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## **DOCTOR OF PHILOSOPHY**

### **A modelling approach to assessing the environmental impacts of harvesting marine bivalves from natural populations**

Feather, Alastair

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A modelling approach to assessing the  
environmental impacts of harvesting marine  
bivalves from natural populations



PRIFYSGOL  
**BANGOR**  
UNIVERSITY

A thesis presented for the degree of Doctor of Philosophy

By

**Alastair Feather**

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School of Ocean Sciences, Menai Bridge, Anglesey, LL59 5AB

## Thesis summary

Estuaries support diverse ecological communities which perform many important biological functions and provide a variety of goods and services. As a result of direct and indirect human impacts the world's estuaries are currently being degraded at unprecedented rates and their functionality and services are under threat. The conservation and sustainable use of estuarine resources is of global significance due to their role in food production (e.g., aquaculture, nursery habitats), mitigating climate change (e.g., carbon storage, coastal defence) and water quality (e.g., nutrient cycling). A key challenge in estuarine management is determining how to manage the many ecosystem services simultaneously.

Bivalves are an important component of marine environments because they deliver many ecosystem services and contribute markedly to the functioning of coastal ecosystems. Managers must often balance economic value (e.g., harvest) with wider conservation objectives (e.g., coastal birds) and there are often conflicts. Understanding interactions (i.e., trade-offs and synergies) between ecosystem services is key to their sustainable management but knowledge is limited within marine environments due to data scarcity and system complexity (e.g., non-linear, interactive, extensive). Effective conservation and management strategies are regularly informed using ecological models and depend heavily on understanding how environmental change impacts the physiology and behaviour of organisms. Applying mechanistic models which link ecological processes with ecosystem functions and services can help improve understanding.

Coastal birds rely heavily on intertidal invertebrate prey to maintain body condition, particularly throughout winter and while travelling to and from breeding grounds. Human activities within migration routes therefore require careful management to ensure they are sustainable and minimise the negative impacts to ecological communities and functioning. Many coastal bird populations are however experiencing long-term declines and the drivers are thought to be in part associated with the disappearance and degradation of intertidal habitats. This thesis aimed to assess the environmental impacts of harvesting the intertidal bivalve *Mytilus edulis* (Blue mussel), specifically to coastal bird populations in Morecambe Bay.

Chapter three aimed to identify and develop a method for simulating the growth and development of intertidal *M. edulis* in response to environmental conditions. A Dynamic Energy Budget (DEB) model was developed to simulate the growth and development of intertidal *M. edulis* in response to environmental conditions. The condition and growth rates of intertidal *M. edulis* in Morecambe

Bay were observed to increase with decreasing elevation and a DEB growth model which was modified to incorporate an energy conserving, intertidal adaption most accurately predicted the relationship. Increases to the concentration of suspended particles, temperature and elevation were most influential to individual growth.

Chapter four aimed to improve understanding of how to sustainably manage the ecosystem services provided by intertidal *M. edulis*. A DEB population model for intertidal *M. edulis* was developed to simulate the functioning of multiple ecosystem services simultaneously in response to environmental conditions. It was used to quantify the net nutrient (nitrogen, phosphorus and carbon) fluxes (i.e., source or sink) associated with the population, to assess the sensitivity of services to environmental change and to identify potential synergies and trade-offs linked to harvesting *M. edulis*. The population was predicted to serve as a sink for nutrients, particularly carbon and mostly due to biodeposition and shell burial. Changes to the concentration of suspended particles, temperature and pre-settlement mortality were most influential to all ecosystem service rates. The harvest of market size *M. edulis* had a negligible but positive impact on the provision of habitat provisioning (i.e., biomass) while the harvest of culture size individuals had an important and negative effect. Strong synergies were identified between the provision of habitat provisioning and the removal of nutrients and the effects of harvesting *M. edulis* subsequently extended to regulatory services.

Chapter five aimed to assess the long-term risks of harvesting intertidal *M. edulis* to coastal bird populations in Morecambe Bay. An Agent-Based Model (ABM) was developed for simulating both the foraging behaviour of coastal birds and the dynamics of *M. edulis* populations in response to environmental conditions. The model was used to assess the relative importance of *M. edulis* as a resource for coastal bird populations in Morecambe Bay. Changes to the abundance of *M. edulis* in Morecambe Bay were most influential to the annual body condition of the *Somateria mollissima* (Common eider) population. The harvest of market size individuals was uncorrelated with the condition of the *Calidris canutus* (Red knot), *Haematopus ostralegus* (Eurasian oystercatcher) and *Larus argentatus* (Herring gull) populations, and weakly correlated (positive) with that of the *S. mollissima* population. The harvest of culture size individuals was uncorrelated with the condition of the *C. canutus* population, weakly correlated (negative) with that of both the *H. ostralegus* and *L. argentatus* and strongly correlated (negative) with the condition of the *S. mollissima* population. The negative correlations associated with harvesting culture size individuals became stronger when supplementary bivalve (e.g., *Macoma balthica*) resources were low.



This thesis highlighted the advantages of using ABMs for predicting ecological responses to environmental change and provided a practical example for simulating intertidal systems. It developed understanding of how to manage multiple estuarine ecosystem services simultaneously and demonstrated various potential trade-offs when harvesting from natural populations. The overall results underline the threat of climate change to ecosystem functioning and highlight the potential for sustainable harvest practices to mitigate the effects.

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# 1. General Introduction

## 1.1 Increases in human-wildlife conflict

Ecosystem functions are the processes that regulate flows of energy, nutrients and organic matter through the environment (De Groot et al., 2002; Fisher et al., 2008). They are the basis for all goods and services that ecosystems provide (Figure 1.1), and their functionality is maintained by diverse biological communities (Barbier et al., 2011; Cardinale et al., 2011, 2006). Interactions between the biotic and abiotic components of ecosystems drive key ecological processes (e.g., nutrient cycling) which ultimately provide important regulating (e.g., water purification) and provisioning (e.g., food) services (Costanza et al., 2014). The functionality and resilience of earths ecosystems is fundamentally linked to their biological diversity and vulnerable to its degradation (Cardinale et al., 2006; Hooper et al., 2012; Stachowicz et al., 2007).

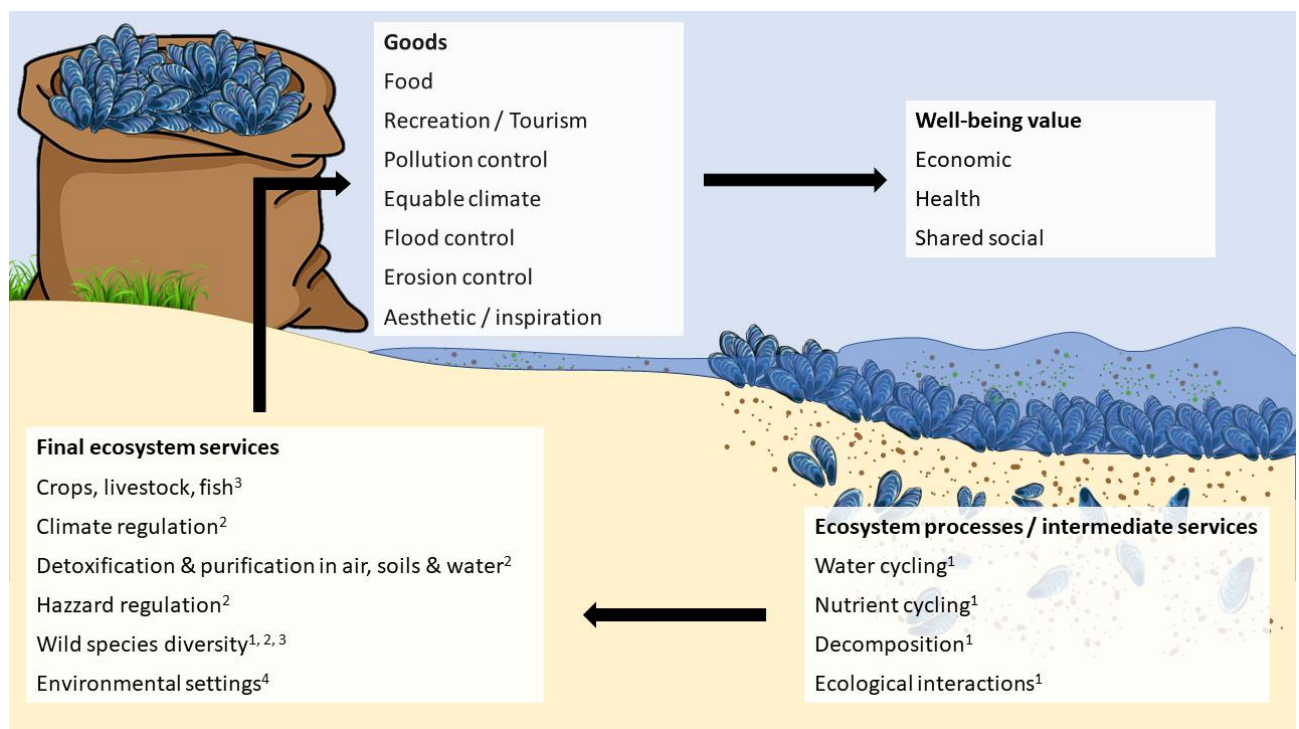


Figure 1.1 Ecosystem processes, services, goods / benefits, and values associated with bivalve natural populations (Ecosystem service type: <sup>1</sup> – Supporting, <sup>2</sup> – Regulating, <sup>3</sup> – Provisioning, <sup>4</sup> – Cultural). Note that some ecosystem services can be both intermediate and final services, and that the term good(s) includes all use and non-use, material and non-material outputs from ecosystems that have value for people. Adapted from Fisher et al., (2008).

Human activities are currently dominating the earth's ecosystems and have modified over 77% and 87% of the world's terrestrial and marine areas, respectively (Allan et al., 2017; Jones et al., 2018; Watson et al., 2016). Such widespread exploitation and destruction of resources and habitats has dramatically reduced biodiversity in extensive tracts of land and sea (Barnosky et al., 2011; Tollefson, 2019). The production of food (e.g., agriculture, aquaculture, harvest) is a major driver of global biodiversity loss which is set to intensify with an increasing human population and changing climate (Crist et al., 2017; Giam, 2017; Isbell et al., 2022; Myers and Worm, 2003; Ray et al., 2019). The biodiversity responsible for ecological processes which support food production (e.g., pollination, nutrient management, soil quality, pest control) is degraded by unsustainable exploitation of the same goods it supports (Kremen, 2020). Sustainable food production is consequently one of the greatest challenges of the twenty-first century and as traditional terrestrial production areas disappear there is growing interest towards aquaculture as an alternative (Godfray et al., 2010; Naylor et al., 2021; Subasinghe et al., 2009).

### **1.1 Importance of estuarine resources**

Estuarine ecosystems are characterised by steep environmental gradients to which diverse ecological communities are adapted (Anderson, 1972; Meire et al., 2005). They provide many important ecological services (e.g., food provisioning, nutrient cycling, water purification, coastal defence, climate regulation) which have long supported large human populations (Barbier et al., 2011; Beaumont et al., 2007; Small and Nicholls, 2003). Centuries of human activity (e.g., food production, transport, development) has degraded the functioning of estuaries worldwide and their supply of goods and services is under threat (Barbier et al., 2011; Worm et al., 2006). Management of estuarine ecosystems therefore commonly aims to restore, maintain and protect their functionality through sustainable use of goods and services (Boerema and Meire, 2017; Needles et al., 2013; zu Ermgassen et al., 2020). Ecosystem services do not operate independently of one another and there are commonly negative impacts (i.e., trade-offs) when one is favoured over another (Barbier et al., 2008). Economic activities in particular, often conflict with regulatory or supportive ecosystem services provided by estuaries (Atkinson et al., 2010; Clarke et al., 2019).

Bivalve populations are an integral component of coastal ecosystems because of the multifunctional role they play in delivering ecosystem services (Carss et al., 2020; Smaal et al., 2018; van der Schatte Olivier et al., 2018). As filter feeders, bivalves consume suspended inorganic and

organic particles from the water column which are then stored (i.e., tissue and shell) or deposited (i.e., biodeposit, dead shell) into the sediments (Cranford, 2018; Fodrie et al., 2017; van der Schatte Olivier et al., 2021). Doing so removes nutrients (e.g., nitrogen, phosphorus, carbon) from coastal waters which improves water quality, mitigates the symptoms of eutrophication (e.g., hypoxia) and alleviates (e.g., carbon storage) climate change (Cranford, 2018; Filgueira et al., 2018b; Rabalais et al., 2009). Some species (e.g., *Mytilus edulis*) form complex, three-dimensional biogenic structures (i.e., reefs) which reduce wave energy, stabilise sediments and protect adjacent habitats (e.g., saltmarsh) from erosion (La Peyre et al., 2015; Walles et al., 2015; Ysebaert et al., 2018). Reefs also provide important habitat for many additional species (e.g., coastal birds) thereby enhancing biodiversity (Craeymeersch and Jansen, 2019; Hogan and Reidenbach, 2021; Kent et al., 2016). The most recognizable service of bivalves from a human perspective is protein (i.e., tissue) and they are harvested worldwide for both direct consumption and cultivation (Kamermans and Capelle, 2019; Kraan et al., 2007; Wijsman et al., 2018). The sustainable management of the ecosystem services delivered by bivalve populations (and the ecological processes underpinning them) is therefore economically, ecologically and socially complex (Figure 1.1).

## **1.2 Status of coastal birds and main drivers of population change**

Coastal birds (e.g., waders, wildfowl and gulls) are an important element of intertidal ecosystems because of the roles they play in food webs, and in physical and chemical processes within mudflat sediments (Kuwae et al., 2012, 2008; Mathot et al., 2018). They also provide a visible indication of ecosystem health, and because many species are experiencing long term population declines, their conservation has become a high priority for scientists and conservationists around the globe (Meltofte et al., 2019; Rosenberg et al., 2019; Studds et al., 2017). Most species of coastal bird are migratory and have large geographic ranges which contain breeding, non-breeding and staging areas (Piersma et al., 2016; Studds et al., 2017; Woodward et al., 2022). Within such large and complex systems individuals are subject to contrasting pressures, requirements and migratory strategies and the specific drivers of declines remain unclear (Murray et al., 2018; Van Roomen et al., 2012).

The processes involved are widely believed linked to changes in the availability of intertidal areas and the invertebrate communities they support (Pearce-Higgins et al., 2017; Sutherland et al., 2012; Van Roomen et al., 2012). The mechanisms believed responsible are generally related to

environmental processes and anthropogenic activities (e.g., coastal development, nutrient inputs, climate change, commercial fisheries, recreation, invasive species) which alter, disturb, degrade or destroy intertidal habitats (Baker et al., 2004; Waser et al., 2016; Whittingham et al., 2019). Migratory coastal birds habitually use intertidal habitats throughout the winter and whilst travelling to and from breeding grounds (Frost et al., 2021; Horn et al., 2020; Mu and Wilcove, 2020). The impacts (e.g., low survival) of intertidal habitat loss are therefore most severe when it occurs in important non-breeding and staging areas (Melville et al., 2016; Piersma et al., 2016; Studds et al., 2017). Such areas often support economically important populations of bivalves and their exploitation potentially conflicts with conservation objectives for coastal birds (Atkinson et al., 2010, 2003; Smit et al., 1998).

### **1.3 Coastal bird life history and seasonal energy requirements**

Millions of coastal birds migrate annually from high latitude breeding habitats to temperate coastlines (Meltofte et al., 2019; Studds et al., 2017). Many species roost and forage in intertidal habitats whilst travelling and exceptionally large numbers gather where resources are sufficient to support them throughout winter (Frost et al., 2021; Meltofte et al., 2019). The daily energy requirements of most coastal birds is mass-specific (i.e., increases with body size) and decreases with temperature (Kersten and Piersma, 1987; Nagy et al., 1999). Some species (e.g., *Somateria mollissima*) are capital breeders and build up body condition during winter in order to arrive at breeding grounds with improved body condition and increased reproductive potential (Laursen et al., 2019a; Lehikoinen et al., 2010). Others (e.g., *Calidris canutus*) make long, energetically demanding journeys and rely more on intertidal resources to restore and maintain fat reserves (Atkinson et al., 2007; McWilliams et al., 2004; Morrison and Hobson, 2004). The extent to which each strategy is achieved, depends on both the quality and quantity of available resources.

Intertidal bivalve populations are a particularly important source of food for coastal birds because they are both relatively abundant and comparatively high in caloric value (Beukema et al., 2010; Laursen et al., 2019b; Van Donk et al., 2019). The distribution of birds is often closely associated with bivalve populations and dietary studies show bivalve species are consumed in high proportions relative to other invertebrates (Cervencel et al., 2015; Enners et al., 2021; Quaintenne et al., 2014). Consuming larger proportions of bivalves relates positively to body condition for a number of species which in turn improves reproductive success (Bustnes et al., 2002; Laursen et al., 2019a;

Laursen and Møller, 2022; Le V Dit Durell et al., 2001). Because coastal birds can meet much of their energy requirements by consuming bivalves, conservation managers commonly focus on ensuring that sufficient bivalve biomass is made available (Goss-Custard et al., 2004; Laursen et al., 2010; West et al., 2007).

#### **1.4 Agent-based models**

Conservation objectives for non-breeding coastal birds are determined from their population size at coastal sites (Frost et al., 2021; Meltofte et al., 2019; Studds et al., 2017). Conservation strategies for coastal birds therefore require a quantitative understanding of how change to intertidal areas affects a populations size (e.g., emigration, mortality, reproduction) which usually involves some form of numerical model (Goss-Custard and Stillman, 2008; Stillman and Goss-Custard, 2010).

Empirical models are relatively easy to develop and can be quickly applied to a range of species, spatial scales and systems. Some (e.g., habitat association models) relate bird abundance to the presence of key environmental variables (e.g., habitat area or type) and use the relationship to predict abundance under new environmental conditions (Mu and Wilcove, 2020; Rehfishch et al., 2000; Wang et al., 2022). Others (e.g., depletion models) make similar predictions by relating bird abundance to resource density via individual searching efficiency and prey handling time (Gill et al., 2001; Mu et al., 2022). Empirical models are limited in their predictive ability because their projections are only valid for the environmental conditions under which the predicting relationships were observed (Evans, 2012; Stillman et al., 2015; Wood et al., 2018). For example, coastal birds respond to habitat loss by relocating, either locally within the system or globally outside of it. Their intake rates are negatively related to foraging density via competition (e.g., interference, exploitation) and therefore will potentially increase or decrease when birds relocate (Goss-Custard, 1977; Goss-Custard and Sutherland, 1997). The predictions of empirical models do not account for the redistribution of birds after habitat loss and the resulting change to intake rates.

Agent-Based Models (ABMs) autonomously simulate the physiology, decisions and behaviour of all individuals that constitute a population within a virtual environment (DeAngelis and Gross, 2018; Grimm and Railsback, 2005; Stillman et al., 2015). Coastal bird ABMs base individual foraging decisions (e.g., diet, location, duration) on fitness optimising rules and calculate intake rates as a function of resource type (e.g., specie, size, density), competitive interactions (e.g., kleptoparasitism, suppression), individual characteristics (e.g., foraging efficiency, dominance,

mass) and physical conditions (e.g., temperature, tide, time). Although ABMs are time consuming to develop, a key advantage is that the basis for predictions (i.e., fitness maximization) is more likely to persist when the birds encounter novel environments than the empirical relationships within traditional models (Stillman et al., 2015; Wood et al., 2018). ABMs have been used for over 20 years to inform the management of coastal bird populations and have provided some valuable insights (Goss-Custard and Stillman, 2008; Stillman et al., 2015; Stillman and Goss-Custard, 2010). They have been successfully applied to a wide range of systems (e.g., estuaries, rivers, saltmarsh) and species (e.g., waders, ducks, geese, swans) to advise conservationists on the potential impact of climate change (e.g., sea level rise), habitat loss (e.g., tidal barrages, wind farms, nuclear power stations), human disturbance (e.g., recreation, hunting, bivalve harvest), food production (e.g., aquaculture) and agriculture (Caldow et al., 2007; Chudzińska et al., 2016; Durell et al., 2008, 2006; Garcia et al., 2016; Stillman et al., 2021, 2003; West et al., 2007; West and Caldow, 2006; Wood et al., 2014).

### **1.5 Conservation challenges and knowledge gaps**

A leading challenge in conserving migratory coastal birds is safeguarding their annual cycles such that sites and habitats across the breeding, passage and wintering grounds are protected (Pearce-Higgins et al., 2017; Runge et al., 2015; Szabo et al., 2016; Yong et al., 2018). Most threats are increasing in intensity, particularly in non-breeding areas (i.e., passage and wintering grounds) where habitat loss (e.g., coastal development, aquaculture, disturbance, invasive species, pollution and climate change) is regarded as having the greatest impact (Aharon-Rotman et al., 2016; Pearce-Higgins et al., 2017; Studds et al., 2017). Preserving and maintaining robust networks of coastal habitat (intertidal and supratidal) for migrating and wintering populations is therefore an important and challenging component of long-term conservation strategies (Xu et al., 2019). Coastal ecosystems (e.g., estuaries) are however experiencing mounting pressure from anthropogenic activities and understanding the ecological consequences to coastal bird populations is critical if adverse impacts are to be minimized and conservation measures prioritized (Evans, 2012; Stillman et al., 2015; Wood et al., 2018).

Coastlines and estuaries are large and complex systems for which experiments are not easy to design and long term data sets are rare (Beukema et al., 2017b, 2010; Møller et al., 2019). ABMs provide an alternative means to explore such systems and quantify the sensitivity of bird populations to multiple drivers simultaneously (Grimm, 2018; Thiele et al., 2014). Many studies have



used ABMs to independently assess management strategies, site quality and environmental impacts in relation to the survival of non-breeding birds (Brown and Stillman, 2021). Very few studies have assessed the long term response of coastal bird populations to environmental change even though long-term population viability is a fundamental objective for most conservation strategies (Martin et al., 2007; Stillman et al., 2001). To do so, coastal bird ABMs would need to incorporate each species breeding habitat (i.e., non-intertidal), behaviour (e.g., migration, incubation, chick rearing) and success (i.e., recruitment), which is beyond their current capabilities. A potential solution is to focus on the long-term body condition of a population which for many species of coastal bird is positively related to survival, breeding success, migratory performance (Duijns et al., 2017; Gibson et al., 2018; Laursen et al., 2019a). They must also better link the population dynamics of resources to environmental conditions as these also respond to environmental change (Beukema et al., 2017b, 2010). For example, long-term variability in bivalve recruitment, mortality and growth (i.e., resources for coastal birds) is sensitive to changes in temperature and food availability (Beukema et al., 2017b, 2010; Beukema and Dekker, 2019).

The current coastal bird ABMs took approximately 40 years to develop but once tested they could be rapidly applied to a range of species and systems (Brown and Stillman, 2021; Goss-Custard and Stillman, 2008; Stillman et al., 2015; Stillman and Goss-Custard, 2010). Their success results from the standardized and re-usable sub-models which were developed to represent the behaviours, mechanisms and characteristics of a large number of species and systems (Goss-Custard et al., 2006; Stillman, 2008; Stillman et al., 1996). If this flexibility is to continue, then a sub-model to represent resource dynamics must also be standardized and re-usable. A potential framework under which this model might be developed is Dynamic Energy Budget (DEB) theory, which links physiological processes of individual organisms (i.e., ingestion, assimilation, respiration, growth and reproduction) under a single framework (Kooijman, 2010, 2000, 1986). A DEB model of an individual organism describes the rates at which it assimilates and utilises energy for maintenance, growth and reproduction, as a function of the state of the organism and of its environment (Nisbet et al., 2000; van der Meer, 2006). It is thereby capable of simulating the complete life cycle of an organism in dynamic (e.g., intertidal) environmental conditions (Monaco and McQuaid, 2018). DEB models use the same model structure for all heterotrophic species, with species differing only in parameter values (van der Veer et al., 2006). Parameters have been estimated for over 3000 species to date (including 141 bivalves) and there are standardised methods for estimating unknown values (Lika et al., 2011a; Marques et al., 2018; Saraiva et al., 2011; van der Veer et al., 2006).

## 1.6 Morecambe Bay

The waterbird assemblage in Morecambe bay has been declining for more than 25 years (Woodward et al., 2019). Not all species are declining but many of the bivalve specialists are (e.g., *S. mollissima*, *H. ostralegus*) and for some (e.g., *C. canutus*) the decline appears to be site specific (Woodward et al., 2019). The bay is situated in northwest England and marks the confluence of five estuaries. It is a large (530 km<sup>2</sup>), shallow and predominantly sandy bay which is lined with saltmarshes, shingle beaches and dunes (Gray, 1972; Gray and Bunce, 1972; Gray and Scott, 1977). The region experiences a spring tidal range of 9 m which intermittently exposes up to 420 km<sup>2</sup> of intertidal flats. It is the largest area of continuous intertidal flats in the UK and is of international significance for the biodiversity it supports (Anderson, 1972; Clapham, 1979, 1978; Clare et al., 1971; Dare, 1976; Dare and Mercer, 1973; Davidson, 1971; Elliott and Corlett, 1972; Gray and Bunce, 1972; Gray and Scott, 1977; Jones and Clare, 1977; Jones and Miller, 1966; Prater, 1972; Sloan and Aldridge, 1981; Wilson, 1973). Under the EU Birds Directive Morecambe Bay is designated a Special Protection Area (SPA), and under the EU Habitats Directive it is designated a Special Area of Conservation (SAC). The area is also designated a Special Site of Scientific Interest (SSSI), a national nature reserve (NNR), a natura 2000 site and a Ramsar site.

The benthic community in Morecambe Bay is characterised by bivalves (e.g., *C. edule*, *M. edulis*, *M. balthica*) which play an important, provisionary role in the ecosystem. They are a major food source for the internationally important assemblage of wetland birds which inhabit the area (Frost et al., 2021). It is the third largest gathering of water birds in the UK and includes considerable numbers of molluscivorous (e.g., *H. ostralegus*, *C. canutus* and *S. mollissima*) which consume large quantities of bivalves (Dare and Mercer, 1973; Goss-Custard et al., 1977; Prater, 1972). Bivalves are also economically important to the area and have been harvested commercially there for more than a century. The most frequently harvested species are *C. edule* and *M. edulis*, while both species are harvested for direct consumption (i.e., market size), *M. edulis* is also harvested undersize (or culture size) and grown to market size at aquacultural sites (Dare and Davies, 1975; Dare and Edwards, 1976). Commercial bivalve harvest in Morecambe Bay creates employment and income, which supports the small businesses that are important to coastal communities. Management of the bivalve populations in Morecambe Bay aims to provide sufficient food such that coastal bird populations remain in good condition.

The reduction in coastal bird numbers might therefore be due to a decrease in site quality (i.e., food availability) and is a potential source of conflict between the local bivalve harvesters and

conservationists. Within this framework the focus is currently on the harvesting of undersize *M. edulis* from the bay. In Morecambe Bay this practice is restricted to areas within the *M. edulis* population which are considered unstable and have a low chance of survival (Dare, 1976). Such aggregations can disappear within months after appearing due to winter storms or predation (e.g., *A. rubens*). By harvesting and relaying them elsewhere the bivalve industry ensures they remain available to coastal birds while creating a valuable source of income. Conservationists however are concerned that such aggregations are of value to coastal birds.

## **1.7 Research aims and thesis structure**

The overall aim of this PhD was to improve understanding of the mechanisms by which intertidal bivalve harvest impacts the environment and its ecological communities. The approach used builds on three existing ABMs which were created to simulate a) the growth and development of individual bivalves, b) the dynamics of bivalve populations and c) the foraging behaviour of coastal birds, all in response to environmental conditions (Rosland et al., 2009; Saraiva et al., 2014; Stillman et al., 2000). The response of multiple ecological populations to environmental change can thereby be assessed simultaneously. Such a holistic approach is needed due to the complexity which underscores coastal ecosystems but to date has not been achieved (Simpson et al., 2021). The approach taken here is therefore novel and will improve the manner in the ecological populations within coastal environments are managed. The thesis begins by developing an existing bivalve growth model to incorporate intertidal environmental conditions, it then focuses on the coupling of individual bivalve growth to population dynamics and finally introduces the foraging behaviour of coastal birds. There were three objectives:

- 1. Identify and develop a method for simulating the growth and development of intertidal *M. edulis* in response to environmental conditions.**
- 2. Improve understanding of how to sustainably manage the ecosystem goods and services provided by intertidal *M. edulis*.**
- 3. Assess the long-term risks of harvesting intertidal *M. edulis* to coastal birds in Morecambe Bay.**

To meet the research aims and objectives the thesis follows the following structure:

Chapter 1 – Introduction to the research topic, aims and objectives

Chapter 2 – Description of common methods

Chapter 3 – Simulating the energy dynamics of intertidal organisms for improved coastal management

Chapter 4 – Towards the sustainable management of temperate intertidal bivalve reefs

Chapter 5 – Balancing the conservation of coastal birds with commercial bivalve harvest

Chapter 6 – Discussion and conclusion

The overall aim of this PhD is to simulate the potential environmental impacts of harvesting intertidal bivalves and both themes and information flow from chapters 3 to 5 (Figure 1.2).

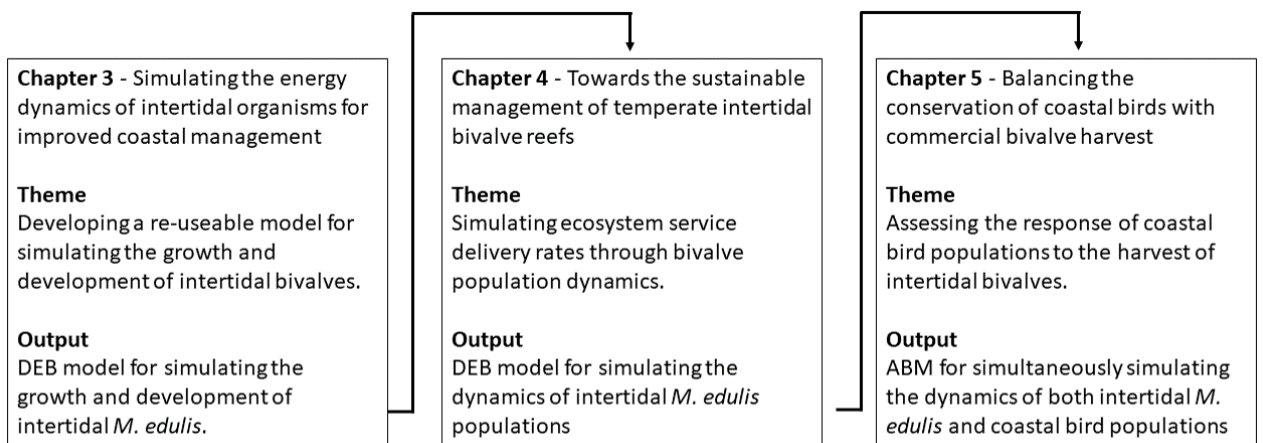


Figure 1.2 Overview highlighting the distribution of themes across chapters and how information flows between them.

The theme of chapter 3 is centred on the development of a re-usable submodel for simulating the growth and development of intertidal organisms. The final growth model and accompanying data is used again in both chapters 4 and 5. The premise of chapter 4 is a coupling of the growth model with various mortality submodels and environmental conditions, both of which contain values and parameters which are specific to Morecambe Bay. In chapter 5 the population model for intertidal

*M. edulis* is modified further to incorporate an additional submodel for simulating the foraging behaviour of coastal birds.

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## 2. General methods

### 2.1 Latin Hypercube Sampling

Efficient sampling strategies that scale with the size of the problem and computational budget are essential for various sampling-based analyses (Cariboni et al., 2007; Thiele et al., 2014). Latin hypercube sampling (LHS) is widely used for model calibration, sensitivity analysis and uncertainty analysis (Marino et al., 2008; Thiele et al., 2014). It is stratified sampling without replacement, belongs to the Monte Carlo class of sampling methods and requires fewer samples to achieve the same accuracy as simple random sampling (McKay et al., 2000).

The distribution of each parameter ( $k$ ) is divided into a fixed number of equal probability intervals ( $n$ ) which are then sampled (Marino et al., 2008). The size of each interval depends on the distribution of the parameter (uniform distributions all have the same size) and the sample size ( $n$ ) should be at least  $k + 1$  but is usually much larger to ensure accuracy (Figure 2.1). The sampling involves randomly selecting values from each probability density function. All probability intervals are sampled once without replacement so that the complete range of each parameter is included.

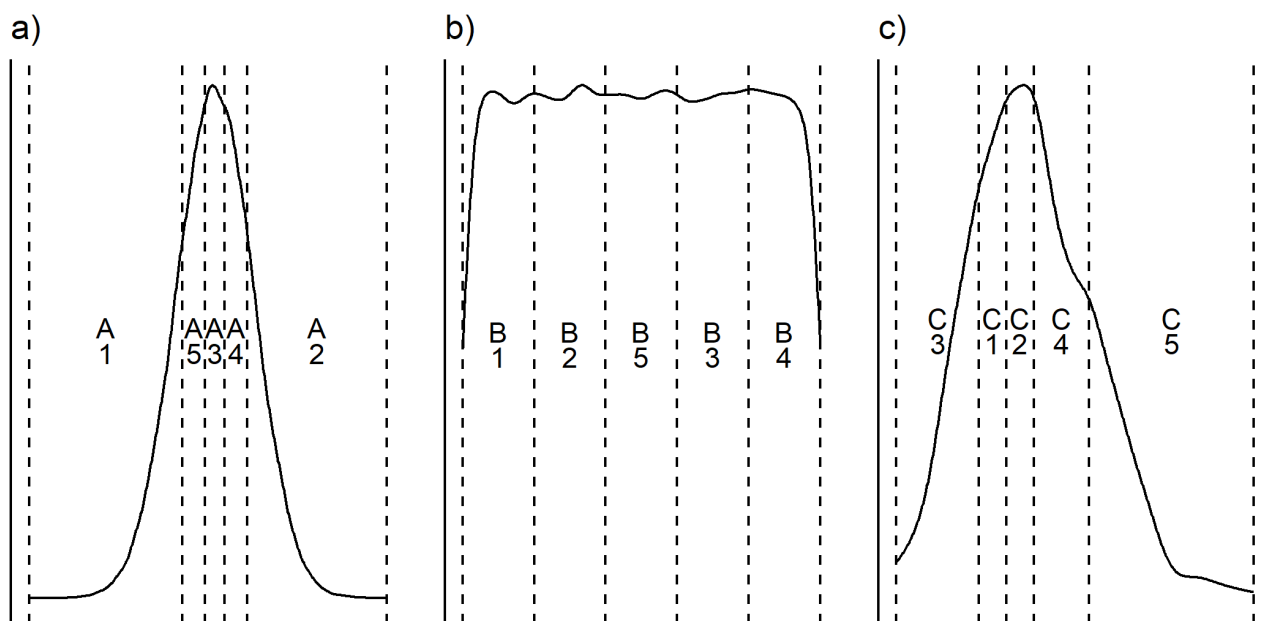


Figure 2.1 Example of probability density functions (pdfs) assigned to three hypothetical model parameters (a, b and c) for which a Latin hypercube is to be constructed. The theoretical sample size ( $n$ ) is five and each parameter range is divided into five equiprobable subintervals. Independent samples are then drawn from each pdf (a = normal, b = uniform and c = non-normal).

A matrix is generated that consists of  $n$  rows and of  $k$  columns corresponding to the sample size and the number of varied parameters (Table 2.1). The model is then run using each combination of parameter values (each row of the matrix) and the model output of interest is collected from each run. Different model outputs can be studied if more than one model output is of interest.

Table 2.1 The LHS matrix created by assembling the samples from each pdf in figure 1. Each row of the LHS matrix represents a unique combination of parameter values sampled without replacement.

A1	B1	C1
A2	B2	C2
A3	B3	C3
A4	B4	C4
A5	B5	C5

## 2.2 Morris sensitivity analysis

A global sensitivity analysis provides a general understanding of how sensitive the model outputs are to changes in parameter values (Cariboni et al., 2007). The results can help to measure model adequacy and can be used to identify parameters or parameter groups to which outputs are sensitive. Once identified, high sensitivity can be used to establish research priorities (e.g., better measure of parameter) and can provide insight into the process and mechanisms most critical to the stability of model outputs (i.e., risk assessment).

The Morris method provides a measure of global sensitivity for each parameter which can be used to both rank and group them by importance (Campolongo et al., 2007; Morris, 1991). It is free of assumptions about the model (e.g., linear relationships) and qualifies whether parameters have a negligible, first order (e.g., linear or additive) or second order (e.g., non-linear or interactive) relationship with model outputs. The method uses individually randomised ‘one-factor-at-a-time’ (OAT) experiments in which each parameter  $x_i$  ( $i = 1, \dots, k$ ) is varied along a path of step size  $\Delta$  to create a trajectory (or multiple trajectories) through the parameter space. Each trajectory results in an estimate of the elementary effect (EE) for the  $i^{\text{th}}$  parameter (i.e., the ratio of the change in model output to the change in that parameter). A single EE ( $d$ ) is calculated by:

$$d(x) = \left( \frac{y(x_1, \dots, x_i + \Delta_i, \dots, x_k) - y(x)}{\Delta_i} \right)$$

where  $\Delta_i$  is the trajectory step size for parameter  $x_i$ ,  $\mathbf{x}$  is the vector of parameters of size  $k$  and  $y(\mathbf{x})$  is the model output. The number of levels ( $p$ ) is determined by the user and used to estimate the value for  $\Delta$  ( $\Delta = p / [2 \cdot (p - 1)]$ ). A single trajectory for each parameter serves as a local sensitivity measure which, on its own, is highly dependent on the location of the trajectories starting point and does not account for interactions between parameters. Multiple trajectories are usually aggregated to a global measure, the number of trajectories ( $r$ ) translates to model runs ( $n$ ) using the equation:  $n = r \cdot (k + 1)$  (Morris, 1991). Values for  $r$  can vary greatly (e.g., 10 to 2500) and without proper consideration the sensitivity analysis can fail to identify the correct parameters (Campolongo et al., 2007; Ruano et al., 2012, 2011; Vanrolleghem et al., 2015). Three sensitivity measures are computed: the mean ( $\mu$ ) and absolute mean ( $\mu^*$ ) of the elementary effects, which assess the overall influence of the parameter on the output, and the standard deviation ( $\sigma$ ), which estimates the extent of the parameters higher order effects (i.e., non-linear and/or due to interactions) with other factors.

The total effect of each parameter is computed as both the mean ( $\mu$ ) and the absolute mean ( $\mu^*$ ) of the EEs for all trajectories. Both are needed because if the model output responds in a non-monotonic (positive and negative) way to parameters,  $\mu$  is prone to type II errors (Campolongo et al., 2007). Using  $\mu^*$  solves this problem but in the process loses information on the sign of the effect. To retain this information  $\mu$  and  $\mu^*$  can be examined simultaneously which both provides the sign of effect and indicates whether it changes as parameter values vary. Simultaneously large values of both  $\mu$  and  $\mu^*$  mean that the model output is sensitive to the parameter, on average, throughout the parameters range, the sign (+ve or -ve) of  $\mu$  indicates the direction of the effect. If  $\mu^*$  is large and  $\mu$  is small, the output is sensitive to the parameter in a non-monotonic manner. Low values of  $\mu^*$  (and therefore  $\mu$ ) indicate the parameter value does not influence the output.

The standard deviation of the elementary effects ( $\sigma$ ) is an aggregated measure of the intensity of the interactions of each parameter with all others and reflects the degree of nonlinearity in model response to changes in the parameter (Morris, 1991). If  $\sigma$  is large, it means that the sensitivity of the parameter varies markedly between different points in the parameter space. For a completely linear model, elementary effects are the same everywhere (because the local gradients are the same everywhere), and  $\sigma$  is zero. Therefore, a higher  $\sigma$  entails a more nonlinear relationship with more interactive components. Plotting  $\sigma$  against  $\mu^*$  is a common method for establishing the type of effect each parameter change has on model outputs (Morris, 1991; Ruano et al., 2011; Vanrolleghem et al., 2015). The lines corresponding to  $\mu^* = 2 \cdot (\sigma \cdot r)^{-0.5}$  (2SEM) and a threshold value

for  $\mu^*$  ( $CT_{Morris}$ ) divide the plot into non-influential, influential and interactive / non-linear effects (Figure 2.2). Parameters with  $\mu^*$  values less than  $CT_{Morris}$  are considered non-influential. Those with  $\mu^*$  values greater than  $CT_{Morris}$  and  $\sigma$  values less than 2SEM are considered influential. Parameters with  $\mu^*$  values greater than  $CT_{Morris}$  and  $\sigma$  values greater than 2SEM are considered interactive or non-linear (Morris, 1991; Ruano et al., 2011; Vanrolleghem et al., 2015).

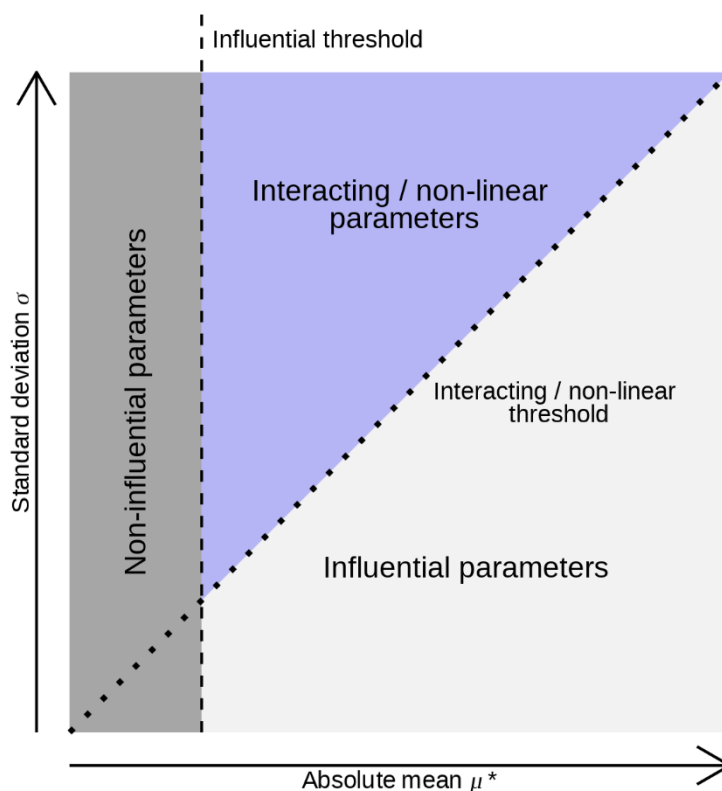


Figure 2.2 Schematic overview of the suggested terminology for differentiating parameters according to the Morris screening method.

The Morris method produces multiple rankings of importance for each input parameter and the extent to which rankings agree is helpful for assessing the quality and robustness of the analysis. The top-down coefficient of concordance (TDCC) provides a useful measure in which emphasis is placed on agreement between high ranking parameters (Helton et al., 2005; Iman and Conover, 1987; Marino et al., 2008). The TDCC is calculated for each output variable by first ranking  $r(s_{ij})$  all input parameters ( $k_i$ ) by replicate ( $r_j$ ) and sensitivity measure ( $s_{ij}$ ). These ranks are then replaced by the corresponding savage scores  $ss(s_{ij})$  (Savage, 1959):

$$ss(S_{ij}) = \sum_{i=r(S_{ij})}^{nk} 1/i$$

where  $nk$  is the maximum number of input parameters (i.e.,  $i = 1, 2, 3...nk$ ). The result is an array of the form:

	$R_1$	$R_2$	...	$R_{nr}$
$k_1$	$ss(S_{11})$	$ss(S_{12})$	...	$ss(S_{1, nr})$
$k_2$	$ss(S_{21})$	$ss(S_{22})$	...	$ss(S_{2, nr})$
$\vdots$	$\vdots$	$\vdots$	...	$\vdots$
$K_{nk}$	$ss(S_{nk,1})$	$ss(S_{nk,2})$	...	$ss(S_{nk, nr})$

where  $nr$  is the total number of replicates (i.e.,  $j = 1, 2, 3...nr$ ). The TDCC calculated as:

$$TDCC = \frac{\left\{ \sum_{i=1}^{nk} \left[ \sum_{j=1}^{nr} ss(S_{ij}) \right]^2 - nr^2 \cdot nk \right\}}{\left\{ nr^2 \cdot \left( nk - \sum_{i=1}^{nk} 1/i \right) \right\}}$$

The TDCC values and their corresponding p-values provide an indication of analysis consistency. Values for the TDCC range between 0 and 1, those close to one ( $> 0.9$ ) indicate a high degree of reproducibility, which decreases with TDCC. The p-values for each TDCC (under the null hypothesis of zero concordance between parameter rankings) are calculated using the statistics T (approximating a  $\chi^2$ -distribution with  $k-1$  degrees of freedom), derived from TDCC using the following formula:

$$T = nr \cdot (nk - 1) \cdot TDCC$$

The concordance between rankings is statistically significant when  $p < 0.05$ .

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### 3. Simulating the energy dynamics of intertidal organisms for improved coastal management

A. Feather<sup>1</sup>, J. G. Hiddink<sup>1</sup>, L. S. Cordes<sup>1</sup>

<sup>1</sup> School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB

#### 3.1 Abstract

Marine bivalves provide many ecosystem services and are a key component of functioning coastal ecosystems. A key challenge in estuarine management is determining how to sustainably manage multiple ecosystem services simultaneously. Effective conservation and management strategies are informed using ecological models and depend on understanding how environmental change impacts the physiology and ecology of marine organisms. Intertidal habitats are however periodically exposed to the air and organisms exhibit behaviours (e.g., valve closure) and adaptations (e.g., metabolic depression) to cope with the stress. Growth models may therefore need to include additional mechanisms if accuracy across shore levels is to be maintained. In this study the extent to which growth (annual growth rate, maximum size) and condition of *Mytilus edulis* is related to position on the shore (elevation) is assessed at three sites in Morecambe Bay, UK. Two intertidal Dynamic Energy Budget (DEB) models (a basic intertidal model in which there is no change in physiological rates during periods of aerial exposure, and a modified intertidal model in which rates are reduced) are then compared in their ability to describe the observed relationship between growth, condition and elevation. Growth and condition of *M. edulis* was observed to decrease significantly with increasing tidal shore level. Both DEB models predicted condition in response to elevation accurately, the modified intertidal model however proved more precise when simulating individual growth. Changes to the concentration of suspended particles (organic and inorganic) most influenced model growth rates relative to other environmental drivers. The *M. edulis* populations in Morecambe Bay are therefore compensated during periods of aerial exposure, most likely through the depression of metabolic rates. Sustainable management of coastal systems will increasingly require predictions of responses to novel environmental conditions, for multiple species and at a range of spatial scales. DEB growth models can do just this and are therefore powerful and promising tools for informing coastal management.

#### 3.2 Introduction

The world's ecosystems are under increasing pressure due to unprecedented rates of change in climate and land use (Hoegh-Guldberg and Bruno, 2010; Tilman et al., 2001; Vitousek et al., 2017). Global food production is a major threat to biodiversity as many practices remove or modify large areas of important habitats (Phalan et al., 2011; Tscharrntke et al., 2012). The expansion and intensification of terrestrial agricultural practices has resulted in the large-scale loss of ecosystem services and the extinction of numerous species (Green et al., 2005). Aquaculture is now the fastest growing food production sector and is viewed with increasing importance with respect to food security (Béné et al., 2016). Bivalve aquaculture accounts for approximately 14% of food produced in the world's oceans and for some species (e.g., *Mytilus edulis*), the practice is reliant on the harvest of undersize individuals from populations (subtidal and intertidal) which occur naturally in coastal areas (Kamerms and Capelle, 2019; Wijsman et al., 2018). Harvesting bivalves from natural populations often conflicts with conservation objectives (e.g., European Birds Directive (Directive, 2009/147/EC)) and it is essential to develop innovative tools and approaches for assessing how ecological populations and ecosystem services might respond (de Silva, 2012; Ens, 2006; Goss-Custard et al., 2004).

Substantial efforts have been made to better understand the dynamics of bivalve populations, in particular the biological and physical factors that affect growth rates (Bayne, 1976; Grant et al., 1993). Ecological models are typically used to simulate bivalve growth and are routinely used for selection of culture sites, optimization of culture practices, and the estimation of ecosystem service provisioning rates (Filgueira et al., 2018a; Grant and Pastres, 2019; Newell et al., 2019). They function at the scale of the individual and use either empirical or mechanistic relationships to describe energy intake and expenditure rates (Beadman et al., 2002; Larsen et al., 2014; Rosland et al., 2009). Empirical models are based on the Scope For Growth (SFG) concept which uses the intake and expenditure rates of a 'standard' organism and allometric relationships which scale the rates to animals of different sizes (Bayne, 1976; Gangnery et al., 2003; Hawkins et al., 2002). Mechanistic models are based on Dynamic Energy Budget (DEB) theory and assume energy intake rates to be proportional (also via allometric relationships) to the structural surface area of the organism and expenditure rates to the structural volume. (Kooijman, 2010, 2000, 1986).

DEB theory is empirically grounded, well-tested and has been applied in a range of disciplines, and to species from a wide range of taxonomic groups (Marques et al., 2018; Saraiva et al., 2014). DEB growth models have increased in popularity over the past decade largely due to their mechanistic nature, replicability and flexibility (Rosland et al., 2009; Saraiva et al., 2012; Thomas and Bacher, 2018). They mechanistically link the physiological processes of individual organisms (e.g., ingestion,

assimilation, respiration, maintenance and reproduction) and relate them to environmental drivers (e.g., temperature, food), thereby simulating complete life cycles (i.e., feeding, growth, development, reproduction and death) in dynamic environments (Nisbet et al., 2000; Sousa et al., 2008; van der Meer, 2006). The same generic model structure is used for all species (differing only in parameterization) and parameters have been estimated for 3195 species (including 141 Bivalvia) to date (Marques et al., 2018). DEB models have long been employed for modelling bivalve growth and the focus has largely been on relatively stable subtidal conditions (Rosland et al., 2009; Thomas and Bacher, 2018; Van Haren and Kooijman, 1993). Fewer models simulate the growth of intertidal bivalves where environmental conditions are more variable (Monaco and McQuaid, 2018; Sarà et al., 2011; Saraiva et al., 2020).

Intertidal habitats are periodically exposed to the air and individuals must change behaviour or risk desiccation (McMahon, 1988; Somero, 2002; Suchanek, 1978). Bivalves can respond to emersion by either permanently closing their valves and switching to anaerobic metabolism, or periodically opening and closing (gaping) their valves which permits continued aerobic respiration (Demers and Guderley, 1994; McMahon, 1988; Nicastro et al., 2010). By closing its valves an individual conserves water (buffering against thermal stress) and increases its defence against predators (Reimer and Tedengren, 1996). Anaerobic metabolism however causes rapid depletion of energy reserves and the accumulation of harmful anaerobic end products (Byrne et al., 1990; McMahon, 1988; Weihe and Abele, 2008; Yin et al., 2017). Bivalves can conserve energy and reduce the negative effects of anaerobic respiration by depressing metabolic rates (metabolic depression) during periods of aerial exposure (Griffiths, 1981a; Tagliarolo et al., 2012; Widdows and Shick, 1985). Rates of respiration can reduce by up to 95 % when individuals are exposed, though this behaviour is variable and most prominent in individuals and populations which are acclimatised to intertidal conditions (Tagliarolo et al., 2012).

Bivalve growth rates are typically variable depending on multiple intrinsic (e.g., genetic), environmental (e.g., temperature, food), and social (e.g., inter- or intra-specific competition) factors (Beukema et al., 2010; Seed, 1969). Both somatic (i.e., tissue) and shell (i.e., length) growth are generally observed to decrease with increasing aerial exposure (Buschbaum and Saier, 2001; Rodhouse et al., 1984; Yin et al., 2017). Longer emersion times reduce both digestion and growth rates via a reduction of feeding time and, if valves are closed, by prompting a switch to anaerobic metabolism (De Zwaan and Mathieu, 1992). Additional costs of aerial exposure can occur in summer when high air temperatures increase maintenance costs and reduce growth further (Almada-Villela et al., 1982). Feeding and growth rates are however negatively related to population density and

growth might be reduced at low shore levels if competition is increased (Buschbaum and Saier, 2001; Jones et al., 2011; King et al., 2006; Tang et al., 2020). Shell mass has been shown to increase with aerial exposure for some species which is attributed to the slower growth of the animals at higher tidal elevations and is therefore likely broadly related to age (Beadman et al., 2003; Brown et al., 1976; Seed, 1968).

DEB growth models for intertidal bivalves may therefore need to include additional adaptive mechanisms (e.g., metabolic depression) if accuracy across shore levels is to be maintained (Monaco and McQuaid, 2018). Here, we focus on an intertidal population of *M. edulis* in Morecambe Bay, a large shallow inlet located on the northwest coast of England, UK. Several DEB models have been developed for *M. edulis* which have been used to better understand the influence of environmental conditions (e.g., temperature, food availability, salinity, pH, toxins) on growth, metabolism and reproduction (Rosland et al., 2009; Saraiva et al., 2012; Van Haren and Kooijman, 1993). Energetic costs associated with environmental stress are attached to standard model structures with relative ease which has enabled researchers to assess the physiological response of *M. edulis* to a wide range of novel conditions (Maar et al., 2015; Rosland et al., 2012; Thomas and Bacher, 2018). No model so far however has addressed the energetic costs for intertidal individuals when exposed to the air. *M. edulis* close their valves when exposed to air and are shown to be largely anaerobic during this period (Widdows et al., 1979; Widdows and Shick, 1985). Rates of both oxygen consumption and carbon dioxide production simultaneously decrease to values between 5 and 25 % of those observed under aquatic conditions (Tagliarolo et al., 2012; Widdows et al., 1979; Widdows and Shick, 1985). Physiological rates (e.g., growth) of *M. edulis* are therefore expected to be reduced in individuals living higher up the shore (Buschbaum and Saier, 2001; Gillmor, 1982; Sukhotin and Pörtner, 1999; Tagliarolo et al., 2012). It remains unclear what modifications, if any, should be applied to DEB growth models of intertidal *M. edulis*. A better understanding of how to predict intertidal bivalve growth will improve decisions made by coastal managers who are increasingly informed via ecological models (Goss-Custard et al., 2019; Kotta et al., 2020; Rullens et al., 2022).

The overall aim of this study is to develop a DEB model for simulating the growth of *M. edulis* in response to intertidal environmental conditions. We first quantify the extent to which individual growth and condition of *M. edulis* in Morecambe Bay differs across shore levels. Then we identify the environmental conditions and individual behaviours most important in driving these differences, using two DEB models which differ in complexity. The difference between the two model structures occurs when individuals are emerged, one structure assumes that intake rates are suppressed but

all physiological rates remain the same, and the other assumes all physiological rates are reduced (metabolic depression) by a constant value.

### 3.3 Methods

Field data were collected to 1) describe the growth and physiological condition of *M. edulis* in Morecambe Bay in relation to shore level, 2) calibrate DEB growth models and 3) evaluate DEB growth model performance. Shell length (cm) frequency plots are used to generate age-specific length data and obtain growth trajectories (e.g., shell length to age) and growth parameters (von Bertalanffy). Individual biometric measurements are used to estimate dry tissue mass growth trajectories (via the relationship between dry tissue mass, shell length and elevation) and describe the relationship between condition index and elevation. The extent to which growth and condition are related to elevation is assessed using growth parameters and condition index. The DEB models are calibrated on growth trajectories (dry tissue mass and shell length) for each station and their performance across shore levels is evaluated against growth parameters and condition index.

#### 3.3.1 Field surveys

Surveys were conducted on three *M. edulis* reefs in Morecambe Bay (Figure 3.1). The Bay is the largest continuous area of intertidal flats in UK and experiences a tidal range of up to 10.5 m at spring tides with an ebbing tide that can retreat 12 km. The intertidal *M. edulis* population here is exposed between 5 – 60 %  $y^{-1}$  which facilitates the study of variation in intertidal behaviour and adaptation. The three sites represent three broad regions and were chosen due to their accessibility. Sampling took place between 2017 and 2019 during March and September, covered an elevation range of -4.0 m to 1.0 m above sea level and an annual aerial exposure of 5 to 60 % (Table 3.1).

Table 3.1 Overview of the sampled *M. edulis* reefs, showing the mean elevation (above sea level m)  $\pm$  standard deviations and range [min, max], the mean annual exposure (%  $y^{-1}$ )  $\pm$  standard deviations and range [min, max], the number of visits during the sampling period and the number of sample stations by site.

Site	Sampling period	Elevation (m)	Annual exposure (%)	Visits	Stations
Fleetwood	2017-05-15 to 2019-03-15	-2.51 ± 0.70 [-3.4, -1.6]	16.0 ± 1.0 [4, 29]	6	7
Foulney	2017-05-15 to 2019-03-15	-1.93 ± 1.11 [-3.8, 0.9]	24.0 ± 1.4 [2, 57]	6	25
Heysham	2017-06-15 to 2019-03-15	-2.49 ± 0.10 [-3.4, -0.5]	16.0 ± 1.3 [5, 43]	5	8

Forty sampling stations of 100 m<sup>2</sup> were distributed across the three reefs and five 0.1 m<sup>2</sup> samples were collected from within each station during each survey. Each sample was taken by removing all mussels found within a 0.1 m<sup>2</sup> quadrat and freezing for further processing in the laboratory. All sampling stations and points were placed randomly throughout the *M. edulis* reefs using the *sp* package (Pebesma and Bivand, 2005) for the software R (R Core Team, 2018).

