shore levels to make this analysis robust. It had been hoped that comparisons could be made between feeding rates on existing algae and previous algae coverage. As this was not possible, it is acknowledged that there are a greater number of recordings on ‘0’ algae in winter than autumn

## 7.8 Potential further research

*Ecology of the macroalgal-mat*

There is a further gap in our understanding of the ecology of the macroalgal-mat itself. It was apparent from the bird behavioural observations and video analysis that there was suitable prey available within the macroalgal-mat rather than only in the sediment. Invertebrates retained from the macroalgal-mat biomass samples could be analysed to determine whether there were any differences between communities. In addition these could be related back to the algae samples (also retained) to determine whether the invertebrate community is impacted by different species of algae. In addition, it might be possible to determine whether invertebrate species are moving upwards within the sediment column in response to increased macroalgal-mat biomass and resultant changes in the sediment chemistry.

*Individual-based model*

This research has demonstrated that macroalgal-mats are transforming the intertidal habitat and the benthic macro-invertebrate community within Poole Harbour with implications for the overwintering bird population. A logical next-step would be the development of an individual-based model (IBM) to predict the wading bird population response to the macroalgal-mat coverage and biomass across the whole intertidal mudflat habitat in Poole Harbour. Using existing data and aerial images, an IBM would enable predictions of impacts on overwintering wading birds should the macroalgal-mat increase in biomass or extent across Poole Harbour. Developing an IBM would address the constraints present in all ecological studies – length of time available for studying a system.

*Remote sensing*

Aerial photography is acknowledged as an appropriate methodology for assessing the extent of macroalgal-mats; particularly when the study site is large (Vadas and Beal 1987; Nedwell et al. 2002; Patrício et al. 2007; Scanlan et al. 2007). By using aerial photographs it would have been possible to show the full extent of the macroalgal-mat development in Poole Harbour – particularly those areas which are inaccessible on foot yet may provide a ‘bare-mud’ refuge for invertebrates or wading birds.

However, had aerial imagery been available, there would remain some limitations to this method.  A costly flight would have been scheduled for the month in which peak macroalgal-mat growth and extent was anticipated in Poole Harbour (August 2013). Although peak % coverage of algae was recorded in August 2013 in Holes Bay and Newton Bay, the peak occurred later in Brands Bay (September 2013) and Ower Bay (October 2013) (Fig. 2.5); after the aerial images would have been obtained.  This type of remote sensing is costly therefore it may not have been possible to schedule a repeat flight for October to allow for the increased coverage.  In Poole Harbour there are additional constraints from the limited time within each low tide period during which the mudflats are exposed and, due to the ‘double high-water’ in Poole, timing for low spring tide is often later in the afternoon resulting in a reduced light level for photography.  Technology has advanced in the field of remote sensing particularly the use of unmanned aerial vehicles (UAVs), also known as ‘drones’ (Ogden 2013; Ivoševic et al. 2015).  These could provide a much more cost effective method by which the extent of the macroalgal-mat could be determined with flights carried out on more than one occasion during a macroalgal-mat growth season; although flights over estuaries may be restricted in autumn to avoid disturbance to the populations of overwintering wading birds.

## 7.9 Conservation recommendations

Management proposals currently being considered in northern France involve the wholescale clearance of the macroalgal mat (Smetacek and Zingone 2013).  A similar proposal is being considered for Poole Harbour (Capuzzo and Forster 2014; N. Hopkins, Catchment Co-Ordinator, Wessex Water, pers. com.)  However, as shown in Chapter 4, Fig. 4.4 and 4.5, removing the macroalgal-mat would have a similarly negative impact upon the benthic invertebrate abundance and biomass and wading bird BIM as algae biomass >2000 g (ww) $m^{-2}$, resulting in the removal of important prey resources within the sediment.  In addition, as the birds appear to be feeding on invertebrates on the surface of the macroalgal-mat, clearing this food resource without allowing the sediment benthic invertebrate community to recover would further reduce the availability of suitable prey.  It is likely that the anoxic/hypoxic conditions would remain within the sediment for a longer period before returning to levels where the invertebrate community begins to re-establish; reducing the availability of prey still further. Sediment is currently dominated by smaller, pollution tolerant, species and these would be likely to remain until the larger species were able to return.

## 7.10 Final comment

Underpinning this research are a number of legislative frameworks emanating from Europe; although transposed into UK law. It is likely that the UK is entering a period of unprecedented change as a result of the EU Referendum vote yet as we continue to transform the estuarine environment through excess nutrient input, there is a need to understand the processes involved in ecosystems through applied and theoretical collaborative research. As discussed throughout this thesis, although there are site-specific variations in the development of macroalgal-mats, the issue of excessive nutrient input into an ‘open’ estuarine ecosystem is a global problem not restricted by borders.

As this research developed, it became apparent that the macroalgal-mat itself is not a barren green mass of ‘slime’ but a habitat in its own right. This was further supported by recording a diversity of *Ulva* species and invertebrate taxa within the mat; supporting the need for more research on this naturally occurring primary producer before it is removed. Perhaps renaming it an ‘intertidal green-belt’ or ‘intertidal lawn’ might encourage people to consider its function within the estuarine ecosystem and understand that, just like a lawn, the macroalgal-mat requires controlling and maintaining rather than clearing.

*But more than mundane weeds are there,*
*And mud, celestially fair;*

(from ‘Heaven’, Rupert Brooke 1913)

**BLANK**

# 8.0 References

Adams, D., 1987. *Dirk Gently's Holistic Detective Agency.* London: Pan Books

Agardy, T., Alder, J., Dayton, P., Curran, S., Kitchingman, A., Wilson, M., Catenazzi, A., Restrepo, J., Birkeland, C., Blaber, S., Saifullah, S., Branch, G., Boersma, D., Nixon, S., Dugan, P., Davidson, N. and Vörösmarty, C., 2005. Coastal Systems. *In*: Hassan, R., Scholes, R. and Ash, N. eds. *Millennium Ecosystem Assessment: Ecosystems and Human Well-being: Current State and Trends, Volume 1.* London: Island Press.

Airoldi, L. and Beck, M. W., 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology: An Annual Review*, 45, 345-405.

Alexander, D. J., Hart, D. E. and Marsden, I. D., 2008. *Evaluation and Development of Techniques to Map Macroalgae in the Avon-Heathcote Estuary Ihutai.* Christchurch, New Zealand: University of Canterbury.

Altman, J., 1974. Observational study of behaviour: sampling methods. *Behaviour*, 49 (3/4), 227-267.

Alves, J. A., Lourenço, P. M., Piersma, T., Sutherland, W. J. and Gill, J. A., 2010. Population overlap and habitat segregation in wintering Black-tailed Godwits Limosa limosa*.* *Bird Study*, 57 (3), 381-391.

Alves, J. A., Sutherland, W. J. and Gill, J. A., 2012. Will improving wastewater treatment impact shorebirds? Effects of sewage discharges on estuarine invertebrates and birds. *Animal Conservation,* 15, 44-52.

Anders, N. R., Churchyard, T. and Hiddink, J. G., 2009. Predation of the shelduck *Tadorna tadorna* on the mud snail *Hydrobia ulvae*. *Aquatic Ecology*, 43, 1193-1199.

Anderson, D. M., Glibert, P. M. and Burkholder, J. M., 2002. Harmful Algal Blooms and Eutrophication: Nutrient Sources, Composition, and Consequences. *Estuaries*, 25 (4b), 704-726.

Anderson, M. J., Gorley, R. N. and Clarke, K. R., 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* Plymouth: PRIMER-E Ltd.

Ausden, M. and Drake, M., 2006. Invertebrates. *In*: Sutherland, W. J., ed. 2006. *Ecological Census Techniques* 2nd edition. Cambridge: Cambridge University Press, 214-249.

Axelsson, M., Dewey, S., Allen, C. and Hawes, J. 2012. *Investigations into wader and wildfowl density and behaviour in relation to algal cover density in Poole Harbour*. Southampton: Seastar Survey Ltd. for Natural England.

Barbosa, A., 1997. Foraging strategy and predator avoidance behaviour: an intraspecific approach. *Acta Oecologica*, 18 (6), 615-620.

Barnes, R. S. K., 1994. *The Brackish-water Fauna of Northwestern Europe.* Cambridge: Cambridge University Press.

Barto, E. K. and Rillig, M. C., 2012. Dissemination biases in ecology: effect sizes matter more than quality. *Oikos*, 121, 228-235.

Bennett, L., 2011. *Poole Harbour Aquatic Management Plan* (Amendment to Drake, W., 2006). Poole: Poole Harbour Steering Group.

Bibby, C. J., Burgess, N. D., Hill, D. A. and Mustoe, S. H., 2005. *Bird Census Techniques* 2nd edition. London: Elsevier.

Bolam, S. G., Fernandes, T. F., Read, P. and Raffaelli, D., 2000. Effects of macroalgal mats on intertidal sandflats: an experimental study. *Journal of Experimental Marine Biology and Ecology,* 249, 123-137.

Bolam, S. G. and Fernandes, T. F., 2002. The effects of macroalgal cover on the spatial distribution of macrobenthic invertebrates: the effect of macroalgal morphology. *Hydrobiologia*, 475/476, 437-448.

Borja, A., Basset, A., Bricker, S., Dauvin, J-C., Elliott, M., Harrison, T., Marques, J., Weisberg, S and West, R., 2012. Classifying ecological quality and integrity of estuaries. *In:* Wolanski, E. and McLusky, D., eds. *Treatise on Estuarine and Coastal Science.* Waltham: Academic Press, 125-162.

Borja, A., Elliott, M., Henriksen, P. and Marbà, N. 2013. Transitional and coastal waters ecological status assessment: advances and challenges resulting from implementing the European Water Framework Directive. *Hydrobiologia,* 704, 213-229.

Bowen, J. L. and Valiela, I., 2001. The ecological effects of urbanization of coastal watersheds: historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1489-1500.

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

Boyer, K. E. and Fong, P., 2005. Macroalgal-mediated transfers of water column nitrogen to intertidal sediment and salt marsh plants. *Journal of Experimental Marine Biology and Ecology*, 321, 59-69.

Bricker, S. B., Longstaff, B., Dennison, W., Jones, A., Boicourt, K., Wicks, C., and Woerner, J., 2008. Effects of nutrient enrichment in the nation's estuaries: A decade of change. *Harmful Algae,* 8 (1), 21-32.

British Trust for Ornithology, 2016. *Welcome to Bird Facts.* Thetford: British Trust for Ornithology. Available from: http://www.bto.org/about-birds/birdfacts [Accessed 29 May 2016].

Brodie, J., Maggs, C. A. and John, D. M., (Eds.), 2007. *Green Seaweeds of Britain and Ireland.* Scarborough: British Phycological Society.

Brooke, R. 1913. *The Collected Poems of Rupert Brooke.* Cirencester: The Echo Library (2006).

Bryan, G., Jonas, P., Money, R., Kite, D. and Bardon, R., 2012. *Final draft strategy for managing nitrogen in the Poole Harbour Catchment to 2035.* Technical Report drafted by: Environment Agency, Natural England, Wessex Water.

Bryant, D. M., 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuarine and Coastal Marine Science*, 9, 369-384.

Burton, N. H. K., Armitage, M. J. S., Musgrove, A. J. and Rehfisch, M M., 2002. Environmental Assessment. Impacts of man-made landscape features on numbers of estuarine waterbirds and low tide. *Environmental Management*, 30, 857-864.

Cabral, J. A., Pardal, M. A., Lopes, R. J., Múrias, T. and Marques, J C., 1999. The impact of macroalgal blooms on the use of the intertidal area and feeding behaviour of waders (Charadrii) in the Mondego estuary (west Portugal). *Acta Oecologica,* 20 (4), 417-427.

Caldow, R., McGrorty, S., West, A., Durell, S. E. A. le V. dit, Stillman, R. and Anderson, S., 2005. Macro-invertebrate Fauna in the Intertidal Mudflats. *In:* Humphreys, J. and May, V. eds. *The Ecology of Poole Harbour*. Oxford: Elsevier, 91-108.

Capuzzo, E. and Forster, R. M., 2014. *Removal and subsequent uses of opportunistic green macro-algae (Ulva lactuca) in Poole Harbour.* Lowestoft: Centre for Environment, Fisheries & Aquaculture Science. Cefas contract report C6285.

