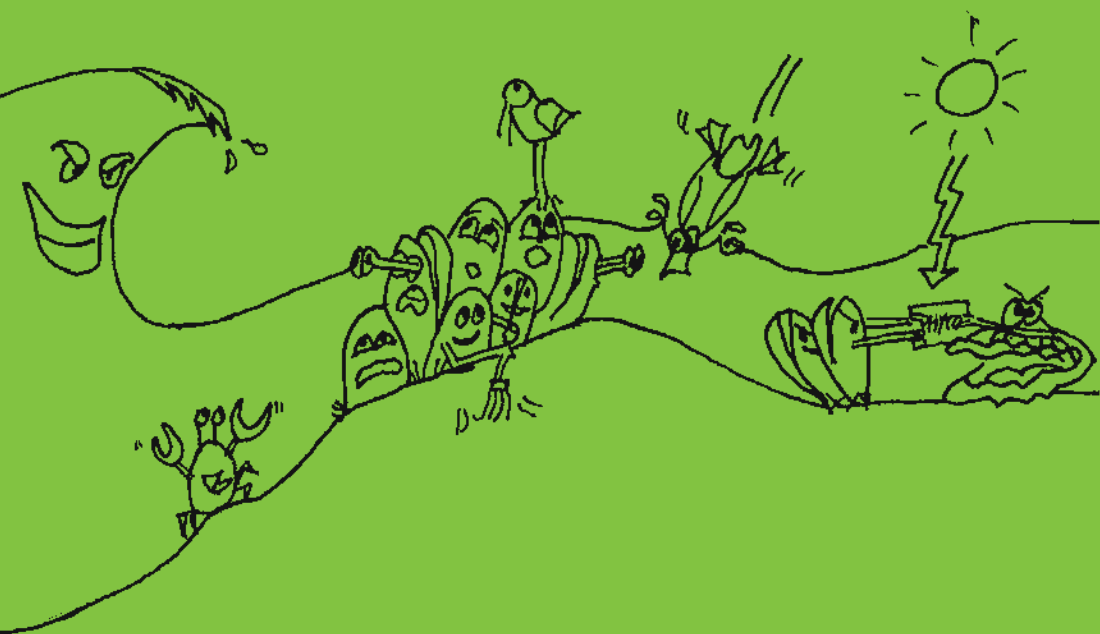


Modelling bivalves in estuaries and coastal areas

Sofia Saraiva



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The research presented in this thesis was carried out at the Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), The Netherlands; Faculty of Earth & Life Sciences, Department of Theoretical Biology, VU University Amsterdam, The Netherlands; and Environment and Energy Section, Instituto Superior Técnico (MARETEC), Portugal.

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Modelling Bivalves in estuaries and coastal areas

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in het openbaar te verdedigen
ten overstaan van de promotiecommissie
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door

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geboren te Covilhã, Portugal

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Best wishes for all of you!

Sofia Sensitive

*Complex problems in science, as in life,
can always be decomposed in several smaller,
hopefully simpler, problems...*

Sofia Saraiva

to my family,

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1. General Introduction

Coastal areas in general and estuaries in particular belong to the most productive ecosystems in the world. They provide critical habitat for species that are commercially, recreational, and culturally valued. Many species rely on estuaries for food and shelter to nest and breed, including Humans.

One reason why estuaries make some of the most fertile ecosystems on Earth, is that water flowing into them carries nutrients from the surrounding watershed. Often the same water also washes pollutants from the watershed, thus making estuaries into some of the most polluted ecosystems. The pressure is high and the need to protect them is imperative. Reconciling environmental objectives (eutrophication abatement, conservation of biodiversity) with an economic use of these ecosystems requires extensive analysis of all the complex interactions taking place. The key for effective protection of the ecosystem is knowledge. Knowledge is required on the main processes, the main actors, their needs, their role, their impact. This basic knowledge allows the prediction of environmental impacts, either of natural or anthropogenic origin. Such predictions are needed to know how much advantage we can actually take from these systems in a sustainable way.

Bivalves as ecosystem engineers

Bivalves, which are common to many coastal habitats, are probably ecologically and economically the best studied benthic suspension feeding group. Particularly oysters and mussels often dominate ecosystem processes, in many cases due to intensive aquaculture (Dame et al., 2001). Suspension-feeding bivalves obtain their food from the surrounding water by retaining suspended organic particles when water is transported through the gills (Winter, 1978). Attached on specific bottom types, they take advantage of waves, tides and wind-driven currents to transport oxygen and particulate food to them, but also carry away waste, and disperse larvae (Dame et al., 2001). Often bivalves inhabit coastal waters where turbidity may be high, due to natural processes (e.g. resuspension of deposited material due to waves and currents) and human activities (e.g. dredging) resulting in broad fluctuations in both quality and quantity of suspended particulate matter. Their food intake is related to both plankton and detritus concentrations (Widdows et al., 1979; Kiørboe et al., 1981; Velasco and Navarro, 2003; Newell et al., 1989, 2005) and the non-assimilated material is returned to the water column as pseudofaeces (material rejected prior to the gut passage) and faeces (material rejected prior to absorption). Because these organisms can process large amounts of material, they can cause significant changes in the concentrations of particles and substances and they are often major agents of benthic-pelagic coupling and nutrient cycling, through various feedback systems (Prins et al., 1998). Their filtration directly reduces the concentration of phytoplankton and bacterial communities. However, bivalves can also increase deposition rates (Dame, 1993), enrich sediments and stimulate mi-

crobial growth, providing an important resource for surrounding benthos (Norkko et al., 2001; Asmus and Asmus, 1993) and primary production. They may thus alter the prevailing environmental conditions, change nutrient cycling at the ecosystem scale (Zemlys et al., 2003; Dolmer, 2000) and ultimately affect the growth rate of their own population (Dowd, 1997). Moreover, bivalves serve as food for many other groups of organisms in the different stages of their life cycle. Main predators include shrimps, crabs, starfish, and birds (Brinkman et al., 2002). Thus, changes in the bivalve population may produce effects on lower and upper trophic levels and *vice versa*.

Bivalve individual and population dynamics

In the study of population dynamics not only the abundance of a population is important but also its composition in terms of the relative frequency of individuals with different stages of development or body size. Size determines the nature of many ecological interactions, e.g. food choice, foraging capacity, growth, reproduction and mortality (Peters, 1983; Ebenman and Persson, 1988b,a), hence size also influences population dynamics. By describing the physiological processes at the individual level and simulating their life history events (reproduction, mortality), the population dynamics is the result of tracing all individuals over time.

Populations are maintained by reproduction and bivalve individuals produce large quantities of eggs (Bayne, 1976) that are distributed through the system by wind and tidally driven currents (Brinkman et al., 2002). A few weeks after hatching, when reaching a certain size, post-larvae leave the water column and search for a suitable substrate to settle (de Vooy, 1999), preferably empty shells and biodeposited material. The production of byssus threads allow individual mussels to attach to substrata and to each other and actively maintain position on the benthic surface and still have access to the water (Dame et al., 2001; wa Kangeri et al., 2014). But only a small proportion of the organisms will actually find some substrate to attach and from those, only a small fraction will survive the intense physical processes induced by strong currents, waves and sand deposition (Brinkman et al., 2002). After settlement, in many of those places, small mussels have to cope with emersion time that limits the available food, as well as some more intense biological processes. Those processes include inter and intra-specific competition for food and space (Troost et al., 2008), the size-dependent predation pressure by shrimps (Campos and van der Veer, 2008; Campos et al., 2010; Andresen and van der Meer, 2010), adult bivalves (Bayne, 1976; André and Rosenberg, 1991) and later on by crabs (Dankers and Zuidema, 1995), starfish (Saier, 2001) and birds (Brinkman et al., 2002). Thus, mortality rates in the first year of bivalves' life are extremely high. The overall predation pressure at this stage and also through their life cycle, will depend on the individual performance to outgrow the predation size spectrum (dependent upon availability of food and temperature) and also on

the predation intensity during the vulnerable stage, which is linked with the predators consumption rates and their abundance in the system. However, despite all the risks, bivalve suspension feeders form beds on intertidal flats and rocky shores. Some beds can even succeed for many years as complex communities of several year classes of mussels and their associated biofauna. Some others can only maintain themselves for a short period of time (Nehls and Thiel, 1993). The persistence of the bed, *i.e.* the persistence of the bivalve population and its dynamics, is thus the integrated result of all these processes (bottom-up and top-down) in addition to their feedback on the biogeochemical cycle of nutrients.

Problem statement and modelling approach

The ability to predict the dynamics of bivalve populations in response to environmental change, natural or human induced, is quite useful for the management of coastal ecosystems, either with the purpose of commercial exploitation optimization, environmental impact assessment, climate changes implications or assessing the impact of exotic species introduction. Mathematical models have been used to address some of these questions. Although they can vary enormously in terms of complexity, their focus is either more oriented on (i) the eco-physiology of the individual bivalves, coupled or not with biogeochemical and biological models, but with 'simplified' descriptions of physical processes (e.g. Brinkman and Institute for Forestry and Nature Research (Wageningen), 1993; Baretta et al., 1995; Dowd, 1997; Scholten and Smaal, 1998; Ren and Ross, 2001; Savina and Ménesguen, 2008; Brigolin et al., 2009; Ferreira et al., 2009) or on (ii) physical transport, using complex physical models where only 'simple' formulations for biogeochemical/biological processes were introduced, e.g. GETM (Burchard and Bolding, 2002), COHERENS (Luyten et al., 1999), MOHID Water Modelling System (Miller and Pinder, 2004). Generally, the first group of models aims to predict the bivalve production and the second group aims to predict the impact of bivalves activity on system properties, such as primary production. The constant developments in computer hardware and programming languages enable the development of models that couple complex descriptions of both ecological and physical processes. The challenge is now to get better predictions of the bivalve production and their population dynamics in interaction with an ever changing environment by improving the description of the availability of their food and physical processes. Such descriptions can be supplied by 'physical transport' type of models.

Several difficulties arise compared with the traditional modelling approach followed for phytoplankton and zooplankton. Most of these difficulties are caused by two facts: (i) bivalves have both a pelagic stage, where they are transported in the water column and directly depend on physical processes, and a benthic stage; (ii) their food requirement (bottom-up processes) and their interactions with other species (competition and top-down processes) strongly change

throughout their life cycle (embryo, juvenile and adult stages). One of the main consequences is that reproduction and recruitment success are not easy to predict if these two facts are not properly addressed. In some of the current modelling approaches the problem is solved either by imposing spawning events at a specific time (e.g. Maar et al., 2010) or by considering them dependent on environmental variables (e.g. Gerla et al., 2014), but the reproduction is detached from the bivalve development stage. In addition, understanding top-down control requires the simulation of the change in size of individual bivalves, throughout their main live stages (larvae, juvenile and adult), since predators have a size preference. Size structure in the population has been normally neglected or imposed, though. Probably because most models have been developed for environmental impact assessment, where either the size structure is artificially controlled, as in aquaculture systems, or simply because it is found too complex. However, model aims go now beyond aquaculture assessments and new questions are raised, for example on population responses to climate change. Other examples are related to the introduction of new species in lower, same and upper trophic levels, changes in food quality, changes in habitat morphology, changes in hydrodynamics, temperature or salinity. All these questions can only be addressed if size structure is considered in the population, through the simulation of the individual bivalve development. For this purpose, energy budget models have received some attention (Beadman and Kaiser, 2002), in particular the DEB theory, proposed by Kooijman (1986, 2000, 2010). It is based on a mechanistic view of an organism's metabolic processes, including growth, maturation and reproduction, where the basic principles and formulations are valid for all different stages of the individual. In practice, this means that the same set of equations can be used to simulate the complete life cycle of a bivalve. Recent developments have facilitated its use, which makes DEB theory a good option to build a model of the bivalve individual and to further couple it to hydrodynamic and biogeochemical models that already have a high level of complexity. Yet, this approach can significantly increase model complexity, *i.e.* higher number of state variables, more/different uncertainties to cope with, higher number of parameters to estimate, larger amount and variability of input data, higher computational time, and also larger volumes of output results to analyse. Now comes the time where it is possible, though challenging, to move a step forward on bivalve population modelling and to combine the best knowledge of the individual metabolic processes, synthesized in the DEB theory (www.bio.vu.nl/thb/deb/), used as model unit in a individual based population model approach, with the already established knowledge on hydrodynamics and biogeochemical cycles described by MOHID Water Modelling System (www.mohid.com). A summary of the main features of the two worlds is given below.

Dynamic Energy Budget (DEB) theory

The Dynamic Energy Budgets theory, developed at the VU University Amsterdam, is a metabolic theory that aims to describe the physiological response of an organism to changes in its environment. The theory uses a set of assumptions and principles to translate functional description

of the organisms into differential equations. It assumes that the various energetic processes, such as assimilation and maintenance, are dependent either on surface area or on body volume (Kooijman, 2010). The standard DEB model assumes that the body mass of the organism is partitioned into the abstract quantities of 'structure' and 'reserve', which act as state variables. All assimilated energy is first stored as reserve; subsequently the reserve is utilized to fuel the other metabolic processes, following the so-called κ -rule: a fixed fraction of mobilized reserve is used for somatic maintenance and growth (increase in structure), the rest is used for maturity maintenance and maturation (embryos and juveniles) or reproduction (adults). Maturity is also a key concept in the theory and represents the total energy invested in the development of the organism. During the juvenile stage, the fraction of energy allocated to reproduction is used to develop reproductive organs and regulation systems, increasing the maturation level of the organism. After reaching a particular threshold, no more development is needed and the organism becomes an adult. Hereafter, it allocates this flux to the reproduction buffer, for further gametes production and release into the water. Based on the principle of mass conservation of each element in the system (e.g. C, H, O, N, P), and the computed organic fluxes, the mineral fluxes to (and from) the water column are the result of a mass balance. The feedback of the individual processes on the system can thus be straightforwardly followed. The main advantage of the DEB models is that they are based on a generic theory, meaning that the same model structure can be applied to different species, where only parameter values differ. Variability in growth and reproduction between individuals of the same species are assumed to be mainly caused by differences in environmental conditions (temperature, food).

In recent years, important improvements have been made around the DEB theory. The theory itself still uses the same core principles, although new or particular topics have been developed to explain, verify or test the model against specific features that turn up in the observations. The clarification of the concepts and variables, and their relation and translation into real measurable quantities (Sousa et al., 2008, e.g.), as well as the recent developments on the parameter estimation (Lika et al., 2011, e.g.), facilitates the theory implementation and promotes its use.

MOHID Water modelling system

MOHID Water Modelling System is a three dimensional (3D) water modelling system developed over the last 30 years at Instituto Superior Técnico (IST), University of Lisbon. It consists in a set of coupled models that aim to simulate the main physical and biogeochemical processes occurring in the aquatic systems (ocean, coastal areas, estuaries, rivers, lakes and reservoirs) (Miller and Pinder, 2004).

MOHID has been extensively implemented and validated in different coastal/estuarine areas (Leitão et al., 2005; Trancoso et al., 2005; Saraiva et al., 2007; Vaz et al., 2009, e.g.) in a wide range of applications, namely hydrodynamic characterization, sediment transport, contaminant dispersion, eutrophication assessment studies. The system is programmed using an object oriented approach and it is organized in a hierarchical modular structure including over 80 mod-

ules. These modules are responsible for computing, among others, hydrodynamics, turbulence, eulerian and lagrangian transport, sediment transport, biogeochemical/ecological processes and water quality.

In terms of algorithm approach, the entire system is based on the finite volume concept. The hydrodynamic model solves the primitive continuity and momentum equations for the surface elevation and 3D velocity field for incompressible flows, in orthogonal horizontal coordinates and generic vertical coordinates, assuming hydrostatic equilibrium and Boussinesq approximation (Martins et al., 2001). Density is computed depending on salt, temperature and pressure, by the UNESCO equation of state (Burchard et al., 1981). The model includes a variety of turbulence models including GOTM (Burchard et al., 1999). Momentum, mass and heat transport is computed using a generic 3D advection-diffusion library including high order advection schemes. Water properties can be dissolved in the water, therefore transported solely by currents or in a particulate phase (e.g. adsorbed on to particulate matter), thus being additionally subjected to settling. Particulate properties can deposit in the bottom and become part of the sediment compartment and can be resuspended back to the water column. There are three different pelagic biogeochemical modules which can simulate, in different levels of complexity, nutrient and organic matter cycling (nitrogen, phosphorus, silica), primary production, zooplankton and oxygen dynamics. Additional features MOHID comprise robust and versatile handling of initial and boundary conditions, sub-model nesting and a generic ocean-atmosphere interface module.

Aim and Outline of the thesis

The aim of this thesis is to study the bivalve population dynamics and quantify their influence on the pelagic system, through the development and use of a modelling tool. To achieve this, an individual-based population model for bivalves (based on the Dynamic Energy Budget theory), was developed and coupled to a hydrodynamic/biogeochemical model (MOHID Water Modelling System). The result is a process oriented modelling tool that integrates physical, biogeochemical, ecological and physiological factors governing bivalve populated marine ecosystems, describing and quantifying mass and energy fluxes between all the involved actors. Such a model can be used to characterize ecosystem response to different environmental scenarios and to serve as an effective and reliable management tool. Moreover, the tool can be potentially used to simulate human engineered ecosystems (e.g. mussel farms in built structures such as beds, rafts or long lines), and study efficiency and productivity rates and sustainability. The originality of this work lies, among others, in the integration of several fields of knowledge to achieve a better understanding of the relative importance of the processes. The integrated modelling tool was successively tested throughout its development and it was implemented in a real ecosystem (Balgzand, Wadden Sea, The Netherlands). The structure of the thesis mirrors

the steps towards the final goal of building and implementing the integrating modelling tool. Chapter 2 deals with detailing feeding processes in bivalves, particularly on mussels. An extension of the standard DEB model was developed, using a novel mechanistic description to deal with the observed changes in food quantity and quality in estuaries and coastal areas. Filtration, ingestion and assimilation are assumed as three different steps and pseudofaeces production is computed as the difference between filtered and ingested fluxes. The concept of Synthesizing Units described by the DEB theory was used to develop generic formulations to account for different types of food, with type-specific ingestion and assimilation efficiencies. The model performance was evaluated by comparison with the literature data for the blue mussel for a wide range of experimental conditions.

In Chapter 3 a new set of DEB parameters for the blue mussel *Mytilus edulis* is presented. The new estimation is based on the recently developed covariation method – that consists on the simultaneous minimization of the weighted sum of squared deviations between data sets and model predictions in one single procedure. It also includes a set of physiological constraints by introducing the concept of pseudo-data. Different data sets, obtained from the literature, were used in the estimation procedure and model results using the new and the previous estimations were compared with observations.

Chapter 4 presents a validation of a generic individual model for bivalves. The model is based on the DEB theory and includes the extension of the standard DEB model to cope with changing food quantity and quality presented in Chapter 2, parameters presented in Chapter 3, as well as some additional specific assumptions for bivalves. The results were tested against field observations obtained at four different locations in the North Sea – Wadden Sea, Sean Gas Field(UK), Oyster Grounds and North of Dogger Bank (UK). At these locations, labelled mussels (*Mytilus edulis*) were kept under natural conditions. Shell length was measured for each mussel repeatedly during the experiment and dry weight was determined at the end of the experiment for some of the mussels. Temperature, salinity, chlorophyll concentration and Secchi-depth (at the Wadden Sea location) were measured next to the experiment sites. The individual model performance was evaluated by comparing predicted and measured shell length, dry weight and growth, at each location for each individual.

The upgrading of the generic individual model from Chapter 4 into a population model is described in Chapter 5. An individual based population model for bivalves was designed, built and tested in a zero-dimensional approach, in order to simulate the population dynamics of a mussel bed located in an intertidal area. The model organizes populations by different bivalve species, each containing a set of cohorts. Each cohort is simulated as an independent entity which can interact with other cohorts from its own or a different species. As population processes, the model includes initial egg mortality, background mortality, food competition, and predation (including cannibalism). Model properties were studied through the analysis of theoretical scenarios and by the simulation using different parameters combinations in a realistic setup with environmental measurements. Realistic criteria were then used to narrow down the

possible parameters combinations and the model predictions were compared with field observations from a long-term and multi-station monitoring program. This chapter was an important stepping stone for the eventual development and implementation of the full integrated model presented in Chapter 6.

Chapter 6 firstly describes the main features of the model and the concepts used in coupling the individual based population model with MOHID water modelling system. This is followed by a fully integrated application to the Balgzand area, a tidal-flat area in the westernmost part of the Wadden Sea, The Netherlands. The model simulates hydrodynamics (currents and water elevations), waves, heat, salt and sediment transport, biogeochemical cycle of nutrients, primary production and bivalve population dynamics. It is initialized and forced by an extensive observations data set for the above mentioned variables and processes during a period of two years representing present ecosystem conditions. A validation of the model is made for selected indicators and the results on mussels population dynamics was explored. In order to quantify the impact of the mussel populations in the ecosystem, an additional scenario without mussels was performed.

The study finalizes with a general discussion (Chapter 7) on the general contribution of the present work, main difficulties and its perspectives.

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2. Modelling feeding processes in bivalves: A mechanistic approach

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Many bivalves species inhabit coastal waters where fluctuations in both quantity and quality of suspended particulate matter occur. The study of interactions between the organism and its environment requires thus a certain level of detail concerning the feeding process, not only from the bivalve point of view – which material can they actually use as food – but also from the ecosystem point of view – to what extent are bivalves able to clear the water column and change ecosystem dynamics? However such detail is commonly neglected in ecosystem modelling and a mechanistic description of the feeding process is still lacking. In this study, the Synthesizing Units concept, part of the Dynamic Energy Budget (DEB) theory, is used to describe the main feeding processes in bivalves. Filtration, ingestion and assimilation are assumed as three different steps and pseudofaeces production computed as the difference between filtered and ingested fluxes. Generic formulations are proposed and discussed, considering several types of food, with type-specific ingestion and assimilation efficiencies. The model performance is evaluated by comparison with literature data for the blue mussel for a wide range of experimental conditions. The lack of data and of detailed information on the experimental setup adds some uncertainty to the parameters estimation. Nevertheless, the model results are in good agreement with observations. The model has the desired flexibility to be implemented as an extension to the standard DEB model, to simulate bivalve growth in estuaries and coastal areas where the organisms experience different food quantity and quality.

Keywords: modelling, bivalves, feeding processes, food quantity, food quality, DEB theory.

Introduction

Suspension-feeding bivalves obtain their food from the surrounding water by retaining suspended organic particles when water is transported through the gills (Winter, 1978). Food intake is related to both plankton and detritus concentrations (Widdows et al., 1979; Kiørboe et al., 1981; Velasco and Navarro, 2003; Newell et al., 1989, 2005). The non-assimilated material is returned to the water column as pseudofaeces (material rejected prior to the gut passage) and faeces (material rejected prior to absorption).

Bivalve filtration can have a large impact on the benthic and pelagic compartments of the ecosystem. Filtration of particles can induce a top-down control of phytoplankton and bacterial communities, as well as changes in the nutrient cycling at the ecosystem scale (Zemlys et al., 2003; Dolmer, 2000). Bivalves can also increase deposition rates (Dame, 1993), enrich sediments and stimulate microbial growth and may thus provide an important resource for surrounding benthos (Norkko et al., 2001; Asmus and Asmus, 1993).

Many suspension-feeding bivalves inhabit coastal waters where turbidity may be high, due to natural processes (e.g. resuspension of deposited material due to waves and currents) and human activities (e.g. dredging) resulting in broad fluctuations in both quality and quantity of suspended particulate matter.

Functional responses of filter-feeding bivalves to variations in seston (total amount of particles in the water) have been discussed by numerous authors (e.g. Foster-Smith, 1975b; Shumway et al., 1985; Bayne et al., 1987; Newell et al., 1989; Navarro and Iglesias, 1993; Riisgård, 2001) but contradictions and uncertainties still exist. Most studies applied empirical relations for filtration, pseudofaeces production and assimilation based on laboratory or field experiments (Scholten and Smaal, 1998; Hawkins et al., 2002). No clear mechanistic process was proposed to explain the feeding processes (Foster-Smith, 1975b; Widdows et al., 1979) and, for example, the effect of non-edible particles or the choice of an appropriate food quantifier has been accounted by considering the half saturation parameter as an environment-specific parameter (van Haren and Kooijman, 1993; Ren and Ross, 2001; Pouvreau et al., 2006; Bacher and Gangnery, 2006; Ren and Schiel, 2008; Ren, 2009; Rosland et al., 2009), where low values of this parameter reflects high-quality. Although useful for model hindcast implementations (reproduce past events), this approach compromises the model use in a forecast approach (scenarios prediction). Kooijman (2006) explicitly included the role of silt (or inedible particles) and Ren (2009) applied this model using a series of feeding experiments with *Perna canaliculus*. Furthermore Ren (2009) proposed a model for pseudofaeces production, although no mechanism is clearly described.

Based on the concepts described in the Dynamic Energy Budget (DEB) theory (Kooijman, 2000), we aim to improve the modelling of the feeding processes in bivalves, by extending Kooijman (2006) approach for generic conditions of food quantity and quality, avoiding the use of an environment-specific half-saturation constant estimation. Model parameters are estimated

using several data sets from literature on *Mytilus edulis* (blue mussel).

Model description

As already proposed in the literature (Foster-Smith, 1975a; Shumway et al., 1985; Bayne et al., 1987) the model presented here considers three main processes in bivalves feeding (Fig.2.1): (i) filtration, extraction of particles from the water column controlled by the ciliary activity on water flow generation (clearance rate, \dot{C}_R) and the retainment of the particles in the gills; (ii) ingestion, pre-ingestive selection at the labial palps, returning the rejected material into the water column (pseudofaeces production); (iii) assimilation, differential absorption in the gut and incorporation of material into the organism reserves, with the production of faeces .

For each particle type i in the water column, with density X_i , a flux of particles is retained through filtration ($X_i \dot{C}_R$). If some of the particles are not retained by the gills, which will mainly depend on the particles characteristics and bivalve filtration efficiency, the corresponding water out flux will transport these rejected particles back to the water column ($X_i^{out} \dot{C}_R$). Once retained in the gills, particles are then lead to the second step (ingestion) where selection occurs by the palps (their transport to the mouth). Here particles handling time limit the amount of particles that can be processed, implying rejection of particles to the water column in the form of pseudofaeces ($\dot{J}_{P_i F}$). The third and last feeding step is assimilation, defined here as the process where the particles are absorbed and converted into the organism's reserves. It is assumed that the chemical composition of absorbed food has to be the same as that of the reserves and the difference in the chemical composition between bivalve reserves and ingested food, determines the production of faeces ($\dot{J}_{P_i A}$). A more detailed description of the model assumptions and also of the main empirical observations for each step, derived from the literature, can be found in the following sections.

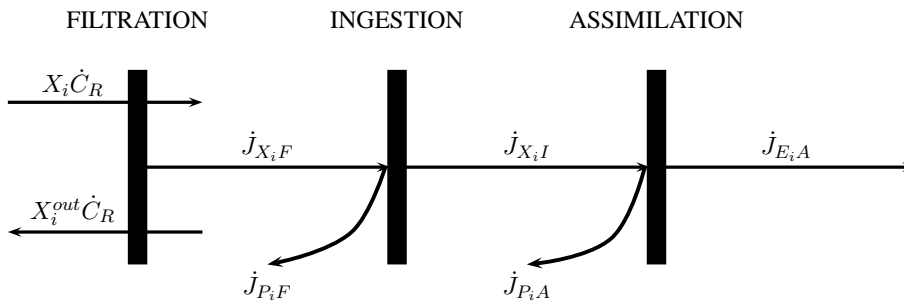


Fig. 2.1. Generic scheme for feeding processes in bivalves. X_i – particle concentration in the environment, ml^{-3} ; X_i^{out} – particle concentration returned to the environment, ml^{-3} ; \dot{C}_R – clearance rate, $\text{l}^3 \text{t}^{-1}$; $\dot{J}_{X_i F}$ – filtration rate, m t^{-1} ; $\dot{J}_{P_i F}$ – pseudofaeces production, m t^{-1} ; $\dot{J}_{X_i I}$ – ingestion rate, m t^{-1} ; $\dot{J}_{P_i A}$ – faeces production, m t^{-1} ; $\dot{J}_{E_i A}$ – assimilation rate, m t^{-1} . Dotted symbols represents a rate (quantity per time unit) and $\dot{J}_{C P}$ represents the mass flux of compound C due to process P. m refers to mass, l to environmental length and t to time.

A generic mechanism

To describe each process included in bivalve feeding, the model makes use of the Synthesizing Units concept introduced in the Dynamic Energy Budget theory by Kooijman (1998, 2000, 2010).

Synthesizing Units (SU) are generalized enzymes that transform arrival fluxes of substrates into a production flux of products (Lika and Papadakis, 2009). It is assumed that the substrate molecules arrive according to a Poisson process and that the binding occurs with a fixed probability. During the production (handling time), no substrate particles are accepted by the SU, i.e. while handling, the binding probability for each arriving substrate will be null. If we identify the SU with an individual, and the product with reserve, the transformation rate is directly given by the functional response, commonly described as the Michaelis–Menten function, equivalent to Holling type II functional response in its simplest scenario. However SU's can assume more complex forms if more than one type of food is considered and depending on the transformation type. Globally the process of transformation is classified according to: (i) the relative role of substrates in product formation (substitutable when any substrate can be separately transformed into the product; complementary when all substrates are required to produce the product) and (ii) their interaction at the binding/production level (parallel if there is no interaction between the substrates; sequential if the binding of one substrate interferes with the binding of the others (Kooijman, 2010; Lika and Papadakis, 2009). More detailed information about the concept and base mathematical formulations, to derive SU's mathematical formulation for specific conditions, can be found in Kooijman (2010). Temperature influence on the feeding processes is described by the Arrhenius relation, with the additional idea that each rate is controlled by SUs having an inactive configuration at low and high temperatures presented in Kooijman (2010):

$$\dot{k}(T) = \dot{k}_1 e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)} \frac{s(T)}{s(T_1)} \text{ with } s(T) = \left(1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T} - \frac{T_{AH}}{T_H}\right)}\right)^{-1}$$

where T is the absolute environment temperature (Kelvin), T_1 is the reference temperature, T_A is the Arrhenius temperature, \dot{k}_1 is the value of the rate at temperature T_1 , $\dot{k}(T)$ is the value of the rate at temperature T , T_L and T_H relate to the lower and upper boundaries of the tolerance range and T_{AL} and T_{AH} are the Arrhenius temperatures (K) for the rate of decrease at both boundaries. As an approximation, we assume that all physiological rates are affected by temperature in the same way (Pouvreau et al., 2006).

Filtration

Filter feeders generate a water flow to obtain a volume of water (clearance rate, \dot{C}_R) which is proportional to the surface area of the gills hence to squared body length (Riisgård, 2001; Kooijman, 2006), from where the particles are extracted.

M. edulis ability to retain suspended particles has been well investigated for particles larger than $1\ \mu\text{m}$ (Vahl, 1972; Møhlenberg and Riisgård, 1978), a size class which includes all of the phytoplankton, zooplankton, and much of detritus. If one wants to simplify the model, it is thus possible to assume that *M. edulis* will be able to retain all particulate matter suspended in the water column, i.e. able to filter all the particles in the water volume defined by the clearance rate, meaning that the out flux ($X_i^{\text{out}} \dot{C}_R$, Fig.2.1) could be considered equals zero.

A negative effect of high concentrations of suspended particles on clearance rate has been also reported in several studies (e.g. Foster-Smith, 1975b; Winter, 1978; Widdows et al., 1979; Riisgård and Møhlenberg, 1979; Kiørboe et al., 1980; Riisgård and Randlov, 1981; Bayne et al., 1989; Riisgård, 2001; Newell et al., 2001) and was interpreted as a result of the saturation of the food handling organs such as cirri, gill filaments, mucus strings, labial palp and gut. Nevertheless, the dependence of clearance rate with the concentration of total suspended particles has been described differently: (i) a constant clearance rate until a threshold concentration (*saturation value*), from which there is a decrease (Winter, 1973; Riisgård and Randlov, 1981; Sprung and Rose, 1988; Riisgård, 2001; Newell et al., 2001) and (ii) a continuous decrease of clearance rate (Widdows et al., 1979; van Haren and Kooijman, 1993).

To better understand the implications of both approaches it is perhaps useful to consider the particle retainment by the bivalve as sequence of two different apparatus systems (processes): (a) water flow generation by the ciliary activity and (b) the retainment of particles by the gill lamellae. The existence of an initial plateau where clearance rate remains constant assumes a constant ciliary activity, bellow the threshold concentration. On the other hand, the continuous decrease of clearance rate assumes that the ciliary activity is always coupled to particle retainment. Measurements on the separate behavior of both processes are technically difficult and usually experimental results only quantify their joint effect (filtration rate). Approach (ii) is a more parsimonious description because does not imply a switching behavior and it will be adopted in this study.

Another important question, when evaluating the effect of suspended inorganic particles on food uptake in suspension feeding bivalves, is whether bivalves are able to filter particles of low and high food value in a different way. While morphological studies and direct observations on the mantle cavity and gills indicate that at least some suspension-feeding bivalves display particle selection at the filtration level, experimental evidence is either weak or contradictory (Kiørboe et al., 1980). Results from Rouillon and Navarro (2003), using two phytoplankton species presenting different structural properties (a diatom and a naked flagellate), suggest the absence of a differential retention by the gill of any microalgal component of the diet, consistent with Widdows et al. (1979) and Cucci et al. (1985). Also in Vahl (1972), *M. edulis* is reported as a non-selective filter-feeder, due to the 100 % efficiency in retaining all particles greater than $2\text{--}5\ \mu\text{m}$ in its gill. Thus, no selection between particles at the filtration level is assumed and implies the same clearance rate for all food types ($\{\dot{C}_R\}$), representing the same 'effective' searching rate that depends on the organism maximum capacity ($\{\dot{C}_{Rm}\}$) and envi-

ronment conditions in terms of particle concentrations. In the model, filtration rate is regulated by substitutable and sequential SU's where any substrate can be separately filtered and the handling of one food type by the filtration apparatus interferes with the possible handling of other food types. The formulation derived under these conditions is then similar to Holling type II functional response, although extended to the situation with several types of food. Formulations derived for the filtration model are presented in Table 2.1.

Table 2.1. Filtration process description. Clearance rate computed as substitutable and sequential SU's. X_i represents particle type: e.g. silt (X_0), algae (X_1), zooplankton (X_2) or detritus (X_3). m refers to mass, l to length, and t to time.

	Symbol	Dimensions	Description
Processes rates	\dot{C}_R	$l^3 t^{-1}$	Clearance rate
	$\dot{J}_{X_i F}$	$m t^{-1}$	Filtration rate
Variables	L_f	l	Organism physical length (total length)
	$V = (\delta_M L_f)^3$	l^{-3}	Organism structural volume
	X_i	$m l^{-3}$	Particle concentration in the environment
Parameters	$\{\dot{C}_{Rm}\}$	$l^3 t^{-1} l^{-2}$	Maximum surface area-specific clearance rate
	$\{\dot{J}_{X_i Fm}\}$	$m t^{-1} l^{-2}$	Maximum surface area-specific filtration rate for X_i
	δ_M	-	Shape coefficient

$$\dot{C}_R = \frac{\{\dot{C}_{Rm}\}}{1 + \sum_i^n \frac{X_i \{\dot{C}_{Rm}\}}{\{\dot{J}_{X_i Fm}\}}} V^{2/3}$$

$$\dot{J}_{X_i F} = \dot{C}_R X_i$$

Ingestion and pseudofaeces production

For various bivalve species, experiments where animals were fed with mixtures of silt and algae have shown a reduction in the relative amount of chlorophyll/fluorescent particles or organic content present in pseudofaeces, compared with the relative amount in food (Kiørboe and Møhlenberg, 1981; Kiørboe et al., 1980; Hawkins et al., 1998; Prins et al., 1991; Bayne et al., 1993; Navarro et al., 2003). These results suggest the existence of particle selection during handling by the palps (where ingestion takes place), although this explanation is rejected by some authors (Jørgensen, 1996) and not confirmed by Foster-Smith (1975b). The selective ingestion of food particles may help animals to maintain food uptake at a high level, in spite of dilution of the food items with indigestible material, increasing the organic material in the ingestion. Some studies revealed that this selectivity does not only concern to inorganic vs. organic particles: organic content has been found in pseudofaeces (Foster-Smith, 1975b; Widdows et al., 1979; Prins et al., 1991; Ren, 2009) and experiments using flow cytometric techniques have indicated selective feeding between algae species using mixed algal suspensions (Shumway et al., 1985). The similarities between filtration and ingestion processes allow the use of the same type of

mechanism (substitutable and sequential SU's) to explain and describe both processes. However, in ingestion, binding and handling time should be particle specific, i.e. the parameters that regulate the process will be specific for each type of particle and their combination will result in the selectivity described in the literature. The selection is made by assuming different binding probability for each type of food ($\rho_{X_i I}$), representing different affinities between each particle type and the ingestion apparatus (palps). Filtration and ingestion are assumed as two SU systems connected by handshaking 'open' protocol, where the first SU releases its products irrespective of the state of the next SU (Kooijman, 2000), with the consequent production of pseudofaeces (filtered material that the ingestion process is not able to handle). Pseudofaeces production rate is in this approach not a process itself but it is the difference between filtration and ingestion. The details for the computation of ingestion and pseudofaeces production are described in Table 2.2.

Table 2.2. Ingestion and pseudofaeces production description. Maximum ingestion rate computed as substitutable and sequential SU's. X_i represents particle type: e.g. silt (X_0), algae (X_1), zooplankton (X_2), detritus (X_3). m refers to mass, l to length, and t to time.