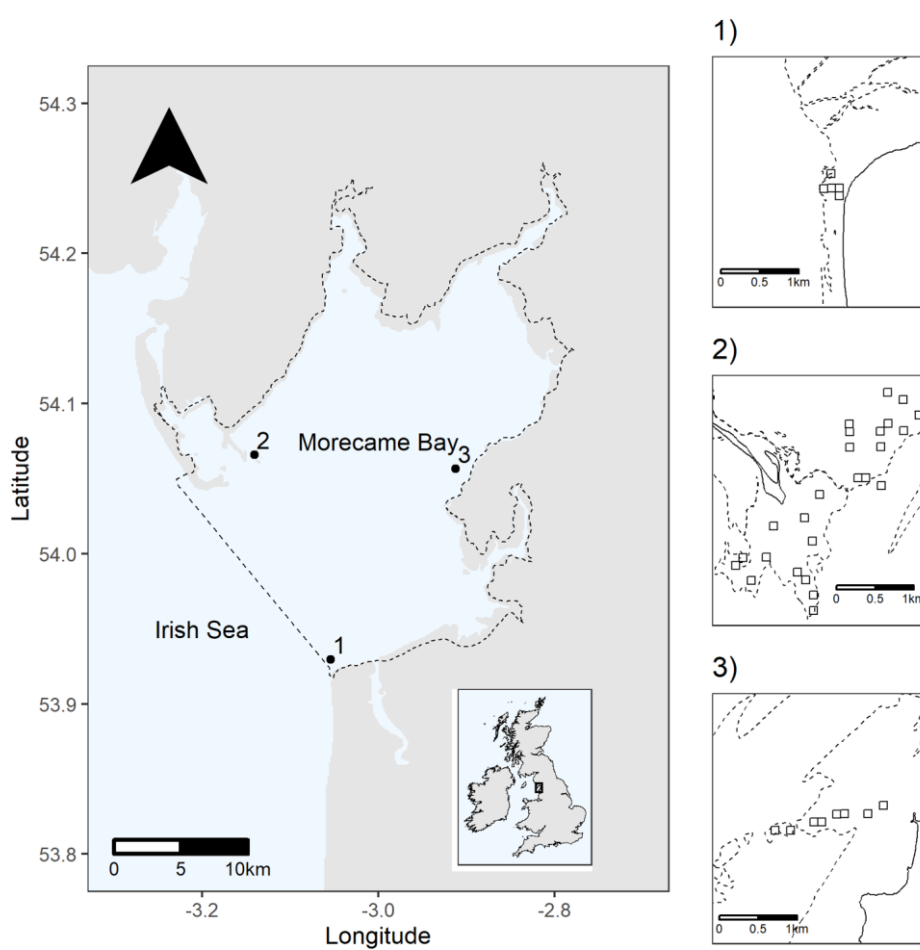


Figure 3.1 Map showing the Special Area of Conservation (dashed line) and sampling sites within Morecambe Bay, UK, 1 – Fleetwood, 2 – Foulney, 3 – Heysham. The three smaller maps correspond to site numbers and show the location of sampling stations (100m<sup>2</sup>) and mean high (solid) and low (dashed) water marks.

### 3.3.2 Individual measurements

In the laboratory each sample was washed, sieved (using 0.5, 2, 10 mm sieves) and the total mass (g) of all individuals present within each sieve was recorded. The smallest sieve size was chosen to ensure new settlement (1.5 mm) would be identified if present. The shell length of all individuals > 10 mm was measured using callipers (0.1 mm), all individuals < 10 mm were measured using the digital analysis software *ImageJ* (Schneider et al., 2012). Individuals < 5 mm were often present in large numbers which was time consuming to measure individually, therefore the mass of all individuals < 5 mm was recorded before a subsample of approximately 5 – 10 g was analysed. The count was then proportionally scaled up to the original < 5 mm sample. An individual from each distinct size class, sampling station and date was selected for dry tissue mass measurements. The wet tissue mass (g) was measured using digital scales (0.001g) before each sample was dried in an oven at 90 °C for 24 hours to determine the dry mass (g). Finally, each tissue sample was placed in a furnace at 450 °C for 3 hours to obtain its ash-free dry mass (g). Condition (*ci*) index is calculated for each sample as:

$$ci = \frac{m}{l^3}$$

where *m* is the dry tissue mass (g), and *l* is the shell length (cm).

### 3.3.3 Age and cohort

Length-frequency histograms for each station and date were analysed using the *mixdist* package in the R statistical programming language (Macdonald, 2018; R Core Team, 2018). Maximum-likelihood estimates are used to fit finite mixture distribution models to length frequency histograms as normal distributions. This approach provides estimates of age distributions: the proportion of each age group relative to the population ( $\pi$ ), mean length at age ( $\mu$ ) and standard deviations of length at age ( $\sigma$ ). Approximate starting values for  $\pi$ ,  $\mu$  and  $\sigma$  are required which must be obtained via visual inspection of the length frequency histograms (Clarke et al., 2019; Hoxmeier and Dieterman, 2011). Histograms for each sample station were therefore visually examined across

all dates simultaneously. Age groups were based on knowledge of growth in the first year of settlement. In Morecambe Bay major settlements occur annually between January and April, and individuals can grow to between 2 and 3 cm by autumn (Dare, 1976). A shell length of < 3 cm in September and October was therefore used as a reference for age 0 individuals. The life span of *M. edulis* in Morecambe Bay is reported to be 3 – 4 years and therefore five age classes (0 – 4) were considered during visual examination (Dare, 1976). In summary, all individuals were assigned an age class (i.e., cohort) based on shell length and these values were used to calculate growth parameters.

### 3.3.4 DEB model description

#### 3.3.4.1 Overview

The model used in this study is based on (Rosland et al., 2009); a detailed description of this model, equations, and parameters is given in (Pouvreau et al., 2006), (van der Meer, 2006), (van der Veer et al., 2006) and (Rosland et al., 2009). The model description uses DEB symbols and notations described in (Kooijman, 2000) where square brackets  $[\ ]$  denote quantities expressed as per unit structural volume, while braces  $\{ \}$  denote quantities expressed as per unit surface area of the structural volume. All rates (i.e., dimension per time) have dots above their symbol. Tables 2, 3 and 4 list the equations and parameters that describe flows of energy and the dynamics of state variables. The model is written in NetLogo (Wilensky, 1999).

The model simulates the growth and development of *M. edulis* in relation to suspended particle concentration (organic and inorganic), temperature (water and air) and tidal dynamics (elevation and water level). The model contains two types of entities, an individual *M. edulis* and the environment. An individual is characterized by four state variables: structural volume ( $v$ ,  $\text{cm}^3$ ), which determines size, feeding rates, and maintenance costs; reserve ( $es$ , J), which serves as an intermediate storage of energy between feeding and mobilization processes, maturity ( $eh$ , J), which regulates the transition between two developmental stages (juvenile, adult) and reproductive buffer ( $er$ , J), an energy buffer of mature individuals for reproduction. The environment is defined by the state variables of chlorophyll-a concentration ( $chl$   $\text{mg m}^{-3}$ ), suspended inorganic particulate matter concentration ( $spim$   $\text{g m}^{-3}$ ), sea surface temperature ( $sst$  °K), near surface air temperature ( $nst$  °K), elevation (m) and water level (m). All model simulations use a single profile of environmental data and progress using hourly time steps. At each time step an individual first feeds



before assimilated energy enters the reserve compartment, from here energy is mobilized to fuel all other processes. Four differential equations specify how the state variables of a mussel change depending on their current values and environmental conditions.

Table 3.2 Dynamic Energy Budget model equations for describing energy flow.

Process	Description	Unit	Equation
Ingestion	Ingestion rate	J d <sup>-1</sup>	$\dot{p}X = \{\dot{p}Xm\} \cdot f \cdot V^{\frac{2}{3}} \cdot T_c$
Ingestion	Functional response	-	$f = \frac{x}{x + X_K \left(1 + \frac{y}{K_Y}\right)}$
Assimilation	Assimilation rate	J d <sup>-1</sup>	$\dot{p}A = ae \cdot \dot{p}X$
Utilisation	Utilisation rate	J d <sup>-1</sup>	$\dot{p}C = \left(\frac{es}{V}\right) \cdot \frac{\left(T_c \cdot [E_G] \cdot ec \cdot V^{\frac{2}{3}}\right) + ([P_M] \cdot T_c \cdot V)}{[E_G] + \left(\frac{es}{V}\right) \cdot k}$
Somatic maintenance	Somatic maintenance rate	J d <sup>-1</sup>	$\dot{p}M = [P_M] \cdot V \cdot T_c$
Growth	Flux allocated to growth	J d <sup>-1</sup>	$\dot{p}G = (k \cdot \dot{p}C) - \dot{p}M$
Growth	Maturity maintenance	J d <sup>-1</sup>	$\dot{p}J = \dot{k}J \cdot eh \cdot T_c$
Maturity and reproduction	Flux allocated to reproduction/maturity	J d <sup>-1</sup>	$\dot{p}R = (1 - k) \cdot \dot{p}C - \dot{p}J$
Somatic maintenance	Gamete resorption rate	J d <sup>-1</sup>	$\dot{p}L1 = \max(\dot{p}M - (k \cdot \dot{p}C), 0)$
Somatic maintenance	Lysis of structure rate	J d <sup>-1</sup>	$\dot{p}L2 = \max(\dot{p}M - (k \cdot \dot{p}C + \dot{p}L1), 0)$
Spawning	Condition to spawn		<i>if GSR ≥ GSRspawn AND T ≥ Tspawn</i>
Spawning	Flux to spawning	J d <sup>-1</sup>	$erspawn = kr \cdot er$
	Arrhenius equation		$T_c = \exp\left(\frac{T_A}{T_1} + \frac{T_A}{T}\right)$

The ingestion rate  $\dot{p}X$  (J d<sup>-1</sup>) is proportional to the surface area of the structural body, which is  $V^{2/3}$ . Ingestion is constrained by the maximum ingestion rate  $\{\dot{p}Xm\}$  (J cm<sup>-2</sup> d<sup>-1</sup>) and scaled by  $f$  according to a Holling II functional response (Holling, 1965). The model assumes individuals filter both organic and inorganic matter but can only convert the organic matter into energy, inorganic matter is rejected and expelled as pseudo-faeces. Therefore, the functional response has been modified to include inorganic particles ( $spim$ ) following (Kooijman, 2006). The organic ( $x$  mg chl m<sup>-3</sup>) and inorganic ( $y$  g  $spim$  m<sup>-3</sup>) matter concentrations are scaled by the organic particle ( $X_K$  mg chl m<sup>-3</sup>) and the inorganic particle ( $K_Y$  g  $spim$  m<sup>-3</sup>) half saturation coefficients. The ingested food is assimilated into the reserve ( $es$ , J cm<sup>-3</sup>) with a constant assimilation efficiency ( $ae$ ). Energy is then allocated from the reserve with the fraction  $\kappa$  to somatic growth and maintenance and the fraction  $(1 - \kappa)$  to maturity, gamete production and reproduction maintenance. Spawning occurs when both a temperature and gonado-somatic index ( $GSI$ ) threshold are reached simultaneously, and when the individual is submerged. When an individual spawns the reproductive buffer ( $er$ ) is emptied. During severe starvation (low energy reserves), the reproductive tissue can pay for somatic maintenance.

All physiological rates depend on the temperature following the Arrhenius function within a species-specific tolerance range.

Table 3.3 Equations to translate Dynamic Energy Budget model quantities (Table 1) to empirical biological metrics.

Biological measurement	Unit	Equation
Shell length	cm	$l = \frac{V^{\frac{1}{3}}}{\delta_m}$
Dry tissue mass	g	$DFM = (V \cdot cf1) + \left( \frac{(es + er)}{cf3} \cdot cf2 \right)$
Gonado-somato index	-	$GSI = \frac{\frac{er}{cf3} \cdot cf2}{(V \cdot cf1) + \left( \frac{(es + er)}{cf3} \cdot cf2 \right)}$

Shell length ( $l$  cm) is proportional to the structural volume ( $v$  cm<sup>3</sup>) via the shape coefficient ( $\delta_m$ ), dry tissue mass (DFM g) is calculated as the reserves, reproductive buffer and structural volume combined and  $GSI$  is defined as a mass ratio between the gametes (reproductive buffer) and total dry tissue mass.

### 3.3.4.2 Environmental drivers

The environmental data needed to drive standard DEB models are a time series of food concentration and temperature. Food concentration (density) is used to determine intake rates while all the physiological rates (assimilation and maintenance) in the model are dependent on body temperature (i.e., water temperature when submerged and air temperature when emerged). Chlorophyll-a ( $chl$ , mg m<sup>-3</sup>) and suspended particulate inorganic matter ( $spim$ , g m<sup>-3</sup>) concentrations are used here as a measure of food quantity and quality. Sea surface ( $sst$ , K) and near surface air temperature ( $nst$ , K) are used as a measure of body temperature. Elevation (height above sea level m) and water level data (Ordnance Datum m) are considered additional environmental drivers which determine if the individual is submerged or emerged, and thereby regulating changes in intake rates and temperature. Environmental data were obtained from 1<sup>st</sup> of January 2015 to the 31<sup>st</sup> of December 2019 for the area designated as a Special Area of Conservation (SAC) for Morecambe Bay (Figure 1). All simulations use a single profile for temperature (water and air) and suspended particle (organic and inorganic) concentration, but a unique elevation value is set for

each run. All processing of spatial data was carried out using the *raster* package (Hijmans et al., 2017) for the software R (R Core Team, 2018).

Daily *chl* and *spim* concentrations were extracted from satellite observations at 1 km resolution obtained using merged data from SeaWiFS, MODIS and MERIS via a regional algorithm specifically designed for coastal waters (Gohin, 2011). Daily *sst* was extracted at 1 km resolution from NOAA-18 satellite measurements (available <https://www.copernicus.eu/en>). Hourly measurements of *nst* for the survey period are available from the Met Office Integrated Data Archive System, (Met Office, 2006), observed *nst* was obtained from Walney Island weather station (54.125 N, -3.258 W, elevation: 15m, (Met Office, 2019). Lidar data collected at 1 m horizontal and 1 mm vertical resolution (available <https://environment.data.gov.uk/>) were used to calculate mean elevation of each sample station. Hourly tidal height data from Heysham tide station (available <https://www.bodc.ac.uk>) was used to simulate tide dynamics in relation to elevation.

#### **3.3.4.3 Model structures**

Two DEB model structures (basic intertidal and modified intertidal) are assessed in relation to the accuracy at which they describe growth of *M. edulis* in response to intertidal environmental conditions. Both simulate an intertidal environment by comparing elevation with water level at every time step to determine whether an individual can feed, and whether physiological processes are dependent on water or air temperature. The difference between the two model structures occurs when individuals are emerged, the basic intertidal model assumes that intake rates are suppressed but all physiological rates remain the same. The modified intertidal model assumes all physiological rates are reduced (metabolic depression) by a constant, *mdr* (-).

#### **3.3.4.4 Parameter values**

The primary DEB parameters are based on those given by (Rosland et al., 2009; Saraiva et al., 2011; van der Veer et al., 2006). Additional parameters are either derived from literature or estimated from biometric data or during the calibration step. All parameters are summarised in Table 3.4.

Table 3.4 Dynamic Energy Budget model parameters for *Mytilus Edulis*.

Parameter	Units	Symbol	Value	Reference
Maximum surface-area specific ingestion rate	J d <sup>-1</sup> cm <sup>-2</sup>	$\{\dot{P}xm\}$	273	(Rosland et al., 2009)
Assimilation efficiency	-	$ae$	0.75	(van der Veer et al., 2006)
Volume specific cost of growth	J cm <sup>-3</sup>	$[EG]$	1900	(van der Veer et al., 2006)
Maximum storage density	J cm <sup>-3</sup>	$[EM]$	2190	(van der Veer et al., 2006)
Energy conductance	cm d <sup>-1</sup>	$ec$	0.094	(Rosland et al., 2009)
Volume specific cost of maintenance	J cm <sup>-3</sup> d <sup>-1</sup>	$[PM]$	27.8	(Rosland et al., 2009)
Allocation fraction to growth and maintenance	-	$k$	0.67	(Saraiva et al., 2011)
Volume-specific maturity maintenance rate coefficient	d <sup>-1</sup>	$kj$	0.0146	(Rosland et al., 2009)
Gonado-somatic ratio to spawn	J J <sup>-1</sup>	$GSI_{spawn}$	0.27	(Cardoso and Dekker, 2007)
Minimum temperature for spawning	°C	$T_{spawn}$	9.6	(Saraiva et al., 2011)
Reproduction efficiency	-	$kr$	0.95	(Kooijman, 2010)
Maturity at puberty	J	$EH_p$	0.0158	(Saraiva et al., 2011)
Shell length growth coefficient	-	$\delta m$	-	(Table 3.8)
Dry mass to wet mass conversion factor	g g <sup>-1</sup>	$cf1$	0.19	This study
Ash-free dry mass to dry mass conversion	g g <sup>-1</sup>	$cf2$	0.60	This study
Ash-free dry mass to joules conversion	kJ g <sup>-1</sup>	$cf3$	22	(Goss-Custard, 1996)
Arrhenius temperature	K	$T_A$	5800	(van der Veer et al., 2006)
Reference temperature	K	$T_{ref}$	293.15	(van der Veer et al., 2006)
Rate of decrease at upper boundary	K	$T_{AH}$	31376	(van der Veer et al., 2006)
Rate of decrease at lower boundary	K	$T_{AL}$	45430	(van der Veer et al., 2006)
Lower boundary of tolerance range	K	$T_H$	296	(van der Veer et al., 2006)
Upper boundary of tolerance Range	K	$T_L$	275	(van der Veer et al., 2006)
Metabolic depression constant	-	$mdr$	-	(Table 3.8)
Half saturation coefficient – chlorophyll-a	mg chl m <sup>-3</sup>	$X_K$	-	(Table 3.8)
Half saturation coefficient – inorganic material	g m <sup>-3</sup>	$K_Y$	-	(Table 3.8)

### 3.3.4.5 Setup and run procedure

For all analyses (calibration, validation and sensitivity) the model was setup and run using the same approach. Simulations began at 1:00 am on March 1<sup>st</sup> with the average environmental conditions for this day and time ( $chl = 3.8 \text{ mg m}^{-3}$ ,  $spim = 28.8 \text{ g m}^{-3}$ ,  $nst = 3.1 \text{ °C}$ ,  $sst = 5.9 \text{ °C}$ , water level = 1.03 m). An individual (shell length = 0.026 cm, ash free dry mas =  $5.72 \cdot 10^{-8} \text{ g}$ ) was then grown for five years using average hourly environmental conditions (2015 – 2019) and variable elevations. Where stochasticity was included (validation), the initial size (ash free dry mass g) of the individual was drawn from a normal distribution (mean = 0.026 cm  $\pm$  0.00005 standard deviation).

### 3.3.5 DEB parameter estimates

The saturation coefficients, shape coefficient and metabolic depression rate are estimated in the calibration step. A non-linear optimisation method is used for parameter calibration in which parameter ranges are simultaneously and systematically searched for values which minimise the difference between observed and predicted values (Nelder and Mead, 1965). Data used for calibration are the average growth trajectories of shell length and tissue mass for each sample station.

Suspension feeders filter both digestible and indigestible particles from the water column. Excess particles can be rejected as pseudofaeces, but high particle concentrations reduce food ingestion rate by saturating the filtration process. The half saturation constants for organic and inorganic particle concentrations modulate this process and are both included in the calibration step. Ingestion rate is related to food density through a Holling type II functional response modified to take into account the negative effects of inorganic particles on filtration rate (Holling, 1965; Kooijman, 2006). The scaled functional response is given by:

$$f = \frac{x}{K'(Y) + x}$$

in which

$$K'(Y) = X_K \left( 1 + \frac{y}{K_Y} \right)$$

where  $x$  is the food concentration ( $\text{mg chl m}^{-3}$ ),  $y$  the inorganic particle concentration ( $\text{g spim m}^{-3}$ ),  $K'(Y)$  is the apparent half saturation constant ( $\text{mg chl m}^{-3}$ ),  $X_K$  is the organic particle half saturation constant ( $\text{mg chl m}^{-3}$ ) and  $K_Y$  the inorganic particle half saturation constant ( $\text{g spim m}^{-3}$ ). The value of  $f$  ranges between 0 and 1 according to the apparent half saturation constant, which, when equal to the food concentration results in an ingestion rate which is half the maximum ( $f = 0.5$ ). When the inorganic particle concentration is zero, the apparent half saturation constant is equal to the organic half saturation constant. As the inorganic particle concentration increases, the organic half saturation constant is increased according to the inorganic particle half saturation constant. The result is reduced ingestion rates in high particle concentrations. The shape coefficient ( $\delta_m$ ) describes the relationship between shell length and structural volume ( $v$ ) and is best estimated using somatic

mass (no gonads) and shell length data. Here, measurements of individual tissue mass include gonads, structure and reserves (i.e., not structure alone) and therefore cannot be used to estimate  $\delta_m$ . The shape coefficient was therefore included in the calibration step. The rate at which *M. edulis* can reduce its metabolism during periods of aerial exposure is thought to be between 0 and 100 %. Given the uncertainty and importance of the parameter, the metabolic depression rate was also included in the calibration step.

The four parameters are estimated via calibration against observed dry tissue mass, shell length and condition by minimizing the weighted sum of squared residuals using the formula:

$$ssr = \sum \frac{(sim - obs)^2}{(obs)^2}$$

where *sim* and *obs* represent the model and observed values for dry tissue mass and shell length.

The parameters are calibrated simultaneously using a fractional factorial design in which the parameter space (defined by the ranges in Table 3.5) is sampled using a Latin Hypercube. Latin Hypercube Sampling (LHS) belongs to the Monte Carlo class of sampling methods and requires fewer samples than simple random sampling to achieve the same accuracy (McKay et al., 2000). All parameter combinations generated using a Latin Hypercube ( $n = 200$ ) were run for each sample station ( $n = 38$ ) and model structure (basic and modified). The set which produced the minimum *ssr* was selected from each and the average of these values used as final estimates. Sampling was undertaken using the R package *nlr* which is designed to setup, run and analyse NetLogo model simulations from R (Salecker, 2020; Salecker et al., 2019; Wilensky, 1999).

Table 3.5 Parameter value ranges used for model calibration

Parameter	Symbol	Min	Max
Organic half saturation coefficient	$X_K$	0	5
Inorganic half saturation coefficient	$K_Y$	0	5
Shape coefficient	$\delta_m$	0.220	0.320
Metabolic depression rate	<i>mdr</i>	0	1

### 3.3.6 DEB parameter quality

Parameters were estimated as the average values from 38 calibration runs. The quality of parameter estimates was assessed for each model structure using linear regressions of observed and predicted values for shell length and dry tissue mass. Simulations were run for each sample station and model structure using the estimated parameter values (see section 3.3.9 Statical analysis).

### **3.3.7 DEB model accuracy**

The purpose of the model is to predict growth in response to intertidal environmental conditions, which relate to elevation. The accuracy at which each model structure predicted across shore levels (elevation) was tested using linear regressions of observed and predicted values for condition index ( $\text{g cm}^{-3}$ ) and von Bertalanffy growth parameters (annual growth coefficient  $K$  and maximum shell length  $L_{\infty}$ ). Simulations were run for each sample station and model structure (see section 3.3.9 Statical analysis).

### **3.3.8 DEB model sensitivity**

A global sensitivity analysis was used to measure how environmental drivers influence the growth of model individuals. When quantified, the variance that each contributes to growth rates can be used to prioritise data collection (i.e., which drivers require a detailed measure) and identify inputs which can be fixed (i.e., negligible influence), thereby reducing the data required and simplifying the model (Cariboni et al., 2007). The Morris screening method is used to rank the drivers according to their influence (Campolongo et al., 2007; Cariboni et al., 2007; Morris, 1991). The method returns rankings similar to the method of Sobol' which often serves as benchmark for other sensitivity analysis methods (Herman et al., 2013; Sobol', 1990). A detailed description of the Morris method is provided in the *general methods*, a brief description is given here.

The complete range of each environmental driver is screened using a one-step-at-a-time approach (OAT) in which each driver is repeatedly and randomly varied over a set number of levels across a predetermined range. The elementary effect of each driver is measured along all its respective trajectories and the respective mean ( $\mu$ ), absolute mean ( $\mu^*$ ) and the standard deviation ( $\sigma$ ) are used as sensitivity measures. The Morris method facilitates a measure of global sensitivity by

simultaneously varying all other input values, thereby relating the standard deviation to their influence. The analysis contains five environmental drivers and uses final dry tissue mass after 5 years for the model output (Table 3.6). The complete range for all environmental drivers is the default value (for each hourly time step)  $\pm$  average standard deviation.

Table 3.6 Input variables for Morris sensitivity analysis

Environmental input	Unit	Range
Suspended particulate inorganic matter	g m <sup>-3</sup>	$\pm$ 6.72
Chlorophyll-a	mg m <sup>-3</sup>	$\pm$ 1.08
Elevation	m	$\pm$ 0.77
Near surface temperature	°C	$\pm$ 2.41
Sea surface temperature	°C	$\pm$ 0.68

The Morris method produces multiple rankings of importance for each input parameter and the extent to which rankings agree is used to assess the quality and robustness of the analysis. The top-down coefficient of concordance (TDCC) provides a measure which emphasises agreement between high ranking parameters (Helton et al., 2005; Iman and Conover, 1987; Marino et al., 2008). The TDCC is calculated for each output variable by first ranking all input parameters by replicate and sensitivity measure. These ranks are then replaced by the corresponding Savage scores and the TDCC and p values are calculated (Helton et al., 2005; Marino et al., 2008; Savage, 1959). Values for the TDCC range between 0 and 1, those close to one ( $> 0.9$ ) indicate a high degree of reproducibility, which decreases with TDCC. The p-values for each TDCC (under the null hypothesis of zero concordance between parameter rankings) can be calculated using the statistics T (approximating a  $\chi^2$ -distribution with  $k-1$  degrees of freedom). The concordance between rankings is considered non-statistically significant for p-values higher than 0.05.

### 3.3.9 Statistical analysis

Statistical analyses are used to empirically describe the observed relationship between a) tissue mass, shell length and elevation, b) condition index and elevation, c) growth and elevation, and d) ash free and wet tissue mass. They are also used to assess both the quality of parameter estimates and the accuracy of model predictions. The relationship between tissue mass, shell length, and elevation was used to estimate growth trajectories of tissue mass at each sample station. Both the



shell length and tissue mass growth trajectories are used to calibrate the models and assess the quality of parameter estimates. The relationships between growth or condition and elevation were used to describe the extent to which growth and develop of *M. edulis* in Morecambe Bay relates to elevation. They are then used to assess the accuracy with which each model structure predicts across shore levels. The conversion factor for ash free to wet tissue mass are used in the DEB model.

The relationship between tissue mass (g), shell length (cm), and elevation (m) was estimated using generalized linear mixed models (GLMMs) in which tissue mass (continuous,  $\log_{10}$  transformed) was regressed against shell length (continuous,  $\log_{10}$  transformed), elevation (continuous) and the two-way interaction between them. The interaction between shell length and elevation was included to account for any potential accumulative difference associated with time. The model included date and station nested within site as random effects (repeated measures, Table 3.1).

The relationship between condition index ( $\text{g cm}^{-3}$ ) and elevation was also estimated using GLMMs whereby condition index (continuous) was regressed against elevation (continuous). The model also included date and station nested within site as random effects (repeated measures).

The conversion factor of wet tissue mass (g) to ash free dry tissue mass (g) was again estimated using GLMMs. Wet tissue mass (continuous,  $\log_{10}$  transformed) was first regressed against dry tissue mass (continuous,  $\log_{10}$  transformed) and dry tissue mass (continuous,  $\log_{10}$  transformed) was then regressed against ash free dry tissue mass (continuous,  $\log_{10}$  transformed). The product of the two coefficients was used as the conversion factor within the DEB model. The model again included date and station nested within site included as random effects (repeated measures).

All GLMMs were constructed and compared in R 4.0.3 using the lme4 package (Bates et al., 2015; Pinheiro et al., 2018; R Core Team, 2018).

Observed and simulated growth parameters for *M. edulis* were estimated by fitting data (age, length) from each sample station to a von Bertalanffy growth function (Beverton and Holt, 1958):

$$E[L/t] = L_{\infty} (1 - e^{-k(t-t_0)})$$

where  $L_t$  is the length at time  $t$ ,  $L_{\infty}$  is the asymptotic length,  $K$  is the growth coefficient, and  $t_0$  the hypothetical time at which length is 0. Observed values of  $K$  and  $L_{\infty}$  from each station were regressed against elevation using GLMMs with station nested within site as a random effect.

The quality of parameter estimates, and the accuracy of each DEB model structure was evaluated using linear regression between observed and predicted values. Parameter quality was assessed using values of shell length and dry tissue mass, model accuracy was tested using condition index, annual growth coefficient and maximum length. The intercept, slope, coefficient of determination ( $R^2$ ) and p value for slope = 1 of regressions are used to identify model bias, assess the consistency of predictions and quantify the amount of the variance explained (Piñeiro et al., 2008; Smith and Rose, 1995).

### **3.4 Results**

#### **3.4.1 Length and age**

The average trajectory of shell length with age for each station was required to estimate growth parameters and calibrate the DEB models. Growth was similar at all sites and the five year classes were identified during cohort analysis using length frequency histograms (Appendix A Figure 3.5-11). The average shell length of individuals was between 0.3 and 0.7 cm during their first year (year class 0), this increased to 3.1 cm in their second year, 4.2 to 4.4 in their third and 4.9 to 5.1 in the fourth and 5.3 to 5.8 in their fifth (Figure 3.2).

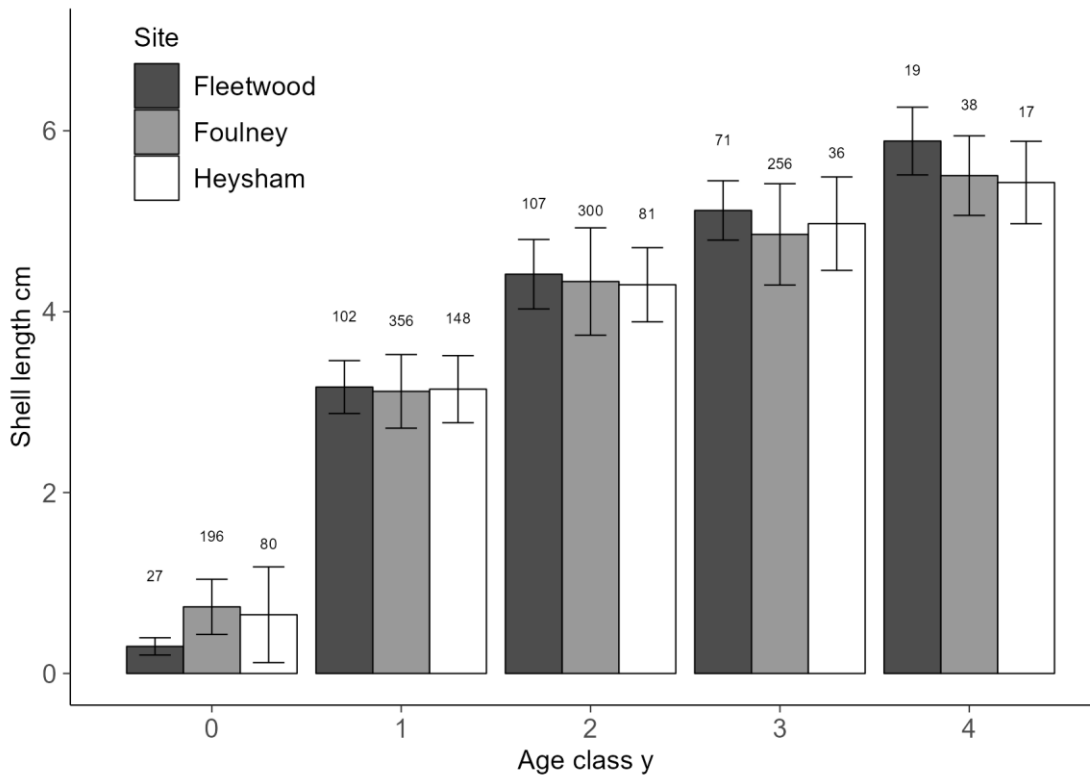


Figure 3.2 Shell length estimates (mean  $\pm$  standard deviation) of *M. edulis* in Morecambe Bay by year class and site. The numbers above each bar show the sample size. A shell length of < 3 cm in September and October was used as a reference for age 0 individuals.

### 3.4.2 Growth and condition

The relationship between individual tissue mass (g), shell length (cm) and elevation (m) was needed to estimate the average trajectory of tissue mass with age for each station. A GLMM was used to relate tissue mass (cm,  $\log_{10}$  transformed) to shell length (cm,  $\log_{10}$  transformed) and elevation (m). The initial model included both the main effects of, and the two-way interaction between shell length and elevation. Date (factor) and sample station (factor) nested within site (factor) were included with random intercepts (random effect). The interaction was not significant and the final model included just the main effects of shell length and elevation ( $F_{(1, 629.32)} = 2.085$ ,  $p = 0.149$ ). The model specifies that, for a given shell length, individuals collected from higher elevations have significantly smaller tissue mass compared to the those from low elevations ( $F_{(1, 36.90)} = 94.48$ ,  $p < 0.001$ , Figure 3.3, Table 3.7).

Table 3.7 ANOVA table for the response of dry tissue mass (g, log transformed) to elevation (m). Degrees of freedom (df), sum of squares (Sum Sq), F statistics (F value) and statistical significance (P value).

Term	Sum of squares	df	F value	P value
Log <sub>10</sub> shell length	465.41	(1, 551.27)	10273.31	< 0.001
Elevation	4.28	(1, 36.90)	94.483	< 0.001

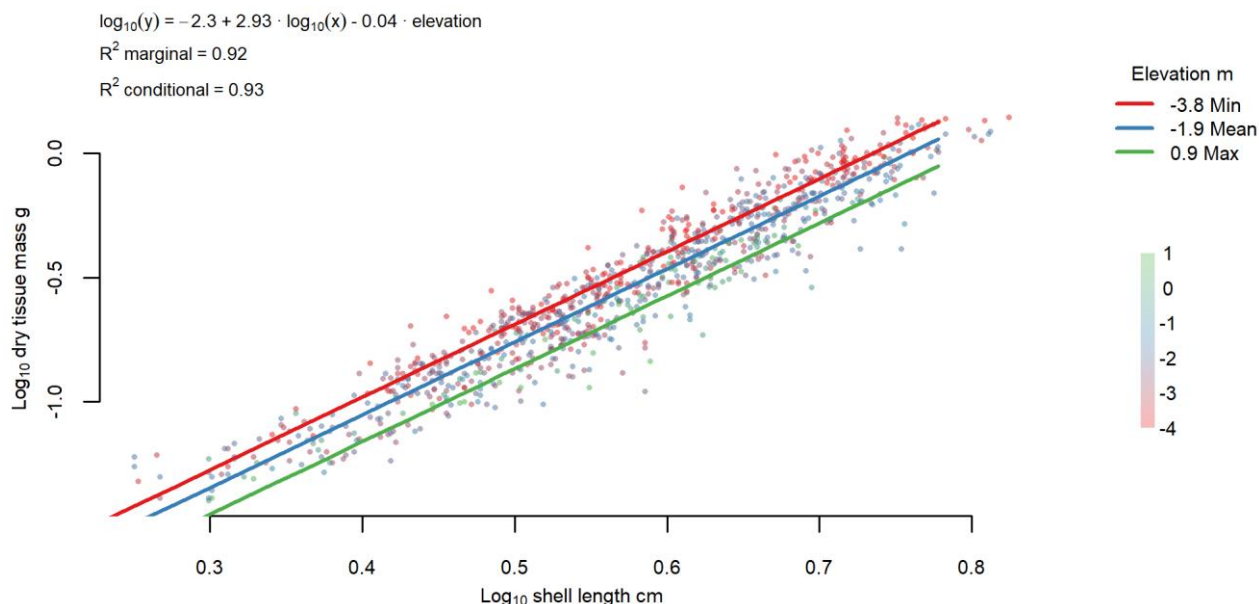


Figure 3.3 Relationship between dry tissue mass (g, log<sub>10</sub> transformed), shell length (cm, log<sub>10</sub> transformed) and elevation (height above sea level m) for *M. edulis* in Morecambe Bay 2017 - 2019. Lines represent glmm predictions for the min (red), mean (blue) and max (green) elevation.

The relationship between both von Bertalanffy growth parameters and condition index, and elevation was needed for each station to quantify the relationship between growth and elevation in Morecambe Bay. It was also needed to assess the ability of the DEB models to describe the relationship. The von Bertalanffy growth equation was fitted to length and age data from 38 sample stations in Morecambe Bay (Appendix A, Figure 3.14). The average condition index was calculated for all stations by age using individual biometric measurements.

A GLMM was used to investigate how growth parameters (annual growth coefficient  $K \text{ y}^{-1}$  and maximum shell length  $L_{\infty} \text{ cm}$ ) and condition index ( $\text{g cm}^{-3}$ ) varied in relation to elevation (m). The models included the main effect of elevation and station nested in site as a random effect. The condition index of *M. edulis* (mean  $0.006 \pm 0.00007$  s.e., range 0.005 – 0.007) significantly decreased ( $-0.0004$ ) with increasing elevation ( $R^2 \text{ marginal} = 0.40$ ,  $R^2 \text{ conditional} = 0.41$ ,  $F_{(1, 81.33)} = 62.90$ ,  $p < 0.001$ , Figure 3.4a). The annual growth coefficient of *M. edulis* (mean  $0.64 \pm 0.04$ , range 0.54 – 0.72) significantly decreased ( $-0.05$ ) with increasing elevation ( $R^2 \text{ marginal} = 0.19$ ,  $R^2 \text{ conditional} = 0.19$ ,

$F_{(1, 36)} = 8.40$ ,  $p < 0.05$ , Figure 3.4b). The maximum shell length of *M. edulis* (mean  $5.58 \pm 0.09$  s.e., range 3.00 – 6.73) also significantly decreased (-0.42) with increasing elevation ( $R^2$  marginal = 0.55,  $R^2$  conditional = 0.61,  $F_{(1, 36)} = 49.54$ ,  $p < 0.001$ , Figure 3.4c).

The growth and development of *M. edulis* therefore varied significantly in relation to shore level. After three years an individual (shell length 3.4 cm, dry tissue mass 0.46 g) growing at 1 m elevation (60 % aerial exposure) was approximately 50 % smaller than one (shell length 5.7 cm, dry tissue mass 1.03 g) growing at -4 m (0 % aerial exposure).

### 3.4.3 Environmental conditions

Between 2015 and 2019 the mean daily sea surface temperature within Morecambe Bay was  $10.4^\circ\text{C} \pm 4.4$  s.d. fluctuating seasonally between a minimum of  $4.1^\circ\text{C}$  and a maximum of  $19.9^\circ\text{C}$  (Figure 3.15c). The mean daily near surface air temperature was similar at  $10.4^\circ\text{C} \pm 4.6$  s.d., but seasonal fluctuations were larger with a minimum of  $-4.5^\circ\text{C}$  and a maximum of  $29.2^\circ\text{C}$  (Appendix A, Figure 3.15d). Chlorophyll-a generally followed a seasonal pattern with values in spring and summer remaining close to the overall mean, while autumn and winter values are relatively more variable. Concentrations ranged from 0.55 to  $10.80 \text{ mg m}^{-3}$  with an average of  $4.32 \text{ mg m}^{-3} \pm 1.4$  s.d. (Appendix A, Figure 3.15a). Suspended particulate inorganic matter also followed a seasonal pattern, with minimum values in spring and summer, and maximum values in autumn and winter. Mean suspended particulate inorganic matter was  $20.13 \text{ g m}^{-3} \pm 10.29$  s.d. with minimum and maximum values 0.04 and  $65.00 \text{ g m}^{-3}$ , respectively (Appendix A, Figure 3.15b). Mean tide height (Ordnance datum) was  $0.32 \text{ m} \pm 0.22$  s.d. with a minimum low water height of -4.84 m and maximum high water of 6.06 m (Appendix A, Figure 3.15e).

### 3.4.4 DEB parameter estimates

Four parameters were estimated via calibration on 38 growth trajectories (shell length, dry tissue mass) for each model structure (Table 3.8). These values were used in all further simulations.

Table 3.8 Calibrated parameter values (mean  $\pm$  standard error) for each model structure.

DEB model	Parameter	Symbol	Mean	Standard deviation
Basic intertidal	Shape coefficient	$\delta m$	0.273	0.01
Basic intertidal	Half-saturation coefficient (organic)	$X_K$	0.72	0.28
Basic intertidal	Half-saturation coefficient (inorganic)	$K_Y$	1.97	0.72
Modified intertidal	Shape coefficient	$\delta m$	0.265	0.01
Modified intertidal	Half-saturation coefficient (organic)	$X_K$	0.94	0.18
Modified intertidal	Half-saturation coefficient (inorganic)	$K_Y$	2.41	0.49
Modified intertidal	Metabolic depression rate	mdr	0.58	0.15

GLMMs were used to estimate conversion factors of wet tissue mass (g,  $\log_{10}$  transformed) to dry tissue mass (g,  $\log_{10}$  transformed) and dry tissue mass (g,  $\log_{10}$  transformed) to ash-free dry tissue mass (g, log transformed). The slope of each model was forced through zero (slope = 1 back transforms to 0 intercept) and date (factor) and station nested within site were included with random intercepts (random effect). The wet to dry tissue mass conversion was estimated to be  $0.19 \pm 0.0004$  s.e. and the dry to ash-free dry tissue mass  $0.60 \pm 0.007$  s.e. (Appendix A, Figure 3.13).

### 3.4.5 DEB parameter quality

The quality of parameter estimates was assessed for each model structure using linear regressions of observed and predicted values for shell length and dry tissue mass. Simulations were run for 5 years using average environmental conditions and station-specific values for elevation (Appendix A, Figure 3.16, 17). Both sets of estimated parameters (basic and modified) predicted shell length accurately (intercept = 0 and slope = 1) but the modified parameter set predicted tissue mass more accurately than the basic set which overestimated (intercept > 0) low values and underestimated high values (slope < 1). Both the intercept and slope from the modified parameter set were again no different from 0 and 1, respectively.

Table 3.9 Results from linear regressions comparing observed and simulated values of length (cm) and dry tissue mass (g) for *M. edulis* in Morecambe Bay. The regression intercept, coefficient (slope), significance values for intercept = 0 (p intercept), slope = 0 (p slope) and slope = 1 (p slope = 1), and the coefficient of determination ( $R^2$ ) are given for two DEB models. A basic intertidal DEB model in which individual metabolic rates remain constant during periods of aerial exposure, and a modified intertidal DEB in which individuals suppress metabolic rates during periods of aerial exposure.

Model	Variable	Intercept	Slope	p intercept	p slope	p slope = 1	$R^2$
Basic intertidal	Shell length (cm)	-0.05	1.01	ns	< 0.001	ns	0.95
	Dry tissue mass (g)	0.05	0.85	< 0.001	< 0.001	< 0.001	0.89
Modified intertidal	Shell length (cm)	-0.10	1.00	ns	< 0.001	ns	0.97
	Dry tissue mass (g)	0.02	0.95	ns	< 0.001	ns	0.93

### 3.4.6 DEB model accuracy

The accuracy at which each model structure predicts across shore levels was evaluated using linear regressions of observed and predicted values for condition index ( $\text{g cm}^{-3}$ ) and von Bertalanffy growth parameters (annual growth coefficient  $K \text{ y}^{-1}$  and maximum shell length  $L_{\infty}$  cm). Simulations were run for 4 years using average environmental conditions and station-specific values for elevation.

The modified intertidal DEB was more accurate when predicting across shore levels compared to the basic one, primarily due to better predictions for annual growth (Table 3.10, Figure 3.4). The basic structure consistently overestimated low values (intercept > 0) and underestimated high values of condition, maximum length and annual growth (slope < 1). The modified structure overestimated low values for condition and maximum length (intercept > 0), consistently overestimated high values for condition (intercept > 0 and slope = 1) and underestimated high values for maximum length (slope < 1). The modified structure accurately predicted values for annual growth (intercept = 0 and slope = 1).

Table 3.10 Results from comparisons of observed and simulated values of condition index, annual growth coefficient ( $K$ ) and maximum shell length ( $L_{\infty}$ ) using linear regressions. The regression intercept, coefficient (slope), significance values for intercept = 0 (p intercept), slope = 0 (p slope) and slope = 1 (p slope = 1), and the coefficient of determination ( $R^2$ ) are given for two DEB models. A

basic intertidal DEB model in which individual metabolic rates remain constant during periods of aerial exposure, and a modified intertidal DEB in which individuals suppress metabolic rates during periods of aerial exposure.

Model	Variable	Intercept	Slope	p intercept	p slope	p slope = 1	R <sup>2</sup>
Basic intertidal	Condition index	0.002	0.64	< 0.05	< 0.001	< 0.05	0.28
	Growth coefficient ( <i>K</i> )	2.562	-2.80	< 0.001	< 0.05	< 0.001	0.17
	Maximum length ( <i>L</i> <sub>∞</sub> )	3.066	0.46	< 0.001	< 0.001	< 0.001	0.53
Modified intertidal	Condition index	0.001	0.80	< 0.05	< 0.001	ns	0.32
	Growth coefficient ( <i>K</i> )	-0.348	1.72	ns	< 0.05	ns	0.16
	Maximum length ( <i>L</i> <sub>∞</sub> )	1.713	0.67	< 0.05	< 0.001	< 0.05	0.55

The relationship between values (observed and simulated) and elevation shows that while both model structures capture the observed decrease with increasing elevation found for condition and maximum length, the basic structure fails to capture the relationship for annual growth (Figure 3.4).

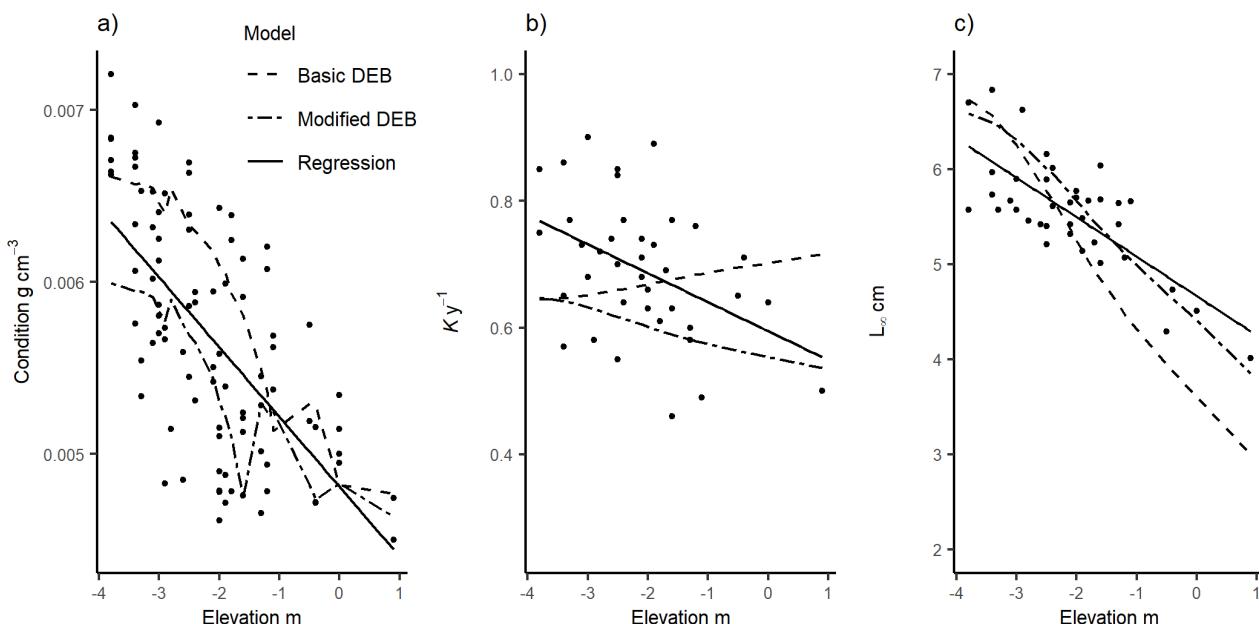


Figure 3.4 Comparison of observed (points) and simulated (lines) values for a) condition index  $ci \text{ g cm}^{-3}$ , b) annual growth coefficient  $K \text{ y}^{-1}$  and c) maximum shell length  $L_{\infty} \text{ cm}$  plotted against elevation  $m$  (aerial exposure). Solid lines represent the relationship estimated using linear regressions of observed values against elevation (condition index –  $F_{(1, 81)} = 62.9$ ,  $R^2$  marginal = 0.40,  $R^2$  conditional = 0.41,  $p < 0.001$ ,  $y = 0.0048 - 0.00041 \cdot x$ , annual growth coefficient –  $F_{(1, 36)} = 8.70$ ,  $R^2$  marginal = 0.19,  $R^2$  conditional = 0.19,  $p < 0.05$ ,  $y = 0.59 - 0.046 \cdot x$  and maximum shell length –  $F_{(1, 36)} = 49.3$ ,  $R^2$  marginal = 0.55,  $R^2$  conditional = 0.61,  $p < 0.001$ ,  $y = 4.67 - 0.41 \cdot x$ ). Dashed lines represent predictions from a basic intertidal DEB model in which individual metabolic rates remain the same during periods of aerial exposure. Two-dashed lines represent predictions from a modified intertidal DEB model in which individuals suppress metabolic rates during periods of exposure



### 3.4.7 DEB model sensitivity

The Morris method was used to rank environmental drivers of the DEB model in order of importance with respect to growth. The analysis was robust (TDCC = 0.99,  $\chi^2 = 179.61.68$ ,  $p < 0.001$ ) and results indicated that the influence of environmental drivers is monotonic (identical values for  $\mu$  and  $\mu^*$ ) and linear (values of  $\sigma$  are less than  $\mu$ ). Environmental drivers can be grouped into three categories; chlorophyll-*a* (positive) and suspended particulate inorganic matter (negative) had the greatest influence on growth, followed by sea surface temperature (positive) and elevation (negative). Changes in near surface temperature (negative) and had the smallest influence on growth (Table 3.11).

Table 3.11 Results from Morris sensitivity analysis of *M. edulis* growth to the variation of 5 environmental drivers. The mean ( $\mu$ ), absolute mean ( $\mu^*$ ), standard deviation ( $\sigma$ ) and the savage score of the elementary effects. Values are given for the all environmental inputs; chlorophyll-*a* ( $\text{mg chl m}^{-3}$ ), suspended particulate inorganic matter ( $\text{g spim m}^{-3}$ ), elevation (m), sea surface temperature (K), near surface temperature (K). The output used was dry tissue mass.

Parameter	Unit	$\mu$	$\mu^*$	$\sigma$	Savage score
Chlorophyll- <i>a</i>	$\text{mg m}^{-3}$	0.44	0.44	0.07	1.64
Suspended particulate inorganic matter	$\text{g m}^{-3}$	-0.41	0.41	0.08	2.28
Sea surface temperature	K	0.20	0.20	0.05	0.32
Elevation	m	-0.17	0.17	0.04	0.79
Near surface temperature	K	-0.04	0.04	0.02	0.52

### 3.5 Discussion

This study aimed to establish a Dynamic Energy Budget (DEB) model for simulating the growth and development of *M. edulis* in response to intertidal environmental conditions. The extent to which individual growth and condition of *M. edulis* in Morecambe Bay varies across shore levels was empirically described before two DEB model structures were assessed in their ability to simulate the observed relationship. Both condition and growth of *M. edulis* were observed to decrease with increasing shore levels. Simulating intertidal growth with no change to physiological rates during periods of aerial exposure (basic intertidal DEB) primarily affects individual size. When exposed, model individuals use energy (without replacement) from their reserve at the standard rate (relative to body size) which limits growth. While both DEB model structures predicted condition index well in relation to elevation, predictions of annual shell growth and maximum shell length were improved

when using a modified intertidal DEB model in which individuals reduce their metabolic rates during periods of aerial exposure.

*M. edulis* collected from higher elevations have lower relative tissue mass, an indication that they are under physiological stress. Intertidal individuals experience reduced feeding times and do not appear to compensate by increasing feeding rates during immersion (Bayne et al., 1988; Griffiths and Buffenstein, 1981). A decline in ingestion rate with increasing shore height is therefore expected but does not directly explain the difference in tissue mass between individuals of similar shell lengths. The difference might be more related to the reproductive cycle which is sensitive to both changes in food abundance and temperature (Duinker et al., 2008; Kautsky, 1982; Philippart et al., 2003). Gonad development is enhanced when food abundance is high and individuals can allocate a larger proportion of assimilated energy to reproduction (Duinker et al., 2008; Kautsky, 1982; Petes et al., 2007). Spawning frequency can also increase in response to environmental stress (e.g. aerial exposure) in an effort to reallocate energy from reproduction towards maintenance (Kluytmans et al., 1988; Petes et al., 2007). Individuals found at low shore levels might therefore be expected to maintain larger gonads compared to those at high shore levels, giving them a relatively larger body mass.

Average growth rates of *M. edulis* are expected to be reduced at higher shore levels due to reduced feeding times and additional physiological costs associated with being exposed at low tide (Buschbaum and Saier, 2001; Gillmor, 1982; Rodhouse et al., 1984; Spencer et al., 1978). Here, the amount by which growth is reduced is not a direct function of aerial exposure which suggests a mechanism by which individuals are compensated for the periods they cannot feed. It is unlikely that individuals living at high shore levels benefit from reduced competition (intra- or inter-specific) for food. The density of *M. edulis* is generally observed to peak at mid to high shore levels where predation rates are relatively low (McGrorty and Goss-Custard, 1991). It is more likely that normal physiological rates are temporarily reduced when individuals are exposed to the air (Tagliarolo et al., 2012; Widdows and Shick, 1985). For bivalves in general, metabolic depression is linked to slow growth and longevity (Philipp and Abele, 2010). Slow growing bivalves are also more resistant to environmental stress and can repair damage to tissue and shell more rapidly than faster growing ones (Ziuganov et al., 2000). Within intertidal habitats, slower growing and older *M. edulis* are found in the higher shore levels (Seed, 1969). Such individuals can also exhibit proportionally heavier shells (Baird and Drinnan, 1957).

Metabolic depression during periods of aerial exposure improved DEB model predictions across shore levels. Observed annual growth was however greater at low elevations compared to model

predictions and its relationship with increasing elevation is more pronounced (Figure 3.4b). The DEB model is therefore somehow limited at low elevations which suggests the observed environmental gradient is influenced by factors other than elevation. The model was most sensitive to changes in suspended particle concentrations and it might be that individuals experience relatively less competition for food at lower elevations where densities are low (Frechette and Bourget, 1985; Nielsen et al., 2016). *M. edulis* also influences sediment properties by depositing large amounts of pseudo-faeces which can readily be resuspended as inorganic particulate matter (de Fouw et al., 2020; van der Zee et al., 2012). In large aggregations of *M. edulis* there is likely a negative relationship between food quantity and quality, and population density, which is not present in the environmental drivers. Individuals living at low densities (i.e., low elevations) may experience relatively improved feeding conditions. Air temperature had little influence on model growth and may not be a suitable proxy for body temperature during periods of aerial exposure. At low tide, air temperature in the intertidal varies between microhabitats (e.g. under rocks) and can differ substantially from the ambient temperature (McFarland et al., 2015; Stillman and Somero, 2000). The body temperature of bivalves might regularly exceed any value observed at Morecambe Bay during the study period (Lima and Wethey, 2009; Monaco and McQuaid, 2018).

The incorporation of mechanisms which link the physiology of organisms to environmental conditions and gradients is an important step for models of coastal systems (Grimm et al., 2017; Grimm and Berger, 2016). The functioning of ecosystems and the services they provide emerge from the behaviours of individual organisms and their interactions with the environment (Carss et al., 2020; Hogan and Reidenbach, 2021; Rullens et al., 2019). Environmental gradients (biotic and abiotic) inherently structure estuarine systems to create mosaics of communities from which important goods and services emerge (Barbier et al., 2011). An important task for coastal managers is the sustainable management of multiple goods and services simultaneously using information gathered through labour intensive methods. If such information should emerge from and be sensitive to the model environment then predictions (e.g., management plans) become inherently more robust, particularly to novel scenarios (Wood et al., 2018).

The use of DEB models for simulating the growth of bivalves in response to environmental conditions (e.g., turbidity, salinity, aerial exposure) is common in aquaculture (Filgueira et al., 2018a, 2014; Maar et al., 2015; Saraiva et al., 2020). Natural bivalve populations play important provisioning and regulatory roles within coastal environments and DEB models are increasingly being used to assess their response to forecasted climate scenarios (Thomas et al., 2016; Thomas and Bacher, 2018). Despite their increasing popularity, DEB models are less frequently used to

develop conservation strategies (Lavaud et al., 2021). This is perhaps because a range of abstract parameters must be estimated, which in the past was difficult to accomplish (e.g., fewer available data). Where conservation is a priority, they are used to improve understanding of the target species and identify risks (e.g., climate change) or identify potential mitigation strategies (Arnall et al., 2019; Augustine et al., 2017; Haberle et al., 2020). Sustainable management of coastal systems will increasingly require predictions of responses to novel environmental conditions, for multiple species and at a range of spatial scales. DEB growth models can do just this and are therefore powerful and promising tools for informing coastal management.