Cardoso, P. G., Lillebø, A. I., Pardal, M. A., Ferreira, S. M. and Marques, J. C., 2002. The effect of different primary producers on *Hydrobia ulvae* population dynamics: a case study in a temperate intertidal estuary. *Journal of Experimental Marine Biology and Ecology*, 277, 173-195.

Cardoso, P. G., Pardal, M. A., Raffaelli, D., Baeta, A., and Marques, J. C., 2004. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. *Journal of Experimental Marine Biology and Ecology,* 308, 207-220.

Cardoso, P. G., Leston, S., Grilo, T. F., Bordalo, M. D., Crespo, D., Raffaelli, D. and Pardal, M. A., 2010. Implications of nutrient decline in the seagrass ecosystem success. *Marine Pollution Bulletin*, 60, 601-608.

Caro, T., 2007. Behaviour and conservation: a bridge too far? *Trends in Ecology and Evolution*, 22 (8), 394-400.

Cascade Consulting, 2012. *AMP5 Wastewater Nutrient Investigations: Poole Harbour SSSI.* Manchester: Cascade Consulting for Wessex Water. Report Number #1388653v3.

Clarke, K. R. and Warwick, R. M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation.* 2nd Edition. Plymouth: PRIMER-E Ltd.

Clarke, K. R. and Gorley, R. N., 2006. *Primer v6: User Manual/Tutorial.* Plymouth: PRIMER-E Ltd.

Clarke, K. R., Somerfield, P. J. and Chapman, M. G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330, 55-80.

Cloern, J. E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series,* 210, 223-253.

Cohen, J., 1994. The Earth is Round (p<.05). *American Psychologist*, 49 (12), 997-1003.

Como, S. and Magni, P., 2009. Temporal changes of a macrobenthic assemblage in harsh lagoon sediments. *Estuarine, Coastal and Shelf Science*, 83, 638-646.

Costanzo, S. D., O'Donohue, M. J., Dennison, W. C., Loneragan, N. R. and Thomas, M., 2001. A new approach for detecting and mapping sewage impacts. *Marine Pollution Bulletin,* 42 (2), 149-156.

Crooks, S. and Turner, R. K., 1999. Integrated Coastal Management: Sustaining Estuarine and Natural Resources. *In:* Nedwell, D. B. and Raffaelli, D. G., eds. *Estuaries: Advances in Ecological Research Vol. 29.* London: Academic Press, 241-290.

Crothers, J., 1997. *A key to the major groups of British marine invertebrates.* Telford: FSC Publications.

Davidson, N. C., Townshend, D. J., Pienkowski, M. W. and Speakman, J. R., 1986. Why do curlews *Numenius* have decurved bills? *Bird Study*, 33, 61-69.

Davidson, N. C., Laffoley, D. d'A., Doody, J. P., Way, L. S., Gordon, J., Key, P., Pienkowski, M. W., Mitchell, R. and Duff, K. L., 1991. *Nature conservation and estuaries in Great Britain.* Peterborough: Nature Conservancy Council.

Day, J. W. Jr., Crump, B. C., Kemp, W. M. and Yáñez-Arancibia, A., 2013. Introduction to Estuarine Ecology. *In*: Day, J. W. Jr., Crump, B. C., Kemp, W. M. and Yáñez-Arancibia, A., eds. *Estuarine Ecology* 2nd ed. Hoboken, New Jersey: John Wiley & Sons, 1-18.

Deegan, L. A., Wright, A., Ayvazian, S. G., Finn, J. T., Golden, H., Merson, R. R. and Harrison, J., 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12, 193-212.

Deegan, L. A., Johnson, D. S., Warren, R. S., Peterson, B. J., Fleeger, J. W., Fagherazzi, S. and Wollheim, W. M., 2012. Letter: Coastal eutrophication as a driver of salt marsh loss. *Nature,* 490, 388-392.

Dias, M. P., Granadeiro, J. P. and Palmeirim, J. M., 2009. Searching behaviour of foraging waders: does feeding success influence their walking? *Animal Behaviour*, 77, 1203-1209.

Dierschke, V., Kube, J., Probst, S. and Brenning, U., 1999. Feeding ecology of dunlins *Calidris alpina* in the southern Baltic Sea, 1. Habitat use and food selection. *Journal of Sea Research,* 42 (1), 49-64.

Dolbeth, M., Pardal, M. A., Lillebø, A. I., Azeiteiro, U. and Marques, J. C., 2003. Short- and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. *Marine Biology*, 143, 1229-1238.

Dolbeth, M., Cardoso, P. G., Ferreira, S. M., Verdelhos, T., Raffaelli, D. and Pardal, M. A., 2007. Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. *Marine Pollution Bulletin,* 54, 576-585.

Dolbeth, M., Cardoso, P. G., Grilo, T. F., Bordalo, M. D., Raffaelli, D. and Pardal, M. A., 2011. Long-term changes in the production by estuarine macrobenthos affected by multiple stressors. *Estuarine, Coastal and Shelf Science*, 92, 10-18.

Dominguez, J., 2002. Biotic and abiotic factors affecting the feeding behavior of the black-tailed godwit. *Waterbirds: The International Journal of Waterbird Biology*, 25 (4), 393-400.

Durell, S. E. A. Le V., 2000. Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biological Reviews*, 75, 503-518.

Durell, S. E. A. Le V., Stillman, R. A., Caldow, R. W. G., McGrorty, S., West, A. D. and Humphreys, J., 2006. Modelling the effect of environmental change on shorebirds: A case study on Poole Harbour, UK. *Biological Conservation,* 131, 459-473.

Dwyer, R. G., Bearhop, S., Campbell, H. A. and Bryant, D. M., 2013. Shedding light on light: benefits of anthropogenic illumination to a nocturnally foraging shorebird. *Journal of Animal Ecology,* 82, 478-485

Eaton, M. A., Aebischer, N. J.,, Brown, A. F., Hearn, R. D., Lock, L., Musgrove, A. J., Noble, D. G., Stroud, D. A. and Gregory, R. D., 2015. Birds of Conservation Concern 4: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Bird*s 108, 708–746.

Elliott, M., Burdon, D., Hemingway, K. L. and Apitz, S. E., 2007. Estuarine, coastal and marine ecosystem restoration: Confusing management and science – A revision of concepts. *Estuarine, Coastal and Shelf Science,* 74, 349-366

Elliott, M. and Whitfield, A. K., 2011. Challenging paradigms in estuarine ecology and management. *Estuarine, Coastal and Shelf Science,* 94, 306-314

Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist,* 100, 611-617.

Eriksson, B. K. and Johansson, G., 2005. Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. *Oecologia,* 143, 438-448.

Escartín, J. and Aubrey, G., 1995. Flow Structure and Dispersion within Algal Mats. *Estuarine, Coastal and Shelf Science,* 40, 451-472.

Evans, P. R., 1976. Energy Balance and Optimal Foraging Strategies in Shorebirds: Some Implications for their Distributions and Movements in the Non-Breeding Season. *Ardea*, 64 (1), 117-139.

Everett, R. A., 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. *Journal of Experimental Marine Biology and Ecology,* 175 (2), 253-274.

Ferns, P. N., 1992. *Bird life of Coasts and Estuaries.* Cambridge: Cambridge University Press.

Ferns, P. N. and Siman, H. Y., 1994. Utility of the curved bill of the Curlew *Numenius arquata* as a foraging tool. *Bird Study*, 41 (2), 102-109.

Ferreira, S. M., Pardal, M. A., Lillebø, A. I., Cardoso, P. G. and Marques, J. C., 2004. Population dynamics of *Cyathura carinata* (Isopoda) in a eutrophic temperate estuary. *Estuarine, Coastal and Shelf Science*, 61, 669-677.

Ferreira, J. G., Wolff, W. J., Simas, T. C. and Bricker, S. B., 2005. Does biodiversity of estuarine phytoplankton depend on hydrology? *Ecological Modelling,* 187, 513-523.

Ferreira, S. M., Brandão, A., Baeta, A., Neto, J. M., Lillebø, A. I., Jensen, K. T. and Pardal, M. A., 2007. Effects of restoration management on the estuarine isopod *Cyathura carinata*: mediation by trematodes and habitat change. *Marine Biology*, 151, 109-118.

Field, A., Miles, J. and Field, Z., 2012. *Discovering Statistics Using R.* London: Sage Publications Inc.

Finn, P. G., Catterall, C. P. and Driscoll, P. V., 2008. Prey versus substrate as determinants of habitat choice in a feeding shorebird. *Estuarine, Coastal and Shelf Science*, 80, 381-390.

Fitzpatrick, S. and Bouchez, B., 1998. Effects of recreational disturbance on the foraging behaviour of waders on a rocky beach. *Bird Study*, 45 (2), 157-171.

Fletcher, R. L., 1996. The occurrence of “green tides” – a review. *In:* Schramm, W. and Nienhuis, P. H., eds. *Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication.* Berlin: Springer, 7-43.

Flindt, M. R., Pardal, M. A., Lillebø, A. I., Martins, I. and Marques, J. C., 1999. Nutrient cycling and plant dynamics in estuaries: A brief review. *Acta Oecologica,* 20 (4), 237-248.

Frost, T.M., Austin, G.E., Calbrade, N.A., Holt, C.A., Mellan, H.J., Hearn, R.D., Stroud, D.A., Wotton, S.R. and Balmer, D.E. 2016. *Waterbirds in the UK 2014/2015: The Westland Bird Survey.* Thetford: British Trust for Ornithology.

Fox, J. and Weisberg, S., 2011. *An {R} Companion to Applied Regression* (2nd edition). [R package car]. Thousand Oaks, California: Sage. Available from URL http://www.jstatsoft.org/v40/i01/.

Fox, S. E., Stieve, E., Valiela, I., Hauxwell, J. and McClelland, J., 2008. Macrophyte abundance in Waquoit Bay: Effects of land-derived nitrogen loads on seasonal and multi-year biomass patterns. *Estuaries and Coasts,* 31, 532-541.

Fox, S. E., Teichberg, M., Olsen, Y. S., Heffner, L. and Valiela, I., 2009. Restructuring of benthic communities in eutrophic estuaries: lower abundance of prey leads to trophic shifts from omnivory to grazing. *Marine Ecology Progress Series,* 380, 43-57.

Fox, S. E., Teichberg, M., Valiela, I. and Heffner, L., 2012. The Relative Role of Nutrients, Grazing, and Predation as Controls on Macroalgal Growth in the Waquoit Bay Estuarine System. *Estuaries and Coasts,* 35, 1193-1204.

Gao, S., Chen, X., Yi, Q., Wang, G., Pan, G., Lin, A. and Peng, G., 2010. A strategy for the proliferation of *Ulva prolifera*, main causative species of green tides, with formation of sporangia by fragmentation. *PLoS ONE*, 5 (1), e8571.

Giere, O., 2006. Ecology and biology of marine oligochaete – an inventory rather than another review. *Hydrobiologia*, 564, 103-116.

Gill, J. A., Norris, K. and Sutherland, W. J., 2001a. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. *Journal of Applied Ecology*, 38, 846-856.

Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W. and Sutherland, W. J., 2001b. The buffer effect and large-scale population regulation in migratory birds. *Nature*, 412, 436-438.

Giordani, G., Zaldívar, J. M. and Viaroli, P., 2009. Simple tools for assessing water quality and trophic status in transitional water ecosystems. *Ecological Indicators,* 9, 982-991.

Google Earth 7.1.5.1557, 2014. *Brands Bay, 50*$^{o}$*39’46.79”N, 1*$^{o}$*58’19.32”W, elevation 0m. Holes Bay, 50*$^{o}$*43’58.78”N, 1*$^{o}$*59’40.15”W, elevation 0m. Ower Bay, 50*$^{o}$*40’34.51”N, 2*$^{o}$*00’22.26”W, elevation 0m.* Available from: *https://earth.google.co.uk/ [Accessed 13 June 2016].*

Goss-Custard, J. D., 1970. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *Journal of Animal Ecology*, 39 (1), 91-113.

Goss-Custard, J. D. and Charman, K., 1976. Predicting how many wintering waterfowl an area can support. *Wildfowl*, 27, 157-158.

Goss-Custard, J. D. and Jones, R. E., 1976. The diets of redshank and curlew. *Bird Study,* 23 (3), 233-243.

Goss-Custard, J. D., 1977. Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. *Animal Behaviour*, 25, 10-29.

Goss-Custard, J. D., Jones, R. E. and Newbery, P. E., 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, 14, 681-700.