	Symbol	Dimensions	Description
Processes rates	$\dot{J}_{X_i I}$	m t^{-1}	Ingestion rate
	$\dot{J}_{P_i F}$	m t^{-1}	Pseudofaeces production rate
	$\dot{J}_{X_i F}$	m t^{-1}	Filtration rate (Table 2.1)
Parameters	$\rho_{X_i I}$	-	Binding probability for X_i
	$\dot{J}_{X_i I m}$	m t^{-1}	Maximum ingestion rate for X_i
	δ_M	-	Shape coefficient

$$\dot{J}_{X_i I} = \frac{\rho_{X_i I} \dot{J}_{X_i F}}{1 + \sum_i^n \frac{\rho_{X_i I} \dot{J}_{X_i F}}{\{\dot{J}_{X_i I m}\}}}$$

$$\dot{J}_{P_i F} = \dot{J}_{X_i F} - \dot{J}_{X_i I}$$

Assimilation and faeces production

Assimilation in DEB theory is the influx of food-derived reserve into the reserve compartment using SU mechanism. The efficiency in the conversion of food into the reserves depends on how the organism is able to absorb food particles, which ultimately depends on the similarity of the chemical composition of food and reserves. Conversion efficiency, therefore, depends on the type of food. In situations where the food quality – food sources and respective chemical composition – does not have significant changes over time, realistic results can be found using a constant assimilation efficiency independent of the feeding rate, thus making the assimilation rate proportional to the ingestion rate (Kooijman, 2000). This simplification can be used for some types of food, e.g. zooplankton or detritus but its applicability is doubtful for algae in estuaries and coastal lagoons because its chemical composition as reflected, for example, by the P:N:C ratio, can have significant changes over time (Sommer, 1994). The total assimilation rate

is then expected to increase with the similarity between the algae and bivalve reserves composition. For this reason the model considers different formulations for the uptake of algae structure and reserves: algal structure is taken up according to the simple rule described above; algal reserves are considered to be complementary substrates for the synthesis of bivalve reserve, which are processed in parallel. Table 2.3 summarizes the assimilation and faeces formulations used by the model, adapted from Kooijman (2000) (pag. 48, equation 2.15) and implemented here, as an example, for the situation where carbon and nitrogen are the complementary elements needed to produce one unit of organism reserves. If different situations are observed, the model is easily expandable by implementing the referred generic equation accordingly.

Table 2.3. Assimilation and faeces production. Algae structure and reserves are represented by X_1^E and X_1^V , respectively. Algae reserves assimilation is computed as complementary and parallel SU's, assuming the handling time as the main step limiting the process; assimilation of other food types assumes a constant efficiency parameter. X_i represents particle type: e.g. silt (X_0), algae (X_1), zooplankton (X_2) or detritus (X_3). m refers to mass, l to length, and t to time.

	Symbol	Dimensions	Description
Processes rates	$\dot{J}_{E_i A}$	$m\ t^{-1}$	Assimilation rate for X_i
	$\dot{J}_{E_1 A}$	$m\ t^{-1}$	Total algae assimilation rate
	$\dot{J}_{E_1^E A}$	$m\ t^{-1}$	Algae reserves assimilation rate
	$\dot{J}_{E_1^V A}$	$m\ t^{-1}$	Algae structure assimilation rate
	$\dot{J}_{X_i I}$	$m\ t^{-1}$	Particle i ingestion rate (Table 2.2)
	$\dot{J}_{X_1^E I}$	$m\ t^{-1}$	Algae reserves ingestion rate (Table 2.2)
	$\dot{J}_{X_1^V I}$	$m\ t^{-1}$	Algae structure ingestion rate (Table 2.2)
Parameters	y_{EX_i}	$m\ m^{-1}$	Yield coefficient of reserves on food X_i
	$y_{EX_1^V}$	$m\ m^{-1}$	Yield coefficient of reserves on algae structure
	$n_{X_1^E}^N$	$m\ m^{-1}$	Chemical index of nitrogen in algae reserve
	n_E^N	$m\ m^{-1}$	Chemical index of nitrogen in bivalve reserves
Algae	$\dot{J}_{E_1 A} = \dot{J}_{E_1^E A} + \dot{J}_{E_1^V A}$		
Reserves	$\dot{J}_{E_1^E A} = \left(\left(\dot{J}_{X_1^E I} \right)^{-1} + \left(\frac{\dot{J}_{X_1^E I} n_{X_1^E}^N}{n_E^N} \right)^{-1} - \left(\dot{J}_{X_1^E I} + \frac{\dot{J}_{X_1^E I} n_{X_1^E}^N}{n_E^N} \right)^{-1} \right)^{-1}$		
Structure	$\dot{J}_{E_1^V A} = y_{EX_1^V} \dot{J}_{X_1^V I}$		
Other Particles	$\dot{J}_{E_i A} = y_{EX_i} \dot{J}_{X_i I}$		

Methodology and data observations

To evaluate model performance, results were compared with experimental data from literature. Most observations result from dedicated experiments using mixtures of algae and silt (Table 2.4). Experimental conditions differed: some authors used laboratory cultured algae suspensions, where cell numbers for each species were counted (Riisgård and Møhlenberg, 1979; Kiørboe et al., 1980; Prins et al., 1991; Bayne et al., 1993); others used algae suspensions from the field, with unidentified species and where chlorophyll-a concentration was measured as a proxy for algae biomass (Widdows et al., 1979). Either dried silt was added (Bayne et al.,

1993), or sediment directly from the field, i.e. with the possible addition of organic material to the suspension (Widdows et al., 1979; Kiørboe et al., 1980; Prins et al., 1991). Algae concentration was kept constant and different amounts of silt/sediment were added (Widdows et al., 1979; Kiørboe et al., 1980) or both varied (Prins et al., 1991; Bayne et al., 1993) or only pure algae was used (Riisgård and Møhlenberg, 1979). Organisms size, temperature ranges and experimental setup also differed between experiments, which makes the results not easily comparable. Our model predictions do account for the various detailed experimental conditions in terms of particles concentration, temperature and organism length. When necessary, model results were converted to the type of variables reported by the authors. Not all necessary details were always available and several assumptions had to be made (Table 2.4). Each model simulation requires two common parameters (shape coefficient, δ_M and maximum clearance rate, $\{\dot{C}_{Rm}\}$) and four parameters specific for each type of particle present in the suspension: i) one in the filtration process (maximum surface area-specific filtration rate, $\{\dot{J}_{X_i Fm}\}$), representing the property handling time; (ii) two in the ingestion process (binding probability, $\rho_{X_i I}$ and maximum ingestion rate, $\dot{J}_{X_i Im}$), representing the binding and the handling time of the property, respectively and (iii) at least one in the assimilation process (yield coefficient of reserves on food, y_{EX_i}). Most of the parameters are unknown and had to be estimated, except for the shape coefficient, $\delta_M = 0.26$ (average between the estimates of van der Veer et al. (2006), Rosland et al. (2009) and van der Meer (2006)), the maximum surface area-specific filtration rate for algae, $\{\dot{J}_{X_1 Fm}\} = 4.8 \times 10^{-4} \text{ molC d}^{-1} \text{ cm}^{-2}$ proposed by Rosland et al. (2009), and the temperature parameters estimated by van der Veer et al. (2006): $T_1 = 293 \text{ K}$; $T_A = 5800 \text{ K}$; $T_L = 275 \text{ K}$; $T_H = 296 \text{ K}$; $T_{AL} = 45430 \text{ K}$ and $T_{AH} = 31376 \text{ K}$. $60 \text{ mgC(algae) mgChla}^{-1}$ (Cloern, 1995); $0.1 \text{ mgDW (algae) mgWW}^{-1}$ and $2.5 \text{ mgDW(algae) mgC}^{-1}$ (Slobodkin and Richman, 1961) were assumed to convert data when needed. Parameters were estimated (minimizing a weighted residual sum of squares) for a particular data set (Table 2.4) and, when available, other data sets were used for validation.

The model was implemented under the FEMME environment (Soetaert et al., 2002), using the directional iterative Levenberg–Marquardt method, assuming one over the data set variance as weight coefficient when using more than one data set. Comparisons between model and observations were made graphically and also by computing the overall error as $E = e^{\sigma^2} - 1$, where σ^2 is the variance of ε and $\varepsilon = \sqrt{\log^2 \left(\frac{\hat{Y}_{pred}}{Y_{obs}} \right)}$ for each data point. This overall error aims to quantify the difference between model and data: assuming a null value for a perfect match and increasing values for increasing errors. The overall error computed for each comparison can be useful for the comparison with future model applications and comparison with other models implementation to the same data set.

Table 2.4. Literature data used in the study: (1)Widdows et al. (1979); (2)Risgaard and Møhlenberg (1979); (3)Kjørboe et al. (1980); (4)Prins et al. (1991); (5)Bayne et al. (1993). X_0 and X_1 represent silt and algae, respectively. TPM represents total particulate matter concentration in the water column. 60 mgC(algae) mgChla⁻¹ (Cloern, 1995); 0.1 mgDW(algae) mgWW⁻¹ and 2.5 mgDW(algae) mgC⁻¹ (Slobodkin and Richman, 1961) were assumed to convert data when needed.

Authors	Experiments		Model scenario								
	Conditions	Data	Main assumptions	Operation	Results						
1	Constant algae	3, 5, 7 cm	Clearance rate	T=15 °C	Fil. par. estimation (3 cm) Fil. validation (57 cm)	Fig.2.2 $\{\dot{C}_{Rm}\} = 0.096 \text{ m}^3 \text{ d}^{-1} \text{ cm}^{-2}$ $\{J_{X_0 Fm}\} = 3.5 \text{ g d}^{-1} \text{ cm}^{-2}$					
	Variable silt										
	TPM [3–330] mg l ^{−1}	7 cm	Total pseudofaeces	T=15 °C	Ing. validation	Fig.2.4					
	Constant algae										
2	Variable algae ^a	132 mg	Clearance rate	Length = 4.8 cm T=15 °C	Fil. validation	Fig.2.2b					
	TPM [0.07–0.3] mg l ^{−1}										
	Constant algae ^a						3.7 cm	Clearance rate	T=15 °C	Fil. validation	Fig.2.2b
	Variable Silt										
3	Variable Silt	5.7–6.4 cm	Ingestion rate	Length=6 cm T=6.5 °C	Fil. validation	Fig.2.4					
	Variable algae ^a										
	Variable silt						Total pseudofaeces	Ing. par. estimation	Ass. par. estimation	Fig.2.3	
	TPM [5–90] mg l ^{−1}										
4	T [5.1–7.9] °C	Algae ingestion Algae faeces	Ass. par. estimation	Ass. par. estimation	Ass. par. estimation	Fig.2.6					
	ρX ₁ I = 0.99										
	ρX ₀ I = 0.45										
	JX ₀ I _m = 0.65 × 10 ⁴ molC d ^{−1}										
5	Variable algae ^a	4–5 cm	Clearance rate	Length = 4.5 cm	Fil. validation	Fig.2.2b					
	Variable silt										
	TPM [0.1–10] mg l ^{−1}						Carbohydrates ≈ Reserves 0.4 gC(CH ₂ O) ^{−1}	Ing. validation	Ass. par. estimation	Fig.2.5	
	T=15 °C										
5	Reserves assimilation	Assimilation rate	Assimilation rate	Assimilation rate	Assimilation rate	Assimilation rate					
	Assimilation efficiency ^b										
	Assimilation efficiency ^b										
	Assimilation efficiency ^b										

^aLaboratory cultured cells

^bDefined by the author

Results and discussion

Filtration

In most experiments a mixture of algae and silt particles was used. In these conditions filtration is controlled by three different parameters: (i) the maximum surface area-specific clearance rate ($\{\dot{C}_{Rm}\}$), constant for all the particles types (no selection); (ii) the maximum surface area-specific filtration rate for algae ($\{J_{X_1Fm}\}$), estimated by Rosland et al. (2009) and (iii) the maximum surface area-specific filtration rate for inorganic particles ($\{J_{X_0Fm}\}$). Unknown parameters were estimated using data from Widdows et al. (1979) on 3 cm mussels because it was the experiment with more data points. Assumptions were made on the conversion factors between dry mass and organic carbon and the chlorophyll content of algae as well as constant temperature during the experiment. Good agreement between model and observations was obtained (Fig.2.2a). Next, the estimated parameter set was used to predict experimental results reported in the literature by other authors (Widdows et al., 1979; Riisgård and Møhlenberg, 1979; Kiørboe et al., 1980; Prins et al., 1991; Bayne et al., 1993). The predicted value for the clearance rate agreed with the observations (Fig. 2.2b) with an error variance equal 0.36. Observations by Widdows et al. (1979) for mussels with 7 cm at small TPM, and of Kiørboe et al. (1980) deviate most. These differences between model and data might be attributed to the lack of detailed information on the experimental setup, namely on temperature (high ranges of temperature are mentioned in both experiments) and food concentration, which was obtained from a seasonal pattern. For all other data sets the agreement is satisfactory.

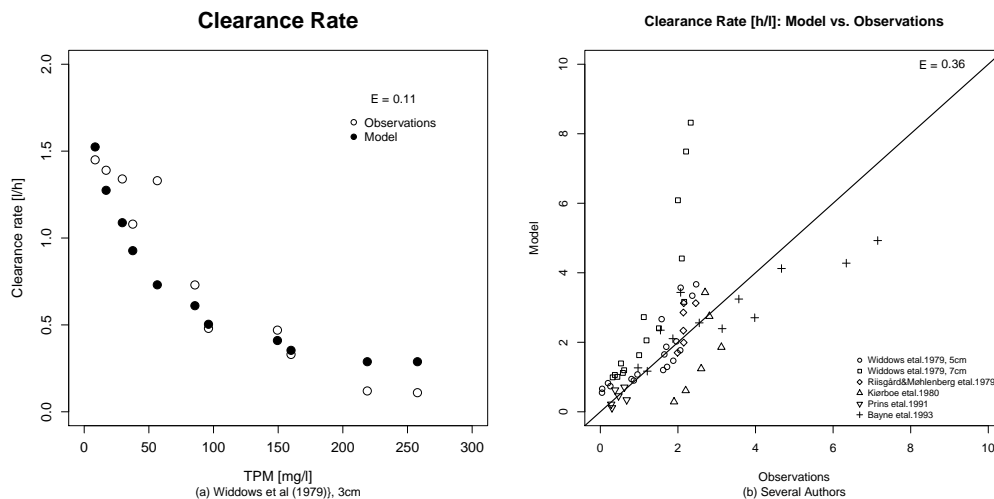


Fig. 2.2. Clearance rate: model results and observations. $\{J_{X_1Fm}\} = 4.8 \times 10^{-4} \text{ molC d}^{-1} \text{ cm}^{-2}$ from Rosland et al. (2009) and estimated parameters: $\{\dot{C}_{Rm}\} = 0.096 \text{ m}^3 \text{ d}^{-1} \text{ cm}^{-2}$ and $\{J_{X_0Fm}\} = 3.5 \text{ g d}^{-1} \text{ cm}^{-2}$. E-value reflects the variance of the error obtained for each data point and TPM represents total particulate matter concentration in the water column.

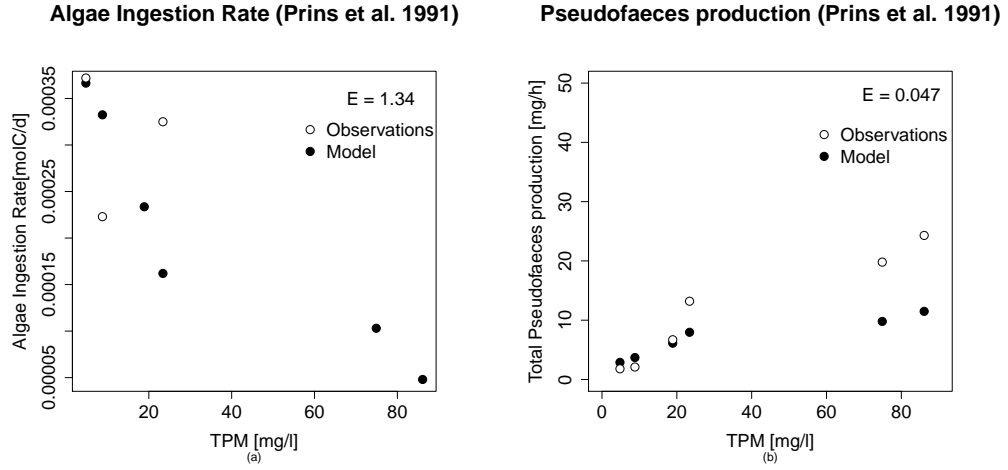


Fig. 2.3. Model results and observations from Prins et al. (1991): (a) ingestion rate; (b) pseudofaeces production. Estimated parameters: $\rho_{X_1 I} = 0.99$; $\rho_{X_0 I} = 0.45$; $\dot{J}_{X_1 Im} = 0.65 \times 10^4 \text{ molC d}^{-1}$ and $\dot{J}_{X_0 Im} = 0.23 \text{ g d}^{-1}$. E-value reflects the variance of the error obtained for each data point and TPM represents total particulate matter concentration in the water column.

Ingestion and pseudofaeces production

Ingestion rate and consequently pseudofaeces production not only depend on the clearance rate and filtration rate, validated before, but also on two additional parameters specific for each type of particle: (i) binding probability $\rho_{X_i I}$ and (ii) maximum ingestion rate $\dot{J}_{X_i Im}$. Parameters were estimated using data from Prins et al. (1991) for organisms of 5.7–6.4 cm length. These authors used constant cultured algae cells (with respective N:C ratio and C:Chla ratio reported) and variable silt concentration to perform experiments where algae ingestion rate and pseudofaeces production were estimated. This detail allowed the estimation of the full parameter set for ingestion. Both model predictions and observations confirm that an increase in total particulate matter in the water column leads to an increase in the pseudofaeces production and a decrease in the ingestion rate (Fig.2.3). Model predictions were then compared with data from other sources using the set of parameters obtained before and the results reveal a satisfactory agreement (Fig.2.4). However some differences are found when comparing with measurements at low TPM reported by Bayne et al. (1993). By performing experiments at very low concentrations, their results suggest the existence of a TPM concentration threshold for pseudofaeces production, i.e. the pseudofaeces production occurs only at concentrations above this threshold (4 mg l^{-1}). Such threshold is not predicted by the model but in absolute amounts, the difference is small and will have no significant influence in the simulation of bivalve growth or performance.

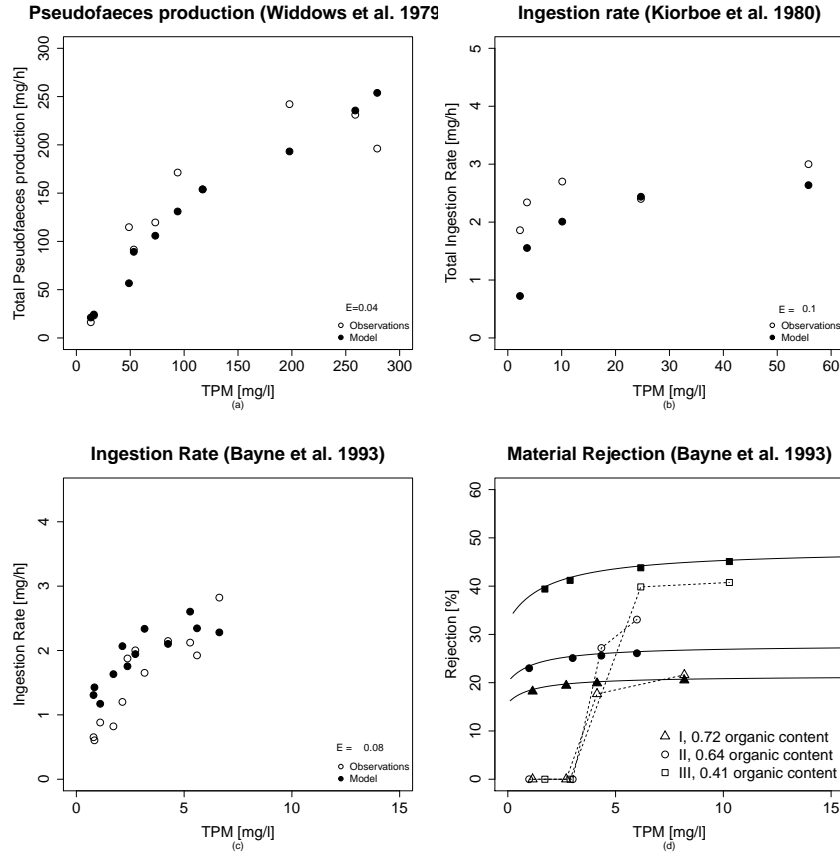


Fig. 2.4. Model validation using ingestion and pseudofaeces production data: model (closed symbols) vs. observations (open symbols). Parameters values used: $\rho_{X_1 I} = 0.99$; $\rho_{X_0 I} = 0.45$; $J_{X_1 I m} = 0.65 \times 10^4 \text{ molC d}^{-1}$ and $J_{X_0 I m} = 0.23 \text{ g d}^{-1}$. E-value reflects the variance of the error obtained for each data point and TPM represents total particulate matter concentration in the water column.

Assimilation

The last step included in the feeding process is the assimilation. The assimilation process modelling requires some additional informations not easily found in the literature, namely algae reserves and structure fraction and the chemical composition of algal and bivalves reserves (N:C ratios). Bayne et al. (1993) reported measurements on carbohydrates concentration in the water and the respective assimilated value. The amount of carbohydrates in algae cell can be used as proxy for algae reserves (Kooijman, 2000) and it was used here to estimate the fraction of reserves in the bivalves food (f_{X_1}) during the experiment. Using this information and establishing a range of bivalve N:C ratio – between 0.17 and 0.22 (Smaal and Vonck, 1997, for overall bivalve), the calibration of the parameters dealing with the assimilation process was performed. Estimates of algae structure assimilation efficiency ($y_{EX_1^V}$) and bivalve reserves N:C ratio (n_E^N) were obtained and the results are presented in Fig.2.5 with relatively good agreement. Considering that algae structure chemical composition does not change significantly during the experiment, the previous values were used to perform a comparison with observations on faeces contribution from algae (using chlorophyll as a marker) obtained by Prins et al. (1991).

An estimation on the algae reserves fraction (f_{X_1}) and bivalve reserves N:C ratio (n_E^N) were obtained (Fig.2.6). It is important to notice that the fraction of algal reserve (f_{X_1}) in the experiments of Prins et al. (1991) and Bayne et al. (1993) differed (0.9 vs. 0.3 till 0.8), revealing the uncertainty in this quantity. Nevertheless, considering the significant lack of available data, the results are satisfactory, with relatively good agreement with the observed patterns of properties.

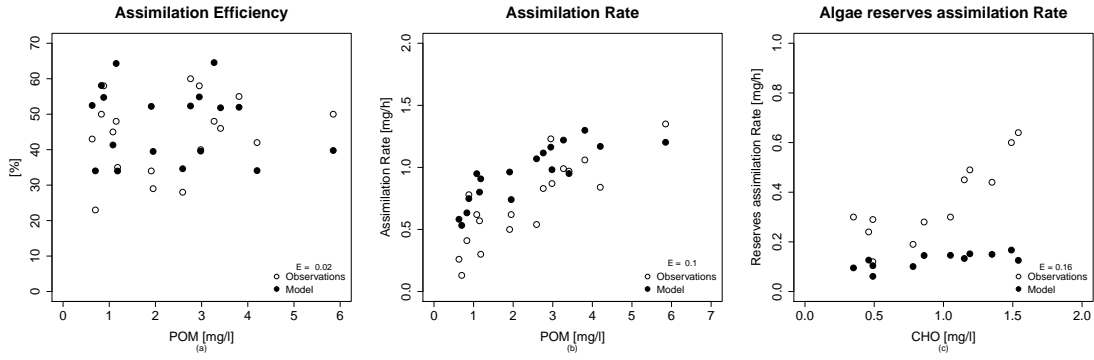


Fig. 2.5. Assimilation Process: model results and observations from Bayne et al. (1993). a) Absorption Rate; b) assimilation rate; c) reserves assimilation rate. Estimated parameters: algae structure assimilation efficiency, $y_{EX_1^V} = 0.4 \text{ molC(reserves) mol(food)}^{-1}$; bivalve NC ratio, $n_E^N = 0.22 \text{ molN molC(reserves)}^{-1}$; algae NC ratio, $n_{X_E}^N = 0.15 \text{ molN molC(reserves)}^{-1}$. E-value reflects the variance of the error obtained for each data point; POM represents total particulate organic matter concentration in the water column and CHO the carbohydrates concentration.

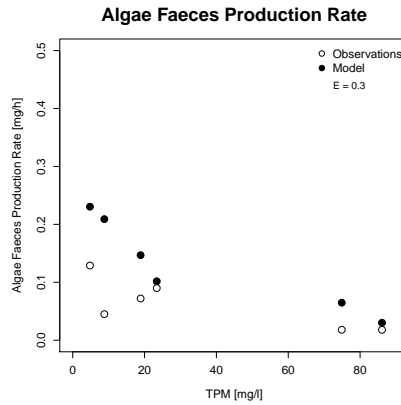


Fig. 2.6. Algae Assimilation Rate: model results and observations from Prins et al. (1991). Estimated parameters: algae reserves fraction, $f_{X_1} = 0.9 \text{ molC(reserves) molC(total)}^{-1}$; bivalve reserves NC ratio, $n_E^N = 0.21 \text{ molN molC(reserves)}^{-1}$. E value reflects the variance of the error obtained for each data point and TPM represents total particulate matter concentration in the water column.

Conclusion

In the past much attention has been given to quantify the feeding processes in bivalves, such as filtration, pseudofaeces production, ingestion and assimilation rates. The ultimate goal was

to understand how bivalve growth rates were affected by food quantity and quality and by temperature. Although important results have been obtained, a formal mechanistic description for many of the observations has not been provided. From a modelling point of view, a mechanistic approach enables model implementation for conditions that differ from the experiment. We showed that the concept of Synthesizing Units described by DEB theory can provide such mechanistic description. Globally, the model performance (estimation and validation) appeared to be satisfactory under a wide range of experimental setups and methodologies. The model was able to reproduce the main patterns found in the observations and the results were also usually quantitatively accurate. This holds in particular for clearance and filtration rate and to a lesser extent for ingestion and pseudofaeces production. The main uncertainty related to ingestion concerned the apparent existence of a pseudofaeces production threshold as observed in laboratory experiments (Bayne et al., 1993). These observations may, however, be explained by a temporary pseudofaeces accumulation inside the bivalve before rejection or by the release of particles in their primary form, without the production of pseudofaeces. Besides, the topic is only important for pseudofaeces production in systems with very low total particulate matter concentration where the implications of the model assumptions should be better addressed. Detailed information on the experimental conditions was often lacking, particularly concerning assimilation. Several assumptions had to be made on the chemical composition of the bivalve, food, pseudofaeces and faeces, and we were unable to check any mass balances. It is also important to notice that the processes are sequential, meaning that the errors found in one step will also show up in the next step, compromising the similarity between model and observations in the later steps. Improvement of the parameter estimation can be achieved by new and dedicated experiments. In short, besides all uncertainties, our model was able to provide a mechanistic explanation for the main patterns observed on the different physiological rates related with feeding process for a wide range of experimental conditions and it represents a further step in the understanding of the complex feeding behavior of bivalves. The model copes with variable food quantity (concentration and number of properties) and quality (chemical composition of each particle) in the water column which assumes extreme importance on the seasonal simulation of bivalves growth. Thus, we conclude that the model has the desired flexibility to be implemented as an extension to the standard DEB model, in order to simulate bivalve growth, enabling the easy coupling with ecosystem models.

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3. DEB parameters estimation for *Mytilus edulis*

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Many bivalves species inhabit coastal waters where fluctuations in both quantity and quality of suspended particulate matter occur. The study of interactions between the organism and its environment. The potential of DEB theory to simulate an organism life-cycle has been demonstrated at numerous occasions. However, its applicability requires parameter estimates that are not easily obtained by direct observations. During the last years various attempts were made to estimate the main DEB parameters for bivalve species. The estimation procedure was by then, however, rather ad-hoc and based on additional assumptions that were not always consistent with the DEB theory principles. A new approach has now been developed - the covariation method - based on simultaneous minimization of the weighted sum of squared deviations between data sets and model predictions in one single procedure. This paper presents the implementation of this method to estimate the DEB parameters for the blue mussel *Mytilus edulis*, using several data sets from the literature. After comparison with previous trials we conclude that the parameter set obtained by the covariation method leads to a better fit between model and observations, with potentially more consistency and robustness.

Keywords: modelling, bivalves, feeding processes, food quantity, food quality, DEB theory.

Introduction

The Dynamic Energy Budget (DEB) theory for metabolic organization has all the essential components to deal with energy and mass balances, including stoichiometry (Kooijman, 2010; Sousa et al., 2008). However, DEB models use state variables that cannot directly be measured, such as 'reserves' and 'structure' both contributing to body mass. Similarly, many biological quantities that are relatively easy to measure have contributions from different basic processes. Respiration rate, as measured by oxygen consumption, for example, does not represent maintenance costs only, but also overhead costs of growth and reproduction. In addition, most DEB parameters, such as the fraction of energy spent on growth and maintenance (κ), the maintenance rate per unit of volume ($[p_M]$), or the maximum energy density ($[E_m]$), cannot be measured directly. This implies that parameter estimation procedures are by necessity complex.

For bivalves, van Haren and Kooijman (1993) presented first estimates of DEB parameters. Data from the literature were used to estimate several parameters, but rather different values were obtained from various data sets. This was attributed to differences in experimental methods, temperature assumptions, salinities, water depths and food conditions and, to some extent, genetic variation (van Haren and Kooijman, 1993). After that, van der Veer et al. (2006) developed a protocol to estimate a complete set of DEB parameters for various bivalve species. The authors advocated the use of data from factorially designed experiments. But such data sets were, and still are, lacking and several compromises had to be made. For example, to estimate the shape coefficient parameter (δ_M , relation between physical and structural length), data on physical length vs. weight was used, thus disregarding the contribution of reserves to the total biomass. Rosland et al. (2009) tried to overcome this problem by estimating this parameter using data from starved organisms, assuming that their body mass would be only structure, but they were confronted with another problem, which is that their set of parameter estimates resulted in physiological inconsistencies. A particularly important quantity is the yield of reserves on structure (y_{VE}), a measure of the growth efficiency, which is the number of C-moles of structure built with 1 C-mol of reserves. A value higher than 1 for this quantity is impossible due to mass conservation. The parameter set previously obtained by Rosland et al. (2009) and van der Veer et al. (2006) resulted in a y_{VE} value higher than one. Thus, the parameter estimation method should be updated in order to avoid such inconsistencies. As suggested by van der Meer (2006), the standard procedure for parameter estimation should combine all available data sets and estimate parameters by means of simultaneous regression. The author presents an exercise using this approach, where part of the estimation procedure of van Haren and Kooijman (1993) was repeated using two statistical approaches (simultaneous regression by means of weighted non-linear regression, and repeated measurements or time-series regressions). The underlying idea was that if two or more functions contain common parameters it is possible to arrive at a single parameter set estimate using a weighted least-squares algorithm. This procedure may at the same time result in lower standard errors of the parameters. Kooijman et al. (2008) pro-

vided further guidance by structuring the estimation of parameters in 10 steps with a minimum set of data and the use of the regression routines included in the software package DEBtool (<http://www.bio.vu.nl/thb/deb/>). These routines used several generic algorithms to obtain the best fit, from slow algorithms with a large domain of attraction (genetic algorithms, Nelder-Mead method), to fast algorithms with a small domain of attraction (Newton-Raphson method). Finally, the contribution by Lika et al. (2011), in this special issue, provides a method based on the simultaneous minimization of the weighted sum of squared deviations between data sets and model predictions in one single-step procedure, including physiological constraints on the estimated parameter set (covariation method). The intended physiological consistency, apart from optimizing the goodness of fit for all available data, can be obtained using the concept of sloppy constraints, where 'pseudo-observations' are fitted for particular parameters, simultaneously with real observations (Kooijman et al., 2008). By choosing the weight coefficients in the regression procedure that minimize the weighted sum of squared deviations, the observations can be obtained (high weight coefficient for observations) without high deviation of the standard parameters (slightly lower weight coefficient). This study presents the implementation of this approach to estimate DEB parameters for *Mytilus edulis*, using several collections of literature data. The results are compared with previous attempts from van der Veer et al. (2006) and Rosland et al. (2009).

Material and methods

Covariation method

The covariation method for the parameters estimation is based on a collection of observations (single data points and/or time series) and a set of pseudo-data (used to restrict the possible parameter combinations, see below). The general idea behind the covariation method is to let all available information compete, or interact, to produce the end result, implying the estimation of all parameters from all data sets simultaneously (Lika et al., 2011). Thus, all the parameters values are estimated in one single step for all the available data, by minimizing the weighted sum of squared deviations between data and model predictions:

$$E_r = \sqrt{\frac{1}{n} \sum_{i=1}^n \beta_i \left(\frac{Y_i - \hat{Y}_i}{Y_i} \right)^2}$$

where n is the total number of data points (real and 'pseudo-data'), β_i the weight coefficient and Y_i and \hat{Y}_i are the observations and the model predictions respectively.

The concept of 'pseudo-data' is used to avoid an unrealistic combination of parameters and to maintain the rules for the covariation of parameter values implied by the physical laws, on

which DEB theory is built. 'Pseudo-data' is in fact a set of values of primary or compound parameters for a generalized animal obtained from a large collection of estimated parameters from various data sets for a wide variety of species (Kooijman, 2010). Estimates should not result in large deviations from these values, since animals share most metabolic properties and machinery (Kooijman, 2010; Lika et al., 2011). Different weight coefficients are associated to both the true observations and the pseudo-data: a high weight coefficient implies high confidence in the data and/or pseudo-data. Pseudo-data typically get lower weight coefficients relative to real data. Among real data, the weight coefficients mainly aim to reflect the certainty of the used data.

The comparison between the different parameter sets (van der Veer et al. (2006), Rosland et al. (2009) and this study) is made by an overall error (E) and a goodness-of-fit mark computed as

$$E = \sqrt{\frac{\sum_{i=1}^n \beta_i \left(\frac{Y_i - \hat{Y}_i}{Y_i} \right)^2}{\sum_{i=1}^n \beta_i}}$$

$$\text{Goodness-of-fit} = 10 \times (1 - E)$$

where n is the number of data points, β_i the weight coefficient and Y_i and \hat{Y}_i are the observations and the model predictions respectively. The inclusion of the weight coefficients in the computation of the overall data will reflect the uncertainty of the data in line with the assumptions made in the estimation procedure. An overall error of 0 (goodness-of-fit mark of 10) represents a perfect model prediction and a high value (low goodness-of-fit mark) represents high discrepancies between model and observations.

Observations

Several observations (zero and uni-variate data) were used in the estimation procedure. Zero-variate data (single data points) include general physical characteristics (a , age; L length and W_W wet weight) on particular stages of *M. edulis* development: i) birth, the moment when they are able to feed; ii) puberty, the moment when they are able to reproduce and iii) adult stage; and also information about the maximum gonado-somatic index (gonadal mass fraction relative to other tissue) found in field. The uni-variate data include: (i) detailed feeding observations on total pseudofaeces production (Widdows et al., 1979; Prins et al., 1991), ingestion rate (Kiørboe et al., 1980; Prins et al., 1991) and algae faeces contribution (Kiørboe et al., 1980; Prins et al., 1991) for different total particulate matter concentrations (TPM) in the water; (ii) field observations on length versus age (Rodhouse et al., 1984) and on wet weight versus length (Borchardt, 1985; Pieters et al., 1979) presented by van Haren and Kooijman (1993); (iii) oxy-

gen consumption rate at different length from experiments where food level was kept constant (Kruger, 1960); (iv) growth rate during starvation (Strömngren and Cary, 1984) and (v) oxygen consumption at different ingestion rates, for two different length groups (Bayne et al., 1987, 1989).

Table 3.1 lists the data and their relative weights used in the parameter estimation. The relative weight coefficients were arbitrary assigned for each observation although following a logical reasoning. Relatively more weight is given to information on ultimate length and weight because it is considered reliable and it is crucial for estimating the feeding parameters, $[\dot{p}_M]$ and κ . Information on the growth versus age also has a high relative weight, because it is important that the model captures the observed main pattern of the organism growth. The weight coefficient of the pseudo-data is set relatively low mainly because their function is to avoid unrealistic parameter combination without forcing too much the estimation. An exception is made for the growth efficiency, κ_G , because it is mandatory that this quantity is lower than 1.

Model Description

To predict observations presented as *Data01* to *Data05*, the standard DEB model was coupled with a detailed model for feeding processes, as suggested by Saraiva et al. (2011). Total assimilation rate is now related to both food quantity (concentration) and quality (composition). Filtration, ingestion and assimilation are three different processes, using the concept of synthesizing units to describe mathematically the fluxes between these processes.

The use of a food density parameter (f) and the maximum specific assimilation rate parameter ($\{\dot{p}_{Am}\}$) as used in the standard DEB model, is no longer needed. $\{\dot{p}_{Am}\}$ is derived from some additional parameters, also estimated in this study. Data sets *Data06* to *Data13* lacked detailed information on feeding conditions. In these cases the standard DEB model was applied using the extra parameter food density, f (ranging from 0, a situation without food, to 1, a situation with optimal conditions). Formulations and specific assumptions used in this study are listed in Table 3.2. Parameters and conversion factors are listed in Table 3.3. Due to the lack of data on the length of birth and puberty at different food levels, the maturity maintenance rate coefficient (\dot{k}_J) is assumed equal to the somatic maintenance rate coefficient (\dot{k}_M), with the implication that these lengths do not depend on food level. In order to compare model predictions and observations, several additional assumptions were made concerning the environmental conditions, including the f parameter estimates (when needed), and/or initial conditions of the organisms in the beginning of the experiment, also listed in Table 3.2. More details about the feeding processes model extension and the standard DEB model and assumptions can be found in Saraiva et al. (2011) and Kooijman (2010).