### 3.6 Author contributions

Supervision: J. G. Hiddink and L. S. Cordes

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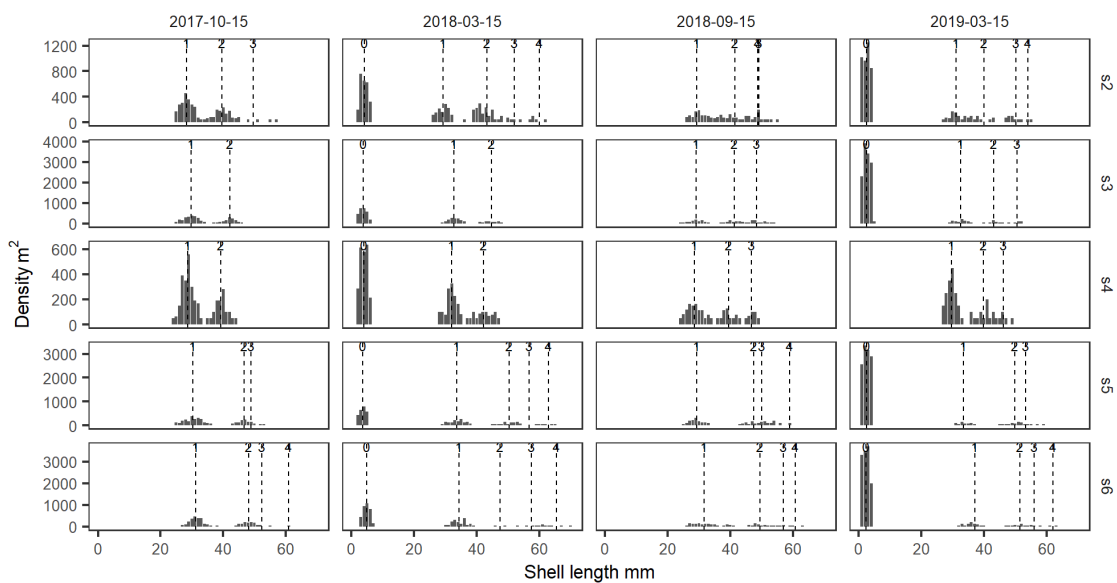


Figure 3.5 Size frequency distribution of *M. edulis* at five sampling stations in Morecambe Bay surveyed between May 2017 and Mar 2019

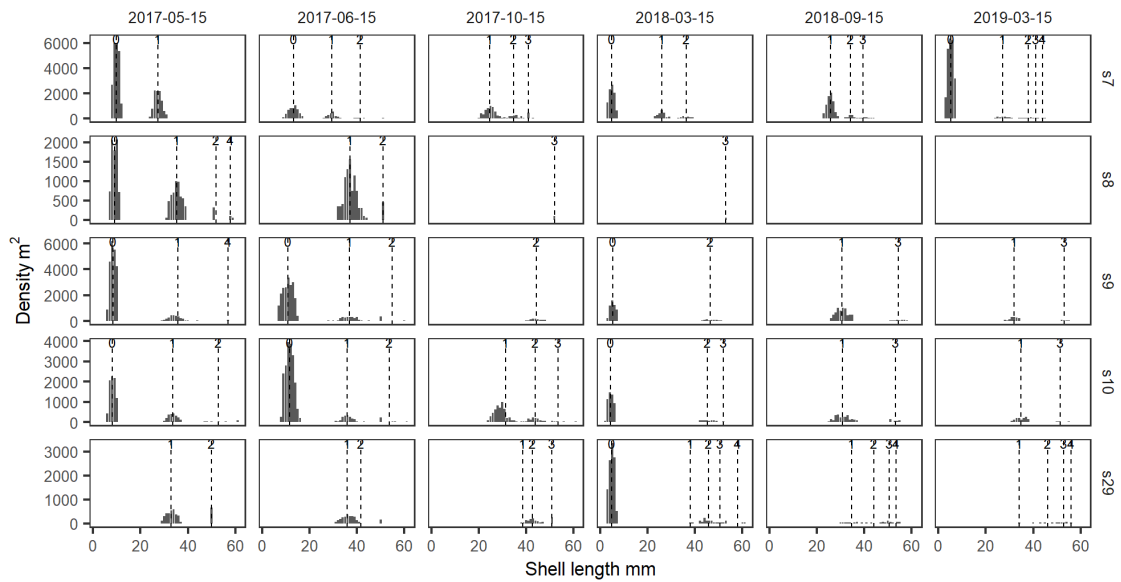


Figure 3.6 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019

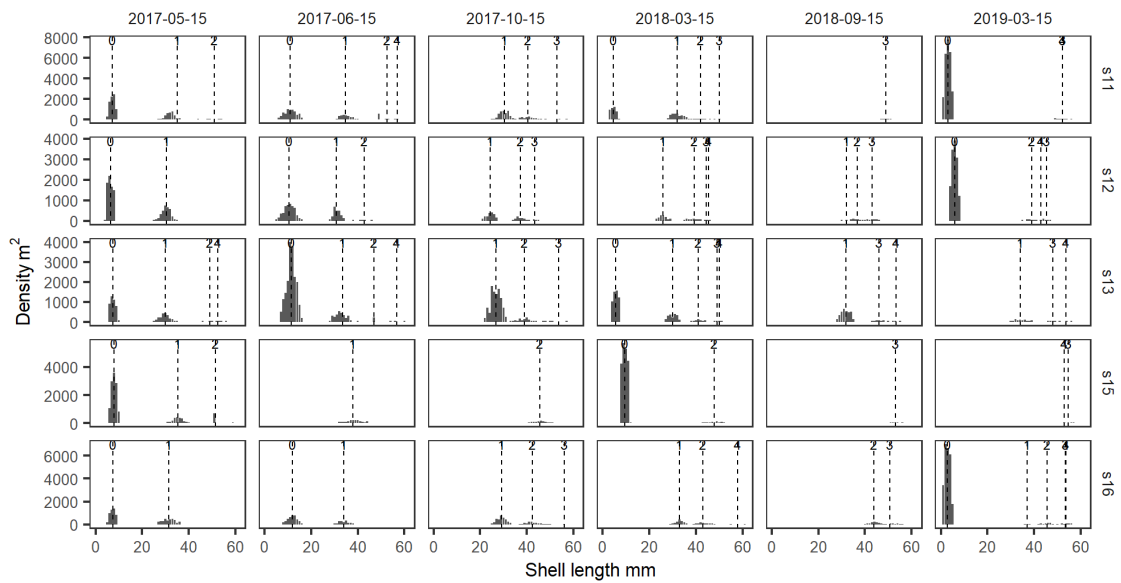


Figure 3.7 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019



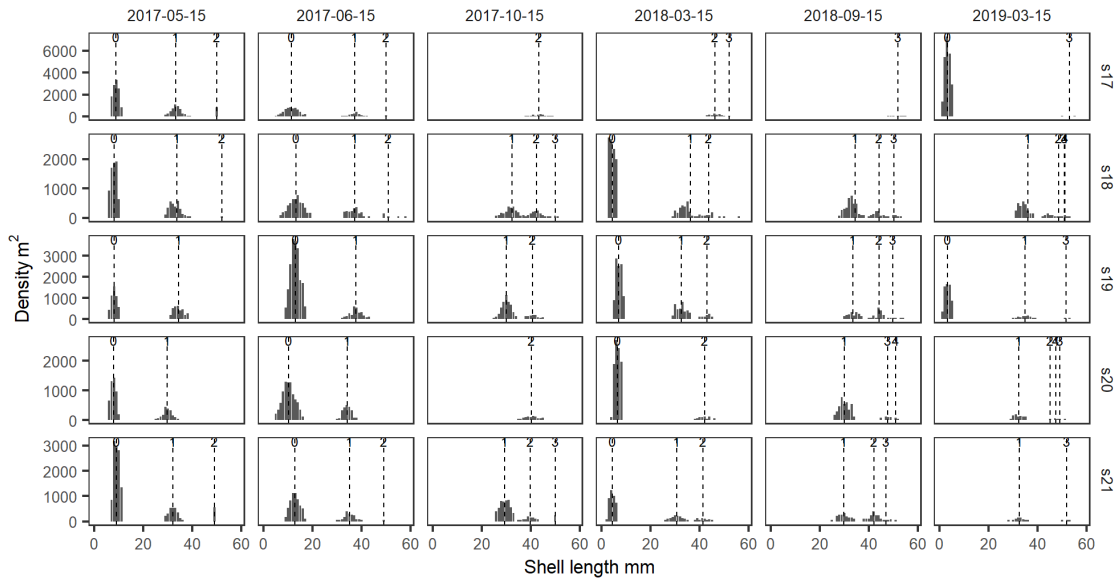


Figure 3.8 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019

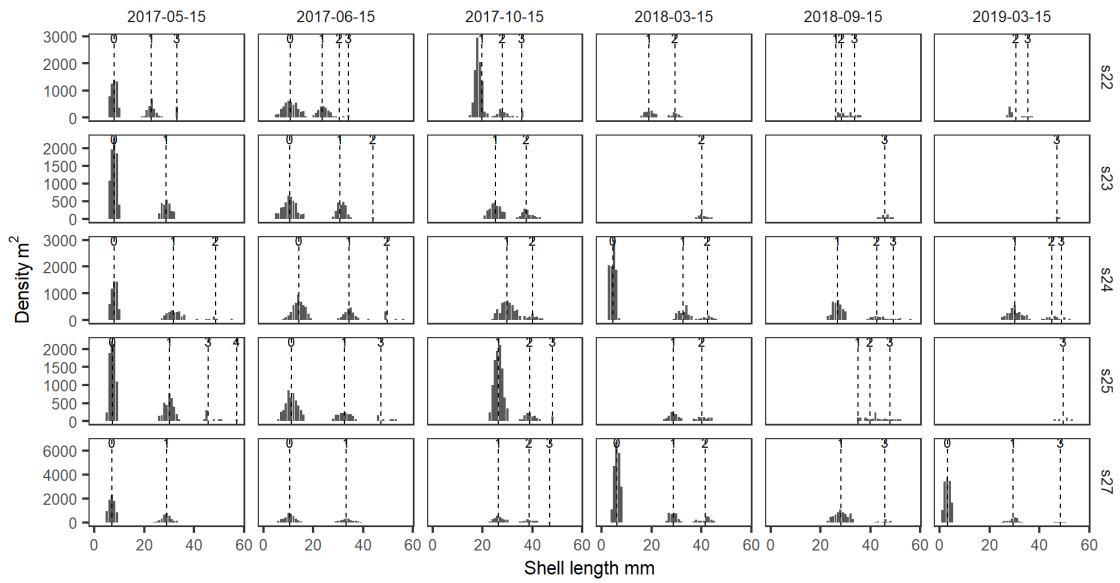


Figure 3.9 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019

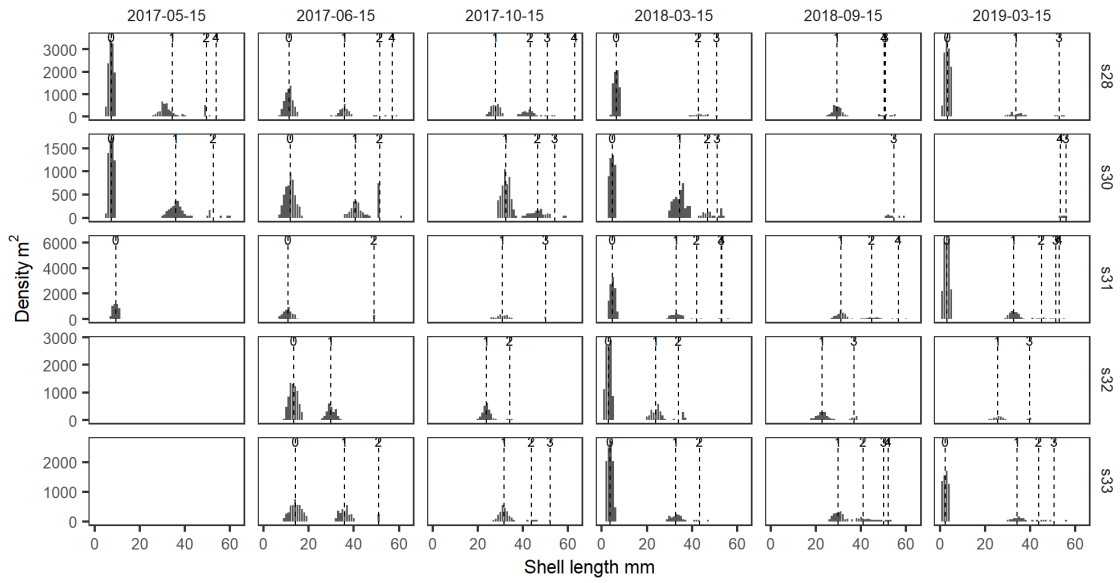


Figure 3.10 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019

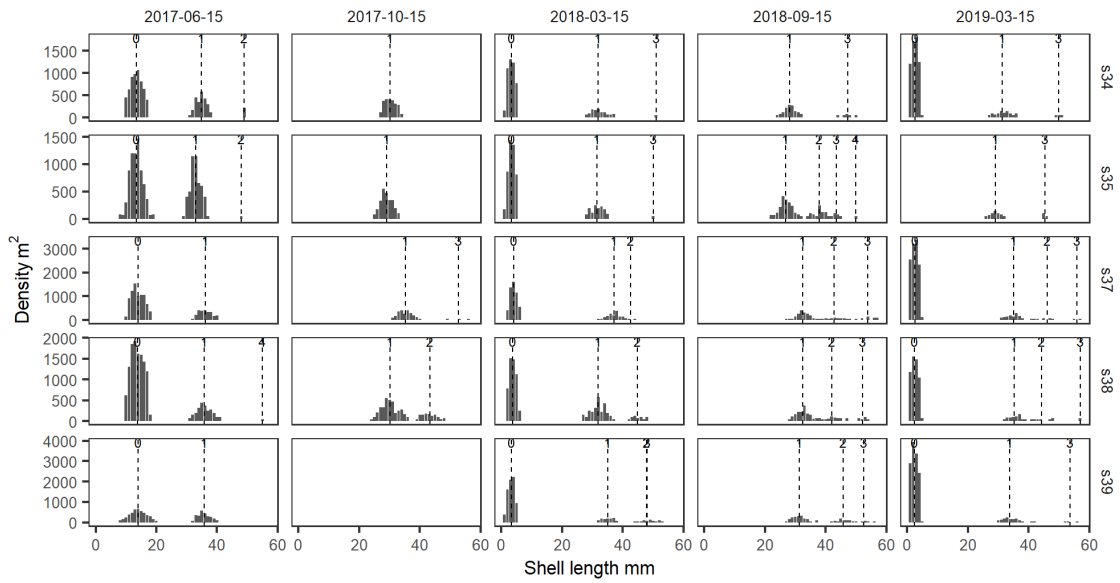


Figure 3.11 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019

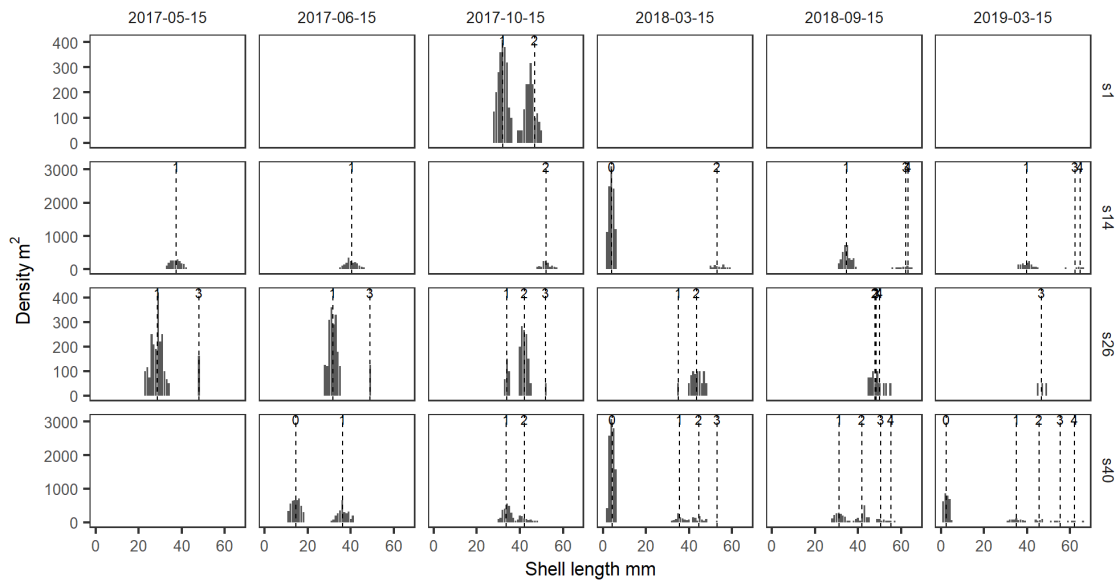


Figure 3.12 Size frequency distribution of *M. edulis* at five sampling stations sampling sites in Morecambe Bay surveyed between May 2017 and Mar 2019

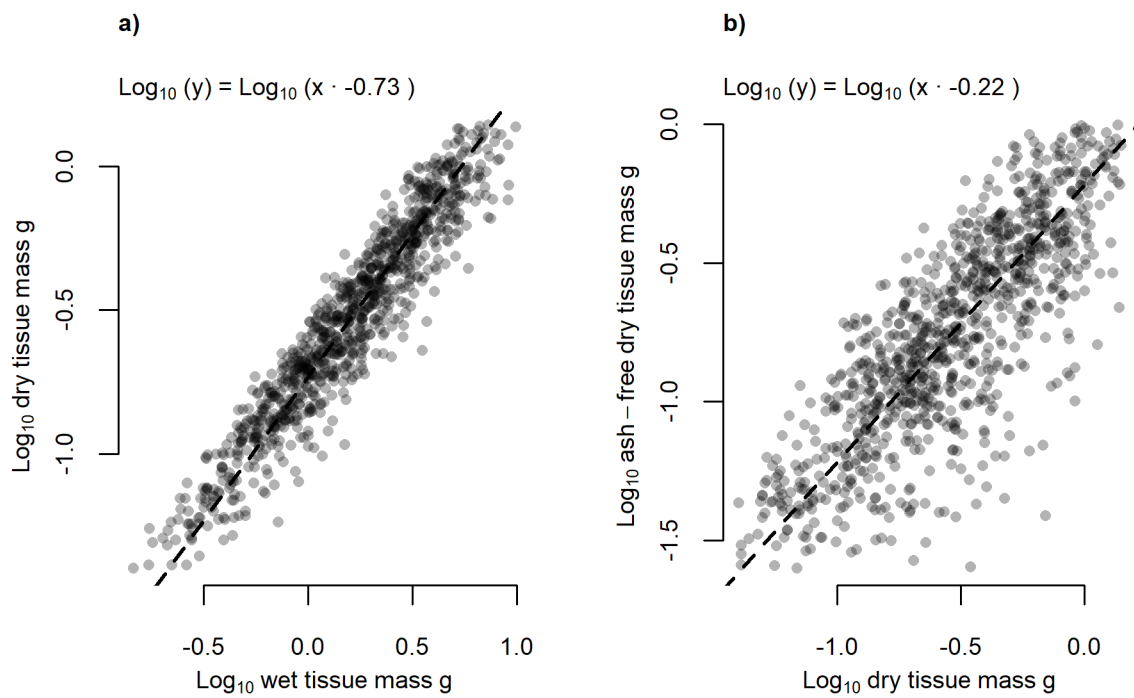


Figure 3.13 Linear regressions ( $\log_{10}$  transformed) of dry tissue mass (g) against wet tissue mass (g) and ash-free dry mass (g) against dry tissue mass (g). Equations are provided on the plots. Dashed lines represent model predictions.

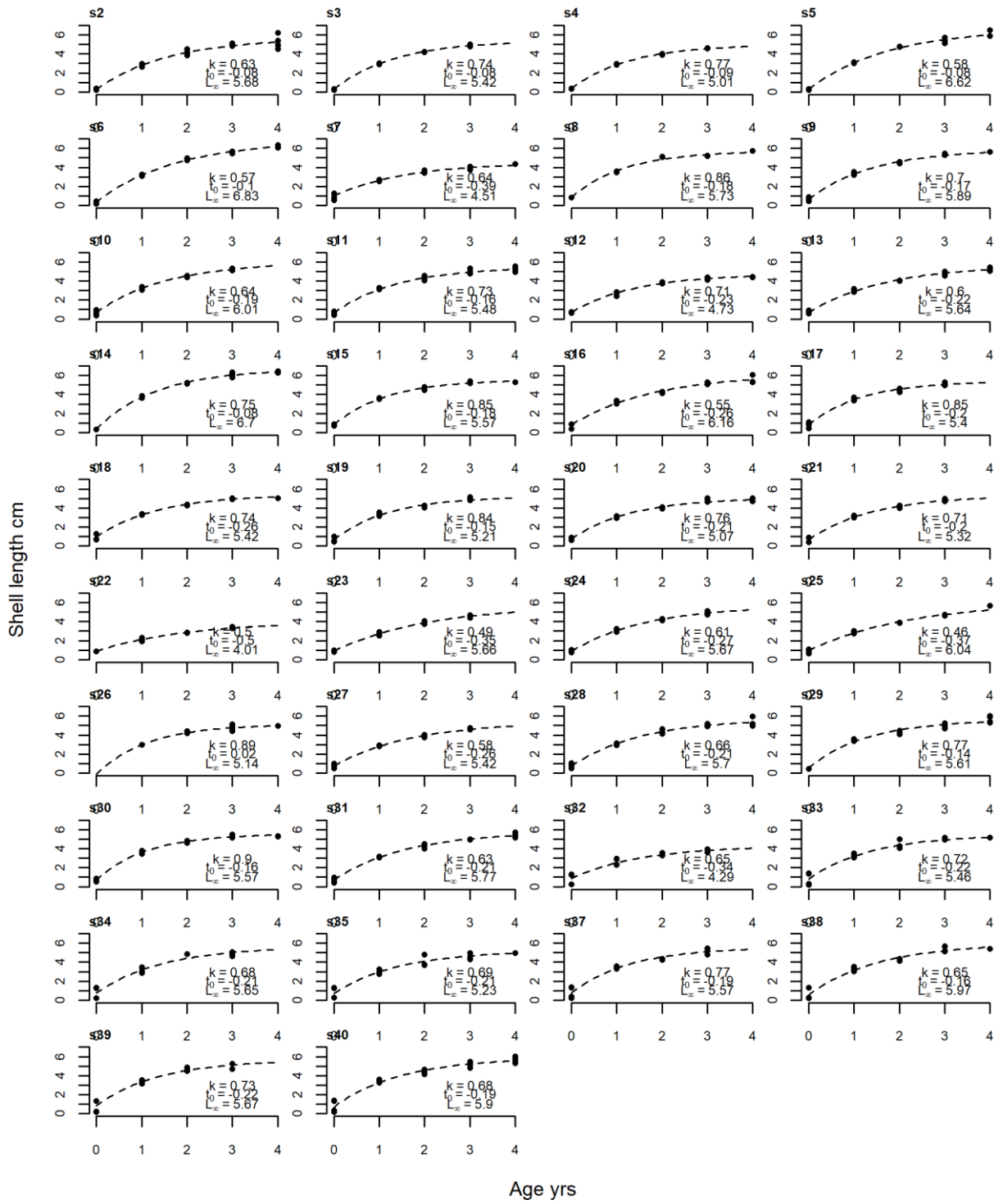


Figure 3.14 Von Bertalanffy growth curves fitted to length-at-age data of *M. edulis* from 38 stations in Morecambe Bay, UK.

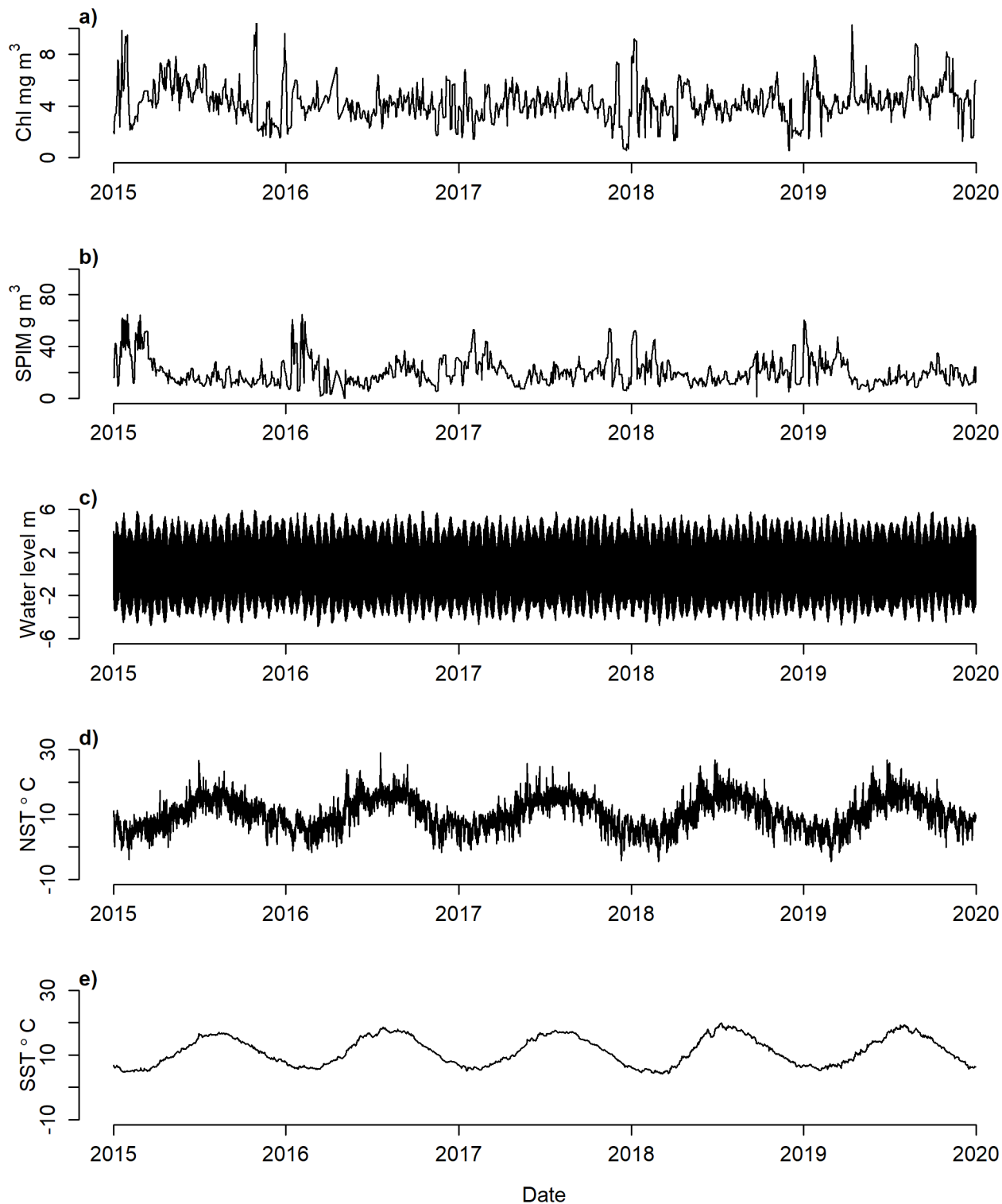


Figure 3.15 Environmental data used in DEB model. a) Chlorophyll-*a* concentration (mg m<sup>3</sup>) and b) Suspended particulate inorganic matter (g m<sup>3</sup>), as measured by SeaWiFS satellite, c) Tide height (m) taken from Heysham tide gauge (54.031643, -2.9211731), d) Near surface temperature (°C) taken from Walney Island weather station and e) Sea surface temperature (°C) measured by NOA-18 satellite, between 2017 and 2020 in Morecambe Bay.

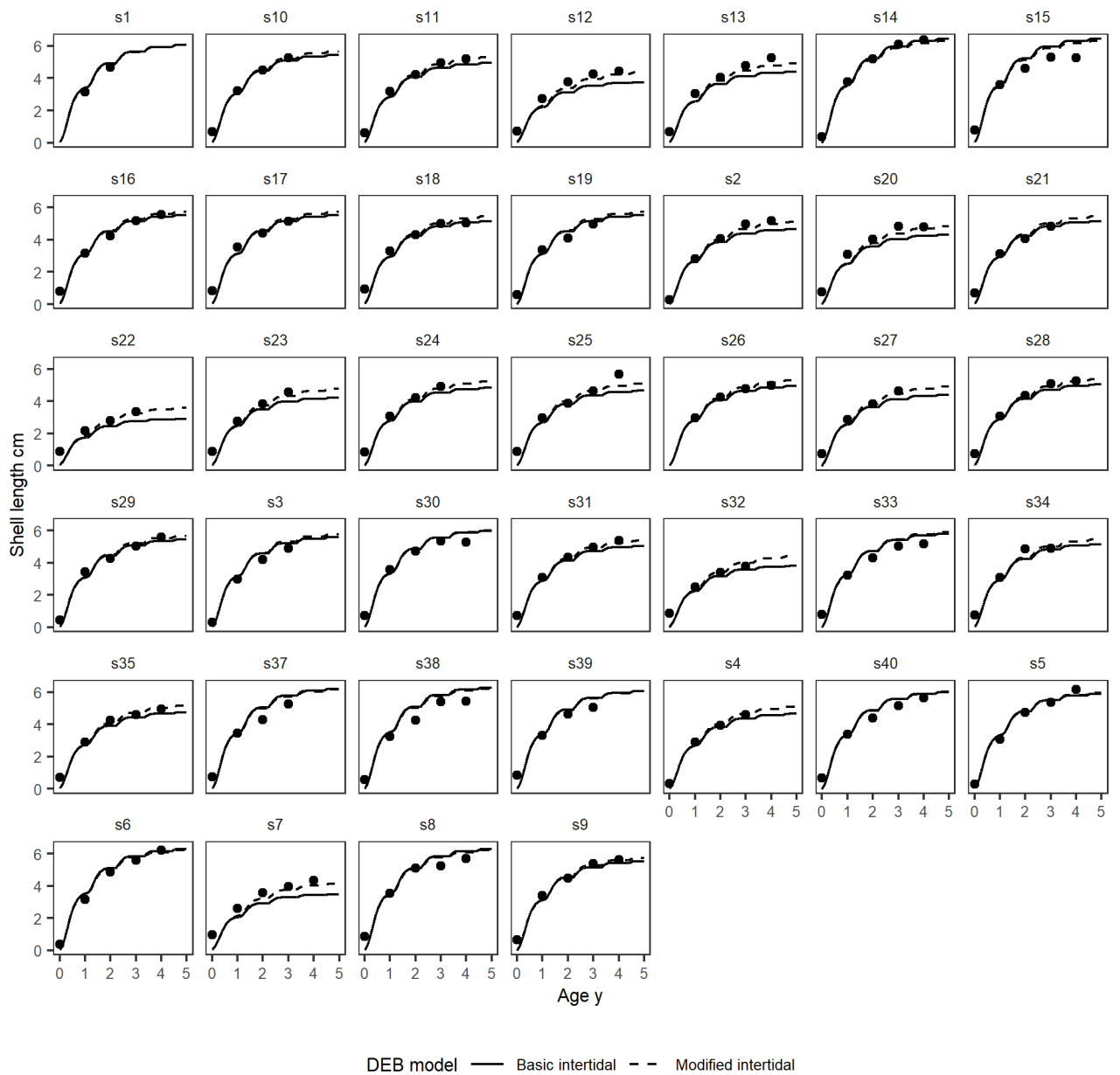


Figure 3.16 Predicted (solid line – basic DEB model structure, dashed line – modified DEB model structure) and observed (points) values of the shell length (cm) for intertidal *M. edulis* from 38 sample stations in Morecambe Bay, UK. Simulations begin on 1<sup>st</sup> March.

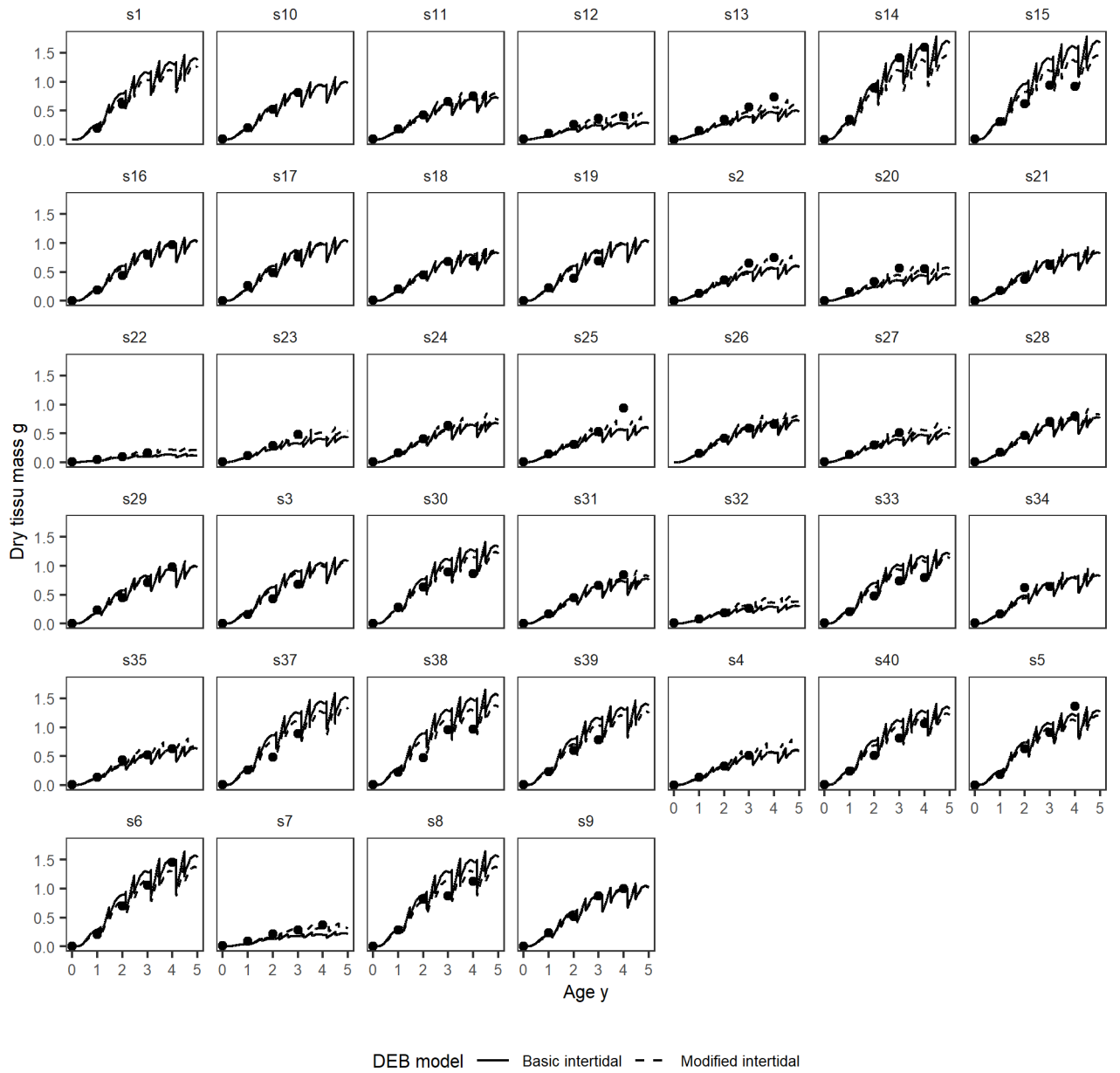


Figure 3.17 Predicted (solid line – basic DEB model structure, dashed line – modified DEB model structure) and observed (points) values of dry tissue mass (g) for intertidal *M. edulis* from 38 sample stations in Morecambe Bay, UK. Simulations begin on 1<sup>st</sup> March.

## 4. Towards the sustainable management of temperate intertidal bivalve reefs

A. Feather<sup>1</sup>, J. G. Hiddink<sup>1</sup>, L. S. Cordes<sup>1</sup>

1 - School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB

### 4.1 Abstract

A key challenge in environmental management is determining how to manage multiple ecosystem services simultaneously. Understanding interactions (trade-offs and synergies) between ecosystem services is key to their sustainable management but knowledge is limited within marine environments due to data scarcity and system complexity. Applying mechanistic models which link ecological processes to ecosystem functions and services can help improve understanding. A Dynamic Energy Budget (DEB) population model was used to quantify two provisioning ecosystem services (food provision direct to market, food provision via aquaculture) and four regulatory services (carbon removal, nitrogen removal, phosphorus removal, habitat provisioning) provided by an intertidal bivalve (*Mytilus edulis*) population. Their sensitivity to changes in environmental conditions was measured and trade-offs and synergies associated with their management were identified. Model populations acted as annual sinks for carbon, nitrogen and phosphorus. Regulatory ecosystem services were more sensitive to environmental change compared to provisioning services and changes to shore height, food availability and water temperature were most influential to all. Moderate trade-offs occurred between the provision of culture-size individuals for aquaculture and all regulatory services while strong synergies occurred between all regulatory services. Sustainable use of the ecosystem services delivered by intertidal bivalve reefs likely requires protection of reef substrate and restricted (quantity, spatial, temporal) harvesting strategies. Such strategies should enhance the functioning of estuarine systems and their resilience to climate change.

### 4.2 Introduction

As a result of direct and indirect human impacts the world's biodiversity is currently disappearing at unprecedented rates and its ecosystems (along with their functionality and services) are being degraded (Barnosky et al., 2011; McCauley et al., 2015; Worm et al., 2006). Preserving the organisms that maintain ecosystem functionality is an urgent priority but human activities habitually conflict



with conservation objectives (O'Hara et al., 2019; Young et al., 2005). Novel management approaches are needed which address the impact of human activities on ecosystem function (i.e., biodiversity loss) while allowing continued but sustainable use of goods and services (Delacámara et al., 2020; Levin et al., 2009). A major challenge is determining how to manage environments which deliver multiple ecosystem services simultaneously (Bennett et al., 2009). Relationships and interactions between ecosystem services are poorly understood and one service is generally prioritised at the expense of others (Raudsepp-Hearne et al., 2010). Research which aims to examine the interactions between ecosystem services and identify the driving mechanisms is required to help guide management practices (Qiu and Turner, 2013).

Coastal and estuarine habitats deliver many important ecosystem services (e.g., food provisioning, nutrient cycling, water purification, coastal defence, climate regulation) and their management is increasingly focussed on preserving and restoring ecological functioning (Barbier et al., 2011; Newton et al., 2018; Weinstein, 2008). Bivalve populations are an integral component of coastal ecosystems because of the functional role they play in delivering ecosystem services (Carss et al., 2020; Smaal et al., 2018; van der Schatte Olivier et al., 2018). The most recognizable provisioning (i.e., material products) service of bivalves from a human perspective is protein (i.e., tissue) and they are harvested for both direct consumption and cultivation (Kamermans and Capelle, 2019; Kraan et al., 2007). The species harvested for use in aquaculture (e.g., *Mytilus edulis*) are collected under market size (> 4.5 cm) and moved to sites where conditions favour growth (Dare and Edwards, 1976). Bivalve shells are usually discarded but as a source of calcium carbonate they are potentially valuable within the construction (e.g., cement production) and agricultural (e.g., fertilizer, livestock supplement) industries (Morris et al., 2019; van der Schatte Olivier et al., 2018). The regulating services (e.g., nutrient removal, carbon sequestration and storage, coastal protection, habitat provisioning) performed by bivalves relate to biotic and abiotic processes and their interaction with ecological and human populations. They are not material but instead improve the quality of human life by sustaining favourable environmental conditions (Mengist et al., 2020). As filter feeders, bivalves remove nutrients (e.g., nitrogen, phosphorus) from coastal waters and mitigate the symptoms (e.g., hypoxia, harmful algal blooms, fish mortality) of eutrophication (Rabalais et al., 2009). As calcifying organisms, carbon is stored in the form of calcium carbonate within bivalve shells which, as a sink in the carbon cycle, play a role in alleviating climate change (Bertolini et al., 2021; Dong et al., 2022; Jansen and van den Bogaart, 2020). Some bivalves (e.g., *M. edulis*) form complex, three-dimensional biogenic structures (i.e., reefs) which reduce wave energy and stabilise sediments (Ysebaert et al., 2018). Bivalve reefs protect adjacent habitats (e.g., saltmarsh) from

erosion and act as natural break waters which mitigate shoreline retreat (La Peyre et al., 2015; Scyphers et al., 2011; Walles et al., 2015). Reefs also provide important habitat for many species (e.g., invertebrates, fish, birds) thereby enhancing biodiversity (Craeymeersch and Jansen, 2019; Hogan and Reidenbach, 2021; Kent et al., 2016). Sustainable management of the ecosystem services delivered by bivalve populations (and the ecological processes underpinning them) is therefore economically, ecologically and socially complex.

The quantification of ecosystem services is fundamental information for their sustainable management. Many studies have quantified the ecosystem services delivered by bivalve populations and research is increasingly focused on their capacity to remove nutrients (e.g., nitrogen, phosphorus, carbon) and provide food (Gentry et al., 2020; van der Schatte Olivier et al., 2018; zu Ermgassen et al., 2020). Nutrient removal estimates are based on the balance between their nutrient accumulation (e.g., tissue, shell, biodeposits) and release (e.g., metabolic waste, decomposition, biocalcification), and the manner by which bivalves leave (e.g., death, harvest) the system (Filgueira et al., 2015; Petersen et al., 2018). Non-harvested individuals remain in the system until death when their tissue becomes part of the food web (i.e., predation, decomposition) and their shells and biodeposits become part of the substrate. The sediments beneath bivalve reefs accumulate large quantities of inorganic and organic nutrients in the form of shells and biodeposits (Fodrie et al., 2017; Lee et al., 2020; Westbrook et al., 2019). Nutrients buried within shallow, aerobic sediments gradually re-enter the system as shells (e.g., bioerosion, abrasion, dissolution) and biodeposits (e.g., decomposition, mineralization) degrade and decay (Van Broekhoven et al., 2014; Waldbusser et al., 2011). Their long term removal requires being buried to depths where the biochemical conditions (i.e., anaerobic, carbonate saturation) favour their preservation (Fodrie et al., 2017; Hu et al., 2011; Kellogg et al., 2014). Harvested individuals are removed (shell and tissue) from the system once they have grown to a target (e.g., market) size. The nutrients contained within their shell and tissue are therefore removed while those in biodeposits remain to decay or be buried. Estimates of nutrient removal for both natural and cultivated populations rarely include all fluxes, sources and sinks (van der Schatte Olivier et al., 2018). Studies of cultured populations focus on the accumulation of nutrients within harvested shell and tissue but often include only a subset of sources (e.g., respiration, biocalcification) associated with production (Rose et al., 2015; Turolla et al., 2020; van der Schatte Olivier et al., 2021). Studies of natural bivalve populations focus on the rates of burial and release from within sediments and often ignore the fluxes associated with living individuals (Fodrie et al., 2017; Hillman et al., 2021; Westbrook et al., 2019).

Managing the ecosystem services provided by bivalve populations is complicated due to the variety of services they deliver (Carss et al., 2020; van der Schatte Olivier et al., 2018; zu Ermgassen et al., 2020). Complex relationships can exist among services and human activities can produce positive (synergistic) and negative (trade-off) changes to the provision of multiple ecosystem services simultaneously (Bennett et al., 2009; Howe et al., 2014). The relationships are both shaped and linked by environmental drivers (biotic and abiotic) which influence provision rates and complicate management further (Dade et al., 2019). Drivers can relate to human activities (e.g., food production) or climatic variables (e.g., temperature) and can influence ecosystem service relationships in multiple (e.g., linear, interactions, nonlinear) ways (Bennett et al., 2009). Mild winters, food competition and increased predation are also known to influence annual biomass and are therefore potential drivers of trade-offs and synergies (Beukema et al., 2017b; Beukema and Dekker, 2005; Philippart et al., 2003). Work on the relationships and interactions between the ecosystem services provided by bivalves is still developing because marine environments are complex (e.g., multi-dimensional, extensive, connected) and appropriate (e.g., scale) data is scarce (Townsend et al., 2018). Areas of high bivalve density (e.g., reefs, cultures) are thought to be important for ecosystem service multifunctionality making them hotspots for interactions (Rullens et al., 2022, 2019; zu Ermgassen et al., 2020). Trade-offs are believed more common and likely to occur when provisioning ecosystem services are involved, synergies are less predictable but thought more likely to entail regulatory services (Howe et al., 2014; Lee and Lautenbach, 2016). Due to the complexity and extent of coastal systems, ecological models play a fundamental role in assessing the goods and services they provide (Bagstad et al., 2013; Rieb et al., 2017; Seppelt et al., 2011).

Biogenic reef habitats have experienced unprecedented global loss due to human activity, in particular unsustainable extraction (Beck et al., 2011; Cook et al., 2013; zu Ermgassen et al., 2020). Reef building species often occupy a restricted area (i.e., suitable substrate) from which multiple ecosystem services are expected to originate. They therefore require careful and measured management approaches to ensure balanced resource usage. This study aims to quantify and assess the sensitivity of six major ecosystem services provided by a population of intertidal *M. edulis* in Morecambe Bay, a large shallow estuary situated in Northwest England, UK. *M. edulis* is an epifaunal species which, in Morecambe Bay, forms extensive and dense, long-lived biogenic reefs (Beukema et al., 2017b, 2010; McGrorty et al., 1990). The reefs support internationally important wildlife populations (e.g., coastal birds) and are harvested commercially for both market and culture size individuals (Dare and Davies, 1975; Frost et al., 2021). Management of the *M. edulis* populations in Morecambe Bay primarily focuses on providing sufficient food for coastal birds while supporting

commercial fisheries. Evaluating the additional ecosystem services provided by *M. edulis* reefs will assist managers in developing an ecosystem approach to fisheries management.

A Dynamic Energy Budget (DEB) driven individual-based population model for intertidal *M. edulis* was calibrated, and its accuracy tested before being used to quantify the services delivered. The sensitivity of ecosystem services to environmental change was assessed via a global sensitivity analysis and their sensitive to each other was assessed using pairwise correlations. The results are used to a) establish whether *M. edulis* reefs act as sinks or sources for carbon, nitrogen and phosphorous, b) identify the environmental factors which most influence the provision of services and c) detect potential trade-offs and synergies associated with commercial harvest.

## **4.3 Methods**

### **4.3.1 Population model**

#### **4.3.1.1 Description**

The main purpose of the model is to predict ecosystem service provisioning rates of an intertidal *M. edulis* population in response to environmental change. The growth and development of individual *M. edulis* is simulated using a Dynamic Energy Budget (DEB) model which is coupled with a population model that incorporates birth and death.

The *M. edulis* population consists of  $i$  cohorts, each treated as  $n$  identical individuals born at the same time and growing under the same environmental conditions (Scheffer et al., 1995). The model environment is spatially gridded (250 m resolution) and operates at discrete hourly time steps. Each grid cell (here after patch  $j$ ) retains a unique elevation (m) which remains constant, and all patches share a common suspended particle concentration (organic and inorganic), temperature (air and water) and water level, which change at every time step. The water level dictates the state (submerged or emerged) of a cell, if it is greater than a cell's elevation the cell is submerged and if it is less the cell is emerged. A submerged cell depends on both water temperature and suspended particle concentrations to drive individual processes (e.g., growth, maintenance, reproduction). An emerged cell depends on air temperature and individual energy reserves to drive processes because suspended particles are set to zero (no intake).

A cohort is identified by its calendar week of birth, each cohort can occupy multiple patches and one patch can contain multiple cohorts. At each time step, for every patch and for every cohort, the model first calculates the average change to individual properties (e.g., tissue mass, shell length, reproductive state) relative to the environmental conditions of the patch, the size of the individual and the number of individuals present (food competition). It then calculates the change in the number of individuals within each cohort (mortality) and the change in the number of cohorts within the population (i.e., birth, death). The type of mortality an individual is vulnerable to depends on the patches state (submerged or emerged) and includes predation (including cannibalism), starvation, commercial harvest and three constant background rates (gamete, pelagic and benthic). An individual will spawn when conditions (individual and environmental) are optimal, and a new cohort is born after each spawning event. Cohorts die when either their size (i.e., constituents) or the condition of an average individual within them falls below a threshold value. The only density dependent process in the model is food competition which allows cohorts to compete for food based on their consumption rates and the number of individuals within them. Ecosystem service provision rates are calculated at every step and relate to individual growth rates, biomass (shell and tissue), and mortality. The model is written in NetLogo (Wilensky, 1999).

#### **4.3.1.2 Individual processes**

A Dynamic Energy Budget (DEB) model describes the rate at which an organism assimilates and utilizes energy for maintenance, growth and reproduction, as a function of the state of the organism and its environment (Kooijman, 2010; van der Meer, 2006). The present model is based on a standard DEB model for bivalves, parameterized for *M. edulis* and modified to include changes in metabolic rates due to intertidal conditions where individuals are periodically exposed to the air (Rosland et al., 2009; Van Haren and Kooijman, 1993).

Individuals are comprised of four state variables: structural body volume ( $v$ , cm<sup>3</sup>), reserve ( $es$ , J), maturity level ( $eh$ , J) and the reproduction buffer ( $er$ , J). The model assumes that *M. edulis* filters both organic and inorganic matter from the surrounding water. Organic matter can be converted to energy, but inorganic material is rejected and expelled as pseudo-feces. Ingestion rates depend on the concentration of particles in the water (organic and inorganic) and individual body size (surface area of gills). A functional response scales ingestion rates in relation to particle concentration and reduces ingestion rates when inorganic particle concentrations are high (Kooijman, 2006). Ingested

particles are assimilated and immediately stored in the reserve from which energy is mobilised to fuel all metabolic processes. A fixed fraction ( $k$ ) of the mobilised reserve is allocated to somatic maintenance and growth, the rest is used for maturity maintenance and maturation (juveniles) or reproduction (adults). The energy allocated to reproduction collects in the reproduction buffer, once the buffer becomes large enough (relative to the rest of its body) the individual can spawn, and the reproductive buffer is emptied. If an individual is ready to spawn it will only do so when environmental conditions are within the spawning thresholds. Individuals can use the reproduction buffer to cope with somatic maintenance costs (re-absorption of gametes) during periods of starvation. Ultimately, somatic structure can be used in response to starvation, causing the body to shrink, though maintaining the same shell length. If immature mussels experience starvation, they reduce their maturity level to cope with maturity maintenance (rejuvenation). A full description of the DEB model and parameter values is given in Chapter 3.

#### 4.3.1.3 Population processes

##### 4.3.1.3.1 Cohort birth and death

When cohorts are born their state ( $state_{cohort}$ ) is set to one, when they die, it is set to zero and they are no longer subject to model processes. An individual will spawn instantaneously once it is both in physiological condition (gonadosomatic index  $\geq 0.27$ ) and the environmental conditions are correct (sea temperature  $\geq 9.6^\circ\text{C}$ , submerged). One cohort is born after each spawning event, the number of gametes released is calculated for all spawning individuals ( $gamete_{cohort}$ ) by multiplying the energy stored within the reproductive buffer ( $er_{cohort}$ ) by the reproductive efficiency ( $kr$ ) and then dividing this by the energy content of a single gamete ( $es_b$ ). The number of gametes produced by all individuals is multiplied by the number of individuals each represents ( $n_{cohort}$ ) and then summed over the entire population ( $gamete_{global}$ ). An equal ratio of male to female is assumed (50:50) and the total number of gametes produced by the population is divided by two (Sprung, 1983; Sunila, 1981). Not all gametes released into the environment survive to become larvae and the initial gamete loss rate ( $z1$ ) groups all the mortality processes during this phase (e.g., egg viability, fertilization probabilities, dispersion). Initial gamete loss is instantaneous and afterwards all surviving gametes ( $n_{cohort\ new}$ ) begin life as a cohort of larvae and are evenly distributed across all patches (Equations 4.1).

Equations 4.1 Model equations for simulating cohort birth.

$$\text{gamete}_{\text{cohort}ij} = \begin{cases} \text{if environment conditions}_{\text{patch}j} = \text{spawning conditions} & \left\{ \frac{\text{er}_{\text{cohort}ij} \cdot \text{kr}}{\text{esb}} \right\} \\ \text{else} & \{0\} \end{cases}$$

$$\text{gamete}_{\text{global}} = \sum_{j=1}^{j_{\text{max}}} \sum_{i=1}^{i_{\text{max}}} \frac{\text{gamete}_{\text{cohort}ij} \cdot n_{\text{cohort}ij}}{2}$$

$$n_{\text{cohort new}} = \text{gamete}_{\text{global}} \cdot z1$$

$$\text{state}_{\text{cohort}ij} = \begin{cases} \text{if age} \geq 20 \text{ y or } n_{\text{cohort}ij} < 1 \text{ or } v < v_b \text{ or } eh < eh_b & \{0\} \\ \text{else} & \{1\} \end{cases}$$

Cohorts die when the number of individuals is  $< 1$ , if age  $> 20$  years (e.g., Seed, 1969) or if maturity level ( $eh$ ) or structural volume ( $v$ ) fall below their respective birth values ( $eh_b$  and  $v_b$ , Equation 4.2).

Equation 4.2 Model equation for calculating cohort death.

$$\text{state}_{\text{cohort}ij} = \begin{cases} \text{if age} \geq 20 \text{ y or } n_{\text{cohort}ij} < 1 \text{ or } v < v_b \text{ or } eh < eh_b & \{0\} \\ \text{else} & \{1\} \end{cases}$$

#### 4.3.1.3.2 Mortality

The number of individuals within each cohort ( $n_{\text{cohort}}$ ) and patch is calculated at every step according to multiple mortality types (Equation 4.3):

Equation 4.3 Model equation for calculating cohort mortality.

$$n_{\text{cohort}ij} = n_{\text{cohort}ij} - m_{\text{pelagic}ij} - m_{\text{ingestion}ij} - m_{\text{benthic}ij} - m_{\text{starvation}ij} - m_{\text{predation}ij} - m_{\text{harvest}ij}$$

Simulating the growth and development of bivalves during their larval phase is not within the scope of the present model because additional DEB parameters are required (Rico-Villa et al., 2010; Thomas et al., 2011). Instead, the pelagic, larval phase is simplified such that larvae begin life at settlement size (0.026 cm) and are instantly distributed evenly over all patches where they exist

without feeding (no growth or development) for 28 days. During this time, they are considered pelagic and are subject to a constant pelagic loss rate ( $z2 \text{ h}^{-1}$ ) which groups all common mortality processes thought to occur throughout the larvae phase (e.g., dispersion, predation, Equation 4.4):

Equation 4.4 Model equation for calculating larvae mortality.

$$m_{pelagic_{ij}} = \begin{cases} \text{if location} = \text{pelagic} \{z2 \cdot n_{cohort_{ij}}\} \\ \text{else} \{0\} \end{cases}$$

Larvae are also subject to cannibalism if the benthic constituents of their patch are feeding. Cannibalism is variable and depends on the combined filtration rate of all benthic individuals found on the patch. The benthic individuals are however simultaneously ingesting organic particles and the larvae concentration is first converted to mg chlorophyll-*a*  $\text{m}^{-3}$  to recalculate the local food concentration and individual intake rates. The ratio of larvae to organic particles is used to calculate the number of larvae consumed (Equations 4.5).

The chlorophyll-*a* content ( $chl_{content} 6.22 \times 10^{-6} \text{ mg}$ ) of each larvae is summed by cohort and patch, converted (using patch area and depth) to  $\text{mg m}^{-3}$  ( $chl_{cohort}$ ) and added ( $chl_{patch}$ ) to each patch's current chlorophyll-*a* concentration ( $chl_{global}$ ). The clearance rate of individual cohorts ( $cr_{cohort}$ ) is the product of the maximum clearance rate ( $crm$ ), a Holling type II function ( $f$ ), individual surface area ( $v^{2/3}$ ) and an Arrhenius temperature function ( $tc$ ).  $f$  consists of the chlorophyll-*a* concentration ( $x$ ), the half saturation coefficient ( $k$ ), the apparent half saturation coefficient ( $ky$ ) and the suspended inorganic particle concentration ( $y$ ).  $tc$  is calculated using the reference ( $t1$ ), Arrhenius ( $ta$ ) and current ( $t$ ) temperature. The patch clearance rate ( $cr_{patch}$ ) is the sum of its benthic constituents which is then applied to  $chl_{patch}$  to calculate the patch filtration rate. The number of larvae in each cohort ( $n_{cohort}$ ) is then reduced by the patch filtration rate relative to all other cohorts of larvae on the patch ( $n_{patch}$ ) and the ratio of larvae chlorophyll-*a* ( $chl_{cohort}$ ) to background chlorophyll-*a* ( $chl_{patch}$ ):



Equations 4.5 Model equations used to calculate cannibalism mortality.

$$f = \frac{x}{x + k \left(1 + \frac{y}{ky}\right)}$$

$$tc = e^{\left(\frac{ta}{t} - \frac{ta}{\tau}\right)}$$

$$cr_{\text{cohort}_{ij}} = crm \cdot f \cdot v_{\text{cohort}_{ij}}^2 \cdot tc$$

$$chl_{\text{cohort}_{ij}} = \begin{cases} \text{if location} = \text{pelagic} & \left\{ \frac{chl_{\text{content}} \cdot n_{\text{cohort}_{ij}}}{\text{depth}_j \cdot \text{area}_j} \right\} \\ \text{else} & \{0\} \end{cases}$$

$$chl_{\text{patch}_j} = chl_{\text{global}} + \sum_{i=1}^{i_{\text{max}}} chl_{\text{cohort}_{ij}}$$

$$cr_{\text{patch}_j} = \begin{cases} \text{if water level} > \text{elevation}_j \text{ and } \text{location}_i = \text{benthic} & \left\{ \sum_{i=1}^{i_{\text{max}}} cr_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}} \right\} \\ \text{else} & \{0\} \end{cases}$$

$$m_{\text{ingestion}_{ij}} = cr_{\text{patch}_j} \cdot chl_{\text{patch}_j} \cdot \left( \frac{chl_{\text{cohort}_{ij}}}{chl_{\text{patch}_j}} \right) \cdot \left( \frac{n_{\text{cohort}_{ij}}}{n_{\text{patch}_j}} \right) \cdot \left( \frac{1}{chl_{\text{content}}} \right)$$

In Morecambe Bay direct settlement (primary) after spawning is rare and the size at settlement is generally > 0.15 cm (Dare, 1976). It is believed that when larvae first attach (at 0.026 cm) it is to algal or hydroid substrate elsewhere in the bay, from which they detach once they have outgrown the temporary substrate. Therefore after 28 days the surviving larvae become postlarvae and begin to feed and grow. During this time, they are considered attached to hydroids and submerged, and remain so until they grow to > 0.15 cm. At this point they are considered part of the intertidal population and are subject to intertidal processes (i.e., exposure to air).