Goss-Custard, J. D., Warwick, R. M., Kirby, R., McGrorty, S., Clarke, R. T., Pearson, B., Rispin, W. E., Durell, S. E. A. le V. dit and Rose, R. J., 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. *Journal of Applied Ecology*, 28 (3), 1004-1026.

Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G. and McGrorty, S., 2002. Carrying capacity in overwintering migratory birds. *Biological Conservation*, 105, 27-41.

Goss-Custard, J. D., Triplet, P., Sueur, F. and West, A. D., 2006a. Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation*, 127, 88-97.

Goss-Custard, J. C., West, A. D., Yates, M. G., Caldow, R. W. G., Stillman, R. A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Durell, S. E. A. Le V. dit., Eighhorn, G., Ens, B. J., Exo, K-M., Udayangani-Fernando, P. U., Ferns, P. N., Hockey, P. A. R., Gill, J. A., Johnstone, I., Kalejta-Summers, B., Masero, J. A., Moreira, F., Velu Nagarajan, R., Owens, I. P. F., Pacheco, C., Perez-Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W. J., Triplet, P., Worrall, D. H., Zharikov, Y., Zwarts, L. and Pettifor, R. A., 2006b. Intake rates and the functional response in shorebirds (*Charadriiformes*) eating macro-invertebrates. *Biological Reviews*, 81, 501-529.

Grall, J. and Chauvaud, L., 2002. Marine eutrophication and benthos: the need for new approaches and concepts. *Global Change Biology,* 8, 813-830.

Granadeiro, J. P., Dias, M. P., Martins, R. C. and Palmeirim, J. M., 2006. Variation in numbers and behaviour of waders during the tidal cycle: implications for the use of estuarine sediment flats. *Acta Oecologica*, 29, 293-300.

Gray, J. S. and Mirza, F. B., 1979. A possible method for the detection of pollution-induced disturbance on marine benthic communities. *Marine Pollution Bulletin,* 10, 142-146.

Gray, J. S., Wu, R. S-s. and Or, Y. Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series,* 238, 249-279.

Gray, J. S. and Elliott, M., 2010. *Ecology of Marine Sediments: From Science to Management* 2nd edition. Oxford: Oxford University Press.

Green, D. R., 2007. Applying geospatial technologies to weedmat monitoring and mapping: The Ythan Estuary, NE Scotland. *In:* Green, D. R., ed. (2010). *Coastal and Marine Geospatial Technologies.* Netherlands: Springer

Green, L., Blumstein, D. T. and Fong, P., 2015. Macroalgal mats in a eutrophic estuary obscure visual foraging cues and increase variability in prey availability for some shorebirds. *Estuaries and Coasts*, 38, 917-926.

Gunnarsson, T. G., Gill, J. A., Potts, P. M., Atkinson, P. W., Croger, R. E., Gélinaud, G., Gardarsson, A. and Sutherland, W. J., 2005a. Estimating population size in black-tailed godwits *Limosa limosa islandica* by colour-marking. *Bird Study*, 52, 153-158.

Gunnarsson, T. G., Gill, J. A., Petersen, A., Appleton, G. F. and Sutherland, W. J., 2005b. A double buffer effect in a migratory shorebird population. *Journal of Animal Ecology*, 74, 965-971.

Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M. and Sutherland, W. J., 2005c. Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society B*, 272, 2319-2323.

Gunnarsson, T. G., Gill, J. A., Atkinson, P. W., Gélinaud, G., Potts, P. M., Croger, R. E., Gudmundsson, G. A., Appleton, G. F. and Sutherland, W. J., 2006. Population-scale drivers of individual arrival times in migratory birds. *Journal of Applied Ecology*, 75, 1119-1127.

Hardison, A. K., Canuel, E. A., Anderson, I. C. and Veuger, B., 2010. Fate of macroalgae in benthic systems: carbon and nitrogen cycling within the microbial community. *Marine Ecology Progress Series*, 414, 41-55.

Hauxwell, J., Cebrián, J., Furlon, C. and Valiela, I., 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology*, 82 (4), 1007-1022.

Hawkins, S. J., 2012. Marine conservation in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 22, 281-287.

Hayden, H. S., Blomster, J., Maggs, C. A., Silva, P. C., Stanhope, M. J. and Waaland, J. R., 2003. Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. *European Journal of Phycology*, 38, 277-294.

Hayward, P. J. and Ryland, J. S. ,(Eds.), 1998. *Handbook of the Marine Fauna of North-West Europe.* Oxford: Oxford University Press.

Herbert, R. J. H., Ross, K., Huebner, R. and Stillman, R. A., 2010. *Intertidal Invertebrates and Biotopes of Poole Harbour SSSI and survey of Brownsea Island Lagoon.* Bournemouth: Bournemouth University for Natural England. Technical Report.

Hofmann, L. C., Nettleton, J. C., Neefus, C. D. and Methieson, A. C., 2010. Cryptic diversity of Ulva (Ulvales, Chlorophyta) in the Great Bay Estuarine System (Atlantic USA): introduced and indigenous distromatic species. *European Journal of Phycology*, 45 (3), 230-239.

Holt, C.A., Austin, G.E., Calbrade, N.A., Mellan, H.J., Hearn, R.D., Stroud, D.A., Wotton, S.R. and Musgrove, A.J. 2015. *Waterbirds in the UK 2013/14: The Wetland Bird Survey.* Thetford: British Trust for Ornithology.

Howarth, R. W. and Marino, R., 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over three decades. *Limnology and Oceanography*, 51 (1:2), 364-376.

Hull, S. C., 1987. Macroalgal Mats and Species Abundance: a Field Experiment. *Estuarine, Coastal and Shelf Science,* 25, 519-532.

Hulscher, J. B., 1996. Food and feeding behaviour. *In:* Goss-Custard, J. D., ed. *The Oystercatcher: From individuals to populations.* Oxford: Oxford University Press.

Humphreys, J., 2005. Salinity and Tides in Poole Harbour: Estuary or Lagoon? *In:* Humphreys, J. and May, V. eds. *The Ecology of Poole Harbour*. Oxford: Elsevier, 35-47.

Humphreys, J. and May, V., 2005. Introduction: Poole Harbour in context. *In:* Humphreys, J. and May, V. eds. *The Ecology of Poole Harbour*. Oxford: Elsevier, 1-8.

Hurd, C. L., Harrison, P. J., Bischof, K. and Lobban, C. S., 2014. *Seaweed Ecology and Physiology* (2nd Edition). Cambridge: Cambridge University Press.

Ivoševic. B., Han, Y.-G., Cho, Y. and Kwon, O., 2015. The use of conservation drones in ecology and wildlife research. *Journal of Ecology and Environment*, 38 (1), 113-118.

JNCC, 2004. *Common Standards Monitoring Guidance for Littoral Sediment Habitats.* Peterborough: Joint Nature Conservation Committee.

JNCC, 2013. *Special Protection Areas.* Peterborough: Joint Nature Conservation Committee. Available from: http://jncc.defra.gov.uk/page-162 [Accessed 29 May 2016].

Jones, M. and Pinn, E., 2006. The impact of a macroalgal mat on benthic biodiversity in Poole Harbour. *Marine Pollution Bulletin,* 53, 63-71.

Kadiri, M., Bockelmann-Evans., B. and Rauen, W. B., 2014. Assessing the susceptibility of two UK estuaries to nutrient enrichment. *Continential Shelf Research*, 88, 151-160.

Kaiser, M. J., Attrill, M. J., Jennings, S., Thomas, D. N., Barnes, D. K. A., Brierley, A. S., Polunin, N. V. C., Raffaelli, D. G. and Williams, P. J. le B., 2005. *Marine Ecology: Processes, Systems, and Impacts.* Oxford: Oxford University Press.

Kersten, M. and Piersma, T., 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea*, 75, 175-187.

Kite, D. J., Bryan, G. and Jonas, P., 2012. *Nitrogen in the Poole Harbour Catchment*: *Technical Report.* Dorchester: Natural England and Environment Agency.

Kong, F., Mao, Y., Cui, F., Zhang, X. and Gao, Z., 2010. Morphology and molecular identification of *Ulva* forming green tides in Qingdao, China. *Journal of Ocean University of China (Oceanic and Coastal Sea Research)*, 10 (1), 73-79.

Kuwae, T., Miyoshi, E., Sassa, S. and Watabe, Y., 2010. Foraging mode shift in varying environmental conditions by dunlin *Calidris alpina. Marine Ecology Progress Series*, 406, 281-289.

Lambeck, R. H. D., Goss-Custard, J. D. and Triplet, P., 1996. Oystercatchers and man in the coastal zone. *In:* Goss-Custard, J. D., ed. *The Oystercatcher: From individuals to populations.* Oxford: Oxford University Press.

Langston, W. J., Chesman, B. S., Burt, G. R., Hawkins, S. J., Readman, J. and Worsfold, P., 2003. *Characterisation of the South West European Marine Sites. Summary Report.* Plymouth: Marine Biological Association. Occasional Publication 14.

Langston, W. J., Pope, N. D., Davey, M., Langston, K. M., O'Hara, S. C. M., Gibbs, P. E. and Pascoe, P. L., 2015. Recovery from TBT pollution in English Channel environments: A problem solved? *Marine Pollution Bulletin*, 95, 551-564.

Leaper, R., Raffaelli, D., Emes, C. and Manly, B., 2001. Constraints on body-size distributions: an experimental test of the habitat architecture hypothesis. *Journal of Animal Ecology*, 70, 248-259.

Lee, N. M. and Hockey, P. A. R., 2001. Biases in the field estimation of shorebird prey sizes. *Journal of Field Ornithology*, 72 (1), 49-61.

Leston, S., Lillebø, A. I. and Pardal, M. A., 2008. The response of primary producer assemblages to mitigation measures to reduce eutrophication in a temperate estuary. *Estuarine, Coastal and Shelf Science*, 77, 688-696.

Lewis, L. J. and Kelly, T. C., 2001. A short-term study of the effects of algal mats on the distribution and behavioural ecology of estuarine birds. *Bird Study*, 48 (3), 354-360.

Lewis, L. J., Davenport, J. and Kelly, T. C., 2003. Responses of benthic invertebrates and their avail predators to the experimental removal of macroalgal mats. *Journal of the Marine Biological Association, U.K.*, 83, 31-36.

Lewis, J. L., Kelly, T. C. and Davenport, J., 2014. Black-tailed godwits *Limosa limosa islandica* and redshanks *Tringa totanus* respond differently to macroalgal mats in their foraging areas. *Wader Study Group Bulletin*, 121 (2), 85-93.

Little, C., 2000. *The Biology of Soft Shores and Sediments.* Oxford: Oxford University Press.

Littler, M. M. and Littler, D. S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *The American Naturalist*, 116 (1), 25-44.

Liu, D., Keesing, J. K., Qinguo, X. and Shi, P., 2009. World's largest macroalgal bloom caused by expansion of seaweed aquaculture in China. *Marine Pollution Bulletin,* 58, 888-895.

Liu, D., Keesing, J. K., Dong, Z., Zhen, Y., Di, B., Shi, Y., Fearns, P. and Shi, P., 2010. Recurrence of the world’s largest green-tide in 2009 in Yellow Sea, China: *Porphyra yezoensis* aquaculture rafts confirmed as nursery for macroalgal blooms. *Marine Pollution Bulletin*, 60, 1423-1432.

Liu, F., Pang, S. J., Chopin, T., Xu, N., Shan, T. F., Gao, S. Q. and Sun, S., 2010. The dominant *Ulva* strain of the 2008 green algal bloom in the Yellow Sea was not detected in the coastal waters of Qingdao in the following winter. *Journal of Applied Phycology*, 22, 531-540.

Longbottom, M. R., 1970. The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. *Journal of Experimental Marine Biology and Ecology*, 5, 138-157.

Lopes, R. J., Pardal, M. A. and Marques, J. C., 2000. Impact of macroalgal blooms and wader predation on intertidal macro-invertebrates: experimental evidence from the Mondego Estuary (Portugal). *Journal of Experimental Marine Biology and Ecology*, 249, 165-179.

Lopes, R. J., Pardal, M. A., Múrias, T., Cabral, J. A. and Marques, J. C., 2006. Influence of macroalgal mats on abundance and distribution of dunlin *Calidris alpina* in estuaries: a long-term approach. *Marine Ecology Progress Series*, 323, 11-20.