Table 3.1. Data used in parameter estimation procedure and the weight coefficient β_i . The generalized animal parameters refer to $T=20^\circ\text{C}$.

type	symbol	description	value/specific conditions	dimensions	β value	references
Zero-variate	a_b	age at birth (18°C)	0.2	d	10^2	Newell (1989)
	a_s	age at first spawning	365	d	10^2	Newell (1989)
	a_m	life span	24×365	d	10^4	Sukhotin et al. (2007)
	L_b	length at birth (18°C)	0.009	cm	10^2	Newell (1989)
	L_p	length at puberty	1.2	cm	10^2	van der Veer et al. (2006)
	L_i	maximum length observed	15	cm	10^4	van der Veer et al. (2006)
	W_W	wet weight at birth	$0.037L_b^3$	g_{WW}	10^2	van Haren and Kooijman (1993)
	W_W^p	wet weight at puberty	$0.037L_p^3$	g_{WW}	10^2	van Haren and Kooijman (1993)
	W_W^i	ultimate wet weight	$0.037L_i^3$	g_{WW}	10^4	van Haren and Kooijman (1993)
	GSI	gonado-somatic index	0.2	molmol^{-1}	10^2	Cardoso et al. (2007)
	\dot{v}	energy conductance	0.02	cm	10^{-1}	
	κ	allocation fraction	0.8	adim	10^{-1}	
Generalized animal parameters	$[p_M]$	volume specific somatic maintenance	18	$\text{Jd}^{-1}\text{cm}^{-3}$	10^{-1}	Kooijman (2010)
	κ_G	growth efficiency	0.8	adim	10^2	
	Data01	TPM vs. pseudofaeces production rate	7 cm, $T=15^\circ\text{C}$	mg_{dw}^{-1} vs. $\text{mg}_{dw}\text{h}^{-1}$	10^2	Widdows et al. (1979)
	Data02	TPM vs. ingestion rate	3.7 cm, $T=15^\circ\text{C}$	mg_{dw}^{-1} vs. $\text{mg}_{dw}\text{h}^{-1}$	10^3	Kjørboe et al. (1980)
	Data03	TPM vs. pseudofaeces production rate	6 cm, $T=6.5^\circ\text{C}$	mg_{dw}^{-1} vs. $\text{mg}_{dw}\text{h}^{-1}$	10^2	Prins et al. (1991)
	Data04	TPM vs. ingestion rate		mg_{dw}^{-1} vs. $\mu\text{gChl}ah^{-1}$	10^2	
	Data05	TPM vs. algae faeces contribution		mg_{dw}^{-1} vs. $\mu\text{gChl}ah^{-1}$	10^2	
	Data06/07/08	time vs. shell length	0, 13 and 33 % of aerial exposure	y vs. mm	10^2	Rodhouse et al. (1984)
	Data09	shell length vs. oxygen consumption	$T=15^\circ\text{C}$	cm vs. $\text{cm}^3\text{O}_2\text{h}^{-1}$	10^2	Kruger (1960)
	Data10	shell length vs. wet weight	field observations	cm vs. g	10	Borchardt (1985); Pieters et al. (1979)
	Data11	time vs. growth	starvation, $T=21.8^\circ\text{C}$, $L=1.7$ cm	d vs. mmd^{-1}	10	Strongren and Cary (1984)
	Data12/13	ingestion vs. oxygen consumption	$T=15^\circ\text{C}$, $L=2.5$ and 4.5 cm	mgPOMh^{-1} vs. $\text{cm}^3\text{O}_2\text{h}^{-1}$	10	Bayne et al. (1987, 1989)

Table 3.2. Model formulations and main assumptions used to estimate parameters and compute data found in literature. Equations and sections refer to Kooijman (2010). Parameters description and dimensions can be found in Table 3.3.

type	data	model formulations	model main assumptions
Zero-variate (step 1)	a_b	eq. 2.39	
	a_p	eq. 2.53	
	a_m	section 6.1.1	
	L_b	eq. 2.46	
	L_p	eq. 2.54	
	L_i	$L_i = fL_m$	$f = 1$
		$L_m = \frac{\dot{v}}{k_M g}$	$k(T) = k_1 e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)}$
		$k_M = \frac{[P_M]}{[E_G]}$	$k_J = k_M$
		$g = \frac{[E_G]}{\kappa [E_m]}$	
		$[E_m] = \frac{\{P_{Am}\}}{\dot{v}}$	
Uni-variate	$\frac{W_W^b}{W_W^p}, \frac{W_W^i}{W_W^p}$	$W_W = V \left(1 + \frac{f[E_m]w_E}{\mu_E d_V}\right)$	
	GSI	eq. 4.89	$f = 0.8, T=12^\circ\text{C}$
	Data01	$\dot{J}_{PI} = \sum_i^n (\dot{J}_{X_i F} - \dot{J}_{X_i I})$ $\dot{J}_{X_i I} = \frac{\rho_{X_i I} \dot{J}_{X_i F}}{1 + \sum_i^n \frac{\rho_{X_i I} \dot{J}_{X_i F}}{\{J_{X_i Im}\}}}$ $\dot{J}_{X_i F} = \dot{C}_R X_i$ $\dot{C}_R = \frac{\{\dot{C}_{Rm}\}}{1 + \sum_i^n \frac{X_i \{\dot{C}_{Rm}\}}{\{J_{X_i Fm}\}}} V^{2/3}$	$i = 1$, inorganic material $i = 0$, algae X_i particle concentration
	Data02	$\sum_i^n \dot{J}_{X_i I}$	$\rho_{X_1 I} = \rho_{X_0 I}$
	Data03	\dot{J}_{PI} , similar to Data01	assumptions described in Saraiva et al. (2011)
	Data04	$\sum \dot{J}_{X_i I}$, similar to Data02	
	Data05	$\dot{J}_{PA} = \sum_i^n (\dot{J}_{X_i I} - \dot{J}_{E_i A})$	
	Data06/07/08	$\frac{d}{dt} l = \dot{k}_M \frac{g}{3} \frac{e-l}{e+g}$ $\frac{d}{dt} e = \frac{(f-e)g \dot{k}_M}{l}$	$f_{initial} = 1$ (assumed), $T=12^\circ\text{C}$ $f = 0.60$, 0% aerial exposure (estimated) $f = 0.52$, 13% aerial exposure $f = 0.40$, 33% aerial exposure
	Data09	$p_D = \kappa l^3 + (1 - \kappa) e l^2 \frac{g+l}{g+e}$ $p_G = \kappa l^2 \frac{e-l}{1+\frac{e}{g}}$ J_O , oxygen mass balance	$e = f = 1$, aclimated organisms (estimated)
	Data10	$W_W = V \left(1 + \frac{f[E_m]w_E}{\mu_E d_V}\right)$	$e = f = 1$, aclimated organisms (estimated)
	Data11	$U_{E_{initial}} = \frac{L_v^3}{\dot{v}} f_{initial}$ $\frac{d}{dt} l, \frac{d}{dt} e$	$f_{initial} = 0.25$ (estimated) $f = 0$, starvation
	Data12/13	$f = J_X \frac{y_{EX}}{\{J_{EAm}\} L^2}$ $\frac{d}{dt} l, p_D, p_G, J_O$ similar to Data09	$e = f$, aclimated organisms $y_{1EX} = 0.13$, 2.5 cm (estimated) $y_{2EX} = 0.53$, 4.5 cm (estimated)

Table 3.3. DEB parameters for *Mytilus edulis* and other parameters and conversion factors at the reference temperature of $T=20^\circ\text{C}$. (dw) represents dry weight and (sd) represents the standard deviation of the estimated parameters.

symbol	description	units	value (sd)	references
\dot{v}	energy conductance	cm d^{-1}	0.056 (0.0077) 0.094 0.067	this study Rosland et al. (2009) van der Veer et al. (2006)
κ	allocation fraction to growth and somatic maintenance	-	0.67 (0.13) 0.45 0.7	this study Rosland et al. (2009) van der Veer et al. (2006)
$[\dot{p}_M]$	volume specific somatic maintenance	$\text{J d}^{-1} \text{cm}^{-3}$	11.6 (3.52) 27.8 24	this study Rosland et al. (2009) van der Veer et al. (2006)
$[E_G]$	specific cost for structure	J cm^{-3}	5993 (1744) 1900 1900	this study Rosland et al. (2009) van der Veer et al. (2006)
δ_M	shape coefficient	-	0.297 (0.0058) 0.231 0.287	this study Rosland et al. (2009) van der Veer et al. (2006)
$\rho_{X_1 I}$	algae binding probability	-	0.37 (0.06) 0.99	this study Saraiva et al. (2011)
$\rho_{X_0 I}$	inorganic material binding probability	-	0.37 (0.06) 0.45	this study Saraiva et al. (2011)
$\dot{J}_{X_1 I m}$	algae maximum ingestion rate	mol C d^{-1}	1.3×10^4 (7×10^{10})	this study
$\dot{J}_{X_0 I m}$	inorganic material maximum ingestion rate	mol C d^{-1} g d^{-1}	0.65×10^4 0.11 (0.078) 0.23	Saraiva et al. (2011) this study Saraiva et al. (2011)
E_{Hb}	maturity at birth	J	2.95×10^{-5} (1.4×10^{-4})	this study
E_{Hp}	maturity at puberty	J	1.58×10^2 (2.5×10^2)	this study
\hat{h}_a	Weibull aging acceleration	d^{-1}	5.23×10^{-10} (2.23×10^{-9})	this study
$\{\dot{C}_{Rm}\}$	maximum surface area-specific clearance rate	$\text{m}^3 \text{d}^{-1} \text{cm}^{-2}$	0.096	Saraiva et al. (2011)
$\{\dot{J}_{X_1 Fm}\}$	algae maximum surface area-specific filtration rate	$\text{mol C d}^{-1} \text{cm}^{-2}$	4.8×10^{-4}	Thomas et al. (2011)
$\{\dot{J}_{X_0 Fm}\}$	inorganic material maximum surface area-specific filtration rate	$\text{g d}^{-1} \text{cm}^{-2}$	3.5	Saraiva et al. (2011)
s_G	Gompertz stress coefficient	-	0.0001	Kooijman (2010)
κ_R	reproduction efficiency	-	0.95	Kooijman (2010)
T_{ref}	reference temperature	K	293	this study
T_A	Arrhenius temperature	K	7022	van der Veer et al. (2006)
$d_V = d_E$	structure and reserves specific density	$\text{g}_{(dw)} \text{cm}^{-3}$	0.2	Rosland et al. (2009); Brey (2001)
$w_E = w_V$	reserves and structure relative molecular mass	$\text{g}_{(dw)} \text{mol}^{-1}$	25.22	$C_1 H_{1.8} O_{0.53}$ Kooijman (2010) $N_{0.21}$ Smaal and Vonck (1997)
μ_E	reserves chemical potential	J mol^{-1}	697000	van der Veer et al. (2006)
V_{mol}	oxygen molar volume	J mol^{-1}	22.4	CODATA
$\psi_{dw/C}$	algae dry weight to carbon conversion factor	$\text{mg}_{(dw)} \text{mg}_C^{-1}$	2.5	Slobodkin and Richman (1961)

Results

The parameters estimates obtained in this and previous studies are presented in Table 3.3. To enable a better evaluation of the results, the observations were predicted using the three different DEB parameter sets: van der Veer et al. (2006), Rosland et al. (2009) and this study. Besides, two ingestion parameter sets are used: Saraiva et al. (2011) and this study (Table 3.4 for the zero-variate data and Figures 3.1 to 3.4 for the uni-variate data). Additionally, Table 3.5 presents some quantities useful to verify the consistency and realism of the parameters combination and species comparison. It should be noted that additional information was often needed to perform a model simulation, mainly concerning the conditions of the organisms in the beginning of the experiments, the food availability and also the parameters defining the maturity level at birth and puberty (controlling the transition stages) and the Weibull aging acceleration (which controls the life span of the organism). In this study these additional parameters were included in the estimation procedure. Because the parameter sets found in literature do not include these quantities, they were separately estimated while keeping the main parameters fixed.

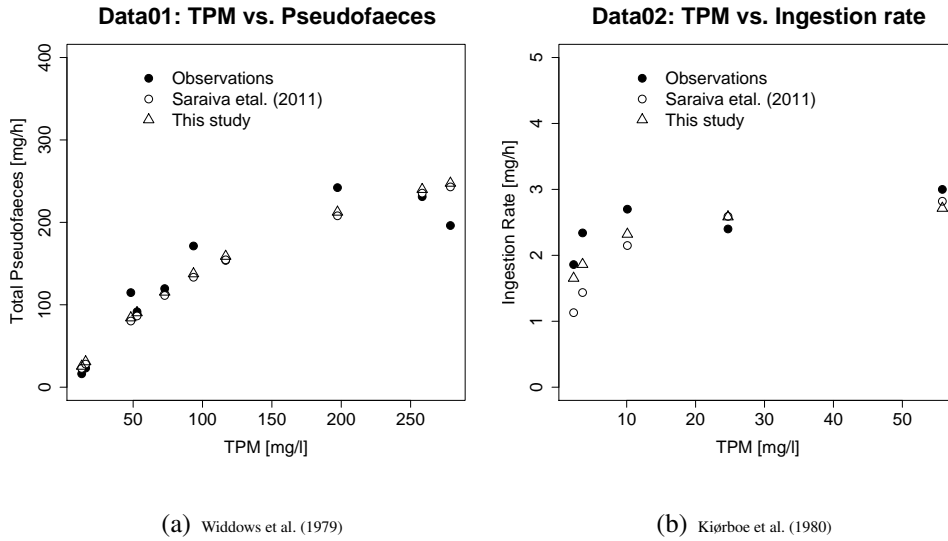


Fig. 3.1. Observations vs. Model Predictions: pseudofaeces production from Widdows et al. (1979) and ingestion rate from Kjørboe et al. (1980). Simulations were performed using two different parameters set: (i) Saraiva et al. (2011) and (ii) this study.

The volume specific somatic maintenance, $[\dot{p}_M]$ and also the maximum specific assimilation rate, $\{\dot{p}_{Am}\}$ (a parameter in the standard DEB model but in this study a quantity computed by the feeding processes model, Table 3.5) obtained in this study are much lower than in the other studies. This means that the organism is not able to obtain so much food as previously thought, but it also spends less energy on somatic maintenance. On the other hand, the obtained specific cost for structure, $[E_G]$, is much higher and closer to 4600 Jcm^{-3} , which is the estimated energy content of bivalve structure assuming $23 \text{ kJ/g}_{(AFDW)}$ (van der Veer et al., 2006),

$0.2g_{(AFDW)}/g_{(WW)}$ (Rosland et al., 2009; Brey, 2001) and $1gcm^{-3}$. The total overhead costs for growth represents then about 20 %, which is a plausible value. The estimates for the energy conductance, ψ , are close between studies. The allocation fraction to growth and somatic maintenance, κ , obtained here ($\kappa=0.67$) is very close to the value obtained by van der Veer et al. (2006) ($\kappa=0.7$) and higher than obtained by Rosland et al. (2009) ($\kappa=0.45$). Those differences imply differences on the reproduction strategy of the organism: a higher value of κ represents higher investment on growth and lower gonado-somatic index as a direct consequence. In Table 3.4 besides the overall error and the goodness-of-fit mark, the relative error by data type is presented, computed as $E_r = \sum \left| \frac{Y_i - \hat{Y}_i}{Y_i} \right|$. As expected, lower relative errors, E_r , are obtained for the data with higher weight coefficients: life span, a_m and ultimate length and weight (L_i and W_W^i). High values are found for the weight of birth, W_b , and age at puberty a_p , for all the data sets. W_b is very difficult to measure and a_p is a very rough estimate. Although it is commonly assumed that bivalves can spawn one year after birth, not much information is available for the exact moment of puberty. Overall, predictions from this study imply much lower E_r for most data used compared with previous estimates. a_m , L_i and *Data10* are exceptions but the differences are not significant. Figure 3.2 and Figure 3.1 concern the detailed feeding processes using Saraiva et al. (2011) and parameters from this study. Both predictions approximate the observations, with a slightly better result from previous estimations. Yet, decrease in goodness of fit for these particular data sets are balanced with a better goodness of fit for the other data sets.

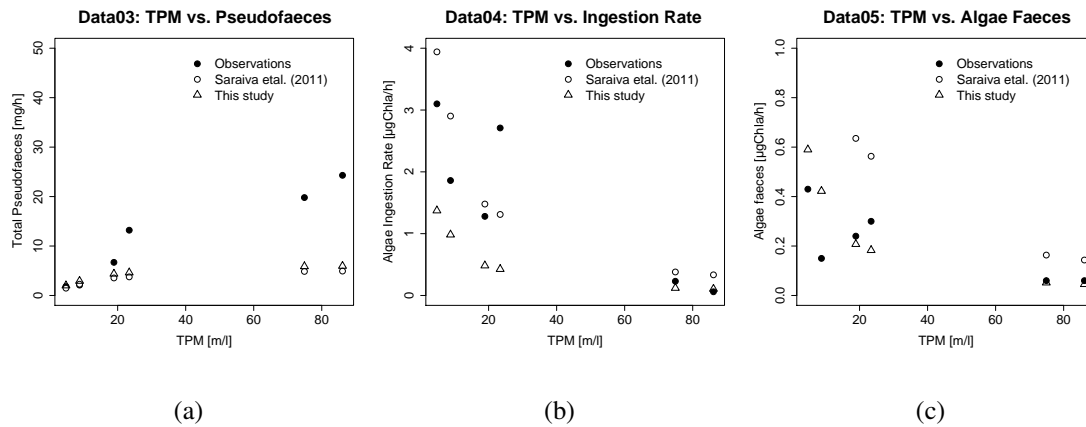


Fig. 3.2. Observations vs. Model Predictions: pseudofaeces production, ingestion rate and algae faeces production from Prins et al. (1991). Simulations were performed using two different parameters set: (i) Saraiva et al. (2011) and (ii) this study.

The newly estimated parameter set yielded much better fits for the uni-variate data (Figure 3.3 and Figure 3.4), with the oxygen consumption rates as an exception. The oxygen consumption rate depends very much on the biochemical composition of the organic compounds (mussel structure and reserves, food and faeces), which can be different from the values assumed in this study due to lack of data. The overall error, E , obtained in this study is much lower than before and the obtained goodness-of-fit mark is very close to 10.

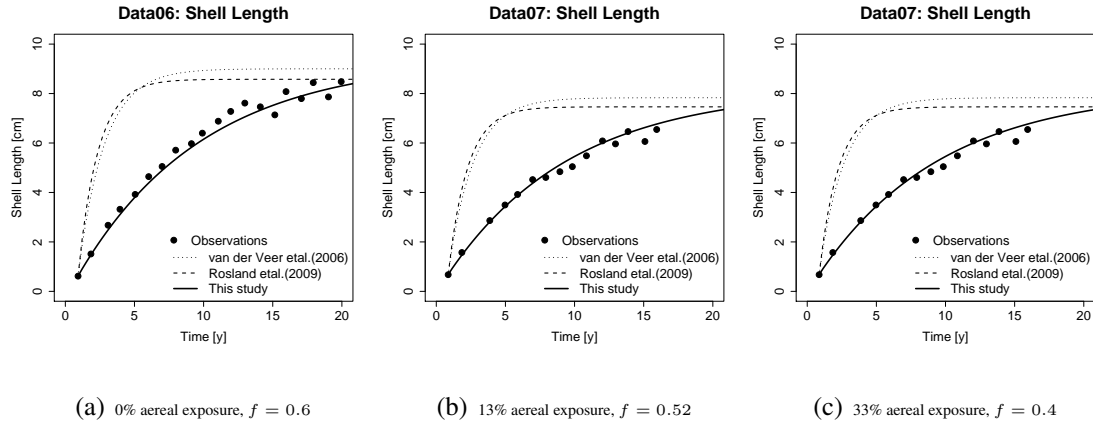


Fig. 3.3. Observations vs. Model Predictions: shell length over time from Rodhouse et al. (1984). Simulations were performed using three different parameters set: (i) van der Veer et al. (2006); (ii) Rosland et al. (2009) and (iii) this study.

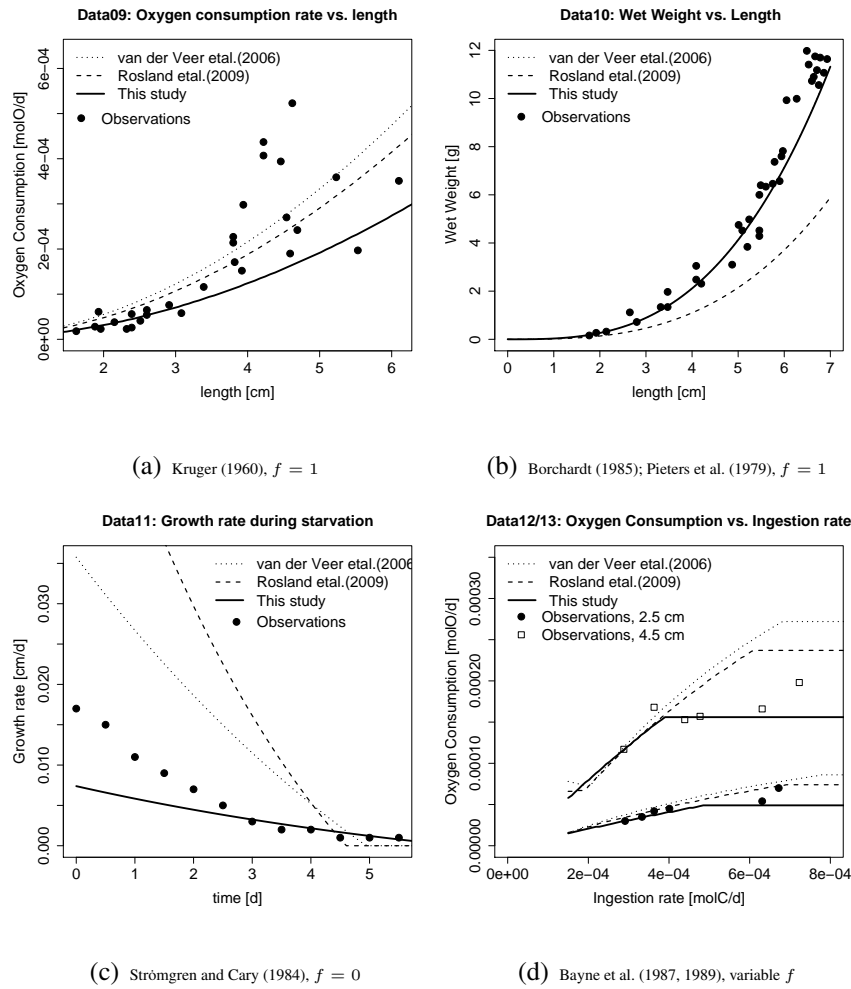


Fig. 3.4. Observations vs. Model Predictions: several authors. Simulations were performed using three different parameters set: (i) van der Veer et al. (2006); (ii) Rosland et al. (2009) and (iii) this study.

Table 3.4., Model predictions by data type for each parameter set: overall error and goodness-of-fit mark. $E_r = \frac{\sum_i^n \left(\frac{Y_i - \hat{Y}_i}{Y_i} \right)}{n}$.

		van der Veer et al. (2006)	Rosland et al. (2009)		Saraiva et al. (2011)		This study	
zero-variate data	value	prediction	E_r	prediction	E_r	prediction	E_r	prediction
a_b	0.2	0.48	1.40	0.39	0.93	0.23	0.23	0.13
a_p	365	17.26	0.95	34.5	0.97	151.3	-	0.58
a_{rn}	8760	8078	0.078	8760	0.0011	8777	-	0.003
L_b	0.009	0.026	1.89	0.034	2.79	0.0073	-	0.200
L_p	1.2	0.61	0.49	1.53	0.55	1.27	-	0.057
L_i	15	15	0	14.3	0.047	15.7	-	0.043
W_b^a	2.7×10^{-8}	5.88×10^{-7}	20.83	6.89×10^{-7}	24.40	1.26×10^{-8}	-	0.53
W_b^y	0.064	0.0077	0.88	0.062	0.96	0.067	-	0.057
W_w^y	124.6	111.6	0.10	50.1	0.60	126.6	-	0.016
W_w^y	0.2	0.33	0.64	1.09	4.44	0.20	-	0.0043
uni-variate data								
Data01		-	-	-	0.32	-	0.32	0.46
Data02		-	-	-	0.26	-	0.26	0.13
Data03		-	-	-	0.16	-	0.16	0.24
Data04		-	-	-	4.3	-	4.3	0.74
Data05		-	-	-	1.96	-	1.96	0.31
Data06		0.32	0.36	0.36	-	-	-	0.012
Data07		0.32	0.34	0.34	-	-	-	0.014
Data08		0.53	0.56	0.56	-	-	-	0.014
Data09		0.034	0.026	0.026	-	-	-	0.011
Data10		0.12	0.45	0.45	-	-	-	0.12
Data11		2.19	3.85	3.85	-	-	-	0.34
Data12		0.0085	0.0047	0.0047	-	-	-	0.0032
Data13		0.036	0.027	0.027	-	-	-	0.0094
Overall E		0.01	0.02	0.005	0.005	0.001	0.001	0.001
Goodness-of-fit		9.92	9.831	9.94	9.94	9.99	9.99	9.99

Table 3.5. Other quantities computed by the model (at T=20 °C).

symbol	description	units	van der Veer et al. (2006)	Rosland et al. (2009)	this study
M_E^0	initial reserve mass at optimal food conditions	mol	2.97×10^{-9}	4.50×10^{-9}	1.49×10^{-10}
W^0	initial weight at optimal food conditions	g	7.48×10^{-8}	1.14×10^{-7}	3.75×10^{-9}
$U_E b / U_{E0}$	fraction of reserve left at birth	-	0.45	0.34	0.14
M_V^b	structural mass at birth	mol	3.33×10^{-9}	3.89×10^{-9}	7.92×10^{-11}
W^b / W_m	birth weight as fraction of maximum	-	5.23×10^{-9}	1.36×10^{-8}	9.94×10^{-11}
M_V^p	structural mass at puberty	mol	4.36×10^{-5}	3.5×10^{-4}	4.24×10^{-4}
W^p / W_m	puberty weight as fraction of maximum	-	6.89×10^{-5}	1.24×10^{-3}	5.32×10^{-4}
M_V^i	ultimate structural mass	mol	0.63	0.28	0.80
del_V	fraction of weight that is structure	-	0.72	0.72	0.79
f_{Gb}	f for growth ceasing at birth	-	1.74×10^{-3}	2.39×10^{-3}	4.63×10^{-4}
f_{Jb}	f for maturation ceasing at birth	-	1.74×10^{-3}	2.39×10^{-3}	4.63×10^{-4}
f_{Jp}	f for maturation and growth ceasing at puberty	-	0.041	0.11	0.081
$[E_m] / [p_M]$	maximum survival time when starved	d	91.2	78.1	124
z	zoom factor relative to reference $L_m = 1cm$	-	4.30	3.30	4.65
$\{\dot{p}_{Am}\}$	maximum specific assimilation rate	$Jd^{-1}cm^{-2}$	147.6	204	80.5
$\{\dot{J}_{EA_m}\}$	maximum surface-specific assimilation rate	$mold^{-1}cm^{-2}$	2.11×10^{-4}	2.93×10^{-4}	1.15×10^{-4}
t_E	maximum reserve residence time	d	64.2	35.1	83.03
$[E_m]$	reserve capacity	Jcm^{-3}	2203	2170	1438
\dot{k}_M	somatic maintenance rate coefficient at T	d^{-1}	0.0126	0.0146	0.0019
\dot{k}_J	maturity maintenance rate coefficient at T	d^{-1}	0.0126	0.0146	0.0019
k	maintenance ratio	-	1	1	1
$[J_{EM}]$	volume-specific somatic maintenance costs	$mold^{-1}cm^{-3}$	3.44×10^{-5}	3.99×10^{-5}	1.66×10^{-5}
RQ	respiration quotient at maximum length	$molCmolO^{-1}$	0.97	0.97	0.97
UQ	urination quotient at maximum length	$molNmolO^{-1}$	0.20	0.20	0.20
WQ^i	watering quotient at maximum length	$molHmolO^{-1}$	0.57	0.57	0.57
\dot{J}_O	dioxygen use per gram at maximum length	$lg^{-1}h^{-1}$	1.21×10^{-4}	1.46×10^{-4}	6.49×10^{-5}
GSI	Gonado-somatic index at optimal food	$molmol^{-1}$	0.49	1.6	0.30
R_m	ultimate reproduction rate	d^{-1}	3.77×10^5	3.70×10^5	5.26×10^6
y_{VE}	yield of structure on reserve	$molmol^{-1}$	2.91	2.91	0.92
g	energy investment ratio	-	1.23	1.95	6.2
r_B	von Bertalanffy growth rate	d^{-1}	2.32×10^{-3}	3.22×10^{-3}	5.6×10^{-4}
$[M_V]$	volume-specific structural mass	$molcm^{-3}$	7.93×10^{-3}	7.93×10^{-3}	7.93×10^{-3}
$[E_V]$	volume-specific structural energy	Jcm^{-3}	5527	5527	5527
ψ_{EW}	energy density of whole body	Jg^{-1}	2.76×10^4	2.76×10^4	2.76×10^4

Discussion

The parameters related with the filtration process (maximum clearance rate, $\{\dot{C}_{Rm}\}$ and the maximum filtration rates, $\{\dot{J}_{X_1Fm}\}$) were estimated and validated by Saraiva et al. (2011) using several observations from several authors. Those parameter values were not further estimated in this study. In contrary, the ingestion parameters (binding probability, ρ_{X_1I} , and maximum ingestion rate \dot{J}_{X_1Im}) were not kept fixed because the previous estimates were less reliable due to lack of detailed data and other type of relevant data are now available.

The results indicate that the parameter set obtained using the covariation method is a considerable improvement compared to those obtained before, using ad-hoc procedures. However, the implementation of the method is not trivial and requires a consistent choice of the data to be used and a careful establishment of assumptions. The choice of different weight coefficients for the different data is an important step in the estimation procedure, not only to normalize the error to a dimensionless number, but also to account for the uncertainty and relative importance of the data. Though it should be admitted that there is subjectivity in the assignment of weight coefficients. Data available in the literature are not always suitable mainly because: i) information is lacking and too many assumptions have to be made to run the model and/or ii) the extended standard DEB model could still be too simple to cope with the observations. The use of the standard DEB model in the covariation method is not imperative. The model can be as complex as the user wants, but it is important to keep in mind that technical problems, namely on the convergence of the estimation method, increase with the complexity of the model and complex models require more detailed input data. In this study, the use of an additional parameter to quantify the food density, f , to predict some of the experiments/field measurements is an example of a model simplification, disregarding for instance the seasonal pattern of food density and quality. However, this parameter, when used, was estimated or adjusted for each data type and it is believed that this approximation is consistent with the type of data used in the procedure, particularly for the growth prediction at the scale of years. This study uses also observations directly linked with the feeding processes (particularly ingestion) in order to improve previous estimations of the respective parameters. The use of observations on oxygen consumption during starvation was avoided. In order to correctly simulate extreme starvation, the model would have to account with the possible utilization of the reproduction buffer contents (gametes) and the possible shrinking of the organism, which would imply more complexity and, even more important, more accurate information about the reproduction processes, which are in this study summarized by the gonado-somatic index observation. More information on the eggs production and/or energy content would improve the κ parameter estimation as well as the reproduction efficiency, k_R , assumed constant in this study.

Conclusion

The optimal parameter set for a model is the one that best predicts the observations but without losing physiological realism. The parameters estimation procedure implemented in this study - the covariation method - is based not only on minimization of the weighted sum of squared deviations for all data sets simultaneously, but also on the inclusion of physiological constraints by introducing the concept of pseudo-data. The parameter set obtained reveals not only more consistency and realism but also better predictions than previous estimates. For that reason, the use of the new parameter set should be used in future implementations of a DEB model on *M. edulis* energetics.

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4. Validation of a Dynamic Energy Budget (DEB) model for the blue mussel *Mytilus edulis*

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A model for bivalve growth was developed and the results were tested against field observations. The model is based on DEB theory and includes an extension of the standard DEB model to cope with changing food quantity and quality. At four different locations in the North Sea -Wadden Sea, Sean GasField(UK), Oyster grounds and North of Dogger bank (UK) -labeled mussels (*Mytilus edulis*) were kept under natural conditions. Shell length was measured for each mussel repeatedly during the experiment and dry weight was determined at the end of the experiment for some of the mussels. Temperature, salinity, chlorophyll concentration and Secchi-depth (at the Wadden Sea location) were measured next to the experiment sites. Model performance was evaluated by comparing predicted and measured shell length, dry weight and growth, at each location for each individual. The results show that the model was able to reproduce the main patterns of the observations, implying that the main metabolic processes at the individual level are well described.

Keywords: modelling, DEB theory, bivalves' growth, model validation, *Mytilus edulis*.

Introduction

Bivalves have been extensively studied and a wide range of modelling approaches were used to describe their ecology. Each of the existing models has been developed from a particular perspective and with a particular set of objectives, ranging from a simple filtration model, with feeding and excretion being the main processes, to more complex models, where filtration, particle rejection and selection, food absorption efficiency and reproduction are described as functions of environmental conditions. Most of these models describe nutrition and resource allocation as allometric relationships. The so-called net-production models assume that assimilated energy is immediately available for maintenance and that the remaining energy is available for growth, or stored as reserve (e.g. Bacher et al., 1991; Grant and Bacher, 1998; Scholten and Smaal, 1998; Ren and Ross, 2001). The Dynamic Energy Budget (DEB) theory, proposed by Kooijman (1986) and extensively discussed in Kooijman (2000, 2010), is based on a more mechanistic view and has already been successfully applied to model bivalve dynamics (e.g. Ross and Nisbet, 1990; van Haren and Kooijman, 1993; Bacher and Gangnery, 2006; Pouvreau et al., 2006; Troost et al., 2010).

The DEB theory is conceptually different from the net-production models approach, because it assumes that all assimilated energy is first stored as reserve (which does not require maintenance), subsequently the reserves is utilized to fuel other metabolic processes such as maintenance, growth, development and reproduction. In addition, DEB models do not use empirical allometric relationships but simply state that food uptake is proportional to surface area of the body, whereas maintenance scales mainly to structural body volume. One of the main advantages of a DEB model is that it is based on a generic theory meaning that the same model structure can be applied to different species, where only parameter values differ. Variability in growth and reproduction between individuals of the same species are assumed to be mainly be caused by differences in environmental conditions (temperature, food). Interspecific variability (between several species) is caused both by differences in parameters values as well as environmental conditions (Kooijman, 2000, 2010).

The present paper aims to test to what extent a generic model for an individual mussel is realistic enough to be used for population modelling in the future. The obtained model results are compared with real observations on the growth of the blue mussel, *Mytilus edulis*, at four different locations in the North Sea with one station in a coastal environment and three stations in the open sea (off shore).

Material and Methods

DEB Model

The standard DEB model, described in Kooijman (2010) was adapted and extended using the feeding processes model proposed by Saraiva et al. (2011a).

The basic assumptions of the DEB model are:

1. an organism is characterized by a structural body (individual structure biomass), reserve (biomass available for direct use), maturity level (amount of energy spent in the organism development) and a reproduction buffer (biomass allocated to future gametes production);
2. the chemical composition (C, H, O, N, and P assumed as the main elements) of reserve and structure are constant (strong homeostasis);
3. if food density is constant then the ratio between reserve and structure (reserve density) tends to a constant value (weak homeostasis);
4. the life cycle of the individual has three different life-stages: embryonic (no feeding, the embryo relies on stored energy supplies), juvenile (feeding starts but resources are not yet allocated to the reproduction buffer), and adult (organism is mature and able to reproduce);
5. the metabolic switching (from embryo to juvenile and juvenile to adult) is linked to maturity level;
6. κ -rule: a fixed fraction of mobilized reserve is used for somatic maintenance and growth (increase of structural mass), the rest for maturity maintenance and maturation (increase of maturity in embryos and juveniles) or reproduction (adults);
7. the reserve density at constant food density does not depend on the amount of structure (weak homeostasis);
8. somatic maintenance is proportional to the amount of structure and maturity maintenance proportional to the level of maturity.

In addition, for the specific case, the presented model also assumes:

1. the bivalve is an isomorph organism (its shape does not change during growth);
2. the conversion between the real and the structural length is made by a fixed dimensionless shape coefficient (δ_M);
3. the organism is able to use the reproduction buffer to cope with somatic maintenance costs (re-absorption of gametes) during starvation periods and if that is not enough, structure will be used;
4. the bivalve is able to reduce its maturity level in order to cope with maturity maintenance.

Figure 4.1 represents a scheme of the model and Tables 4.1 to 4.4 the main formulations and necessary parameters used in the model. A more detailed description of the model and its specific assumptions can be found in the following sections.