Background benthic loss ( $z3 \text{ h}^{-1}$ ) begins once larvae have settled and is constant for the algal and benthic population. It accounts for all possible natural causes of death except harvest and predation by predators represented in the model (e.g., water currents, storms, disease, Equation 4.6).

Equation 4.6 Model equation used to calculate benthic mortality.

$$m_{\text{benthic}ij} = \begin{cases} \text{if location}_{\text{cohort}ij} = \text{benthic or hydroid} \{z3 \cdot n_{\text{cohort}ij}\} \\ \text{else } \{0\} \end{cases}$$

Food competition is a density dependent process in which food is shared locally by all individuals. Each patch has a potential filtration rate based on the local environmental conditions, and the size and number of the resident benthic individuals. If the amount of food in the local environment is less than the patches potential filtration rate, the food is redistributed among the patch residents based on their relative potential filtration (i.e., individuals with the greatest potential filtration are allocated more food). Frequent starvation can result in individuals reducing both their size and maturity level to cope with maintenance costs (Cleuvers et al., 1997; Vanoverbeke, 2008). While a model individual's maturity level and structural volume remain greater than the values given at birth, the effects of starvation are reversible without any physiological consequences. If maturity level and structural volume fall below their respective birth values, the starvation effects become irreversible, and the individual (and all its constituents) will die. The starvation loss rate ( $s1 \text{ h}^{-1}$ ) prevents the sudden death of many individuals by simulating a population level response to periods of starvation. An individual's energy reserve ( $es_{\text{cohort}}$ ) is scaled (*scaled reserves* $_{\text{cohort}}$ ) to its maximum potential ( $em_{\text{cohort}}$ ) based on the individuals' size. Starvation is defined as periods when *scaled reserves* $_{\text{cohort}}$  falls below a critical value ( $s2, 0.1$ ). If individuals are in poor physiological condition (*scaled reserves* $_{\text{cohort}} < s2$ ) they experience an increased mortality rate ( $s1 \text{ h}^{-1}$ ) which accounts for the possible differences between individuals (e.g., local food concentration). The starvation loss rate is inversely linked to reserve density so that individuals in the poorest condition are more likely to starve (Martin et al., 2013a, Equations 7). Starvation is not constant, but only occurs during periods when food is limited. Starvation caused by the overcrowding of juveniles is thought to play an important, regulatory role in the population dynamics of marine invertebrates by reducing population density after large peaks in recruitment (Goser and Ratte, 1994; Martin et al., 2013; Preuss et al., 2009).

Equations 4.7 Model equations for calculating starvation mortality.

$$\text{scaled reserves}_{\text{cohort}_{ij}} = \frac{eS_{\text{cohort}_{ij}}}{em_{\text{cohort}_{ij}}}$$

$$m_{\text{starvation}_{ij}} = \begin{cases} \text{if scaled reserves}_{\text{cohort}_{ij}} < s2 \{s1 \cdot (1 - \text{scaled reserves}_{\text{cohort}_{ij}})\} \\ \text{else } \{0\} \end{cases}$$

The main predators of *M. edulis* represented in the model are *Crangon* (brown shrimp), *Carcinus maenas* (shore crab), *Asterias rubens* (common sea star), *Haematopus ostralegus* (Eurasian oystercatcher), *Somateria mollissima* (common eider), *Calidris canutus* (red knot) and *Larus argentatus* (herring gull). For each species of model predator ( $p$ ), the *intake rate* (g AFDM  $h^{-1}$ ) of an average sized individual and the number of individuals present ( $n_{\text{predator}}$ ) gives the mortality rate applied to each cohort and patch. Each predator species occurs seasonally, has a preferred size range and is restricted to certain environmental conditions. A cohort ( $a_{\text{cohort}}$ ) and patch ( $a_{\text{patch}}$ ) are available to predators if they are within the preferred size range and environmental conditions are correct (i.e., low or high tide). Each respective predator-specific mortality rate is applied to all available algal and benthic individuals. The mortality rates are distributed between these individuals in proportion to their relative abundance ( $n_{\text{patch}}$ ). All predator sizes, intake rates, preferred prey size ranges and dietary information are given (Table 4.6, Equations 4.8).

Equations 4.8 Model equations for calculating predation mortality.

$$a_{\text{cohort}_{ijp}} = \begin{cases} \text{if minimum size preference}_p \geq \text{shell length}_{ij} \geq \text{maximum size preference}_p \{1\} \\ \text{else } \{0\} \end{cases}$$

$$a_{\text{patch}_{jp}} = \begin{cases} \text{if environmental conditions}_j = \text{environmental conditions}_p \{1\} \\ \text{else } \{0\} \end{cases}$$

$$n_{\text{patch}_{jp}} = \sum_{i=1}^{i_{\text{max}}} a_{\text{cohort}_{ijp}} \cdot n_{\text{cohort}_{ijp}}$$

$$m_{\text{predation}_{ij}} = \sum_{p=1}^{p_{\text{max}}} \text{intake rate}_p \cdot \left( \frac{n_{\text{cohort}_{ijp}}}{n_{\text{patch}_{jp}}} \right) \cdot \left( \frac{1}{\text{AFDM}_{ijp}} \right) \cdot n_{\text{predator}_{jp}} \cdot a_{\text{cohort}_{ijp}} \cdot a_{\text{patch}_{jp}}$$

All benthic individuals are subject to commercial harvest ( $\% h^{-1}$ ) once they have grown to  $> 2$  cm. There are two harvest methods ( $h$ ), the harvest of consumer size individuals ( $\geq 4.5$  cm) occurs only by hand while the population is emerged. The harvest of culture size individuals (2 – 4 cm) occurs both by hand and boat and can therefore take place while the population is emerged and submerged. All harvesting is restricted to daylight hours when all commercial fisheries activity in

Morecambe Bay must take place. The harvest of undersize individuals via boat is also restricted to an area of 16.5 ha during periods of high tide and when water depth > 5m. A patch ( $a_{patch}$ ) is available for harvest when environmental conditions are correct, and a cohort ( $a_{cohort}$ ) is available for harvest when it is the correct size. The harvest rates are distributed between all individuals in proportion to their relative abundance ( $n_{patch}$ , Equations 4.9).

Equations 4.9 Model equations for calculating harvest mortality.

$$a_{patch_{jh}} = \begin{cases} \text{if patch conditions}_j = \text{harvest conditions}_h \{1\} \\ \text{else } \{0\} \end{cases}$$

$$a_{cohort_{ijh}} = \begin{cases} \text{if minimum harvest size}_h \geq \text{shell length}_{ij} \geq \text{maximum harvest size}_h \{1\} \\ \text{else } \{0\} \end{cases}$$

$$n_{patch_{jh}} = \sum_{i=1}^{i_{max}} a_{cohort_{ijh}} \cdot a_{patch_{jh}}$$

$$\text{harvest}_{cohort_{ij}} = \sum_{h=1}^{h_{max}} \text{harvest rate}_h \cdot \left( \frac{n_{cohort_{ij}}}{n_{patch_{jh}}} \right) \cdot \left( \frac{1}{\text{biomass}_{cohort_{ij}}} \right) \cdot a_{cohort_{ijh}} \cdot a_{patch_{jh}}$$

#### 4.3.1.4 Ecosystem services

Six ecosystem services are simulated: nutrient removal (carbon, nitrogen and phosphorus), food provisioning (market and culture) and habitat provisioning. Nutrients accumulate in, and are released from tissue, shell and biodeposits. Their net flux ( $\text{t ha}^{-1} \text{y}^{-1}$ ) is calculated as the balance between the sinks (biodeposits, live and dead shell, harvested tissue and shell) and sources (biocalcification, respiration, excretion, mineralisation, dissolution), negative values indicate sinks (Figure 4.1).

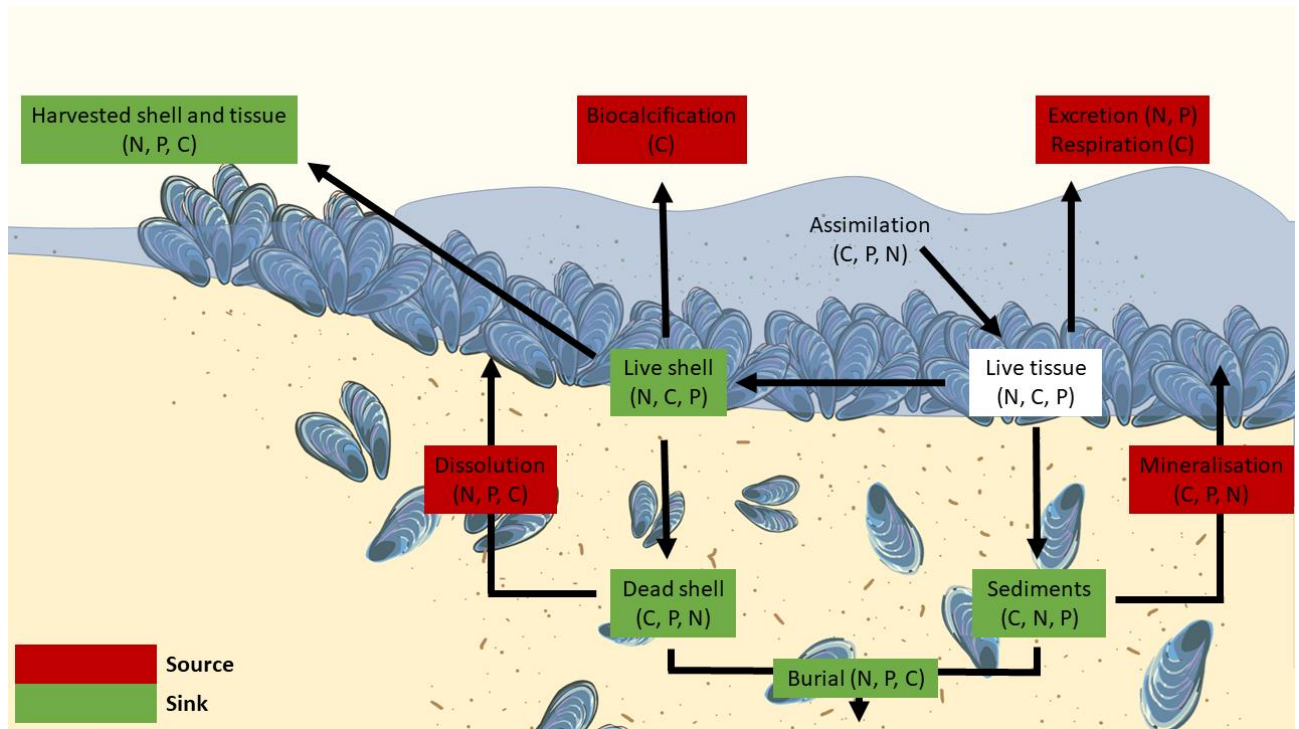


Figure 4.1 Simulated flows between model nutrient (C- carbon, P – phosphorous, N - nitrogen) sinks (biodeposits, live and dead shell, harvested tissue and shell) and sources (biocalcification, respiration, excretion, mineralisation, dissolution).

Food provisioning is calculated as the total biomass (shell and tissue) removed via harvest and habitat provisioning is calculated as the total biomass of all living individuals. All incorporated fluxes are those considered by environmental assessments of bivalve aquaculture (e.g., Aubin et al., 2018; Jansen and van den Bogaart, 2020; Kotta et al., 2020).

Table 4.1 Values used to calculate nitrogen (N), phosphorous (P) and carbon (C) accumulation (tissue, shell, biodeposit) and release (respiration, excretion, biocalcification, mineralisation, dissolution) by model *M. edulis* (Jansen et al., 2012; Kautsky et al., 1990; Morris and Humphreys, 2019; Ries et al., 2016; Van Broekhoven et al., 2015; van der Schatte Olivier et al., 2021).

Nutrient	Description	Symbol	Unit	Value
Nitrogen	Tissue content	$N_{tissue}$	ratio	0.087
	Excretion rate	$N_{excrete}$	$\text{mg g}^{-1} \text{h}^{-1}$	0.011
	Biodeposit accumulation rate	$N_{deposit}$	$\text{mg g}^{-1} \text{h}^{-1}$	0.013
	Biodeposit mineralisation rate	$N_{mineralise}$	$\text{ratio h}^{-1}$	0.0003
	Shell content	$N_{shell}$	ratio	0.047
Phosphorous	Tissue content	$P_{tissue}$	ratio	0.01
	Excretion rate	$P_{excrete}$	$\text{mg g}^{-1} \text{h}^{-1}$	0.001
	Biodeposit accumulation rate	$P_{deposit}$	$\text{mg g}^{-1} \text{h}^{-1}$	0.001
	Biodeposit mineralisation rate	$P_{mineralise}$	$\text{ratio h}^{-1}$	0.0002
	Shell content	$P_{shell}$	ratio	0.0001
Carbon	Tissue content	$C_{tissue}$	ratio	0.410
	Respiration rate	$C_{respire}$	$\text{mg g}^{-1} \text{h}^{-1}$	0.187
	Biodeposition accumulation rate	$C_{deposit}$	$\text{mg g}^{-1} \text{h}^{-1}$	0.112
	Biodeposit mineralisation rate	$C_{mineralise}$	$\text{ratio h}^{-1}$	0.320
	C released per g of $\text{CaCO}_3$ shell formed	$C_{calcification}$	ratio	0.079
	Proportion of $\text{CaCO}_3$ in shell	$\text{CaO}_{3shell}$	ratio	0.950
	Proportion of C in shell	$C_{shell}$	ratio	0.127
	Molecular ratio of $\text{CaCO}_3$ to C	$\text{CaO}_3 \alpha C$	ratio	0.120
All	Shell decay rate	$Decay_{shell}$	$\text{ratio h}^{-1}$	0.00002

All nutrients accumulate in tissue ( $dT/dt$ ) and shell ( $dS/dt$ ) relative to growth rate, they both accumulate in biodeposits ( $nutrient_{deposit}$ ) and are released from tissue ( $nutrient_{respire}$ ,  $nutrient_{excrete}$ ) relative to body size ( $AFDM_{cohort}$ ). Carbon released from shell is dependent on growth rate ( $dS/dt$ ) and calcium carbonate content ( $\text{CaO}_{3shell}$ ), there is no simulated nitrogen or phosphorus release from shell. Nutrients in dead shell relate to the benthic mortality, predation and starvation rates experienced by each cohort. All nutrients are released from biodeposits ( $nutrient_{mineralise}$ ) and dead shell ( $decay_{shell}$ ) as an hourly proportion. Physiological processes (tissue growth, excretion, biodeposition) involved depend on temperature via the Arrhenius equation ( $tc$ ), all values and equations used to calculate nutrient fluxes are provided (Table 4.1, Equations 4.10, 11).

Equations 4.10 Equations used to describe the nitrogen (N) and phosphorous (P) fluxes for a model *M. edulis*.

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$$\text{tissue source}_{\text{cohort}_{ij}} = \text{tc} \cdot \text{nutrient}_{\text{excrete}} \cdot \text{AFDM}_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{live shell source}_{\text{cohort}_{ij}} = 0$$

$$\text{biodeposit source}_{\text{cohort}_{ij}} = \text{biodeposit source}_{\text{cohort}_{ij}} \cdot \text{nutrient}_{\text{mineralise}} \cdot \text{AFDM}_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{dead shell source}_{\text{cohort}_{ij}} = \text{dead shell sink}_{\text{cohort}_{ij}} \cdot \text{Decay}_{\text{shell}}$$

$$\text{tissue sink}_{\text{cohort}_{ij}} = \text{tc} \cdot \text{nutrient}_{\text{tissue}} \cdot \left( \frac{dT}{dt} \right)_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{biodeposit sink}_{\text{cohort}_{ij}} = \text{tc} \cdot \text{nutrient}_{\text{deposit}} \cdot \text{AFDM}_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{live shell sink}_{\text{cohort}_{ij}} = \text{nutrient}_{\text{shell}} \cdot \left( \frac{dS}{dt} \right)_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{dead shell sink}_{\text{cohort}_{ij}} = \text{shell sink}_{\text{cohort}_{ij}} \cdot \left( m_{\text{benthic}_{ij}} + m_{\text{predation}_{ij}} + m_{\text{starvation}_{ij}} \right)$$

$$\text{harvest sink}_{\text{cohort}_{ij}} = m_{\text{harvest}_{ij}} \cdot \left( \text{tissue sink}_{\text{cohort}_{ij}} + \text{shell sink}_{\text{cohort}_{ij}} \right)$$


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Equations 4.11 Equations used to describe all carbon fluxes for a model *M. edulis*.

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$$\text{tissue source}_{\text{cohort}_{ij}} = \text{tc} \cdot C_{\text{respired}} \cdot \text{AFDM}_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{live shell source}_{\text{cohort}_{ij}} = \left( \frac{dS}{dt} \right)_{\text{cohort}_{ij}} \cdot C_{\text{calcification}} \cdot \text{CaCO}_{3\text{shell}} \cdot \text{CaO}_3 \propto C \cdot n_{\text{cohort}_{ij}}$$

$$\text{biodeposit source}_{\text{cohort}_{ij}} = \text{tc} \cdot C_{\text{mineralise}} \cdot \text{AFDM}_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{dead shell source}_{\text{cohort}_{ij}} = \text{dead shell sink}_{\text{cohort}_{ij}} \cdot \text{Decay}_{\text{shell}}$$

$$\text{tissue sink}_{\text{cohort}_{ij}} = \text{tc} \cdot C_{\text{tissue}} \cdot \left( \frac{dT}{dt} \right)_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{live shell sink}_{\text{cohort}_{ij}} = C_{\text{shell}} \cdot \left( \frac{dS}{dt} \right)_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{biodeposit sink}_{\text{cohort}_{ij}} = \text{tc} \cdot C_{\text{deposit}} \cdot \text{AFDM}_{\text{cohort}_{ij}} \cdot n_{\text{cohort}_{ij}}$$

$$\text{dead shell sink}_{\text{cohort}_{ij}} = \text{shell sink}_{\text{cohort}_{ij}} \cdot \left( \text{benthic}_{\text{cohort}_{ij}} + \text{predation}_{\text{cohort}_{ij}} + \text{starvation}_{\text{cohort}_{ij}} \right)$$

$$\text{harvest sink}_{\text{cohort}_{ij}} = \text{harvest mortality}_{\text{cohort}_{ij}} \cdot \left( \text{tissue sink}_{\text{cohort}_{ij}} + \text{shell sink}_{\text{cohort}_{ij}} \right)$$


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All sources (tissue, biodeposit, live and dead shell) and sinks (biodeposit, live and dead shell, harvested tissue and shell) for each nutrient ( $n$ ) were summed for each cohort ( $i$ ) and patch ( $j$ ), and the balance calculated (Equations 4.12):

Equations 4.12 Model equations for calculating net the flux of nitrogen, phosphorous and carbon.

$$\text{total nutrient source}_{\text{cohort}_{ij}} = \sum_{s=1}^{s_{\max}} \text{source}_{\text{cohort}_{ij}}$$

$$\text{total nutrient sink}_{\text{cohort}_{ij}} = \sum_{s=1}^{s_{\max}} \text{sink}_{\text{cohort}_{ij}}$$

$$\text{net nutrient flux}_n = \sum_{j=1}^{j_{\max}} \sum_{i=1}^{i_{\max}} \text{net nutrient source}_{\text{cohort}_{ij}} - \text{net nutrient sink}_{\text{cohort}_{ij}}$$

The provisioning of food and habitat (*biomass<sub>cohort</sub>*) was calculated using the sum of wet tissue mass, shell mass and the mass of water contained within the valves when close (biomass, Equations 4.13).

Equations 4.13 Model equations for calculating cohort biomass.

$$\text{shell length}_{\text{cohort}_{ij}} = \frac{v^{\frac{1}{3}}}{\delta m}$$

$$\text{wet tissue mass}_{\text{cohort}_{ij}} = (v_{\text{cohort}_{ij}} \cdot \text{dtm} \propto \text{wtm}) + \left( \frac{e_{s_{\text{cohort}_{ij}}} + e_{r_{\text{cohort}_{ij}}}}{j \propto \text{wtm}} \right)$$

$$\text{shell mass}_{\text{cohort}_{ij}} = 10^{-1.44 + 3.31 \cdot \log_{10} \text{shell length}_{\text{cohort}_{ij}}}$$

$$\text{water mass}_{\text{cohort}_{ij}} = e^{-8.503 + 2.703 \cdot \ln\left(\frac{\text{shell length}_{\text{cohort}_{ij}}}{10}\right)}$$

$$\text{biomass}_{\text{cohort}_{ij}} = \text{wet tissue mass}_{\text{cohort}_{ij}} + \text{shell mass}_{\text{cohort}_{ij}} + \text{water mass}_{\text{cohort}_{ij}}$$

The only provisioning service included is commercial harvest for direct consumption (shore) and for culture (shore and boat) at aquacultural sites (Dare and Davies, 1975). Commercial harvest was two services: the provision of either market size individuals ( $\geq 4.5$  cm) or culture size individuals (2 – 4 cm). The number of individuals removed via each harvest type is calculated for each cohort and patch ( $m_{\text{harvest}}$ ). These rates are multiplied by each cohort's biomass to obtain the biomass removed (Equation 4.14).



Equation 4.14 Model equation for calculating hourly harvest rates.

$$\text{food provision}_h = \sum_{j=1}^{j_{\max}} \sum_{i=1}^{i_{\max}} m_{\text{harvest}_{ijh}} \cdot \text{biomass}_{\text{cohort}_{ij}}$$

The final service of *M. edulis* is as habitat provisioning (e.g., nursery, foraging) for important species (e.g., coastal birds). The total biomass of the benthic population is considered a proxy for habitat provisioning (Equation 4.15).

Equation 4.15 Model equation for calculating population biomass.

$$\text{habitat provisioning} = \sum_{j=1}^{j_{\max}} \sum_{i=1}^{i_{\max}} \begin{cases} \text{if location} = \text{benthic} \{n_{\text{cohort}_{ij}} \cdot \text{biomass}_{\text{cohort}_{ij}}\} \\ \text{else } \{0\} \end{cases}$$

All fluxes were calculated as tonnes per hectare per year for analysis (t service ha<sup>-1</sup> y<sup>-1</sup>) for comparison with other studies.

#### 4.3.1.5 Setup

The model was always initialised in the same manner. The initial population structure (i.e., age and density) was setup using the average observed on each site during autumn surveys in Morecambe Bay (Table 4.2). The state variables (*es*, *er*, *eh*, *v*) used by the DEB model are setup by pre-running the model for all individuals under constant, submerged environmental conditions until initial sizes are reached (Table 4.2, Table 4.3). For simulations where stochasticity was included the initial values were drawn from a normal distribution using the mean ± standard errors.

Table 4.2 Initial *M. edulis* age, density and size for all simulations. Values are the average from autumn surveys in Morecambe Bay 2017 – 2019.

Site	Age	Density m <sup>-2</sup>	Standard error	AFDM g	Standard error
Fleetwood	1	1529	249	0.11	0.01
	2	815	34	0.29	0.03
	3	107	47	0.45	0.04
	4	40	4	0.79	0.08
Foulney	1	3117	476	0.08	0.01
	2	791	28	0.23	0.02
	3	108	23	0.39	0.03
	4	40	4	0.77	0.08
Heysham	1	1997	129	0.10	0.01
	2	360	185	0.24	0.04
	3	40	4	0.50	0.03

Because the *M. edulis* population in Morecambe is patchy only 75 % of patches receive an initial population (average coverage estimate, NWIFCA), the remaining 25 % (randomly assigned) begin the simulation with no adult individuals present. All patches are however initialised with a population of larvae ( $2.6 \times 10^7 \text{ m}^{-2}$ ) which is the mean annual value generated during calibration. Simulations begin on the 15<sup>th</sup> of September at 1 am (when largest biomass was recorded) using environmental conditions for this date and time (Table 4.3).

Table 4.3 Pre-run and initial values for model environmental drivers.

Model driver	Symbol	Unit	Pre-run	Initial
<b>Environmental</b>				
Chlorophyll- <i>a</i>	<i>chl</i>	mg m <sup>-3</sup>	4	4.2
Suspended particulate inorganic matter	<i>spim</i>	g m <sup>-3</sup>	20	21.2
Sea temperature	<i>sst</i>	°C	14	15.6
Air temperature	<i>nst</i>	°C	14	13.2
Water level		m	10	-0.032
<b>Predator</b>				
<i>A. rubens</i>		ind m <sup>-2</sup>	0	75
<i>C. crangon</i>		ind m <sup>-2</sup>	0	1.7
<i>C. maenas</i>		ind m <sup>-2</sup>	0	0.6
<i>C. canutus</i>		ind	0	1535
<i>H. ostralegus</i>		ind	0	22349
<i>L. argentatus</i>		ind	0	3595
<i>S. mollissima</i>		ind	0	3064

#### 4.3.2 Data

The temporal and spatial extent of the model environment is explicit to the region designated a Special Area of Conservation within Morecambe Bay (Figure 4.2).

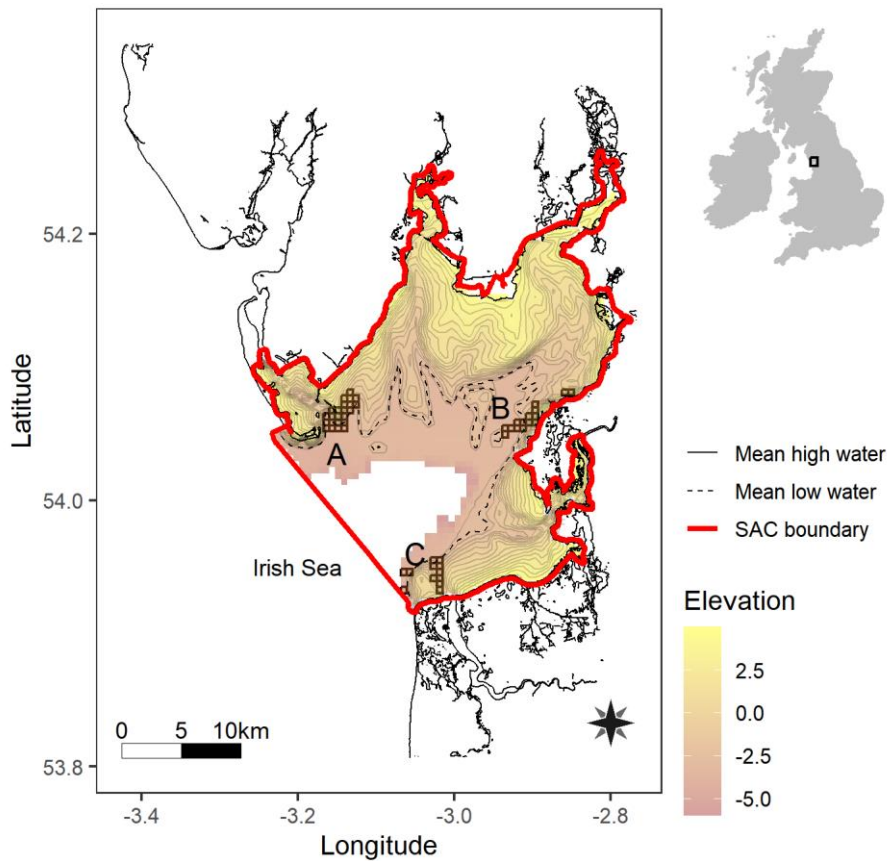


Figure 4.2 Special Area of Conservation (SAC) for Morecambe Bay, UK. The three main sites of *M. edulis* reefs (A = Foulney, B = Heysham, C = Fleetwood) are shown within 250m grids used in simulations. The coloured gradient corresponds to elevation (m), the solid red line to the SAC extent in Morecambe Bay, solid black lines to mean high water (mhw) and dashed lines to mean low water (mlw).

#### 4.3.2.1 Field surveys

Field data are collected to 1) describe the biomass of intertidal *M. edulis* populations in Morecambe Bay in relation to shore level, season and age, 2) estimate initial model values and 3) evaluate model accuracy. Shell length frequency plots and individual biometric measurements were used previously (see Chapter 3) to estimate individual age, tissue and shell mass and mass conversion values. Values for biomass were calculated as the sum of both tissue and shell mass, and the volume of water contained when the valves were closed. Biomass values were summarised by elevation, season and age to describe the relationship, and test model accuracy. They were summarised by age and season to calculate initial model values.

Fieldwork was undertaken on three mature *M. edulis* reefs in Morecambe Bay between May 2017 and March 2019. Forty sampling stations of 100m<sup>2</sup> were established across the three reefs covering an elevation range of -4.0 m to 0.1 m above sea level and an annual aerial exposure of 0 to 60 %. In Morecambe Bay the major settlements of post-larvae take place between March and June, the main period of growth (shell, tissue) occurs between July and December (Dare, 1976). To coincide with seasonal peaks in both the number of individuals and total biomass all stations were sampled once in spring and again in autumn during the survey period. On every visit, five samples were collected from each station by removing all individuals found within a 0.1m<sup>2</sup> quadrat and freezing for processing in the laboratory. The location of each sampling station remained the same throughout the sampling period and the location of sampling points was changed each time a station was sampled. All sampling stations and points were placed randomly throughout the *M. edulis* reefs using the *sp* package (Pebesma and Bivand, 2005) for the software R (R Core Team, 2018). If no *M. edulis* were present at a sample point it was recorded as empty.

Each sample was washed, sieved (using 0.5, 2, 10 mm sieves) and the total mass (g) of all *M. edulis* present within each sieve was recorded. The shell length of all individuals > 10 mm was measured using callipers (0.1 mm), all individuals < 10 mm were measured using the digital analysis software *ImageJ* (Schneider et al., 2012). Individuals < 5 mm were often present in large numbers which were time consuming to measure individually, therefore the mass of all individuals < 5 mm was recorded and a subsample of approximately 5 – 10 g was analysed. The number of individuals was then scaled up using the original sample – sub-sample ratio. Age was estimated on shell length using von Bertalanffy growth parameters, tissue and shell mass were estimated on shell length using allometric relationships (see Chapter 3). Density and biomass within each sample station (per sample date) was estimated as the mean (n = 5) of their respective values (multiplied by 100).

#### **4.3.2.2 Environmental**

The present model environment aims to simulate the conditions experienced by *M. edulis* in intertidal habitats. The suspended particulate matter concentration (organic and inorganic) and temperature (water and air) of each patch drive the individual processes (feeding, ingestion, maintenance, growth, reproduction) of all *M. edulis* within it. Hourly water level measurements combined with elevation are used to determine whether a cell is submerged (underwater) or emerged (exposed to the air). Elevation and water level values therefore work together to create a

structurally realistic spatial and temporal gradient between the marine and terrestrial environment. All temporal and spatial environmental data were obtained from 1<sup>st</sup> January 2015 to the 31<sup>st</sup> of December 2019 for the region designated a Special Area of Conservation (SAC) for Morecambe Bay (Figure 4.2). Temporal data were converted to an hourly time series and spatial data were converted to 250 m resolution. A single time series of temperature, suspended particle concentration and water level was used by all patches while elevation was assigned to all patches according to observed values extracted from spatial data. All processing of spatial data was carried out using the *raster* package (Hijmans et al., 2017) for the software R (R Core Team, 2018).

Chlorophyll-*a* (*chl*, mg m<sup>-3</sup>) and suspended particulate inorganic matter (*spim*, g m<sup>-3</sup>) concentrations are used as a measure of suspended particle concentration. Daily *chl* and *spim* concentrations were extracted from satellite observations at 1 km resolution obtained using merged data (SeaWiFS, MODIS and MERIS) via a regional algorithm specifically designed for coastal waters (Gohin, 2011; Gohin et al., 2005; Gohin and Druon, 2002). Sea surface (*sst*, K) and near surface air (*nst*, K) are used as measures of temperature. Mean daily *sst* was extracted from merged satellite (NOAA-18, NOAA-19, MetOpB, NPP, GCOM-W, GOES13, MSG4, DMSP-F17, DMSP-F15) measurements at approximately 6 km resolution (Donlon et al., 2012). Discrete hourly *nst* was obtained from the Met Office Integrated Data Archive System (available <https://catalogue.ceda.ac.uk>) for the Walney Island weather station (54.125, -3.258, elevation: 15 m, (Met Office, 2019, 2006). Elevation values were extracted from lidar data collected at 1 m horizontal and 1 mm vertical resolution (available <https://environment.data.gov.uk/>) and hourly water level data were obtained from Heysham tide station (available <https://www.bodc.ac.uk>). Daily sunrise and sunset times for Morecambe Bay were calculated using the R package *sunCalc* (Benoit and Elmarhraoui, 2019)

#### 4.3.2.3 Long-term biomass

Annual biomass estimates (g m<sup>2</sup> y<sup>-1</sup>) from 1968 to 2019 are provided by NWIFCA and are used to both calibrate the model and test the quality of parameter estimates (Table 4.4, Appendix B, Figure 4.14). The long-term trend in the bay is stable, but inter-annually variable. The model is calibrated such that simulated annual biomass falls within the lower and upper values observed for the entire Bay (see 4.3.3 Parameter estimation), the quality of parameter estimates is assessed by comparing model outputs with site values.

Table 4.4 Median annual biomass ( $\text{g m}^{-2} \text{yr}^{-1}$ ) of *M. edulis* in Morecambe Bay between 1968 and 2019. Values are given by site (Fleetwood, Foulney, Heysham, Bay) and include the number of samples (N), lower (25%) and upper quantiles (75%).

Site	N	From	To	Median $\text{g m}^{-2} \text{yr}^{-1}$	Quantile	
					25%	75%
Foulney	22	1968	2019	8843.67	6974.11	11419.60
Heysham	16	1968	2019	7677.32	6475.77	9371.44
Fleetwood	9	2001	2019	8987.56	6892.33	9987.77
Bay	47	1968	2019	8345.67	6851.89	11081.14

#### 4.3.2.4 Commercial harvest

In Morecambe Bay, commercial harvest of *M. edulis* takes place both from the shore by hand and from boats using dredges. Hand gatherers target both culture and market size individuals while dredging harvests culture size *M. edulis* only. Annual harvest rates ( $\text{t yr}^{-1}$ ) for market and culture size *M. edulis* in Morecambe were provided by NWIFCA (Table 4.5, Appendix B, Figure 4.15). Total harvest rates (market and culture size) were used to calibrate the model such that annual harvest rates fell within the maximum and minimum of observed values. Values for market and culture size individuals were used separately to assess the quality of estimated parameters.

Table 4.5 Annual harvest ( $\text{t yr}^{-1}$ ) of *M. edulis* in Morecambe Bay between 1971 and 2019. Values are given by harvest size (total, consumer size, undersize) and include the number of samples (N), lower (25%) and upper quantiles (75%).

Harvest	From	To	N	Median $\text{t yr}^{-1}$	Quantile	
					25%	75%
Total	1971	2019	37	1813.9	170.9	3515.9
Market size	2006	2019	7	402.7	342.9	462.6
Culture size	1975	2018	22	3050.0	1310.7	4260.0

#### 4.3.2.5 Predators

The rate ( $\text{g AFDM h}^{-1}$ ) at which individual *M. edulis* are consumed by each predator species is estimated using the average intake rate of an individual of each species (determined by size) and their abundance. For each predator species, an individual intake rate and a time series of abundance is estimated (Table 4.6 and 4, Figure 4.3 and 3). All intake rates are converted to  $\text{g AFDM h}^{-1}$  for use

in the model, where intake rates were given as 'individuals of length  $x$  (cm)  $h^{-1}$ ' they were converted using the equation:  $AFDM \text{ (g)} = 0.093 \cdot x^{2.283}$  (this study), and intake rates given or estimated as  $J h^{-1}$  were converted using  $1 \text{ g AFDM} = 22000 \text{ J}$  (Goss-Custard, 1996).

#### 4.3.2.5.1 Intake rates

Individual intake rates for each invertebrate predator species are adapted from values found in the literature (Campos et al., 2009; Dare et al., 1983; Kamermans et al., 2009; Mascaró and Seed, 2001, 2000; Murray et al., 2007; Saier, 2001). In the Irish sea, intertidal *C. crangon* populations consist of predominantly juveniles (carapace width 0.7 cm) which are less than 1 year old (Oh et al., 1999). Their individual intake rate can be related to size ( $J \text{ cm}^{-2} \text{ h}^{-1}$ ) and differs between sexes (Campos et al., 2009; Oh et al., 1999). Here, an average (between sexes) intake rate of  $2.01 \text{ J cm}^{-2} \text{ h}^{-1}$  (adapted from (Campos et al., 2009)) is used and it is assumed that the population is all juvenile (carapace width 0.7 cm). *C. maenas* (carapace width 4.5 – 7.5 cm) consume on average 0.68 individuals (shell length 1.5 – 3.0 cm) per hour (Dare et al., 1983; Murray et al., 2007). The average size (carapace width) of *C. maenas* observed within *M. edulis* populations is 4.5 cm, at this size the maximum shell length *C. maenas* can process is around 2.5 cm which in this study equates to 0.075 g AFDM (Dare et al., 1983; Mascaró and Seed, 2001, 2000). In Morecambe Bay the average size (arm length) of *A. rubens* within aggregations is  $7.13 \pm 1.12$  cm and they are generally observed feeding on juvenile settlements with shell lengths of less than 3.5 cm (Dare, 1982, 1976; Sloan and Aldridge, 1981). Intake rates are calculated assuming an average prey size of 2.5 cm (0.075 g AFDM) and an intake rate of 0.02 individuals per hour (Allen, 1983; Kamermans et al., 2009; Saier, 2001). Additionally, not all individuals within a population of *A. rubens* are actively feeding, some have not located prey and others are digesting prey previously consumed (Gil and Zaixso, 2008; Sloan and Aldridge, 1981; Town, 1980). The average proportion of *A. rubens* observed feeding simultaneously is estimated to be 0.44 and intake rates are adjusted further by this amount (Sloan and Aldridge, 1981).

Table 4.6 Body size (cm) and intake rates of model invertebrate predators. The mean size of each predator species and their intake rate is estimated as the average from a number of studies (Baeta et al., 2006; Campos et al., 2009; Dare et al., 1983; Dolmer, 1998; Hiddink et al., 2002; Kamermans et al., 2009; Murray et al., 2007; Oh et al., 1999; Saier, 2001; Sloan and Aldridge, 1981; Sommer et al., 1999). The ash-free dry mass of each preferred prey size is estimated from this study and 1 g AFDM = 22 KJ (Goss-Custard, 1996).

Species	Mean size cm	Intake rate (literature)	Intake rate (model)
<i>A. rubens</i>	7.1	0.02 (0.01 – 0.05) Individual h <sup>-1</sup>	8.47 · 10 <sup>-4</sup> g AFDM h <sup>-1</sup>
<i>C. maenas</i>	4.5	0.68 (0.13 – 1.35) Individual h <sup>-1</sup>	3.19 · 10 <sup>-2</sup> g AFDM h <sup>-1</sup>
<i>C. crangon</i>	0.7	2.01 (1.57 – 2.45) J cm <sup>-2</sup> h <sup>-1</sup>	6.36 · 10 <sup>-5</sup> g AFDM h <sup>-1</sup>

The body mass of the four bird predator species was taken from values found in the literature (Robinson, 2005). The individual energy requirements (Field metabolic rate, FMR KJ h<sup>-1</sup>) of each species is calculated using the all bird equation of (Nagy et al., 1999) and converted to g AFDM h<sup>-1</sup>:

$$FMR = \left( \frac{10.5 \cdot \text{body mass}^{0.681}}{24} \right) \cdot \frac{ae}{1}$$

Birds can only assimilate a fraction of all the energy available from their food intake and the energy requirement is corrected according to an assimilation efficiency (ae). The assimilation efficiency is estimated to be 0.75 for *C. canutus*, *S. mollissima* and *L. argentatus*, which swallow whole mussels (Nehls, 1995; Prater, 1972). A higher assimilation efficiency (0.85) is used for *H. ostralegus* because they remove bivalve shells before consuming the tissue (Cadée, 1989; Durell et al., 2006; Kent, 1981; Norton-Griffiths, 1967; Stillman et al., 2000).

Table 4.7 Body mass (g), individual energy intake requirement (KJ h<sup>-1</sup>), assimilation efficiency and mussel intake rates (g ash-free dry mass h<sup>-1</sup>) of model bird predators. Daily energy requirements are calculated by substituting average body mass (g) in the 'all bird daily energy requirements' equation of (Nagy et al., 1999) and assuming 1 g AFDM = 22 KJ (Goss-Custard, 1996).

Species	Mass (g)	Energy requirement KJ h <sup>-1</sup>	Assimilation efficiency	Intake rate g AFDM h <sup>-1</sup>
<i>L. argentatus</i>	971	47.3	0.85	2.15
<i>C. canutus</i>	138	12.5	0.75	0.57
<i>S. mollissima</i>	2276	84.6	0.75	3.84
<i>H. ostralegus</i>	546	32.0	0.85	1.45

#### 4.3.2.5.2 Abundance



The abundance (individual  $m^{-2}$ ) of *C. crangon* and *C. maenas* in Morecambe Bay is taken from the Isle of Man, 120 km to the west and from the Menai Strait in Wales, 120 km to the south west (Murray et al., 2007; Oh et al., 1999). The abundance of *A. rubens* (individual  $m^{-2}$ ) in Morecambe Bay has been estimated as part of a number of historic studies, such occurrence still occur today and values are therefore adapted from these (Dare, 1982, 1976, 1973; Sloan and Aldridge, 1981). Around the Isle of Man, *C. crangon* are absent in the winter and move inshore in spring with numbers peaking (12  $m^{-2}$ ) in mid-summer (Figure 4.3). In the Menai Strait, *C. maenas* (carapace width 4.4 cm) begin to move onto subtidal and intertidal cultivated *M. edulis* populations in spring. The density peaks in mid-summer (1.5  $m^{-2}$ ) and is at its lowest (0.2  $m^{-2}$ ) throughout winter (Figure 4.3). In Morecambe Bay there is an annual occurrence of dense ( $245 \pm 100 m^{-2}$ ) and extensive ( $2.025 \pm 0.267 ha$ ) aggregations of *A. rubens* which begin to move into the low intertidal (< 5% aerial exposure) and subtidal zones in spring (Dare, 1982, 1976, 1973; Sloan and Aldridge, 1981). Numbers rapidly decline again in September and *A. rubens* are absent from October to March (Figure 4.3).

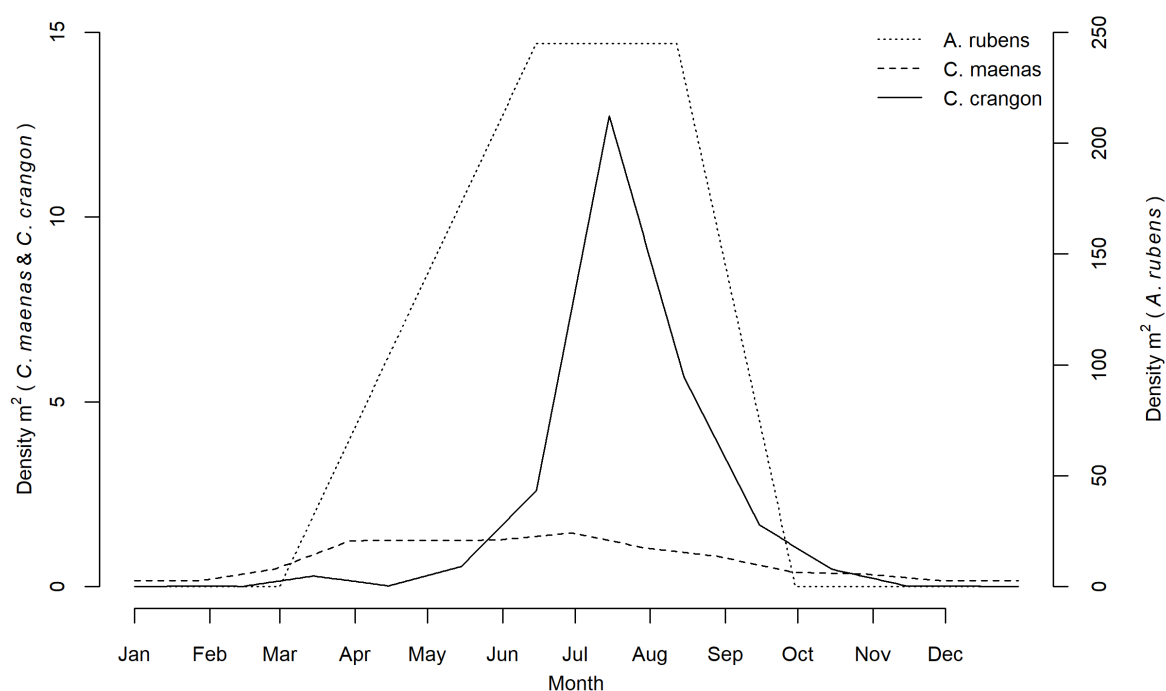


Figure 4.3 Abundance (individual  $m^{-2}$ ) of the main invertebrate predators of *M. Edulis* in Morecambe Bay. Line type represents: solid – *A. rubens* adapted from (Dare, 1982; Sloan and Aldridge, 1981), dashed – *C. Crangon* adapted from (Oh et al., 1999) and, dotted – *C. maenas* adapted from (Murray et al., 2007).

In the UK all coastal birds are counted once per month as part of the Wetland Birds Survey (WeBS) and Morecambe Bay regularly supports > 40000 *H. ostralegus*, > 20000 *C. canutus*, > 13000 *L. argentatus* and > 6000 *S. mollissima* ((Frost et al., 2019). When foraging these birds do not disperse evenly over the entire bay but aggregate on preferred feeding areas. The WeBS monitoring scheme typically includes high and low tide counts to determine where birds are roosting and feeding, however in Morecambe Bay the area uncovered during periods of low tide is vast and all surveys of wetland birds are restricted to counting roosting birds at high tide (Banks et al., 2006; Frost et al., 2019; Marsh et al., 2012). In the absence of low tide counts, the number of birds present on *M. edulis* reefs is estimated to be those roosting on shores which contain *M. edulis* reefs. The density of each species (individual m<sup>-2</sup>) is estimated using the number of each species observed roosting and the total area (m<sup>2</sup>) of the *M. edulis* population (401 ha).

In Morecambe Bay the numbers of *H. ostralegus* and *C. canutus* peak during the autumn when large numbers travel to wintering grounds (Prater, 1972; Wilson, 1973). The number of *C. canutus* peaks slightly later in winter after the arrival of the Scandinavian breeding populations, which temporarily pause at sites along the North Sea coast before travelling to Morecambe (Prater, 1972). During this time numbers of *H. ostralegus* and *C. canutus* can reach 40,000 and 20,000 respectively (Figure 3c and 3d). The aggregations of *C. canutus* in Morecambe are largely winter populations and numbers decrease in early spring when most return to breeding sites (Frost et al., 2019; Wilson, 1973). *H. ostralegus* are however also present in substantial numbers (< 10,000 immature, local breeding and non-breeding birds) during the summer, (Dare and Mercer, 1973; Frost et al., 2019; Wilson, 1973). *S. mollissima* are resident breeders in Morecambe Bay and numbers remain high (> 2,000) throughout the year (Frost et al., 2019). Numbers peak in spring (3,000) and in autumn (5,000) when the local breeding population is joined by birds on route to or returning from breeding grounds further north. In summer, once breeding is complete, most adult birds move away from the colony for their annual moult. *L. argentatus* are also resident breeders in Morecambe Bay and their numbers also remain high (> 2,000) throughout the year (Frost et al., 2019; Kim and Monaghan, 2006; Sibly and McCleery, 1983, Figure 4.4b). Numbers increase throughout spring and initially peak in summer (2,500) once all birds have returned to the breeding colony (Camphuysen et al., 2011). Their numbers then temporarily decrease as adult birds disperse after moulting and numbers peak again in Autumn (3,000) when more northern populations are temporarily present in the Bay (Hickling, 1954; Verbeek, 1977a, 1977b).

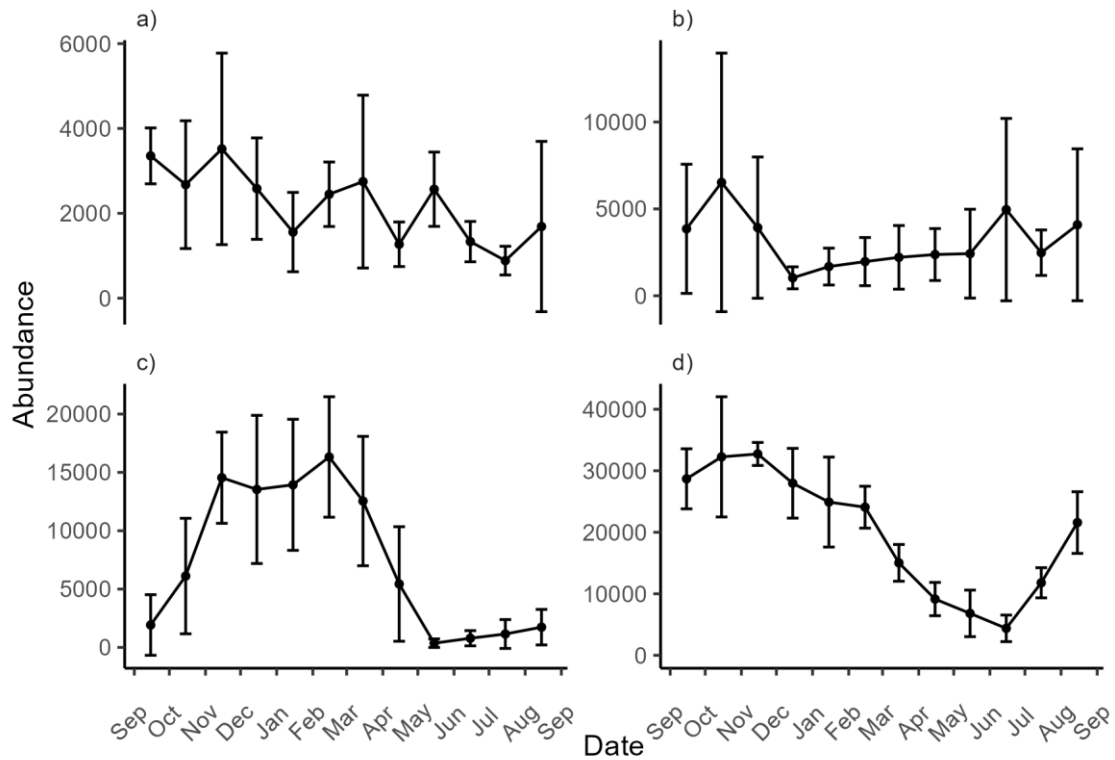


Figure 4.4 Mean ( $\pm 1$  standard deviation) monthly counts of a) *S. mollissima*, b) *L. argentatus*, c) *C. canutus* and d) *H. ostralegus* in Morecambe Bay between 2015-01-01 and 2019-12-31.

#### 4.3.2.5.3 Prey size

The average size of *M. edulis* consumed by each predator species is taken from values found in the literature (Bustnes and Erikstad, 1990; Cadée, 1989; Cayford and Goss-Custard, 1990; Dare, 1982; Davidson, 1971; Dolmer, 1998; Goss-Custard et al., 2006; Hiddink et al., 2002; Leopold et al., 1989; Mascaró, 2000; Mascaró and Seed, 2001; Oh et al., 2001; Pierotti and Annett, 1991; Prater, 1972; Saier, 2001; Sommer et al., 1999; Sutherland and Ens, 1987). All preferred prey size values and feeding conditions are provided (Table 4.8).

Table 4.8 Minimum and maximum prey size preference and feeding conditions of the model predator species

Species	Min prey size cm	Max prey size cm	Feeding conditions
<i>A. rubens</i>	1.00	4.00	Submerged
<i>C. maenas</i>	0.50	2.50	Submerged
<i>C. crangon</i>	0.02	0.20	Submerged
<i>H. ostralegus</i>	2.00	5.00	Emerged
<i>L. argentatus</i>	0.50	5.00	Emerged
<i>S. mollissima</i>	0.50	5.00	Submerged
<i>C. canutus</i>	0.10	1.50	Emerged

### 4.3.3 Parameter estimation

Seven parameters for which values are unknown were used to calibrate the model (Table 4.9). They were calibrated simultaneously using an approach in which a sample ( $k$ ) of all possible parameter combinations is evaluated systematically against a set of observed data (Lika et al., 2011b, 2011a; Saraiva et al., 2011; Thiele et al., 2014). The aim is to find the parameter combination that best fits the data by minimizing the weighted sum of squared residuals ( $ssr$ ). A hybrid solution was used by defining conditional equations which transform categorical criteria to a best-fit criterion:

$$ssr_{kc} = \begin{cases} \text{if } xmin_c \leq y_k \leq xmax_c \{0\} \\ \text{else } \left\{ \left( \frac{\bar{x}_c - y_k}{\bar{x}_c} \right)^2 \right\} \end{cases}$$

$$ssr_k = \sum_{c=1}^{c_{max}} S_{kc}$$

where the quality measure ( $ssr$ ) for each parameter combination ( $k$ ) is calculated independently for each of the observed data ( $c$ ). Its value is set to 0 if the simulated value ( $y$ ) falls within the minimum ( $xmin$ ) and maximum ( $xmax$ ) of observed values, if it falls outside of this range the relative deviation to the mean ( $\bar{x}$ ) is used. The quality measure for each observation is then summed by parameter set and the minimum value is selected.

The range of possible values for the seven parameters was estimated from the literature and described below (Table 4.9). Latin Hypercube Sampling (LHS), a method for generating a stratified sample of values from multiple parameters, was used to generate the random parameter set (Iman et al., 1981; McKay et al., 2000). The sampling was undertaken using the R package *tgp* and

simulations were run using the R package *nlr* which is designed to setup, run and analyse NetLogo model simulations from R (Gramacy, 2007; Salecker, 2020; Salecker et al., 2019). A Latin Hypercube of 2000 samples was generated, and the parameter set which best fit the criteria selected.

Table 4.9 Parameter names, code, units and range used during Latin Hypercube Sampling.

Parameter	Code	Unit	Minimum	Maximum
Initial egg loss	<i>z1</i>	proportion h <sup>-1</sup>	0.01	0.99
Pelagic loss rate	<i>z2</i>	proportion h <sup>-1</sup>	0.00001	0.0015
Benthic and hydriodic loss rate	<i>z3</i>	proportion h <sup>-1</sup>	0.000001	0.00011
Reserve dependent mortality rate	<i>s1</i>	proportion h <sup>-1</sup>	0.000005	0.00046
Harvest rate consumer (hand)	<i>h1</i>	proportion h <sup>-1</sup>	0.00002	0.0021
Harvest rate undersize (hand)	<i>h2</i>	proportion h <sup>-1</sup>	0.00002	0.0021
Harvest rate undersize (dredge)	<i>h3</i>	proportion h <sup>-1</sup>	0.01	0.99

The criteria used for parameter estimation are based on data from long-term monitoring and annual landings. Firstly, only parameter sets (generated via LHS) for which the population persisted for 30 years are considered because the intertidal *M. edulis* population in Morecambe has been established for > 100 years (Daniel, 1921; Dare, 1976, 1973; Dare and Davies, 1975; Johnstone, 1898). After this only two further criteria were applied; simulated values of both annual biomass (g m<sup>-2</sup> y<sup>-1</sup>) and harvest (t y<sup>-1</sup>) must fall within the minimum and maximum of observed values.