Lyons, D. A., Arvanitidis, C., Blight, A. J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H., Queirós, Rilov, G., Somerfield, P. J. and Crowe, T. P., 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. *Global Change Biology*, 20, 2712 – 2724.

MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. *American Naturalist,* 100, 603-609.

Martins, R. C., Catry, T., Santos, C. D., Palmeirim, J. M. and Granadeiro, J. P., 2013. Seasonal Variations in the Diet and Foraging Behaviour of Dunlins *Calidris alpina* in a South European Estuary: Improved Feeding Conditions for Northward Migrants. *PLoS ONE* 8(12): e81174.

McLusky, D. S. and Elliott, M., 2004. *The Estuarine Ecosystem: Ecology, Threats and Management* 3rd edition. Oxford: Oxford University Press.

Ménesguen, A. and Piriou, J-Y., 1995. Nitrogen loadings and macroalgal (*Ulva* sp.) mass accumulation in Brittany (France). *Ophelia*, 42, 227-237.

Ménesguen, A. and Cugier, P., 2006. A new numerical technique for tracking chemical species in a multisource, coastal ecosystem applied to nitrogen causing *Ulva* blooms in the Bay of Brest (France). *Limnology and Oceanography*, 51 (1, 2), 591-601.

Met Office, 2016. *Climate Summaries*. Exeter: Met Office. Available from http://www.metoffice.gov.uk/climate/uk/summaries [Accessed 28 May 2016].

Monbet, Y., 1992. Control of phytoplankton biomass in estuaries: A comparative analysis of microtidal and macrotidal estuaries. *Estuaries,* 15 (4), 563-571.

Montgomery, H. A. C. and Soulsby, P. G., 1980. Effects of Eutrophication on the intertidal Ecology of Langstone Harbour, U.K., and proposed control measures. *Progress in Water Technology*, 13, 287-294.

Morand, P. and Merceron, M., 2005. Macroalgal Population and Sustainability. *Journal of Coastal Research,* 21 (5), 1009-1020.

Moreira, F., 1994. Diet, prey-size selection and intake rates of Black-tailed Godwits *Limosa limosa* feeding on mudflats. *Ibis*, 136, 349-355.

Mouritsen, K. N., 1994. Day and night feeding in Dunlins *Calidris alpina*: choice of habitat, foraging technique and prey. *Journal of Avian Biology,* 25, 55-62.

Mouritsen, K. N. and Jensen, K. T., 1992. Choice of microhabitat in tactile foraging dunlins *Calidris alpina*: the importance of sediment penetrability. *Marine Ecology Progress Series*, 85, 1-8.

Múrias, T., Cabral, J. A., Marques, J. C. and Goss-Custard, J. D., 1996. Short-term Effects of Intertidal Macroalgal Blooms on the Macrohabitat Selection and Feeding Behaviour of Wading Birds in the Mondego Estuary (West Portugal). *Estuarine, Coastal and Shelf Science,* 43, 677-688.

Natural England, 2013. *Natura 2000: European Wildlife Sites* [online]. Sheffield: Natural England. Available from: http://www.naturalengland.org.uk/images/natura-european-wildlife-sites_tcm6-27665.pdf [Accessed 28 May 2016].

Natural England, 2016. *Department Brief. Poole Harbour potential Special Protection Area*. Peterborough: Natural England

Navedo, J. G., Arranz, D., Herrera, A. G., Salmón, P., Juanes, J. A. and Masero, J. A., 2013. Agroecosystems and conservation of migratory waterbirds: importance of coastal pastures and factors influencing their use by wintering shorebirds. *Biodiversity Conservation*, 22, 1895-1907.

Nedwell, D. B., Sage, A. S. and Underwood, G. J. C., 2002. Rapid assessment of macro algal cover on intertidal sediments in a nutrified estuary. *Science of the Total Environment,* 285, 97-105.

Neilson, B. J. and Cronin, L. E., 1981. Preface. *In*: Neilson, B. J. and Cronin, L. E., eds. *Estuaries and Nutrients.* Clifton, New Jersey: The Humana Press Inc.

Newton, C. and Thornber, C., 2012. Abundance and species composition surveys of macroalgal blooms in Rhode Island salt marshes. *Northeastern Naturalist*, 19 (3), 501-516.

Newton, C. and Thornber, C., 2013. Ecological impacts of macroalgal blooms on salt marsh communities. *Estuaries and Coasts*, 36, 365-376.

Ogden, L. A., 2013. Drone Ecology. *BioScience*, 63 (9), 776.

Österling, M. and Pihl, L., 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. *Journal of Experimental Marine Biology and Ecology*, 263, 159-183.

Painting, S. J., Devlin, M. J., Malcolm, S. J., Parker, E. R., Mills, D. K., Mills, C., Tett, P., Wither, A., Burt, J., Jones, R. and Winpenny, K., 2007. Assessing the impact of nutrient enrichment in estuaries: Susceptibility to eutrophication. *Marine Pollution Bulletin,* 55, 74-90.

Patrício, J., Neto, J. M., Teixeira, H. and Marques, J. C., 2007. Opportunistic macroalgae metrics for transitional waters. Testing tools to assess ecological quality status in Portugal. *Marine Pollution Bulletin,* 53, 1887-1896.

Pearson, T. H. and Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology – An Annual Review,* 16, 229-311.

Pedersen, M. F. and Borum, J., 1997. Nutrient control of estuarine macroalgae: Growth strategy and the balance between nitrogen requirements and uptake. *Marine Ecology Progress Series,* 161, 155-163.

Perrot, T., Rossi, N., Ménesguen, A. and Dumas, F., 2014. Modelling green macroalgal blooms on the coasts of Brittany, France to enhance water quality management. *Journal of Marine Systems*, 132 (38-53).

Peters, G., 2016. *userfriendlyscience: Quantitative analysis made accessible.* [R package userfiendlyscience version 0.4-0]. Vienna: CRAN R-project. Available from: URL: http://CRAN.R-project.org/package=userfriendlyscience.

Piazzi, L. and Cinelli, F., 2003. Evaluation of benthic macroalgal invasion in a harbour area of the western Mediterranean Sea. *European Journal of Phycology,* 38, 223-231.

Pickess, B. and Underhill-Day, J., 2002. *Important Birds of Poole Harbour.* Wareham: Poole Harbour Study Group.

Pohlert, T., 2014. *The Pairwise Multiple Comparison of Mean Ranks (PCMR).* [R package PCMR]. Vienna: CRAN R Project. Available from: URL: http://CRAN.R-project.org/package=PMCMR.

Prater, A. J., 1981. *Estuary Birds of Britain and Ireland.* Calton, Staffordshire: T & A D Poyser Ltd.

R Core Team 2016. *R: A language and environment for statistical computing*. Version [3.3.0 "Supposedly Educational"]. Vienna: R Foundation for Statistical Computing. Available from: URL https://www.R-project.org/.

Raffaelli, D., Hull, S. and Milne, H., 1989. Long-term changes in nutrients, weed mats and shorebirds in an Estuarine System. *Cahiers de biologie marine*, 30, 259-270.

Raffaelli, D., Limia, J., Hull, S. and Pont, S., 1991. Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. *Journal of the Marine Biological Association U.K.*, 71, 899-908.

Raffaelli, D. G., Raven, J. A. and Poole, L. J., 1998. Ecological Impact of Green Macroalgal Blooms. *In:* Ansell, A. D., Gibson, R. N. and Barnes, M., eds. *Oceanography and Marine Biology: an Annual Review, Volume 36*. London: Routledge, 97-125.

Raffaelli, D. G., 1999. Nutrient enrichment and trophic organisation in an estuarine food web. *Acta Oecologica*, 20 (4), 449-461.

Raffaelli, D. G., Balls, P., Way, S., Patterson, I. J., Hohmann, S. and Corp, N., 1999. Major long-term changes in the ecology of the Ythan estuary, Aberdeenshire, Scotland; how important are physical factors? *Aquatic Conservation: Marine and Freshwater Ecosystems,* 9 (2), 219-236.

Raffaelli, D., Hall, S., Emes, C. and Manly, B., 2000. Constraints on body size distributions: an experimental approach using a small-scale system. *Oecologia*, 122, 389-398.

Raffaelli, D., 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology Progress Series,* 311, 285-294

Raven, J. A. and Taylor, R., 2003. Macroalgal growth in nutrient enriched estuaries: a biogeochemical and evolutionary perspective. *Water, Air, and Soil Pollution*, 3, 7-26.

Rees-Jones, S., 2004. *Investigation into the impact of macroalgae on intertidal macrobenthos in Southern Regions Estuaries.* West Mailing: Southern Region Environment Agency. Technical Report No. 10204.

Riedel, B., Zuschin, M. and Stachowitsch, M., 2012. Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: a realistic scenario. *Marine Ecology Progress Series*, 458, 39-52.

Rippe, H. and Dierschke, V., 1997. Picking out the plum jobs: feeding ecology of curlews *Numenius arquata* in a Baltic Sea wind flat. *Marine Ecology Progress Series,* 159, 239-247.

Rosenberg, R., Nilsson, H. C. and Diaz, R. J., 2001. Respone of Benthic Fauna and Changing Sediment Redox Profiles over a Hypoxic Gradient. *Estuarine, Coastal and Shelf Science,* 53, 343-350.

RSPB, undated. *The European Birds Directive – safeguarding special places for people and wildlife.* Available from: *https://www.rspb.org.uk/Images/birdsdirectivereport_tcm9-133074.pdf [Accessed 30 March 2016].* Sandy: RSPB

Santiago-Quesada, F., Estrella, S. M., Sánches-Guzmán, J. M. and Masero, J. A., 2014. Why water birds forage at night: a test using black-tailed godwits *Limosa limosa* during migratory periods. *Journal of Avian Biology*, 45, 406-409.

Santos, C. D., Granadeiro, J. P. and Palmeirim J. M., 2005. Feeding Ecology of Dunlin *Calidris alpina* in a Southern European Estuary. *Ardeola,* 52, 235-252.

Scanlan, C. M., Foden, J., Wells, E. and Best, M. A., 2007. The monitoring of opportunistic macroalgal blooms for the water framework directive. *Marine Pollution Bulletin,* 55, 162-171.

Sfriso, A., Pavoni, B., Marcomini, A. and Orio, A. A., 1992. Macroalgae, Nutrient Cycles, and Pollutants in the Lagoon of Venice. *Estuaries*, 15 (4), 517-528.

Shen, Q., Li, H., Li, Y., Wang, Z., Liu, J. and Yang, W., 2012. Molecular identification of green algae from the rafts based infrastructure of *Porphyra yezoensis. Marine Pollution Bulletin*, 64, 2077-2082.

Smetacek, V. and Zingone, A., 2013. Green and golden seaweed tides on the rise. *Nature*, 504, 84-88.

Soulsby, P. G., Lowthion, D. and Houston, M., 1982. Effects of macroalgal mats on the ecology of intertidal mudflats. *Marine Pollution Bulletin,* 13 (5), 162.

Statham, P. J., 2012. Nutrients in estuaries – An overview and the potential impacts of climate change. *Science of the Total Environment*, 434, 213-227.

Stillman, R. A., West, A. D., Goss-Custard, J. D., McGrorty, S., Frost, N. J., Morrisey, D. J., Kenny, A. J. and Drewitt, A. L., 2005. Predicting site quality for shorebird communities: a case study on the Humber Estuary, UK. *Marine Ecology Progress Series*, 305, 203-217.

Stillman, R. A., 2008. MORPH – An individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling,* 216, 265-276.

Stillman, R. A. and Goss-Custard, J. D., 2010. Individual-based ecology of coastal birds. *Biological Reviews*, 85, 413-434.

Stillman, R. A., Moore, J. J., Woolmer, A. P., Murphy, M. D., Walker, P., Vanstaen, K. R., Palmer, D. and Sanderson, W. G., 2010. Assessing waterbird conservation objectives: An example for the Burry Inlet, UK. *Biological Conservation*, 143, 2617-2630.

Sutherland, W. J., Newton, I. and Green, R. E., 2005. *Bird Ecology and Conservation: A Handbook of Techniques.* Oxford: Oxford University Press.

Sutherland, W. J., 2006. *Ecological Census Techniques* 2nd edition. Cambridge: Cambridge University Press

Svensson, L., Mullarney, K. and Zetterström, D., 2010. *Collins Bird Guide* 2nd edition. London: Harper Collins.