Table 4.1. Model state variables and forcing functions. See Tables 4.3, Tables 4.2 and Tables 4.4 for further variable descriptions.

symbol	description	units	formulation
M_V	Bivalve structure biomass	molC^V	$\frac{dM_V}{dt} = J_{VG}$
M_E	Bivalve reserve biomass	molC^E	$\frac{dM_E}{dt} = J_E = J_{EA} - J_{EC}$
M_H	Bivalve maturity investment	molC^E	$\frac{dM_H}{dt} = j_{ER}^M$
M_R	Bivalve reproduction buffer	molC^E	$\frac{dM_R}{dt} = j_{ER}^R$
T	Temperature	K	
X_0	Inorganic particles concentration	mg l^{-1}	
X_1	Algae concentration	molCl^{-1}	
$n_{X_1}^N$	Algae nitrogen/carbon ratio	$\text{molN mol}^{-1}\text{C}$	
$n_{X_1}^P$	Algae phosphorus/carbon ratio	$\text{molP mol}^{-1}\text{C}$	

Table 4.2. Model auxiliary compound parameters and other quantities. Tables 4.1, Tables 4.3 and Tables 4.4 for further variable descriptions

symbol	description	units	formulation
$V^{1/3}$	Volumetric length	cm	$V^{1/3} = \left(\frac{M_V}{[M_V]} \right)^{1/3}$
$[M_V]$	Volume specific structural mass	$\text{molC}^V \text{cm}^{-3}$	$[M_V] = \frac{dV}{w_V}$
$[E]$	Reserves density	$\text{molC}^E \text{cm}^{-3}$	$[E] = \frac{M_E}{V}$
M_H^b	Cumulative maturity spent until birth	molC^E	$M_H^b = \frac{E_{Hb}}{\mu_E}$
M_H^p	Cumulative maturity spent until puberty	molC^E	$M_H^p = \frac{E_{Hp}}{\mu_E}$
Y_{VE}	Yield coefficient of structures on reserves	$\text{molC}^V \text{mol}^{-1}\text{C}^E$	$Y_{VE} = \frac{[M_V] \mu_E}{[E_G]}$
\dot{k}_M	Somatic maintenance rate coefficient	d^{-1}	$\dot{k}_M = \frac{[p_M]}{[E_G]}$
\dot{k}_J	Volume specific maturity maintenance	d^{-1}	$\dot{k}_J = \dot{k}_M$
GSR	Gonado-somatic ratio	$\text{molC}^R \text{mol}^{-1}\text{C}$	$\text{GSR} = \frac{M_R}{M_V + M_E + M_R}$
L	Organism length	cm	$L = \frac{V^{1/3}}{\delta_M}$
DW	Organism total dry weight	$\text{g}(dw)$	$DW = M_V w_V + (M_E + M_R) w_E$

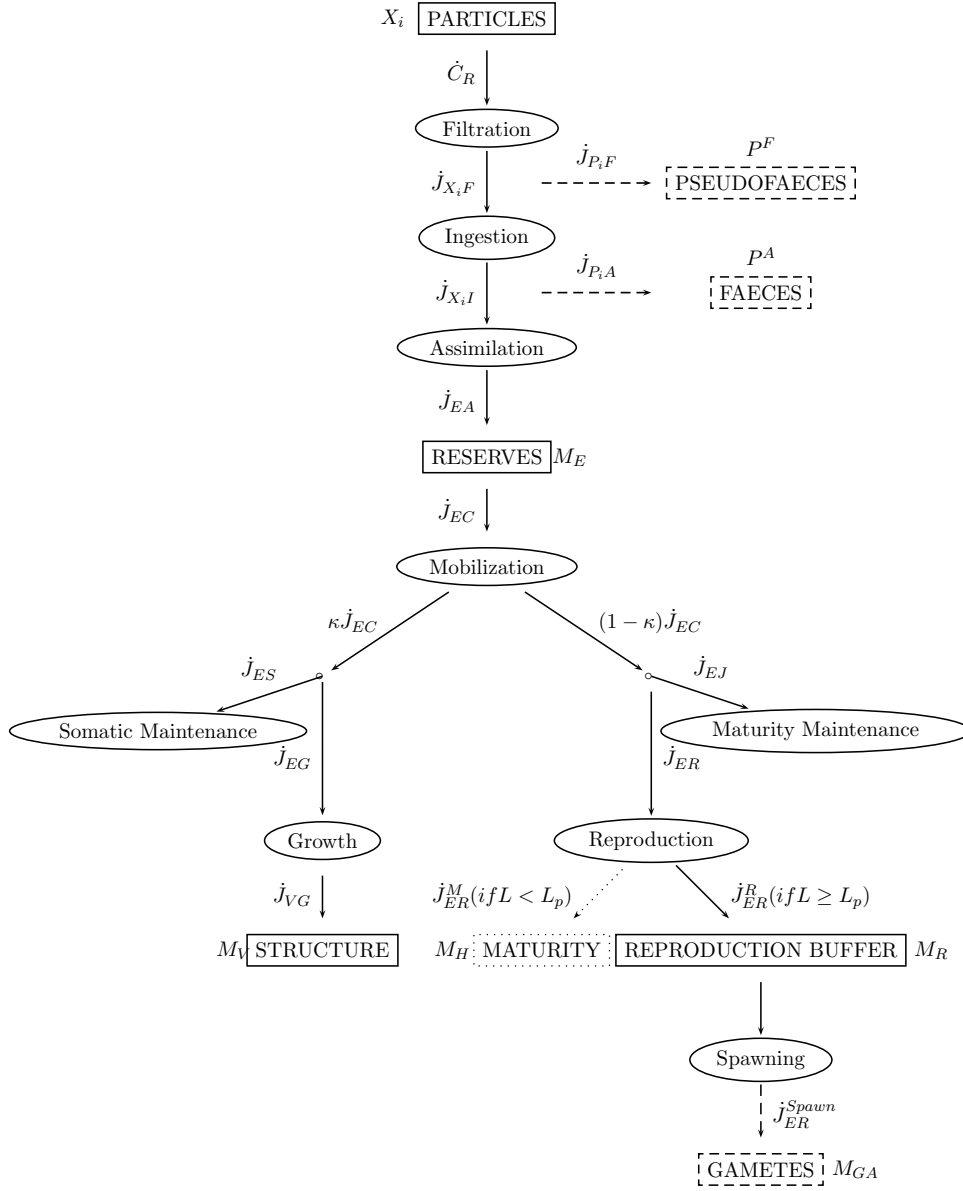


Fig. 4.1. Global Scheme for the DEB Model for bivalve. Ellipses represent the main processes involved in the organism metabolism and mass fluxes are indicated as \dot{j}_* . Boxes with solid lines represent the organism mass compartments and solid arrows the associated flux; dotted box represents energy investment and dotted arrow its inflow; dashed line box represents a mass compartment outside the organism and the dashed arrow represents the respective outflow from the organism.

Table 4.3. Model formulations: feeding process description adapted from Saraiva et al. (2011a) and standard DEB model adapted from Kooijman (2010). See Tables 4.1, Tables 4.2 and Tables 4.4 for further variable descriptions.

process	symbol	description	units	formulation
Filtration	\dot{C}_R	Clearance rate	$\text{m}^3 \text{d}^{-1}$	$\dot{C}_R = \frac{\{\dot{C}_{Rm}\}}{1 + \sum_{i=0}^n \frac{X_i \{\dot{C}_{Rm}\}}{\{J_{X_i F m}\}}} V^{2/3}$
	$\dot{J}_{X_i F}$	Filtration rate	$\text{molC d}^{-1} \text{g d}^{-1}$	$\dot{J}_{X_i F} = \dot{C}_R X_i$
Ingestion	$\dot{J}_{X_i I}$	Ingestion rate	$\text{molC d}^{-1} \text{g d}^{-1}$	$\dot{J}_{X_i I} = \frac{\rho_{X_i I} \dot{J}_{X_i F}}{1 + \sum_{i=1}^n \frac{\rho_{X_i I} \dot{J}_{X_i F}}{\{J_{X_i I m}\}}}$
	$\dot{J}_{P_i F}$	Pseudofaeces production rate	$\text{molC d}^{-1} \text{g d}^{-1}$	$\dot{J}_{P_i F} = \dot{J}_{X_i F} - \dot{J}_{X_i I}$
Assimilation	\dot{J}_{EA}	Assimilation rate	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{EA} = \dot{J}_{EAE} + \dot{J}_{EAV}$
	\dot{J}_{EAV}	Algae structure assimilation rate	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{EAV} = y_{EXV} \dot{J}_{X_1 I} (1 - f_E)$
	\dot{r}_C	-	$\text{molC}^E \text{d}^{-1}$	$\dot{r}_C = \dot{J}_{X_1 I} f_E$
	\dot{r}_N	-	$\text{molC}^E \text{d}^{-1}$	$\dot{r}_N = \dot{J}_{X_1 I} f_E \frac{n_{X_1}^N}{n_N^N}$
	\dot{r}_P	-	$\text{molC}^E \text{d}^{-1}$	$\dot{r}_P = \dot{J}_{X_1 I} f_E \frac{n_{X_1}^P}{n_P^P}$
	\dot{J}_{EAE}	Algae reserves assimilation rate	$\text{molC}^E \text{d}^{-1}$	
	$\dot{J}_{EAE} = \left(\frac{1}{\dot{r}_C} + \frac{1}{\dot{r}_N} + \frac{1}{\dot{r}_P} - \frac{1}{\dot{r}_C + \dot{r}_N} - \frac{1}{\dot{r}_C + \dot{r}_P} - \frac{1}{\dot{r}_N + \dot{r}_P} + \frac{1}{\dot{r}_C + \dot{r}_N + \dot{r}_P} \right)^{-1}$			
	$\dot{J}_{P_i I}$	Faeces production rate	molC d^{-1}	$\dot{J}_{P_i I} = \dot{J}_{X_i I} - \dot{J}_{EA}$
	\dot{J}_{EC}	Mobilization flux	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{EC} = \frac{[E]}{\frac{[EG]}{\mu_E} + \kappa[E]} \left(\frac{[EG]}{\mu_E} \dot{V}^{2/3} + \dot{J}_{ES} \right)$
Somatic Maintenance	\dot{J}_{ES}	somatic maintenance	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{ES} = \frac{[\dot{p}_M]}{\mu_E} V$
Growth	\dot{J}_{EG}	Flux allocated to growth	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{EG} = \kappa \dot{J}_{EC} - \dot{J}_{ES}$
	\dot{J}_{VG}	Growth	$\text{molC}^V \text{d}^{-1}$	$\dot{J}_{VG} = y_{VE} \dot{J}_{EG}$
Maturity and Reproduction	\dot{J}_{EJ}	Maturity maintenance	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{EJ} = k_J M_H$
	\dot{J}_{ER}	Flux allocated to reproduction/maturity	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{ER} = (1 - \kappa) \dot{J}_{EC} - \dot{J}_{EJ}$
	\dot{J}_{ER}^M	Flux to maturity	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{ER}^M = \begin{cases} \dot{J}_{ER}, & \text{if } M_H < M_H^P \\ 0, & \text{otherwise} \end{cases}$
	\dot{J}_{ER}^R	Flux to reproduction buffer	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{ER}^R = \begin{cases} 0, & \text{if } M_H < M_H^P \\ \dot{J}_{ER}, & \text{otherwise} \end{cases}$
Spawning	\dot{J}_{ER}^{spawn}	Spawning	$\text{molC}^E \text{d}^{-1}$	$\dot{J}_{ER}^{spawn} = \begin{cases} k_R M_R / R^{spawn}, & \text{if } GSR \geq GSR^{spawn} \wedge T \geq T^{spawn} \\ 0, & \text{otherwise} \end{cases}$
	N^{spawn}	Number of gametes released	$\# \text{d}^{-1}$	$N^{spawn} = \dot{J}_{ER}^{spawn} / M_E^0$
Inorganic Fluxes	\dot{J}_{NH_3}	Ammonia flux	molNd^{-1}	
	$\dot{J}_{NH_3} = -(-\dot{J}_{X_i F} n_{X_1}^N + \dot{J}_{P_i F} n_{X_1}^N + \dot{J}_{P_i I} n_{X_1}^N + \dot{J}_{VG} n_V^N + \dot{J}_E n_E^N + \dot{J}_{ER}^R n_E^N)$			
	\dot{J}_{PO_4}	Phosphate flux	molPd^{-1}	
	$\dot{J}_{PO_4} = -(-\dot{J}_{X_i F} n_{X_1}^P + \dot{J}_{P_i F} n_{X_1}^P + \dot{J}_{P_i I} n_{X_1}^P + \dot{J}_{VG} n_V^P + \dot{J}_E n_E^P + \dot{J}_{ER}^R n_E^P)$			
	\dot{J}_{H_2O}	Water flux	molHd^{-1}	
	$\dot{J}_{H_2O} = -(-\dot{J}_{X_i F} n_{X_1}^H + \dot{J}_{P_i F} n_{X_1}^H + \dot{J}_{P_i I} n_{X_1}^H + 3 \dot{J}_{NH_3} + \dot{J}_{VG} n_V^H + \dot{J}_E n_E^H + \dot{J}_{ER}^R n_E^H)$			
	\dot{J}_{CO_2}	Carbon dioxide flux	molCd^{-1}	
	$\dot{J}_{CO_2} = -(-\dot{J}_{X_i F} + \dot{J}_{P_i F} + \dot{J}_{P_i I} + \dot{J}_{NH_3} + \dot{J}_{VG} + \dot{J}_E + \dot{J}_{ER}^R)$			
	\dot{J}_{O_2}	Dioxygen flux	$\text{molO}_2 \text{d}^{-1}$	
	$\dot{J}_{O_2} = -\frac{1}{2}(-\dot{J}_{X_i F} n_{X_1}^O + 4 \dot{J}_{PO_4} + 2 \dot{J}_{H_2O} + 2 \dot{J}_{CO_2} + \dot{J}_{P_i F} n_{X_1}^O + \dot{J}_{P_i I} n_{X_1}^O + \dot{J}_{VG} n_V^O + \dot{J}_E n_E^O + \dot{J}_{ER}^R n_E^O)$			

Table 4.4. DEB parameters for *Mytilus edulis* and other parameters and conversion factors. (*dw*): dry weight, max: maximum, s.a.: surface area.

symbol	description	units	value	reference
$\{\dot{C}_{Rm}\}$	Maximum surface area specific clearance rate	$\text{m}^3 \text{d}^{-1} \text{cm}^{-2}$	0.096	Saraiva et al. (2011a)
$\{\dot{J}_{X_1 Fm}\}$	Algae maximum surface area-specific filtration rate	$\text{molC d}^{-1} \text{cm}^{-2}$	4.8×10^{-4}	Rosland et al. (2009)
$\{\dot{J}_{X_0 Fm}\}$	Inorganic material maximum surface area-specific filtration rate	$\text{g d}^{-1} \text{cm}^{-2}$	3.5	Saraiva et al. (2011b)
$\rho_{X_1 I}$	Algae binding probability	-	0.4	Saraiva et al. (2011b)
$\rho_{X_0 I}$	Inorganic material binding probability	-	0.4	Saraiva et al. (2011b)
$\dot{J}_{X_1 Im}$	Algae maximum ingestion rate	molC d^{-1}	1.3×10^4	Saraiva et al. (2011b)
$\dot{J}_{X_0 Im}$	Inorganic material maximum ingestion rate	g d^{-1}	0.11	Saraiva et al. (2011b)
y_{EXV}	Yield coefficient of reserves in algae structure	$\text{molC}^E \text{mol}^{-1} \text{C}^V$	0.75	this study
\dot{v}	Energy conductance	cmd^{-1}	0.056	Saraiva et al. (2011b)
κ	Allocation fraction to growth and somatic maintenance	-	0.67	Saraiva et al. (2011b)
$[\dot{p}_M]$	Volume specific somatic maintenance	$\text{Jd}^{-1} \text{cm}^{-3}$	11.6	Saraiva et al. (2011b)
$[E_G]$	Specific cost for structure	Jcm^{-3}	5993	Saraiva et al. (2011b)
δ_M	Shape coefficient	-	0.297	Saraiva et al. (2011b)
M_E^0	Initial reserve mass at optimal food conditions	molC^E	1.48×10^{-10}	Saraiva et al. (2011b)
E_{Hb}	Maturity at birth	J	2.99×10^{-5}	Saraiva et al. (2011b)
E_{Hp}	Maturity at puberty	J	1.58×10^2	Saraiva et al. (2011b)
κ_R	Reproduction efficiency	-	0.95	Kooijman (2010)
R^{spawn}	Spawning period	d	1	this study
GSR^{min}	Minimum gonado-somatic ratio in the organism	$\text{molC}^R \text{mol}^{-1} \text{C}$	0.1	Cardoso et al. (2007)
GSR^{spawn}	Gonado-somatic ratio to spawn	$\text{molC}^R \text{mol}^{-1} \text{C}$	0.2	this study
T^{spawn}	Minimum temperature for spawning	$^{\circ}\text{C}$	9.6	Hummel et al. (1989)
T_{ref}	Reference temperature	K	293	this study
T_A	Arrhenius temperature	K	7022	van der Veer et al. (2006)
$d_V = d_E$	Bivalve structure and reserves specific density	$\text{g}_{(dw)} \text{cm}^{-3}$	0.2	Rosland et al. (2009); Brey (2001)
$\psi_{afdw/dw}$	Bivalve ash-free dw to dw conversion factor	$\text{g}_{(afdw)} \text{g}_{(dw)}^{-1}$	0.85	this study
μ_E	Bivalve reserves chemical potential	Jmol^{-1}	6.97×10^5	van der Veer et al. (2006)
$\psi_{dw/C}$	Algae dry weight to carbon conversion factor	$\text{g}_{(dw)} \text{gC}^{-1}$	2.5	Slobodkin and Richman (1961)
f_E	Reserves fraction in algae biomass	-	0.5	this study
$n_{X_1}^*$	Chemical composition of food	mol^*/molC	$\text{C}_1\text{H}_{1.8}\text{O}_{0.53}$	Kooijman (2010)
$n_E^* = n_V^*$	Chemical composition of bivalve reserve/structure	mol^*/molC	$\text{C}_1\text{H}_{1.8}\text{O}_{0.53}$	Kooijman (2010)
$*$	=C, H, O, N, P		$\text{N}_{0.18}\text{P}_{0.006}$	Smaal and Vonck (1997)
$w_E = w_V$	Bivalve reserves/structure relative molecular mass	$\text{g}_{(dw)} \text{mol}^{-1}$	25.22	this study

State variables and forcing functions

Four state variables characterize the organism, i.e. the individual structure biomass, M_V (molC^V); reserve, M_E (molC^E); maturity level, M_H (molC^E) and reproduction buffer, M_R (molC^E) (Table 4.1). The forcing functions of the model are ambient temperature and the concentration of particles in the water, either inorganic (non food material, expressed in mg/l) or algae (food, expressed in molC/l for C,N, and P).

Feeding

Filtration, ingestion and assimilation are assumed to be separate processes (Saraiva et al., 2011a). The Synthesizing Units concept (SU), introduced in the DEB theory by Kooijman (1998, 2000, 2010), is used to describe those processes. For each particle type i in the water column, with density X_i , a flux of particles is retained through filtration (the product of clearance rate by the particles concentration, $X_i \dot{C}_R$). In the model, clearance rate is regulated by

substitutable and sequential SU's where any substrate can be separately filtered and the handling of one food type by the filtration apparatus interferes with the possible handling of other food types. Once retained in the gills, particles are then lead to the palps, where the selection is made between particles transported to the mouth to be ingested and particles which are rejected and transported back to the water as pseudofaeces (\dot{J}_{P_iF}). The same type of mechanism (substitutable and sequential SU's) is used to explain and describe both filtration and ingestion. The formulation derived is then similar to Holling type II functional response, although extended to the situation with several types of food. Filtration and ingestion are assumed as two SU systems connected by open handshaking protocol, i.e. the first SU releases its products irrespective of the state of the next SU, with the consequent production of pseudofaeces (filtered material that the ingestion process is not able to handle). The selection of particles in the ingestion process is made by assuming a different binding probability for each type of food (ρ_{X_iI}), representing a different affinity of the ingestion apparatus(palps) for each particle.

The third and last feeding step is assimilation, defined as the process where the particles are absorbed and converted into the organism's reserve. The efficiency in the conversion of food into the reserves depends on how the organism is able to absorb food particles, which ultimately depends on the similarity of the chemical composition of food and reserves. Conversion efficiency, therefore, depends on the type of food. The adopted assimilation formulation for algal reserves assumes a parallel and complementary substrate for the synthesis of bivalve reserve tissue. Differences in the chemical composition between bivalve reserve tissue and ingested food, determines the production of faeces (\dot{J}_{P_iA}). More details on the model assumptions, formulations and parameter estimation can be found in Saraiva et al. (2011a).

Mobilization

The mobilization rate, \dot{J}_{EC} , is the rate at which energy is used from the reserve. As a consequence of the homeostasis assumption, the mobilization of the reserve occurs at a rate proportional to the reserve density, which is the ratio between reserves (mass, molC) and structure (volume, m³), and thus inversely proportional to structure (Kooijman, 2010).

Somatic Maintenance

Somatic maintenance, \dot{J}_{ES} , stands for all processes necessary to 'stay alive', or to maintain the integrity of the animal's body and this maintenance term can generally be decomposed in contributions that are proportional to structural body volume (structure maintenance costs) and to surface area (e.g. osmotic work in brackish waters, endotherms) (Kooijman, 2010). This second type of contribution to maintenance (proportional to the organism surface area) is considered to be null because we assume that the bivalve is not affected by the possible changes in salinity at the study locations and also because bivalves are ectotherms, not spending energy on temperature regulation.

Growth

Growth, J_{VG} , represents the increase of structural body mass of the organism. The flux of reserve available for growth, \dot{J}_{EG} , is computed as the difference between the amount of energy allocated to growth/maintenance, following the κ - rule, and the somatic maintenance. The increase in structural body mass, i.e. the growth, is computed by assuming a yield coefficient (y_{VE}) resulting from the stoichiometric balance of mass transformations (Kooijman, 2010).

Maturity and Reproduction

During the juvenile stage, the fraction of energy allocated to reproduction is used to develop reproductive organs and regulation systems, increasing the maturation level of the organism. Maturity represents the mass, or energy, investment in the development of the organism. When the organism reaches a particular maturity level (M_H^p), no more development is needed and it becomes an adult. Hereafter, it allocates this flux, \dot{J}_{ER} , to the reproduction buffer for further gametes production and release into the water. Thus, this maturity threshold controls stage transitions. Maturity requires maintenance, proportional to the maturity level, which can be thought to relate to the maintenance of regulating mechanisms and concentration gradients (Kooijman, 2010). The present model assumes, for simplicity, that the maturity maintenance rate coefficient is equal to the somatic maintenance rate coefficient, $k_M = k_J$, implying that the stage transitions occur at fixed amount of structure.

Spawning

The allocation of energy to reproduction is accumulated in a reproduction buffer. This leads to an increasing of the gonad-somatic mass ratio (GSR, gonadal tissue fraction of the total biomass) over time. Spawning events occur if the GSR and the temperature are above the respective thresholds (GSR^{spawn} and T^{spawn}). The model considers that the gametes production, i.e. the conversion of the reproduction buffer content into embryo reserve has overhead costs. The dimensionless factor, k_R , represents the fraction that is fixed in eggs and $1 - k_R$ the dissipation fraction. In line as field observations from (Cardoso et al., 2007), the model assumes that one spawning event does not empty the reproduction buffer content completely but that a minimum value of GSR is maintained inside the organism. For simplicity, the model considers that each gamete (sperm cell or egg) produced will have a constant value of reserve density that equals the reserve density of the mother when in optimal condition and that the spawning events are instantaneous.

Inorganic Compounds

Mineral fluxes are represented by the amount of CO_2 , H_2O , O_2 , NH_3 and PO_4 used or released by the individual in the processes described above. They can be computed on basis of the

principle of mass conservation for each element in the system (C,H,O, N, P) using the organic fluxes computed before.

Temperature effect

All physiological rates depend on the body temperature. This dependency is usually well-described by the Arrhenius relation, within a species-specific tolerance range of temperatures:

$$\dot{k}(T) = \dot{k}_1 \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)$$

with T being the absolute temperature (K), T_1 the reference temperature, T_A the Arrhenius temperature, \dot{k}_1 the value of the rate at temperature T_1 , and $\dot{k}(T)$ the value of the rate at temperature T . It is assumed that all physiological rates are affected by temperature in the same way.

Model parameters

The model parameters used in this study were estimated by Saraiva et al. (2011b) using several data sets from the literature on the blue mussel (*Mytilus edulis*), following the covariation method described in Lika et al. (2011). This method is based on the minimization of the weight sum of squares deviation between data and model results. The data include a collection of observations (single data points and/or time series) and a set of pseudo-data (average of parameters obtained from a large collection of organisms, used to restrict the possible parameter combinations). The general idea behind the covariation method is to let all available information compete, or interact, to produce the end result, implying the estimation of all parameters from all data sets simultaneously. Saraiva et al. (2011b) also provides a comparison with previous parameter sets in terms of model performance and approximation to the data, concluding that the new parameter set should lead to better results. The parameters used in this study are listed in Table 4.4.

Field Observations

Mussels

Intertidal mussels from the Dutch coast (Egmond) and the UK coast (Lowestoft and Wash), with size range from 2 to 6 cm, were collected and individually marked. Marks consisted of miniature labels (www.hallprint.com) which were glued on one of the valves with a gel type of superglue. At the start of the experiment each individual shell length was measured to the nearest 1/10 mm with digital callipers, and a subset ($n = 195$) of animals was sacrificed and dissected to determine initial soft tissue weight and condition. The labelled mussels were then

transplanted to four locations in the North Sea: Wadden Sea, Sean Gas Field (UK), Oyster Grounds (NL) and North of Dogger Bank (UK) (Fig. 4.2). Fig. 4.3 presents the size distribution of the transplanted mussels at each location. The mussels were transplanted in series of small nets (10×20 cm, with a mesh size of 1.5 cm) which were filled with 15 mussels each, Table 4.5. The resulting 'density of mussels' is in the range to those found in natural mussel banks. At an inshore part of the North Sea, the Wadden Sea, mussels were located in the surface water layer on December 2005. At this location the mussels were collected, cleaned and measured individually every month and a subset of the mussels was sacrificed in the first year for weight determination. During the experimental period (from December 2005 until August 2009), four new transplantations were done at this location (November 2006, April 2007, June 2008 and November 2008). The transplantations followed the same methodology as the first deployment. For this location growth data from 148 mussels is available.

Table 4.5. Experiment details at the four locations.

name	location	origin	depth (m)	experiment period	Number of mussels
1. Wadden Sea	53.01N 4.80E	Egmond	surface	Dec 2006 to Aug 2009	148
2. Sean Gas Field	53.17N 2.81E	Wash/Lowestoft	31	Jan 2008 to Aug 2008	45
3. Oyster Grounds	54.41N 4.04E	Egmond/Wash/Lowestoft	45	Nov 2007 to Aug 2008	132
4. Dogger Bank	55.68N 2.28E	Wash/Lowestoft	surface	Nov 2007 to Aug 2008	59
5. Dogger Bank	55.68N 2.28E	Wash/Lowestoft	85	Nov 2007 to Aug 2008	98

At the other locations (off shore North Sea) the same procedure was applied and the nets were tied to bottom moorings which were deployed from October 2007 to September 2008. Between the start and end of this deployment period two interim retrievals of the moorings took place (January 2008 and April 2008) during which the individually marked mussels were re-measured and small sets of individuals were taken out for weight determination. For the North Dogger Bank location nets with mussels were also positioned at the surface. Hence for this location growth data from both surface and bottom were collected.

The mortality of the entire experimental population of mussels at all locations was low ($\tilde{2} \%$). At the Dogger Bank surface location some fouling by macroalgae in the surface nets occurred during the spring summer period. The nets transplanted to the Wadden Sea location experience fouling by barnacles and adhering mud. This fouling was removed at a monthly frequency at the times the mussels were remeasured. Hence the negative effects on mussel growth and performance are expected to be small.

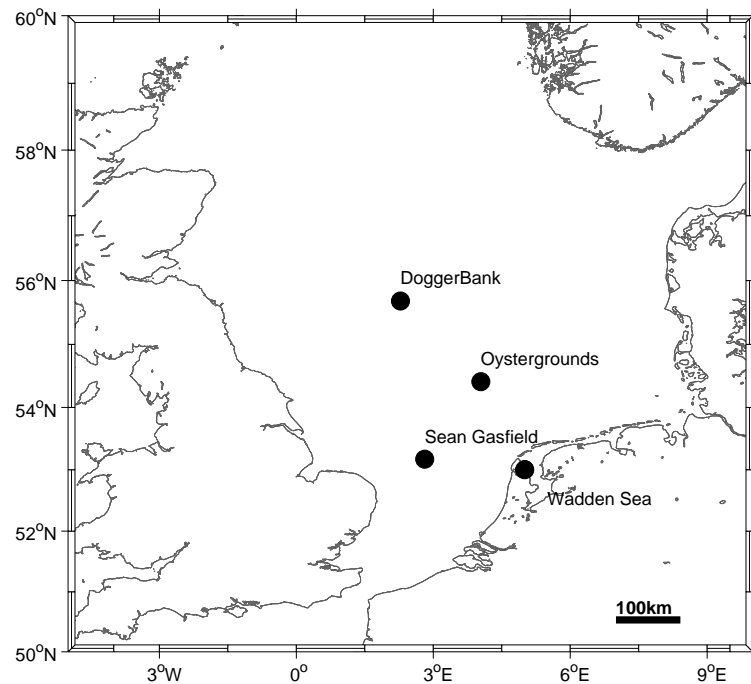


Fig. 4.2. Transplantation locations of blues mussels *Mytilus edulis* in the North Sea.

Environmental Conditions

Environmental conditions were quantified from field measurements of water temperature and chlorophyll a concentration at each location. For the Wadden Sea, the Royal Netherlands Institute for Sea Research maintains a research jetty, situated on the northern shore of the Marsdiep, a tidal inlet, which connects the Western Dutch Wadden Sea with the North Sea. At this location continuous observations are being made on sea surface temperature (SST) and salinity (SSS) van Aken (2008a,b) and on chlorophyll-a concentrations Philippart et al. (2010). Since this monitoring station is located close to the transplantation location of the mussels (see next section), these measurements were used as input data for the model (Fig. 4.4). At this location, total particulate matter (TPM) were estimated and inorganic material concentration was computed as the difference between TPM and the algae weight. TPM estimation used an empirically based model, proposed by Håkanson (2006), to quantify the relationship between TPM, salinity, and Secchi depth. The formulation was tested for a period when all the measurements were available (Fig. 4.4c) and then used to estimate TPM concentrations for the periods in which no measurements were available.

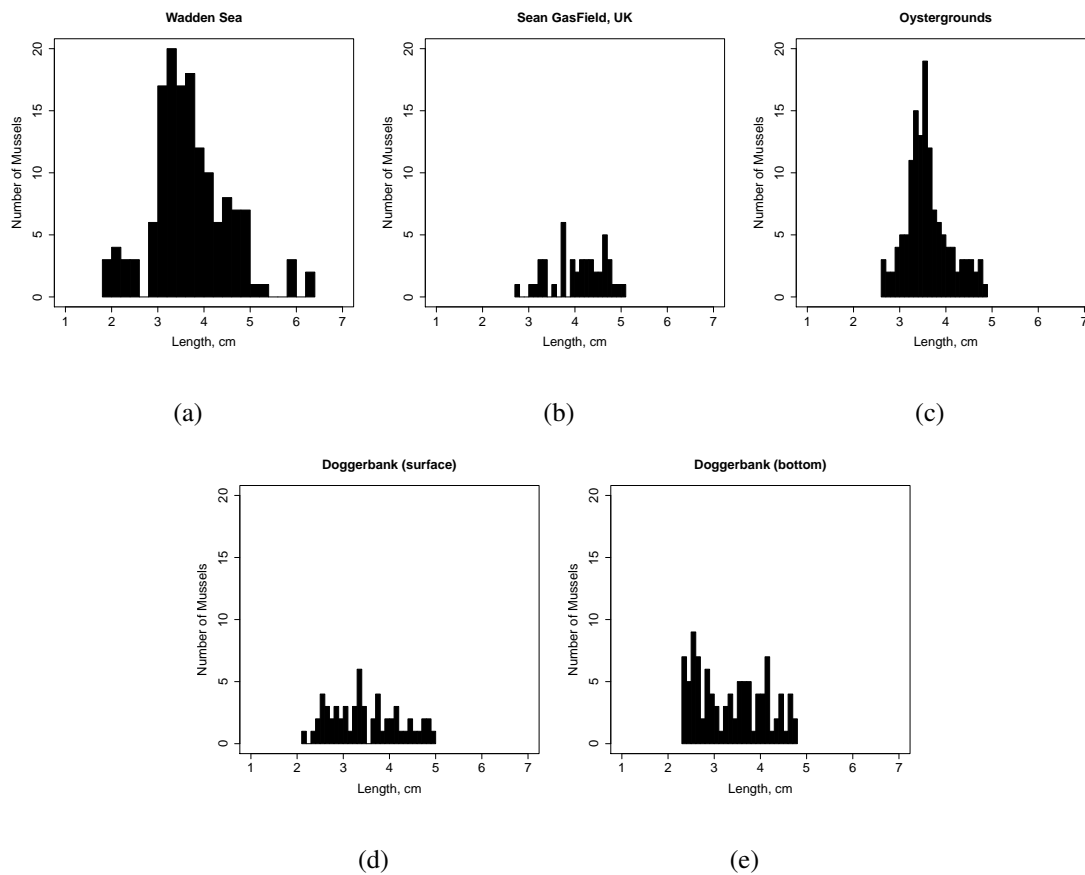


Fig. 4.3. Initial mussel size distribution transplanted to each location: a) Wadden Sea, b) Sean Gas field, c) Oyster Grounds, d) and e) Dogger Bank.

The environmental conditions for the off-shore North Sea locations were measured with semi autonomous moorings and lander systems, to which the mussels were attached. The mooring systems were equipped with self-logging Fluorescence, Turbidity and CTD sensors. Details of the moorings and landers are given in Suratman et al. (2010) and in Painting (2010). Chlorophyll-a to Carbon and Nitrogen/Phosphorus to Carbon ratios were used to convert chlorophyll observations into food concentration in terms of carbon, nitrogen and phosphorus content, necessary as model input. Average results from the GETM-ERSEM model were used to obtain a seasonal pattern of those nutrient ratios at all four locations, also shown in Fig. 4.4. More detailed description on the GETM-ERSEM model and its implementation in the North Sea can be found at www.nioz.nl/northsea_model and Baretta-Bekker et al. (1997). To assess the implications of the assumptions made on the forcing functions, namely on the determination of the inorganic material concentration and conversion from chlorophyll-a to carbon, nitrogen and phosphorus, some additional model scenarios were performed. The first scenario is a repetition of the reference scenario but assuming 50% lower inorganic material concentrations to assess the importance of the food quality on the mussel growth. Two other scenarios were performed: i) assuming a constant average value for the Carbon/Chlorophyll ratio, to assess the importance of the seasonal variation of food quantity; (ii) assuming a constant average value for Nitro-

gen/Carbon and Phosphorus/Carbon, to quantify the importance of the seasonal variation of food composition.

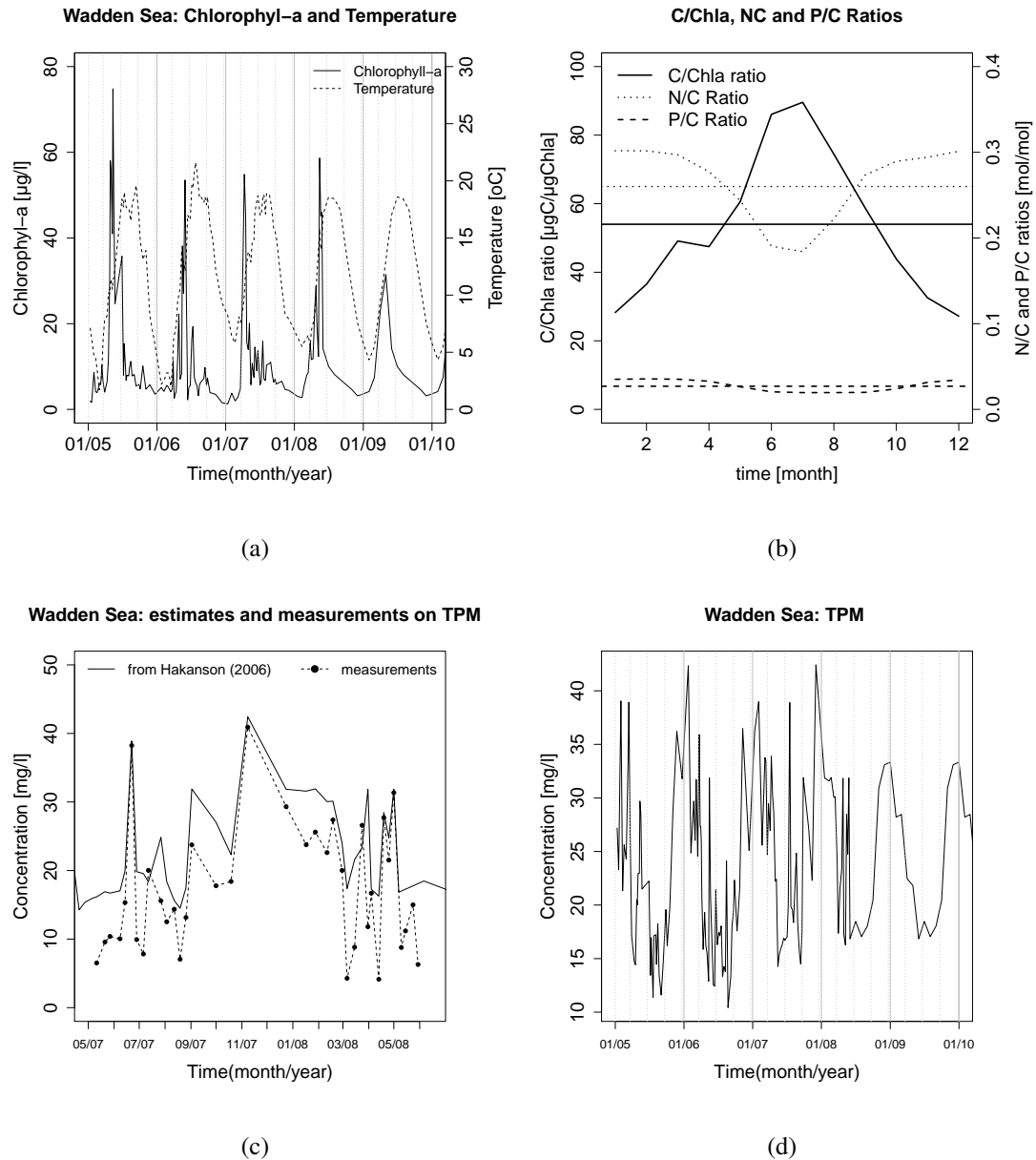


Fig. 4.4. Environmental conditions measured at the Wadden Sea location and used as model input data: (a) Temperature and Chlorophyll-a; (b) seasonal pattern of Chlorophyll-a, Nitrogen and Phosphorus to Carbon ratios in food particles (the straight lines represent their annual average value) - model results provided by GETM-ERSEM model (www.nioz.nl/northsea_model); (c) measured and estimated TPM (Total Particulate Matter) concentrations for the period with available data and (d) TPM concentrations.

Comparison between predictions and observations

The same model and the same parameter set were used to model length and weight growth of each mussel at each of the four locations.

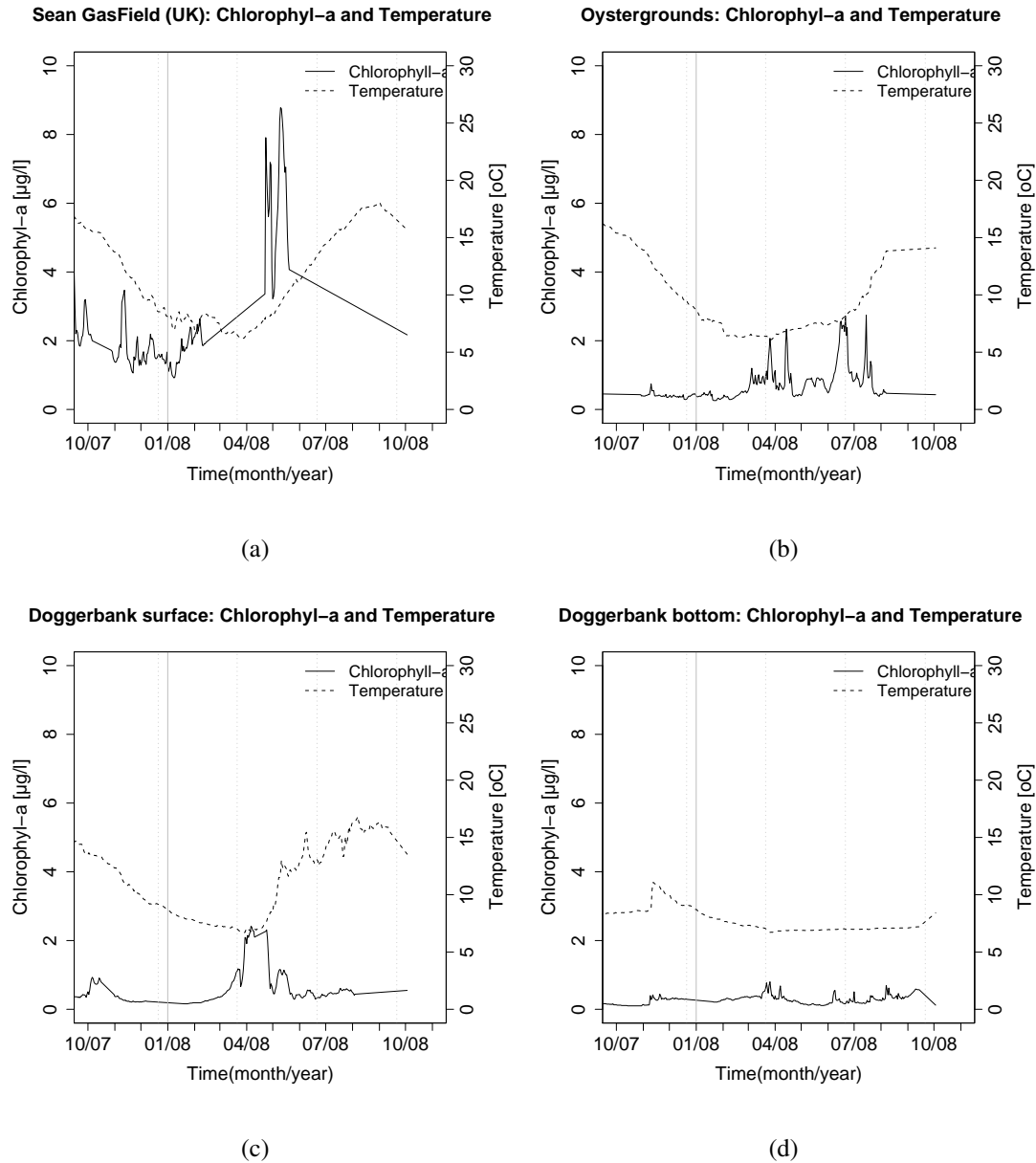


Fig. 4.5. Environmental conditions (Temperature and Chlorophyll-a concentration) measured at Sean Gas Field (UK), Oyster Grounds and Dogger Bank (surface and bottom).