Initial egg loss (*z1*), pelagic loss rate (*z2*) and benthic loss rate (*z3*) are three constant mortality rates which occur during each of the three main life stages (gamete, larvae, postlarvae). The three parameters have been estimated using field and laboratory experiments, and these values are used to select the ranges to be searched. The initial egg loss of *M. edulis* can be low under laboratory conditions (< 0.3), (Sprung and Bayne, 1984), but it is unclear whether it remains so in natural systems where water currents and animal spacing are more variable (Hollows et al., 2007; Levitan et al., 1992; Pennington, 1985; Peterson and Kimmerer, 1994). Therefore, the complete range (0.01 – 0.99) is included in the search for this parameter. Pelagic disappearance rates are estimated to fall between 0.03 – 0.34 d<sup>-1</sup>, the highest of which would result in the loss of an entire cohort over a 28 day period (Bayne, 1965; Fotel et al., 1999; Hansen, 1999; Hansen et al., 1997; Jørgensen, 1981; Pedersen et al., 2008; Philippart et al., 2003; Rumrill, 1990; Stenalt et al., 1998; Tapia and Pineda, 2007). The pelagic loss rate is therefore assumed to fall between 0.000 and 0.015 h<sup>-1</sup>, the upper of which would result in the loss of > 0.999 of a cohort in 28 days. Benthic loss rates are estimated to lie between 0.30 – 0.99 yr<sup>-1</sup> and model values are searched for between 1.0 x 10<sup>-6</sup> and 1.0 x 10<sup>-3</sup> h<sup>-1</sup>, where the maximum would result in the loss of > 99 % of a cohort in one year ((Beukema et al., 2010; Dare, 1976; Fotel et al., 1999; Jørgensen, 1981; Philippart et al., 2003).

The reserve dependant mortality coefficient ( $s1$ ) determines the proportion of individuals currently experiencing starvation that will die. Starvation is an intermittent mortality rate which only occurs during prolonged periods where food is limited. The parameter is estimated to have a maximum value of  $0.0005 \text{ h}^{-1}$  which, when a cohort is starving, would result in the loss of all individuals in 3 months (Maar et al., 2009; Martin et al., 2013; Preuss et al., 2009).

Commercial harvest of *M. edulis* occurs in Morecambe Bay via three methods: the harvest of market size individuals by hand ( $h1$ ), of culture size individuals by hand ( $h2$ ) and of culture size by dredge ( $h3$ ). Harvest rates are controlled by environmental conditions (e.g., tide), local authorities (e.g., open and closed periods), and the method used. In Morecambe Bay, *M. edulis* populations located at the mean spring low water mark (-3 m) are exposed during daylight hours for 468.2 hours per year (estimated using environmental drivers). The maximum value for the harvest of market and culture size individuals from the shore was set to  $0.0021 \text{ h}^{-1}$ , which would result in 99% of individuals being removed during this time. Harvesting via boat is restricted to a small area (17.5 ha) and was assumed to remove a maximum of 99 % in one hour.

#### **4.3.4 Parameter quality**

Parameters estimates via calibration were selected based on their ability to reproduce the average annual biomass and total annual harvest observed in Morecambe Bay. Their quality was assessed by comparing simulated values (using parameter estimates) of annual biomass and annual harvest (market and culture) by size with their respective observed values. The results indicate the quality to which estimated parameters distribute both biomass and harvest between three distinct geographical regions and two harvest sizes respectively. Variation in values (observed and simulated) of biomass between sites and harvest between sizes was described using Kruskal-Wallis tests and Dunn tests. Comparisons between observed and predicted values were made using Wilcoxon's tests.

#### **4.3.5 Model accuracy**

The main purpose of the model is to predict the response of ecosystem services provided by intertidal *M. edulis* populations to environmental change, predominantly through growth rates and

biomass. The accuracy with which it does this was assessed by comparing predicted values for annual biomass by season, elevation and age with observed ones. The results indicate the extent to which simulated biomass values describe the age, seasonal and spatial structure observed in natural intertidal *M. edulis* populations. Differences in the simulated and observed values of biomass by season were described using Kruskal-Wallis and Dunn tests, comparisons were made using Wilcoxon's tests. The relationship observed between biomass and elevation was described and compared with simulated values via linear regression. Observed and simulated distributions of annual biomass between age groups was compared using chi-squared tests.

#### 4.3.6 Ecosystem service assessment

Six ecosystem services delivered by *M. edulis* were quantified and their sensitivity to environmental change and each other (i.e., trade-offs and synergies) assessed (Table 4.14). The results were used to establish whether intertidal *M. edulis* populations serve as sources or sinks to important nutrients, identify the environmental parameters to which services are most sensitive (i.e., at risk) and to identify sets (bundles) of associated services (Saidi and Spray, 2018). All simulations are run for 30 years, and the outputs for analysis are carbon removal ( $\text{t C ha}^{-1} \text{y}^{-1}$ ), nitrogen removal ( $\text{t N ha}^{-1} \text{y}^{-1}$ ), phosphorous removal ( $\text{t P ha}^{-1} \text{y}^{-1}$ ), food provisioning ( $\text{t biomass ha}^{-1} \text{y}^{-1}$ ) and habitat provisioning ( $\text{t biomass ha}^{-1} \text{y}^{-1}$ ).

Simulations were first run using default parameter settings to estimate the annual flux of each service (Table 4.14). A global sensitivity analysis was then used to provide a general understanding of how sensitive ecosystem services are to changes in parameter values (Cariboni et al., 2007). The results can identify parameters and parameter groups to which services are highly sensitive and thereby establish research priorities (e.g., better measure of parameter) and provide insight into the mechanisms most critical to the stability of ecosystem services (i.e., risk assessment). The Morris method was used to provide a measure of global sensitivity for each parameter which can both rank and group them by importance (Morris, 1991, see Chapter 2 General Methods for detailed description). This method is free of assumptions about the model (e.g., linear relationships) and qualifies whether parameters have a negligible, first order (e.g., linear or additive) or second order (e.g., non-linear or interactive) relationship with model outputs. Individually randomised 'one-factor-at-a-time' (OAT) experiments are generated in which each parameter is repeatedly varied through the parameter space, over a predetermined number of levels, while all other parameters

are simultaneously varied. Three sensitivity measures are computed:  $\mu$  (mean) and  $\mu^*$  (absolute mean), which assess the overall influence of the parameter on the output, and  $\sigma$  (standard deviation), which estimates the extent to which each parameter is influenced (i.e., non-linear, interaction) by other factors. Non-influential parameters are those with  $\mu^* < 0.1$ , important factors are those for which  $\mu^* > 0.1$  and interacting / nonlinear factors are those for which  $\mu^* > 0.1$  and  $\sigma > 2 \times (\sigma/\sqrt{n})$ .

The number of repetitions (n) was 20, the number of parameters included in the analysis was 17 and each was divided into 8 levels (Table 4.10). Both model outputs and model parameters were scaled between 0 and 1 to allow for comparison between ecosystem services and to avoid an incorrect interpretation of factors that have different orders of magnitude (Iooss et al., 2020).

Table 4.10 Value range (minimum and maximum) of parameters used in the Morris sensitivity analysis by parameter group, parameter and code. Where  $\pm$  is given, default values were adjusted accordingly.

Group	Parameter	Code	Value	Unit
Elevation	Elevation	e1	$\pm 0.92$	m
Suspended particles	Chlorophyll-a	f1	$\pm 1.10$	$\text{mg m}^{-3} \text{h}^{-1}$
	Inorganic	f2	$\pm 8.43$	$\text{g m}^{-3} \text{h}^{-1}$
Temperature	Near surface temperature	t1	$\pm 5.70$	$^{\circ}\text{C h}^{-1}$
	Sea surface temperature	t2	$\pm 6.40$	$^{\circ}\text{C h}^{-1}$
Invertebrate abundance	<i>A. rubens</i>	i1	$\pm 72.81$	individual $\text{m}^{-2} \text{h}^{-1}$
	<i>C. crangon</i>	i2	$\pm 0.41$	individual $\text{m}^{-2} \text{h}^{-1}$
	<i>C. maenas</i>	i3	$\pm 0.75$	individual $\text{m}^{-2} \text{h}^{-1}$
Bird abundance	<i>C. canutus</i>	b1	$\pm 6723.00$	individual $\text{h}^{-1}$
	<i>H. ostralegus</i>	b2	$\pm 13929.00$	individual $\text{h}^{-1}$
	<i>L. argentatus</i>	b3	$\pm 1936.50$	individual $\text{h}^{-1}$
	<i>S. mollissima</i>	b4	$\pm 1341.00$	individual $\text{h}^{-1}$
Background mortality	Initial egg loss	z1	$\pm 0.23$	proportion $\text{h}^{-1}$
	Background pelagic loss	z2	$\pm 0.0005$	proportion $\text{h}^{-1}$
	Background benthic loss	z3	$\pm 0.00001$	proportion $\text{h}^{-1}$
Commercial harvest	Market	h1	$\pm 0.0005$	proportion $\text{h}^{-1}$
	Culture hand	h2	$\pm 0.0005$	proportion $\text{h}^{-1}$
	Culture dredge	h3	$\pm 0.25$	proportion $\text{h}^{-1}$

The Morris method produces multiple rankings of importance for each input parameter and the extent to which rankings agree is helpful for assessing the quality and robustness of the analysis. The top-down coefficient of concordance (TDCC) provides a useful measure in which emphasis is placed on agreement between high ranking parameters (Helton et al., 2005; Iman and Conover, 1987; Marino et al., 2008). The TDCC is calculated for each output variable by first ranking all input parameters by replicate and sensitivity measure ( $\mu^*$ ), and then replacing the ranks with their



corresponding savage scores (Savage, 1959). The TDCC values (0 – 1) and their corresponding p-values provide an indication of consistency. High values (> 0.9) indicate a high degree of reproducibility, which decreases with TDCC. The p-values for each TDCC (under the null hypothesis of zero concordance between parameter rankings) were calculated using the statistics T (approximating a  $\chi^2$ -distribution with  $k-1$  degrees of freedom) and the concordance between rankings is considered statistically significant when  $p < 0.05$ .

Once ecosystem services were quantified and their sensitivity evaluated, associations among them were quantitatively assessed via pairwise Spearman’s correlation coefficients (Mouchet et al., 2014). Positive correlations indicated a synergy between ecosystem services while negative correlations suggested a trade-off. Latin Hypercube sampling (multi-dimensional stratified sampling,  $n = 500$ ) was used to generate the simulation experiment on which correlation coefficients were calculated (Iman et al., 1981; McKay et al., 2000). The 18 model parameters considered for sensitivity analysis were included in the hypercube and the same ranges were used for its creation (Table 4.10).

## 4.4 Results

### 4.4.1 Environmental drivers

All temporal environmental data were extracted from the 1<sup>st</sup> of January 2015 to the 31<sup>st</sup> of December 2019 for the area designated a SAC within Morecambe Bay and converted to an hourly time series (Table 4.11, Figure 4.5).

Table 4.11 Average environmental conditions (temperature, suspended particles, water level, daylight) in Morecambe Bay, UK. Median, maximum and minimum values are given with units.

Driver	Unit	Median	Minimum	Maximum
Air temperature	°C y <sup>-1</sup>	11.0	1.4	22.8
Water temperature	°C y <sup>-1</sup>	11.8	6.4	19.2
Chlorophyll-a	mg m <sup>-3</sup> y <sup>-1</sup>	4.3	2.2	6.5
Inorganic particles	g m <sup>-3</sup> y <sup>-1</sup>	18.7	9.1	45.5
Water level	m y <sup>-1</sup>	0.2	-4.8	5.9
Day length	h y <sup>-1</sup>	13.5	8.8	19.0

Chlorophyll-*a* varied relatively little over the year while inorganic particle concentration was larger in the winter months. Temperature (air and water) and day length followed seasonal patterns, increasing over the summer months and decreasing during winter. Water levels followed monthly cycles during which extremes occurred twice.

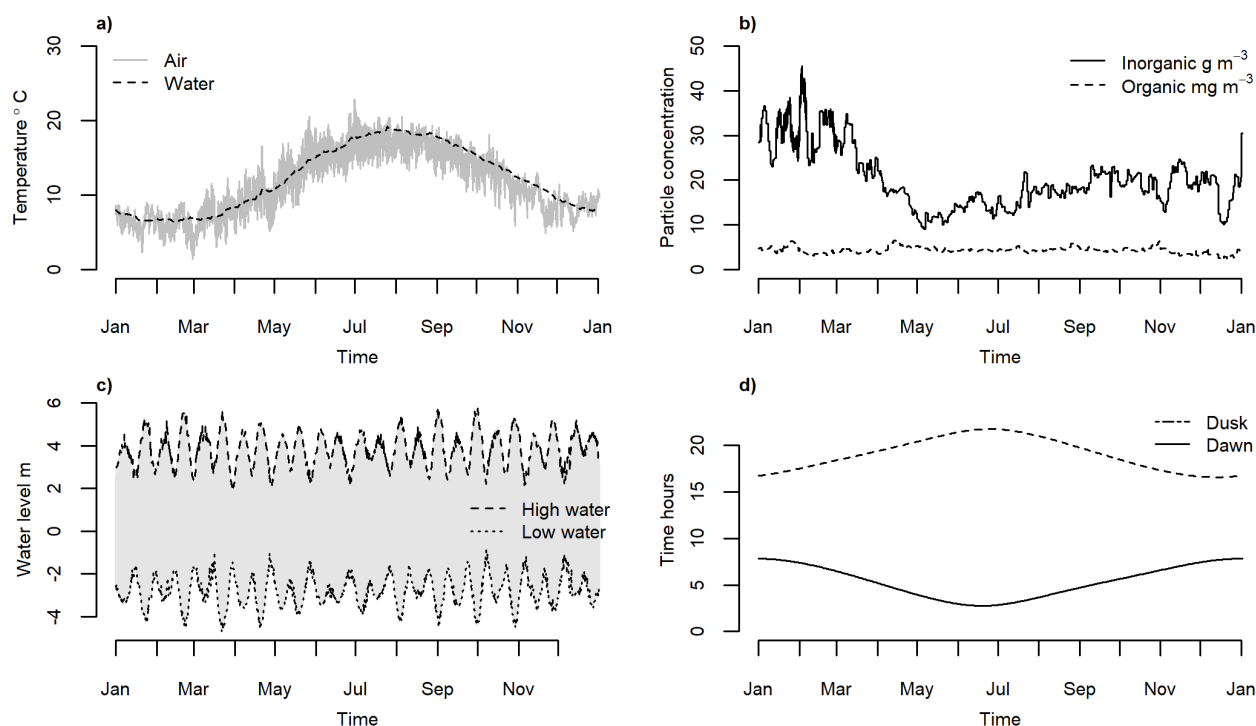


Figure 4.5 Environmental drivers of the global model environment. a) Temperature (black = water °C, grey = air °C), b) Suspended particle concentration (dashed = Chlorophyll-*a* mg m<sup>-3</sup>, black = suspended particulate inorganic matter g m<sup>-3</sup>), c) Tide height m (dashed line = high water mark m, dotted line = low water mark m) and d) Daylight hours (dashed = dusk, solid = dawn). Both Chlorophyll-*a* and suspended particulate inorganic matter are extracted from data measured by the SeaWiFS satellite, air temperature was taken from Walney Island weather station, water temperature is extracted from data measured by the NOA-18 satellite, water levels are taken from the Heysham tide gauge and daylight hours were predicted using R package *sunCalc*. a), b) and d) are averages from 2015-01-01 to 2019-12-31. c) is data from 2019.

#### 4.4.2 Parameter estimates

Seven parameters were estimated via calibration in which 2000 different parameter sets were assessed in their ability to meet two specified criteria. Parameter sets were selected on their ability to reproduce long-term estimates of annual biomass and landings. Final values for the seven parameters are the parameter set which best fit the criteria (Table 4.12).

Table 4.12 Estimates for 7 parameters: initial gamete loss, pelagic loss rate and benthic loss rate, reserve dependent mortality rate and harvest rate (market and culture).

Parameter	Unit	Code	Estimate	Standard deviation
Initial egg loss	% h <sup>-1</sup>	z1	29.087	23.9
Pelagic loss rate	% h <sup>-1</sup>	z2	0.058	0.046
Benthic loss rate	% h <sup>-1</sup>	z3	0.009	0.002
Reserve dependent mortality rate	% h <sup>-1</sup>	s1	0.031	0.01
Harvest consumer size (hand)	% h <sup>-1</sup>	h1	0.14	0.053
Harvest undersize (hand)	% h <sup>-1</sup>	h2	0.115	0.048
Harvest undersize (dredge)	% h <sup>-1</sup>	h3	33.831	25.768

#### 4.4.3 Parameter quality

The quality of parameter estimates was assessed by comparing simulated values for annual biomass by site and annual harvest by size (market, culture) with their respective observed values.

Observed values for annual biomass of intertidal *M. edulis* populations in Morecambe Bay did not differ between the three sites (Kruskal-Wallis,  $\chi^2(2) = 1.28$ ,  $p = 0.52$ , Figure 4.6b). Simulated values however did differ between sites (Kruskal-Wallis,  $\chi^2(2) = 8.7$ ,  $p < 0.05$ , Figure 4.6b), the largest values were predicted at Fleetwood (Dunn, median = 10879.03 g m<sup>-2</sup> y<sup>-1</sup>) compared to both Heysham (Dunn, median = 5709.87,  $z = 2.0$ ,  $p < 0.05$ ) and Foulney (Dunn, median = 4895.69,  $z = 3.0$ ,  $p < 0.05$ ). There was no difference in simulated annual biomass between Heysham and Foulney (Dunn,  $z = -1.15$ ,  $p = 0.25$ ). Compared to observed values, simulated annual biomass was underestimated (-36%) at Foulney (Wilcoxon's, difference = -3818.16 g m<sup>-2</sup> y<sup>-1</sup>,  $W = 180$ ,  $p < 0.05$ ) and overestimated (23%) at Fleetwood (Wilcoxon's, difference = 3059.83 g m<sup>-2</sup> y<sup>-1</sup>,  $W = 9$ ,  $p < 0.05$ ). There was no significant difference between observed and simulated values for annual biomass at Heysham (Wilcoxon, difference = -1634 g m<sup>-2</sup> y<sup>-1</sup>,  $W = 104$ ,  $p = 0.22$ ) or the average for Morecambe Bay (Wilcoxon, difference = 1353.28 g m<sup>-2</sup> y<sup>-1</sup>,  $W = 168$ ,  $p = 0.19$ , Figure 4.6a).

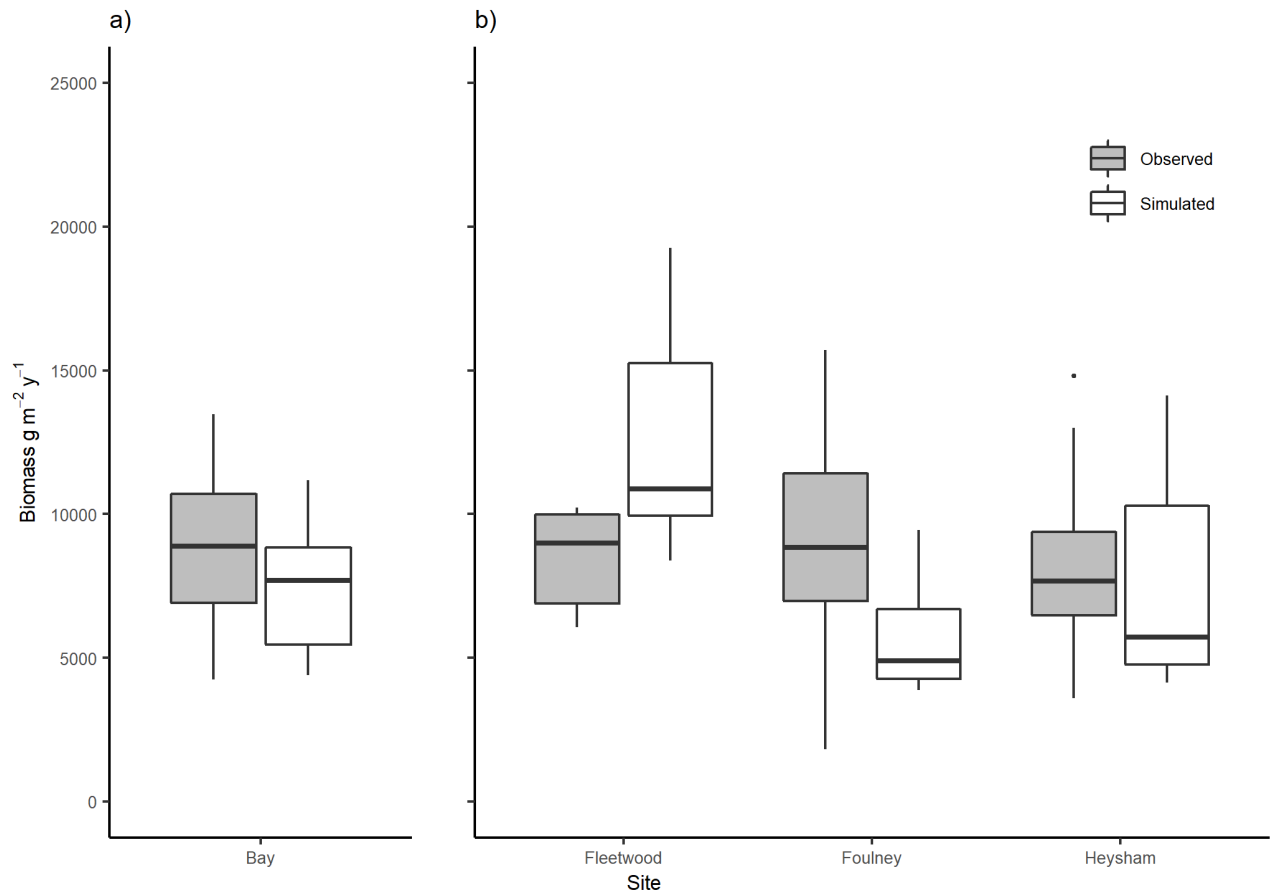


Figure 4.6 Observed (grey) and simulated (white) values of annual biomass  $\text{g m}^{-2} \text{y}^{-1}$  given by a) Morecambe bay and b) site (Fleetwood, Foulney, Heysham).

The observed annual harvest of market size (median =  $402.7 \text{ t y}^{-1}$ ) *M. edulis* in Morecambe Bay was significantly less (-86.8%) than that of culture size (median =  $3050 \text{ t y}^{-1}$ ) individuals (Wilcoxon's, difference = 2501,  $W = 14$ ,  $p < 0.001$ , Figure 4.7b, 6c). The simulated annual harvest of consumer size ( $423.8 \text{ t y}^{-1}$ ) *M. edulis* in Morecambe Bay was also significantly lower (-88.8%) than the harvest of undersize ( $3784.9 \text{ t y}^{-1}$ ) individuals (Wilcoxon's, difference = 3361.51,  $W = 0$ ,  $p < 0.001$ , Figure 4.7b, 6c).

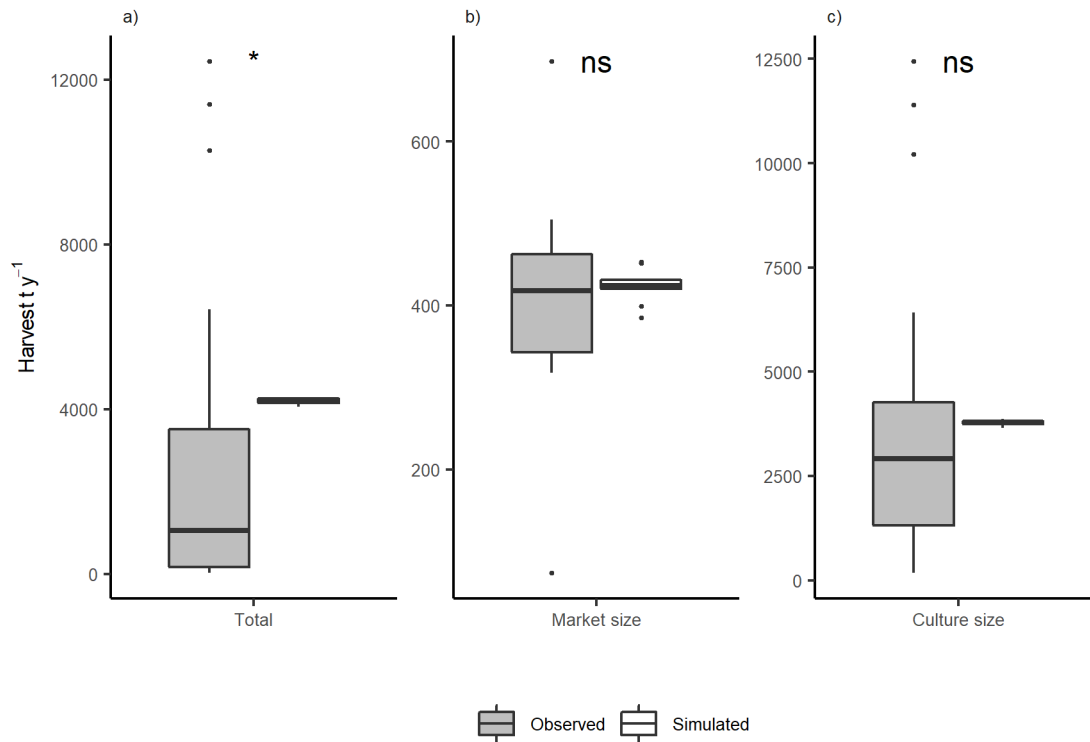


Figure 4.7 Observed (grey) and simulated (white) values of annual harvest rate  $t^{-1}$  in Morecambe Bay, UK. a) total harvest, b) – market size  $> 4.5$  cm and c) culture size 2 – 4 cm (note differing y axis scales).

There was no significant difference between observed and simulated values for annual harvest of both market size (Wilcoxon's, difference = 13.2,  $W = 25$ ,  $p < 0.36$ , Figure 4.7b) or culture size (Wilcoxon's, difference = 857.1,  $W = 70$ ,  $p < 0.11$ , Figure 4.7c) individuals. Simulated values for both harvest sizes were however greater than their respective observed values and the total simulated harvest was significantly larger than observed values (Wilcoxon's, difference = 3155.2,  $W = 60$ ,  $p < 0.001$ , Figure 4.7a).

#### 4.4.4 Model accuracy

Model accuracy was assessed temporally and spatially by comparing simulated values of biomass with observed values by season and elevation. Variation in observed and simulated seasonal biomass was described using Kruskal-Wallis and Dunn tests (post hoc), the two were compared using Wilcoxon's tests. The relationship between annual biomass (observed and simulated) and elevation was described and compared using linear regressions and an ANCOVA. The ANCOVA included biomass ( $g\ m^{-2}\ y^{-1}$ ) as the response variable with elevation (continuous, cube root transformed) and

value type (factor, 2 levels) as predictor variables. Observed and simulated values were compared further using a linear regression.

When evaluated by season, observed biomass varied significantly between spring and autumn (Wilcoxon's, difference = -3280.7,  $W = 1553$ ,  $p < 0.001$ , Figure 4.8). Values were significantly greater in autumn (median = 7644.3  $\text{g m}^{-2}$ ) compared to those in spring (median = 4389.8  $\text{g m}^{-2}$ ). Simulated values of monthly biomass also varied significantly between seasons (Wilcoxon's, difference = -2028.6,  $W = 0$ ,  $p < 0.001$ , Figure 4.8). Simulated biomass was again greater in autumn (median = 5902.3  $\text{g m}^{-2}$ ) compared to spring (median = 5687.7  $\text{g m}^{-2}$ ). Observed and simulated values of biomass did not differ significantly when comparing values for both spring (Wilcoxon's, difference = -1685.5,  $W = 238$ ,  $p = 0.06$ , Figure 4.8) and autumn (Wilcoxon's, difference = 260.9,  $W = 357$ ,  $p = 0.81$ , Figure 4.8).

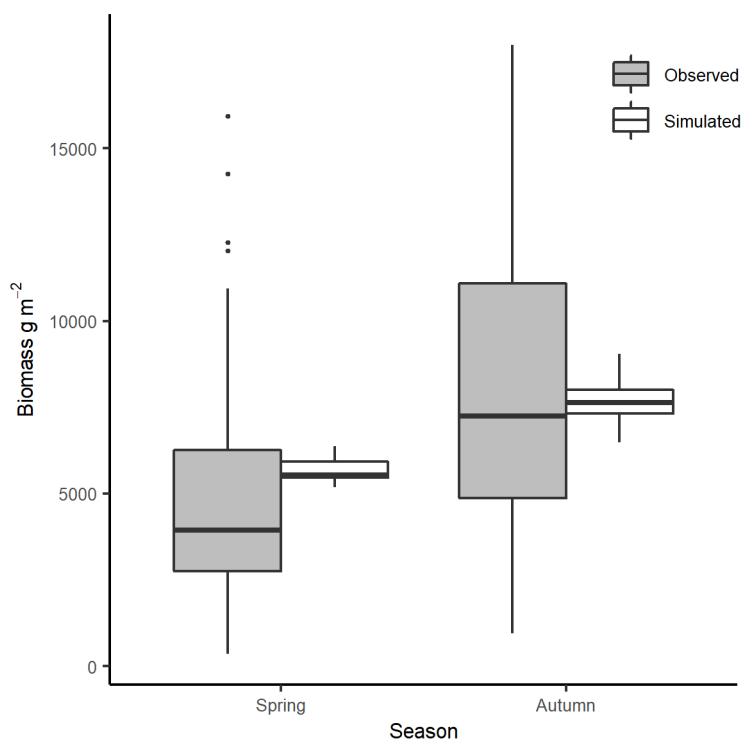


Figure 4.8 Observed (grey) and simulated (white) values biomass  $\text{g m}^{-2}$  season<sup>-1</sup> in Morecambe Bay, UK. Values are given by season (spring and autumn).

Observed annual biomass decreased significantly with increasing elevation (Linear regression,  $F_{(1, 67)} = 15.29$ ,  $R^2 = 0.16$ ,  $p < 0.001$ , Figure 4.9a). Simulated annual biomass also decreased significantly with increasing elevation (Linear regression,  $F_{(1, 67)} = 9.679$ ,  $R^2 = 0.11$ ,  $p < 0.05$ , Figure 4.9a). Data type (observed or simulated) had no significant effect on the slope of the relationship (ANCOVA,  $F_{(1,$

136) = 0.839,  $p = 0.361$ ). Simulated values of annual matched observed values reasonably well but low values were overestimated (intercept > 0) and high values were underestimated (slope < 1,  $F_{(1, 67)} = 34.14$ ,  $R^2 = 0.33$ ,  $p < 0.001$ , Figure 4.9b).

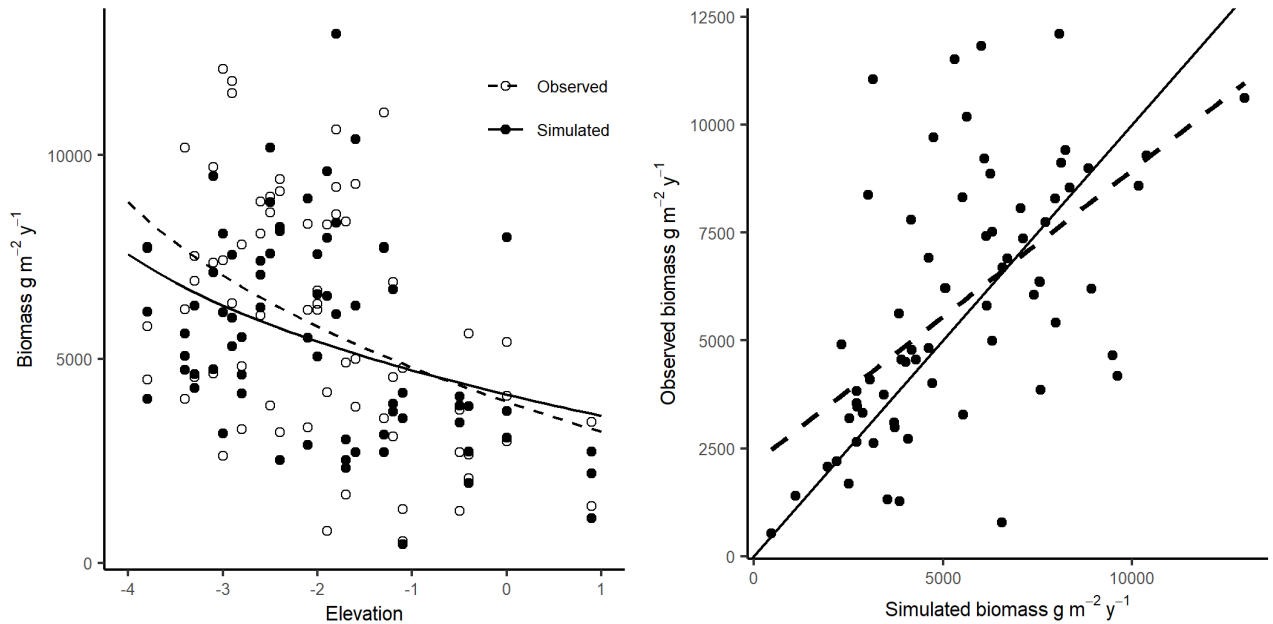


Figure 4.9 a) Observed (white) and simulated (black) values of annual biomass ( $\text{g m}^{-2} \text{y}^{-1}$ ) against elevation (m). The solid line is the prediction from a linear regression of simulated annual biomass against elevation back transformed ( $y = 12428 - 4853 * (x + 5)^{1/3}$ ,  $F_{(1, 67)} = 18.11$ ,  $R^2 = 0.20$ ,  $p < 0.001$ ). The dashed line is the prediction from a linear regression of observed annual biomass against elevation back transformed ( $y = 15723 - 6883 * (x + 5)^{1/3}$ ,  $F_{(1, 67)} = 18.11$ ,  $R^2 = 0.20$ ,  $p < 0.001$ ). b) Linear regression of observed against simulated annual biomass by elevation, the dashed line represents model the prediction ( $y = 2154.6 + 0.68x$ ,  $F_{(1, 67)} = 34.14$ ,  $R^2 = 0.33$ ,  $p < 0.001$ ) and the solid line represents a slope of 1.

When evaluated by age, there was no significant difference between observed and simulated values of mean annual biomass (chi squared,  $\chi^2 = 450$ ,  $df = 435$ ,  $p = 0.30$ , Figure 4.10).

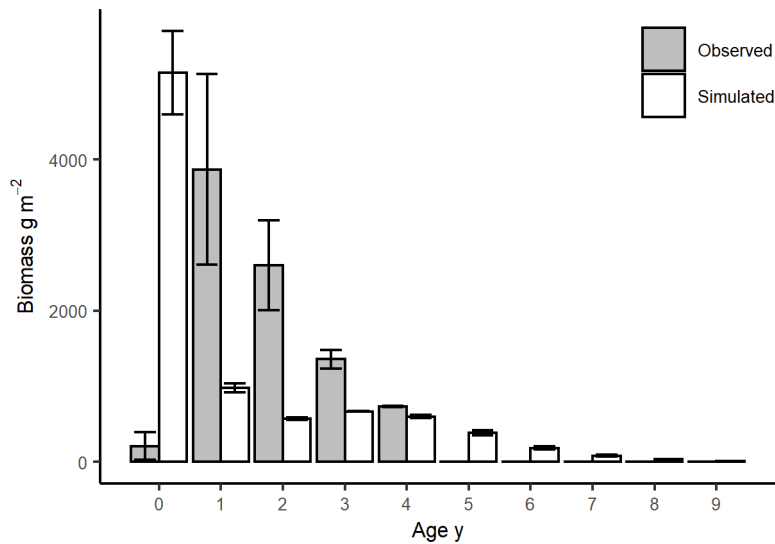


Figure 4.10 Observed (grey) and simulated (white) values for mean annual biomass ( $\text{g m}^{-2} \text{y}^{-1}$ )  $\pm$  standard error in Morecambe Bay. Values are given by age (0 – 9).

#### 4.4.5 Ecosystem services

Six ecosystem services were quantified and their sensitivity to environmental change and each other (i.e., trade-offs and synergies) were assessed. For correlation and sensitivity analysis both nitrogen and phosphorous removal were combined and considered to be one service, nutrient removal.

Ecosystem services were quantified by running simulations ( $n = 10$ ) for 30 years using default parameter values with the annual net (carbon, nitrogen and phosphorous) flux, harvest (market size and undersize) and biomass output (Table 4.13, 17). The intertidal *M. edulis* population in Morecambe Bay was predicted to act as an annual sink for carbon ( $-4416.8 \pm 118.7 \text{ t C y}^{-1}$ ), nitrogen ( $-225.5 \pm 5.2 \text{ t N y}^{-1}$ ) and phosphorous ( $-106.6 \pm 3.8 \text{ t P y}^{-1}$ ). The annual provision of food for direct consumption ( $408.2 \pm 12.2 \text{ t y}^{-1}$ ) and use in aquaculture ( $3488.9 \pm 28.4 \text{ t y}^{-1}$ ) accounted for 10% of the population's annual biomass ( $34932.4 \pm 1241.3 \text{ t y}^{-1}$ , Table 4.13).



Table 4.13 Estimated annual quantities of six ecosystem services delivered by an intertidal *M. edulis* population in Morecambe Bay, UK. All values are given as tonnes per hectare per year ( $\text{t ha}^{-1} \text{y}^{-1}$ ) and as tonnes per year ( $\text{t y}^{-1}$ ) for Morecambe Bay. Estimates were made using default settings. Negative values represent sinks and positive values represent sources.

Description	$\text{t ha}^{-1} \text{y}^{-1}$		$\text{t y}^{-1}$	
	Mean	S.E.	Mean	S.E.
Net carbon flux	-10.59	0.28	-4416.84	118.73
Net nitrogen flux	-0.54	0.01	-225.47	5.16
Net phosphorus flux	-0.26	0.01	-106.6	3.76
Biomass	83.78	2.98	34932.43	1241.29
Harvest market	0.98	0.03	408.22	12.24
Harvest culture	8.37	0.04	3488.92	18.54

The largest nutrient sinks were dead shell ( $7.6 \text{ t C ha}^{-1} \text{y}^{-1}$ ), dead shell and tissue ( $0.3 \text{ t N ha}^{-1} \text{y}^{-1}$  and  $0.3 \text{ t N ha}^{-1} \text{y}^{-1}$ ) and tissue ( $0.3 \text{ t P ha}^{-1} \text{y}^{-1}$ ) for carbon, nitrogen and phosphorous respectively (Table 4.14). The largest source of carbon was respiration ( $1.6 \text{ t C ha}^{-1} \text{y}^{-1}$ ) while the largest source of nitrogen ( $0.1 \text{ t N ha}^{-1} \text{y}^{-1}$ ) and phosphorus ( $0.03 \text{ t P ha}^{-1} \text{y}^{-1}$ ) was excretion (Table 4.14).

Table 4.14 Estimated annual fluxes (source or sink) of three ecosystem services (carbon, nitrogen, phosphorous removal) delivered by an intertidal *M. edulis* population in Morecambe Bay, UK. All values are given as tonnes per hectare per year ( $t\ ha^{-1}\ y^{-1}$ ) and as tonnes per year ( $t\ y^{-1}$ ) for Morecambe Bay.

Nutrient	Flux	Direction	$t\ ha^{-1}\ y^{-1}$		$t\ y^{-1}$	
			Mean	S.E.	Mean	S.E.
Carbon	Dead shell	Sink	7.6	0.3	3154.9	116.7
	Biodeposit	Sink	1.0	0.02	406.5	10.1
	Harvest	Sink	1.1	0.01	447.6	2.7
	Live shell	Sink	5.2	0.1	2153.5	44.3
	Tissue	Sink	1.3	0.01	546.3	3.5
	Dead shell	Source	1.1	0.04	441.7	16.3
	Biodeposit	Source	0.3	0.01	130.1	3.2
	Live shell	Source	1.2	0.02	495.5	10.3
	Tissue	Source	1.6	0.04	678.5	16.8
Nitrogen	Dead shell	Sink	0.3	0.01	116.9	4.3
	Biodeposit	Sink	0.1	0.003	46.8	1.2
	Harvest	Sink	0.1	0.001	38.3	0.2
	Live shell	Sink	0.2	0.004	79.8	1.6
	Tissue	Sink	0.3	0.002	115.7	0.7
	Dead shell	Source	0.04	0.001	16.4	0.6
	Biodeposit	Source	0.003	0.0001	1.4	0.04
	Tissue	Source	0.1	0.002	38.6	1.0
	Phosphorus	Dead shell	Sink	0.01	0.0003	3.2
Biodeposit		Sink	0.01	0.0002	3.4	0.1
Harvest		Sink	0.01	0.0001	3.5	0.02
Live shell		Sink	0.01	0.0001	2.2	0.05
Tissue		Sink	0.03	0.0002	13.7	0.1
Dead shell		Source	0.001	0.00004	0.5	0.02
Biodeposit		Source	0.000002	0.0000001	0.001	0.00002
Tissue		Source	0.01	0.0002	3.0	0.1

The sensitivity of ecosystem services to environmental change was assessed via a global sensitivity analysis. The Morris method was used to provide a measure of sensitivity for each ecosystem service in relation to 17 environmental parameters. The results were used to rank the ecosystem services in order of sensitivity and identify highly influential parameters. The analysis showed a high level concordance in the ranking of influential parameters for food provisioning (market and culture), habitat provisioning, nutrient removal and carbon sequestration (Table 4.15).

Table 4.15 Top-down concordance coefficient (TDCC),  $\chi_2$  and associated p value for the Morris method sensitivity analysis.

Output	TDCC	$\chi_2$	p value
Food provisioning market	0.79	268.35	< 0.001
Food provisioning culture	0.64	218.42	< 0.001
Habitat provisioning	0.70	169.61	< 0.001
Carbon removal	0.79	200.09	< 0.001
Nutrient removal	0.60	203.31	< 0.001

More parameters were identified as influential to regulatory services compared to provisory services. Of the 17 parameters included in the sensitivity analysis, 6 were identified as influential to carbon, nitrogen and phosphorous removal, 7 to habitat provisioning and 4 to the provision of market and culture size individuals. All influential parameters were also classed as interactive to their respective ecosystem services (Figure 4.11).

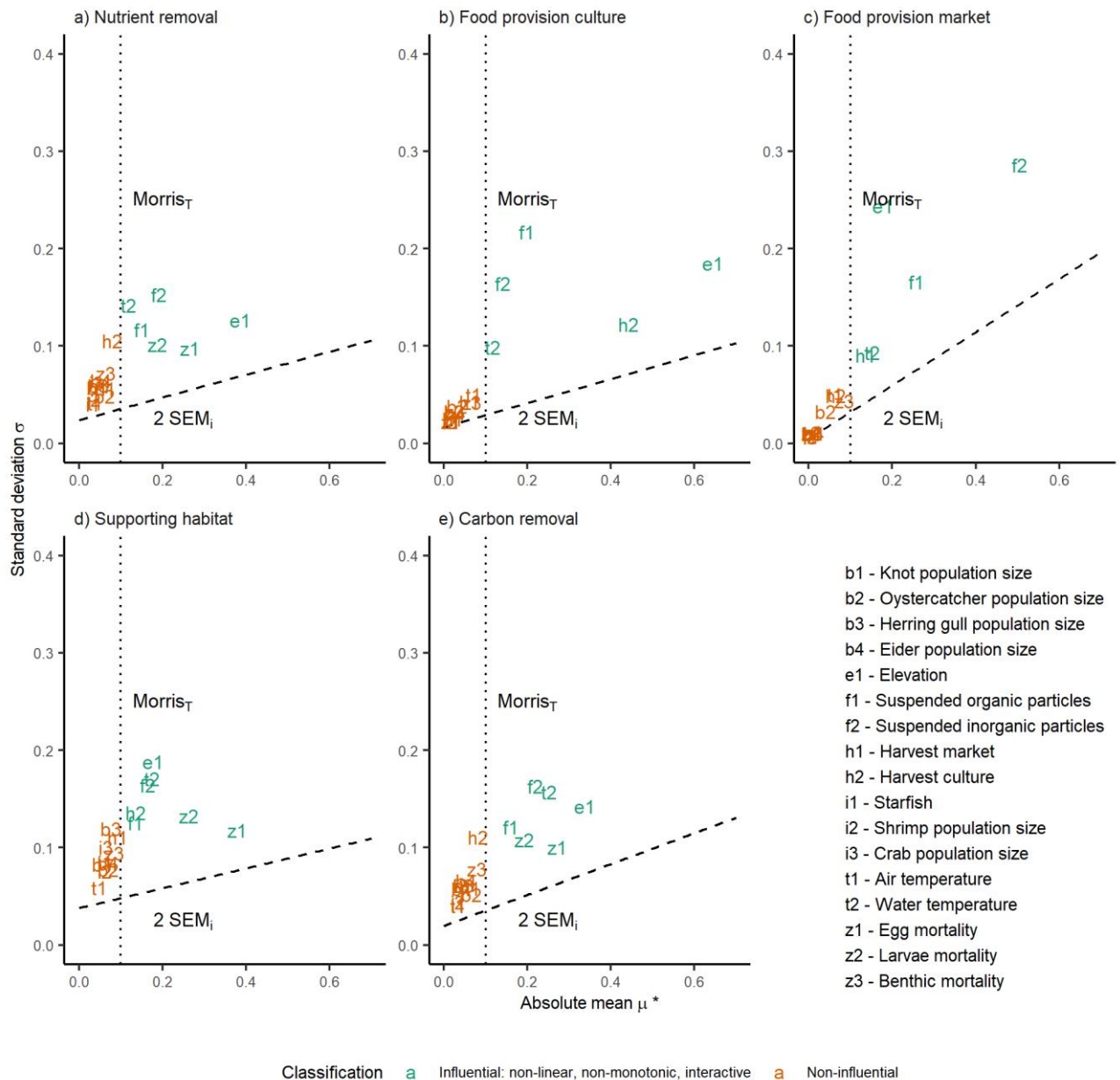


Figure 4.11 Results from the Morris sensitivity analysis in which 17 parameters (see plot legend) were assessed in relation to their influence over five model outputs (Nutrient removal, Food provision culture, Food provision market, Habitat provisioning, Carbon removal). Plots show standard deviation ( $\sigma$ ) against absolute mean ( $\mu^*$ ) of the scaled (0 – 1) elementary effects. Values (orange) <  $Morris_T$  are considered non-influential, values  $\geq Morris_T$  and <  $2 SEM_i$  are influential but not interactive and values (green)  $\geq Morris_T$  and  $\geq 2 SEM_i$  are influential and interactive.

The mean of elementary effects provides an indication of the direction of change (positive or negative) each parameter produced (Figure 4.12). The provision of both market and culture size individuals was sensitive to changes in the concentration of suspended inorganic (negative) and organic (positive) particles, elevation (positive), sea temperature (market: positive, culture: negative) and the rate at which each was harvested (positive). Nutrient removal, carbon removal

and habitat provisioning were all influenced by changes to elevation (negative), suspended inorganic (negative) and organic (positive) particle concentration, initial gamete (negative) and background pelagic mortality (negative), and water temperature (negative). Habitat provisioning was also sensitive to changes in the rate at which culture size individuals were harvested by hand (negative). All mean elementary effects are shown (Figure 4.12).

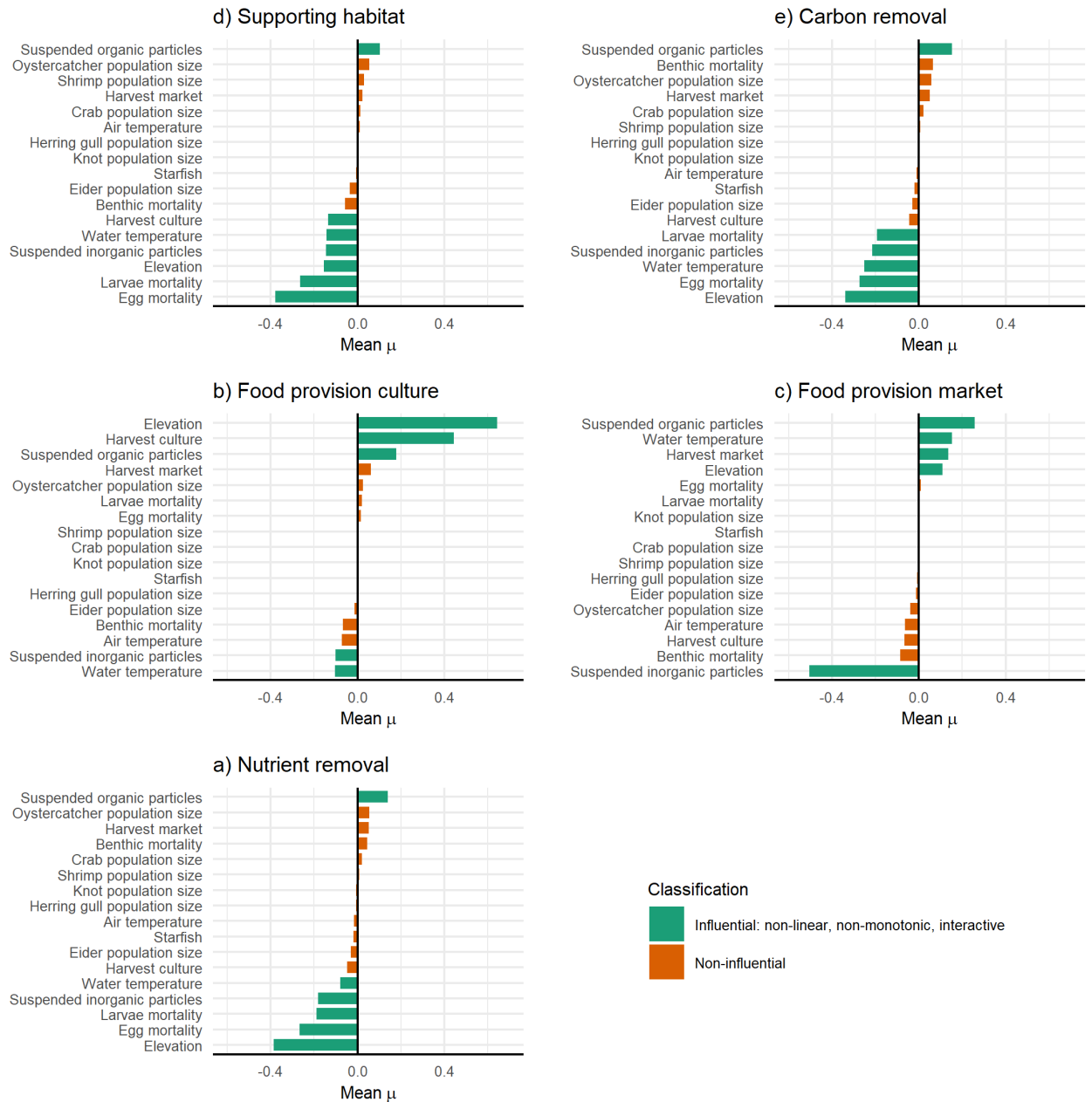


Figure 4.12 Mean elementary effect of the Morris sensitivity analysis for each parameter and ecosystem service. Negative numbers represent negative influences while positive numbers represent positive influences. Parameters classed as influential are coloured green and those classed as non-influential are colour orange.

Interactions between ecosystem services were assessed using Spearman's rank correlation coefficients (Figure 4.13). All ten ecosystem service pairs were significantly correlated, a negative correlation (trade-off) occurred between the provision of culture size individuals and three other services (carbon removal, nutrient removal and biomass). The remaining seven pairs of ecosystem services were positively (synergy) correlated.

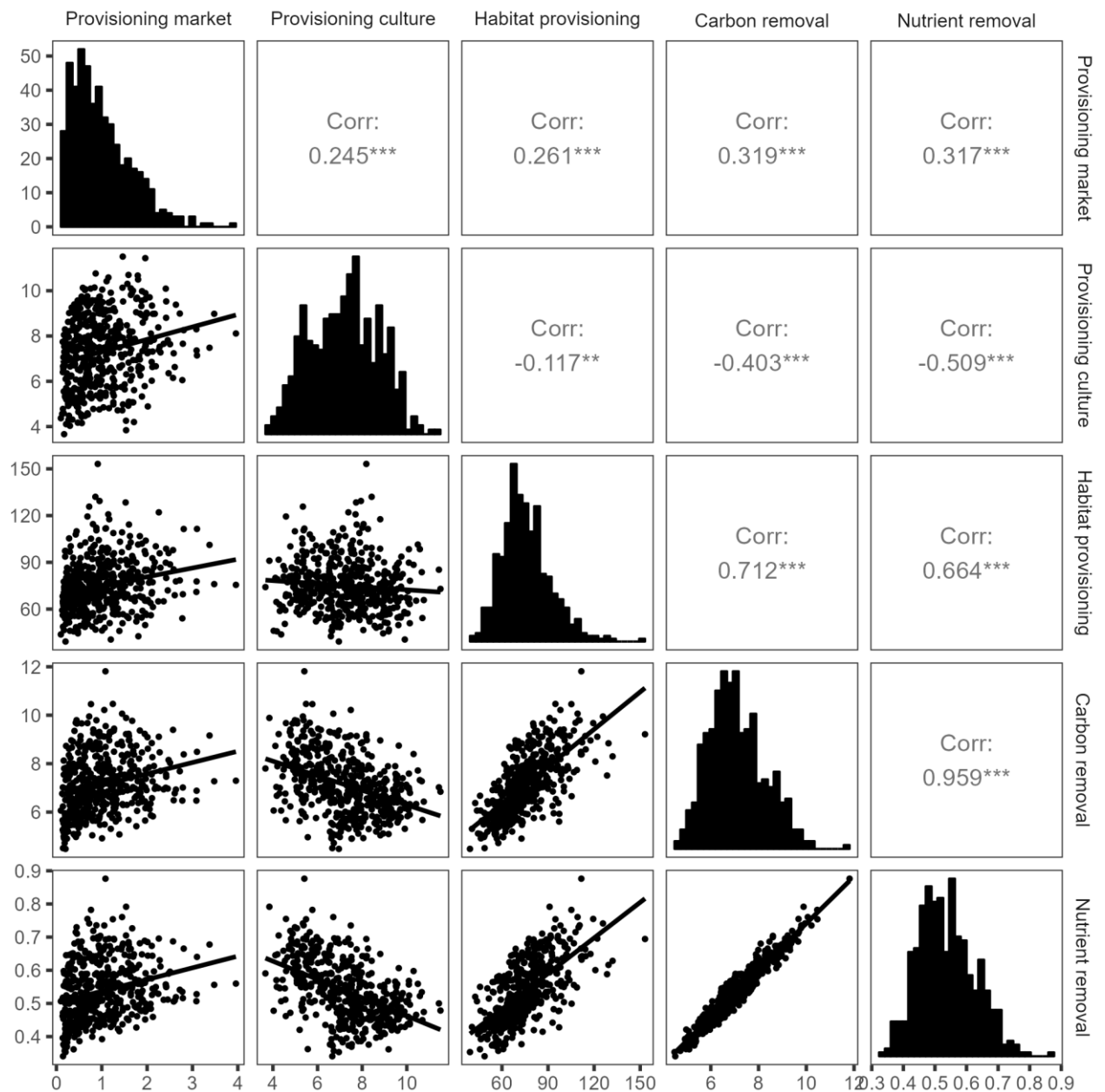


Figure 4.13 Spearman's correlation plot, histograms and coefficients between five ecosystem services provided by *M. edulis* (n = 500, \* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001). Food provisioning market = harvest of individuals > 4.5 cm, Food provisioning culture = harvest of individuals 2 - 4 cm, habitat provisioning = population biomass, carbon removal, nutrient removal = nitrogen + phosphorus removal.

All trade-offs involved the provision of culture sized individuals and occurred with nutrient removal (moderate), carbon removal (moderate) and habitat provisioning (weak). The strongest synergy occurred between nutrient and carbon removal (very strong), there were also notable synergies between biomass and both carbon (strong) and nutrient removal (strong). The final synergies involved the provision of market sized individuals and occurred with nutrient (weak) and

carbon removal (weak), habitat provisioning (weak) and the provision of culture size individuals (weak).

#### 4.5 Discussion

Marine ecosystems are characterized by complex interactions between biological and physical processes (Barbier et al., 2008). Bivalve populations deliver a myriad of ecosystem services which must be strategically managed to ensure their sustainable use (Barbier et al., 2011). Interactions between ecosystem services complicate management because human activities can inadvertently impact (trade-offs and synergies) multiple ecosystem services simultaneously (Bennett et al., 2009; Howe et al., 2014). Identifying these interactions and assessing their relative sensitivity and strength is the focus of this study. A set of ecosystem services delivered by a commercially harvested intertidal bivalve (*M. edulis*) population were quantified and their sensitivity to changes in environmental drivers and each other assessed. The population acted as an annual sink for nutrients (carbon, nitrogen and phosphorous) of which approximately 10% was attributed to commercial harvest. A sensitivity analysis indicated that ecosystem services were generally more sensitive to changes in environmental drivers (e.g., elevation, suspended matter concentrations, temperature) and pre-settlement mortality (egg and larvae) compared to mortality throughout the benthic life stage. Trade-offs were associated with provisioning services and synergies with regulatory services. The sustainable management of natural bivalve populations is discussed.