Taylor, R., Fletcher, R. L. and Raven, J. A., 2001. Preliminary Studies on the Growth of Selected 'Green Tide' Algae in Laboratory Culture: Effects of Irradiance, Temperature, Salinity and Nutrients on Growth Rate. *Botanica Marina,* 44, 327-336.

Teichberg, M., Fox, S. E., Olsen, Y. S., Valiela, I., Martinetto, P., Iribarnes, O., Yuriko Muto, E., Petti, M. A. V., Corbisier, T. N., Soto-Jiménez, M., Páez-Osuna, F., Castro, P., Freitas, H., Zitell, A., Cardinaletti, M. and Tagliapietra, D., 2010. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. *Global Change Biology,* 16, 2624-2637.

Thiel, M., Stearns, L. M. and Watling, L., 1998. Effects of green algal mats on bivalves in a New England mud flat. *Helgoländer Meeresuntersunchungen Helgoländer Meeresunters*, 52, 15-28.

Thomas, N. S., Caldow, R. W. G., McGrorty, S., Durrell, S. E. A. le V., West, A. D. and Stillman, R. A., 2004. *Bird Invertebrate Prey Availability in Poole Harbour.* Wareham, Dorset: Poole Harbour Study Group.

Townsend, C. R., Begon, M. and Harper, J. L., 2008. *Essentials of Ecology*, 3rd edition. Oxford: Blackwell Publishing.

Tubbs, C. R., 1977. Wildfowl and waders in Langstone Harbour. *British Birds*, 70, 177-199.

Tubbs, C. R. and Tubbs, J. M., 1980. Wader and Shelduck feeding distribution in Langstone Harbour, Hampshire. *Bird Study,* 27 (4), 239-248.

Underhill-Day, J., Underhill-Day, N., White, J. and Gartshore, N., 2010. *Poole Harbour SSSI Condition Assessment.* Wareham: Footprint Ecology for Natural England.

United Kingdom Hydrographic Office Admiralty Easy Tide. *Tidal Prediction Chart: Poole* [online]. Taunton: United Kingdom Hydrographic Office. Available from: http://www.ukho.gov.uk/easytide/EasyTide/index.aspx [Accessed as required from March 2013 – March 2015].

Valiela, I., McClelland, J., Hauxwell, J., Behr, P. J., Hersh, D., Foreman, K., 1997. Macroalgal Blooms in Shallow Estuaries: Controls and Ecophysiological and Ecosystem Consequences. *Limnology and Oceanography,* 42 (5, 2), 1105-1118.

Van Alstyne, K. L., Gifford, S.-A., Dohman, J. M. and Savedo, M. M., 2015. Effects of environmental changes, tissue types and reproduction on the emissions of dimethyl sulphide from seaweeds that form green tides. *Environmental Chemistry*, 13 (2), 220-230.

van de Kam, J., Ens, B., Piersma, T. and Zwarts, L., 2004. *Shorebirds. An illustrated behavioural ecology*. Utrecht: KNNV.

van de Pol M., Ens B.J., Oosterbeek K., Brouwer L., Verhulst S., Tinbergen J.M., Rutten A.L. and de Jong M., 2009. Oystercatchers' bill shapes as a proxy for diet specialization: more differentiation than meets the eye. *Ardea* 97(3), 335–347.

Venier, C., Figueiredo da Silva, J., McLelland, S. J., Duck, R. W. and Lanzoni, S., 2012. Experimental investigation of the impact of macroalgal mats on flow dynamics and sediment stability in shallow tidal areas. *Estuarine, Coastal and Shelf Science,* 112, 52-60.

Verdelhos, T., Neto, J. M., Marques, J. C. and Pardal, M. A., 2005. The effect of eutrophication abatement on the bivalve *Scrobicularia plana. Estuarine, Coastal and Shelf Science*, 63, 261-268.

Warwick, R. M., 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology*, 92, 557-562.

Warwick, R. M. and Clarke, K. R., 1994. Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. *Marine Biology*, 118, 739-744.

WFD-UKTAG, 2009. *UKTAG Transitional and Coastal Water Assessment Methods: Macroalgae. Macroalgal Bloom Assessment (Opportunistic Macroalgae).* Edinburgh: Water Framework Directive – United Kingdom Technical Advisory Group. Report.

WFD-UKTAG, 2013. *UKTAG Biological Status Methods Coastal and Transitional Waters – Opportunistic macroalgae. Annex 15 Transitional and coastal waters. Practitioners Guide to the Opportunistic Macroalgal Blooming Tool.* Edinburgh: Water Framework Directive – United Kingdom Technical Advisory Group. Report: Version 08.071212. Available from http://www.wfduk.org [Accessed 02 May 2013].

West, A. D., Goss-Custard, J. D., Durell, S. E. A. Le V. and Stillman, R. A., 2005. Maintaining estuary quality for shorebirds: towards simple guidelines. *Biological Conservation*, 123, 211-224.

West, A. D., Yates, M. G., McGrorty, S. and Stillman, R. A., 2007. Predicting site quality for shorebird communities: A case study on the Wash embayment, UK. *Ecological Modelling*, 202, 257-539.

Whitfield, A. K., Elliott, M., Basset, A., Blaber, S. J. M. and West, R. J., 2012. Paradigms in estuarine ecology – A review of the Remane diagram with a suggested revised model for estuaries. *Estuarine, Coastal and Shelf Science*, 97, 78-90.

Wickham, H. 2009. *Elegant Graphics for Data Analysis* [R package ggplot2]. New York: Springer Verlag.

Wildsmith, M. D., Rose, T. H., Potter, I. C., Warwick, R. M., Clarke, K. R., and Valesini, F. J., 2009. Changes in the benthic macroinvertebrate fauna of a large microtidal estuary following extreme modifications aimed at reducing eutrophication. *Marine Pollution Bulletin,* 58, 1250-1262.

Wilson, J. G. and Fleeger, J. W., 2013. Estuarine Benthos. *In*: Day, J. W. Jr., Crump, B. C., Kemp, W. M. and Yáñez-Arancibia, A., eds. *Estuarine Ecology* 2nd ed. Hoboken, New Jersey: John Wiley & Sons, 303-325.

Wolff, W. J., 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. *Ardea*, 57, 1-28.

WoRMS Editorial Board, 2016. *World Register of Marine Species*. Available from http://www.marinespecies.org. [Accessed as required from March 2013].

Yardley, J., 2008. To Save Olympic Sailing Races, China Fights Algae. *New York Times* [online], 1 July 2008. Available from: http://www.nytimes.com/2008/07/01/world/asia/01algae [Accessed 15 June 2016].

Yarrington, C. S., Tyler, A. C. and Altieri, A. H., 2013. Do snails facilitate bloom-forming macroalgae in a eutrophic estuary? *Journal of Experimental Marine Biology and Ecology*, 446, 253-561.

Zwarts, L. and Wanink, J. H., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, 31 (4), 441-476.

Zwarts, L., 1996. *Waders and their estuarine food supplies.* Lelystad: RIZA Report Van Zee tot Land 60.

Zwarts, L., Crayford, J. T., Hulscher, J. B., Kersten, M., Miere, P. M. and Triplet, P., 1996. Prey size selection and intake rate. *In:* Goss-Custard, J. D., ed. *The Oystercatcher: From individuals to populations.* Oxford: Oxford University Press.

BLANK

# Appendix 1a

**Mean air temperature ($^{o}$C), sunshine (hours) and rainfall (mm) for 1981-2010 average and monthly from January 2013 – March 2015 (www.metoffice.gov.uk).**

| Month | Year | Mean temperature $^{o}$C | Sunshine (hours) | Rainfall (mm) |
|---|---|---|---|---|
| Jan | 1981-2010 | 5.0 | 66.5 | 86.9 |
| Feb | 1981-2010 | 4.9 | 84.5 | 62.5 |
| Mar | 1981-2010 | 6.9 | 121.4 | 64.7 |
| Apr | 1981-2010 | 8.7 | 185.1 | 53.9 |
| May | 1981-2010 | 12.1 | 218.5 | 49.5 |
| Jun | 1981-2010 | 14.8 | 229.5 | 51.6 |
| Jul | 1981-2010 | 17.0 | 232 | 47.8 |
| Aug | 1981-2010 | 16.8 | 214.6 | 51.8 |
| Sep | 1981-2010 | 14.4 | 159.1 | 65.3 |
| Oct | 1981-2010 | 11.2 | 115.2 | 100.7 |
| Nov | 1981-2010 | 7.6 | 80.1 | 100.5 |
| Dec | 1981-2010 | 5.2 | 60.3 | 100.0 |
| Jan | 2013 | 3.9 | 43.5 | 81.4 |
| Feb | 2013 | 3.2 | 67.6 | 38.1 |
| Mar | 2013 | 3.4 | 66.5 | 70.3 |
| Apr | 2013 | 7.6 | 166.9 | 41.8 |
| May | 2013 | 10.7 | 191.9 | 56.2 |
| Jun | 2013 | 14.2 | 188.1 | 22.8 |
| Jul | 2013 | 18.7 | 291.9 | 31.9 |
| Aug | 2013 | 17.6 | 214.4 | 38.9 |
| Sep | 2013 | 14.4 | 126.8 | 52.6 |
| Oct | 2013 | 12.8 | 97.9 | 138.7 |
| Nov | 2013 | 6.7 | 78.8 | 71.8 |
| Dec | 2013 | 6.3 | 53.8 | 161.4 |
| Jan | 2014 | 6.2 | 63.7 | 205.2 |
| Feb | 2014 | 6.7 | 96.6 | 147.7 |
| Mar | 2014 | 8.1 | 159.7 | 37.9 |
| Apr | 2014 | 10.6 | 167.5 | 75.1 |
| May | 2014 | 12.5 | 201.6 | 74.1 |
| Jun | 2014 | 15.8 | 241.7 | 37.8 |
| Jul | 2014 | 18.6 | 269.2 | 46.2 |
| Aug | 2014 | 15.9 | 199.4 | 102.0 |
| Sep | 2014 | 15.8 | 144.8 | 14.8 |
| Oct | 2014 | 13.3 | 106.9 | 111.4 |
| Nov | 2014 | 9.0 | 58.3 | 135.6 |
| Dec | 2014 | 5.5 | 75 | 53.9 |
| Jan | 2015 | 4.9 | 70.2 | 99.0 |
| Feb | 2015 | 4.1 | 80 | 60.4 |
| Mar | 2015 | 6.9 | 142.2 | 24.5 |

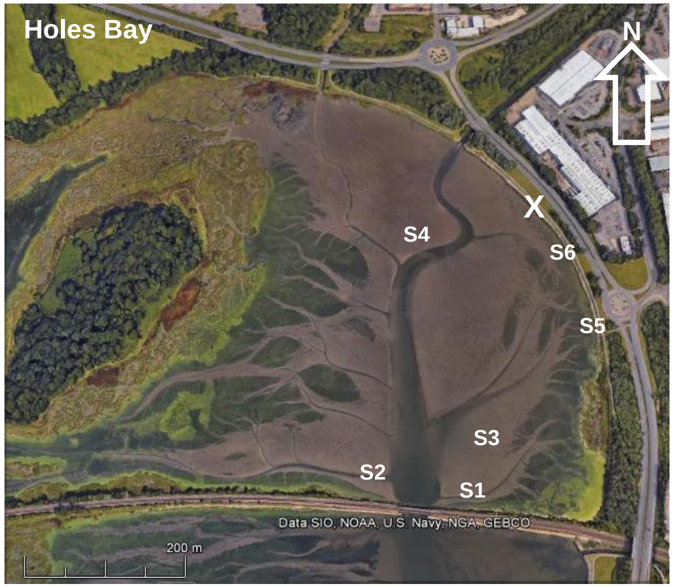
# Appendix 1b

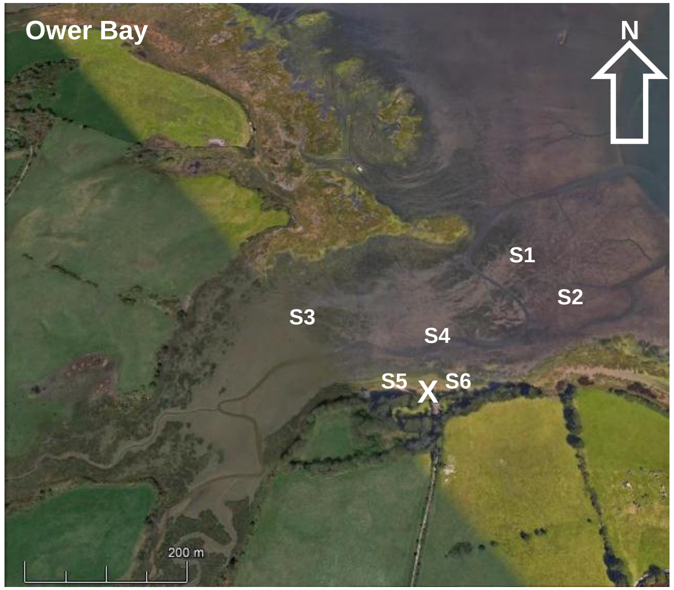
## Site temperature $^{o}$C and mean sediment temperature $^{o}$C recorded during algae biomass sampling March 2013 – March 2015.