The model simulations in the present study only differed with respect to location-specific forcing function (food, temperature) and initial conditions (amounts of reserve, structure, reproduction buffer and level of maturity). The initial conditions for each mussel were estimated by using the results of a pre-run of the model for a 'born and raised' mussel living in average environmental conditions. Initial structure was estimated by length measured at the beginning of the experiment and initial reserve content estimated by combining the seasonal pattern of reserve density resulted from the pre-run simulation with the Julian day of the start of the experiment. For each location, the results were analyzed on an individual basis, i.e. comparing

observations and model predictions for each mussel separately, and then the overall results were analyzed in terms of the average performance of the model predictions. The difference between model predictions and field observations was quantified in terms of an relative error computed as $E_r = \left| \frac{Y - \hat{Y}}{Y} \right|$, where Y and \hat{Y} are the observations and the model predictions respectively.

Results

Wadden Sea

Fig. 4.6 presents model predictions for mussel characteristics for a 'born and raised' mussel under average daily environmental conditions, as measured in the Marsdiep (temperature, chlorophyll-a and inorganic particles concentration) obtained at the Wadden Sea location. Total mussel dry weight was computed as the sum of structure, reserve and reproduction buffer content of the bivalve, as described in Table 4.2. In Fig. 4.6 (a), dry weight vs. length predictions are compared with observations from the subset of mussels sacrificed in the beginning of the experiment.

For the same predicted length, a range of predicted dry weight values was found, depending on the reproduction buffer content. This buffer is determined by the number and timing of spawning events also predicted by the model. The difference between model estimates and real observations is higher for mussels with higher length, but it is also in this range that the observations show more scatter. After 16 years of simulation the average 'born and raised' mussel is about 7 cm long, which is within the common range of lengths found in field observations which is between 5 and 10 cm (MarLIN, 2009, www.marlin.ac.uk). All the model results indicate a strong seasonal pattern with: high growth in spring/summer season and low growth during autumn/winter season. This pattern is consistent with the seasonal cycle of temperature and food availability for a typical year (Fig. 4.4). Temperature starts to increase during the beginning of spring (April) followed by an increase in chlorophyll concentration. The increase of food availability and temperature promotes high growth for the mussel during a period of about 5 months. The decline in chlorophyll during summer until the end of the year and the temperature decrease in autumn, result in a lower mussel growth. In this period of low food availability the mussel is using its reserve to maintain itself. Model results shows that mussels of more than 4.5 cm may even use the reproduction buffer content to fuel the high somatic maintenance costs, shown in Fig. 4.6 (d). Spawning events, controlled by temperature and the fraction of gametes in the organisms (T^{spawn} and GSR^{spawn} thresholds), are responsible for the sharp decline of the reproduction buffer content. The model predicts an interval of about one year between spawning events (late spring/summer), but also indicates that in some years a second spawning event if the first event is early in spring. Both predictions are consistent with field observations (Cardoso et al., 2007). As described before, the 'mussel born and raised' scenario was used to establish the initial conditions (structure, reserve and reproduction buffer from measured initial length)

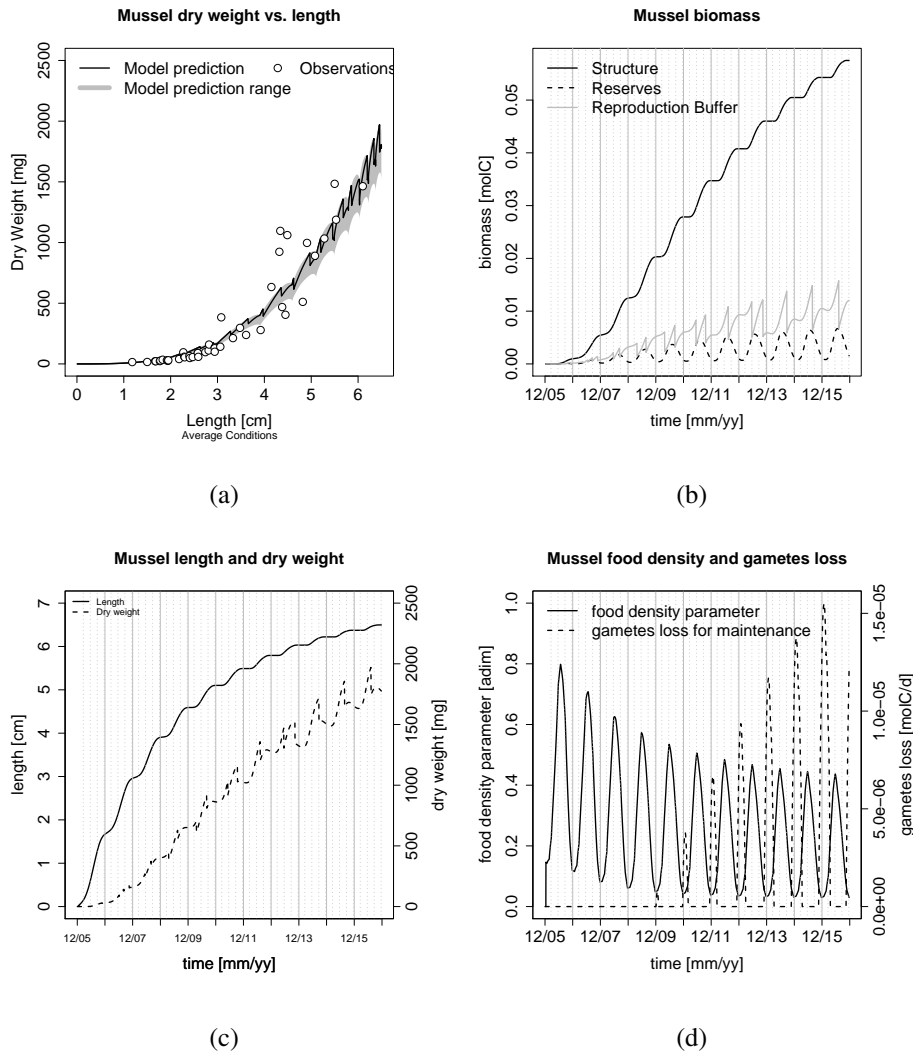


Fig. 4.6. Model predictions for a 'born and raised' mussel living on average environmental conditions at the Wadden Sea: (a) mussel length vs. dry weight; (b) mussel biomass distribution by compartment; (c) mussel growth over time and (d) food density parameter and gametes use for somatic maintenance needs.

of the mussels. Model simulations were then performed for each mussel (148 mussels) considering the same forcing functions and individual parameters, changing only the initial conditions of each mussel. Fig. 4.7 represents some of the obtained results; (a) and (b) represent examples of shell length observations in comparison with the predicted length for four particular mussels (B209, B127, B144 and B219). This shows that the main seasonal pattern observed both in data and in the model: the mussel growing season starts with the increase of the temperature and chlorophyll-a concentration in the water column during spring. This contrasts with slow growth observed during autumn and winter. Although the model is able to predict this pattern, the particular predictions for mussel B127 and B209 show a higher growth during the growing season of the first year, compared with the observations (Fig. 4.7b). For mussels B144 and B219, in Fig. 4.7 (a), the model predictions are close to the observations even with very different initial length. The overall relative error (relative difference between observation and model) for these

mussels is about 2%, showing that the initial length is not determining the goodness of fit of the model prediction. It is also interesting to notice that mussels B209 and B219, white dots in Fig. 4.7 (a) and (b), with about the same size in the beginning of the experiment, have a significant difference in their observed growth pattern. Fig. 4.7 also presents the overall result for model predictions vs. observations for growth: (c) in terms of shell length and (d) in terms of weight, for each data point (white dots) and its average (black dots). The high variability in growth in the observations is well shown. The relative difference between model and observations is about 30% and there is a tendency for lower predicted values. In terms of weight increase, the average relative error is much higher (about 75%).

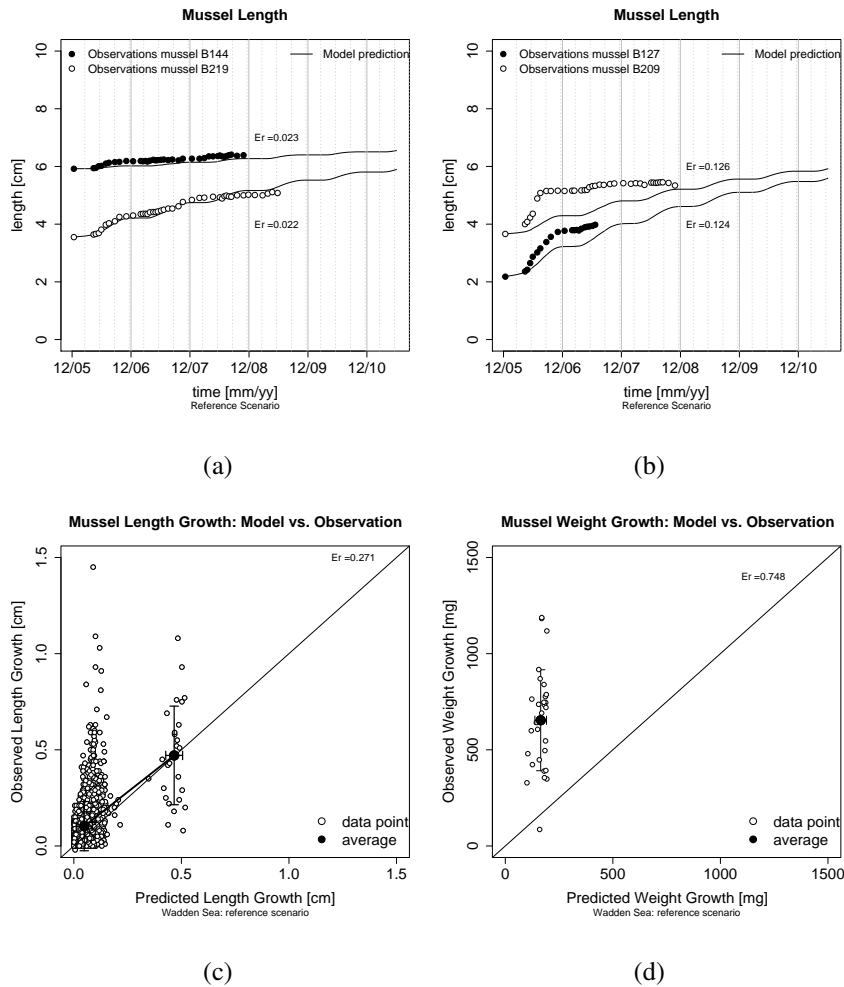


Fig. 4.7. *Mytilus edulis*. Model predictions vs. observations in the Wadden Sea: (a) shell length comparison for bivalve B144 and bivalve B219 as good examples of model predictions; (b) shell length comparison for bivalve B127 and bivalve B209 as not so good examples of model predictions; (c) shell length growth and (d) weight growth. See 'Results: Wadden Sea' for further details. The relative error is computed as $E_r = \left| \frac{Y - \hat{Y}}{Y} \right|$, where Y and \hat{Y} are the observations and the model predictions respectively.

Fig. 4.8 (a) and (b) show the comparison between observed length and model prediction in the simulated scenarios for two particular mussels, and (c) and (d) represents the average result of shell length and weight growth for the reference scenario (black dots) and for the scenario with

half inorganic material concentration (white dots). The results show that the decrease in the inorganic material concentration does have a significant effect increasing the mussels growth. The overall result suggests that this higher growth rate compared with the reference scenario, slightly improves in the model predictions, reducing the tendency for lower model predictions. In fact, for about 90% of the mussels, being Fig. 4.8 (a) an example of those and Fig. 4.8 (b) an example of the remaining 10% the first scenario, with half inorganic material, results in better model predictions. The differences between the scenarios on food quantity and composition and the reference situation are not very significant – the highest difference is about 0.2cm in a mussel with a 5cm long shell, which represents a change of about 4% in length.

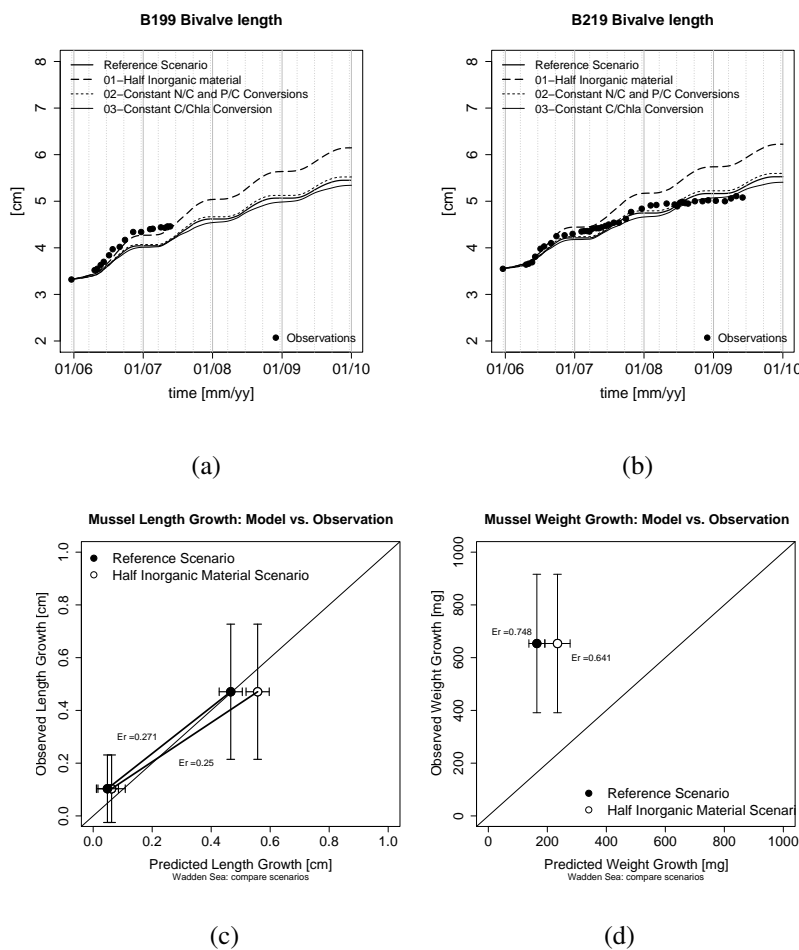


Fig. 4.8. Model predictions vs. observations in the Wadden Sea: (a) and (b) bivalve B199 and bivalve B219 as examples of shell length predictions in four different scenarios of food quality; (c) and (d) length and weight growth, respectively, in the reference scenario and in the scenario with half inorganic material concentration. The relative error is in Fig. 4.7.

All locations North Sea

The same modelling methodology was followed for the other locations in the North Sea and the results obtained for the reference scenarios are summarized in Fig. 4.9. The model goodness of

fit can be assessed by the distance between the dots and the diagonal line which represents the perfect fit. Length growth results for each location are summarized in terms of a straight line connecting the average values of growth observed for all the mussels. Dogger Bank (bottom) is represented by a single dot because at this location all the mussels showed low growth and where all averaged (Fig. 4.9). The Wadden Sea (1) and Sean Gas Field (2) are close to the diagonal and for the Oyster Grounds (3), the results show the correct slope but with higher observed values. The low length growth found for the Dogger Bank bottom location (5) is in agreement with the model predictions, and the strong contrast with the results obtained at Dogger Bank surface location (4). In terms of weight, Fig. 4.9 (d), the results obtained for the Wadden Sea show the largest difference between estimates and observations. For the other locations, despite the high variability in the data, the comparison between model predictions and observations is relatively close to the perfect fit.

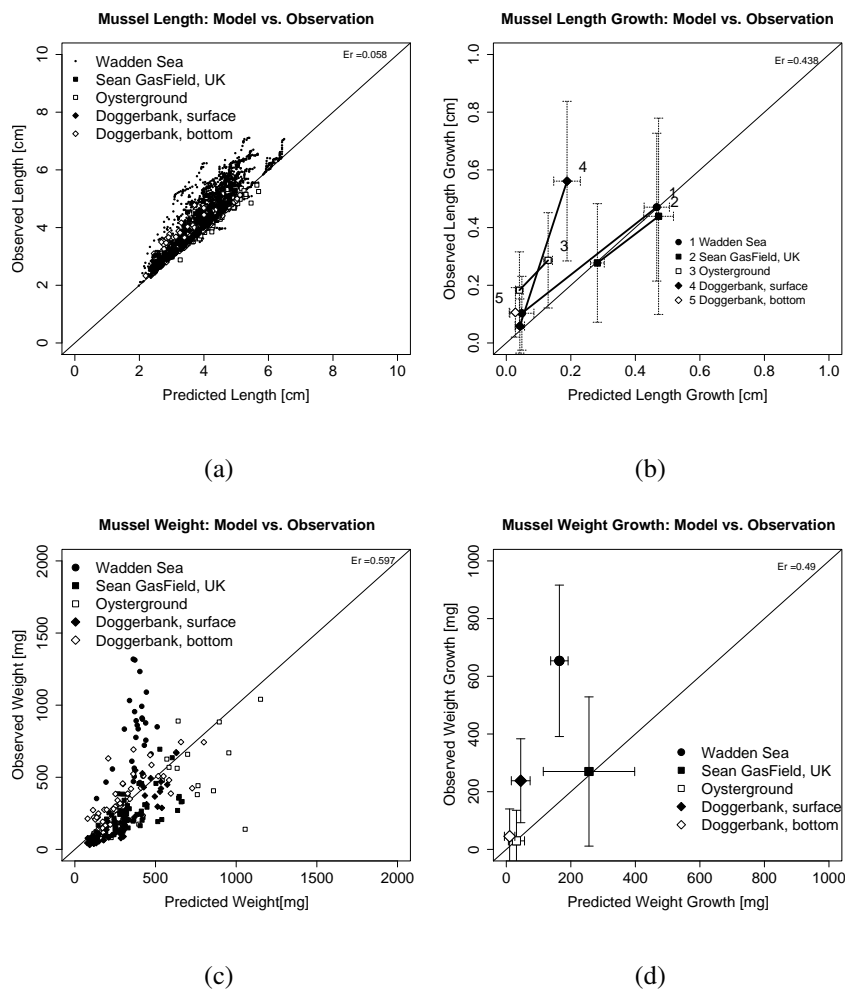


Fig. 4.9. Model predictions vs. observations at the four locations: (a) shell length; (b) shell length growth; (c) weight and (d) weight growth. The relative error is in Fig. 4.7.

Discussion

The same model and parameter set were used to predict mussel growth in the transplantation experiments at all four locations. The underlying idea is that a generic mussel model should represent an average (growth) performance of mussels under given environmental conditions. The observations used in the study refer to particular mussels and it is not always correct to average the data, particularly if mussels have different sizes. For that reason, the model was evaluated by the combination of two different methodologies: comparing observations and predictions for individual mussels and secondly by computing the average relative error per location. The individual mussel observations show a clear seasonal pattern. The growing season is driven by an increasing temperature and food availability during spring and summer. The model is well able to reproduce this for all the locations, suggesting that the main and seasonal processes are well described. The analysis of the overall results of predictions on length and weight growth (Fig. 4.9) are also satisfactory especially when considered that the model was not calibrated nor fitted to these particular experimental observations. However, several assumptions and choices had to be made and with that some uncertainties are associated with the results. Temperature and Chlorophyll-a measurements were used to characterize the environmental conditions at each of the location. This information, although fundamental, is not fully representative of the conditions at the site. Chlorophyll-a is used as a proxy for food concentration and composition, combined with chlorophyll to carbon and nitrogen/phosphorus conversion factors. To include the seasonal variation of these ratios in the North Sea we had to use ERSEM model outcomes as this type of information was not available from the measurements at these different locations. Additionally, the Wadden Sea simulations used estimates of inorganic material concentration in the water column obtained by an empirical relationship between this property and measurements of Secchi depth and salinity, proposed by Håkanson (2006). The use of these assumptions instead of measured data can also cause some deviations between model predictions and observations on the mussels length or weight. The feeding processes model extension enables the evaluation of some of the assumptions made on the food characterization due to the incorporation of food quality and composition in the assimilation rate computation. Differences in the mussel growth between the different modelling scenarios performed are shown in Fig. 4.8 (a) and (b), for 2 individual mussels. The scenario analysis confirms the negative effect of high suspended inorganic particles on mussel's filtration and consequently on the growth of the organism, which is in agreement with several other studies (see review by Riisgård (2001), and references therein). This is an important result and strengths the model potential for mussel's growth simulation in estuarine and coastal environments.

The model predictions improved in the scenario of half inorganic material concentration. This could be explained by the fact that the experiment was conducted inside the harbour and the measurements were taken at the Jetty station, located outside the harbour, more exposed to coastal transport of TPM and wind-induced waves. The scenarios comparison also suggests

that the influence of inorganic particles is much more important than the influence of seasonal changes in food composition. These are important results also for the design of future experiments meaning that with limited resources the main effort in measurements should be on the TPM determinations rather than frequent seasonal food composition estimations. Therefore, to obtain better model predictions especially data should be available on TPM concentrations, the temperature and food concentration (phytoplankton concentration and/or chlorophyll concentrations combined with C:Chla ratios). The measurements should be at high measurement frequency (order of weeks or monthly at least) and food composition (mainly C, N and P) at the experiment location preferable at a seasonal time scale. Frequent mussel length monitoring and periodic mussels sacrifices for weight determination is essential for a more detailed comparison with the model predictions. Monitoring of gonadal development and spawning events could also be of great help to evaluate the reproduction buffer handling rules assumed in the model. Knowledge on the start conditions of each mussel (length and reserve density) is also critical for the model implementation, particularly if the simulation period is short and if the results are compared in terms of growth (different between the end point value and the start). In this study, start conditions of mussels were based on a previous model simulation for a 'born and raised' mussel living in average seasonal environmental conditions, resulting in a clear seasonal pattern of the organism reserves density. This seasonal pattern, combined with the starting date of the experiment was used to estimate the initial reserves density of each mussel.

The agreement between predictions and observations is higher, and also more reliable, for length measurements than for weight. In fact, the uncertainties associated with weight can be very significant. The organism weight depends very much on the spawning events and on the usage of energy reserves in long periods of food shortage (Bayne et al., 1978, 1982). There is a large variability in observed length and weight growth of the mussels within each site. This variability is attributed to different individual performance, different initial conditions and to some extent to differences in experiencing the ambient conditions despite the careful planning of the experiment. Individual performance will also depend on the organism condition, i.e. reserves density and health. Even when mussels have similar length, they can differ in condition since they were collected in a natural population living in a spatial and temporally variable environment. The model is not able to reproduce specific adaptations of the individual to specific environmental conditions, e.g. temperature ranges or sediment concentrations in the water column. The parameters used in the model were estimated by Saraiva et al. (2011b) using literature data describing results collected from different locations, experiments and authors and as such pretends to represent a parameter set for an 'average mussel' and not so much a specific individual from a specific location. Therefore, it is believed that, if needed, the model performance for each location could be improved by using detailed data and/or use site-specific assumptions. Although there is a significant variability in the observed growth of the mussels they all follow the same seasonal pattern and that is well predicted by the model at all locations.

Conclusions

This study aimed to evaluate the performance of a generic individual model for mussels to predict length and weight growth given the environmental conditions. The model results were compared with observations made at the individual level. Despite the high variability found in the field observations, the model was able to reproduce the seasonal pattern of the observations on length and weight growth. Length is better predicted than weight probably due to the high influence of spawning events and food limitation periods on the total mussel weight ($\pm 10 - 15\%$), as well as the high uncertainty on the initial weight conditions. One important conclusion of this study is that the influence of inorganic material concentration on the mussel growth is significant and the model suggests that it could even be more important than the seasonal changes in food composition. Model predictions can be improved if measurements of inorganic material concentration are available. The model was tested at four different locations, with different environmental conditions. From the results we conclude that the 'average mussel' model can reasonably reproduce the average of the mussels in each location. This supports the model's ability to correctly describe the main processes involved in the mussel growth and confirms its potential use in up scaling these processes to the level of population dynamics.

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5. Bivalves: from individual to population modelling

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An individual based population model for bivalves was designed, built and tested in a 0D approach, to simulate the population dynamics of a mussel bed located in an intertidal area. The processes at the individual level were simulated following the Dynamic Energy Budget theory, whereas initial egg mortality, background mortality, food competition, and predation (including cannibalism) were additional population processes. Model properties were studied through the analysis of theoretical scenarios and by simulation of different mortality parameter combinations in a realistic setup, imposing environmental measurements. Realistic criteria were applied to narrow down the possible combination of parameters values. Field observations obtained in the long-term and multi-station monitoring program were compared with the model scenarios. The realistically selected modelling scenarios were able to reproduce reasonably the timing of some peaks in the individual abundances in the mussel bed and its size distribution but the number of individuals was not well predicted. The results suggest that the mortality in the early life stages (egg and larvae) plays an important role in population dynamics, either by initial egg mortality, larvae dispersion, settlement failure or shrimp predation. Future steps include the coupling of the population model with a hydrodynamic and biogeochemical model to improve the simulation of egg/larvae dispersion, settlement probability, food transport and also to simulate the feedback of the organisms' activity on the water column properties, which will result in an improvement of the food quantity and quality characterization.

Keywords: population, IBM modelling, DEB theory, *Mytilus edulis*.

Introduction

Population ecology aims to understand how populations of organisms change over time and space, and how these populations interact with their environment (Akçakaya et al., 1999). In classical models (e.g., Lotka–Volterra) population abundance (number of organisms) over time is computed assuming that per capita birth and death rates as well as interspecific competition are the same for all members of the population. This approach could only be considered a good approximation if the population structure is relatively constant over time, e.g., age and size, so that the individuals can be represented by a mean-field approximation (Łomnicki, 1992). But the structure of natural populations is commonly not constant and the individuals of a population are usually far from identical. Moreover, many mechanisms determining population behaviour are directly related to those individual differences (Metz et al., 1988). Huston et al. (1988) introduced the concept of 'individual-based models' (IBM) as an alternative approach, adopting the individual as the basic entity. By describing the physiological processes at the individual level and simulating their life history events (reproduction, mortality), the population dynamics, i.e., the variation in time of the number or biomass of individuals, is the result of tracing all individuals over time. The most important source of individual variation relates to size and the state of development or maturation (de Roos and Persson, 2012), which determines to a large extent the type and strength of ecological interactions, e.g. food choice, foraging capacity, growth, reproduction and mortality (Peters, 1983; Ebenman and Persson, 1988b,a). The individual model should thus realistically describe the size, development and maturation of the individual.

The Dynamic Energy Budget (DEB) theory, proposed by Kooijman (1986, 2000, 2010), is based on a mechanistic view of an organism's metabolic processes, including growth, maturation and reproduction. In the last years, DEB models at the level of the individual bivalve have been developed and tested against field and/or laboratory observations (e.g., Ross and Nisbet, 1990; van Haren and Kooijman, 1993; van der Veer et al., 2006; Pouvreau et al., 2006; Troost et al., 2010; Saraiva et al., 2012). The main advantages of these models is that they are based on a generic theory, meaning that the same model structure can be applied to different species, where only parameter values differ. Variabilities in growth and reproduction between individuals of the same species are assumed to be mainly caused by differences in environmental conditions (temperature, food), explaining seasonal and geographical distribution of individuals (e.g., Kearney, 2012). Thus, a population model based on a DEB individual model will surely have a high potential, although only a few studies actually focus on the topic Kooijman and Metz. (e.g., 1983); Kooijman (e.g., 1986); Kooijman et al. (e.g., 1989, 1999); Martin et al. (e.g., 2012) for more generic studies; and specifically for the bivalves Bacher and Gangnery (e.g. 2006) (oyster *Crassostrea gigas*), Kooi and van der Meer (2010) (*Macoma Baltica*), Savina and Ménesguen (2008) (benthic bivalve *Paphia rhomboides*), and Maar et al. (2009, 2010) (blue mussel).

In the present study, an individual based population model, based on the DEB theory, was de-

signed and built for the blue mussel, *Mytilus edulis*. The model differs from the study presented in Maar et al. (2009, 2010) by linking the birth of a new cohort to the spawning events computed by the individual model. The number of cohorts in the system is therefore not imposed and theoretically unlimited. The model was used in a stand alone setup, 0D, forced by food and temperature measurements.

The model performance was studied through the analysis of theoretical scenarios and by the schematic simulation of a mussel bed located at the Balgzand (Wadden Sea, The Netherlands) considering different mortality parameter combinations. The aim of this study is to understand and identify the main processes determining the population dynamics, as well as identify possible gaps in the model and data. This is an important stepping stone for the coupling of the population model to a hydrodynamic and biogeochemical model.

Material and Methods

Population model

In the model, the population consists of several cohorts, and each cohort consists of identical individuals born at the same time. The underlying idea is that organisms of the same species, born at the same time and place, will experience the same environmental conditions and will consequently follow the same growth and development trajectory over time. The population dynamics will be represented by the cohort trajectories, characterized by their individual properties (e.g. size, biomass, state of development), and also by its number of individuals. The population model is, in fact, responsible for the book-keeping of the information generated by the individual model over time (one for each cohort), with all the state variables representing every cohort. It also includes the effect of processes at the population level, namely mortality by predation (including cannibalism) or by natural causes. While the individual model is responsible for the computation of the changes in the individual variables, i.e., size, biomass, and state of development, the population model is responsible for the changes in the number of individuals in each cohort (by mortality) and the change in the number of cohorts (by managing births and deaths of cohorts).

One other important topic within a population is food competition. When an individual consumes a food item, that item cannot be consumed again by other individuals. Total food intake of the population (summing over all individuals) has a major impact on the resource density, which in turn affects the individual food intake. Thus, this feedback is crucial for the population dynamics and is included in the present model.

The model is written in FORTRAN 95 using object oriented programming (OOP) paradigms. Although FORTRAN 95 is not an object oriented programming language (OOL), FORTRAN modules can act as classes of common OOL (Decyk et al., 1997; Akin, 1999; Miller and Pinder, 2004). The model uses several object oriented features such as encapsulation, polymorphism,

function overloading and inheritance. Such features allow for the versatility of the model for complex ecosystem simulations through maintaining a simple and organized code, especially when dealing with multiple species, large number of cohorts, species interaction (e.g., predation and competition) as well as multiple types of food. State variables, main formulations and parameters of the population model are listed in Tables 5.1 to 5.4. A more detailed description of the processes included in the model and its specific assumptions can be found in the following sections.

Table 5.1. Model state variables and forcing functions. i represents the number of the cohort.

level	symbol	description	units	formulation
Environment	T	size temperature	K	
	X_0	inorganic particles	mg l^{-1}	
	X_1	algae	mol Cl^{-1}	
	N_{X_1}	algae N/C ratio	$\text{mol N mol}^{-1} \text{C}$	
	$n_{X_1}^F$	algae P/C ratio	$\text{mol P mol}^{-1} \text{C}$	
	P^S	shrimp abundance	$\# \text{m}^{-2}$	
	P^C	crab abundance	$\# \text{m}^{-2}$	
Individual	P^B	bird abundance	$\# \text{m}^{-2}$	
	M_{Vi}	structure	mol C^V	Saraiva et al. (2012)
	M_{Ei}	reserve	mol C^E	Saraiva et al. (2012)
	M_{Hi}	maturity	mol C^E	Saraiva et al. (2012)
	M_{Ri}	reproduction buffer	mol C^E	Saraiva et al. (2012)
Population	A_i	age	y	
	N_i	individuals in cohort i	#	$\frac{dN_i}{dt} = -m_i^S P^S - m_i^C P^C - m_i^B P^B - m^N N_i -$
	n_C	number of cohorts	#	$\frac{dn_C}{dt} = B - D$

Table 5.2. Population model main formulations. * represents the predator (S for shrimp, C for crab or B for bird).

process	symbol	description	units	formulation
Cohort Birth	B	new cohort	#	$B = \begin{cases} 1, & \text{if } \sum_{i=1}^{n_C} N_i^{spawn} > 0 \\ 0, & \text{otherwise} \end{cases}$
	N_i^{spawn}	gametes released	$\# \text{d}^{-1}$	Saraiva et al. (2012)
	N^0	individuals in the new cohort	#	$N^0 = N_i^{spawn} (1 - m^{egg})$
Starvation	m_i^F	starvation extra mortality	d^{-1}	$m_i^F = \frac{1}{100} \exp(-70e_i) (-1)^{-1}, \text{ if } e_i \leq -1$ Maar et al. (2009)
Predation	m_i^S	shrimp predation	$\# \text{d}^{-1}$	$m_i^S = \rho^S \{j_{X_m}^S\} \frac{N_i}{N_t^S} \frac{1}{w_i} A_{Ci}^S$
	m_i^C	crab predation	$\# \text{d}^{-1}$	$m_i^C = \rho^C m_t^C \frac{N_i}{N_t^C} A_{Ci}^C$
	m_i^B	bird predation	$\# \text{d}^{-1}$	$m_i^B = \rho^B j_X^B \frac{N_i}{N_t^B} \frac{1}{AFDW_i} A_{Ci}^B$
	$\{j_{X_m}^S\}$	shrimp max ingestion rate	$\text{mol C d}^{-1} \text{cm}^{-2}$	$\{j_{X_m}^S\} = \frac{\{p_{X_m}^S\}}{\mu_E} L_S^2$
	N_t^*	prey available for predator *	#	$N_t^* = \sum_{i=1}^{n_C} N_i A_{Ci}^*$
	A_{Ci}^*	cohort availability for predator *	adim	$A_{Ci}^* = \begin{cases} 1, & \text{if } L_{mP}^* \leq L_i \leq L_{MP}^* \\ 0, & \text{otherwise} \end{cases}$
Cohort Death	D	number of cohorts to die	#	$D = \sum_{i=1}^{n_C} D_i$
	D_i	cohort i state	adim	$D_i = \begin{cases} 1, & \text{if dead} \\ 0, & \text{if alive} \end{cases} \begin{cases} N_i < \text{MinValue, or} \\ M_{Hi} < M_H^b \wedge M_{Vi} < M_V^b, \text{ or} \\ M_{Vi} < M_V^b \wedge L_i < L_b, \text{ or} \\ A_i > a^\dagger \end{cases}$

Table 5.3. Population model main formulations: other quantities.

symbol	description	units	formulation
L_i	organism length	cm	$L_i = \frac{V_i^{1/3}}{\delta_M}$
$V_i^{1/3}$	volumetric length	cm	$V_i^{1/3} = \left(\frac{M_{V_i}}{[M_V]}\right)^{1/3}$
$[M_V]$	volume specific structural mass	$\text{molC}^V \text{cm}^{-3}$	$[M_V] = \frac{d_V}{w_V}$
$[E_i]$	reserves density	$\text{molC}^E \text{cm}^{-3}$	$[E_i] = \frac{M_{E_i}}{V_i}$
e_i	scaled reserves density	adim	$e_i = \frac{[E_i] \mu_E}{[E_m]}$
DW_i	organism total dry weight	g	$DW_i = M_{V_i} w_V + (M_{E_i} + M_{R_i}) w_E$
$AFDW_i$	organism ash free dry weight	g	$AFDW_i = DW_i \psi$

Table 5.4. Model parameters. (dw) represents dry weight and (afdw) ash free dry weight.

process/level	symbol	description	units	value	reference (Balgzand setup)
shrimp	$\{\bar{p}_{Xm}^S\}$	shrimp max ingestion rate	$\text{Jd}^{-1} \text{cm}^{-2}$	48.35	Campos et al. (2009)
predation	$L_{m\text{prey}}^S$	shrimp average size	cm	1.2	Beukema (1992)
	$L_{m\text{prey}}^S$	shrimp minimum prey size	cm	0	this study
	$L_{M\text{prey}}^S$	shrimp maximum prey size	cm	0.2	10% of their size
	ρ^S	fraction of mussels in shrimp diet	adim	[0,1]	this study
crab	m_t^C	crab average ingestion rate	$\# \text{d}^{-1} \#^{-1}$	15	Murray et al. (1992)
predation	$L_{m\text{prey}}^C$	crab minimum prey size	cm	0.5	Mascaró and Seed (2000, 2001)
	$L_{M\text{prey}}^C$	crab maximum prey size	cm	2.5	Mascaró and Seed (2000, 2001)
	ρ^C	fraction of mussels in crab diet	adim	[0,1]	this study
bird	j_X^B	bird average ingestion rate	$\text{g}(\text{afdw}) \text{d}^{-1} \text{cm}^{-2}$	49	adapted from Laursen et al. (2010)
predation	$L_{m\text{prey}}^B$	bird minimum prey size	cm	3	Mascaró and Seed (2000, 2001)
	ρ^B	fraction of mussels in birds diet	adim	[0,1]	this study
mortality	m^N	background mortality	d^{-1}	[0,1]	this study
	m^{egg}	initial egg mortality	d^{-1}	[0,1]	this study
individual	ψ	(afdw) to (dw) conversion factor	$\text{g}(\text{afdw}) \text{g}(\text{dw})^{-1}$	0.85	this study
parameters	μ_E	reserves chemical potential	Jmol^{-1}	6.97×10^5	van der Veer et al. (2006)
	$d_E = d_V$	reserves/structure specific density	$\text{g}(\text{dw}) \text{cm}^{-3}$	0.2	Rosland et al. (2009); Brey (2001)
	$w_E = w_V$	reserves/structure relative molecular mass	$\text{g}(\text{dw}) \text{mol}^{-1}$	25.22	$C_1 H_{1.8} O_{0.53}$ Kooijman (2010)
	M_V^b	structure at birth	molC^V	7.92×10^{-11}	Saraiva et al. (2011b)
	M_E^b	reserves at birth	molC^E	6.0×10^{-11}	Saraiva et al. (2011b)
	M_H^b	maturity at birth	molC^E	4.24×10^{-11}	Saraiva et al. (2011b)
	$[E_m]$	reserve capacity	Jcm^{-3}	1438	Saraiva et al. (2011b)
	a^\dagger	life span	y	24	Sukhotin et al. (2007)

Individual processes

The individual model is based on the standard DEB model (Kooijman, 2000, 2010) coupled with a feeding process model, specifically designed for bivalves (Saraiva et al., 2011a). The model was tested by Saraiva et al. (2012), for different locations in the North Sea, which showed that the main metabolic processes at the individual level were well described.