Natural intertidal populations of *M. edulis* were predicted to serve as annual sinks for carbon ( $-10.6 \pm 0.3 \text{ t C ha}^{-1} \text{ y}^{-1}$ ), nitrogen ( $-0.5 \pm 0.01 \text{ N t ha}^{-1} \text{ y}^{-1}$ ) and phosphorous ( $-0.03 \pm 0.01 \text{ t P ha}^{-1} \text{ y}^{-1}$ ). These estimates suggest that *M. edulis* reefs deposit similar amounts of carbon and nitrogen per hectare as other coastal habitats (e.g., saltmarsh, mangroves, sea grass) making them potentially valuable for mitigating climate change and the symptoms of eutrophication (Aoki et al., 2020; Bilkovic et al., 2017; McLeod et al., 2011). The permanency with which nutrients are removed by bivalve populations is however widely discussed. Many assessments of bivalve aquaculture for example consider harvested individuals as being permanently removed from the ecosystem (Aubin et al., 2018; Higgins et al., 2011; Kotta et al., 2020). Tissue is however consumed and therefore re-enters systems via digestion or as waste material, while bivalve shells are generally discarded to be buried at land fill sites. Burial in the sediments is perhaps the most permanent sink simulated as nutrients can be sequestered in deep sediments for hundreds to thousands of years (Fodrie et al.,



2017). Shell (dead or live) formed the largest sink indicating that its burial and dissolution rate are important fluxes for which measurements are valuable (Waldbusser et al., 2013). Very few studies have reported burial rates, but they are thought to depend primarily on the reworking of sediments by storms and currents (Davies et al., 1989; Parsons-Hubbard et al., 1999). Relatively more is known of dissolution rates (predominantly *C. virginica*) which vary considerably ( $2 - 70 \% \text{ y}^{-1}$ ) in relation to shell type (condition, species, age), environmental conditions (e.g., pH, epibionts, temperature) and time (Pace et al., 2020; Ries et al., 2016; Tomašových et al., 2014; Waldbusser et al., 2011). Dead shell is a fundamental part of bivalve reef functioning (e.g., biodiversity, nutrient sink, sedimentation) and persistence (e.g., recruitment, survival), its removal or disturbance degrades reef structure and increases their potential to act as nutrient sources (Baldocchi, 2008; Evans and Belnap, 1999; Running, 2008; Shigeta et al., 2022). Not returning shell material to the habitat from which it was extracted has been implicated as a major driver where overexploitation has resulted in a populations collapse (Blake and Ermgassen, 2015). Sustainable management of bivalve reefs therefore includes protecting shell accumulation, minimising its disturbance and replacing that which is removed (Craeymeersch and Jansen, 2019; Kent et al., 2017; Powell and Klinck, 2007).

Low elevations held more biomass and removed a greater quantity of nutrients (carbon, nitrogen, phosphorous) compared to high and are therefore potential sites for conservation or restoration of these ecosystem services. Efforts to restore bivalve reefs have focused on *Ostreidae* spp. and have proved more successful within high intertidal zones (Schulte et al., 2009; zu Ermgassen et al., 2020). High shore reefs experience greater rates of survival and recruitment, and also provide shoreline protection and erosion control (Hogan and Reidenbach, 2022; Schulte et al., 2009; Walles et al., 2015). Restoration of *Mytilidae* spp. takes place within low intertidal and subtidal zones and has proved less successful (Fariñas-Franco and Roberts, 2014; Temmink et al., 2022; Wilcox et al., 2018). The protection of existing *Mytilidae* spp. reefs and habitats suitable for settlement is thought more likely to protect and promote reef development (van der Meer et al., 2019). The degree to which services are provided is variable (spatially, temporally, species) and the incorporation of local knowledge will be important when designating protected areas (Fodrie et al., 2017; Hogan and Reidenbach, 2022; zu Ermgassen et al., 2020).

All ecosystem service pairs were significantly correlated which underlines the complex interactions found between coastal ecosystem services (Boerema and Meire, 2017; Townsend et al., 2018). The trade-offs among ecosystem services exclusively involved the harvest of culture size individuals which is understood to subsequently reduce the size (i.e., biomass) of the populations on which it occurs (Dolmer et al., 1999; Smaal et al., 2021). Overexploitation of undersize individuals

has also been frequently implicated as a driver where bivalve (*Mytilidae* spp.) fisheries have collapsed (Dare et al., 2004; Ens et al., 2004; Jeffs et al., 1999). Synergies occurred between provisioning and regulatory services when the harvest was temporally restricted (i.e., minimum landing size). Management of bivalve populations often constrains harvest to reduce negative environmental impacts (Hall-Spencer et al., 2003; Nielsen et al., 2021; Smaal et al., 2021; Troost et al., 2022). The ability to anticipate trade-offs and adapt management strategies accordingly is thought more likely to produce synergies than planning for a them from the outset (Howe et al., 2014). The strongest synergies occurred between the removal of nutrients (nitrogen, phosphorous and carbon) and the provision of habitat provisioning (i.e., biomass). Management which aims to improve, preserve and restore bivalve reefs is therefore expected to best promote the provision of regulatory services (McLeod et al., 2019; zu Ermgassen et al., 2020).

The present model does not incorporate the hydrological processes associated with estuaries which transport the physical, biological and chemical properties of water (e.g., salinity temperature, phytoplankton, nutrients) throughout the system (Hoeksema et al., 2018; Masson and Peña, 2009; Sutherland and O'Neill, 2016). Hydrodynamic conditions are significant drivers of interactions between organisms and environments (Plenty et al., 2018; Poh et al., 2019; Trancoso et al., 2005). Bivalves for example are transported in the water column during their pelagic stage and directly depend on such processes (Beukema and de Vlas, 1989; Knights et al., 2006). Recruitment success was highlighted as influential to ecosystem services but cannot be deterministically predicted without incorporating these mechanisms. The next stage of development would be to couple the current model with a hydrodynamic model in order to improve current predictions and allow for additional assessments such as the impact of changes in the estuary morphology to ecosystem functioning (Saraiva et al., 2017).

Decision makers around the world are looking to the ecosystem services framework to make better decisions about the environment (Granek et al., 2010). Such information allows managers to set conservation priorities and exploit natural resources in an informed and inclusive manner. The complexity and connectivity of coastal ecosystems is challenging, and ecological models can provide important insights (Rieb et al., 2017). No single management strategy is likely to address the many trade-offs associated with marine ecosystem-based management, approaches will differ between systems and most likely must change through time. Robust and sustainable management of coastal ecosystems will require detailed knowledge (e.g., location, quantity, value) of all the goods and services involved, as well as an understanding of how they respond to environmental change (Dade et al., 2019; Rullens et al., 2022; van der Schatte Olivier et al., 2018). The ongoing conflict between

food provision and ecosystem function demands a continued effort to develop theory and understanding using all forms of experimental (natural, laboratory, simulation) setups.

#### 4.6 Author contributions

Supervision: J. G. Hiddink and L. S. Cordes

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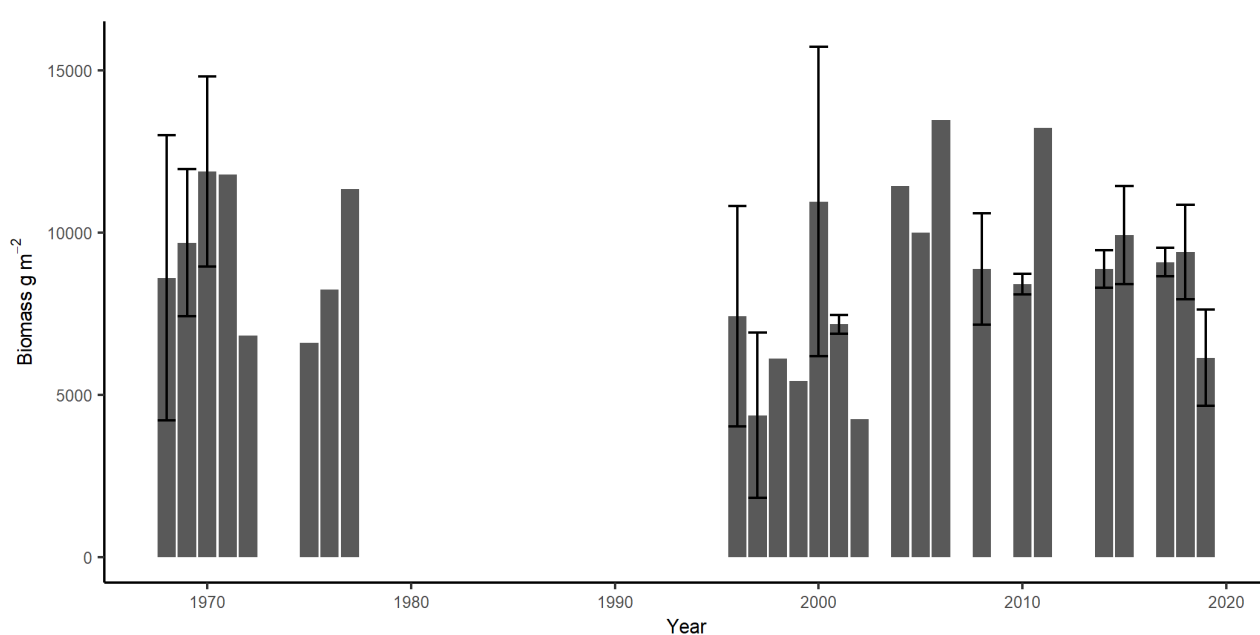


Figure 4.14 Annual biomass ( $\text{g m}^{-2} \text{yr}^{-1}$ ) estimates  $\pm 1$  standard deviation for *M. edulis* population in Morecambe Bay between 1968 and 2019. Values were provided by NWIFCA, 2020.

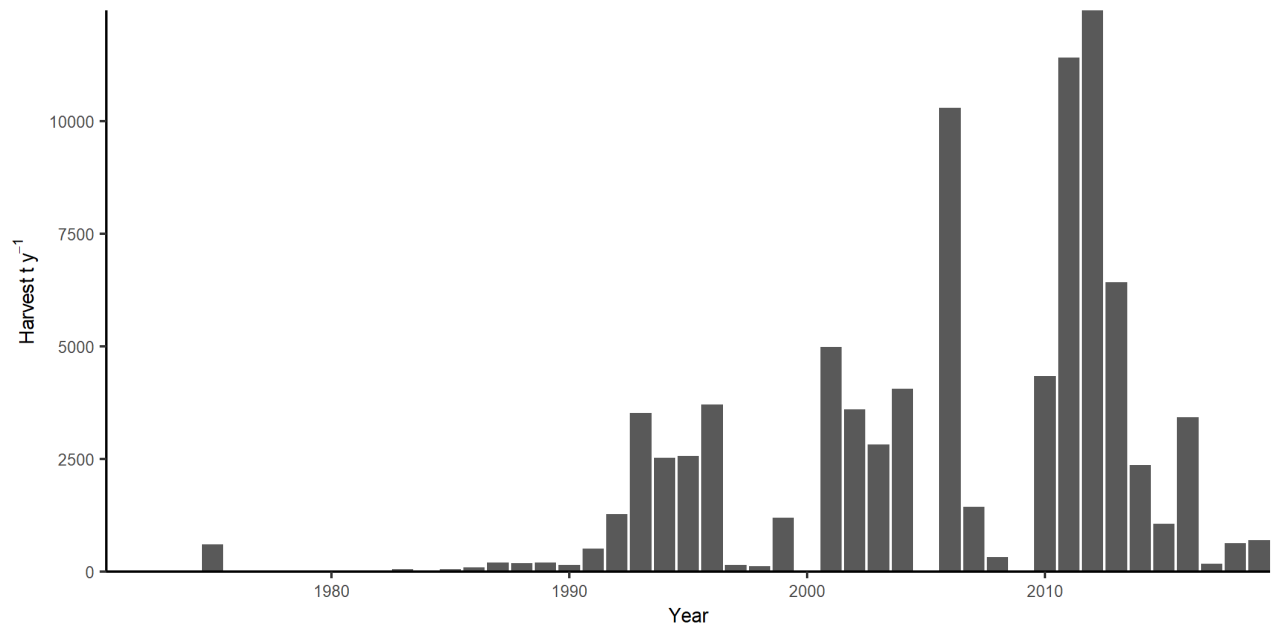


Figure 4.15 Annual harvest (t yr<sup>-1</sup>) of *M. edulis* in Morecambe Bay between 1971 and 2019. Values were provided by NWIFCA, 2020.

## 5. Balancing coastal bird conservation with commercial bivalve harvest

A. Feather<sup>1</sup>, J. G. Hiddink<sup>1</sup>, L. S. Cordes<sup>1</sup>

*1 - School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB*

### 5.1 Abstract

Many species of coastal bird are experiencing long-term population declines and changes in the availability of intertidal invertebrate resources are thought partly responsible. The complexity (e.g., non-linear, interactive, extensive) of estuarine systems complicates analysis via traditional methods and novel tools are required if the drivers of long-term declines are to be understood. This study developed an existing Agent-based model (ABM) for simulating the foraging behaviour of coastal birds in Morecambe Bay in response to environmental change. The foraging decisions (e.g., location) of individual birds were based on fitness-seeking behaviours and their intake rates were calculated as a function of the environment (e.g., resource density). The model predicted average annual body condition for four species of coastal bird (*Calidris canutus*, *Haematopus ostralegus*, *Larus argentatus* and *Somateria mollissima*) in response to environmental conditions. The sensitivity of each species condition to changes in resource abundance was systematically assessed to identify possible drivers of declines with particular focus on the harvest of *Mytilus edulis*, a commercially important bivalve. The density of bivalve (commercial and non-commercial) populations was highlighted as important to all species and the density of terrestrial resources was important to *H. ostralegus* and *L. argentatus*. Both *S. mollissima* and *C. canutus* were notably sensitive to changes in small, non-commercial bivalve species (e.g., *Macoma balthica*) which were relatively widespread compared to commercial species (e.g., *Cerastoderma edule*). *S. mollissima* was found to be most sensitive to the harvest of *M. edulis*, specifically culture sized individuals and particularly when other bivalve abundance was low. The results indicate that current long-term population declines experienced by the molluscivorous birds of Morecambe Bay might be linked to a decrease in the abundance of non-commercial bivalve species. Overexploitation of culture size *M. edulis* has likely exacerbated the situation by driving *S. mollissima* to feed on resources preferred or required by other species. Balancing the conservation of coastal birds with commercial bivalve harvest therefore requires knowledge of non-commercial species and an understanding of the terrestrial resources available.



## 5.2 Introduction

Intertidal wetlands provide a wide range of ecosystem services and support many conservation interests (Carss et al., 2020; Zedler and Kercher, 2005). Human activities (e.g., development, recreation, fishing) within coastal environments are currently driving biodiversity loss and degrading the goods and services they provide (Halpern et al., 2008; Worm et al., 2006). Coastal birds are an important element of intertidal ecosystems because of the roles they play in food webs, and in physical and chemical processes within mudflat sediments (Kuwae et al., 2012, 2008; Mathot et al., 2018). Most species are migratory and primarily use intertidal habitats throughout the winter and whilst travelling (spring and autumn) to and from breeding grounds (Frost et al., 2021; Møller et al., 2019). Their distribution and behaviour during this time reflects the underlying ecological conditions within intertidal habitats and therefore provides an indication of local ecosystem health (Atkinson et al., 2010; Prosser et al., 2017; Van Roomen et al., 2012). Monitoring of non-breeding coastal bird numbers indicates that long-term population declines are occurring for a number of species across the globe (Møller et al., 2019; Piersma et al., 2016; Studds et al., 2017; Wang et al., 2018). The drivers of declines are not well understood and research aiming to improve understanding is needed.

The drivers of declines are thought in part linked to changes in the availability (spatial and temporal) of intertidal invertebrate resources (Pearce-Higgins et al., 2017; Sutherland et al., 2012; Van Roomen et al., 2012). The mechanisms believed responsible are generally related to processes and activities (e.g., nutrient inputs, climate change, exploitation, commercial fisheries, disturbance, invasive species) which alter the size, structure and diversity of benthic invertebrate communities (Baker et al., 2004; Laursen and Møller, 2014; Maclean et al., 2008; Waser et al., 2016; Whittingham et al., 2019). Long term variation (increase and decrease) in nutrient input rates (e.g., agricultural runoff, sewage treatment) is correlated with changes to the community structures of both phytoplankton and macrozoobenthos (Philippart et al., 2007). High inputs favour phytoplankton and filter feeding (e.g., bivalves) communities while low inputs limit phytoplankton and favour deposit feeding (e.g., polychaetes) communities (Hutchings, 1998; Laursen and Møller, 2014; Philippart et al., 2007). Warming temperatures in temperate regions are increasing species diversity (e.g., immigration) and abundance, enhancing individual growth and overwinter survival, but they are reducing recruitment for many bivalve species (Beukema et al., 2017b; Beukema and Dekker, 2020a, 2014, 2011; Dekker and Beukema, 2021). Exploitation of intertidal invertebrates has occasionally but significantly reduced the abundance of target and non-target species from which it takes years

for benthic communities to recover (Baker et al., 2004; Beukema, 1995, 1993; Beukema and Cadée, 1996; Clarke et al., 2017; Piñeiro-Corbeira et al., 2018; Smaal et al., 2021). Many human activities (e.g., recreation, aquaculture, hunting) also temporarily (i.e., disturbance) and permanently (i.e., habitat loss) exclude coastal birds from preferred foraging and roosting habitats (Stillman et al., 2007; Whittingham et al., 2019). Ultimately, the processes and mechanisms which degrade the quality (i.e., diversity, density, abundance, size) of, or exclude birds from their preferred feeding areas can potentially drive them to poorer quality areas where increased densities intensify interference and competition for food (Goss-Custard, 1977).

Intertidal bivalve populations are a particularly important source of food for coastal birds because they are both relatively abundant and comparatively high in caloric value (Beukema et al., 2010; Laursen et al., 2019b; Van Donk et al., 2019). Large aggregations of bivalves can support internationally important numbers of coastal birds and decreases in bivalve abundance can have a considerable impact on coastal bird populations (Atkinson et al., 2010; Camphuysen et al., 2002; Laursen and Møller, 2014; Van Gils et al., 2006a). Intense exploitation of bivalves has coincided with increased starvation and mortality within coastal bird populations causing a long standing conflict between conservationists and industry (Atkinson et al., 2003; Camphuysen et al., 2002, 1996; Laursen et al., 2009; Smit et al., 1998; Verhulst et al., 2004). Commercial harvesting of bivalves has strong ecological effects on benthic invertebrate communities (Clarke et al., 2018, 2017; Piersma et al., 2001). Harvesting routinely removes the larger individuals which can cause phenotypic change, changes to population size and structure, and can ultimately result in population collapse (Clarke et al., 2019; Laursen et al., 2009). Many practices (e.g., hand gathering) temporarily disturb areas which again reduces the ability of birds to feed and roost (Stillman and Goss-Custard, 2002; West et al., 2002). Where conservation objectives are prioritised, management of commercially important bivalve populations commonly attempts to balance the conservation of coastal birds with annual harvest (Laursen et al., 2010; Nehls et al., 1997; Stillman and Wood, 2015).

Balancing conservation objectives for overwintering shorebirds typically involves estimating the food requirements of the resident bird population and limiting the annual bivalve harvest accordingly (Hilgerloh, 1997; Laursen et al., 2010; Meire et al., 1994). Estimates are made using ecological models which are fundamentally based on the energy requirements of the bird population (species, size, prey preference). Agent-based models (ABMs) have been used for over 20 years to inform the management of coastal bird populations and have provided some valuable insights (Goss-Custard and Stillman, 2008; Stillman et al., 2015; Stillman and Goss-Custard, 2010). ABMs autonomously simulate the physiology, decisions and behaviour of all individuals that

constitute a population (DeAngelis and Gross, 2018; Grimm and Railsback, 2005; Stillman et al., 2015). Coastal bird ABMs base individual foraging decisions (e.g., diet, location, duration) on fitness optimising rules and calculate intake rates as a function of resource type (species, size, density), competitive interactions (kleptoparasitism, suppression), individual characteristics (e.g., foraging efficiency, dominance, mass) and physical conditions (e.g., temperature, tide, time). The demographic rates and properties of model populations thereby emerge from the individual behaviour of their constituents. A key advantage of coastal bird ABMs is that the basis for predictions (fitness maximization) is more likely to persist when the birds encounter novel environments than the empirical relationships within traditional models (Stillman et al., 2015; Wood et al., 2018). ABMs have been successfully applied to a wide range of systems (e.g., estuaries, rivers, saltmarsh) and species (e.g., waders, ducks, geese, swans) to advise conservationists on the potential impact of climate change (e.g., sea level rise), habitat loss (e.g., tidal barrages, wind farms, nuclear power stations), human disturbance (e.g., recreation, hunting, bivalve harvest), food production (e.g., aquaculture) and agriculture (Caldow et al., 2007; Chudzińska et al., 2016; Durell et al., 2008, 2006; Garcia et al., 2016; Stillman et al., 2021, 2003; West et al., 2007; West and Caldow, 2006; Wood et al., 2014).

Despite an improved understanding of how to manage the conservation of coastal birds, numerous species are still experiencing long-term population declines (Moltofte et al., 2019; Woodward et al., 2022, 2019). Many studies have used ABMs to independently assess management strategies, site quality and environmental impacts in relation to the annual survival of non-breeding birds (Brown and Stillman, 2021). Very few studies have assessed the long term response of coastal bird populations to environmental change even though long-term population viability is a fundamental objective for most conservation strategies (Martin et al., 2007; Stillman et al., 2001). To do so coastal bird ABMs would need to incorporate each species breeding habitat (i.e., non-intertidal), behaviour (e.g., migration, incubation, chick rearing) and success (i.e., recruitment), which is beyond their current capabilities. A potential solution is to focus on the long-term body condition of a population which for many species of coastal bird is positively related to survival, breeding success, migratory performance (Duijns et al., 2017; Gibson et al., 2018; Laursen et al., 2019a). They must also better link the population dynamics of resources to environmental conditions as these also respond to environmental change (Beukema et al., 2017b, 2010). For example, long-term variability in bivalve recruitment, mortality and growth (i.e., resources for coastal birds) is sensitive to changes in temperature and food availability (Beukema et al., 2017b, 2010; Beukema and Dekker, 2019).

Morecambe Bay contains the largest area of continuous intertidal flats in the UK and is of international significance for the biodiversity it supports (Anderson, 1972; Clapham, 1979, 1978; Clare et al., 1971; Dare, 1976; Dare and Mercer, 1973; Davidson, 1971; Elliott and Corlett, 1972; Gray and Bunce, 1972; Gray and Scott, 1977; Jones and Clare, 1977; Jones and Miller, 1966; Prater, 1972; Sloan and Aldridge, 1981; Wilson, 1973). The benthic community in Morecambe Bay is characterised by bivalves (e.g., *Cerastoderma edule*, *Mytilus edulis*, *Macoma balthica*) which are a major food source for the internationally important assemblage of wetland birds which inhabit the area (Anderson, 1972; Frost et al., 2021). It is the third largest gathering of water birds in the UK and includes considerable numbers of molluscivores (e.g., *Haematopus ostralegus*, *Calidris canutus* and *Somateria mollissima*) which consume large quantities of bivalves (Dare and Mercer, 1973; Goss-Custard et al., 1977; Prater, 1972). The area is designated a Special Protection Area (SPA), a Special Area of Conservation (SAC), a Special Site of Scientific Interest (SSSI), a National Nature Reserve (NNR), a Natura 2000 site and a Ramsar site. Bivalves are also economically important to the area and have been harvested commercially there for more than a century. The most frequently harvested species are *C. edule* and *M. edulis*, while both species are harvested for direct consumption (i.e., consumer size), *M. edulis* is also harvested undersize and grown to consumer size at aquacultural sites (Dare and Davies, 1975; Dare and Edwards, 1976). Management of the bivalve populations in Morecambe Bay aims to provide sufficient food such that coastal bird populations remain in good condition. The waterbird assemblage in Morecambe bay has however been declining for more than 25 years and alerts have been triggered for ten species, and for the waterbird assemblage as a whole (Nager and O’Hanlon, 2016; Woodward et al., 2019). While not all species are declining, many of the bivalve specialists are (e.g., *S. mollissima*, *H. ostralegus*) and for some (e.g., *C. canutus*) the decline might be driven or exacerbated by site specific pressures (Woodward et al., 2019). The reduction in numbers might therefore be due to a decrease in site quality (i.e., food availability) and is a potential source of conflict between the local bivalve industry and conservationists.

The overall aim of this study is to identify the invertebrate resources for which changes in abundance have most likely influenced site quality for foraging coastal birds and assess the extent to which birds have been impacted by the harvest of consumer and culture size *M. edulis*. An ABM was developed which simulates the movement and foraging success of bird populations in response to environmental change. The population dynamics of *M. edulis* are simulated using a Dynamic Energy Budget (DEB) sub-model which simulates their growth, reproduction and mortality in response to environmental conditions (temperature and food availability). A global sensitivity

analysis was used to identify and rank the resources to which foraging success was most influenced. A series of scenarios were then used to assess how and when birds might be sensitive to the harvest of *M. edulis*.

## **5.3 Methods**

### **5.3.1 Model**

The model description is based on the standardized description ODD (overview, design concepts, details) protocol that was originally developed for the documentation of individual-based and agent-based models (Grimm et al., 2020, 2010, 2006).

#### **5.3.1.1 Overview**

##### **5.3.1.1.1 Purpose**

The model was developed to improve our understanding of the manner and extent to which intertidal *M. edulis* populations affect the conservation objectives for coastal bird populations in Morecambe Bay. Its main purpose was to simulate the foraging of coastal birds in response to environmental change, specifically the commercial harvest of *M. edulis*. The model is written in NetLogo (Wilensky, 1999).

The model simulates the birth, growth, reproduction and death of all individuals within an intertidal *M. edulis* population, while simultaneously tracking the location, behaviour and condition of all individuals within a foraging coastal bird population. The foragers utilise several resource types which vary in size, density and location. The model incorporates variation in both the physiological rates of *M. edulis*, and the foraging and competitive ability of coastal birds. Changes to the *M. edulis* population (e.g., size) are driven by the physiological response of its constituents to environmental change. Individual birds respond to change by altering their feeding location, consuming different food or by adjusting the amount of time they spend feeding.

### 5.3.1.1.2 Entities, state variables, and scales

A global environment is applied throughout the system consisting of time, temperature (water and air), sea level and suspended particle concentration (organic and inorganic). Time progresses in discrete hourly time steps and space is divided into 250 m<sup>2</sup> habitat patches with fixed locations. Each patch operates under a local environment in which elevation is fixed and, at any given time, all processes and patch-specific variables are governed by the tide. Patches contain resources which can be consumed by both birds and *M. edulis*, and resources contain energy which is assimilated into the consuming organism. *M. edulis* remain at fixed locations while birds can alter their location to maximise fitness (e.g., body condition). *M. edulis* are characterized by four primary state variables: volume ( $v$ , units cm<sup>-3</sup>), reserves ( $es$ , units J), maturity ( $eh$ , unit J) and reproductive buffer ( $er$ , unit J). Each coastal bird species (*C. canutus*, *H. ostralegus*, *Larus argentatus* and *S. mollissima*) is characterized by three primary state variables: dominance (units -), foraging efficiency (units -) and body mass (units  $g$ ).

Chlorophyll-*a* is commonly used as a proxy for bivalve food and is available to *M. edulis* on any patch which is submerged (Handå et al., 2011). There are eight types of invertebrate resources available to the coastal birds and each is distributed amongst patches according to their elevation (Table 5.1). Bivalves are an important resource for coastal birds in Morecambe Bay and four species are present, *M. edulis*, *Tellina tenuis*, *M. balthica* and *C. edule*. Depending on the species, bivalves occur on patches with elevations between -4 and 2.7 m. *Hydrobia ulvae* and *Corophium volutator* were wide spread in Morecambe Bay and occur on patches with elevations between 1.8 and 4.6 m (Anderson, 1972). Both can feature prominently in the diet of coastal birds, particularly when low intertidal resources are submerged (Prater, 1972). One species of polychaete is available, *Nereis diversicolor*. These marine worms occur on patches with elevations between 0 and 4.6 m. *Oligochaeta spp.* (earth worms) are a major part of coastal bird diets when feeding on terrestrial habitats (Ambrose, 1986; Dare and Mercer, 1973; Gotmark, 1984; Pennycott et al., 2020; Sibly and McCleery, 1983a). This resource is only available to *H. ostralegus* and *L. argentatus* when the air temperature is > 0 °C. All resources have a size class, an hourly mortality rate and annual recruitment rate.

Table 5.1 Species, size range, increment size, elevation range and literary source for eight invertebrate resources available to model foragers. The full tidal range is -5 to 6 m.

Species	Size cm			Elevation m		Source
	Min	Max	Increment	Min	Max	
Oligochaeta spp.	0	25	5	-	-	(Sibly and McCleery, 1983a)
C. volutator	1.2	1.2	1.2	2.7	4.6	(Anderson, 1972)
M. balthica	1	2	1	1.8	2.7	(Anderson, 1972)
H. ulvae	0.6	0.6	0.6	1.8	2.7	(Anderson, 1972)
C. edule	1	4	1	0.9	1.8	(Anderson, 1972)
N. diversicolor	1.5	12	1.5	0.0	4.6	(Anderson, 1972)
T. tenuis	1	3	1	-1.0	0.9	(Anderson, 1972)
M. edulis	1	6	1	-4.0	1.0	(NWIFCA, 2020)

*M. edulis* consumes chlorophyll-*a* in units of energy ( $\text{J hr}^{-1}$ ) with a set assimilation efficiency of 0.75. The hourly energy requirements of *M. edulis* are calculated using DEB theory which scales requirements to body size and relates them to temperature through an Arrhenius equation (Kooijman, 2010). Birds consume invertebrate resources in units of mass ( $\text{mg afdm h}^{-1}$ ) and except for *M. edulis*, the ash-free dry mass of each resource type and size class is estimated using allometric equations (Table 5.2).

Table 5.2 Equations relating the mass (mg afdm) of model invertebrate resources to body size.

Resource	Equation	Source
M. balthica	$\text{afdm mg} = \exp(-4.335 + 2.919 \cdot \ln(\text{shell length mm}))$	(Zwarts, 1991)
C. edule	$\text{afdm mg} = \exp(-4.977 + 3.157 \cdot \ln(\text{shell length mm}))$	(Zwarts, 1991)
Oligochaeta	$\text{afdm g} = \exp(-11.9047 + 2.2853 \cdot \ln(\text{length mm}))$	(Hale et al., 2004)
Hydrobia spp.	$\text{afdm mg} = \exp(-2.538307 + 1.441 \cdot \log(\text{shell length mm}))$	(Eklöf et al., 2017)
N. diversicolor	$\text{afdm mg} = \exp(-0.898 + 2.208 \cdot \log(\text{body length cm}))$	(Zwarts and Wanink, 1993)
N. diversicolor	$\text{body length cm} = 3.6 \cdot \text{jaw length mm} - 0.49$	(James and Olive, 1981)
Corophium spp.	$\text{afdm mg} = \exp(-5.244 + 2.8 \cdot \ln(\text{carapace length mm}))$	(Zwarts and Wanink, 1993)
T. tenuis	$\text{afdm mg} = \exp(-13.5 + 3.01 \cdot \log(\text{shell length mm}) + 0.21/2)$	(Caldow et al., 2007)

The energy density of all invertebrate resources is assumed to be  $22 \text{ kJ g afdm}^{-1}$  and the assimilation efficiency of birds varies depending on the species of bird and the resource type. The energy assimilated by birds is converted to mass assuming that 33 kJ of energy is stored in each g of storage tissues (Kersten M and Piersma, 1987). The thermoneutral energy requirements for each forager is calculated using an equation which relates field metabolic rates with body size for all birds (Nagy et al., 1999). Thermostatic costs are included when temperatures fall below a lower critical threshold (LCT) and are calculated using published values (Jenssen et al., 1989; Kersten M and Piersma, 1987; Lustick et al., 1978).

### 5.3.1.1.3 Process overview and scheduling

At each step the global environment updates (time, suspended particulate matter, temperature and water level) and all patches determine whether they are submerged or emerged before calculating the local temperature (air or water) and suspended particulate concentration (0 or > 0). All *M. edulis* then filter both organic and inorganic particles from the water column (if submerged) but only ingest and assimilate organic particles into their energy reserves. Then, regardless of whether they have fed or not, they calculate the energy which is to be drawn from their reserves (utilisation rate) and allocated to growth, maintenance and reproduction. If they do not have sufficient reserves to pay maintenance costs, they will die. If they do, they update their reserves and calculate the change to their body size and reproductive compartment. All *M. edulis* then determine whether both they and the environment are in condition to spawn and if true, calculate the number of gametes they will produce and empty their reproductive compartment. The global environment then determines if any *M. edulis* have released gametes and if so, collects and distributes the gametes as larvae across all *M. edulis* patches evenly as a new cohort. Each patch then applies several mortality rates to its resident *M. edulis*, most of which (e.g., commercial harvest, predation) are dependent on whether the patch is submerged or emerged. All patches then update their resource densities before all coastal birds calculate their energy requirements and locate the nearest patch and resource which maximises their intake. Once located, they move to (or remain on) their selected patch, consume the chosen resource, assimilate its energy and update their body mass. Finally, all *M. edulis* update their numbers to reflect all mortality experienced within the step and patches update their resources according to background mortality and consumption by birds.

### 5.3.1.2 Design concepts

The *M. edulis* population model is based on the Dynamic Energy Budget theory (Kooijman, 2010, 2000; Van Haren and Kooijman, 1993). An overview of DEB concepts can be found in (Nisbet et al., 2000; van der Meer, 2006). The theory is based on the general principle that metabolic processes are proportional to surface area or body volume and a full balance for mass and energy. Individual birds behave to maximise their own chances of survival using decisions based on general principles (optimal foraging and game theory) and intake rates which are functional to environmental conditions. Birds can adapt to environmental change by altering their foraging location and time, all



possible decisions (e.g., diet) have an associated fitness measure (i.e., energy increase) and model birds make the decision that has the maximum value. Individual *M. edulis* interact with each other indirectly via competition for food and directly through the predation of pelagic larvae by benthic individuals. *M. edulis* interacts with coastal birds as a resource and coastal birds interact with each other via competition for resources (depletion, interference).

Model birds have some knowledge of the system (e.g., the fitness consequences of occupying different patches and consuming different diets) but the extent to which they utilise this knowledge depends on whether they are losing mass (i.e., starving). If they are not losing mass, birds choose to feed at the nearest location and resource on which their energy-intake rate equals or exceeds their energy-expenditure rate. If they are losing mass, birds use rate-maximising decisions to determine their location and diet by searching their local region for the greatest energy intake. If an individual is considered starving (body mass < 0.75 % of target body mass) they will search all regions to maximise their intake rates.

Each *M. edulis* and coastal bird represents more than one individual (super-individual). The number of individuals represented by each modelled *M. edulis* is initially set at the start of each simulation and then set at the birth of each new cohort. Their number decreases as the model progresses due to mortality. The number of individuals within each coastal bird is set at every step so that each model individual represents the same proportion of the population. Two model outputs (annual forager body mass and winter foraging time) were used to calibrate the model, one (annual forager distribution) was used to assess model accuracy and one (annual body mass) was used for sensitivity analyses harvest simulations. All were compared with independent empirical data (See sections 5.3.2 and 5.3.3).

### **5.3.1.3 Details**

#### **5.3.1.3.1 Initialisation**

Simulations begin 15<sup>th</sup> September (01:00:00) using the global environment for this date and time (Appendix C, Table 5.13). There are four distinct geographical regions (three in which *M. edulis* occurs) and all are assigned roost and region specific terrestrial (wet grassland) and intertidal (flats) supplementary habitats (Appendix C, Table 5.14). The location and area of *M. edulis* patches is fixed during each simulation to the values and locations observed in Morecambe Bay (Appendix C, Table

5.14, Figure 5.1). The area of each supplementary terrestrial patch is set to the area of coastal flood plain and grazing marsh within 3 km of each region (Appendix C, Table 5.14, Figure 5.1). The area of supplementary intertidal patches is calculated using LIDAR data of Morecambe Bay as the summed area by region and elevation (Appendix C, Table 5.14, Figure 5.1).

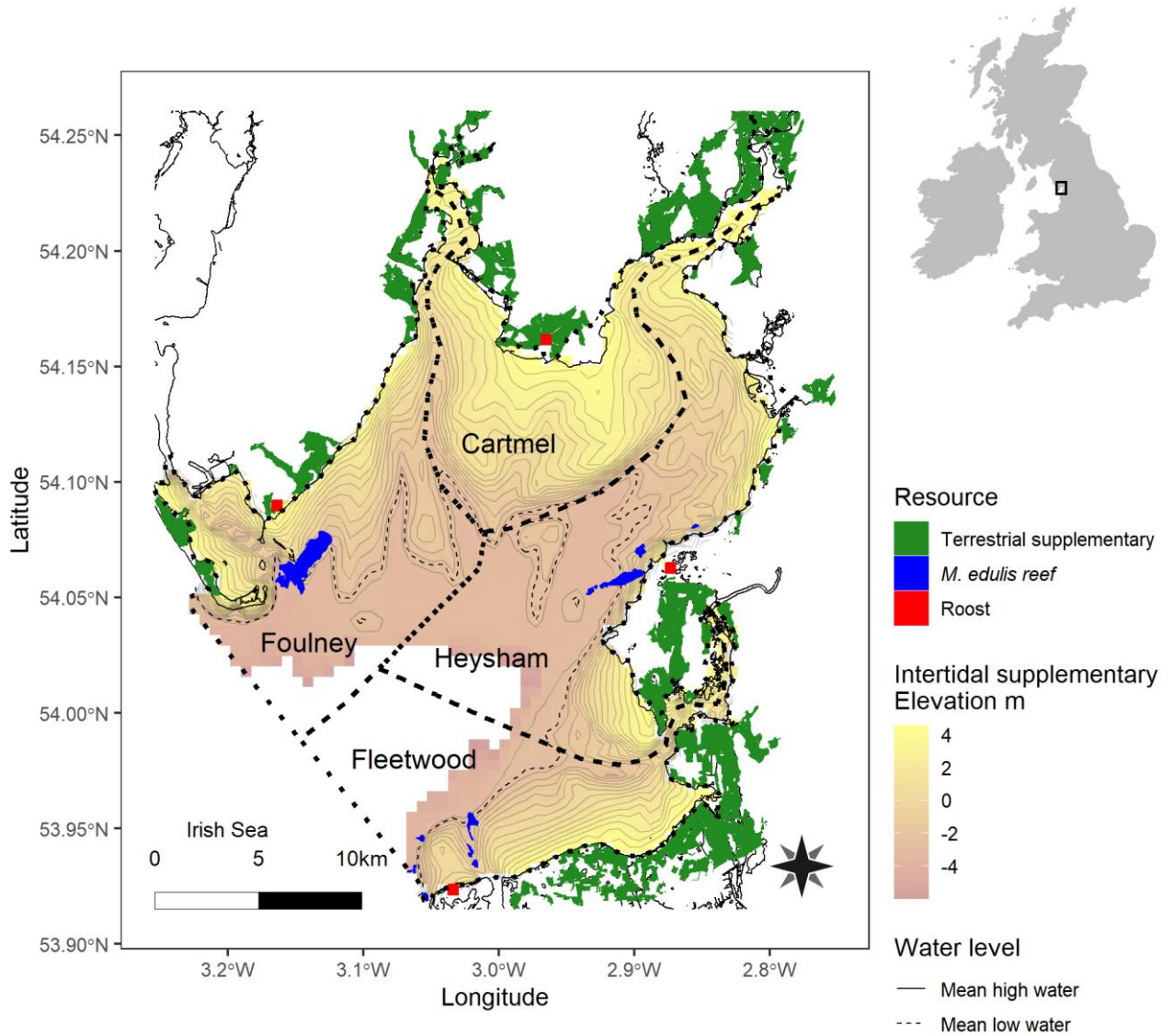


Figure 5.1 Stylised depiction of model setup showing the elevation and location of resources, and roosts in the context of Morecambe Bay. Blue polygons depict the location of *M. edulis* reefs, yellow to brown gradient represents intertidal flats, red and green patches represent roosting sites and terrestrial resources (coastal flood plain and grazing marsh) respectively. The thick dashed line depicts four regions (Cartmel, Fleetwood, Foulney, Heysham) with the SAC for Morecambe Bay. The thin dashed line circumnavigating the bay represents the mean low water mark (-2.8 m) while the solid line represents the 5 m mark. Contour lines range from -3 – 4.5 m at 0.5 m intervals.

Both *M. edulis* and terrestrial patches contain only one resource type (*M. edulis* and *Oligochaeta* spp. respectively) while each supplementary intertidal patch contains multiple types (according to its elevation). The initial density, size and distribution of each resource type is given (Appendix C, Table 5.15).

The model forager population consisted of 160 individuals, 40 for each species ( $n = 4$ ). The initial population size of each species was distributed evenly among each model forager by species. This resulted in each model *C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima* representing 41.5, 138.3, 87.4 and 65.9, respectively. All foragers are assigned several fixed state variables, some of which are drawn from known distributions (Table 5.3).

Table 5.3 State variables, model parameters and initial population size of model foragers (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*). <sup>a</sup> sea temperature

Description	<i>C. canutus</i>	<i>H. ostralegus</i>	<i>L. argentatus</i>	<i>S. mollissima</i>
Initial population size	1658	5533	3494	2635
Assimilation efficiency bivalve	0.75	0.85	0.75	0.75
Assimilation efficiency non-bivalve	0.75	0.75	0.75	0.75
Foraging efficiency	0.125	0.125	0.125	0.125
Terrestrial foraging efficiency	-	0.94	0.71	-
Nocturnal foraging efficiency	0.49	0.46	0.64	0.38
Dominance	0 - 1	0 - 1	0 - 1	-
Starvation mass g	90	350	610	1476
Basal mass g	140	540	1075	2276
Target mass g	140	540	1075	2276
Initial mass g	140	540	1075	2276
Lower critical temperature (LCT) °C	25	10	10	15 <sup>a</sup>
Thermoneutral energy requirements kJ hr <sup>-1</sup>	12.3	31.6	53.5	96.8
Thermostatic costs below LCT kJ deg <sup>-1</sup> hr <sup>-1</sup> (nst)	0.70	1.33	1.49	1.99
Thermostatic costs below LCT kJ deg <sup>-1</sup> hr <sup>-1</sup> (sst)	-	-	-	13.88
Patch use, tidal state	Emerged	Emerged	Emerged	Submerged

### 5.3.1.3.2 Input

The global environment is driven by an hourly time series of temperature, suspended particle concentration, water level and time of day (Figure 5.2). All temporal and spatial environmental data were obtained from 1<sup>st</sup> January 2015 to the 31<sup>st</sup> of December 2019 for the region designated a Special Area of Conservation (SAC) for Morecambe Bay (Figure 5.1). Temporal data were converted to an hourly time series and spatial data were converted to 100 m resolution. A single time series of temperature, suspended particle concentration and water level was used by all patches while elevation was assigned to all patches according to observed values extracted from spatial data. All

processing of spatial data was carried out using the *raster* package (Hijmans et al., 2017) for the software R (R Core Team, 2018).

Chlorophyll-*a* (*chl*, mg m<sup>-3</sup>) and suspended particulate inorganic matter (*spim*, g m<sup>-3</sup>) concentrations are used as a measure of suspended particle concentration. Daily *chl* and *spim* concentrations were extracted from satellite observations at 1 km resolution obtained using merged data (SeaWiFS, MODIS and MERIS) via a regional algorithm specifically designed for coastal waters (Gohin, 2011; Gohin et al., 2005; Gohin and Druon, 2002). Sea surface (*sst*, K) and near surface air (*nst*, K) are used as measures of temperature. Mean daily *sst* was extracted from merged satellite (NOAA-18, NOAA-19, MetOpB, NPP, GCOM-W, GOES13, MSG4, DMSP-F17, DMSP-F15) measurements at approximately 6 km resolution (Donlon et al., 2012). Discrete hourly *nst* was obtained from the Met Office Integrated Data Archive System (available <https://catalogue.ceda.ac.uk>) for the Walney Island weather station (54.125, -3.258, elevation: 15 m, (Met Office, 2019, 2006). Elevation values were extracted from lidar data collected at 1 m horizontal and 1 mm vertical resolution (available <https://environment.data.gov.uk/>) and hourly water level data were obtained from Heysham tide station (available <https://www.bodc.ac.uk>). Daily sunrise and sunset times for Morecambe Bay were calculated using the R package 'sunCalc' (Benoit and Elmarhraoui, 2019).

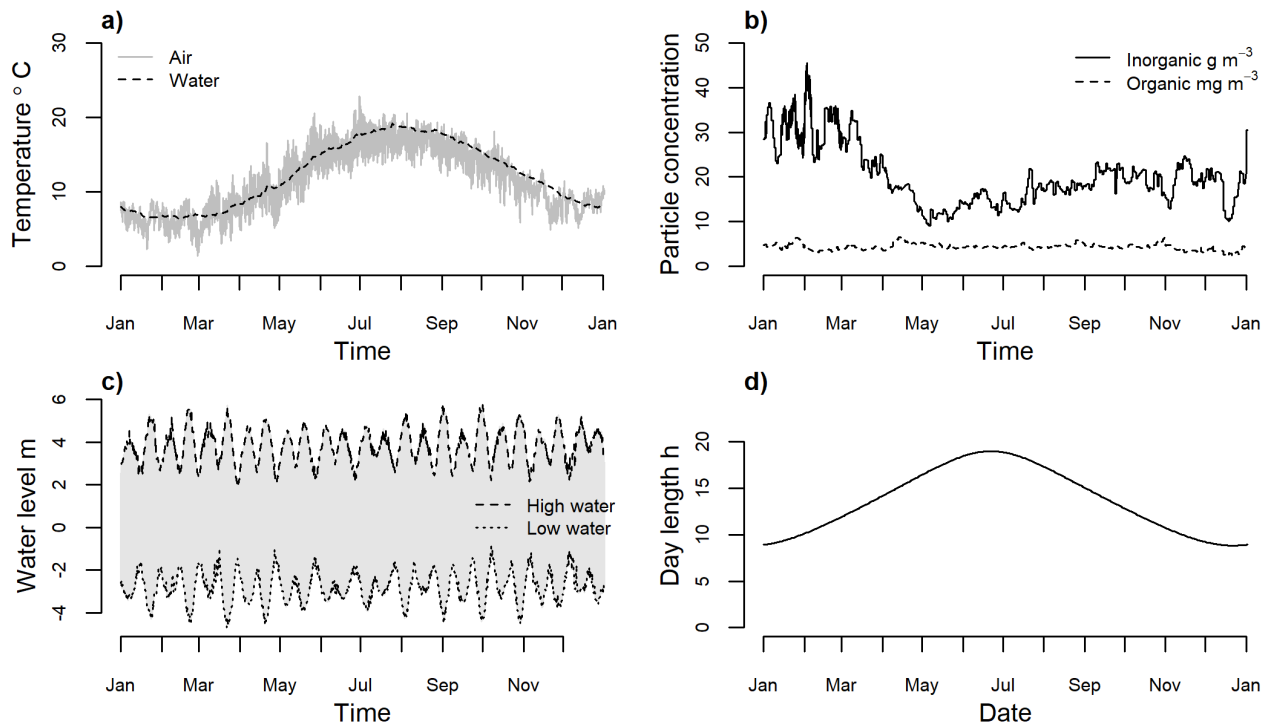


Figure 5.2 Environmental drivers of the global model environment, a) air (solid) and water (dashed) temperature °C, b) Chlorophyll-*a*  $\text{mg m}^{-3}$  (dashed) and suspended particulate inorganic matter  $\text{g m}^{-3}$  (solid), c) water level m and d) daylight hours.

The population size of each forager species changes according to monthly WeBS data (Frost et al., 2019), the values are the average count for each month between 2015 and 2019 (Figure 5.3).

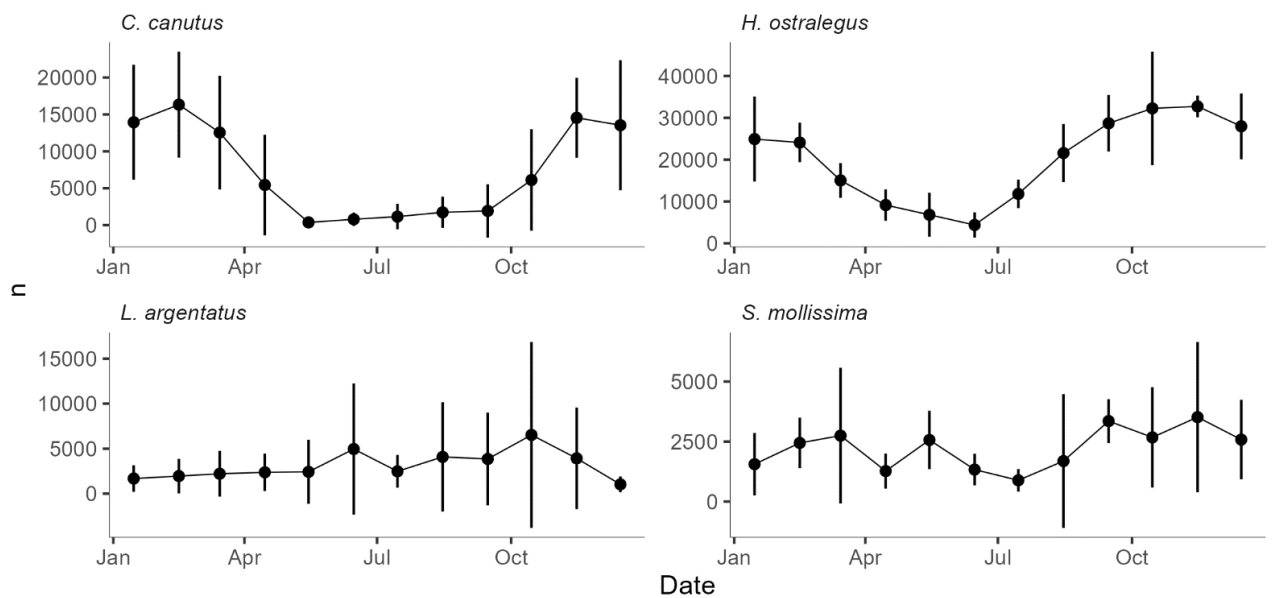


Figure 5.3 Mean ( $\pm$  95% confidence intervals) observed monthly high tide counts for four species (*C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima*) between 2015 and 2019 in Morecambe Bay, UK. The values are adapted from BTO WeBS counts and are used as the model population size for each species at every step.

### 5.3.1.3.3 Sub models

Recruitment, growth and mortality of the *M. edulis* population is simulated via a Dynamic Energy Budget (DEB) population model. Dynamic Energy Budget theory is a formal metabolic theory which dynamically describes the aspects of metabolism (energy and mass budgets) for all living organisms at the individual level (Kooijman, 2010; Nisbet et al., 2000; van der Meer, 2006). See the general methods for a detailed overview and chapter 3 and 4 which explain the DEB sub-models.

The interference-free intake rate (IFIR, mg AFDM s<sup>-1</sup>) of each forager is calculated for all resource types within their search area. It is related to resource density through a type II functional response which increases with resource density up to an asymptotic or maximum value, after which they are limited by handling time (Goss-Custard et al., 2006; Richman and Lovvorn, 2003):

$$IFIR = f \frac{IFIR_{max} \cdot b}{b_{50} + b}$$

where  $IFIR_{max}$  is the maximum intake rate,  $b$  is the density of each resource within the size range consumed and  $b_{50}$  is the resource density at which the intake rate is half of its maximum. All intake rates are multiplied by a foraging efficiency  $f$  drawn from a normal distribution (mean = 1, standard deviation = 0.125) which is proportionally (*C. canutus* = 0.49, *H. ostralegus* = 0.46, *L. argentatus* = 0.64, *S. mollissima* = 0.38) reduced at night.

The maximum interference-free intake rate ( $IFIR_{max}$  mg AFDM s<sup>-1</sup>) for *C. canutus*, *H. ostralegus* and *L. argentatus* is estimated using the mass of an average bird and prey item (Goss-Custard et al., 2006):

$$\ln(IFIR_{max}) = -2.08 + 0.245 \cdot \ln(M_{spec}) + 0.365 \cdot \ln(M_{prey})$$

where  $M_{spec}$  is the average body mass (g) of each species and  $M_{prey}$  is the mean ash-free dry mass (mg) of the prey being consumed. For these three species  $b_{50}$  is unrelated to bird or prey mass and fixed to a value of 0.761 g AFDM m<sup>-2</sup> (Goss-Custard et al., 2006).

Values of the asymptote and gradient used in the functional response for *S. mollissima* are derived from observations of captive velvet scoter *Melanitta fusca* feeding on *M. balthica* and of wild *S. mollissima* feeding on *M. edulis* (Caldow et al., 2007; Nehls, 1995; Richman and Lovvorn, 2003). In most cases, two sets of coefficients are used for each species of bivalve resource, one for small individuals and one for large. The maximum intake rates for *M. edulis* are adapted from observations of *S. mollissima* feeding on small (2 cm) and large (4 cm) *M. edulis* (Caldow et al., 2007; Nehls, 1995). The gradient of the functional response for *S. mollissima* feeding on *M. edulis* is fixed to that of *M. fusca* feeding on small *M. balthica* (2.4 – 3 cm) which are buried at a depth of < 4 cm (Richman and Lovvorn, 2003). For *C. edule*, *M. balthica* and *T. tenuis* the coefficients for *M. fusca* feeding on small (1.8 – 2.4 cm) and large (2.4 – 3 cm) *M. balthica* which are shallowly (< 4 cm) buried (Richman and Lovvorn, 2003). All values are and size class are given (Appendix C, Table 5.16).

The influence of conspecific competitors on a bird's intake rate is incorporated using an interference function (Stillman et al., 1996):

$$\text{if } D \geq D_0$$

$$IR = IFIR \left( \frac{g \cdot D + 1}{D_0 + 1} \right)^{-(m_{max} - (m_{max} - m_{min}) \cdot d)}$$

$$\text{if } D < D_0$$

$$IR = IFIR$$

where *IR* is the intake rate (mg AFDM s<sup>-1</sup>), *D* is the conspecific competitor density in patch (ha<sup>-1</sup>), *D*<sub>0</sub> is the conspecific competitor density above which interference reduces intake rate, *g* is the aggregation factor, *d* is the dominance of focal individual (drawn from a uniform distribution 0 – 1, (Goss-Custard et al., 1995)), *m*<sub>max</sub> is the susceptibility to interference from the least dominant individual (*d* = 0) and *m*<sub>min</sub> is the susceptibility to interference from the most dominant individual (*d* = 1). *D*<sub>0</sub> was set to 100 birds ha<sup>-1</sup> as this is an approximate threshold for systems which interference occurs through kleptoparasitism (Stillman et al., 1996; Triplet et al., 1999). The aggregation factor accounts for the fact that birds will usually be aggregated in a patch, rather than being spread uniformly. The default aggregation factor was assumed to be 10, the value measured for cockle-feeding oystercatchers on the Burry Inlet, UK (West et al., 2003). The values of *m*<sub>max</sub> and *m*<sub>min</sub> for each species were estimated from previous studies and are based on prey size, behaviour and

handling time. Interference is assumed to be absent ( $m_{max} = 0$ ,  $m_{min} = 0$ ) when consuming *H. ulvae* because they are small and can be quickly consumed (minimising interference through kleptoparasitism, (Stillman et al., 1997). They are also relatively immobile with limited ability to escape as birds' approach which reduces interference through prey depression. Interference is assumed to occur through kleptoparasitism when feeding on *M. edulis* which is relatively large and immobile. The extent to which intake rates are reduced is weakest when birds are dominant ( $m_{max} = 0$ ) and strongest when they are not. *C. canutus* consume relatively small *M. edulis* and the handling time is short ( $< 10$  s). The strength of interference between *C. canutus* feeding on *M. edulis* ( $m_{max} = 0$ ,  $m_{min} = 0.08$ ) is the value estimated for short handling times by an interference model (Stillman et al., 2002). The strength of interference between *H. ostralegus* and *L. argentatus* feeding on *M. edulis* ( $m_{max} = 0$ ,  $m_{min} = 0.5$ ) represents a strong level of interference amongst bivalve feeding *H. ostralegus* (Caldow et al., 2007; Triplet et al., 1999). There is little evidence of interference between *M. mollissima* when feeding on *M. edulis* and no quantitative relationship between intake rate and bird density is reported (discussed in detail: (Caldow et al., 2007). Interference is assumed not to occur between *M. mollissima* ( $m_{max} = 0$ ,  $m_{min} = 0$ ) feeding on *M. edulis* in the model. Worms are considered mobile prey which can escape into the sediment as predators' approach. Interference is assumed to occur through prey depression and is independent of dominance ( $m_{max} = 0.48$ ,  $m_{min} = 0.48$ ). The values used are those observed between redshank feeding on *Corophium* (Yates et al., 1996).

The diving sub model is based on data collected by (Dewar, 1924) and is described in detail (Caldow et al., 2007; Kaiser, 2002). All equations used are given (Table 5.4), briefly, the relationship between water depth, dive time and surface time is used to estimate the proportion of time *S. mollissima* spend feeding during a dive cycle, which is applied to the instantaneous intake rate. The time taken to complete a whole dive cycle (under water and surface) is first estimated from the water depth. The average underwater swimming speed of *S. mollissima* is then used to estimate the time spent travelling to and from the water surface as a function of water depth. This value is subtracted from the underwater time to give the amount of time spent at the seabed which is divided by the duration of a complete dive cycle to give the proportion spent feeding.



Table 5.4 Equations used within the diving sub-model of *S. mollissima* (Guillemette, 1998; Guillemette et al., 2004).