| Site | Date | Site temperature $^{o}$C | Mean sediment temperature $^{o}$C | Sediment temperature 95% C.I. |
|---|---|---|---|---|
| Brands Bay | Mar-13 | 2 | 4.62 | 0.08 |
| Brands Bay | Apr-13 | 20 | 19.58 | 0.18 |
| Brands Bay | May-13 | 13 | 14.98 | 0.05 |
| Brands Bay | Jun-13 | 15 | 16.54 | 0.09 |
| Brands Bay | Jul-13 | 26 | 26.02 | 0.15 |
| Brands Bay | Aug-13 | 22 | 20.86 | 0.06 |
| Brands Bay | Sep-13 | 19 | 17.36 | 0.07 |
| Brands Bay | Oct-13 | 15 | 19 | 0.10 |
| Brands Bay | Nov-13 | 9 | 9.7 | 0.02 |
| Brands Bay | Dec-13 | 10 | 11.24 | 0.04 |
| Brands Bay | Jan-14 | 7 | 10.36 | 0.00 |
| Brands Bay | Feb-14 | 9 | 11.99 | 0.00 |
| Brands Bay | Apr-14 | 16 | 16.6 | 0.13 |
| Brands Bay | Jun-14 | 18 | 20.44 | 0.07 |
| Brands Bay | Aug-14 | 21 | 19.9 | 0.12 |
| Brands Bay | Oct-14 | 13 | 14.6 | 0.02 |
| Brands Bay | Dec-14 | 10 | 9.58 | 0.02 |
| Brands Bay | Feb-15 | 6 | 12.12 | 0.03 |
| Holes Bay | Mar-13 | 0 | 5.78 | 0.09 |
| Holes Bay | Apr-13 | 7 | 9.44 | 0.07 |
| Holes Bay | May-13 | 10 | 15.12 | 0.05 |
| Holes Bay | Jun-13 | 19 | 19 | 0.10 |
| Holes Bay | Jul-13 | 30 | 26.72 | 0.08 |
| Holes Bay | Aug-13 | 22 | 20.14 | 0.07 |
| Holes Bay | Sep-13 | 17 | 16.32 | 0.06 |
| Holes Bay | Oct-13 | 19 | 17.4 | 0.08 |
| Holes Bay | Nov-13 | 9 | 12.18 | 0.01 |
| Holes Bay | Dec-13 | 6 | 10.8 | 0.00 |
| Holes Bay | Jan-14 | 7 | 9.84 | 0.00 |
| Holes Bay | Feb-14 | 9 | 10.27 | 0.00 |
| Holes Bay | Apr-14 | 18 | 18.2 | 0.00 |
| Holes Bay | Jun-14 | 20 | 24.26 | 0.05 |
| Holes Bay | Aug-14 | 21 | 21.92 | 0.16 |
| Holes Bay | Oct-14 | 17 | 16.76 | 0.09 |
| Holes Bay | Dec-14 | 8 | 10.68 | 0.03 |
| Holes Bay | Feb-15 | 8 | 12.32 | 0.04 |
| Newton Bay | Mar-13 | 2 | 5.6 | 0.09 |
| Newton Bay | Apr-13 | 15 | 20.48 | 0.11 |

| Site | Date | Site temperature $^{o}C$ | Mean sediment temperature $^{o}C$ | Sediment temperature 95% C.I. |
|---|---|---|---|---|
| Newton Bay | May-13 | 15 | 19.96 | 0.18 |
| Newton Bay | Jun-13 | 18 | 19.36 | 0.17 |
| Newton Bay | Jul-13 | 25 | 26.52 | 0.24 |
| Newton Bay | Aug-13 | 23 | 26.62 | 0.22 |
| Newton Bay | Sep-13 | 16 | 20.9 | 0.12 |
| Newton Bay | Oct-13 | 14 | 15.94 | 0.05 |
| Newton Bay | Nov-13 | 9 | 11.08 | 0.02 |
| Newton Bay | Dec-13 | 11 | 11.2 | 0.00 |
| Newton Bay | Jan-14 | 7 | 10.24 | 0.00 |
| Newton Bay | Feb-14 | 9 | 10.27 | 0.00 |
| Newton Bay | Apr-14 | 12 | 14.94 | 0.04 |
| Newton Bay | Jun-14 | 22 | 22.5 | 0.19 |
| Newton Bay | Aug-14 | 21 | 20.38 | 0.08 |
| Newton Bay | Oct-14 | 13 | 14.5 | 0.05 |
| Newton Bay | Dec-14 | 10 | 10.32 | 0.02 |
| Newton Bay | Feb-15 | 10 | 12.96 | 0.05 |
| Ower Bay | Mar-13 | 2 | 4.76 | 0.04 |
| Ower Bay | Apr-13 | 17 | 17.28 | 0.75 |
| Ower Bay | May-13 | 13 | 18 | 0.21 |
| Ower Bay | Jun-13 | 17 | 16.66 | 0.08 |
| Ower Bay | Jul-13 | 27 | 25.98 | 0.18 |
| Ower Bay | Aug-13 | 22 | 22.62 | 0.34 |
| Ower Bay | Sep-13 | 16 | 19.4 | 0.07 |
| Ower Bay | Oct-13 | 16 | 16.2 | 0.16 |
| Ower Bay | Nov-13 | 9 | 9.72 | 0.03 |
| Ower Bay | Dec-13 | 11 | 11.22 | 0.03 |
| Ower Bay | Jan-14 | 7 | 10.65 | 0.00 |
| Ower Bay | Feb-14 | 9 | 10.43 | 0.00 |
| Ower Bay | Apr-14 | 12 | 14.8 | 0.08 |
| Ower Bay | Jun-14 | 22 | 21.44 | 0.11 |
| Ower Bay | Aug-14 | 21 | 19.34 | 0.05 |
| Ower Bay | Oct-14 | 15 | 15.78 | 0.03 |
| Ower Bay | Dec-14 | 10 | 9.2 | 0.03 |
| Ower Bay | Feb-15 | 10 | 12.62 | 0.03 |

# Appendix 2





**Locations of benthic invertebrate core sampling stations and vantage point for bird observations.**

**S1 and S2: lower shore**

**S3 and S4: mid shore**

**S5 and S6: upper shore**

**X bird observation point**

Each point comprised six replicate core samples taken on three dates (September 2013, December 2013, September 2014).

Images © Google Earth 2014.

# Appendix 3a

**Head-width to length conversions calculated for samples collected in Poole Harbour September 2013, December 2013, and September 2014.**

*Hediste diversicolor:* $\log_{(e)}$ length = $1.2901*\log_{(e)}$head + 2.9143, $r^2 = 0.939$, n=507

*Nephtys hombergii:* $\log_{(e)}$ length = $3.73375+\log_{(e)}$head*0.6082, $r^2 = 0.391$, n=25

No significant difference was found between actual length and length calculated using the equations above ($p = >0.05$).

# Appendix 3b

**Length to AFDM (mg) equations from Thomas et al. (2004) and Herbert et al. (2010) for species recorded in Poole Harbour Sept. 2013, Dec. 2013, Sept. 2014.**

| Species | Length to AFDM (mg) |
|---|---|
| *Hediste diversicolor* | EXP(-4.8+1.88*LN(x)+0.5*0.175 |
| *Nephtys hombergii* | EXP(-6.47+2.4*LN(x)+0.5*0.043) |
| *Cyathura carinata* | EXP(-4.3179+2.1435*LN(x)+0.5*0.2182) |
| *Peringia ulvae* | EXP(-1.6752+1.1748*LN(x)+0.5*0.0762) |
| *Corophium volutator* | EXP(-2.9967+1.5479*LN(x)+0.5*0.129) |
| Small worms* | 0.019 mg per worm |
| *Abra tenuis* | EXP(-2.0287+1.7031*LN(x)+0.5*0.0412) |
| *Limecola (Macoma) balthica* | EXP(-2.0287+1.7031*LN(x)+0.5*0.0412) |
| *Mya arenaria* | EXP(-2.0287+1.7031*LN(x)+0.5*0.0412) |
| *Cerastoderma edule* | EXP(-5.68+3.315*LN(x)+0.5*0.046) |
| *Ruditapes philippinarum* | EXP(-4.9+2.98*LN(B23)+0.5*0.057) |
| *Gammarus locusta* | EXP(-5.2531+2.6753*LN(B10)+0.5*0.0787) |
| *Melita palmata* | EXP(-5.2531+2.6753*LN(B10)+0.5*0.0787) |
| *Microdeutopus gryllotalpa* | EXP(-5.2531+2.6753*LN(B10)+0.5*0.0787) |
| *Microprotopus maculatus* | EXP(-5.2531+2.6753*LN(B10)+0.5*0.0787) |
| *Carcinus maenas* | EXP(-1.757+2.2739*LN(B13)+0.5*0.104) |
| *Arenicola marina* | 358 mg per individual |
| *Littorina spp.* | EXP(-5.6481+3.59194*LN(B12)+0.5*0.09) |
| *Idotea balthica* | EXP(-5.2531+2.6753*LN(B10)+0.5*0.0787) |
| *Retusa obtusa* | EXP(-2.0287+1.7031*LN(x)+0.5*0.0412) |

*Small worms: *Ampharete acutifrons, Aphelochaeta marioni,* Capitellidae, *Chaetozone* sp., Chironomidae, *Desdemona ornata*, Dolichopodidae, *Eteone longa, Glycera tridactyla, Melinna palmata, Phyllodoce mucosa, Polydora* sp., *Pygospio elegans, Scolelepsis* sp., *Scoloplos armiger, Streblospio shrubsolii, Tubificoides* spp.

# Appendix 4a

## Mean abundance (m$^{-2}$) and mean biomass (mg AFDM m$^{-2}$) of invertebrates recorded at each site (Brands Bay, Holes Bay and Ower Bay).

| | **Brands Bay** | | **Holes Bay** | | **Ower Bay** | |
|---|---|---|---|---|---|---|
| | Mean abundance (m$^{-2}$) | Mean biomass (mg AFDM m$^{-2}$) | Mean abundance (m$^{-2}$) | Mean biomass (mg AFDM m$^{-2}$) | Mean abundance (m$^{-2}$) | Mean biomass (mg AFDM m$^{-2}$) |
| **Annelida** | | | | | | |
| *Ampharete acutifrons* | 8.25 | 9.82 | 0 | 0 | 1.18 | 8.23 |
| *Aphelochaeta marioni* | 239.31 | 284.78 | 341.88 | 406.83 | 190.98 | 227.27 |
| *Arenicola marina* | 3.54 | 1266.13 | 1.18 | 422.04 | 1.18 | 422.04 |
| *Capitellid* | 180.37 | 214.64 | 11.79 | 14.03 | 194.52 | 231.47 |
| *Chaetozone* sp. | 1.18 | 1.4 | 0 | 0 | 0 | 0.00 |
| *Desdemona ornata* | 1.18 | 1.4 | 1.18 | 1.4 | 2.36 | 2.81 |
| *Eteone longa* | 8.25 | 9.82 | 4.72 | 5.61 | 30.65 | 36.47 |
| *Glycera tridactyla* | 0 | 0 | 0 | 0 | 1.18 | 1.40 |
| *Hediste diversicolor* | 163.87 | 232.76 | 1936.91 | 10019.56 | 403.18 | 1811.50 |
| *Melinna palmate* | 7.07 | 8.42 | 0 | 0 | 2.36 | 2.81 |
| *Nephtys hombergeii* | 9.43 | 350.9 | 8.25 | 308.25 | 40.08 | 1241.17 |
| *Phyllodoce musoca* | 10.61 | 12.63 | 0 | 0 | 7.07 | 8.42 |
| *Polydora* sp. | 5.89 | 7.01 | 40.08 | 47.7 | 5.89 | 7.01 |
| *Pygospio elegans* | 2.36 | 2.81 | 1.18 | 1.4 | 1.18 | 1.40 |
| *Scolelepsis* sp. | 0 | 0 | 0 | 0 | 2.36 | 2.81 |
| *Scoloplos armiger* | 17.68 | 21.04 | 0 | 0 | 1.18 | 1.40 |
| *Streblospio shrubsolii* | 56.59 | 67.34 | 631.88 | 726.69 | 48.33 | 57.52 |
| *Tubificoides* spp. | 3653.38 | 4347.52 | 1033.89 | 1230.32 | 2578.23 | 3068.09 |
| **Crustacea** | | | | | | |
| *Carcinus maenas* | 17.68 | 655.53 | 4.72 | 434.01 | 12.97 | 375.13 |
| *Corophium volutator* | 211.02 | 87.29 | 1.18 | 0.56 | 5.89 | 2.84 |
| *Cyathura carinata* | 1.18 | 0.97 | 2.36 | 3.67 | 16.5 | 9.12 |
| *Dynamene bidentata* | 7.07 | 13.65 | 0 | 0 | 0 | 0.00 |
| *Gammarus* sp. | 5.89 | 1.82 | 22.4 | 4.05 | 50.69 | 9.74 |
| *Idotea balthica* | 5.89 | 3.41 | 3.54 | 4.6 | 20.04 | 21.64 |
| *Melita palmate* | 7.07 | 2.99 | 21.22 | 8.3 | 4.72 | 1.55 |
| *Microdeutopus grillotalpa* | 113.17 | 17.91 | 21.22 | 3.18 | 55.41 | 6.92 |
| *Microprotopus maculatum* | 1.18 | 0.07 | 1.18 | 0.07 | 3.54 | 0.20 |
| *Sphaeroma* sp. | 0 | 0 | 2.36 | 2.81 | 0 | 0.00 |