The model assumes that different types of particles, food and/or inorganic material larger than $1 \mu\text{m}$ can be retained by the organism through filtration (the product of clearance rate by the particle concentration). This size includes all of the phytoplankton, zooplankton, and much of detritus meaning that the bivalve is able to filter all (most) of the suspended matter in the water

column. The clearance rate depends on the total amount of particles in the water (organic and inorganic), in a way that the rate reaches a maximum value (species-specific) with null concentration of particles and it is very close to zero if the amount of particles is very high (simulating the clog of the capture apparatus). Once retained in the gills, particles are then lead to the palps, where the selection is made between particles transported to the mouth and ingested, and particles which are rejected and transported back to the water as pseudofaeces. The third and last feeding step is assimilation, defined as the process where particles are absorbed and converted into the organism's reserve, depending directly on the type of food. The differences in the chemical composition between bivalve reserve tissue and ingested food determines the production of faeces. More details on the feeding model assumptions, formulations and parameter estimation can be found in the study of Saraiva et al. (2011a). The DEB theory assumes that all assimilated energy is first stored as reserve; subsequently the reserve is utilized to fuel the other metabolic processes, following the so-called κ -rule: a fixed fraction of mobilized reserve is used for somatic maintenance and growth, the rest is used for maturity maintenance and maturation (embryos and juveniles) or reproduction (adults). The allocation of energy to reproduction is accumulated in a reproduction buffer. A spawning event corresponds to the emptying of the reproduction buffer which is dependent on the temperature and gonad-somatic mass ratio (GSR). The model also assumes that the organism is able to use the reproduction buffer to cope with somatic maintenance costs (re-absorption of gametes) during starvation periods. During extreme starvation even structure can be used, meaning that the organism's flesh shrinks, though maintaining the same shell length. In the same line, the bivalve is able to reduce its maturity level in order to cope with maturity maintenance (rejuvenation). A detailed description of the individual model, including the formulations and parameters used can be found in the study of Saraiva et al. (2012).

Population processes

Birth of a new cohort

The birth of a new cohort (B) occurs if there is a spawning event. Spawning events occur instantaneously if the GSR and the temperature are above respective thresholds, in agreement with field and laboratory observations performed by different authors (e.g. Chipperfield, 1953; Wilson and Seed, 1974; Podniesinski and McAlice, 1986; Hummel et al., 1989; Thorarinsdóttir, 1996). For simplicity, the model assumes that all the individuals will have maximum reserve density at hatching. This assumption implies a constant egg size, which is thus independent of the condition of the mother. Also, the new cohort will start with the (juvenile) stage immediately following hatching, thus neglecting the short embryonic stage. From the reproduction buffer content of the parents and knowing the newborn properties, a number of gametes are expected N_i^{spawn} . From these, only a part will succeed and become a newborn individual (N^0), as an effect of the initial egg mortality.

Initial egg mortality

Initial egg mortality parameter (m^{egg}) pretends to include all the mortality processes during the egg and larvae phase: e.g., dispersion, egg viability, fertilization probabilities, settlement failure, and possible predation by other predators besides shrimps, crabs and birds. These processes are grouped in the model as a single constant parameter.

Background mortality

The concept of background mortality is commonly used in fish population dynamics, where it includes all possible causes of death except fishing (Pauly, 1980). We assume in this study that the background mortality (m^N) is constant and accounts for e.g., mortality due to diseases and storms.

Food competition and extra starvation mortality

Food competition is one of the main density dependent processes happening within the population. Food is limited and the model assumes that it is shared by all the individuals in the population depending on their filtration skills and abundance. For each cohort a potential filtration is computed based on the environmental conditions, their individual size and the number of individuals. From these values, a whole population potential filtration is computed, summing all the filtration of all the cohorts. If the amount of food in the environment is not enough to fulfil the mussel needs, the food will be redistributed to all the cohorts based on their relative potential filtration, i.e., the more demanding cohorts will benefit from more food items. This assumption is consistent with the assumption made before, that the individuals in each cohort will always remain identical, suffering from starvation exactly in the same way. As described before, the intense starvation can lead to the use of structure to cope with the somatic maintenance (shrinking) and to the reduction of its maturity level (rejuvenation). The model assumes that these processes are reversible if the maturity and structure amounts are higher than the assumed birth values, meaning that the organisms can increase again their maturity and reach adult stage without any physiological consequences. If the state variables reach irreversible values (lower than the values reached at birth), the individuals will die. However, to simulate possible differences between individuals (e.g. position and extreme local food depletion), an extra starvation mortality suggested by Maar et al. (2009) is considered when the condition of the individuals is low and the scaled reserves density is lower than 0.1. This assumption pretends to simulate the death of individuals in the cohort due to local food depletion preventing the sudden death of the whole cohort.

Predation

In the Wadden Sea, and specifically in the Balgzand area, three main predators of mussels can be identified: shrimps, crabs and birds. The brown or common shrimp *Crangon crangon* is one

of the most abundant benthic species in shallow soft areas along the European coast and it preys heavily upon bivalve spat, including mussels, as well as juvenile flatfish (Campos and van der Veer, 2008; Campos et al., 2010). Due to their huge numbers, they exert a significant influence on the survival of their prey and are, therefore, an important structuring force of benthic shallow-water communities (Mattila et al., 1959; Reise, 1985; Andresen et al., 2013). In winter, nearly all shrimps retreat to deeper, generally more offshore waters (Boddeke, 1975) and the abundance of shrimps in the tidal becomes null. Crabs, and the shore crab (*Carcinus maenas*) in particular, can reduce mussel densities substantially (Dankers and Zuidema, 1995). In late autumn and winter, adult crabs move to deeper waters where they stay until the end of winter, after which they migrate back towards the shallower gullies and mudflats (Klein Breteler, 1975). The predation by birds also affects the abundance of mussels, particularly Oystercatchers (*Hematopus ostralegus*), Eider duck (*Somateria mollissima*) and Herring gull, which are mainly present in the Balgzand area during the winter (Brinkman et al., 2002). Oystercatchers and gulls forage on higher elevated tidal flats (Brinkman et al., 2002) while the Eider ducks can be important in the subtidal or near-subtidal areas (Nehls et al., 1997). Predator abundance and intake are considered a forcing function in the model, meaning that there is no feedback from the bivalve population on the predator variables. It is assumed that each predator has a prey size range preference, and the impact of their predation on the number of individuals in each cohort is proportional to the fraction of total prey available in the system that the cohort represents.

Cannibalism

Cannibalism is included in the model by the allowing the adults mussels to feed on their on larvae. Filtration and ingestion are assumed to be equal to any other particle. Assimilation is considered 100% efficient since both individuals (predator and prey) have the same biomass composition.

Cohort death

The whole cohort dies when: (1) reaches an age limit, (2) by intense starvation (described before) or (3) a insignificant number of individuals remain. The first two causes are biological and the last one is basically imposed for technical reasons, to avoid following a constantly increasing number of cohorts, being some of them not significantly important for the population state due to their low number of individuals.

Model setup

Two different model setups were used: a theoretical one testing model parameterizations and a realistic one describing natural population dynamics. The theoretical setup is a simplified version using one single newborn mussel as an initial condition and one food type. This setup is used to study the model properties and test, as much as possible, the effect of each popu-

lation process on the final result. The realistic setup aims to schematically simulate a mussel bed located in the Balgzand area. The tide effect is simulated using a very simple approach: flooding occurs instantaneously, meaning an input of water with Wadden Sea properties (food and temperature) to the mussel bed; high tide is maintained for a fixed number of hours, and during this period mussels continually filter (and re-filter) the water, depleting food concentration; ebb also occurs instantaneously and during the low tide the mussels are outside the water, meaning that they are not able to feed; after the 5 hours of low tide, flood occurs and brings again water with more particles and food, completing the tidal cycle. At the NIOZ research jetty, situated on the northern shore of the Marsdiep, continuous sea surface temperature and salinity observations are being recorded for more than 30 years (van Aken, 2008a,b), as well as chlorophyll-a concentrations (Philippart et al., 2010). Chlorophyll-a concentrations are used as proxy for food quantity. Food composition is imposed by assuming a seasonal pattern on Chlorophyll-a to Carbon and Nitrogen/Phosphorus to Carbon ratios, used to convert chlorophyll observations into food concentration in terms of carbon, nitrogen and phosphorus contents, necessary as a model input. The results from the GETM-ERSEM model were used to obtain a seasonal pattern of those nutrient ratios, as assumed in Saraiva et al. (2012). A more detailed description on the GETM-ERSEM model and its implementation in the North Sea can be found at http://www.nioz.nl/northsea_model and in Baretta-Bekker et al. (1997). Not far from the NIOZ sampling station is the Balgzand area, where data on benthic fauna have been collected twice annually since 1970.

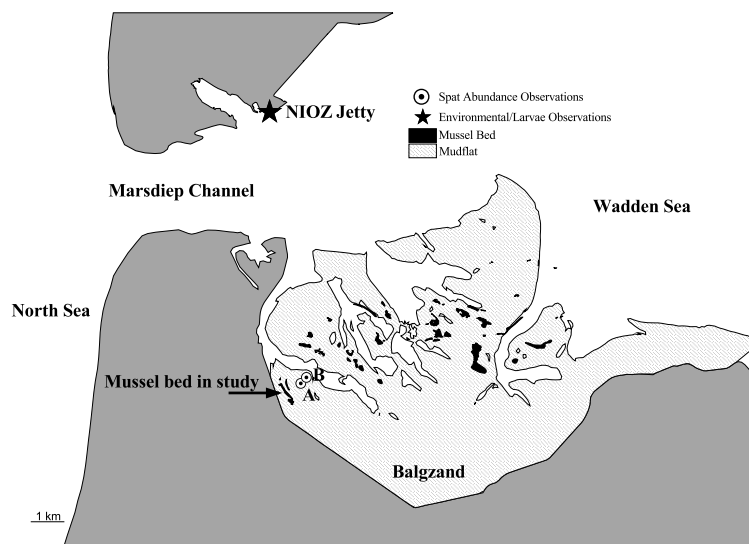


Fig. 5.1. The Balgzand tidal flat area. Locations from: NIOZ research jetty station (water properties by van Aken (2008a,b); Philippart et al. (2010) and larvae observations by de Vooys (1999)); mussel beds (2004 data, provided by Institute for Marine Resources and Ecosystem Studies, IMARES, Wageningen UR); A and B represent locations where spat abundances were measured by Rob Dekker (unpublished data); and the mussel bed which data was used in this study for the initial size distribution of mussels (Beukema and Dekker, 2007).

At 15 fixed stations, numerical densities and ash-free dry weights were determined of all large-sized species of benthic animals, using a 1-mm sieve (Beukema, 1989, 1991; Beukema and Cadeé, 1986; Beukema and Cadée, 1997; Beukema et al., 2002; Beukema and Dekker, 2007). In the summer and autumn of 1990, nearly all mussels and cockles were fished from the tidal flats of the Dutch Wadden Sea (Beukema et al., 2002) and, as a management solution, mussel fisheries were forbidden in the area from 1991 on. One particular mussel bed lost all the mussels, recovering some mussels in the year after. Because this mussel bed has a long time series of observations and because from 1991 no fishery was allowed, it is potentially useful for comparison between model and field observations.

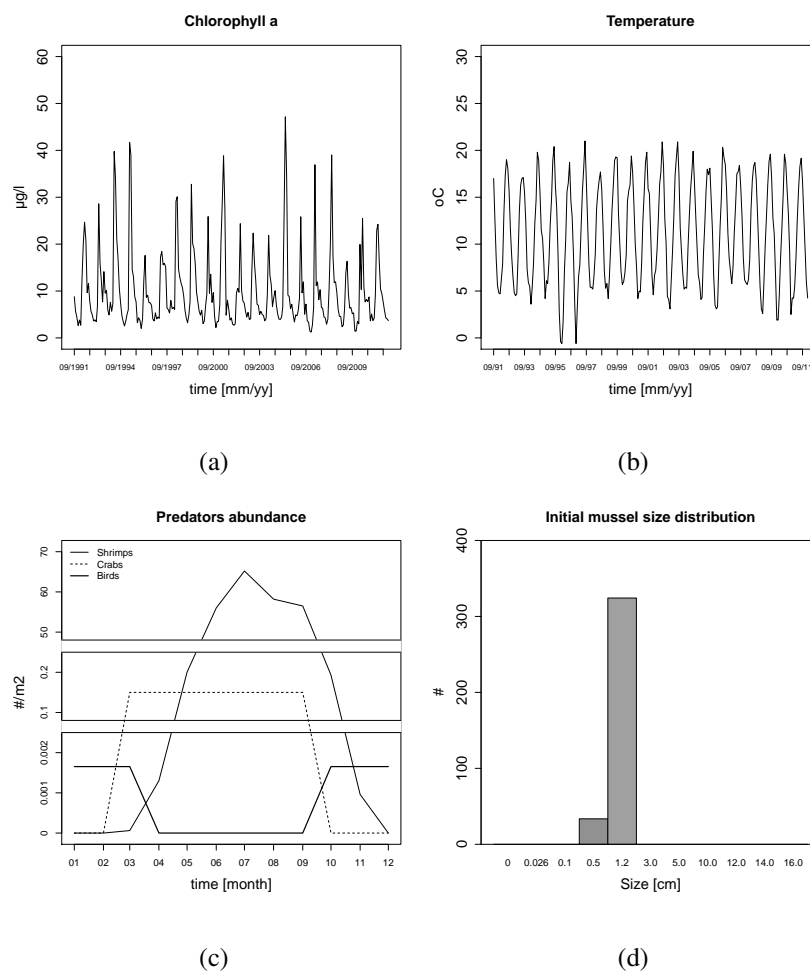


Fig. 5.2. Field observations used for the schematic mussel bed simulation: (a) chlorophyll-a concentration (Philippart et al., 2010); (b) temperature (van Aken, 2008a,b); (c) predators: shrimps adapted from Beukema (1992), crabs adapted from Smallegange et al. (2009) and birds adapted from Andreas Waser, unpublished data; (d) initial conditions for the mussel size distribution (Beukema and Dekker, 2007).

The size distribution at this location, in the winter of 1991, is used as initial conditions for the model, and the field observations made within the long-term monitoring program, are compared with model results. Predator abundance is assumed to have seasonal variation in the system: shrimp abundance was adapted from Beukema (1992); crabs from Smallegange et al. (2009) and birds from Andreas Waser (unpublished data). The location of the mussel bed and the water column monitoring station is presented in Fig.5.1 and the field observations used in the study are presented in Fig.5.2.

Results

Mortality promotes life

To assess the effect of the different types of mortality (except predation) on the population dynamics, a theoretical setup of the model was used with one single newborn mussel as initial condition, one constant food type and constant temperature in three different scenarios: (1) only starvation, where no other type of mortality is considered; (2) starvation and aging; and (3) starvation and background mortality. Some of the main results are presented in Fig.5.3. Without any other type of mortality but starvation, the population evolves to a stable, but unproductive, state. The simulation starts with a single mussel that grows and reproduces well, producing new cohorts. The number of individuals in the system increases and due to food limitations, the amount of food available for each individual decreases substantially. Starvation events become frequent and organisms decrease their reproduction buffer, and ultimately their maturity (Fig.5.3f) and structure (Fig.5.3d and Fig.5.3e), to cope with maintenance costs. Under these conditions, spawning events do not occur anymore (Fig.5.3c) and, because no mortality is imposed in the model, the population consists of a constant number of immature organisms (Fig.5.3a and Fig.5.3b). In the scenario with aging, death was imposed to organisms older than the maximum life span of the species. The difference from the previous scenario is that the aging effect results in the death of the whole population after some time. The effect of the background mortality in the system is, however, very significant. The death of some organisms will benefit others, through an increase in food availability and, as a consequence, some individuals will actually be able to grow and reproduce generating new cohorts and inducing a clear cycle in the number of organisms in the population. The period of the cycles will depend on a balance between food concentration, gamete production and the value of the background mortality.

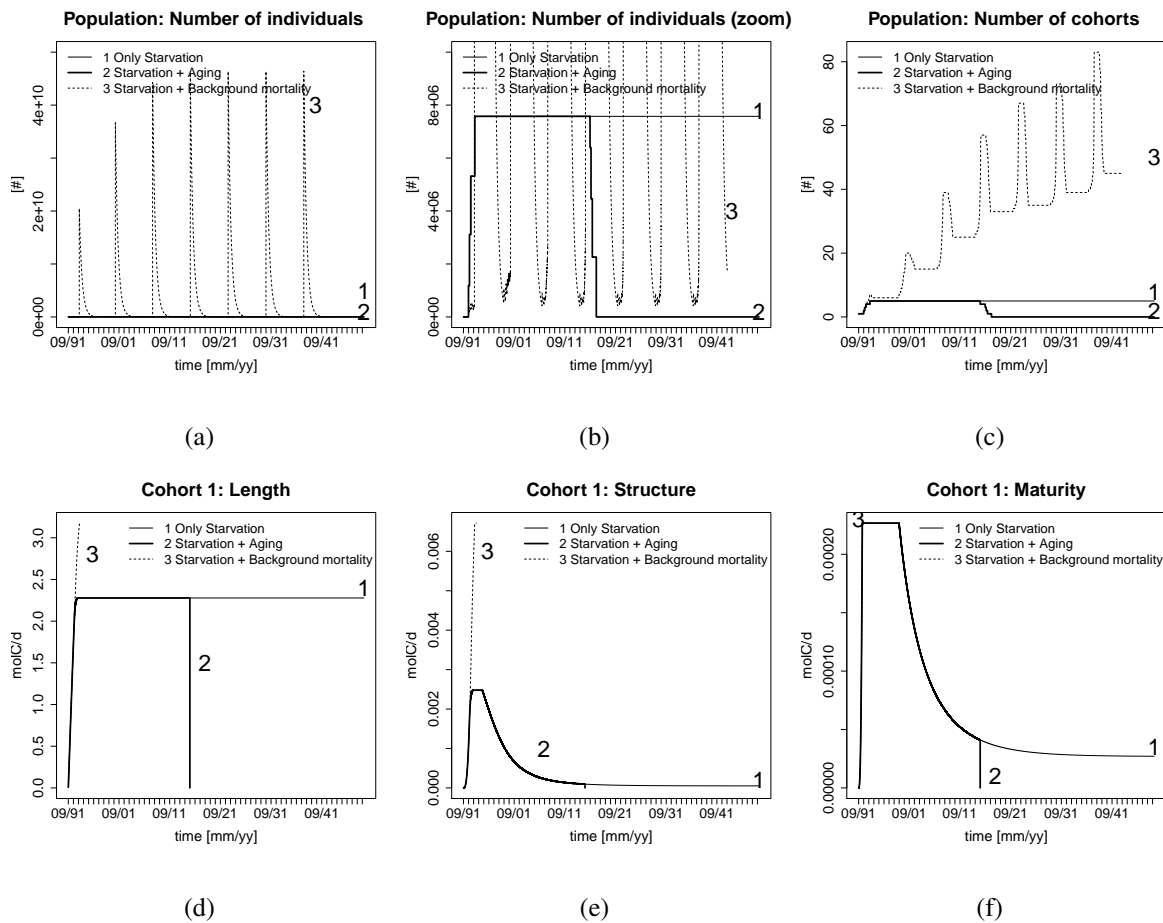


Fig. 5.3. Model predictions for the population and cohort dynamics resulting from a newborn single mussel living in constant environmental conditions (12°C and 0.5 mgC/l) in three different mortality scenarios: (1) only starvation, (2) starvation and aging and (3) starvation and constant background of 0.005 d^{-1} . (a) and (b) represent total number of individuals in the population; (c) represents the number of cohorts; (d), (e), and (f) represent length, structure, and maturity level of the first cohort, respectively.

Tide defines the population state

In the current setup of model, the main effect of tide is the change in food availability. It is assumed that during low tide the mussel bed is completely above water and individuals are not able to feed. However, individuals still have to cope with their maintenance costs during that time. For that reason, one of the expected consequences of tide is that the individuals living in an intertidal environment will be smaller than individuals living in subtidal areas, if all the other processes are the same.

Fig.5.4 presents some of the model results obtained with and without the tidal effect. The reserve dynamics of each individual clearly depends on the existence of tide (Fig.5.4a). During low tide periods, without food, and with the continuous need of maintenance, the reserve biomass decreases, increasing again during high tide. This decrease in reserve has the ultimate consequence of limiting the growth of the individual and the predicted length is considerably different between the two scenarios (Fig.5.4b). The main consequence for the population itself

is a decrease in numbers and also the intensity of the spawning events (Fig.5.4c), as well as a decrease of the maximum individual length in the population (Fig.5.4d). In fact, the scenario with tide reveals two extreme starvation events, leading to the death of some cohorts, shown in this figure as the two periods where the maximum individual size is higher in the scenario with tide: the growth of some individuals benefited from the death of others. However, those periods do not present values higher than the overall maximum value obtained in the scenario without tide. With tide, i.e., with more food availability, the population presents a higher number of cohorts, individuals and also a higher biomass, as shown in Fig.5.4e and Fig.5.4f.

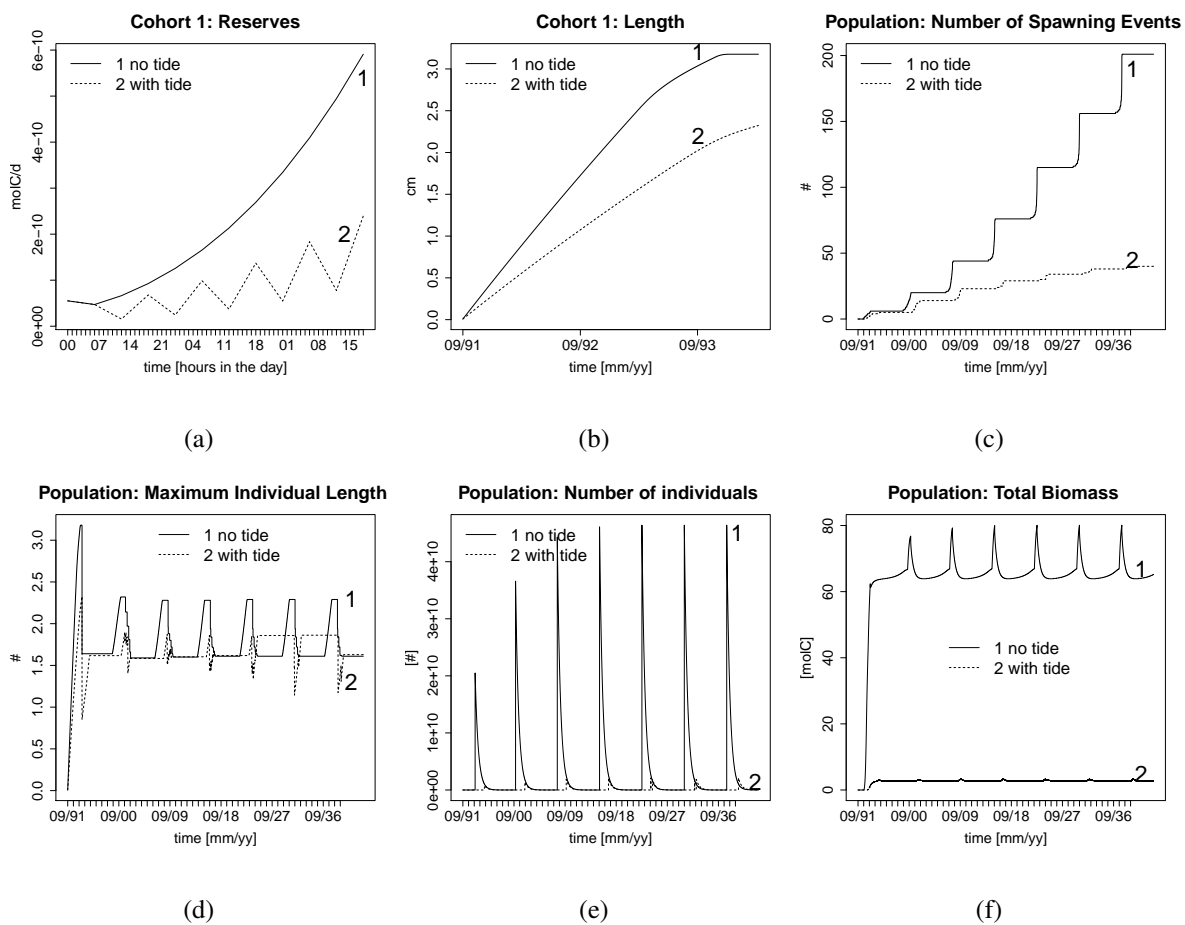


Fig. 5.4. Model predictions for the population and cohort dynamics resulting from a newborn single mussel living in constant environmental conditions (12°C and 0.5 mgC/l) and aging and background mortality (0.005 d^{-1}) (1) with and (2) without tide. (a) reserves for the first cohort during the first 3 days of simulation; (b) length of the first cohort; (c) number of spawning events from the beginning of the simulation; (d) maximum individual length in the population; (e) total number of individuals in the population and (f) total biomass.

Mortality controls persistence

Mortality promotes life, but it also controls persistence. Under realistic mussels initial size distribution, seasonal average conditions of temperature, food concentration and abundance of

predators, described in a previous section and presented in Fig.5.2, several scenarios on different mortality rates were performed. The scenarios were planned to cover, as much as possible, the range for the mortality related parameters: background mortality, m^N , [0-0.05]; initial egg mortality, m^{egg} , [0-1]; fraction of mussels in the shrimp' diet, ρ^S , [0-1]; fraction of mussels in the crab' diet ρ^C , [0-1]; fraction of mussels in the birds' diet, ρ^B , {0, 0.5, 1}. Fig.5.5 presents the results of the persistence analysis of the population for all the scenarios, after 30 years of simulations. Each panel in the figure represents results for one of the three tested values of the fraction of mussels in birds diet (ρ^B), where different values of background and egg mortality were used. Each small plot (example shown in Fig.5.5a) presents the results obtained by different combinations of shrimps (horizontal axis) and crabs (vertical axis) diet fraction parameters for fixed values of background and egg mortality.

The first conclusion is that significant differences can be found depending on the combination of parameters used in the study. Several combinations result in the extinction of the population, particularly when the background mortality is higher than 0.01. The results also show that high values of initial egg mortality, higher than ~ 0.95 , restricts the range of possible values of the fraction of mussels in the shrimps diet, in order to verify the persistence of the population after 30 years. On the contrary, the balance between shrimp and crab predation does not play a significant role in the population persistence with lower values of initial egg mortality and background mortality. Crab predation only become determinant in a very specific range of parameter combination, when initial egg mortality is lower than 0.8 and the background mortality is 0.006 and 0.008. In the same way, the comparison between the three maps obtained for the different values of the fraction of mussels in the birds' diet shows that the predation pressure of the birds seems to be important for the sustainability of the mussel population only in a few scenarios, particularly when the background mortality is low.

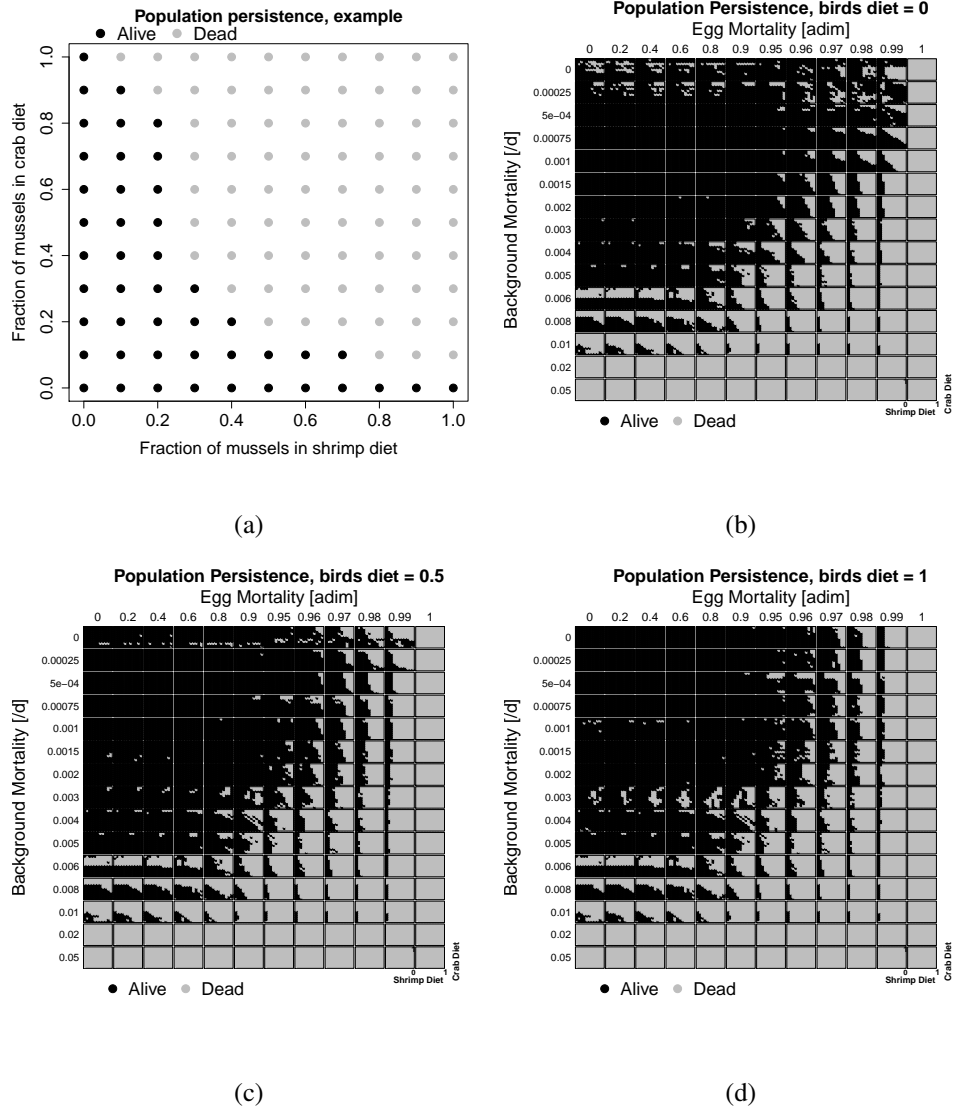


Fig. 5.5. Model predictions for the population persistence under realistic conditions of seasonal temperature food concentration and predator abundance. Several combinations of mortality parameters were tested: background mortality, m^N [0-0.05]; initial egg mortality, m^{spat} [0-1]; fraction of mussels in shrimp diet, ρ^S [0-1]; fraction of mussels in crab diet, ρ^C [0-1], and fraction of mussels in bird diet, ρ^B {0, 0.5, 1}. a) represents an example of each plot in each panel, corresponding to the model results for different combinations of shrimp and crab diets for fixed values of initial egg and background mortality. Each model simulation is represented by a dot. The color black represent scenarios where alive mussels were found, after 30 years of simulation, and gray represent scenarios where all the mussels died. b), c) and, d) represent, respectively, a map of the results found for the three tested values of the fraction of mussels in bird diet, ρ^B {0, 0.5, 1}.

Model and Field Observations

The use of different parameter combinations resulted in a considerable amount of model scenarios. Population persistence was the first criteria to select for a possible range of parameters. The following realistic criteria were subsequently included:

- Predation: parameters concerning the fraction of mussels in the predators diet (ρ^S , ρ^C , ρ^B) should not be zero, because the predation pressure exists;
- Length: the maximum size in the end of the simulation should be higher than 4cm, because field observations show the presence of individuals with this size;
- Spawning: the number of spawning events should be higher than 12, in the 30 year simulation, because this is the number of peaks clearly shown in the observations of the total number of individuals ;

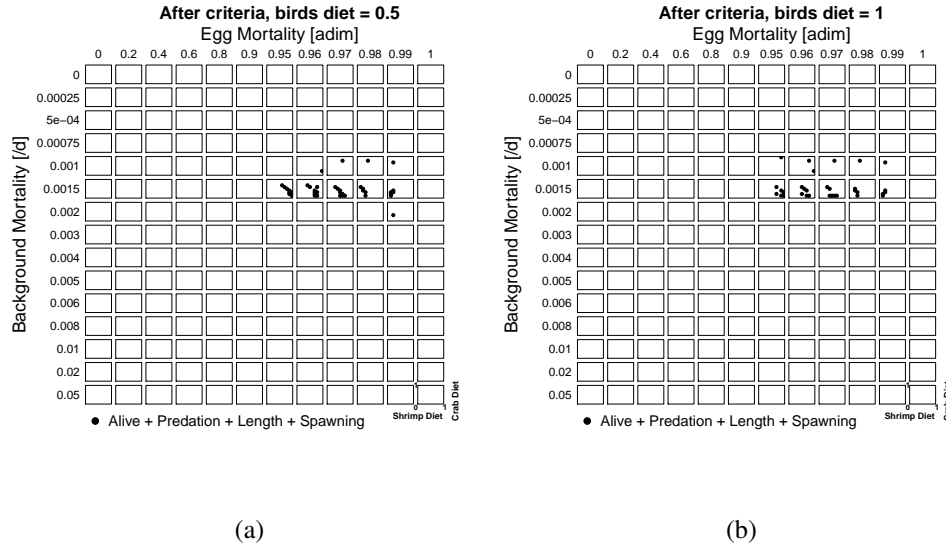


Fig. 5.6. Parameter combinations that after 30 year of simulation produce results on the mussel population dynamics that fulfil the realistic criteria: population persist, predation, maximum length in the population higher than 4 cm and number of spawning events higher than 12, for ρ^B values of 0.5 and 1.

From a total of 65227 parameter combinations, 11702 scenarios lead to the population persistence (Fig.5.5), and only 73 fulfil all the realistic criteria (Fig.5.6). The figure show that the possible values are restricted to a particular area in the plot where background mortality is between 0.001 and 0.0015 and initial egg mortality is higher than 0.95. Nevertheless, the range of possible values for the predation pressure is still significant. Fig.5.7 represents an example of the model results using one particular parameter combination as an example and the available field observations. The presented model results are similar to the other model outcomes using the other realistic selected parameter combinations.

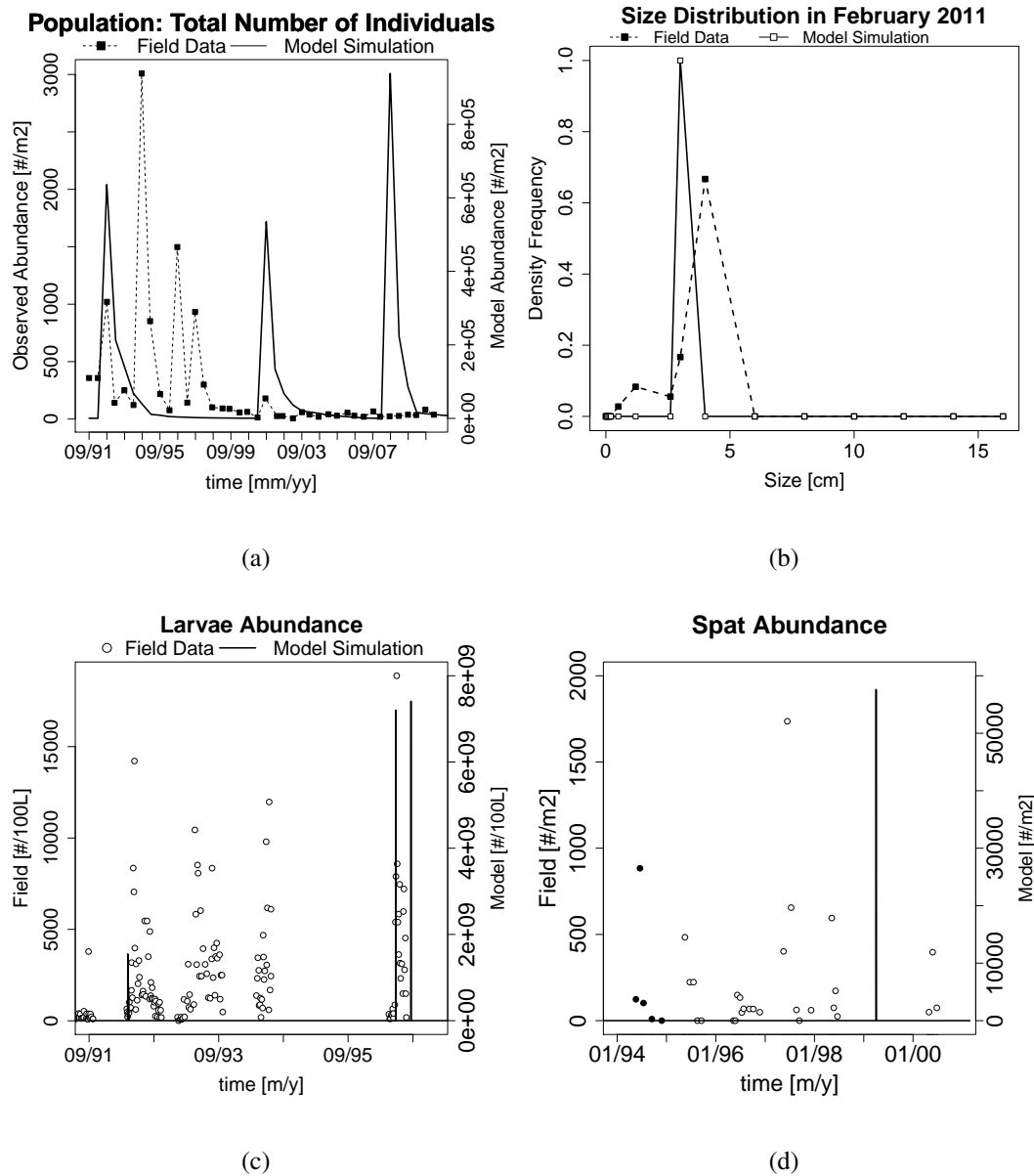


Fig. 5.7. Example of model vs. Observations. Model simulation assumed $\rho^S = 0.2$; $\rho^C = 0.7$; $\rho^B = 1$; $m^N = 0.001$; $m^{egg} = 0.98$. Field observations were obtained by: a) and b) (Beukema and Dekker, 2007) on the total number of individuals in the mussel bed at the Balgzand area with size above 0.1 cm and size distribution; c) and d) (de Vooy, 1999) on the abundance of mussel larvae on the western part of the Dutch Wadden Sea, and e) Rob Dekker (unpublished data) on spat abundance of mussels at locations A and B represented in Fig. 5.1. Larvae correspond to an organism of size range [0.0073; 0.026[cm in the model and size higher than 0.007cm in the field data. Individuals with size [0.03; 0.15[are considered to be spat in the model and in the observations.