Description	Equation	Units
Dive time	$5.5147 \cdot \text{depth m} + 9.9204$	s
Travel time	$(\text{depth m} \cdot 2) / \text{swim speed m s}^{-1}$	s
Surface time	$3.5886 \cdot \text{depth m} + 7.3881$	s
Dive cycle time	Surface time s + dive time s	s
Forage time	Dive time s – travel time s	s
Proportion	Forage time s / dive cycle time s	-
Swim speed	0.95	m s <sup>-1</sup>

### 5.3.2 Calibration

The model was calibrated such that over ten years the mean annual body mass and time spent foraging of birds during winter by each species both fell within observed values (Table 5.5). Eight parameters for which values were uncertain were included in the calibration step: the terrestrial and intertidal (excluding *M. edulis*) foraging area, and the terrestrial (2 species) and nocturnal (4 species) foraging efficiency.

The terrestrial foraging area (0 - 7804 ha) and efficiency (0 – 1) apply to *H. ostralegus* and *L. argentatus*, both of which feed on wet grassland (Dare and Mercer, 1973; Pennycott et al., 2020). While the area for this habitat type is representative of that available in the real system, the resource distribution is uniform across all patches which is unrealistic. The distribution of *Oligochaeta* spp. within wet grasslands is naturally variable (spatially and temporally) and dependent on soil characteristics (e.g., humidity) and atmospheric conditions (e.g., precipitation, temperature, (Curry, 2004; Hendrix et al., 1992). Similarly, the area of wet grasslands available to foraging birds is related to management intensity (e.g., natural grazing, silage production) and its effect on vegetation structure (Atkinson et al., 2005).

Nocturnal foraging efficiency applied to all forager species when consuming resources in the intertidal habitat at night. Coastal birds are regularly observed feeding at night, mainly within intertidal habitats where nocturnal predators are less active (Merkel and Mosbech, 2008; Piersma et al., 2006; Sitters et al., 2001). Little is known of the efficiency with which they do so, it is generally thought to be related to environmental conditions (e.g. visibility, wind) and differ between species and foraging behaviour (Kuwae, 2007; Santos et al., 2010; Turpie and Hockey, 1993).

The intertidal foraging area was defined in relation to elevation but the intertidal flats of Morecambe are dynamic, and subtidal channels and sandbanks can migrate considerable distances each year (Mason et al., 2010, 1999). Invertebrate distribution is also related to additional gradients

within the substrate (particle size, nutrient content) and water column (e.g., salinity, temperature), and is unlikely to be uniform with elevation (Anderson, 1972; Woodland et al., 2021).

Calibration involved simultaneously sampling ( $n = 2000$ ) the complete range of each parameter using Latin Hypercube sampling, a form of stratified sampling for multiple continuous variables (McKay et al., 2000). The model was then run for each parameter set while outputting the mean annual mass and winter feeding time for each forager species. The parameter set for which simulated outputs most closely matched observed values was selected.

Table 5.5 Minimum and maximum values for the proportion of time spent foraging throughout winter and annual body mass (g) for *C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima* (Guillemette, 2001, 1998; Sibly and McCleery, 1983a; van der Kolk et al., 2021; Van Donk et al., 2020; Van Gils et al., 2006b, 2005). The values were used to calibrate the model.

Species	Parameter	Min	Max
<i>C. canutus</i>	Winter foraging time	0.4	0.7
<i>H. ostralegus</i>		0.3	0.5
<i>L. argentatus</i>		0.3	0.6
<i>S. mollissima</i>		0.5	0.7
<i>C. canutus</i>	Annual body mass	103.5	158.0
<i>H. ostralegus</i>		409.5	640.0
<i>L. argentatus</i>		728.3	1264.0
<i>S. mollissima</i>		1707.0	2392.0

The final parameter set was selected using the sum of the relative squared residuals (*ssr*), which was computed for each observed ( $x$ ) and simulated ( $y$ ) value ( $j$ ) and summed by parameter set ( $i$ ):

$$ssr_i = \sum_{j=1}^{j_{max}} \left( \frac{x_{ij} - y_{ij}}{x_{ij}} \right)^2$$

The parameter set with the minimum *ssr* was selected.

### 5.3.3 Accuracy

Model accuracy was assessed by comparing observed monthly counts of roosting birds with simulated values. The estuary was arbitrarily divided into four regions whose boundaries were depicted by the estuary mouth and river boundaries (Figure 5.1). Observed WeBS counts (2010 – 2019) were summed by region and species for each month to estimate average monthly values.

Simulations were then run ( $n = 10$ ) for 10 years to generate values for comparison. Observed and simulated values were compared using linear regressions (Piñeiro et al., 2008; Smith and Rose, 1995).

#### **5.3.4 Food requirements**

The annual food requirements (intake rate and resource preference) for each species were predicted via simulations which used default parameter values. Both were summarised by season (autumn-winter, spring-summer) and intake rates were calculated for each population (t afdm season<sup>-1</sup>) and for an average individual (kg afdm season<sup>-1</sup>).

#### **5.3.5 Sensitivity**

##### **5.3.5.1 Screening**

A Global Sensitivity Analysis (GSA) is used to measure how individual input factors or factor sets influence the model output (body mass of foragers). When quantified, the variance that each contributes to the model output can be used to focus research (i.e., which input factors require a better measure) and improve understanding of how, and the accuracy with which, it can be predicted (i.e., risk assessment). Changes in the availability of intertidal invertebrate resources are believed in part responsible for the long term population declines observed in many species of coastal bird (Piersma et al., 2016; Van Roomen et al., 2012). Identifying the resource types for which changes in abundance significantly influence the annual condition of coastal bird populations is fundamental to robust long term conservation management strategies. The GSA therefore focuses on the sensitivity of coastal bird populations to changes in resource density.

The complete range of each parameter of interest is screened using the Morris method (Campolongo et al., 2007; Morris, 1991). This is a one-step-at-a-time approach (OAT) in which each input factor ( $k$ ) is repeatedly ( $r$ ) and randomly varied over a set number of levels ( $p$ ) across its range. The elementary effect ( $ee$ ) of each input is measure along all its respective trajectories and the respective mean ( $\mu$ ), absolute mean ( $\mu^*$ ) and standard deviation ( $\sigma$ ) are used as sensitivity measures. The Morris method facilitates a measure of global sensitivity by simultaneously varying

all other input values, thereby relating the standard deviation to their influence. Both  $\mu$  (mean) and  $\mu^*$  (absolute mean) assess the overall influence of the parameter on the output,  $\sigma$  (standard deviation) estimates the extent to which each parameter is influenced (i.e., non-linear, interaction) by other factors. Non-influential parameters are those with  $\mu^* < 0.1$ , important factors are those for which  $\mu^* > 0.1$  and interacting factors are those for which  $\mu^* > 0.1$  and  $\sigma > 2 \times (\sigma/\sqrt{n})$ .

The computational cost ( $c$ ) of the Morris experiment is a linear function of the number of factors  $c = r \cdot (k + 1)$ . Here, 20 trajectories ( $r = 20$ ) are generated across 8 levels ( $p = 8$ ) for each input factor ( $k = 8$ ), resulting in a total number of 360 model evaluations ( $c = 360$ ). The sensitivity analysis included 8 environmental parameters that control the density of available resources (Table 5.6). The output of interest was the average annual body mass of each species after 10 years.

Table 5.6 Parameters and respective ranges used for Morris sensitivity analyses showing the unit, code, minimum, default and maximum values.

Parameter	Unit	Code	Minimum	Maximum
<i>Oligochaeta spp.</i>	g afdm m <sup>-2</sup>	<i>r1</i>	0	33.9
<i>N. diversicolor</i>	g afdm m <sup>-2</sup>	<i>r2</i>	0	0.5
<i>Hydrobia spp.</i>	g afdm m <sup>-2</sup>	<i>r3</i>	0	1.3
<i>Corophium spp.</i>	g afdm m <sup>-2</sup>	<i>r4</i>	0	3.8
<i>M. balthica</i>	g afdm m <sup>-2</sup>	<i>r5</i>	0	31.5
<i>C. edule</i>	g afdm m <sup>-2</sup>	<i>r6</i>	0	5.9
<i>T. tenuis</i>	g afdm m <sup>-2</sup>	<i>r7</i>	0	4.4
<i>M. edulis</i>	g afdm m <sup>-2</sup>	<i>r8</i>	0	566.8

The Morris method produces multiple rankings of importance for each input parameter and the extent to which rankings agree was used to assess the quality and robustness of the analysis. The top-down coefficient of concordance (TDCC) provides a useful measure in which emphasis is placed on agreement between high ranking parameters (Helton et al., 2005; Iman and Conover, 1987; Marino et al., 2008). The TDCC values and their corresponding p values provide insightful indications of analysis consistency. Values for the TDCC range between 0 and 1, those close to one (> 0.9) indicate a high degree of reproducibility, which decreases with TDCC. The concordance between rankings is considered non-statistically significant for p-values higher than 0.05. See Chapter 2 general methods for detailed description of the Morris method.

### 5.3.5.2 Resource thresholds

Predictions which can be easily understood by stakeholders and non-modelling specialists alike are important if models are to support environmental decision-making (Stillman et al., 2016). This can be achieved by predicting threshold values for environmental perturbations (e.g., climate change, habitat or resource loss, sea level rise) associated with negative impacts on ecosystems. These thresholds can then be used by stakeholders to inform decision-making. The conservation objectives of SPAs are to maintain the population sizes of birds present at the time of site designation. To support the conservation of coastal birds and bivalve management in Morecambe Bay the model is used to predict the resource abundance required if bird populations are to remain in good condition. Here it is assumed that the bay will support the SPA population size if the mean annual condition of birds is 100%. All resource types identified as influential by the screening process are included and varied simultaneously between 0 and 100% of their default values. The model is run over ten years for each category and density, and the mean annual condition of each bird species is output.

### 5.3.5.3 Commercial harvest

The overexploitation of intertidal bivalves has coincided with high mortality rates of molluscivorous coastal birds and is implicated as a driver of population declines (Atkinson et al., 2010; Smit et al., 1998; Van Gils et al., 2006a). Understanding the relationship between harvest rates and the condition of coastal bird populations is key to the sustainable management of natural bivalve populations.

The relationship between the annual body condition of each species and the harvest of *M. edulis* was assessed via pairwise Spearman's correlation coefficients. Harvest rates (market and culture) of *M. edulis* were simultaneously varied ( $0 - 0.02 \text{ \% h}^{-1}$ ) for all patches and under a range of scenarios in which non-commercial bivalve (*M. balthica*, *T. tenuis*) and terrestrial resources were set to either high (default values) or threshold (bivalve – 70%, terrestrial – 40 %) abundances. A full factorial design resulted in four resource scenarios, involved two harvest sizes (market and culture), 11 harvest rates (from 0 to 0.02 by 0.002) and was repeated 10 times to create an experiment which required 880 model runs. A four-way ANOVA was used then to describe the correlation coefficients in relation to bird species, target harvest size and alternative resource abundance. A bidirectional stepwise linear regression was used to identify the best predictors. The full model contained correlation coefficients (continuous) as the response variable and included the main effects of bird

species (factor, 4 levels), harvest size (factor, 2 levels), bivalve abundance (factor, 2 levels) and terrestrial resource abundance (factor, 2 levels), and all pairwise interactions between them. At each step, variables were added and removed based on AIC values.

## **5.4 Results**

### **5.4.1 Calibration**

The model was calibrated by simultaneously varying the foraging efficiency of each forager species and foraging area such that both the mean annual body mass and winter foraging time of each species were within the range of their respective observed values (Table 5.5). Calibrated values for foraging efficiency and area are provided (Appendix C, Table 5.14, Table 5.3).

### **5.4.2 Accuracy**

Model accuracy was assessed by comparing observed monthly counts of roosting birds with simulated values. The average count (observed and simulated) was calculated by month, species and region over ten years (observed: 2010 – 2019). Observed and simulated values were compared using linear regressions (Table 5.7, Figure 5.4).

Table 5.7 Results from linear regressions of the observed and predicted number of roosting coastal birds in Morecambe Bay. The model intercept, slope, p-value (intercept, slope and slope  $\neq 1$ ) and correlation coefficient ( $R^2$ ) are given by region (Cartmel, Fleetwood, Foulney and Heysham) and species (*C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima*).

Site	Species	Intercept	slope	p intercept	p slope	p slope $\neq 1$	$R^2$
Cartmel	<i>C. canutus</i>	-542.57	0.48	0.138	< 0.05	< 0.05	0.80
Cartmel	<i>H. ostralegus</i>	-639.42	0.71	0.429	< 0.05	0.054	0.71
Cartmel	<i>L. argentatus</i>	13.22	0.07	0.535	< 0.05	< 0.05	0.56
Cartmel	<i>S. mollissima</i>	51.15	1.27	0.587	0.413	0.860	-0.03
Fleetwood	<i>C. canutus</i>	135.66	1.59	0.615	< 0.05	< 0.05	0.78
Fleetwood	<i>H. ostralegus</i>	978.48	0.45	0.088	< 0.05	< 0.05	0.57
Fleetwood	<i>L. argentatus</i>	219.04	0.14	0.091	0.422	< 0.05	-0.03
Fleetwood	<i>S. mollissima</i>	57.68	-0.01	< 0.05	0.906	< 0.05	-0.10
Foulney	<i>C. canutus</i>	332.20	1.54	0.446	< 0.05	0.243	0.51
Foulney	<i>H. ostralegus</i>	607.92	1.07	0.296	< 0.05	0.528	0.89
Foulney	<i>L. argentatus</i>	1692.67	2.38	< 0.05	< 0.05	0.061	0.53
Foulney	<i>S. mollissima</i>	1047.82	1.17	< 0.05	< 0.05	0.530	0.64
Heysham	<i>C. canutus</i>	-247.74	2.26	0.523	< 0.05	< 0.05	0.93
Heysham	<i>H. ostralegus</i>	-2064.17	1.63	< 0.05	< 0.05	< 0.05	0.91
Heysham	<i>L. argentatus</i>	164.97	0.11	< 0.05	0.355	< 0.05	-0.01
Heysham	<i>S. mollissima</i>	-37.75	0.25	0.600	0.115	< 0.05	0.15

Model predictions were not distinguishable from observed values (slope = 1 and intercept = 0) for the region Foulney and the species *C. canutus* and *H. ostralegus*, and the region Cartmel and the species *H. ostralegus*. Predictions closely matched observed values (slope = 1 and intercept  $\neq 0$ ) for the region Foulney and the species *L. argentatus* and *S. mollissima*, but they were consistently underestimated. Predicted values for *C. canutus* and *L. argentatus* at the region Cartmel, and *H. ostralegus* at the region Fleetwood were overestimated when large (slope < 1 and intercept = 0). Predicted values for *C. canutus* at the regions Fleetwood and Heysham were underestimated when large (slope > 1 and intercept = 0). There was no relationship between observed and predicted values for the regions Cartmel, Fleetwood and Heysham, and the species *S. mollissima*. There was also no relationship between observed and predicted values for the regions Fleetwood and Heysham, and the species *L. argentatus*.

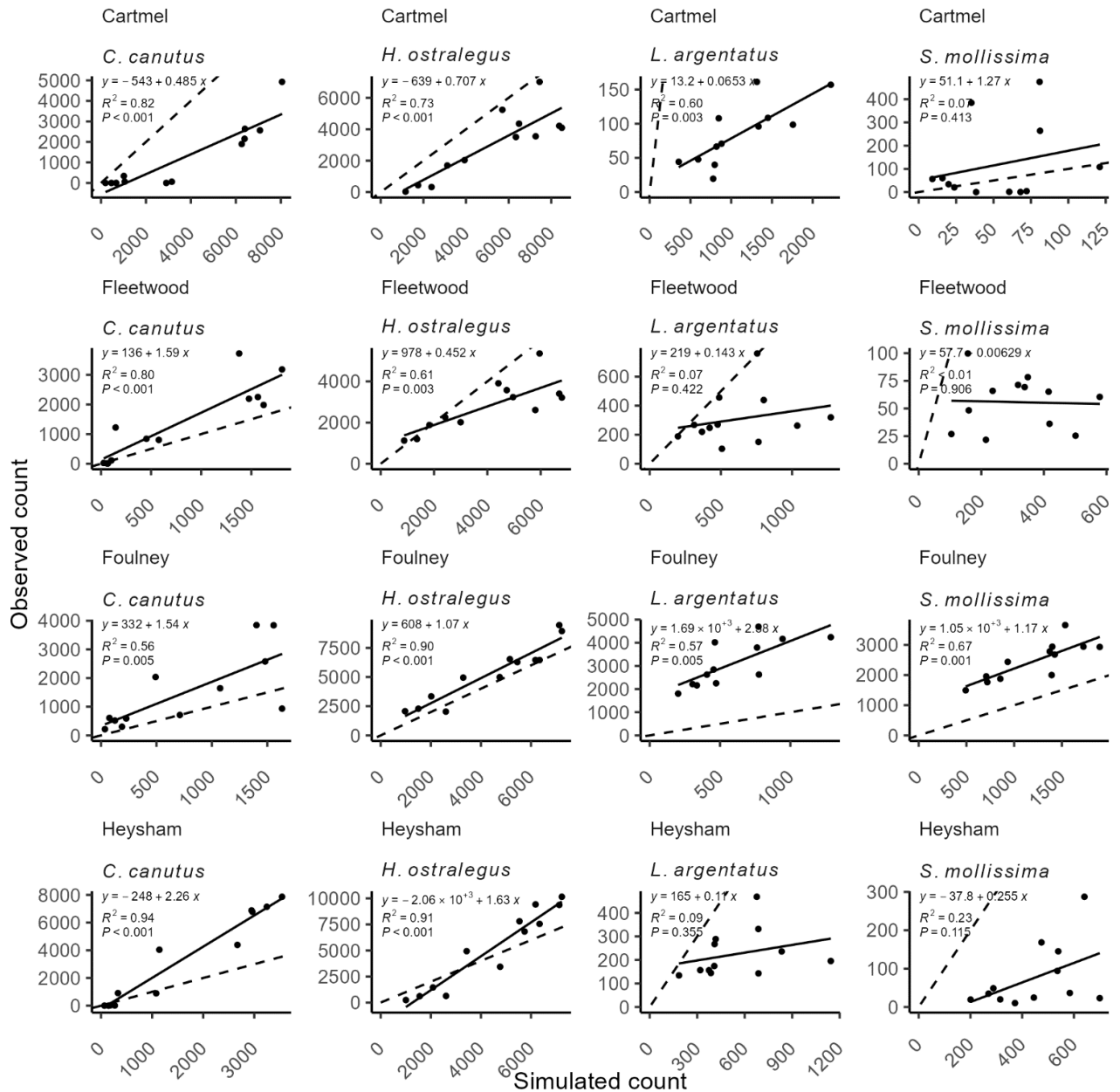


Figure 5.4 Linear regressions of the observed and predicted number of roosting coastal birds in Morecambe Bay. The model equation, correlation coefficient ( $R^2$ ) and p-value are displayed on each plot. The solid lines represent the predicted relationship, and the dashed line represents slope = 1 and intercept = 0. Plots are given by region (Cartmel, Fleetwood, Foulney and Heysham) and species (*C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima*).

In summary model predictions most closely matched observed values for the region Foulney and the species *H. ostralegus*. Values were generally underestimated for the regions Heysham, Fleetwood and Foulney, and overestimated for the region Cartmel.



### 5.4.3 Food requirements

Intake rates of individual foragers and complete populations were estimated by species and season (Table 5.8). Individual intake rates were larger (3 – 12%) during autumn-winter compared to spring-summer and increased with forager body size. Population intake rates also increased from spring-summer to autumn-winter (44 – 631%) for *C. canutus*, *H. ostralegus* and *S. mollissima* but not *L. argentatus* (-9%). Population intake rates were largest for *H. ostralegus* followed by *S. mollissima*, *L. argentatus* and *C. canutus*.

Table 5.8 Estimated intake rates for four species (*C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima*) of coastal bird in Morecambe Bay, UK. Values are given in kilograms (kg) of ash-free dry mass (afdm) and are calculated for an individual and the total population of each species. The intake rates are summarised by species and season (April - September and October - March). The difference (%) between seasons is also provided.

Species	Population			Individual		
	afdm kg season <sup>-1</sup>	afdm kg season <sup>-1</sup>	% Difference	afdm kg season <sup>-1</sup>	afdm kg season <sup>-1</sup>	% Difference
<i>C. canutus</i>	11208.8	81893.2	630.6	5.649	6.332	12.1
<i>H. ostralegus</i>	134349.9	263642.8	96.2	9.818	10.093	2.8
<i>L. argentatus</i>	46880.6	42478.5	-9.4	13.990	14.647	4.7
<i>S. mollissima</i>	52078.2	75052.6	44.1	28.356	29.119	2.7

The proportion of time model foragers spent consuming each resource was also predicted by season (Table 5.9). Both *C. canutus* and *S. mollissima* fed almost exclusively on one resource type throughout the year, *M. balthica* and *M. edulis* respectively. Throughout the spring and summer months *H. ostralegus* and *L. argentatus* foraged on *M. balthica*, *T. tenuis* and terrestrial resources in approximately equal proportions. During the autumn and winter months both species spent more time foraging on *C. edule* and slightly less on *T. tenuis* and terrestrial resources.

Table 5.9 Proportion of time model foragers (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*) spent feeding on each resource (Terrestrial, *H. ulvae*, *C. volutator*, *M. balthica*, *M. edulis*, *C. edule*, *N. diversicolor*, *T. tenuis*) by season.

Summer								
Species	Terrestrial	<i>H. ulvae</i>	<i>C. volutator</i>	<i>M. balthica</i>	<i>M. edulis</i>	<i>C. edule</i>	<i>N. diversicolor</i>	<i>T. tenuis</i>
<i>C. canutus</i>	0.000	0.000	0.187	0.723	0.009	0.000	0.000	0.080
<i>H. ostralegus</i>	0.227	0.000	0.000	0.355	0.072	0.034	0.000	0.313
<i>L. argentatus</i>	0.283	0.000	0.000	0.343	0.038	0.037	0.000	0.298
<i>S. mollissima</i>	0.000	0.000	0.000	0.174	0.613	0.000	0.000	0.212
Winter								
Species	Terrestrial	<i>H. ulvae</i>	<i>C. volutator</i>	<i>M. balthica</i>	<i>M. edulis</i>	<i>C. edule</i>	<i>N. diversicolor</i>	<i>T. tenuis</i>
<i>C. canutus</i>	0.000	0.000	0.101	0.887	0.001	0.000	0.000	0.011
<i>H. ostralegus</i>	0.187	0.000	0.000	0.194	0.062	0.340	0.000	0.216
<i>L. argentatus</i>	0.227	0.000	0.000	0.173	0.043	0.370	0.000	0.187
<i>S. mollissima</i>	0.000	0.000	0.000	0.266	0.591	0.000	0.000	0.142

## 5.4.4 Sensitivity

### 5.4.4.1 Screening

A global sensitivity analysis was used to assess the response of model foragers to environmental change. The Morris method was used to identify the resources which most influence the annual body mass of foragers (Campolongo et al., 2007; Morris, 1991). Top-down concordance coefficients (TDCC) were calculated to assess the level to which the analysis agreed in the ranking of highly influential parameters (Iman and Conover, 1987). TDCCs range between 0 (no agreement) and 1 (complete agreement).

Table 5.10 Top-down concordance coefficients (TDCC), chi-squared ( $\chi^2$ ) and related p-values obtained from comparisons between results of the Morris sensitivity analysis.

Output	Replicates	TDCC	$\chi^2$	p-value
<i>C. canutus</i>	20	0.74	103.0	< 0.001
<i>H. ostralegus</i>	20	0.68	80.8	< 0.001
<i>L. argentatus</i>	20	0.60	84.7	< 0.001
<i>S. mollissima</i>	20	0.70	98.6	< 0.001

The TDCC and associated p values indicate the analysis was robust and repeatable for all forager species (Table 5.10). A larger number of influential ( $\mu^* > \text{Morris}_T$ ) food resources were identified for *H. ostralegus* and *L. argentatus* ( $n = 4$ ), compared to *S. mollissima* ( $n = 3$ ) and *C. canutus* ( $n = 1$ ). All

influential parameters were also classified as non-monotonic, interactive or non-linear ( $\mu^* > \text{Morris}_T$  and  $\sigma > 2 \text{ SEM}_i$ , Figure 5.5).

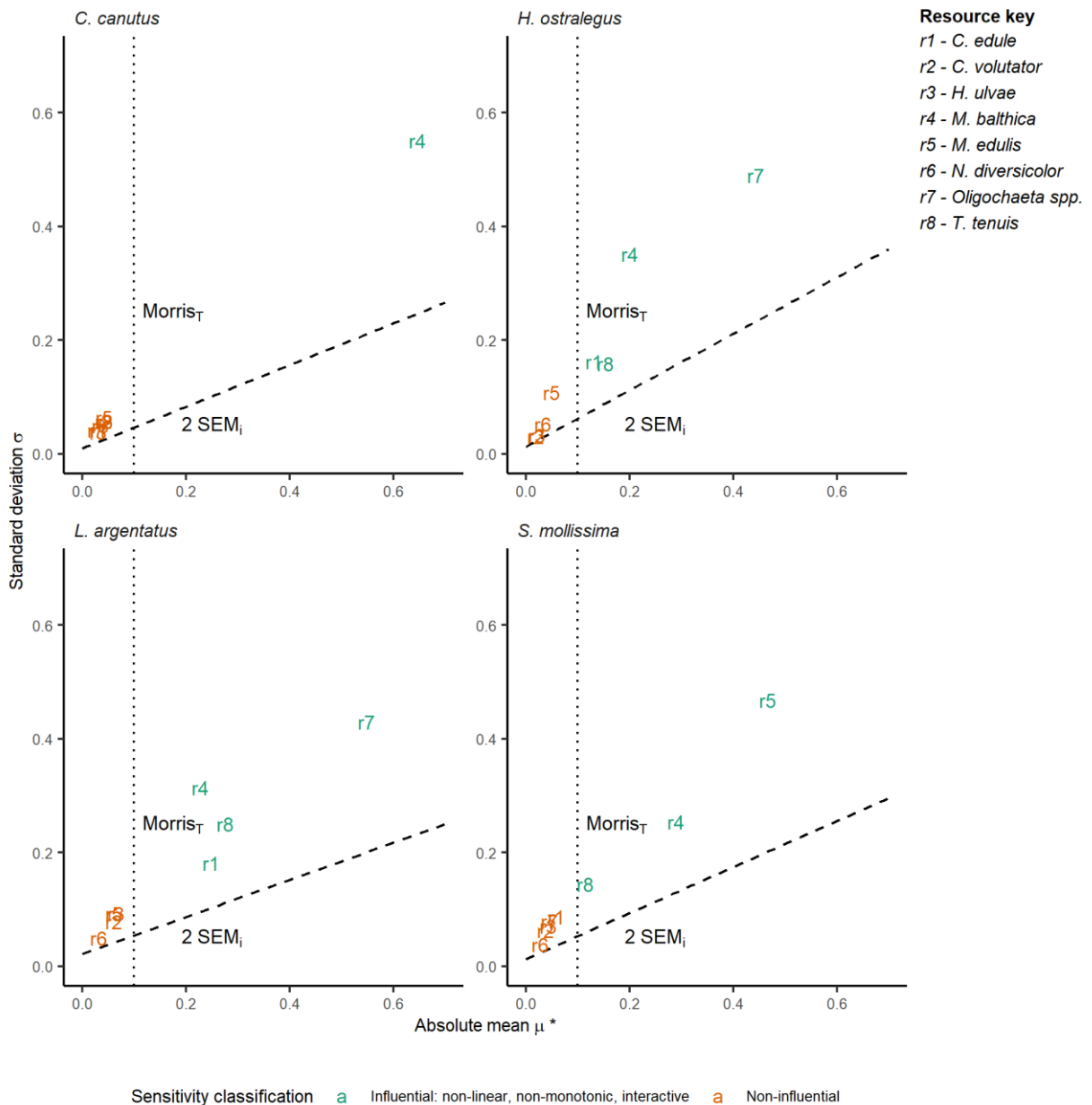


Figure 5.5 Results from Morris sensitivity analysis of forager body mass to the variation of 8 resource types (*C. edule*, *M. edulis*, *Oligochaeta spp.*, *H. ulvae*, *C. volutator*, *M. balthica*, *N. diversicolor*, *T. tenuis*). Plots show standard deviation ( $\sigma$ ) against absolute mean ( $\mu^*$ ) of the scaled (0 – 1) elementary effects for each forager species (*C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima*). Values (orange)  $< \text{Morris}_T$  are considered non-influential, values  $\geq \text{Morris}_T$  and  $< 2 \text{ SEM}_i$  are influential but not interactive and values (green)  $\geq \text{Morris}_T$  and  $\geq 2 \text{ SEM}_i$  are influential and interactive.

All foragers were positively influenced by changes to resource density and the density of *M. balthica* was identified as influential to all. Both *H. ostralegus* and *L. argentatus* were also sensitive

to changes in the density of *Oligochaeta* spp., *C. edule* and *T. tenuis*. *S. mollissima* was also sensitive to changes in the density of *T. tenuis* but was most sensitive to changes in the density of *M. edulis*. All values from the Morris sensitivity analysis are provided (Appendix C, Table 5.19).

#### 5.4.4.2 Resource thresholds

The densities of all influential resource types were simultaneously varied between 0 – 100% to provide simple predictions of the values required for each forager species to maintain good condition. Resource biomass was calculated as the mean value with each forager species preferred sized range in September ( $\text{g afdm m}^{-2} \text{y}^{-1}$ ) and each point represents the mean annual body condition of birds over ten years relative to their target mass. All predicted relationships between biomass and body condition of *C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima* populations are shown (Figure 5.6). For threshold plots, biomass density values are calculated as the sum of all resources (preferred size range) divided by either the total intertidal area (*C. canutus*, *S. mollissima*) or the total intertidal and terrestrial area (*H. ostralegus*, *L. argentatus*). All resource specific densities are also provided (Table 5.11).

The condition of *C. canutus* reached 100 % when intertidal resource density was  $9.9 \text{ g afdm m}^{-2} \text{y}^{-1}$  (Figure 5.6a). The condition of *H. ostralegus* and *L. argentatus* reached 100 % when the intertidal and terrestrial resource density was 9.9 and 8.7  $\text{g afdm m}^{-2} \text{y}^{-1}$  respectively (Figure 5.6b, 6c). The condition of *S. mollissima* reached 100 % when the intertidal resource density was  $15.0 \text{ g afdm m}^{-2} \text{y}^{-1}$  (Figure 5.6d).

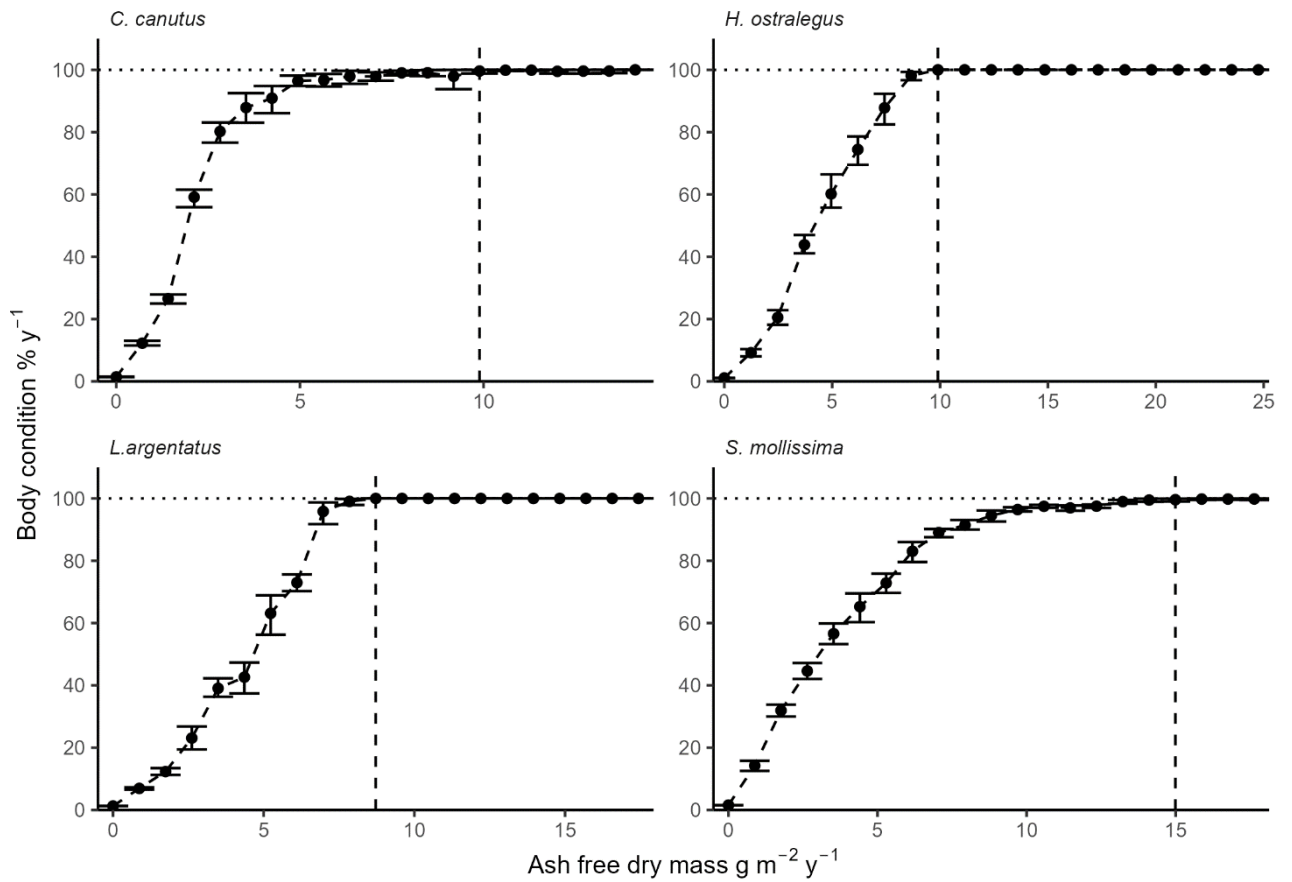


Figure 5.6 Predicted effect of changes to influential resource biomass ( $\text{g afdm m}^{-2} \text{y}^{-1}$ ) on the mean annual body condition  $\pm$  95% confidence intervals of model foragers (*C. canutus*, *H. ostralegus*, *L. argentatus* and *S. mollissima*). All influential resources within each foragers preferred size range were varied from 0% to 100% of the default autumn biomass. Simulations were based on current population sizes of each species and runs lasted for ten years. Vertical dashed lines represent the threshold after which condition is 100 % and horizontal lines represent a condition of 100 %.

Each threshold represents the total resource density for all intertidal (*C. canutus* and *S. mollissima*) and all intertidal and terrestrial (*H. ostralegus* and *L. argentatus*) areas. The density of each resource type at the threshold value provides additional insight into what each threshold represents (Table 5.11).

Table 5.11 Predicted density (g afdm m<sup>-2</sup>) and biomass (t) thresholds for five resource types (*M. edulis*, *C. edule*, *T. tenuis*, *M. balthica*, *terrestrial*) below which the condition of model foragers (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*) was less than 100 %. Density thresholds (g m<sup>-2</sup>) of the size range consumed are given for each resource and forager species. Biomass (t) thresholds are the product of each resource specific density threshold and its respective area (ha). The total area for *C. canutus* and *S. mollissima* is the intertidal region only while the total area for *H. ostralegus* and *L. argentatus* is the intertidal and terrestrial area. Total density estimates are the summed biomass values divided by the total area by species. Bold values represent resources classed as influential to the respective forager.

Resource	<i>C. canutus</i>		<i>H. ostralegus</i>		<i>L. argentatus</i>		<i>S. mollissima</i>		ha
	g m <sup>-2</sup>	t	g m <sup>-2</sup>	t	g m <sup>-2</sup>	t	g m <sup>-2</sup>	t	
<i>M. edulis</i>	12.9	53.7	235.6	982.5	27.8	116.0	<b>127.0</b>	<b>529.7</b>	417.0
<i>C. edule</i>	1.0	80.3	<b>2.3</b>	<b>190.9</b>	<b>2.9</b>	<b>238.6</b>	4.9	405.7	8195.9
<i>T. tenuis</i>	0.6	75.6	<b>1.7</b>	<b>234.0</b>	<b>2.2</b>	<b>292.5</b>	<b>3.7</b>	<b>497.3</b>	13498.0
<i>M. balthica</i>	<b>22.1</b>	<b>2582.3</b>	<b>11.3</b>	<b>1321.3</b>	<b>14.1</b>	<b>1651.6</b>	<b>24.0</b>	<b>2807.8</b>	11711.2
Terrestrial	0.0	0.0	<b>13.3</b>	<b>281.1</b>	<b>16.7</b>	<b>351.4</b>	0.0	0.0	2110.0
Totals									
Total biomass t	2791.9		3009.9		2650.2		4240.4		
Total area ha	28287.0		30397.0		30397.0		28287.0		
Total density g m <sup>-2</sup>	9.9		9.9		8.7		15.0		

#### 5.4.4.3 Commercial harvest

The relationship between the annual body condition of each species and the harvest of *M. edulis* was assessed via pairwise Spearman's correlation coefficients. Harvest rates (market and culture) of *M. edulis* were simultaneously varied (0–0.02 % h<sup>-1</sup>) for all patches and under a range of scenarios in which bivalve (*M. balthica*, *T. tenuis*, *C. edule*) and terrestrial resources were set to either high (default values) or threshold (bivalve – 70 %, terrestrial – 40 %) abundances. A full factorial design resulted in four resource scenarios, involved two harvest sizes (market and culture), 11 harvest rates (from 0 to 0.02 by 0.002) and was repeated 10 times to create an experiment which required 880 model runs.

A four-way ANOVA was used then to describe the correlation coefficients in relation to bird species, target harvest size and alternative resource abundance. A bidirectional stepwise linear regression was used to identify the best predictors. The full model contained correlation coefficients (continuous) as the response variable and included the main effects of bird species (factor, 4 levels, *C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*), harvest size (factor, 2 levels, market, culture), bivalve abundance (factor, 2 levels, low, default) and terrestrial resource abundance (factor, 2 levels, low, default), and all pairwise interactions between them. At each step, variables were added and removed based on AIC values. The final model included the main effects of bird species, harvest

size, bivalve abundance and the interaction between bird species and harvest size ( $F_{(8, 311)} = 52.78$ ,  $R^2 = 0.57$ ,  $p < 0.001$ , Table 5.12).

There was a significant difference in correlation coefficient between species ( $F_{(3, 317)} = 13.0$ ,  $p < 0.001$ ). The coefficient of *S. mollissima* (-0.31) was moderately negative, followed by weak negative coefficients of both *L. argentatus* (-0.16) and *H. ostralegus* (-0.14), and no correlation for *C. canutus* (-0.05). Pairwise comparisons revealed the mean coefficient of *S. mollissima* was significantly stronger than all other species ( $p < 0.05$ ) while *L. argentatus* and *H. ostralegus* had coefficients stronger than *C. canutus* ( $p < 0.05$ ) but not each other. The condition of *S. mollissima* was therefore more negatively correlated with the harvest of *M. edulis* than all other species and *C. canutus* was not affected.

There was also a significant difference in average correlation coefficient between harvest size ( $F_{(1, 315)} = 94.4$ ,  $p < 0.001$ ). A moderately negative coefficient of harvesting culture size *M. edulis* (-0.37) was significantly stronger than that of harvesting market size individuals for which there was no correlation (-0.07,  $p < 0.001$ ). Harvesting culture size *M. edulis* was therefore moderately and negatively correlated with the annual body condition of coastal birds while harvesting market size individuals was not.

Table 5.12 ANOVA table for the response of correlation coefficients between harvest rate and body condition to harvest size (market, culture), bird species (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*), bivalve abundance (low, default) and the interaction between bird species and harvest size. Degrees of freedom (Df), sum of squares (Sum Sq), mean square (Mean Sq), F statistics (F value) and statistical significance (Pr(>F)).

Variable	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Harvest size	1	12.99	12.99	153.87	< 0.001
Species	3	5.36	1.79	21.18	< 0.001
Bivalve abundance	1	0.33	0.33	3.91	< 0.05
Species: Harvest size	3	16.96	5.65	66.97	< 0.001
Residuals	311	26.26	0.08		

There was again a significant difference in average correlation coefficient relating to supplementary bivalve abundance ( $F_{(1, 312)} = 3.9$ ,  $p < 0.05$ ). A weak, negative coefficient (-0.17) under low supplementary bivalve abundance was significantly stronger than when abundance was set to default values (-0.11,  $p < 0.05$ ). Harvesting *M. edulis* was therefore moderately and negatively correlated with the annual body condition of coastal birds when supplementary bivalve abundance was low.

The average correlation coefficient varied in relation to a significant interaction between harvest size and species ( $F_{(3, 314)} = 67.0$ ,  $p < 0.001$ ). Pairwise comparisons show significantly stronger negative coefficients for *H. ostralegus* (-0.22), *L. argentatus* (-0.22) and *S. mollissima* (-1.20) when harvest was for culture size individuals ( $< 0.001$ ). Harvesting culture size *M. edulis* was therefore negatively correlated with body condition of *H. ostralegus*, *L. argentatus* and *S. mollissima*.

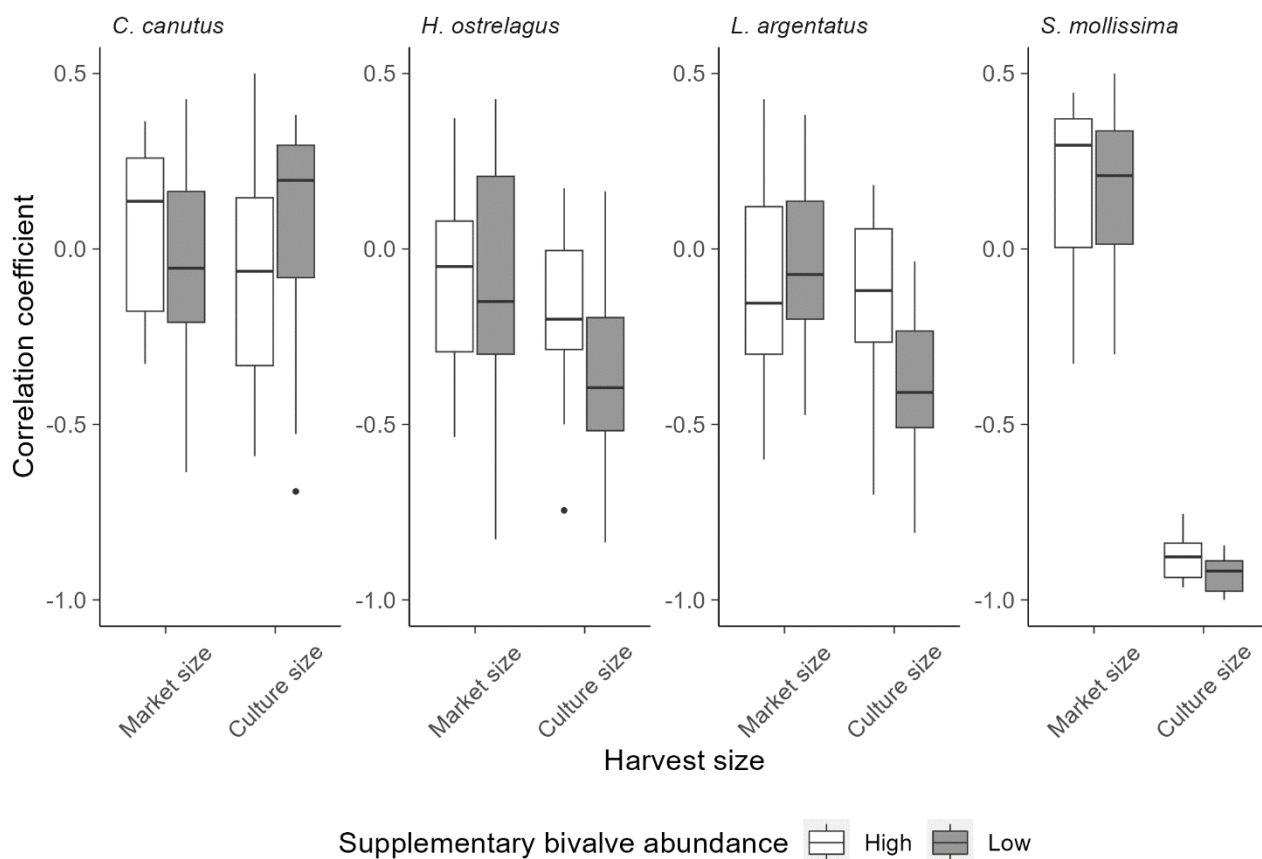


Figure 5.7 Boxplots of correlation coefficients between annual forager body mass and the harvest rate of *M. edulis*. Values are summarised by forager species (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*), supplementary bivalve abundance (low, default) and harvest size (market, culture). Negative correlation coefficients signify a negative correlation between harvest rate and body condition.

## 5.5 Discussion

Many species of coastal bird for which temperate estuaries are an important foraging habitat are experiencing long-term population declines (Meltotte et al., 2019; Piersma et al., 2016; Woodward et al., 2019). Changes in the availability of intertidal invertebrate resources are thought broadly responsible but the drivers (e.g., eutrophication, climate change, commercial bivalve harvest,



disturbance) remain poorly understood (Ens et al., 2009; Van Roomen et al., 2012). The complexity (e.g., non-linear, interactive, extensive) of estuarine systems complicates analysis via traditional methods and novel tools are required if long-term declines are to be understood. This study developed an agent-based model (ABM) for simulating the foraging behaviour of coastal birds in Morecambe Bay in response to environmental change. The sensitivity of each species foraging success to changes in resource density was systematically assessed to identify possible drivers of declines, with particular focus on the harvest of *M. edulis*. The density of bivalves (commercial and non-commercial) populations was highlighted as important to all species and the density of terrestrial resources was important to *H. ostralegus* and *L. argentatus*. The condition of *S. mollissima* was most negatively correlated with the harvest *M. edulis*, specifically culture size individuals and particularly if additional resource densities (e.g., *M. balthica*) were low. Both the likelihood and drivers of resource change are discussed under the topic of balancing the conservation of coastal birds with the harvest of intertidal invertebrate resources.

Bivalve (commercial and non-commercial) abundance was identified as influential to all bird species which confirms their historical importance to site quality in Morecambe Bay (Dare and Mercer, 1973; McCleery and Sibly, 1986; Prater, 1972). Long term trends of change to bivalve populations are increasingly being linked to variation in two environmental conditions; temperature and nutrient concentration (Atkinson et al., 2010; Beukema and Dekker, 2020a; Callaway, 2022). A general relationship of reduced recruitment but enhanced growth and survival with increasing temperature is apparent for many bivalve species (Beukema et al., 2017b, 2017a; Beukema and Dekker, 2020a, 2020b). Another common relationship of reduced biomass with decreasing nutrient inputs is noticeable (Callaway, 2022; Compton et al., 2017; Laursen and Møller, 2014; Philippart et al., 2007). The annual input of nutrients into the Irish sea has been declining since the 1990s and water temperatures have increased by approximately 1.5°C over the last 50 years (Allen et al., 1998; Greenwood et al., 2019; Nedwell et al., 2002; Tinker et al., 2020).

Changes to the abundance of small, non-commercial bivalves (i.e., *M. balthica* and *T. tenuis*) strongly influenced all model species, particularly *C. canutus*. The historical importance of small bivalves to the coastal birds in Morecambe Bay is well described but their current role is not known (Anderson, 1972; Dare and Mercer, 1973; Prater, 1972; Sibly and McCleery, 1983a). Some species (e.g., *M. balthica*) are sensitive to warming temperatures (reduced recruitment, growth and survival) and have been declining in the southern regions of western Europe for almost 50 years (Beukema et al., 2017a, 2017b; Beukema and Dekker, 2019; Dekker and Beukema, 2021; Jansen et al., 2007; Yates et al., 2002). Others (e.g., *Abra tenuis* and *T. tenuis*) favour warmer temperatures

(increased recruitment, growth and survival) and are increasing in abundance which to some extent may counter the declines (Beukema and Dekker, 2011; Dekker and Beukema, 2021). It might be the abundance of *M. balthica* in Morecambe Bay has declined in response to warming temperatures which is contributing to population declines. Routine monitoring of small, non-commercial bivalves is therefore a priority when managing estuaries where conservation objectives for coastal birds are important. The species considered here are predicted to require densities of small bivalves (i.e., *M. balthica* and *T. tenuis*) at  $0.6 - 22.4 \text{ g afdm m}^{-2} \text{ y}^{-1}$  and these values can be used to assess the site quality for Morecambe Bay.

Changes to the abundance of *C. edule* were influential to *H. ostralegus* and *L. argentatus*, both of which predominantly consumed the resource throughout winter. *C. edule* is comparatively less sensitive to warming temperatures (reduced recruitment, increased growth and survival) compared to other species (e.g., *M. balthica*) but a recent decline in biomass of larger (> 2cm) individuals is reported in the Irish Sea (Beukema et al., 2017b; Beukema and Dekker, 2020b; Callaway, 2022). The species experiences inherently variable rates of mortality and recruitment, and low abundance is commonly associated with the coincidence of low recruitment and either overexploitation, severe weather events or pathogen infections (Beukema et al., 2010; Dare et al., 2004; Magalhães et al., 2016; Skujina et al., 2022).

Between 1972 and 2015 the annual commercial harvest of *C. edule* in Morecambe Bay occurred 28 times and removed 36,740 tonnes respectively (NWIFCA, 2020). Polychaete abundance is observed to increase in sediments which are routinely disturbed by harvesting practices (particularly dredging) and evidence that bird numbers have decreased in response might be an increase in the number of polychaete specialists (Atkinson et al., 2010; Clarke et al., 2017; Kraan et al., 2007). In Morecambe Bay many polychaete specialists (e.g., *Pluvialis squatarola*, *Limosa lapponica*) are also undergoing population declines which indicates this has not occurred (Woodward et al., 2019).

Mass mortalities within *C. edule* populations have been intermittently reported throughout western Europe (including Morecambe Bay) for over a century (Burdon et al., 2014; Callaway et al., 2013; Malham et al., 2012; Orton, 1933). Long-term biomass estimates for *C. edule* are generally <  $5 \text{ g afdm m}^{-2} \text{ y}^{-1}$  which alone is not predicted enough to support coastal bird populations (Beukema et al., 2010; Beukema and Dekker, 2006; Fujii, 2007; Stillman et al., 2005; Yates et al., 2002). In the Irish Sea severe winters and elevated pathogen loads are thought to have contributed to high mortality rates and prolonged periods of relatively low biomass (Callaway et al., 2013; Skujina et al., 2022). Low biomass of *C. edule* is currently common in Morecambe Bay and further reductions are predicted to negatively impact some coastal bird populations (e.g., *H. ostralegus* and *L. argentatus*).

This underlines the importance of adjacent sites and secondary habitats for buffering against the effects of changes to resource availability (Bowgen et al., 2022).

The abundance of terrestrial resources was highlighted as important for *H. ostralegus* and *L. argentatus*. Terrestrial habitats are a valuable food source for some coastal birds and are occasionally used in preference to intertidal habitats (Alves et al., 2010; Furnell and Hull, 2014; Smart and Gill, 2003). In Morecambe Bay the *L. argentatus* population has historically used landfill sites and agricultural grasslands to find non-intertidal resources, while *H. ostralegus* used only agricultural grasslands (Dare and Mercer, 1973; Sibly and McCleery, 1983b, 1983a). There has been a significant reduction in the use of landfill sites by *L. argentatus* and agricultural grassland is now the populations preferred non-intertidal habitat (Clewley et al., 2021). Increased competition for food on the agricultural grasslands around Morecambe Bay may therefore be contributing to the decline of its bird assemblage. Biodiversity loss on wet grasslands is high and associated with a decrease in soil moisture and higher soil nutrient contents (Diekmann et al., 2019). Long term declines of insectivorous birds (including waders) are primarily associated with agricultural intensification and loss of grassland habitat (Bowler et al., 2019). The role of agricultural grasslands as foraging grounds for coastal birds is poorly understood. Sea level rise will likely increase dependence on terrestrial resources with projected losses of intertidal habitat ranging between 20% and 70% (Galbraith et al., 2002). Monitoring the number of birds using supplementary habitats such as agricultural grasslands is a convenient way of assessing the extent to which birds depend on terrestrial habitats (Fujii and Raffaelli, 2008).

The condition of *S. mollissima* was strongly influenced by changes to *M. edulis* biomass and negatively correlated with the harvest rate of culture sized individuals. *S. mollissima* are generally found to prefer sites with high densities of *M. edulis* where they consume smaller individuals due to the higher energy content and less resistant shells (Cervencel et al., 2015; Varennes et al., 2015). The model population consumed  $1525.6 \pm 4.5 \text{ t y}^{-1}$  of *M. edulis* and required densities of approximately  $2.5 \text{ kg m}^{-2}$  to do so. This equates to an average individual intake rate of  $3.1 \pm 0.005 \text{ kg d}^{-1}$ , which is comparable to estimates ( $0.9 - 3.7 \text{ kg d}^{-1}$ ) for populations in the Wash, the Wadden Sea and the North Sea (Caldow et al., 2007; Camphuysen et al., 2002; Hilgerloh, 1997; Laursen et al., 2010; Nehls, 1995).

The harvest of culture size individuals was negatively correlated with annual body condition of *H. ostralegus*, *L. argentatus* and *S. mollissima*. Overexploitation therefore potentially conflicts with their conservation objectives in Morecambe Bay. The harvest of culture size *M. edulis* in Morecambe Bay is only permitted when their survival is thought unlikely. Settlements can be extremely dense

and rapid growth (and biodeposition) rates can create unstable aggregations which quickly wash away through natural processes (Dare, 1976; Troost et al., 2022). Despite restrictions the annual harvest rate of culture size *M. edulis* in Morecambe has increased by approximately 100 t y<sup>-1</sup> since the 70s. It is therefore possible that the harvest of culture size individuals has contributed to the population declines of coastal birds in Morecambe Bay.

Negative correlations between the harvest rate of culture size *M. edulis* and body condition were strongest for *S. mollissima* and relatively high harvest rates reduced condition to values observed for starving individuals (Cabanac, 2003; Camphuysen et al., 2002; Garbus et al., 2018). The result suggests the risk to the species is comparatively high because *M. edulis* is their main source of food in Morecambe Bay. While many studies observe *S. mollissima* feeding predominantly on *M. edulis*, others find higher proportions of gastropods, crustaceans and other small bivalves (Guillemette et al., 1996; Kristjánsson et al., 2013; Merkel et al., 2007). Large crustaceans and gastropods were not included as model resources but are numerous in Morecambe Bay and may supplement *S. mollissima* when *M. edulis* abundance is low (Anderson, 1972). Both *H. ostralegus* and *L. argentatus* were not influenced directly by changes to the abundance of *M. edulis* but their condition was negatively correlated with its harvest. As a large predator which exerts high predation pressure on macrobenthic fauna *S. mollissima* may negative influence other species via increased competition (Blicher et al., 2011).

Sustainable management of intertidal invertebrate resources for conservation and economic purposes increasingly requires detailed knowledge of the distribution and abundance of all important resources within the area of interest (Beukema et al., 2010; Beukema and Dekker, 2019). There have been significant changes to both the intertidal and terrestrial invertebrate communities of western Europe over the last 50 years to which coastal bird populations are responding (Beukema and Dekker, 2020a; Outhwaite et al., 2020; Pilotto et al., 2020). Increasing temperatures and rising sea levels are likely altering the foraging decisions of coastal birds at large spatial scales and conservation plans must adapt and expand (Gillings et al., 2006; Maclean et al., 2008; Meltofte et al., 2019; Pearce-Higgins and Holt, 2013). Terrestrial resources in particular are often simplified or ignored when assessing conservation issues, but their influence on site quality is likely to increase (Austin and Rehfisch, 2003; Sutherland et al., 2012). Sea level rise for example is expected to increase the density of birds foraging on intertidal flats which will increase competition and reduce intake rates. The density of wader species is predicted to decrease under management scenarios that provide sufficient wet grassland or allow land behind existing sea defences to be reclaimed by the sea (Austin and Rehfisch, 2003). The impacts of harvesting intertidal invertebrates to coastal

bird populations will likely vary in relation to the environmental change currently occurring in coastal regions. Ecological models must be continuously developed (e.g., DEB sub-models) if they are to keep pace with the rapidly changing environments that coastal birds are experiencing (Grimm et al., 2017, 2006).

## 5.6 Author contributions

Supervision: J. G. Hiddink and L. S. Cordes

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Table 5.13 Initial values for the global model environment.

Global environment	Initial value
Date	15 <sup>th</sup> September 01:00:00
Air temperature	13.2 °C
Sea temperature	15.6 °C
Suspended inorganic particles	21.2 g m <sup>-3</sup>
Chlorophyll-a	4.2 mg m <sup>-3</sup>
Water level	-0.03 m

Table 5.14 Area (ha) of all patches within the global environment by elevation (m), habitat type (terrestrial, intertidal flat and *M. edulis* reef) and region (Foulney, Fleetwood, Heysham and Cartmel). Roost patches have no area and an elevation of 10 m. All



terrestrial (wet grassland) patches have region specific areas, and their elevation is set to 10 m. All intertidal patches have region specific areas and elevations.