| | **Brands Bay** | | **Holes Bay** | | **Ower Bay** | |
|---|---|---|---|---|---|---|
| | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) |
| **Mollusca** | | | | | | |
| *Abra tenuis* | 196.87 | 427.24 | 122.6 | 389.02 | 78.99 | 212.90 |
| *Cerastoderma edule* | 30.65 | 1191.83 | 18.86 | 1690.95 | 21.22 | 769.73 |
| *Gibbula umbilicalis* | 1.18 | 1.41 | 0 | 0 | 0 | 0.00 |
| *Lepidochitona cinerea* | 1.18 | 2.28 | 0 | 0 | 0 | 0.00 |
| *Littorina* spp. | 15.33 | 39.62 | 4.72 | 46.06 | 5.89 | 12.27 |
| *Limecola (Macoma) balthica* | 10.61 | 264.18 | 4.72 | 54.74 | 10.61 | 104.40 |
| *Mya arenaria* | 7.07 | 5.15 | 20.04 | 854.38 | 15.33 | 198.90 |
| *Peringia (Hydrobia) ulvae* | 1171.82 | 1608.79 | 2212.77 | 3328.87 | 1549.06 | 2180.42 |
| *Retusa obtusa* | 1.18 | 0.81 | 0 | 0 | 0 | 0.00 |
| *Ruditapes philippinarum* | 2.36 | 64.57 | 21.22 | 2196.79 | 7.07 | 1062.17 |
| **Other** | | | | | | |
| Actinaria | 11.79 | 14.03 | 4.72 | 5.61 | 5.89 | 7.01 |
| Chironomidae | 2403.75 | 2860.47 | 8.25 | 9.82 | 511.64 | 608.85 |
| Dolichopodid | 4.72 | 5.61 | 0 | 0 | 0 | 0.00 |
| Nemertea sp. | 28.29 | 197.49 | 7.07 | 49.37 | 14.15 | 98.74 |

# Appendix 4b

## Mean abundance ($m^{-2}$) and mean biomass (mg AFDM $m^{-2}$) of invertebrates recorded in September 2013, December 2013, and September 2014 across all sites (Brands Bay, Holes Bay and Ower Bay).

| | **September 2013** | | **December 2013** | | **September 2014** | |
|---|---|---|---|---|---|---|
| | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) |
| **Annelida** | | | | | | |
| *Ampharete acutifrons* | 3.54 | 4.21 | 4.72 | 5.61 | 1.18 | 16.13 |
| *Aphelochaeta marioni* | 299.44 | 356.33 | 233.42 | 277.77 | 239.31 | 240.94 |
| *Arenicola marina* | 0 | 0 | 1.18 | 422.04 | 4.72 | 2569.27 |
| *Capitellid* | 12.97 | 15.43 | 347.77 | 413.85 | 25.94 | 32.14 |
| *Chaetozone* sp. | 0 | 0 | 1.18 | 1.4 | 0.00 | 0.00 |
| *Desdemona ornata* | 3.54 | 4.21 | 1.18 | 1.4 | 0.00 | 0.00 |
| *Eteone longa* | 5.89 | 7.01 | 28.29 | 33.67 | 9.43 | 12.15 |
| *Glycera tridactyla* | 0 | 0 | 1.18 | 1.4 | 0.00 | 0.00 |
| *Hediste diversicolor* | 716.76 | 3409.04 | 911.28 | 3177.9 | 875.91 | 3308.40 |
| *Melinna palmate* | 2.36 | 2.81 | 5.89 | 7.01 | 1.18 | 2.74 |
| *Nephtys hombergeii* | 27.11 | 1045.8 | 15.33 | 463.47 | 15.33 | 588.59 |
| *Phyllodoce musoca* | 2.36 | 2.81 | 10.61 | 12.63 | 4.72 | 5.00 |
| *Polydora* sp. | 4.72 | 5.61 | 23.58 | 28.06 | 23.58 | 33.69 |
| *Pygospio elegans* | 1.18 | 1.4 | 3.54 | 4.21 | 0.00 | 0.00 |
| *Scolelepsis* sp. | 0 | 0 | 2.36 | 2.81 | 0.00 | 0.00 |
| *Scoloplos armiger* | 8.25 | 9.82 | 8.25 | 9.82 | 2.36 | 3.76 |
| *Streblospio shrubsolii* | 93.13 | 110.83 | 489.24 | 556.94 | 154.43 | 133.01 |
| *Tubificoides* spp. | 2261.11 | 2690.72 | 3013.24 | 3585.76 | 1991.14 | 769.08 |
| **Crustacea** | | | | | | |
| *Carcinus maenas* | 15.33 | 327.07 | 8.25 | 445.6 | 11.79 | 709.25 |
| *Corophium volutator* | 172.12 | 73.87 | 25.94 | 12.46 | 20.04 | 5.94 |
| *Cyathura carinata* | 2.36 | 3.67 | 5.89 | 3.99 | 11.79 | 10.11 |
| *Dynamene bidentata* | 4.72 | 9.1 | 2.36 | 4.55 | 0.00 | 0.00 |
| *Gammarus* sp. | 5.89 | 1.94 | 53.05 | 9.52 | 20.04 | 3.51 |
| *Idotea balthica* | 5.89 | 11.91 | 21.22 | 15.34 | 2.36 | 3.39 |
| *Melita palmate* | 15.33 | 6.82 | 5.89 | 1.55 | 11.79 | 4.80 |
| *Microdeutopus grillotalpa* | 50.69 | 6.97 | 37.72 | 2.43 | 101.38 | 27.20 |
| *Microprotopus maculatum* | 5.89 | 0.33 | 0 | 0 | 0.00 | 0.00 |
| *Sphaeroma* sp. | 2.36 | 2.81 | 0 | 0 | 0.00 | 0.00 |

| | September 2013 | | December 2013 | | September 2014 | |
|---|---|---|---|---|---|---|
| | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) | Mean abundance ($m^{-2}$) | Mean biomass (mg AFDM $m^{-2}$) |
| **Mollusca** | | | | | | |
| *Abra tenuis* | 174.48 | 499.91 | 113.17 | 226.24 | 110.82 | 162.46 |
| *Cerastoderma edule* | 24.76 | 1301.03 | 16.5 | 782.42 | 29.47 | 889.92 |
| *Gibbula umbilicalis* | 0 | 0 | 0 | 0 | 1.18 | 2.76 |
| *Lepidochitona cinerea* | 0 | 0 | 1.18 | 2.28 | 0.00 | 0.00 |
| *Littorina* spp. | 15.33 | 67.66 | 8.25 | 29.87 | 2.36 | 0.76 |
| *Limecola (Macoma) balthica* | 5.89 | 43.45 | 10.61 | 144.38 | 9.43 | 177.81 |
| *Mya arenaria* | 9.43 | 438.79 | 18.86 | 267.96 | 14.15 | 379.99 |
| *Peringia (Hydrobia) ulvae* | 1826.1 | 2571.72 | 1710.57 | 2415.74 | 1396.98 | 1074.69 |
| *Retusa obtusa* | 0 | 0 | 1.18 | 0.81 | 0.00 | 0.00 |
| *Ruditapes philippinarum* | 3.54 | 544.72 | 11.79 | 586.37 | 15.33 | 1686.15 |
| **Other** | | | | | | |
| Actinaria | 2.36 | 2.81 | 9.43 | 11.22 | 10.61 | 12.17 |
| Chironomidae | 600.05 | 714.06 | 1881.51 | 2238.99 | 442.08 | 558.23 |
| Dolichopodid | 0 | 0 | 4.72 | 5.61 | 0.00 | 0.00 |
| Nemertea sp. | 3.54 | 24.69 | 27.11 | 189.26 | 18.86 | 93.55 |

# Appendix 5

## Results from SIMPER analysis for significant pairs of sites (Brands Bay and Holes Bay, Ower Bay and Holes Bay) for species driving up to 90% of variation in community structure between sites.

**Brands Bay and Holes Bay**

Average dissimilarity = 62.27

| | **BB** | **HB** | | |
|---|---|---|---|---|
| Species | Average Abundance (indiv. m$^{-2}$) | Average Abundance (indiv. m$^{-2}$) | Contributory % | Cumulative % |
| *H. diversicolor* | 6.06 | 42.1 | 15.11 | 15.11 |
| Chironomid | 36.37 | 0.93 | 13.79 | 28.9 |
| *Tubificoides* | 57.47 | 29.04 | 13.03 | 41.93 |
| *P. ulvae* | 25.95 | 40.97 | 11.43 | 53.36 |
| *S. shrubsolii* | 3.41 | 21.9 | 7.78 | 61.14 |
| *A. marioni* | 10.11 | 13.74 | 5.73 | 66.87 |
| *Corophium volutator* | 8.39 | 0.26 | 3.57 | 70.44 |
| *Abra tenuis* | 13 | 9.06 | 3.21 | 73.65 |
| *Microdeutopus gryllotalpa* | 6.55 | 1.49 | 2.84 | 76.49 |
| Capitellid | 7.09 | 1.24 | 2.83 | 79.32 |
| *Cerastoderma edule* | 4.01 | 2.94 | 1.67 | 81 |
| Nemertine | 3.57 | 1.24 | 1.48 | 82.48 |
| *Mya arenaria* | 0.83 | 3.28 | 1.44 | 83.92 |
| *Polydora* sp. | 0.96 | 3.19 | 1.34 | 85.26 |
| *Melita palmata* | 0.83 | 2.72 | 1.2 | 86.46 |
| *Carcinus maenas* | 2.83 | 0.87 | 1.18 | 87.65 |
| *Ruditapes philippinarum* | 0.51 | 2.76 | 1.16 | 88.81 |
| *Gammarus* sp. | 1.13 | 2.39 | 1.13 | 89.94 |
| *Littorina* spp. | 2.2 | 0.51 | 0.97 | 90.91 |

| **Ower Bay and Holes Bay**<br>Average dissimilarity = 53.33 | | | | |
|---|---|---|---|---|
| | **OB** | **HB** | | |
| Species | Average Abundance (indiv. $m^{-2}$) | Average Abundance (indiv. $m^{-2}$) | Contributory % | Cumulative % |
| *H. diversicolor* | 14.3 | 42.1 | 15.76 | 15.76 |
| *P. ulvae* | 32.92 | 40.97 | 13.3 | 29.06 |
| *Tubificoides* spp. | 48 | 29.04 | 12.97 | 42.03 |
| *S. shrubsolii* | 2.38 | 21.9 | 10.6 | 52.63 |
| *A. marioni* | 9.98 | 13.74 | 6.79 | 59.42 |
| Chironomid | 12.78 | 0.93 | 6.02 | 65.44 |
| *Abra tenuis* | 6.75 | 9.06 | 3.9 | 69.34 |
| Capitellid | 6.96 | 1.24 | 3.36 | 72.7 |
| *Nephtys hombergeii* | 4.09 | 1.32 | 2.53 | 75.23 |
| *Microdeutopus gryllotalpa* | 4.09 | 1.49 | 2.35 | 77.59 |
| *Gammarus* sp. | 2.79 | 2.39 | 2 | 79.59 |
| *Cerastoderma edule* | 3.47 | 2.94 | 1.9 | 81.49 |
| *Mya arenaria* | 2.7 | 3.28 | 1.76 | 83.24 |
| *Polydora* sp. | 0.96 | 3.19 | 1.73 | 84.98 |
| *Ruditapes philippinarum* | 1.24 | 2.76 | 1.61 | 86.59 |
| *Eteone longa* | 2.78 | 0.7 | 1.54 | 88.13 |
| *Melita palmata* | 0.87 | 2.72 | 1.48 | 89.61 |
| Nemertine | 2.3 | 1.24 | 1.35 | 90.96 |

# Appendix 6

## Algae biomass (g m$^{-2}$), algae % cover, % organic content and % sand (particle size >63 µm) for combined core samples.