Discussion

An individual based population model can be seen as a book-keeping tool for all the cohorts in a population generated by the individual model. Its design and implementation are straightforward, from the conceptual point of view, once an individual model is constructed and the technical (programming) problems are overcome. But the population model also includes two

additional features: food competition, with starvation as a possible outcome, and mortality. These features control the population state, as much as the processes at the individual level. In fact, that is the reason why it is so interesting to use a population model, where all the important processes are included and integrated. However, the use of such a tool also implies the availability of a significant amount of information: knowledge on processes, mechanisms, and measurements, concerning both the target population state variables and the environmental conditions, which include the characteristics of the main predators. This modelling exercise started by testing the model responses to changes in input variables (food conditions, through tide effect) and ecological processes (types of mortality). General results from the theoretical scenarios were in line with expectations, i.e., the model is correctly responding to changes in the imposed values.

Model parameters are the critical aspects of every model and this study also shows that changes in the parameters can have significant changes in model outcome. The presented model requires many parameters. The number of parameters at the individual level necessary for the DEB model is higher than many alternative models, but it also deals with many more processes that are included in interaction. The number of parameters per included process cannot be lower, because many of them just have a single parameter and mechanisms prescribe which processes are interacting and why. In the last decades, an important effort was made to assess the DEB parameters of several bivalve species, including the blue mussel (e.g., van Haren and Kooijman, 1993; van der Veer et al., 2006; van der Meer, 2006; Rosland et al., 2009; Lika et al., 2011; Saraiva et al., 2011b). This effort resulted in a set of parameter values, or at least a set of parameter ranges, that can be used with some confidence (e.g., Saraiva et al., 2012). The different types of data that can be fitted with the model are unprecedented. The confidence in the population process parameters is, however, much lower. Some studies on the predation of mussels by other organisms could be used to assess the relevant parameters (Table 5.4). Nevertheless, in the current model setup, five (or at least four) important parameter estimates are still missing: fraction of mussels in shrimp diet (ρ^S), fraction of mussels in crab diet (ρ^C), fraction of mussels in birds diet (ρ^B), background mortality (m^N) and initial egg mortality (m^{egg}). The first three are the parameters concerning the fraction of mussels in the predators' diet (shrimp, crab and birds). Most of the available studies on the feeding rates of the predators and energy requirements are based on laboratory experiments that usually use only one type of prey. In a mussel bed, most of the organisms in the shrimps/crabs/birds eating size range would be mussels, but not only. It is, in fact, very unlikely that predators will select only mussels if similar organisms, within their possible feeding size range, are available. Thus, the question is: what is the proportion of mussels in shrimps' diet, in a mussel bed? The same question can be addressed for the crab and bird predation on mussels. No studies were found that could reveal the proportion of mussels in the crab diet in the field. Concerning the birds, the present study does not distinguish between different species of birds, despite differences in abundance and ingestion rate. The reason was mainly to simplify and reduce the number of unknown parameters in the model. The

proportion of mussels in the Oystercatcher diet can be estimated as about 50% based on seasonal measurements made by Ens et al. (2010). Thanks to this knowledge, the number of tested values concerning the birds diet could be kept substantially lower than for the other predators. Information on the background and initial egg mortality is also lacking. Initial egg mortality is indeed very difficult to estimate. In the current model setup this parameter is supposed to group not only egg viability to growth, but also the effect of the larvae dispersal due to the water flow. Sprung (1984) suggests that more than 99% of the eggs would not survive, but, so far, no quantitative measurements were performed to make a more accurate estimation of this parameter. Finally, the last completely unknown parameter is the background mortality, which intends to include all the natural causes of death as diseases, storms and also other predators not included explicitly in the model. As to our knowledge, no estimates are available for this parameter on bivalves, although it has an important effect in the dynamics of the populations. Pauly (1980) presents a relationship between natural mortality, defined by the author as all possible causes of death except fishing, and the size of the individuals, based on the collection of several data on different organisms and habitats, from different sources. Fig.5.8a presents the comparison between the relationship proposed by Pauly (1980) and the values obtained in this study for the total mortality (that can be directly compared with the natural mortality from literature), considering the maximum size that the bivalve can possibly reach (16 cm). The model values correspond to the scenarios with the outcome that fulfill all the realistic criteria. The values are in the same order of magnitude as the estimates collected by Pauly (1980).

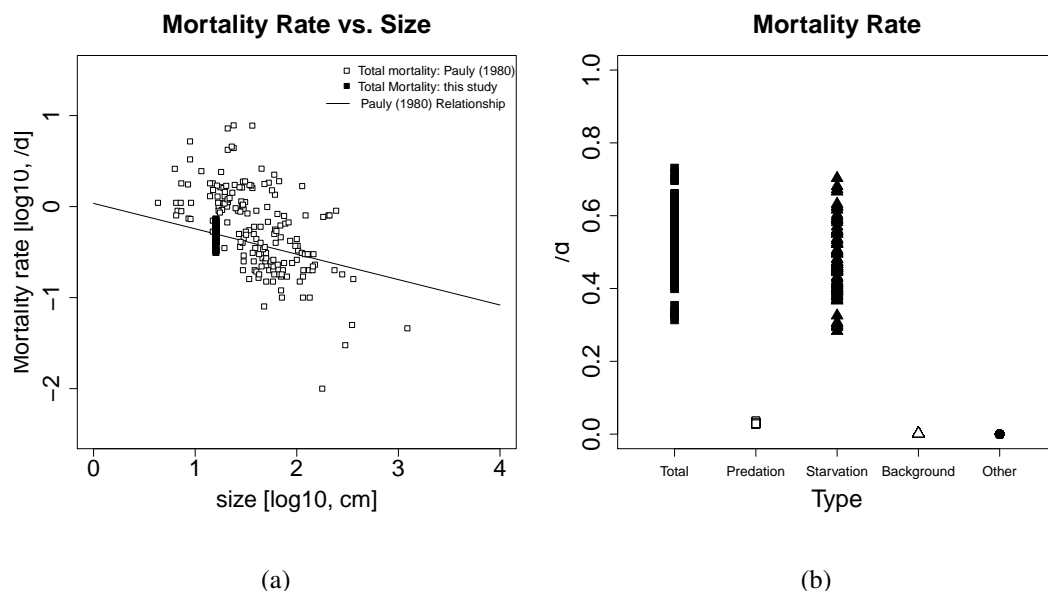


Fig. 5.8. Mortality rate: a) comparison between estimations of natural mortality (as all possible causes of death except fishing) by size, collected by Pauly (1980) and the values of total mortality computed by the model in the possible scenarios (fulfill the realistic criteria); b) different types of mortality computed by the model.

As shown, different outcomes are possible when considering a different combination of param-

eters. The use of realistic criteria made it possible to narrow the parameter range but results do not allow the selection of one unique best scenario. The example on the model results presented in Fig.5.7 shows that the model captures some of the peaks in the total number of individuals and larvae abundance, although the number of individuals and the spat abundances, available only for some years, are not well reproduced. The size distribution after the 30 years of simulation compares reasonably well with the observations, showing that there is a predominant size class of individuals with relatively high sizes (4cm in the model, about 5 cm in the observations). All the realistically selected model scenarios produced similar results and unfortunately there was no (to our knowledge) acceptable criteria that could excel one particular scenario. The most common criteria, the relative error, computed as the difference between model and observation are, in this case, insufficient due to the very high and very similar values between scenarios and the choice was to make no selection. However, the study revealed some interesting results and conclusions that can be used in further studies. The test on the persistence of the population shown that in most of the combinations bird predation is not determinant for the population persistence. Also, that crab predation only becomes determinant in a very specific range of parameter combination, when initial egg mortality is small (lower than 0.8), which is somehow unlikely (Sprung, 1984). Thus, the shrimp predation assumes a high importance in the population persistence together with the initial egg mortality and background mortality. Fig.5.8b presents the range of the geometric average of the different types of mortality considered in the realistically selected model scenarios. It shows that starvation mortality is very important compared with other types of mortality, although it only occurs in very specific moments of low food events. Thus, food quantity and quality characterization will be the determinant in predicting realistic population dynamics. In the current setup of the model there is however a significant uncertainty concerning the environmental conditions, which are based on the measurements made at the northern shore of the Marsdiep and not exactly next to the mussel bed in study (Fig.5.1). The underlying idea of the presented model setup is that the water that flows from the Marsdiep channel will cover the mussel bed and that the subsequent measurements on the environmental conditions will include the effect of the intertidal area ecological activity on the water column properties. Processes within the intertidal area, such as local primary production are not explicitly included in the model. Moreover, it is assumed that all the phytoplankton species that contribute to the chlorophyll measurement are suitable for mussel filtration, which does not need to be the case during specific seasonal events, e.g. picoplankton blooms (Vahl, 1972; Møhlenberg and Riisgård, 1978) or phaeocystis blooms (Smaal and Twisk, 1997). The number of individuals predicted by the model is, in general, higher than the observations. In addition to the uncertainties in the food quality and quantity, other factors can contribute to this result. Likely, the constant value of initial egg mortality parameter is not enough to simulate properly the larvae dispersion and also the possible settlement failure of spat and it is also possible that there is a maximum in the individual abundance caused by e.g., space competition, which was not taken into account. The choices made in this study to simplify the approach were

done not only due to lack of data at the study site on these particular topics, but also because it would increase the complexity of the population model and perhaps interfere with the analysis of its properties at this point. The results suggest that a realistic setup will also need more realistic description of the processes. The coupling of the population model to a hydrodynamic and biogeochemical model will be the next step. The hydrodynamic/transport model will enable the simulation of larval dispersion and the exchange of water properties, specifically food, with other areas in the system and the simulation of the biogeochemical processes will also allow the feedback of the mussels in the water properties.

Conclusion

An individual based population model for bivalves was designed, built and tested to simulate the population dynamics of a mussel bed located in the Balgzand intertidal area. The processes at the individual level were simulated following the DEB theory and as population processes the model includes egg mortality, background mortality, predation and food competition. The realistically selected modeling scenarios are able to reproduce the timing of some peaks in individual abundances in the mussel bed and produce in a similar size distribution of individuals, but the number of individuals is not well predicted. Possible causes for this result were identified and suggestions were made to overcome the discrepancy. Now that the population model is tested and the range of possible parameter values is narrow, the model can be further developed in order to fill the identified gaps and different approaches and complexities can be tested in the future. This study is an important stepping stone in the simulation of the population dynamics in coastal areas and the future step is now to couple it to a hydrodynamic and biogeochemical model, that could simulate the transport of properties (nutrients, food and egg/larvae) in the water column and consequently the exchange between the different areas in the system, as well as the losses due to settlement failure and feedback of mussels in the system dynamics.

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6. The role of bivalves in the Balgzand: first steps on an integrated modelling approach

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The present paper describes a process oriented modelling tool that integrates physical, biogeochemical, ecological and physiological factors governing bivalve populated marine ecosystems. This modelling tool is the result of the coupling between an individual-based population model for bivalves (based on the Dynamic Energy Budgets theory, DEB) and a hydrodynamic/biogeochemical model (MOHID Water Modelling System). The model was implemented in the Balgzand area (Wadden Sea, The Netherlands) in a fine resolution domain to study mussel population dynamics and to quantify the influence of mussel communities on the pelagic system. Model results for a reference scenario (2009/2010) are in good agreement with observations, and provide a consistent quantitative description of local hydrodynamics and biogeochemical cycles. The Balgzand acts as a sink of phytoplankton due to bivalves' filtration, and a source of ammonia, exporting about 40% more than the input flux. These results suggest significant ammonia regeneration. Results show that despite the long and almost continuous spawning season, only a few cohorts are able to survive. Early stage mortality (top-down) can control the persistence of new cohorts in the first month, in particular cannibalism and shrimp predation, although starvation (bottom-up) represent the main loss process in an overall analysis, in terms of biomass. The tendency is that new mussel beds are formed in areas adjacent to existing mussel beds and channel edges, depending on the settlement probability. Bivalves' activity intensifies the seasonal patterns of food and nutrients in areas close to the mussel beds, though not changing their overall spatial distribution. This study not only confirms but quantifies mussels' potential to influence ecosystem functioning due to their role in nutrient cycling. As the first integrated modelling study that focus on the mussels' beds in the Balgzand, the main difficulties on the model design, setup and results analysis were overcome. The model can now be further used, tested and improved in the same or other systems in order to serve as an effective and reliable scientific and management tool.

Keywords: mussel bed, IBM, ecosystem model, DEB theory, MOHID, Balgzand

Introduction

Bivalves, which are common to many coastal habitats, are probably ecologically and economically the best studied benthic suspension feeding group (Dame et al., 2001). The ability to predict the dynamics of bivalve populations in response to environmental change, natural or human induced, is quite useful for the management of coastal ecosystems, either with the purpose of commercial exploitation optimization, environmental impact assessment, climate changes implications or assessing the impact of exotic species introduction. Mathematical models have been used to address some of these questions. Although they can vary enormously in terms of complexity, their focus is either more oriented on (i) the eco-physiology of the individual bivalves, coupled or not with biogeochemical and biological models, but with 'simplified' descriptions of physical processes (e.g. Brinkman and Institute for Forestry and Nature Research (Wageningen), 1993; Baretta et al., 1995; Dowd, 1997; Scholten and Smaal, 1998; Ren and Ross, 2001; Savina and Ménesguen, 2008; Brigolin et al., 2009; Ferreira et al., 2009) or on (ii) physical transport, using complex physical models where only 'simple' formulations for biogeochemical/biological processes were introduced, e.g. GETM (Burchard and Bolding, 2002), COHERENS (Luyten et al., 1999), MOHID Water Modelling System (Miller and Pinder, 2004). Generally, the first group of models aims to predict the bivalve production and the second group aims to predict the impact of bivalves activity on system properties, such as primary production. The constant developments in computer hardware and programming languages enabled the development of models that couple complex descriptions of both ecological and physical processes. The challenge is now to get better predictions of the bivalve production and their population dynamics in interaction with an ever changing environment by improving the description of the availability of their food and physical processes. Such descriptions can be supplied by 'physical transport' type of models.

Several difficulties arise compared with the traditional modelling approach followed for phytoplankton and zooplankton. Most of these difficulties are caused by two facts: (i) bivalves have both a pelagic stage, where they are transported in the water column and directly depend on physical processes, and a benthic stage; (ii) their food requirement (bottom-up processes) and their interactions with other species (competition and top-down processes) strongly change throughout their life cycle (embryo, juvenile and adult stages). One of the main consequences is that reproduction and recruitment success are not easy to predict if these two facts are not properly addressed. In some of the current modelling approaches the problem is solved either by imposing spawning events at a specific time (e.g. Maar et al., 2010) or by considering them dependent on environmental variables (e.g. Gerla et al., 2014), but the reproduction is detached from the bivalve development stage. In addition, understanding top-down control requires the simulation of the change in size of individual bivalves, throughout their main live stages (larvae, juvenile and adult), since predators have a size preference. Size structure in the population has been normally neglected or imposed, though. Probably because most models have been

developed for environmental impact assessment, where either the size structure is artificially controlled, as in aquaculture systems, or simply because it is found too complex. However, model aims go now beyond aquaculture assessments and new questions are raised, for example on population responses to climate change. Other examples are related to the introduction of new species in lower, same and upper trophic levels, changes in food quality, changes in habitat morphology, changes in hydrodynamics, temperature or salinity. All these questions can only be addressed if size structure is considered in the population, through the simulation of the individual bivalve development. For this purpose, energy budget models have received some attention (Beadman and Kaiser, 2002), in particular the DEB theory, proposed by Kooijman (1986, 2000, 2010). It is based on a mechanistic view of an organism's metabolic processes, including growth, maturation and reproduction, where the basic principles and formulations are valid for all different stages of the individual. In practice, this means that the same set of equations can be used to simulate the complete life cycle of a bivalve. Recent developments have facilitated its use, which makes DEB theory a good option to build a model of the bivalve individual and to further couple it to hydrodynamic and biogeochemical models that already have a high level of complexity. Yet, this approach can significantly increase model complexity, *i.e.* higher number of state variables, more/different uncertainties to cope with, higher number of parameters to estimate, larger amount and variability of input data, higher computational time, and also larger volumes of output results to analyse.

Advantages and disadvantages of complex models use have been discussed in the last years (Fulton et al., 2003; Cury et al., 2008; Hannah et al., 2010, *e.g.*), although with more focus on fisheries and end-to-end models. Conclusions are not yet established, but the fact is that very simplistic models fail to capture critical interactions and system components, but extremely complicated models can be impacted by uncertainty, computational cost and lack of accuracy (Fulton, 2010; Hannah et al., 2010). Models are suitably complex if all critical processes, drivers and components under scrutiny are captured (Fulton, 2010), which can be difficult to assess. In this paper, with the aim of predicting the bivalve population dynamics and quantify their influence on the pelagic system we propose that the model should be able to simulate the size structure of the population, based on the individual development, through its main life stages (larvae, juvenile and adult) in a dynamic environment with changes in nutrients, temperature, and food driven by physical processes, as well as predators' seasonal abundance. Following this idea, the present paper describes a process oriented modelling tool that couples an individual-based population model for bivalves (based on the Dynamic Energy Budgets theory, DEB) and a hydrodynamic/biogeochemical model (MOHID Water Modelling System) and its implementation in the Balgzand area (Wadden Sea, The Netherlands).

Material and Methods

Model Description

MOHID Water Modelling System

MOHID (www.mohid.com) is a three dimensional (3D) water modelling system developed at Instituto Superior Técnico (IST), University of Lisbon. It consists of a set of coupled models that aim to simulate the main physical and biogeochemical processes in aquatic systems (Miller and Pinder, 2004). MOHID has been implemented and validated in different coastal/estuarine areas (e.g. Leitão et al., 2005; Trancoso et al., 2005; Saraiva et al., 2007; Vaz et al., 2009). The system is based on the finite volume concept and it is designed in a hierarchical modular structure, using an object oriented approach. The hydrodynamic model solves the primitive continuity and momentum equations for the surface elevation and 3D velocity field for incompressible flows, in orthogonal horizontal coordinates and generic vertical coordinates, assuming hydrostatic equilibrium and Boussinesq approximation (Martins et al., 2001). Momentum, mass and heat transport are computed using a generic 3D advection-diffusion library including high order advection schemes. It also includes a fine sediment transport module simulating settling, deposition and erosion for a generic class of particles and/or particulate matter. Erosion and deposition fluxes depend on bottom shear stresses that are calculated as function of near bottom currents and wave induced stress. The model comprises several modules to compute pelagic biogeochemical processes. The current study uses the Water Quality Module, based on formulations initially developed by the US Environmental Protection Agency (EPA) (Bowie et al., 1985). It can be considered as a NPZD model and its base features include: explicit simulation of nitrogen and phosphorous cycles; assumption of constant C:N:P ratios for organic matter and plankton; one group of phytoplankton, one group of zooplankton, dissolved nutrients and dissolved and particulate phases of organic matter. The pelagic ecological processes parametrization is mainly adapted from EPA. Modelled benthic ecological processes, occurring in deposited sediments, include the mineralization of organic matter. Detailed information on the model structure, formulations and default parametrization can be found in www.mohid.com.

Individual based population model for bivalves

The population of bivalves is represented by several cohorts. Each cohort consists of a number of identical individuals born at the same time and with the same properties (e.g. size, biomass, state of development). The individual model is the standard DEB model (Kooijman, 2000, 2010), but coupled with a feeding processes model, specifically designed for bivalves (Saraiva et al., 2011). DEB theory assumes that the assimilated energy is first stored as reserve; subsequently the reserve is utilized to fuel the other metabolic processes, following the so-called κ -rule: a fixed fraction κ of mobilized reserve is used for somatic maintenance and growth, the rest is used for maturity maintenance and maturation (embryos and juveniles) or reproduction

(adults). The allocation of energy to reproduction is temporarily accumulated in a reproduction buffer. A spawning event, which is dependent on temperature and gonad-somatic mass ratio (GSR), empties the reproduction buffer. Each spawning event gives origin to a new cohort in the system. To avoid the possible exponential increase in cohorts, a minimum time between spawning events can be imposed (7 days in this study). Different types of particles, food and/or inorganic material, can be retained by bivalves through filtration. A detailed description of the individual model can be found in Saraiva et al. (2012) where the model performance was tested for different locations in the North Sea.

At the population level the model includes: initial egg mortality, background mortality, food competition, cannibalism, and imposed predation by shrimps, crabs and birds. Predator abundance and intake are considered a forcing function in the model, meaning that there is no feedback from the bivalve population on the predators. Each predator has a prey size range preference, and the predation impact in each cohort is proportional to the fraction of the number of individuals in the cohort and the total number of prey available. More detail on the population model formulations, assumptions and setup can be found in Saraiva et al. (2014). The coupling with the ecosystem model enabled the inclusion of two additional mortality effects in the population: (i) mortality by velocity above 0.5 m/s, assuming that bivalves are flushed away and eventually die, and (ii) mortality by wrong settlement, meaning that a settlement probability is imposed on each location, based on the fact that mussels have a preference to settle on substrates with coarse shell debris (wa Kangeri et al., 2014). The underlying assumption is that non-settled bivalves will eventually die, due to the effect of currents or burying. The settlement occurs instantaneously when, and where, the individual length is higher than 0.026 cm (de Vooy, 1999).

Coupling biological and physical processes

The coupling philosophy assumes that the biogeochemical processes only depend on the environmental and physiological conditions of the individuals in a particular place and time. In MOHID, which is based on a computational grid to solve the transport equations, the methodology consists in building a biogeochemical module, organized in such form that the *sinks and sources* term is independent of the grid and of the grid cell location. This term is solved separately, but consistently, from the advection and diffusion terms. This independence allows for the biogeochemical module to be implemented in any type of grid (1D, 2D, 3D) and thus can be seen as a zero-dimensional model, where external forcing conditions are provided (ex: light, temperature, salinity) and mass fluxes between state variables (e.g. phytoplankton, ammonia, bivalve) are computed for each control volume using only the *sinks and sources* term of equations. This is also an efficient way to guarantee a high level of robustness in the code and to maintain it. The present study followed this methodology by building a Module Bivalve that computes the time evolution of bivalve properties (e.g. reserves, structure, length) for each cohort in each grid cell, as well as the correspondent effect on other water properties concentra-

tions (*e.g.* phytoplankton, ammonia) due to their activity. MOHID structure also enables that almost any process can be switched on/off. As a result, the model is flexible and easy to use in different systems, conditions, scenarios and most of all, enables the study of particular processes within the system. The bivalves' state variables make use of this structure. For example, bivalve larvae transport can be switched on/off depending on the individual length. During the larvae phase the individual is subject to transport by currents and turbulence, and once it reaches a certain size, the individuals settle, and the transport is switched off.

Study area

The model is implemented for the Balgzand, an intertidal area approximately 50 km² in size, and located in the westernmost part of the Dutch Wadden Sea (Fig.6.1). A long term sampling program at Balgzand started in 1970 and many studies have been performed in the area (and in the Wadden Sea) over a wide range of topics: physical processes, biogeochemical cycles in the water column and sediment, primary production, zooplankton, bivalves, shrimps, crabs, birds. The sum of all these studies constitutes an important source of knowledge on the system processes and dynamics. As a result, the Wadden Sea, and in particular the Balgzand, is suited to perform an integrated modelling study as proposed, as a high volume of information and data in several fields is required. Fig.6.1 presents selected monitoring stations from different sources and projects. These locations correspond to field data stations with recent and consistent field data records that are further used to calibrate and validate the model. At the same time, their distribution provides an insight about the range of concentration and model performance in the different areas. Station 01 (Den Helder), 04 (Oudeschild) and 10 (Den Oever buiten), represent stations managed by Rijkswaterstaat with information on the water level. Station 02 (Marsdiep Noord), also from Rijkswaterstaat, has information on the concentration of some of the target water properties. At Station 03 (NIOZ Jetty), a continuous sea surface temperature and salinity observations that are being recorded for more than 30 years (van Aken, 2008a,b), as well as chlorophyll-a concentrations and total suspended matter, managed by Royal NIOZ (<http://www.nioz.nl/colours>). Stations 05, 06 and 08 are monitoring stations included in the IN PLACE project (NWO), carried out by the Royal NIOZ (C. Leote et al., 2014). Stations 07 and 09 correspond to stations where the model results will be shown in more detail. Stations M01 to M06 correspond to mussel beds included in a long monitoring program performed by IMARES within the WOT Fisheries program, commissioned by the Dutch Ministry of Economic Affairs (van den Ende et al., 2012). Finally, station M07 represents one mussel bed included in a long term monitoring program that provides information on the benthic fauna in the Balgzand, twice annually since 1970 (Beukema and Dekker, 2007).

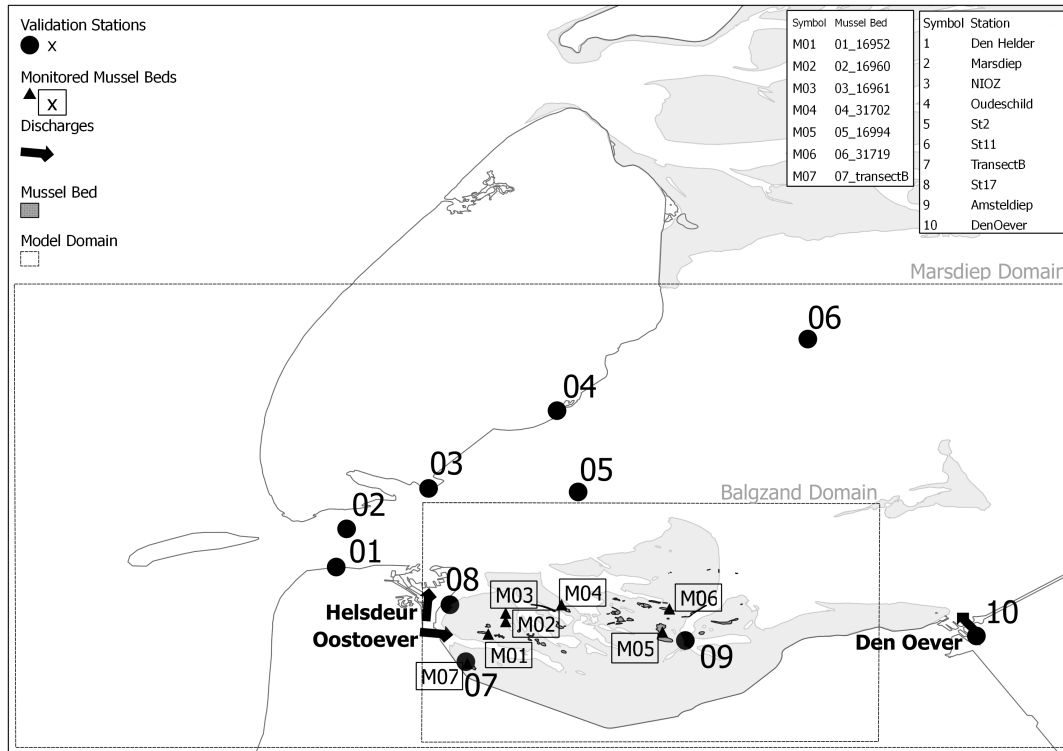


Fig. 6.1. Balgzand Area: mussel bed location, fresh water discharges and monitoring stations used for model validation.

Methodology

Simulation runs from August 2008 until December 2010, representing the nowadays system conditions and will be considered as reference scenario. This time period corresponds to the period with most information available. The conditions imposed were, as much as possible, based on observations from this period reported in papers, reports and/or websites. When not possible, the model was forced with average conditions. Initial values on the water column concentrations were obtained by a previous model run of two years. Results are analysed and compared with field data, in order to validate and test the model performance to describe the main processes. Next, the effect of the mussel beds in the system dynamics is quantified by a simulation without mussels. Results, with and without mussels, are compared in terms of temperature, salinity, total suspended matter, phytoplankton, ammonia, nitrate, inorganic phosphorus concentrations and bivalves' density time series in particular sites. Model results were also integrated over larger areas (integrated boxes) and fluxes across areas were computed by integrating the solution along the box boundary.

Model Setup

Morphologically, the Balgzand is a small but complex shallow area of the Wadden Sea with extensive tidal flats. A significant fraction of the total area, about 70%, is dry during low tide. Hydrodynamic circulation in this area is made through a series of small channels and it is mainly driven according to the local bathymetry, tide, wind and fresh water discharges. Tide and wind driven circulation is greatly influenced by processes occurring in the North Sea and the Wadden Sea. Although there are extensive amounts of data describing environmental conditions in these two systems, it is not always possible to provide boundary conditions for all model variables. Thus, in order to provide a higher quality estimation of boundary conditions, a general model was setup for the Marsdiep area in which a sub-model for the Balgzand area was nested (Fig.6.1). The Marsdiep model uses a regular computational grid with 400 m resolution. The Balgzand model uses a nesting ratio of 1:4 (i.e. 100 m horizontal resolution). The Balgzand domain high resolution is required in order to accurately simulate the narrow channels and correctly estimate water flows and drying and flooding of intertidal areas, particularly important when studying mussels dynamics. The bathymetry data was derived from the Vaklodingen data set published by Rijkswaterstaat (<http://publicwiki.deltares.nl/display/OET/OpenEarth>) and interpolated to the computational grids. In terms of vertical discretization, the model was setup in depth integrated model (2D). This option was made mainly due to computational restrictions and was deemed an acceptable approximation for the Balgzand area due to its shallowness. This model is forced at the open boundary by the water elevations and current velocities derived from The Rijkswaterstaat Kuststrook-fijn model (Philippart and Hendriks, 2005), a storm surge model for the North Sea, which results are provided by Deltares OpenDAP server. At the water surface, meteorological data from the De Kooy station was used to calculate momentum and heat fluxes. A statistical comparison with neighboring stations (Texelhors and Vlieland) showed minor variability in the measured parameters (particularly wind intensity and direction). De Kooy time series data was thus selected based on the higher frequency of observations and less data gaps. Horizontal gradients in meteorological parameters were not considered. At the bottom, shear stresses were computed based on currents and waves (simulated by a limited area wind fetch based model), and used to estimate particulate matter fluxes due to deposition and erosion.

Several water discharges can be found in the study area but only three, presented in Fig.6.1, are considered relevant: Helsdeur (next to the inlet), Den Oever (with a significant flow) and Oostoever (closer to the study area). Den Oever discharge is located in one extremity of the Afsluitdijk that closes the IJsselmeer, and for that reason the discharge properties are assumed to be equal to the conditions found in the lake. Data from several monitoring stations, managed by Rijkswaterstaat, is used to estimate the discharges properties. The necessary assumptions and considerations made to estimate the discharges and boundaries properties are summarized in Table 6.1. Because no specific information was found for Helsdeur and Oostoever discharges,

the model assumes the same properties as considered for Den Oever discharge (except flow, temperature and salinity). It is right to note that observations were used as much as possible, although data prior to 2000 was not considered as an important reduction of nutrients loads to the system has being detected in the last decade (Philippart et al., 2010). When possible, the seasonal variation of properties was imposed, by using the data itself or by using a computed average seasonal pattern (by monthly or daily averaging the available values) for the periods without data. When this was not possible, a constant average value was used. Temperature and salinity at the Wadden Sea boundary were obtained by the interpolation of several time series results (vertically averaged) obtained from an implementation of the GETM model for the Wadden Sea, recently presented by Duran-Matute et al. (2014).

Mussel beds and predators

The initial mussel bed distribution in the model simulation was based on the mussel bed contours and densities (number of mussels per m²), as estimated by IMARES 2008. Some of the mussel beds are monitored on a continuous basis (Fig.6.1). For the mussels beds without further information, an average density value was assumed. The size distribution observed in mussel bed M07 was assumed for all other mussel beds, since no information was available. Initial conditions for the individual state variables (reserves, structure, maturity, reproduction buffer and age) were estimated from the results of a pre-run the DEB model, considering an average seasonal pattern of temperature and food conditions in the system. Predator abundance (Fig.6.2) is assumed to have seasonal variation in the system: shrimps abundance was adapted from Beukema (1992); crabs from Smallegange et al. (2009) and birds from Andreas Waser (unpublished data).

Settlement probability

The settlement probability map (Fig.6.2) is based on a qualitative index for the amount of shells in samples collected during 2013, in the Wadden Sea, in the SIBES-monitoring program, carried out by Royal NIOZ (Compton et al., 2013). The observations made at several stations were interpolated to the model domain and converted into settlement probability values by assuming that a large amount of shells and the mussel bed areas have 100% probability and that no shells corresponds to a value of 10%.

Table 6.1. Rijkswaterstaat stations and other data sources used to estimate water properties in the discharges and boundaries. Average Year refers to a seasonal pattern obtained by monthly average values (after 2000). Seasonal means that the data source provided seasonal observations of the properties concentrations. Conversions between carbon, nitrogen and phosphorus content assume Redfield Ratios (N/C=0.18; P/C=0.024). The ratio 53 mgC/mgChla was used, which is an average from the ERSEM model results obtained a (<http://nioz.info/getm-ersem-setup>). Total suspended matter is based on salinity and turbidity measurements computed following the Håkanson (2006) formulation.

property	Den Oever	Helsdeur and Oostoever	North Sea	Wadden Sea
Water Flow	Seasonal Duran-Matute et al. (2014)		-	-
Temperature	Seasonal Duran-Matute et al. (2014)	Average Year Den Helder station	Average Year Noordwijk meetpost	Seasonal Duran-Matute et al. (2014)
Salinity		Average Year Vrouwezand 1977-1981	Seasonal Noordwijk 02 1975-2010	Seasonal Duran-Matute et al. (2014) 2000-2011
Total Suspended Matter(TSM)		Seasonal Vrouwezand Station turbidity/salinity	Seasonal Noordwijk 02 turbidity/salinity	Average Year Doove Balg West turbidity/salinity
Oxygen		11.8 mg/l Vrouwezand	9.2 mg/l Noordwijk 02	9.48 mg/l Doove Balg West
Nitrate		Seasonal Vrouwezand	Seasonal Noordwijk 02	Seasonal Doove Balg West
Nitrite		Seasonal Vrouwezand	Seasonal Noordwijk 02	Seasonal Doove Balg West
Ammonia		Seasonal Vrouwezand	Seasonal Noordwijk 02	Seasonal Doove Balg West
Phosphate		Seasonal Vrouwezand	Seasonal Noordwijk 02	Seasonal Doove Balg West
Phytoplankton		Seasonal Vrouwezand	Seasonal Noordwijk 02	Seasonal Doove Balg West
Particulate Organic Nitrogen (PON)		5.05 mg/l Den Oever spuilsuizen Organic detritus (N)	0.94 mg/l Noordwijk 02 Organic detritus (N)	1.3 mg/l Doove Balg West Organic detritus (N)
Dissolved Organic Nitrogen(DON)		Seasonal Vrouwezand Based on DOC	Seasonal Noordwijk 02 station Based on DOC	Seasonal Doove Balg West Based on DOC
Particulate Organic Phosphorus (POP)		0.67 mg/l Based on PON	0.13 mg/l Based on PON	0.17 mg/l Based on PON
Dissolved Organic Phosphorus (DOP)		Seasonal Vrouwezand Station Based on DOC	Seasonal Noordwijk 02 station Based on DOC	Seasonal Doove Balg West Based on DOC

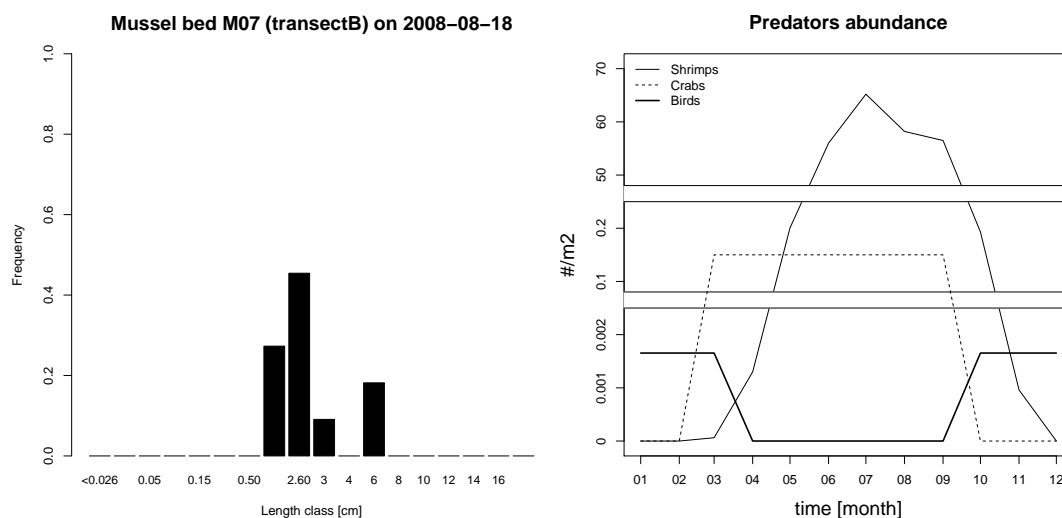
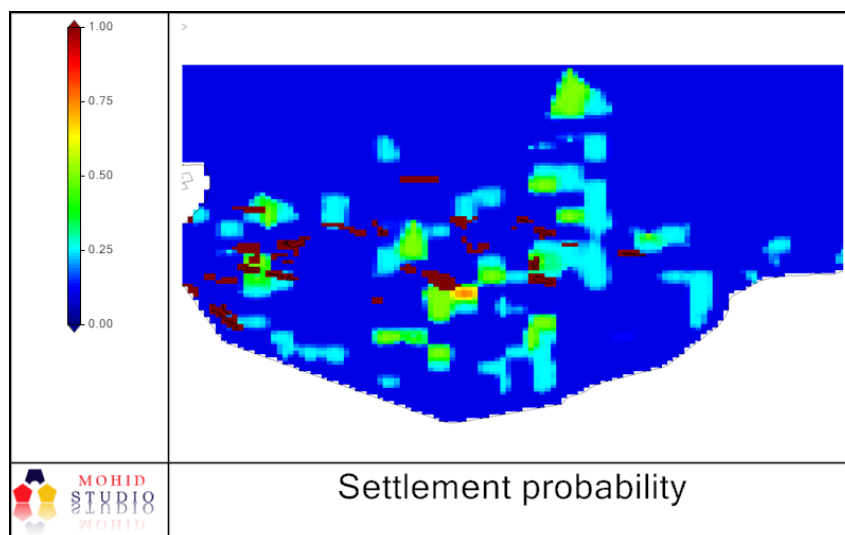


Fig. 6.2. Model input data: settlement probability (based on the on SIBES-monitoring program 2013); size distribution (based on Rob Dekker data) and imposed predators abundance (based on Beukema (1992), Smallegange et al. (2009) and Andreas Waser, unpublished data).