Patch set	Elevation m										
	10.0	-3.5	-2.5	-1.5	-0.5	0.5	1.5	2.5	3.5	4.5	5.5
<b>Terrestrial</b>											
Roost	-	-	-	-	-	-	-	-	-	-	-
Foulney	307.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heysham	340.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fleetwood	640.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cartmel	823.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>Intertidal flats</b>											
Foulney	0.0	0.0	1575	1475	1400	900	925	975	800	350	50
Heysham	0.0	0.0	2150	1425	1325	1075	1350	1225	950	750	100
Fleetwood	0.0	0.0	875	525	775	1125	750	700	650	600	0
Cartmel	0.0	0.0	425	575	750	875	2125	2500	2125	1175	525
<b><i>M. edulis</i> reef</b>											
Foulney	0.0	10.3	27.5	259.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heysham	0.0	13.0	2.6	75.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fleetwood	0.0	7.4	34.6	7.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cartmel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 5.15 Resource density (m<sup>-2</sup>), individual ash-free dry mass (g) and mortality rate (y<sup>-1</sup>) by species, size class (cm) and site (Anderson, 1972; Dekker and Beukema, 1999; Kristensen, 1984; Mossman, 1978).

Resource	Size class cm		Density m <sup>-2</sup>				AFDM g	Mortality y <sup>-1</sup>
	Min	Max	Cartmel	Foulney	Heysham	Fleetwood		
<i>Oligochaeta spp.</i>	1.50	2.99	9	9	9	9	0.0083	0.00
	3.00	4.49	15	15	15	15	0.0267	0.00
	4.50	5.99	24	24	24	24	0.0577	0.00
	6.00	7.49	25	25	25	25	0.1024	0.00
	7.50	8.99	11	11	11	11	0.1620	0.00
	9.00	10.49	7	7	7	7	0.2373	0.00
	10.50	11.99	4	4	4	4	0.3291	0.00
<i>H. ulvae</i>	0.00	0.59	988	988	988	988	0.0010	0.53
<i>C. volutator</i>	0.00	1.19	415	415	415	415	0.0055	0.40
<i>M. balthica</i>	0.00	0.99	172	172	172	172	0.0014	0.49
	1.00	1.99	667	667	667	667	0.0355	0.49
<i>M. edulis</i>	2.00	2.99	161	161	161	161	0.1577	-
	0.00	0.99	0	0	0	0	0.0000	-
	1.00	1.99	0	0	0	0	0.0000	-
	2.00	2.99	0	3787	2426	1857	0.0918	-
	3.00	3.99	0	961	437	990	0.2465	-
	4.00	4.99	0	131	49	130	0.4300	-
<i>C. edule</i>	5.00	5.99	0	49	0	0	0.7762	-
	6.00	6.99	0	0	0	0	0.0000	-
	0.00	0.99	57	57	57	57	0.0011	0.77
	1.00	1.99	10	10	10	10	0.0356	0.77
	2.00	2.99	8	8	8	8	0.1786	0.77
	3.00	3.99	5	5	5	5	0.5166	0.77
<i>N. diversicolor</i>	0.50	1.49	11	11	11	11	0.0013	0.97
	1.50	2.99	25	25	25	25	0.0147	0.97
	3.00	4.49	46	46	46	46	0.0454	0.97
	4.50	5.99	40	40	40	40	0.0955	0.00
	6.00	7.49	28	28	28	28	0.1664	0.00
	7.50	8.99	7	7	7	7	0.2591	0.00
	9.00	10.49	4	4	4	4	0.3747	0.00
<i>T. tenuis</i>	10.50	11.99	1	1	1	1	0.5140	0.00
	0.00	0.99	3	3	3	3	0.1441	0.00
	1.00	1.99	5	5	5	5	0.2637	0.00
	2.00	2.99	4	4	4	4	0.4360	0.00

Table 5.16 Values of the asymptote and gradient used in the functional response for *S. mollissima*

Resource	Size range cm		$b_{50} \text{ m}^{-2}$	IFIR <sub>max</sub> s <sup>-1</sup>
	Min	Max		
<i>M. balthica</i>	0.00	1.99	591	0.748
<i>M. edulis</i>	0.00	2.99	209	0.172
<i>M. edulis</i>	3.00	5.99	209	0.084
<i>C. edule</i>	0.00	1.99	591	0.748
<i>C. edule</i>	2.00	3.99	209	0.496
<i>T. tenuis</i>	0.00	1.99	591	0.748
<i>T. tenuis</i>	2.00	2.99	209	0.496

Table 5.17 Interference coefficients (dimensionless,  $m_{\text{max}}$  = susceptibility to interference of least dominant individual and  $m_{\text{min}}$  = susceptibility to interference of most dominant individual) for eight invertebrate resources (*Oligochaeta spp.*, *Hydrobia spp.*, *Corophium spp.*, *M. balthica*, *M. edulis*, *C. edule*, *N. diversicolor*, *T. tenuis*) and their respective size classes.

Resource	Size range		$m_{\text{max}}$	$m_{\text{min}}$	Description
	Min	Max			
<i>Oligochaeta spp.</i>	1.50	24.99	0.48	0.48	Mobile prey interference
<i>Hydrobia spp.</i>	0.00	0.60	0.00	0.00	No interference
<i>Corophium spp.</i>	0.00	1.20	0.00	0.00	No interference
<i>M. balthica</i>	0.00	1.99	0.00	0.08	Weak kleptoparasitism
<i>M. edulis</i>	0.00	1.99	0.00	0.08	Weak kleptoparasitism
<i>M. edulis</i>	2.00	> 2.00	0.00	0.50	Strong kleptoparasitism
<i>C. edule</i>	0.00	1.99	0.00	0.08	Weak kleptoparasitism
<i>C. edule</i>	2.00	3.99	0.00	0.50	Strong kleptoparasitism
<i>N. diversicolor</i>	0.50	11.99	0.48	0.48	Mobile prey interference
<i>T. tenuis</i>	0.00	1.99	0.00	0.08	Weak kleptoparasitism
<i>T. tenuis</i>	2.00	2.99	0.00	0.50	Strong kleptoparasitism

Table 5.18 Forager prey preference by resource type (*Oligochaeta*, *Hydrobia* spp., *Corophium*, *M. balthica*, *M. edulis*, *C. edule*, *N. diversicolor*, *T. tenuis*), size and forager species (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*). 0 indicates no preference while 1 indicates preference.

Resource	Size range		<i>C. canutus</i>	<i>H. ostralegus</i>	<i>L. argentatus</i>	<i>S. mollissima</i>
	Min	Max				
<i>Oligochaeta</i>	1.50	2.99	1	0	0	0
<i>Oligochaeta</i>	3.00	4.49	0	1	0	0
<i>Oligochaeta</i>	4.50	5.99	0	1	0	0
<i>Oligochaeta</i>	6.00	7.49	0	1	0	0
<i>Oligochaeta</i>	7.50	8.99	0	1	1	0
<i>Oligochaeta</i>	9.00	10.49	0	1	1	0
<i>Oligochaeta</i>	10.50	11.99	0	1	1	0
<i>Hydrobia</i> spp.	0.00	0.59	1	0	0	0
<i>Corophium</i>	0.00	1.19	1	0	0	0
<i>M. balthica</i>	0.00	0.99	1	0	0	0
<i>M. balthica</i>	1.00	1.99	1	1	1	1
<i>M. balthica</i>	2.00	2.99	0	1	1	1
<i>M. edulis</i>	0.00	0.99	1	0	0	0
<i>M. edulis</i>	1.00	1.99	1	1	1	1
<i>M. edulis</i>	2.00	2.99	0	1	1	1
<i>M. edulis</i>	3.00	3.99	0	1	1	1
<i>M. edulis</i>	4.00	4.99	0	1	0	1
<i>M. edulis</i>	5.00	5.99	0	1	0	0
<i>M. edulis</i>	6.00	6.99	0	1	0	0
<i>M. edulis</i>	7.00	7.99	0	0	0	0
<i>M. edulis</i>	8.00	8.99	0	0	0	0
<i>M. edulis</i>	9.00	9.99	0	0	0	0
<i>C. edule</i>	0.00	0.99	1	0	0	0
<i>C. edule</i>	1.00	1.99	1	1	1	1
<i>C. edule</i>	2.00	2.99	0	1	1	1
<i>C. edule</i>	3.00	3.99	0	1	1	1
<i>N. diversicolor</i>	0.50	1.49	1	0	0	0
<i>N. diversicolor</i>	1.50	2.99	1	0	0	0
<i>N. diversicolor</i>	3.00	4.49	0	1	0	0
<i>N. diversicolor</i>	4.50	5.99	0	1	0	0
<i>N. diversicolor</i>	6.00	7.49	0	1	0	0
<i>N. diversicolor</i>	7.50	8.99	0	1	1	0
<i>N. diversicolor</i>	9.00	10.49	0	1	1	0
<i>N. diversicolor</i>	10.50	11.99	0	1	1	0
<i>T. tenuis</i>	4.00	4.99	0	0	1	1
<i>T. tenuis</i>	5.00	5.99	0	0	0	1
<i>T. tenuis</i>	6.00	6.99	0	0	0	1
<i>T. tenuis</i>	7.00	7.99	0	0	0	1
<i>T. tenuis</i>	8.00	8.99	0	0	0	1
<i>T. tenuis</i>	9.00	9.99	0	0	0	1
<i>T. tenuis</i>	10.00	10.99	0	0	0	1
<i>T. tenuis</i>	11.00	11.99	0	0	0	1
<i>T. tenuis</i>	12.00	12.99	0	0	0	1
<i>T. tenuis</i>	13.00	13.99	0	0	0	1

Table 5.19 Results from Morris sensitivity analysis of forager body mass to the variation of 8 resource types. The sensitivity classification (non-influential, influential: second order), mean ( $\mu$ ), absolute mean ( $\mu^*$ ), standard deviation ( $\sigma$ ) and the savage score

of the elementary effects are given by species (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*) and resource type (*C. edule*, *M. edulis*, *Oligochaeta spp.*, *H. ulvae*, *C. volutator*, *M. balthica*, *N. diversicolor*, *T. tenuis*).

Species	Resource	Classification	$\mu$	$\mu^*$	$\sigma$	Savage score
<i>C. canutus</i>	<i>M. balthica</i>	Influential: second order	0.65	0.65	0.55	2.67
<i>C. canutus</i>	<i>T. tenuis</i>	Non-influential	-0.01	0.04	0.06	0.86
<i>C. canutus</i>	<i>M. edulis</i>	Non-influential	0.02	0.04	0.06	0.75
<i>C. canutus</i>	<i>C. volutator</i>	Non-influential	0.03	0.04	0.06	0.83
<i>C. canutus</i>	<i>N. diversicolor</i>	Non-influential	-0.01	0.04	0.05	0.84
<i>C. canutus</i>	<i>C. edule</i>	Non-influential	0.00	0.03	0.04	0.79
<i>C. canutus</i>	<i>H. ulvae</i>	Non-influential	-0.01	0.03	0.04	0.66
<i>C. canutus</i>	<i>Oligochaeta spp.</i>	Non-influential	0.01	0.03	0.04	0.60
<i>H. ostralegus</i>	<i>Oligochaeta spp.</i>	Influential: second order	0.44	0.44	0.49	2.15
<i>H. ostralegus</i>	<i>M. balthica</i>	Influential: second order	0.20	0.20	0.35	0.86
<i>H. ostralegus</i>	<i>T. tenuis</i>	Influential: second order	0.15	0.15	0.16	1.39
<i>H. ostralegus</i>	<i>C. edule</i>	Influential: second order	0.13	0.13	0.16	1.39
<i>H. ostralegus</i>	<i>M. edulis</i>	Non-influential	0.02	0.05	0.11	0.79
<i>H. ostralegus</i>	<i>N. diversicolor</i>	Non-influential	-0.01	0.03	0.05	0.59
<i>H. ostralegus</i>	<i>H. ulvae</i>	Non-influential	0.00	0.02	0.03	0.45
<i>H. ostralegus</i>	<i>C. volutator</i>	Non-influential	0.01	0.02	0.03	0.37
<i>L. argentatus</i>	<i>Oligochaeta spp.</i>	Influential: second order	0.55	0.55	0.43	2.06
<i>L. argentatus</i>	<i>T. tenuis</i>	Influential: second order	0.27	0.28	0.25	1.32
<i>L. argentatus</i>	<i>C. edule</i>	Influential: second order	0.25	0.25	0.18	1.66
<i>L. argentatus</i>	<i>M. balthica</i>	Influential: second order	0.22	0.23	0.31	0.92
<i>L. argentatus</i>	<i>H. ulvae</i>	Non-influential	0.03	0.07	0.09	0.59
<i>L. argentatus</i>	<i>M. edulis</i>	Non-influential	0.04	0.06	0.09	0.53
<i>L. argentatus</i>	<i>C. volutator</i>	Non-influential	0.02	0.06	0.08	0.57
<i>L. argentatus</i>	<i>N. diversicolor</i>	Non-influential	0.01	0.03	0.05	0.36
<i>S. mollissima</i>	<i>M. edulis</i>	Influential: second order	0.47	0.47	0.47	2.03
<i>S. mollissima</i>	<i>M. balthica</i>	Influential: second order	0.29	0.29	0.25	2.05
<i>S. mollissima</i>	<i>T. tenuis</i>	Influential: second order	0.11	0.11	0.14	1.03
<i>S. mollissima</i>	<i>C. edule</i>	Non-influential	0.03	0.06	0.09	0.70
<i>S. mollissima</i>	<i>Oligochaeta spp.</i>	Non-influential	-0.01	0.05	0.08	0.59
<i>S. mollissima</i>	<i>H. ulvae</i>	Non-influential	0.00	0.04	0.07	0.56
<i>S. mollissima</i>	<i>C. volutator</i>	Non-influential	0.00	0.04	0.06	0.47
<i>S. mollissima</i>	<i>N. diversicolor</i>	Non-influential	0.01	0.03	0.04	0.57

Table 5.20 Results from correlation analysis between the harvest rate of *M. edulis* and the annual body condition of model foragers. The correlation coefficient ( $r$ ) and  $p$  value ( $p$ ) are given by species (*C. canutus*, *H. ostralegus*, *L. argentatus*, *S. mollissima*), bivalve abundance scenario (low, high), terrestrial resource abundance scenario (low, high) and harvest size (market or culture).

Species	Bivalve	Terrestrial	Harvest size	r	p
<i>C. canutus</i>	Low	High	Market	-0.636	< 0.05
<i>C. canutus</i>	Low	High	Market	-0.482	0.133
<i>C. canutus</i>	Low	High	Market	-0.382	0.247
<i>C. canutus</i>	High	High	Market	-0.327	0.326
<i>C. canutus</i>	Low	High	Market	-0.318	0.34
<i>C. canutus</i>	High	Low	Market	-0.282	0.401
<i>C. canutus</i>	Low	Low	Market	-0.245	0.467
<i>C. canutus</i>	High	High	Market	-0.227	0.502
<i>C. canutus</i>	High	Low	Market	-0.218	0.519
<i>C. canutus</i>	High	High	Market	-0.2	0.555
<i>C. canutus</i>	Low	Low	Market	-0.173	0.612
<i>C. canutus</i>	High	High	Market	-0.155	0.65
<i>C. canutus</i>	Low	Low	Market	-0.136	0.689
<i>C. canutus</i>	Low	Low	Market	-0.118	0.729
<i>C. canutus</i>	High	Low	Market	-0.109	0.75
<i>C. canutus</i>	Low	Low	Market	-0.091	0.79
<i>C. canutus</i>	Low	Low	Market	-0.055	0.873
<i>C. canutus</i>	High	High	Market	0.009	0.979
<i>C. canutus</i>	Low	Low	Market	0.009	0.979
<i>C. canutus</i>	Low	Low	Market	0.055	0.873
<i>C. canutus</i>	Low	Low	Market	0.073	0.832
<i>C. canutus</i>	High	High	Market	0.118	0.729
<i>C. canutus</i>	High	Low	Market	0.136	0.689
<i>C. canutus</i>	Low	Low	Market	0.155	0.65
<i>C. canutus</i>	High	High	Market	0.155	0.65
<i>C. canutus</i>	High	Low	Market	0.155	0.65
<i>C. canutus</i>	High	Low	Market	0.164	0.631
<i>C. canutus</i>	Low	High	Market	0.173	0.612
<i>C. canutus</i>	High	Low	Market	0.209	0.537
<i>C. canutus</i>	Low	High	Market	0.264	0.433
<i>C. canutus</i>	High	High	Market	0.309	0.355
<i>C. canutus</i>	High	Low	Market	0.345	0.298
<i>C. canutus</i>	High	High	Market	0.355	0.285
<i>C. canutus</i>	High	High	Market	0.355	0.285
<i>C. canutus</i>	High	Low	Market	0.364	0.272
<i>C. canutus</i>	Low	High	Market	0.364	0.272
<i>C. canutus</i>	Low	High	Market	0.4	0.223
<i>C. canutus</i>	Low	High	Market	0.427	0.19
<i>C. canutus</i>	Low	High	Market	0.709	< 0.05
<i>C. canutus</i>	High	Low	Market	0.755	< 0.05
<i>C. canutus</i>	Low	High	Culture	-0.691	< 0.05
<i>C. canutus</i>	High	Low	Culture	-0.591	0.056
<i>C. canutus</i>	Low	Low	Culture	-0.527	0.096
<i>C. canutus</i>	High	High	Culture	-0.518	0.102
<i>C. canutus</i>	High	High	Culture	-0.391	0.235
<i>C. canutus</i>	High	High	Culture	-0.364	0.272
<i>C. canutus</i>	High	Low	Culture	-0.355	0.285
<i>C. canutus</i>	High	High	Culture	-0.264	0.433
<i>C. canutus</i>	Low	Low	Culture	-0.255	0.45

<i>C. canutus</i>	High	High	Culture	-0.236	0.484
<i>C. canutus</i>	High	Low	Culture	-0.2	0.555
<i>C. canutus</i>	Low	Low	Culture	-0.164	0.631
<i>C. canutus</i>	High	Low	Culture	-0.109	0.75
<i>C. canutus</i>	Low	Low	Culture	-0.109	0.75
<i>C. canutus</i>	High	High	Culture	-0.018	0.958
<i>C. canutus</i>	Low	High	Culture	0	1
<i>C. canutus</i>	High	High	Culture	0	1
<i>C. canutus</i>	Low	High	Culture	0.009	0.979
<i>C. canutus</i>	High	High	Culture	0.055	0.873
<i>C. canutus</i>	Low	Low	Culture	0.082	0.811
<i>C. canutus</i>	High	Low	Culture	0.091	0.79
<i>C. canutus</i>	High	Low	Culture	0.164	0.631
<i>C. canutus</i>	Low	High	Culture	0.182	0.593
<i>C. canutus</i>	Low	Low	Culture	0.209	0.537
<i>C. canutus</i>	High	Low	Culture	0.209	0.537
<i>C. canutus</i>	Low	High	Culture	0.273	0.417
<i>C. canutus</i>	Low	High	Culture	0.273	0.417
<i>C. canutus</i>	Low	Low	Culture	0.282	0.401
<i>C. canutus</i>	Low	High	Culture	0.3	0.37
<i>C. canutus</i>	Low	Low	Culture	0.318	0.34
<i>C. canutus</i>	High	High	Culture	0.327	0.326
<i>C. canutus</i>	Low	High	Culture	0.373	0.259
<i>C. canutus</i>	Low	High	Culture	0.373	0.259
<i>C. canutus</i>	Low	Low	Culture	0.382	0.247
<i>C. canutus</i>	High	Low	Culture	0.427	0.19
<i>C. canutus</i>	High	Low	Culture	0.5	0.117
<i>C. canutus</i>	High	High	Culture	0.518	0.102
<i>C. canutus</i>	Low	High	Culture	0.545	0.083
<i>C. canutus</i>	High	Low	Culture	0.618	< 0.05
<i>C. canutus</i>	Low	Low	Culture	0.664	< 0.05
<i>H. ostralegus</i>	Low	Low	Market	-0.827	< 0.05
<i>H. ostralegus</i>	High	High	Market	-0.536	0.089
<i>H. ostralegus</i>	Low	Low	Market	-0.518	0.102
<i>H. ostralegus</i>	Low	High	Market	-0.518	0.102
<i>H. ostralegus</i>	High	High	Market	-0.491	0.125
<i>H. ostralegus</i>	Low	High	Market	-0.427	0.19
<i>H. ostralegus</i>	High	High	Market	-0.345	0.298
<i>H. ostralegus</i>	High	Low	Market	-0.327	0.326
<i>H. ostralegus</i>	High	High	Market	-0.327	0.326
<i>H. ostralegus</i>	Low	High	Market	-0.3	0.37
<i>H. ostralegus</i>	Low	High	Market	-0.3	0.37
<i>H. ostralegus</i>	Low	High	Market	-0.273	0.417
<i>H. ostralegus</i>	Low	High	Market	-0.255	0.45
<i>H. ostralegus</i>	Low	Low	Market	-0.2	0.555
<i>H. ostralegus</i>	High	High	Market	-0.191	0.574
<i>H. ostralegus</i>	High	Low	Market	-0.164	0.631
<i>H. ostralegus</i>	High	High	Market	-0.145	0.67
<i>H. ostralegus</i>	High	Low	Market	-0.109	0.75
<i>H. ostralegus</i>	Low	Low	Market	-0.1	0.77



<i>H. ostralegus</i>	Low	Low	Market	-0.064	0.853
<i>H. ostralegus</i>	Low	High	Market	-0.027	0.937
<i>H. ostralegus</i>	High	High	Market	0.009	0.979
<i>H. ostralegus</i>	High	Low	Market	0.018	0.958
<i>H. ostralegus</i>	High	Low	Market	0.027	0.937
<i>H. ostralegus</i>	Low	Low	Market	0.036	0.915
<i>H. ostralegus</i>	High	Low	Market	0.045	0.894
<i>H. ostralegus</i>	High	Low	Market	0.091	0.79
<i>H. ostralegus</i>	High	Low	Market	0.1	0.77
<i>H. ostralegus</i>	High	Low	Market	0.109	0.75
<i>H. ostralegus</i>	Low	High	Market	0.264	0.433
<i>H. ostralegus</i>	High	High	Market	0.282	0.401
<i>H. ostralegus</i>	Low	Low	Market	0.291	0.385
<i>H. ostralegus</i>	Low	Low	Market	0.3	0.37
<i>H. ostralegus</i>	High	Low	Market	0.373	0.259
<i>H. ostralegus</i>	Low	High	Market	0.391	0.235
<i>H. ostralegus</i>	Low	Low	Market	0.427	0.19
<i>H. ostralegus</i>	High	High	Market	0.536	0.089
<i>H. ostralegus</i>	Low	High	Market	0.582	0.06
<i>H. ostralegus</i>	Low	Low	Market	0.691	< 0.05
<i>H. ostralegus</i>	High	High	Market	0.727	< 0.05
<i>H. ostralegus</i>	Low	High	Culture	-0.836	< 0.05
<i>H. ostralegus</i>	Low	High	Culture	-0.755	< 0.05
<i>H. ostralegus</i>	High	High	Culture	-0.745	< 0.05
<i>H. ostralegus</i>	Low	High	Culture	-0.655	< 0.05
<i>H. ostralegus</i>	Low	Low	Culture	-0.618	< 0.05
<i>H. ostralegus</i>	Low	Low	Culture	-0.545	0.083
<i>H. ostralegus</i>	Low	Low	Culture	-0.509	0.11
<i>H. ostralegus</i>	High	Low	Culture	-0.5	0.117
<i>H. ostralegus</i>	High	High	Culture	-0.491	0.125
<i>H. ostralegus</i>	Low	High	Culture	-0.464	0.151
<i>H. ostralegus</i>	Low	High	Culture	-0.464	0.151
<i>H. ostralegus</i>	Low	Low	Culture	-0.436	0.18
<i>H. ostralegus</i>	Low	High	Culture	-0.4	0.223
<i>H. ostralegus</i>	Low	Low	Culture	-0.391	0.235
<i>H. ostralegus</i>	High	High	Culture	-0.364	0.272
<i>H. ostralegus</i>	Low	Low	Culture	-0.336	0.312
<i>H. ostralegus</i>	Low	High	Culture	-0.3	0.37
<i>H. ostralegus</i>	High	High	Culture	-0.3	0.37
<i>H. ostralegus</i>	Low	High	Culture	-0.291	0.385
<i>H. ostralegus</i>	High	Low	Culture	-0.273	0.417
<i>H. ostralegus</i>	High	Low	Culture	-0.218	0.519
<i>H. ostralegus</i>	High	High	Culture	-0.218	0.519
<i>H. ostralegus</i>	High	Low	Culture	-0.209	0.537
<i>H. ostralegus</i>	High	Low	Culture	-0.2	0.555
<i>H. ostralegus</i>	Low	High	Culture	-0.2	0.555
<i>H. ostralegus</i>	Low	Low	Culture	-0.182	0.593
<i>H. ostralegus</i>	High	High	Culture	-0.155	0.65
<i>H. ostralegus</i>	Low	Low	Culture	-0.109	0.75
<i>H. ostralegus</i>	High	Low	Culture	-0.109	0.75

<i>H. ostralegus</i>	Low	Low	Culture	-0.073	0.832
<i>H. ostralegus</i>	High	High	Culture	-0.027	0.937
<i>H. ostralegus</i>	High	Low	Culture	-0.009	0.979
<i>H. ostralegus</i>	High	Low	Culture	0	1
<i>H. ostralegus</i>	High	High	Culture	0.082	0.811
<i>H. ostralegus</i>	Low	Low	Culture	0.1	0.77
<i>H. ostralegus</i>	High	High	Culture	0.118	0.729
<i>H. ostralegus</i>	High	Low	Culture	0.136	0.689
<i>H. ostralegus</i>	Low	High	Culture	0.164	0.631
<i>H. ostralegus</i>	High	Low	Culture	0.173	0.612
<i>H. ostralegus</i>	High	High	Culture	0.727	< 0.05
<i>L. argentatus</i>	High	Low	Market	-0.6	0.051
<i>L. argentatus</i>	Low	High	Market	-0.473	0.142
<i>L. argentatus</i>	High	High	Market	-0.473	0.142
<i>L. argentatus</i>	Low	Low	Market	-0.4	0.223
<i>L. argentatus</i>	High	Low	Market	-0.4	0.223
<i>L. argentatus</i>	Low	High	Market	-0.318	0.34
<i>L. argentatus</i>	High	Low	Market	-0.309	0.355
<i>L. argentatus</i>	High	Low	Market	-0.309	0.355
<i>L. argentatus</i>	High	High	Market	-0.273	0.417
<i>L. argentatus</i>	Low	High	Market	-0.255	0.45
<i>L. argentatus</i>	High	High	Market	-0.227	0.502
<i>L. argentatus</i>	High	High	Market	-0.209	0.537
<i>L. argentatus</i>	Low	High	Market	-0.2	0.555
<i>L. argentatus</i>	Low	Low	Market	-0.2	0.555
<i>L. argentatus</i>	High	High	Market	-0.164	0.631
<i>L. argentatus</i>	Low	Low	Market	-0.155	0.65
<i>L. argentatus</i>	High	High	Market	-0.145	0.67
<i>L. argentatus</i>	High	Low	Market	-0.145	0.67
<i>L. argentatus</i>	Low	Low	Market	-0.145	0.67
<i>L. argentatus</i>	Low	High	Market	-0.136	0.689
<i>L. argentatus</i>	Low	High	Market	-0.082	0.811
<i>L. argentatus</i>	High	High	Market	-0.082	0.811
<i>L. argentatus</i>	High	High	Market	-0.064	0.853
<i>L. argentatus</i>	Low	High	Market	-0.064	0.853
<i>L. argentatus</i>	Low	Low	Market	-0.055	0.873
<i>L. argentatus</i>	Low	High	Market	-0.018	0.958
<i>L. argentatus</i>	Low	Low	Market	0.045	0.894
<i>L. argentatus</i>	Low	Low	Market	0.136	0.689
<i>L. argentatus</i>	Low	High	Market	0.136	0.689
<i>L. argentatus</i>	High	High	Market	0.182	0.593
<i>L. argentatus</i>	Low	Low	Market	0.182	0.593
<i>L. argentatus</i>	Low	Low	Market	0.191	0.574
<i>L. argentatus</i>	High	Low	Market	0.2	0.555
<i>L. argentatus</i>	High	Low	Market	0.209	0.537
<i>L. argentatus</i>	High	Low	Market	0.227	0.502
<i>L. argentatus</i>	Low	High	Market	0.264	0.433
<i>L. argentatus</i>	Low	Low	Market	0.382	0.247
<i>L. argentatus</i>	High	Low	Market	0.427	0.19
<i>L. argentatus</i>	High	Low	Market	0.518	0.102

<i>L. argentatus</i>	High	High	Market	0.691	< 0.05
<i>L. argentatus</i>	Low	Low	Culture	-0.809	< 0.05
<i>L. argentatus</i>	Low	High	Culture	-0.8	< 0.05
<i>L. argentatus</i>	High	High	Culture	-0.7	< 0.05
<i>L. argentatus</i>	Low	High	Culture	-0.636	< 0.05
<i>L. argentatus</i>	Low	Low	Culture	-0.573	0.066
<i>L. argentatus</i>	Low	Low	Culture	-0.564	0.071
<i>L. argentatus</i>	High	High	Culture	-0.545	0.083
<i>L. argentatus</i>	Low	High	Culture	-0.491	0.125
<i>L. argentatus</i>	High	Low	Culture	-0.482	0.133
<i>L. argentatus</i>	High	Low	Culture	-0.464	0.151
<i>L. argentatus</i>	Low	High	Culture	-0.464	0.151
<i>L. argentatus</i>	Low	High	Culture	-0.445	0.17
<i>L. argentatus</i>	Low	High	Culture	-0.436	0.18
<i>L. argentatus</i>	Low	Low	Culture	-0.427	0.19
<i>L. argentatus</i>	Low	High	Culture	-0.391	0.235
<i>L. argentatus</i>	Low	Low	Culture	-0.364	0.272
<i>L. argentatus</i>	High	Low	Culture	-0.327	0.326
<i>L. argentatus</i>	Low	High	Culture	-0.318	0.34
<i>L. argentatus</i>	Low	Low	Culture	-0.318	0.34
<i>L. argentatus</i>	High	High	Culture	-0.245	0.467
<i>L. argentatus</i>	Low	High	Culture	-0.236	0.484
<i>L. argentatus</i>	Low	High	Culture	-0.227	0.502
<i>L. argentatus</i>	High	Low	Culture	-0.218	0.519
<i>L. argentatus</i>	Low	Low	Culture	-0.209	0.537
<i>L. argentatus</i>	High	High	Culture	-0.2	0.555
<i>L. argentatus</i>	High	Low	Culture	-0.2	0.555
<i>L. argentatus</i>	High	High	Culture	-0.155	0.65
<i>L. argentatus</i>	High	Low	Culture	-0.082	0.811
<i>L. argentatus</i>	Low	Low	Culture	-0.073	0.832
<i>L. argentatus</i>	High	High	Culture	-0.073	0.832
<i>L. argentatus</i>	High	Low	Culture	-0.064	0.853
<i>L. argentatus</i>	Low	Low	Culture	-0.055	0.873
<i>L. argentatus</i>	Low	Low	Culture	-0.036	0.915
<i>L. argentatus</i>	High	Low	Culture	0	1
<i>L. argentatus</i>	High	High	Culture	0.055	0.873
<i>L. argentatus</i>	High	Low	Culture	0.064	0.853
<i>L. argentatus</i>	High	Low	Culture	0.073	0.832
<i>L. argentatus</i>	High	High	Culture	0.127	0.709
<i>L. argentatus</i>	High	High	Culture	0.136	0.689
<i>L. argentatus</i>	High	High	Culture	0.182	0.593
<i>S. mollissima</i>	High	Low	Market	-0.327	0.326
<i>S. mollissima</i>	Low	Low	Market	-0.3	0.37
<i>S. mollissima</i>	High	High	Market	-0.209	0.537
<i>S. mollissima</i>	High	Low	Market	-0.118	0.729
<i>S. mollissima</i>	Low	High	Market	-0.118	0.729
<i>S. mollissima</i>	High	Low	Market	-0.064	0.853
<i>S. mollissima</i>	Low	Low	Market	-0.036	0.915
<i>S. mollissima</i>	Low	Low	Market	0	1
<i>S. mollissima</i>	Low	High	Market	0.027	0.937

<i>S. mollissima</i>	High	High	Market	0.027	0.937
<i>S. mollissima</i>	High	Low	Market	0.055	0.873
<i>S. mollissima</i>	Low	High	Market	0.118	0.729
<i>S. mollissima</i>	Low	High	Market	0.145	0.67
<i>S. mollissima</i>	Low	Low	Market	0.209	0.537
<i>S. mollissima</i>	High	High	Market	0.255	0.45
<i>S. mollissima</i>	Low	High	Market	0.273	0.417
<i>S. mollissima</i>	Low	Low	Market	0.282	0.401
<i>S. mollissima</i>	Low	Low	Market	0.282	0.401
<i>S. mollissima</i>	High	Low	Market	0.291	0.385
<i>S. mollissima</i>	High	Low	Market	0.3	0.37
<i>S. mollissima</i>	High	High	Market	0.336	0.312
<i>S. mollissima</i>	High	High	Market	0.355	0.285
<i>S. mollissima</i>	High	High	Market	0.364	0.272
<i>S. mollissima</i>	High	Low	Market	0.391	0.235
<i>S. mollissima</i>	Low	High	Market	0.391	0.235
<i>S. mollissima</i>	High	High	Market	0.409	0.212
<i>S. mollissima</i>	High	High	Market	0.418	0.201
<i>S. mollissima</i>	Low	Low	Market	0.427	0.19
<i>S. mollissima</i>	High	Low	Market	0.445	0.17
<i>S. mollissima</i>	Low	High	Market	0.5	0.117
<i>S. mollissima</i>	Low	Low	Market	0.5	0.117
<i>S. mollissima</i>	Low	Low	Market	0.518	0.102
<i>S. mollissima</i>	Low	High	Market	0.527	0.096
<i>S. mollissima</i>	Low	Low	Market	0.536	0.089
<i>S. mollissima</i>	High	Low	Market	0.573	0.066
<i>S. mollissima</i>	High	Low	Market	0.645	< 0.05
<i>S. mollissima</i>	Low	High	Market	0.664	< 0.05
<i>S. mollissima</i>	High	High	Market	0.691	< 0.05
<i>S. mollissima</i>	High	High	Market	0.7	< 0.05
<i>S. mollissima</i>	Low	High	Market	0.773	< 0.05
<i>S. mollissima</i>	Low	High	Culture	-1	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.982	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.982	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.982	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.982	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.973	< 0.001
<i>S. mollissima</i>	High	High	Culture	-0.964	< 0.001
<i>S. mollissima</i>	High	Low	Culture	-0.964	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.964	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.945	< 0.001
<i>S. mollissima</i>	High	Low	Culture	-0.945	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.945	< 0.001
<i>S. mollissima</i>	High	Low	Culture	-0.936	< 0.001
<i>S. mollissima</i>	High	High	Culture	-0.936	< 0.001
<i>S. mollissima</i>	High	High	Culture	-0.936	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.918	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.918	< 0.001
<i>S. mollissima</i>	High	High	Culture	-0.918	< 0.001
<i>S. mollissima</i>	High	Low	Culture	-0.909	< 0.001

<i>S. mollissima</i>	Low	High	Culture	-0.909	< 0.001
<i>S. mollissima</i>	High	Low	Culture	-0.909	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.909	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.9	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.891	< 0.001
<i>S. mollissima</i>	High	Low	Culture	-0.891	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.882	< 0.001
<i>S. mollissima</i>	Low	Low	Culture	-0.882	< 0.001
<i>S. mollissima</i>	Low	High	Culture	-0.864	< 0.05
<i>S. mollissima</i>	Low	High	Culture	-0.864	< 0.05
<i>S. mollissima</i>	High	High	Culture	-0.864	< 0.05
<i>S. mollissima</i>	High	Low	Culture	-0.864	< 0.05
<i>S. mollissima</i>	High	Low	Culture	-0.855	< 0.05
<i>S. mollissima</i>	High	High	Culture	-0.845	< 0.05
<i>S. mollissima</i>	Low	Low	Culture	-0.845	< 0.05
<i>S. mollissima</i>	High	Low	Culture	-0.845	< 0.05
<i>S. mollissima</i>	High	High	Culture	-0.818	< 0.05
<i>S. mollissima</i>	High	Low	Culture	-0.818	< 0.05
<i>S. mollissima</i>	High	High	Culture	-0.809	< 0.05
<i>S. mollissima</i>	High	High	Culture	-0.764	< 0.05
<i>S. mollissima</i>	High	High	Culture	-0.755	< 0.05

## 6. General discussion

### 6.1 Overview

The sustainable use of natural resources requires quantitative knowledge of the potential impacts to ecological communities and ecosystem functioning. Many aquacultural practices (e.g., *Mytilus edulis* benthic culture) are dependent on the harvest of individuals from natural populations which are ecologically diverse and multi-functional (Carss et al., 2020; Norling and Kautsky, 2007). Bivalve aggregations filter large quantities of suspended particles from the water column which both improves water quality and removes potentially harmful nutrients (e.g., carbon, nitrogen, phosphorous) to deposit them within sediments (Fodrie et al., 2017; Lee et al., 2020; Westbrook et al., 2019). They also support a greater number of species (e.g., invertebrates, fish, birds) and contain more biomass relative to surrounding areas making them valuable from both conservation and fishery perspectives (Guillemain and Himmelman, 1996; Kristensen et al., 2015; Norling et al., 2015). Potential trade-offs exist when harvesting bivalves from natural populations and environmental managers must often balance economic value with ecological importance (Nehls et al., 1997; Stillman and Wood, 2015). This thesis focused on the trade-offs and synergies associated with harvesting intertidal *M. edulis* with a particular focus on the impacts to coastal bird populations. The aims were:

#### **1. Identify and develop a method for simulating the growth and development of intertidal *M. edulis* in response to environmental conditions.**

A Dynamic Energy Budget (DEB) model was developed to simulate the growth and development of intertidal *M. edulis* in response to environmental conditions. The condition and growth rates of intertidal *M. edulis* in Morecambe Bay were observed to increase with decreasing elevation. A DEB growth model which was modified to incorporate an energy conserving, intertidal adaption (metabolic depression) most accurately predicted the observed relationship. Increases to the concentration of suspended particles (organic and inorganic) were most influential (positive and negative respectively) to individual growth. Increases to water temperature and elevation were also highly influential (positive and negative respectively).

## **2. Improve understanding of how to sustainably manage the ecosystem goods and services provided by intertidal *M. edulis*.**

A DEB population model for intertidal *M. edulis* was developed to simulate the functioning of multiple ecosystem services simultaneously in response to environmental conditions. It was used to quantify the net nutrient (nitrogen, phosphorus and carbon) fluxes (i.e., source or sink) associated with the population, to assess the sensitivity of services to environmental change and to identify potential synergies and trade-offs associated with harvesting *M. edulis*. The population was predicted to serve as a sink for nutrients, particularly carbon and mostly due to biodeposition and shell burial. Increases to the concentration of both organic and inorganic suspended particles were most influential (positive and negative respectively) to all ecosystem service rates. Increases to water temperature and pre-settlement mortality (i.e., egg, larvae) were also highly and negatively influential to all. The harvest of market size (> 4.5 cm) *M. edulis* had a negligible but positive (i.e., synergy) impact on the provision of habitat provisioning (i.e., biomass) by the population. The harvest of culture size (2 – 4 cm) individuals however had an important and negative (i.e., trade-off) effect. Strong synergies were identified between the provision of habitat provisioning and the removal of potentially harmful nutrients. The positive and negative effects of harvesting *M. edulis* subsequently extended to regulatory services, markedly so when harvesting culture size individuals.

## **3. Assess the long term risks of harvesting intertidal *M. edulis* to coastal bird populations in Morecambe Bay.**

An Agent-Based Model (ABM) was developed for simulating both the foraging behaviour of coastal birds and the dynamics of *M. edulis* populations in response to environmental conditions. The model was used to assess the relative importance of *M. edulis* as a resource for coastal bird populations in Morecambe Bay, and to identify the potential risks to birds of harvesting the *M. edulis* population. Increases to the abundance of *M. edulis* in Morecambe Bay were influential (positive) to the annual body condition of the *Somateria mollissima* population. The harvest of market size individuals was uncorrelated with the condition of the *Calidris canutus*, *Haematopus ostralegus* and *Larus argentatus* populations, and weakly correlated (positive) with that of the *S. mollissima*

population. The harvest of culture size individuals was uncorrelated with the condition of the *C. canutus* population, weakly correlated (negative) with that of both the *H. ostralegus* and *L. argentatus* and strongly correlated (negative) with the condition of the *S. mollissima* population. The negative correlations associated with harvesting culture size individuals became stronger when supplementary bivalve resources were low.

## 6.2 Interpretations

Variation in the physical environment (i.e., temperature, turbidity and sea level) most influenced the ecosystem service provisioning rates of *M. edulis* in Morecambe Bay. Long term observations from the Wadden Sea, the English Channel, the Irish Sea show variation in abundance and growth of many bivalve species can be attributed to the same environmental drivers (Beukema and Dekker, 2020a; Callaway, 2022; Southward et al., 2005). Climate change was therefore predicted the primary challenge for coastal managers and sustainable management strategies should aim to promote mitigating services (e.g., carbon storage) while planning for potential impacts (Callaway et al., 2012; Weiskopf et al., 2020).

The biomass of the *M. edulis* population was an important indicator of the rate at which ecosystem services were delivered. Management seeking to protect and improve the *M. edulis* reefs in Morecambe Bay will therefore likely benefit the estuary in multiple (e.g., fisheries, water quality, biodiversity) ways (McLeod et al., 2019; zu Ermgassen et al., 2020). Harvesting the population both positively and negatively influenced the biomass which highlights its potential as a management tool. Removing larger individuals (i.e., market size) from the population was more sustainable (i.e., synergies) while harvesting smaller individuals (i.e., culture size) potentially degraded (i.e., trade-offs) the populations ecological function. Continued efforts to enhance recruitment (e.g., replace harvested shell, artificial substrates) and survival (e.g., reduced harvest) are needed to limit the impacts of climate change (e.g., reduced recruitment, survival and growth) on the populations functioning (Christianen et al., 2018; Frandsen and Dolmer, 2002).

The *S. mollissima* population in Morecambe Bay exploited *M. edulis* in far greater proportions compared to other species. Similar observations have been made on The Wash, the Wadden Sea and the Baltic Sea (Caldow et al., 2007; Laursen et al., 2010). Significant reductions in the abundance (e.g., harvest, mortality) or quality (e.g., disease, turbidity) of *M. edulis* in Morecambe Bay are therefore most likely to negatively impact the *S. mollissima* population (Laursen et al., 2009; Laursen



and Møller, 2014). Negative impacts were avoided when the *M. edulis* reefs contained 127 g afdm m<sup>-2</sup> (2.54 kg biomass m<sup>-2</sup>) of individuals 1 – 4 cm while the surrounding intertidal flats simultaneously supported invertebrates at densities of 15 g afdm m<sup>-2</sup>.

### 6.3 Comparisons

This study aimed to assess the environmental impacts of harvesting intertidal *M. edulis* from natural populations with particular focus on the conservation of coastal birds. The overall results indicate that the impacts differ markedly depending on the size of the individuals being harvested. The harvest of market size *M. edulis* was weakly but positively correlated with other regulatory (e.g., nutrient removal) and provisioning (e.g., habitat provisioning) ecosystem service rates, which positively impacted organisms at higher trophic levels (e.g., *S. mollissima*). The harvest of culture size *M. edulis* on the other hand was negatively correlated with other service rates, particularly the provision of habitat provisioning (i.e., biomass). The effects again extended to coastal birds when harvest rates were high, especially when the biomass of alternative invertebrate resources was low.

Many studies have assessed the environmental impacts of producing *M. edulis* using aquacultural practices (Kaiser et al., 1998; Lacoste et al., 2020; Suplicy, 2020). Cultured populations are increasingly viewed as tools for alleviating ocean eutrophication (e.g., nitrogen removal) and climate change (i.e., carbon fixation), and many additional positive (e.g., enhanced biodiversity) and negative (e.g., pollution) environmental impacts are documented (Aubin et al., 2018; Kotta et al., 2020; Suplicy, 2020). The impacts of harvesting from natural *M. edulis* populations have mostly been assessed in relation to benthic invertebrate communities and coastal bird populations (Clarke et al., 2017; Hiddink et al., 2017; Stillman and Wood, 2015). Descriptive assessments are made by monitoring the environment to identify impacts from culture sites, harvesting methods or harvesting rates (Bromhall et al., 2021; Cervencel et al., 2015; Lacoste et al., 2018). More predictive assessments are made via a combination of behavioural, physical, biogeochemical and physiological models (Aubin et al., 2018; Stillman and Goss-Custard, 2010).

The results here are in broad agreement with experimental studies which have focused on the environmental impacts of harvesting intertidal *M. edulis* populations. The harvest of undersize individuals can result in prolonged periods of reduced biomass within affected areas (Craeymeersch et al., 2013; Dolmer et al., 2001; Smaal et al., 2021). Their overexploitation has resulted in the complete collapse of populations with measurable effects occurring across trophic levels (Atkinson

et al., 2003; Camphuysen et al., 2002, 1996). Results are also in agreement with modelling studies which report that low bivalve harvest rates not significantly impact coastal birds but where changes in management practices (e.g., increasing harvest rates) coincide with extreme climatic events (e.g., severe winter) or a reduction in alternative resources (e.g., *M. balthica*), mortality rates are predicted to rise for some species (Durell et al., 2008; Stillman et al., 2001; West et al., 2003).

This study built on an existing Agent-Based Model (ABM) designed to predict the response of coastal bird populations to environmental change (Goss-Custard and Stillman, 2008; Stillman and Goss-Custard, 2010). The key difference between previous versions and this study is none have incorporated mechanistic sub-models (i.e., DEB model) by which the dynamics (i.e., recruitment, growth, mortality) of invertebrate resource populations respond to environmental conditions. The population dynamics of invertebrate resources are instead traditionally determined according to empirically observed relationships (Durell et al., 2006; Stillman et al., 2010). The current approach was taken because the impacts of harvesting culture size individuals (which occurs in Morecambe Bay) can be detected (e.g., reduced biomass) for a number of years after the action (Smaal et al., 2021). Simulations were therefore ideally required to run for multiples years and predictions would benefit from a model *M. edulis* population that could respond to environmental change in a realistic manner. This again differs from previous versions which have predominantly concentrated on a single non breeding season (Goss-Custard et al., 2004; Stillman et al., 2003; West et al., 2003). The decision to run long-term (i.e., 10 year) simulations lead to the incorporation of migratory and breeding periods, which made using the traditional output of population size difficult. It was decided instead that average body condition of the individuals present would be used thereby serving as a proxy for mortality and breeding success survival, breeding success, migratory performance (Duijns et al., 2017; Gibson et al., 2018; Laursen et al., 2019a). The present ABM therefore simultaneously estimated the condition of both *M. edulis* and coastal bird populations in response to environmental conditions, while previous ABMs estimate the number of individual birds expected to survive the winter in response to environmental conditions.

The dynamics of *M. edulis* populations were simulated via a DEB sub model which mechanistically linked individual growth (tissue and shell) and development (maturity, reproduction) to environmental conditions (e.g., temperature, suspended particles). While these mechanisms increased model complexity, they also improved coherence because they are based on first principles which better captured the key aspects of the systems internal organization (Grimm et al., 2017; Grimm and Berger, 2016).

*M. edulis* intake rates for example increase with decreasing elevation (i.e., aerial exposure) which subsequently created a gradient of biomass from high shore (low biomass) to low shore (high biomass) which is observed in natural populations (Griffiths, 1981b; McGrorty and Goss-Custard, 1993). Upper tidal flats might be disproportionately important for the conservation of coastal birds and their protection and restoration is a priority for conservation managers (Mu and Wilcove, 2020). A small number of coastal bird ABMs have demonstrated increased survival of coastal birds by introducing bivalve populations at relatively high shore levels (Caldow et al., 2004; Stillman et al., 2003). Strategies of this nature can be better understood by using DEB growth models which better quantify the energetic benefits to birds of bivalves living at different shore levels (Monaco and McQuaid, 2018; Saraiva et al., 2020).

Similarly, the *M. edulis* population experiences density dependant competition for food, which includes cannibalism of constituent larvae. As in real systems, reducing (e.g., harvest or mortality) or increasing (e.g., restoration or invasive species) the number of individual *M. edulis* in the model effects both growth and recruitment within the population (Clarke et al., 2019; Dolmer and Stenalt, 2010). Varying resource abundance is very common when using coastal bird ABMs but the resource populations themselves do not respond to the change (Goss-Custard et al., 2004; Stillman et al., 2016). Modelling harvested ecosystems benefits from mechanisms that account for harvest-driven population changes, especially in cases where targeted populations are known to affect important aspects of ecosystem function (Palkovacs et al., 2018).

#### **6.4 Limitations**

The model was not currently able to robustly assess the impacts of climate change on coastal bird populations. Assessing the sensitivity of coastal bird populations to environmental change was instead limited to resource abundance. The limitation exists because the dynamics of only one invertebrate resource type (*M. edulis*) were mechanistically linked to environmental conditions (e.g., temperature, water level, suspended particles). To properly understand the response of coastal birds to climate change all important resources must be realistically sensitive to the novel conditions estuaries will experience (Robins et al., 2016). The response of intertidal invertebrates to climate change is however variable (e.g., temperature thresholds) which will likely increase model complexity that standardised, reusable sub-models (e.g., DEB) are key to minimizing (Augustine and Kooijman, 2019; Beukema and Dekker, 2020a; Kooijman, 2020).

No mechanism for anthropogenic disturbance (e.g., recreational, bivalve harvest) that temporarily and locally depressed feeding rates was incorporated (Stillman et al., 2001; West et al., 2002). Such disturbance in natural systems is observed to induce behavioural responses (e.g., vigilance, movement) which can reduce survival, body condition and site fidelity (Gibson et al., 2018; Whittingham et al., 2019). Assessments of whether anthropogenic disturbance is having a deleterious effect on coastal bird populations is therefore of interest to estuarine managers and can be included in ABMs (Stillman et al., 2007). The effects of harvesting *M. edulis* were instead limited to the removal of resources and subsequent increased competition, and any negative effects of bivalve harvest might therefore be underestimated. ABMs that have included disturbance report that numerous, small disturbances (e.g., walkers) are more damaging to foraging success compared to a few, larger (e.g., bivalve harvest) ones (Durell et al., 2008; Stillman et al., 2001; West et al., 2002). Recreational disturbance of high tide roosts is considered the larger threat to coastal birds in Morecambe Bay and it is likely to increase in intensity (increasing human population) in the future (Liley et al., 2015; Marsh et al., 2012). The incorporation of disturbance sub models can be used to explore the potential impacts.

## 6.5 Implications

Identifying trade-offs between ecosystem services and adapting management plans is thought more likely to result in synergies than planning for them from the outset (Howe et al., 2014). This study identified several potential trade-offs between ecosystem services when harvesting culture size *M. edulis* from natural intertidal populations in Morecambe Bay. Their harvest was found to negatively correlate (trade-off) with the provision of habitat provisioning which in turn reduced the rates at which nutrients (nitrogen, phosphorus and carbon) were removed and negatively affected the supported ecological communities (e.g., coastal birds). Their overexploitation therefore has the potential to degrade ecosystem function and conflict with the conservation of coastal birds (i.e., unsustainable harvesting). Effective and sustainable harvest strategies will consequently require a flexible and proactive approach. In many bivalve producing regions for example (e.g., The Wadden Sea) undersize *M. edulis* are only harvested from subtidal areas where low survival rates are observed (Nehls et al., 1997; Smaal et al., 2021; Troost et al., 2022). While no subtidal aggregations occur in Morecambe Bay the same general approach is taken, undersize *M. edulis* are predominantly harvested from areas where exceptionally high mortality (e.g., winter storms) is expected (Dare, 1982, 1976; Sloan and Aldridge, 1981).

The *S. mollissima* population in Morecambe was predicted to be most at risk from the commercial harvest of undersize *M. edulis*. The species has been declining in the UK for over 25 years, is classified as endangered in Europe and near threatened globally (BirdLife International, 2022; Woodward et al., 2019). Morecambe Bay supports the largest gathering of *S. mollissima* in the UK and is designated a Special Protection Area (SPA) and a Special Area of Conservation (SAC). Conservation objectives for *S. mollissima* would be best served by limiting the harvest undersize individuals in Morecambe Bay. The current wintering population (5 year moving average) of 5,104 individuals was predicted to consume up to 2,973 tonnes of *M. edulis* which must occur at densities of at least 2.54 kg m<sup>-2</sup> (1 – 4 cm) if they are to achieve the intake rates required. At this density only the largest *M. edulis* reef in Morecambe Bay (i.e., Foulney) can support the resources required and this does not always occur because intertidal *M. edulis* populations are also inherently patchy (Dolmer, 1998; Svane and Ompi, 1993). Harvesting undersize individuals when densities are below the threshold is therefore likely to negatively affect the condition of the *S. mollissima* population and should be avoided. In 2006, 2011 and 2012, greater than 10,000 tonnes of undersize *M. edulis* were harvested. Removing such large quantities was predicted to significantly reduce the condition of the *S. mollissima* population in Morecambe Bay and should also be avoided.

The harvest of undersize individuals is occasionally permitted from the larger, mature reefs in Morecambe Bay. The ecosystem services provided by intertidal *M. edulis* populations might be better utilised by no longer permitting harvest from such aggregations, some of which are greater than 100 years old. Marine sediments are one of the planet's primary carbon stores and those beneath intertidal bivalve reefs are no exception (Fodrie et al., 2017; Lee et al., 2020). Destructive human activities (e.g., raking, dredging) that disturb the substrate therefore potentially risk releasing substantial quantities of CO<sub>2</sub> into the atmosphere to exacerbate climate change (Black et al., 2022; Epstein et al., 2022; Fodrie et al., 2017). In Morecambe Bay bivalves are harvested by hand using rakes and from boats using dredges, both of which are destructive to substrates (Clarke et al., 2017). The sediments beneath bivalve reefs should therefore be a priority for protective measures to ensure emissions are minimized.

Passive harvesting strategies (e.g., ropes) which limit the damage to substrates offer a potentially more sustainable approach for obtaining culture size individuals (Buck, 2007; Dare and Davies, 1975; Kamermans and Capelle, 2019). The environmental impacts of using artificial collectors are relatively low but increased competition for food (phytoplankton) among the benthic population may result in overgrazing and possibly affect the local production capacity (Kamermans and Capelle,

2019). This may however have consequences for the yield of market size individuals and for organisms that depend on the population for food (e.g., birds).

## 6.6 Conclusion

The goods and services supplied by marine bivalves are ecologically, economically and culturally valuable (Carss et al., 2020; van der Schatte Olivier et al., 2018). Their sustainable management is of global significance to food production, resilience against climate change and water purification (Smaal et al., 2018). Despite their importance, the economic value of natural bivalve populations is traditionally quantified in terms of food production. This differs from cultured populations for which additional ecosystem services are increasingly being quantified and valued (Aubin et al., 2018; Kotta et al., 2020; van der Schatte Olivier et al., 2018). A major challenge is the complexity and extent of coastal environments for which long term data is scarce. ABMs are well placed to assist in the sustainable management of inshore bivalve populations and many useful and re-useable sub models (e.g., invertebrate growth, foraging birds, hydrodynamic, biogeochemical) have already been developed and tested (Rosland et al., 2009; Saraiva et al., 2017; Stillman et al., 2000). The approach still requires continuous efforts to collect accurate and robust empirical data (e.g., species surveys, environmental monitoring) which can also directly inform management decisions. ABMs ultimately provide a framework under which the multiple disciplines (e.g., ecology, economics, climatology) required for managing coastal ecosystems can come together, ensuring that society continues to develop the benefits that they provide.

## 6.7 Future work

Future coastal bird ABMs might aim to incorporate DEB sub models for all invertebrate resources. Parameters have already been estimated for many of the important bivalve species (e.g., *M. edulis*, *C. edule*, *M. balthica*) and for other essential intertidal (e.g., *C. crangon*, *A. rubens*) and terrestrial (e.g., earthworms) invertebrates (Agüera et al., 2021; Campos et al., 2009; Rakel et al., 2020; van der Veer et al., 2006). Detailed instructions are available for estimating unknown parameters and remote sensing can provide the environmental data needed to drive the models (Saraiva et al., 2011; van der Meer, 2006; van der Veer et al., 2006). DEB models are also standardised and reusable which speeds up model development times, improves interpretation of outputs and increase coherence

in the field (Dade et al., 2019). Changes to temperature for example would simultaneously effect all model organisms as would happen in real systems (Beukema et al., 2017b, 2009; Beukema and Dekker, 2020b). In the present model, temperature was positively related to the individual growth but negatively related to the biomass of *M. edulis* populations which in turn impacted ecosystem services (e.g., habitat provisioning, nutrient removal, carbon removal). If all invertebrate resources responded this way, increases in temperature might be expected to negatively impact coastal bird populations. Increases in temperature however currently benefit model birds by decreasing their daily energy requirements. The incorporation of these mechanisms will be particularly useful for predicting species responses to climate change (Thomas and Bacher, 2018).

## 6.8 References

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