**0913 = September 2013, 1213 = December 2013, 0914 = September 2014. S = Station (e.g. 0913BBS1 = September 2013, Brands Bay, Station 1).**

| **Brands Bay** | **0913 BBS1** | **0913 BBS2** | **0913 BBS3** | **0913 BBS4** | **0913 BBS5** | **0913 BBS6** | **1213 BBS1** | **1213 BBS2** | **1213 BBS3** | **1213 BBS4** | **1213 BBS5** | **1213 BBS6** | **0914 BBS1** | **0914 BBS2** | **0914 BBS3** | **0914 BBS4** | **0914 BBS5** | **0914 BBS6** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Algae (g m$^{-2}$) | 454.53 | 302.60 | 42.02 | 180.37 | 851.56 | 1599.14 | 167.43 | 164.88 | 1282.11 | 74.70 | 1006.68 | 644.66333 | 0 | 47.53 | 268.01 | 239.36 | 388.33 | 2995.84 |
| Algae. % cover | 25 | 25 | 25 | 25 | 50 | 50 | 10 | 10 | 10 | 10 | 30 | 30 | 10 | 10 | 10 | 10 | 75 | 75 |
| % Organic | 5.25 | 4.93 | 5.09 | 9.19 | 1.76 | 6.01 | 1.49 | 5.33 | 7.90 | 5.65 | 0.68 | 5.92 | 2.19 | 4.09 | 4.39 | 6.01 | 1.87 | 6.43 |
| % Sand >63 µm | 18.97 | 3.71 | 3.01 | 3.32 | 43.32 | 18.85 | 14.97 | 2.61 | 8.29 | 4.02 | 62.38 | 17.14 | 26.72 | 4.69 | 3.03 | 5.79 | 37.02 | 14.33 |
| **Holes Bay** | **0913 HBS1** | **0913 HBS2** | **0913 HBS3** | **0913 HBS4** | **0913 HBS5** | **0913 HBS6** | **1213 HBS1** | **1213 HBS2** | **1213 HBS3** | **1213 HBS4** | **1213 HBS5** | **1213 HBS6** | **0914 HBS1** | **0914 HBS2** | **0914 HBS3** | **0914 HBS4** | **0914 HBS5** | **0914 HBS6** |
| Algae (g m$^{-2}$) | 8.70 | 15.49 | 0 | 20.58 | 446.467 | 753.73 | 81.27 | 12.94 | 9.97 | 0.21 | 336.55 | 7.85 | 63.24 | 0 | 223.87 | 168.91 | 787.69 | 697.50 |
| Algae. cover | 100 | 100 | 0 | 100 | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 75 | 100 | 100 | 100 |
| % Organic | 16.54 | 5.89 | 7.95 | 10.02 | 7.45 | 6.50 | 8.48 | 8.78 | 7.54 | 9.10 | 8.54 | 9.02 | 7.93 | 7.71 | 10.04 | 7.86 | 9.11 | 9.26 |
| % Sand >63 µm | 9.49 | 7.10 | 4.10 | 6.66 | 6.32 | 12.83 | 6.09 | 5.1 | 6.41 | 5.11 | 12.3 | 13.07 | 6.01 | 5.44 | 6.49 | 4.71 | 7.33 | 8.73 |
| **Ower Bay** | **0913 OBS1** | **0913 OBS2** | **0913 OBS3** | **0913 OBS4** | **0913 OBS5** | **0913 OBS6** | **1213 OBS1** | **1213 OBS2** | **121 3OBS3** | **1213 OBS4** | **1213 OBS5** | **1213 OBS6** | **0914 OBS1** | **0914 OBS2** | **0914 OBS3** | **0914 OBS4** | **0914 OBS5** | **0914 OBS6** |
| Algae (g m$^{-2}$) | 55.81 | 1465.45 | 13.79 | 13.79 | 884.24 | 2134.52 | 0 | 3.18 | 1107.89 | 779.62 | 377.51 | 1028.32 | 101.645 | 62.38 | 1449.75 | 3344.70 | 1187.68 | 3146.91 |
| Algae. cover | 50 | 50 | 50 | 50 | 100 | 100 | 0 | 0 | 40 | 40 | 40 | 40 | 10 | 10 | 10 | 10 | 75 | 75 |
| % Organic | 4.88 | 5.32 | 5.97 | 4.40 | 5.26 | 2.01 | 5.37 | 7.72 | 3.95 | 6.80 | 2.90 | 2.15 | 5.58 | 5.19 | 4.17 | 7.40 | 12.91 | 3.76 |
| % Sand >63 µm | 5.66 | 3.54 | 6.2 | 3.91 | 15.52 | 30.94 | 2.48 | 6.25 | 16.82 | 4.99 | 31.30 | 31.53 | 2.36 | 5.78 | 8.63 | 7.46 | 13.64 | 25.86 |

# Appendix 7

**Mean prey size used to calculate time required for each wading bird species to reach its daily energy requirement if consuming preferred-size prey (Goss-Custard et al. 2006b). Size class range recorded at each site in parenthesis.**

| **Brands Bay** | **Annelid worms** | **Bivalves** | ***Cerastoderma edule*** | ***Peringia ulvae*** | **Crustaceans** |
|---|---|---|---|---|---|
| Curlew | 81.25 mm<br>(55 mm->105 mm) | 20 mm<br>(5 mm–35 mm) | 12.5 mm<br>(5 mm–20 mm) | - | 16.25 mm<br>(10 mm->20 mm) |
| Black-tailed godwit | 66.25 mm<br>(25 mm->105 mm) | 15 mm<br>(5 mm–25 mm) | - | - | 12.75 mm<br>(3 mm->20 mm) |
| Oystercatcher | 81.25 mm<br>(55 mm->105 mm) | 20 mm<br>(5 mm–35 mm) | 20 mm<br>(5 mm–35 mm) | - | 16.25 mm<br>(10 mm->20 mm) |
| Redshank | 47.5 mm<br>(15 mm–80 mm) | 10 mm<br>(5 mm–15 mm) | - | 3 mm<br>(>5 mm) | 12.75 mm<br>(3 mm->20 mm) |
| Dunlin | 35 mm<br>(10 mm-60 mm) | 5 mm<br>(1 mm-10 mm) | - | 3 mm<br>(>5 mm) | 12.75 mm<br>(3 mm->20 mm) |

| **Holes Bay** | **Annelid worms** | **Bivalves** | ***Cerastoderma edule*** | ***Peringia ulvae*** | **Crustaceans** |
|---|---|---|---|---|---|
| Curlew | 78.75 mm<br>(50 mm->105 mm) | 25 mm<br>(5 mm-45 mm) | 12.5 mm<br>(5 mm-20 mm) | - | 16.25 mm<br>(10 mm->20 mm) |
| Black-tailed godwit | 66.25 mm<br>(25 mm->105 mm) | 15 mm<br>(5 mm–25 mm) | - | - | 12.75 mm<br>(3 mm->20 mm) |
| Oystercatcher | 78.75 mm<br>(50 mm->105 mm) | 25 mm<br>(5 mm-45 mm) | 20 mm<br>(5 mm–35 mm) | - | 16.25 mm<br>(10 mm->20 mm) |
| Redshank | 47.5 mm<br>(15 mm-80 mm) | 10 mm<br>(5 mm-15 mm) | - | 3 mm<br>(>5 mm) | 12.75 mm<br>(3 mm->20 mm) |
| Dunlin | 35 mm<br>(10 mm-60 mm) | 5 mm<br>(1 mm-10 mm) | - | 3 mm<br>(>5 mm) | 12.75 mm<br>(3 mm->20 mm) |

| **Ower Bay** | **Annelid worms** | **Bivalves** | ***Cerastoderma edule*** | ***Peringia ulvae*** | **Crustaceans** |
|---|---|---|---|---|---|
| Curlew | 78.75 mm<br>(50 mm->105 mm) | 25 mm<br>(5 mm-45 mm) | 12.5 mm<br>(5 mm-20 mm) | - | 15 mm<br>(10 mm-20 mm) |
| Black-tailed godwit | 66.25 mm<br>(25 mm->105 mm) | 15 mm<br>(5 mm-25 mm) | - | - | 11.5 mm<br>(3 mm-20 mm) |
| Oystercatcher | 78.75 mm<br>(50 mm->105 mm) | 25 mm<br>(5 mm-45 mm) | 20 mm<br>(5 mm-35 mm) | - | 15 mm<br>(10 mm-20 mm) |
| Redshank | 47.5 mm<br>(15 mm–80 mm) | 10 mm<br>(5 mm-15 mm) | - | 3 mm<br>(>5 mm) | 11.5 mm<br>(3 mm-20 mm) |
| Dunlin | 35 mm<br>(10 mm-60 mm) | 5 mm<br>(1 mm-10 mm) | - | 3 mm<br>(>5 mm) | 11.5 mm<br>(3 mm-20 mm) |

# Appendix 8

## Calculations to obtain each wading bird species' daily energy requirement (kJ). Body weight data provided by BTO Bird Facts (www.BTO.org).

| **Species** | **Body weight (kg)** | **Basal metabolic rate** (BMR)<br>*BMR = 437** *(body weight kg)*$^{0.729}$ | **Daily energy requirement (DER) (kJ)**<br>*DER = 2.1*(BMR)* |
|---|---|---|---|
| Curlew | 0.784 kg | 365.93 | 768.453 kJ |
| Black-tailed godwit | 0.299 kg | 181.016 | 380.134 kJ |
| Oystercatcher | 0.546 kg | 281.197 | 590.514 kJ |
| Redshank | 0.153 kg | 111.363 | 233.862 kJ |
| Dunlin | 0.050 kg | 49.215 | 103.352 kJ |

# Glossary of abbreviations

| | |
|---|---|
| **ABC curve** | Abundance/Biomass Comparison curve |
| **AFDM** | Ash-Free Dry-Mass |
| **ANOSIM** | Analysis of Similarity |
| **BIM** | Benthic Invertebrate Menu |
| **BMR** | Basal Metabolic Rate |
| **BTO** | British Trust for Ornithology |
| **CD** | Chart Datum |
| **CSM** | Common Standards Monitoring |
| **DER** | Daily Energy Requirement |
| **DIN** | Dissolved Inorganic Nitrogen |
| **DISTLM** | Distance-based Linear Model |
| **GAM** | Generalised Additive Model |
| **GPS** | Global positioning system |
| **JNCC** | Joint Nature Conservation Committee |
| **Loess curve** | Locally-weighted smoothing curve |
| **MLWS** | Mean Low-Water Spring |
| **NE** | Natural England |
| **nMDS** | non-Metric Multi-Dimensional Scaling |
| **NVZ** | Nitrate vulnerable zone |
| **PRIMER** | Plymouth Routines In Multivariate Ecological Research |
| **SAC** | Special Area of Conservation |
| **SIMPER** | Similarity Percentages |
| **SPA** | Special Protection Area |
| **SSSI** | Site of Special Scientific Interest |
| **TBT** | Tributyltin |
| **UKHO** | UK Hydrographic Office |
| **WeBS** | Wetland Bird Survey |
| **WFDUKTAG** | Water Framework Directive UK Technical Advice Group |