Results

Hydrodynamics

Hydrodynamic conditions (water elevations and depth integrated currents) were simulated for the period of August 2008 to the end of 2010. Model results were validated by comparing them with water elevations observations for several stations. Coefficients of determination (R^2), bias and root mean square errors asserted the ability of the model to reproduce the observed dynamics (Fig. 6.3). Although no current velocities data were available for validation, the very good water level predictions is a solid indicator of the validity of the hydrodynamic part of the model.

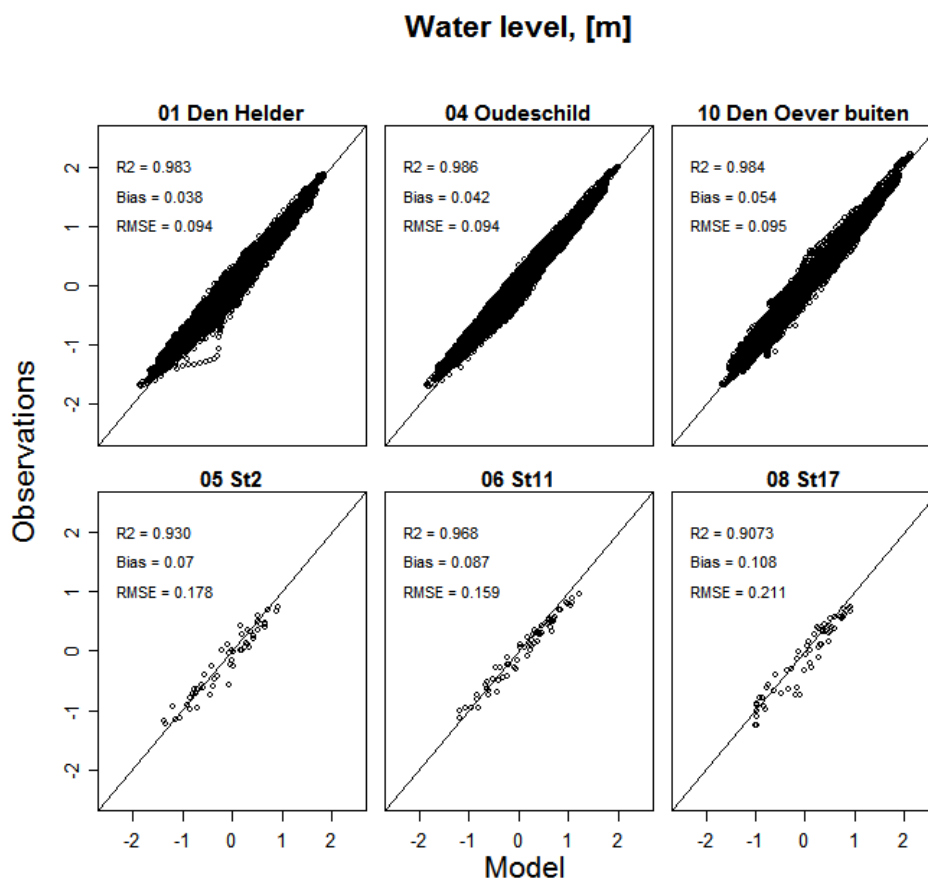


Fig. 6.3. Model vs. observations: water level.

From the hydrodynamic model results, one can derive quantities relevant for describing and understanding the Balgzand ecosystem dynamics, such as residual circulation, emersion times and residence time of water. The residual depth integrated flux (Fig.6.4) was computed by averaging the water fluxes divided by the grid cell width for each grid cell, and then divide the resulting

value for the average water column height for each grid cell. Results show that residual circulation is mainly established along the main channels from east to west. There is low input of water entering directly from the North Sea through the Marsdiep, being this water recirculated along the Balgzand during ebb mixed with the Den Oever fresh water input. Emersion time is shown in percentage of time that each grid cell was emerged, during the year of 2009.

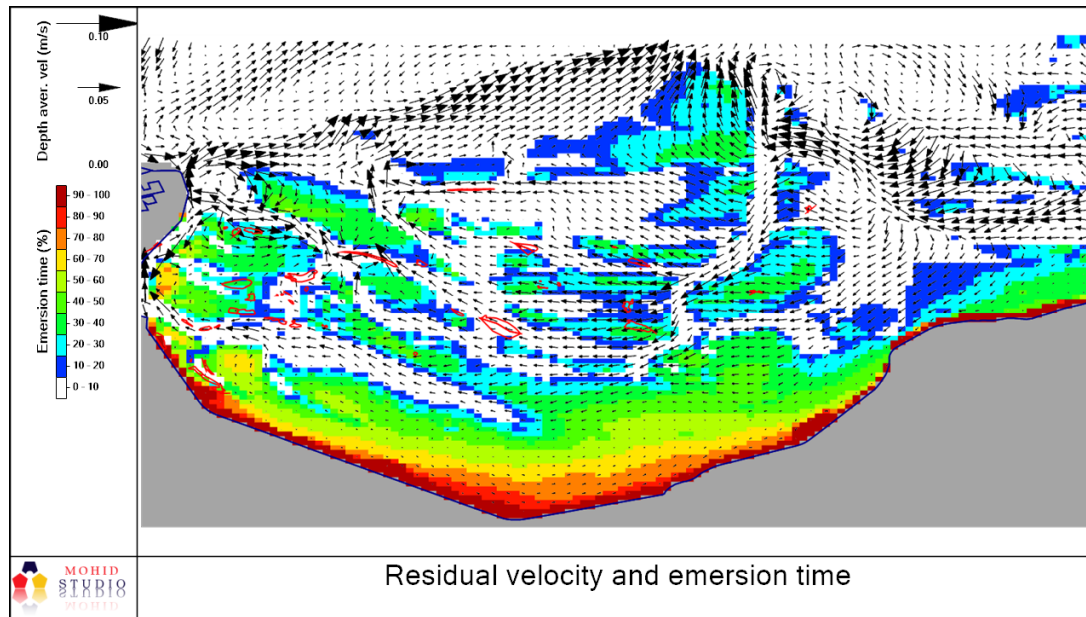


Fig. 6.4. Residual velocities and emersion time in the Balgzand.

Residence time of water in the Balgzand area was determined following the methodology proposed by Braunschweig et al. (2003), using a lagrangian approach. Residence time was computed by releasing an amount of lagrangian tracers, whose summed volume equals the water volume of the Balgzand area. The tracers are transported by currents and their position was tracked in relation to the Balgzand area. The fraction of tracers inside the Balgzand is calculated at each time step. Five scenarios were devised in order to understand residence time variability in relation with wind. The 2008 to 2010 wind data from De Kooy meteorological station were used. For each of the five most frequent wind directions, a period of 15 days was selected. The directions were selected based on frequency and importance in terms of hydrodynamic impact, e.g. East and Northeast wind induces stronger flushing of the water through the Marsdiep towards the North Sea, as Southwest and West winds will tend to block the water inside the Wadden Sea. Residence time was determined for each scenario by considering it as the time that approximately 80% of initial water volume had left the Balgzand area, and values ranged from 3 to 16 days (Fig. 6.5).

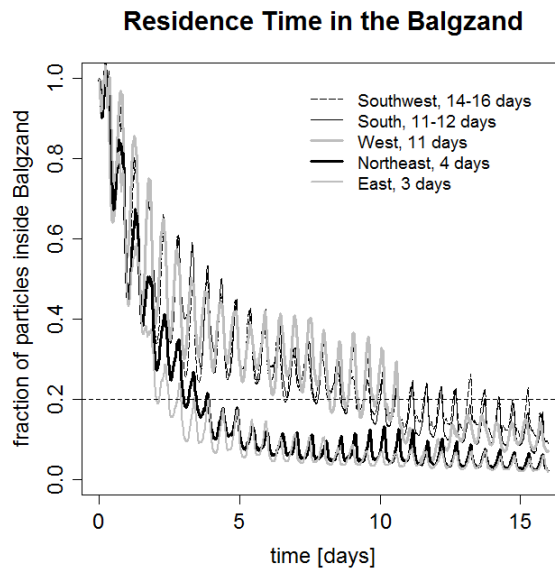


Fig. 6.5. Balgzand residence time: fraction of lagrangian particles inside the Balgzand.

Biogeochemical properties

At all monitoring stations, strong seasonal patterns occur in the data and these patterns are generally well described by the model predictions (examples on Fig. 6.6 to Fig. 6.8). In general, temperature rises during spring and summer and starts to decrease in the beginning of autumn. Phytoplankton concentration shows a bloom in spring (and a smaller bloom in 2010 early autumn) with a consequent decrease in nutrient availability. In addition, the model predicts a daily oscillation that can be explained mainly by tide, although light limitation effects during the night on phytoplankton growth and nutrient uptake can contribute too. The model reproduces not only the dynamics but also the range of the observations, although some differences can be noticed. Salinity and total suspended matter (TSM) range is globally lower in the model, particularly at the stations 05, 06 and 08 where detailed observations were made at different depths during a complete tidal cycle. Those differences can be the result of sediment transport model limitations and related to the 2D setup. Nutrients concentrations are generally higher in the model, but the lower limit is within the range of the observations. Inorganic phosphorus concentration at station 08 (Fig.6.8) is much lower than the observations. The predicted values are in the same order of magnitude as the Oostoever discharge, though, indicating that at this location the effect of the discharge is significant and it is possible that the real discharge concentration is higher.

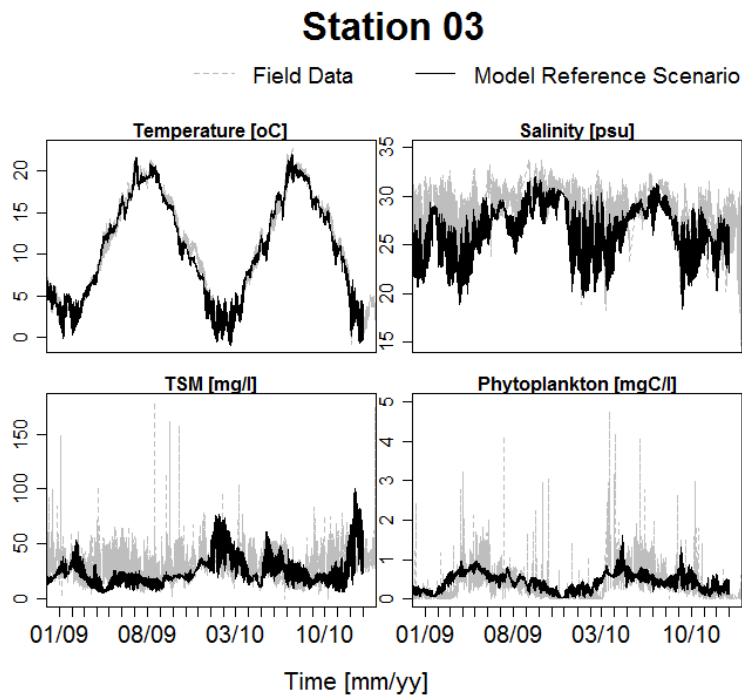


Fig. 6.6. Station 03, NIOZ jetty: model vs. observations.

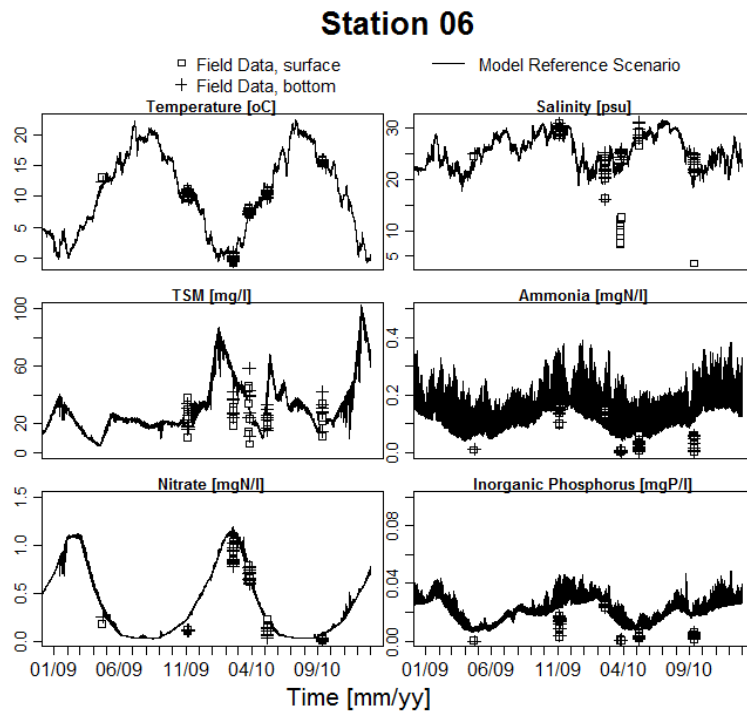


Fig. 6.7. Station 06: model vs. observations.

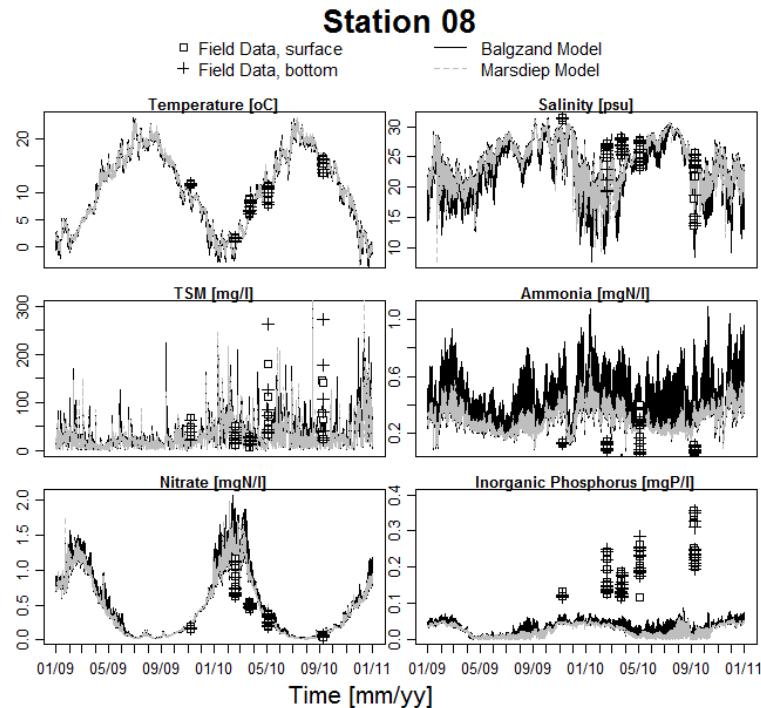


Fig. 6.8. Station 08: model vs. observations.

The spatial distribution of the target variables (Fig.6.9) at high tide in spring and low tide in winter show that the Balgzand has particular conditions that neither directly reflect the conditions from the North Sea nor from the Wadden Sea. In spring, temperature, as well as phytoplankton and ammonia are higher in the Balgzand. In contrast, phosphorus distribution in spring shows lower values. Den Oever (IJsselmeer) discharge influence is clear, both in spring and winter. It has an important effect on the Balgzand, due to its high flow through one important channel that transports water to an extensive area, at least at normal hydrodynamics conditions. Although not possible to be detected in the presented figures, discharges from Oostoever and Helsdeur can also influence the surrounding area but only at the local scale.

The mass fluxes analysis between the integrated boxes (Fig.6.10) confirms that most nutrients and phytoplankton mass flux enter the Balgzand from Box 3 (i.e. contribution from Den Oever discharge) and leaves the area to Box 2. In an overall analysis of the average mass fluxes per year, the Balgzand acts as a sink of phytoplankton by consuming more phytoplankton than the input flux; and a source of ammonia, by exporting more than the input flux.

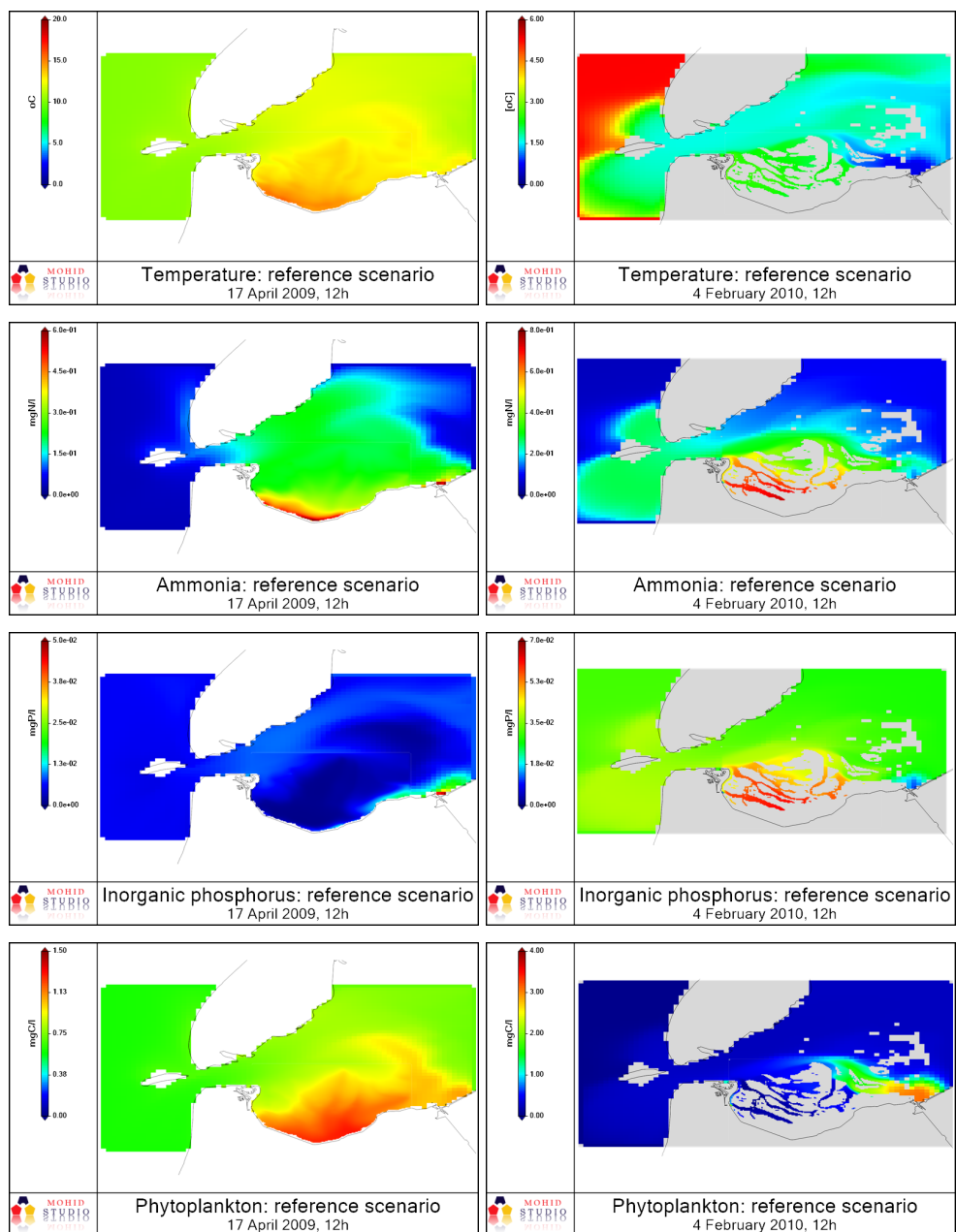


Fig. 6.9. Map distribution of properties in spring (17th April 2009, 12h, high tide) and winter (4th February 2010, 12h, low tide).

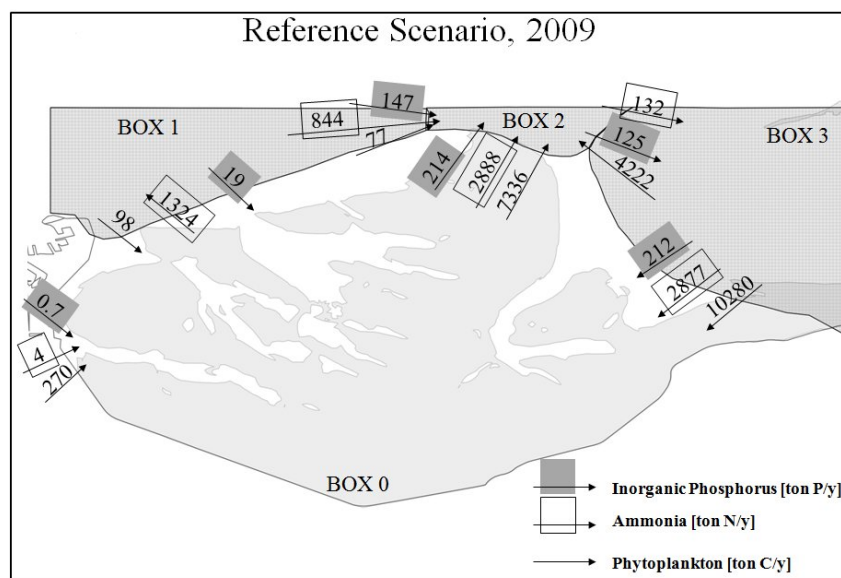


Fig. 6.10. Mass fluxes of properties between integration boxes, in the reference scenario, over 2009.

Mussel beds

Temperature and food availability (phytoplankton), in addition to physical conditions (emersion time and water depth), control mussel bed dynamics. Not surprisingly, mussel growth and development show spatial variability (Fig.6.11). One year after the beginning of the simulation, cohort 1 no longer exist in some areas and the individuals length, which had an initial value of 0.85 cm in all mussel beds, ranges now from 2 cm to 3.5 cm. The other cohorts present the same pattern. Differences can even be observed within a mussel bed (Fig.6.12), since a mussel bed is typically represented by a number of computational grid cells. The variability is high and within the same mussel bed it is possible that some of the mussels will spawn while others do not. The intensity of the spawning event can also differ, as it is shown for mussel bed M07. The comparison with observations is not very clear, due to the high variability and the sparse data, but it is possible to say that for most mussel beds, densities and biomass are in the same order of magnitude, although the biomass results seem to slightly deviate. Mussel beds contours estimations obtained by IMARES for spring 2009, reveals that most of the mussel beds existing in 2008 persist the year after, some of them with a slightly increase in area. Only a few, very small, new mussel beds were formed (Fig.6.13). These results do not have a complete match with the results obtained in the SIBES program in 2009, regarding the presence of mussels in the samples. However, the surveys were done at different times, although in the same year. The model results obtained for June 2009 are generally consistent with IMARES contours, it also predicts the presence of new mussel beds but only a few are actually predicted at the same location as estimated by IMARES. In the model, some the new mussel beds are formed in adjacent areas of existing mussel beds and some others are located in and around the channels, where emersion times are high and velocity was not higher than 0.5 m/s.

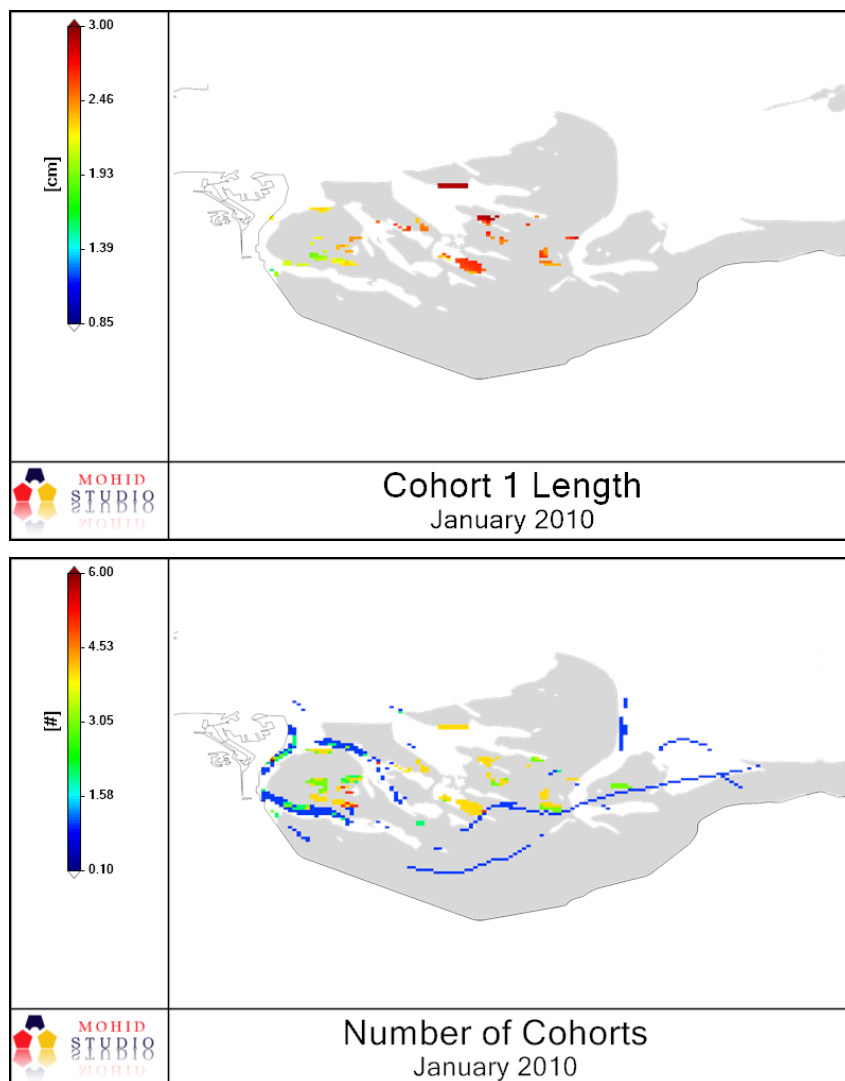


Fig. 6.11. Cohort 1 length and number of cohorts as predicted by the model for January 2010.

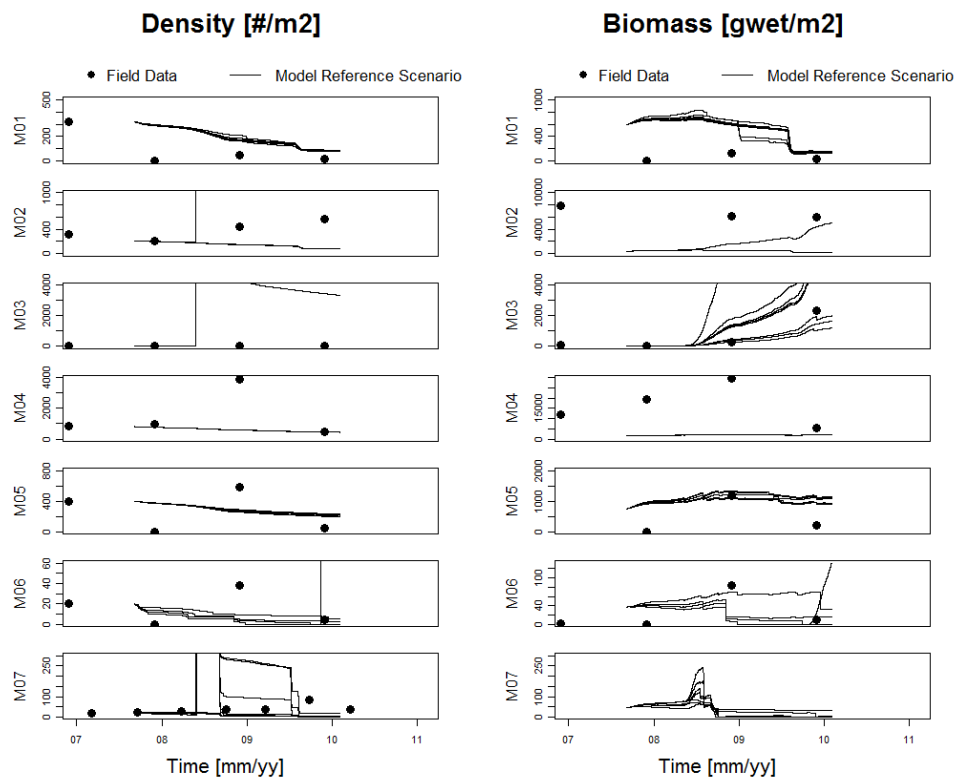


Fig. 6.12. Model vs. observations: density and biomass in the monitored mussel beds. Different lines represent model results in different cell of the domain that belong to the mussel bed.

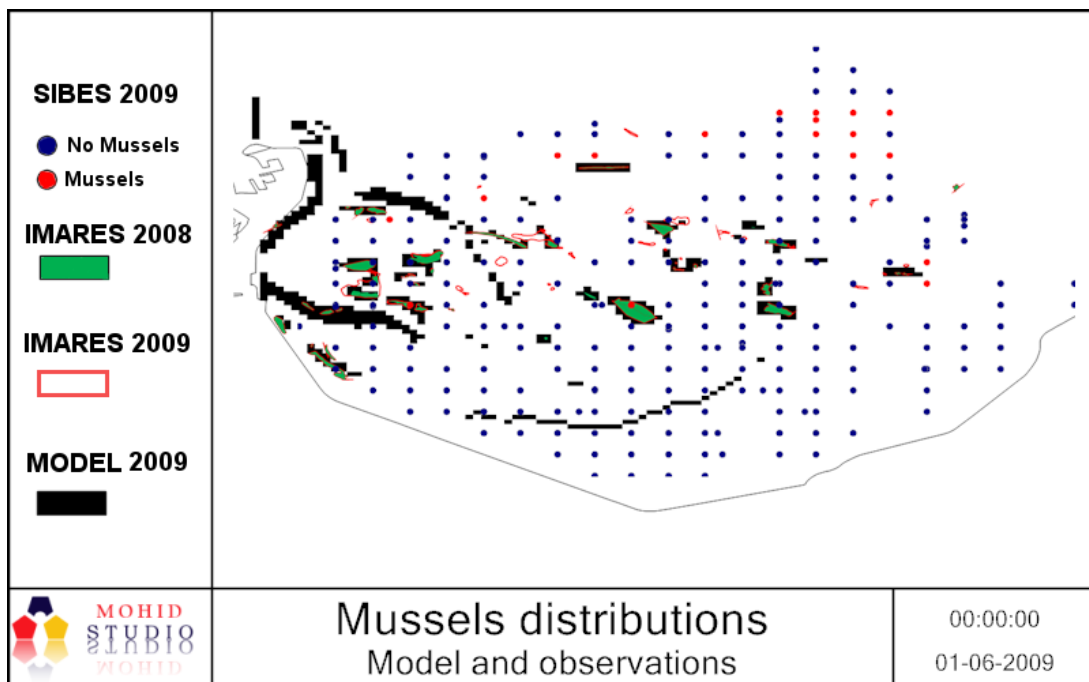


Fig. 6.13. Mussel bed distribution in spring 2009: model results obtained for June 2009; SIBES data obtained for 2009 and IMARES contour data estimated for spring 2009. IMARES 2008 correspond to the imposed initial distribution of mussel beds.

Spatial variability within the same mussel bed is also apparent in the mussel reproduction buffer compartment and consequently in the timing, number and intensity of the spawning events. Spawning events are reflected in the number of cohorts (Fig.6.14). The spawning season starts exactly when temperature rises above the threshold (9.6°C), which in 2009 happened in the beginning of April. From that moment on, the spawning events are almost continuous during spring, summer and beginning of autumn, while the temperature is above the threshold. However, from all the new born cohorts (12 in 2009 and 15 in 2010), only a few (8 in 2009 and 3 in 2010) persist and in the beginning of the new year, most mussel beds have the same (or lower) number of cohorts as in the initial condition (4). Only a few areas, adjacent to existing mussel beds, have more than four cohorts (Fig.6.11). In fact, most cohorts die in their first month of life. Starvation is the main cause of biomass loss in an overall analysis (Table 6.2 and Fig.6.15). It is responsible for more than 98% loss of the bivalve biomass, while total predation is only responsible for about 0.1% of the total biomass loss in 2009 and 0.02% in 2010. However, cannibalism has an extreme influence in the new born cohort density because it represents very high values of instantaneous mortality rate in the population (reaching a value of 10^5), which results in a strong decline in the cohort density and ultimately death of a new cohort (Fig.6.16 and Fig.6.17).

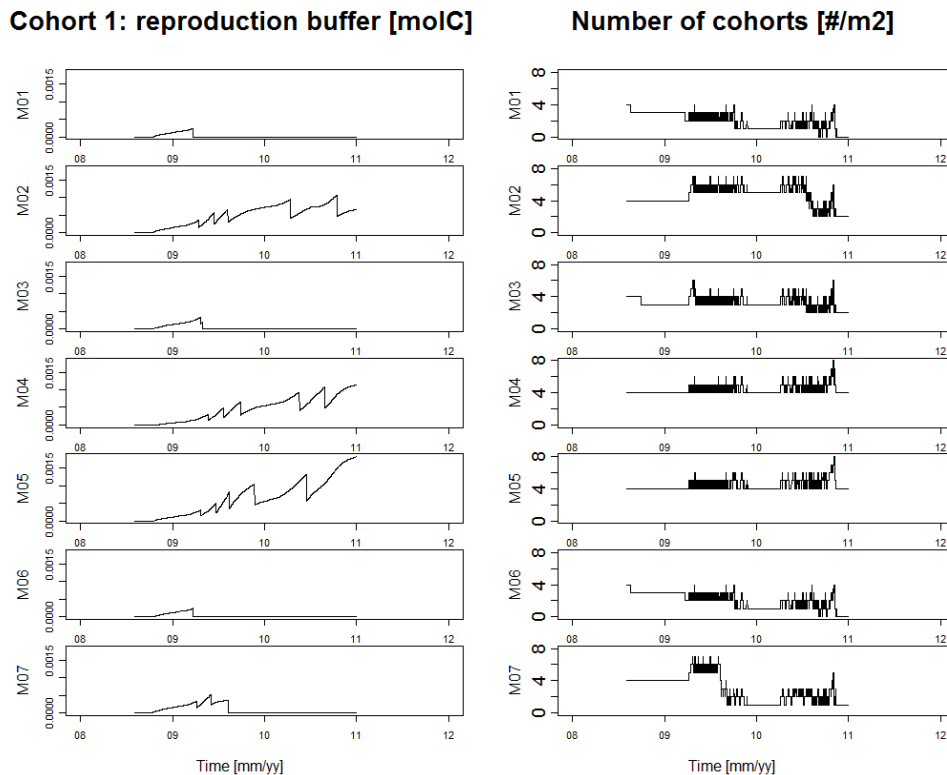


Fig. 6.14. Reproduction buffer and number of cohorts dynamics over time, in the monitored mussel beds.

Mortality per month, molC/m2 (2009)

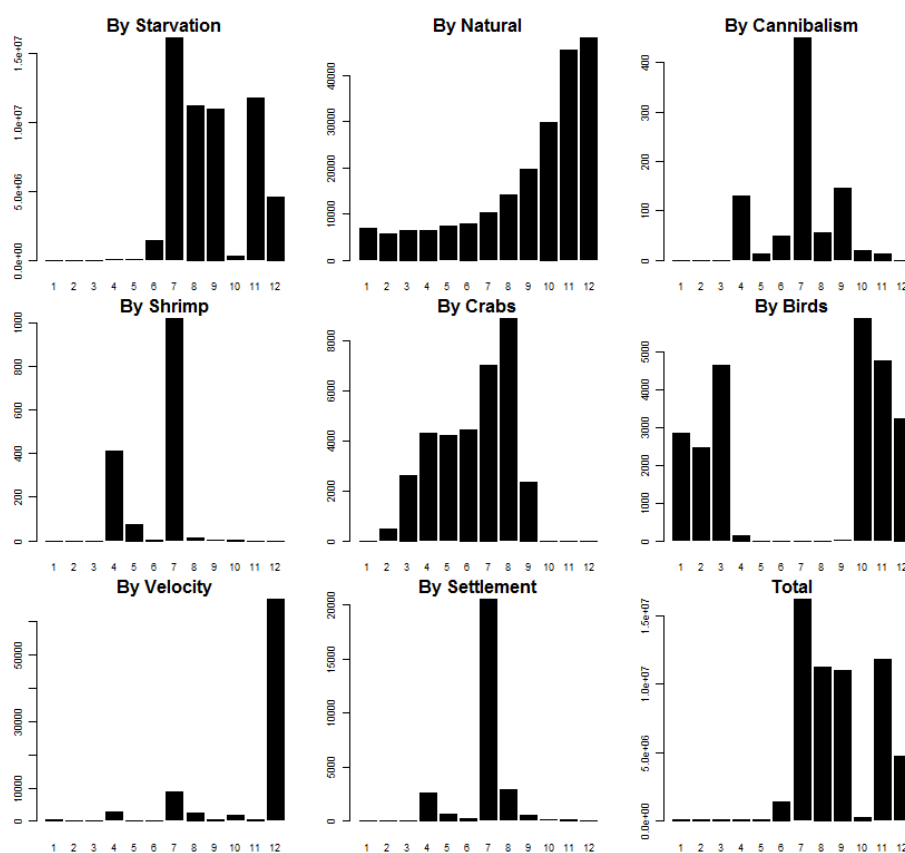


Fig. 6.15. Biomass loss by mortality process in the population, by month, during 2009, in mussel bed M05.

Table 6.2. Relative importance (%) of each mortality process in the total loss of biomass (molC/m²) per year, in mussel bed M05.

mortality	2009	2010
Starvation	99.33	98.03
Natural	0.37	0.87
Settlement	0.049	1.0
Velocity	0.15	0.084
Cannibalism	0.0015	0.0067
Shrimps	0.0027	0.0003
Crabs	0.060	0.0044
Birds	0.042	0.0096

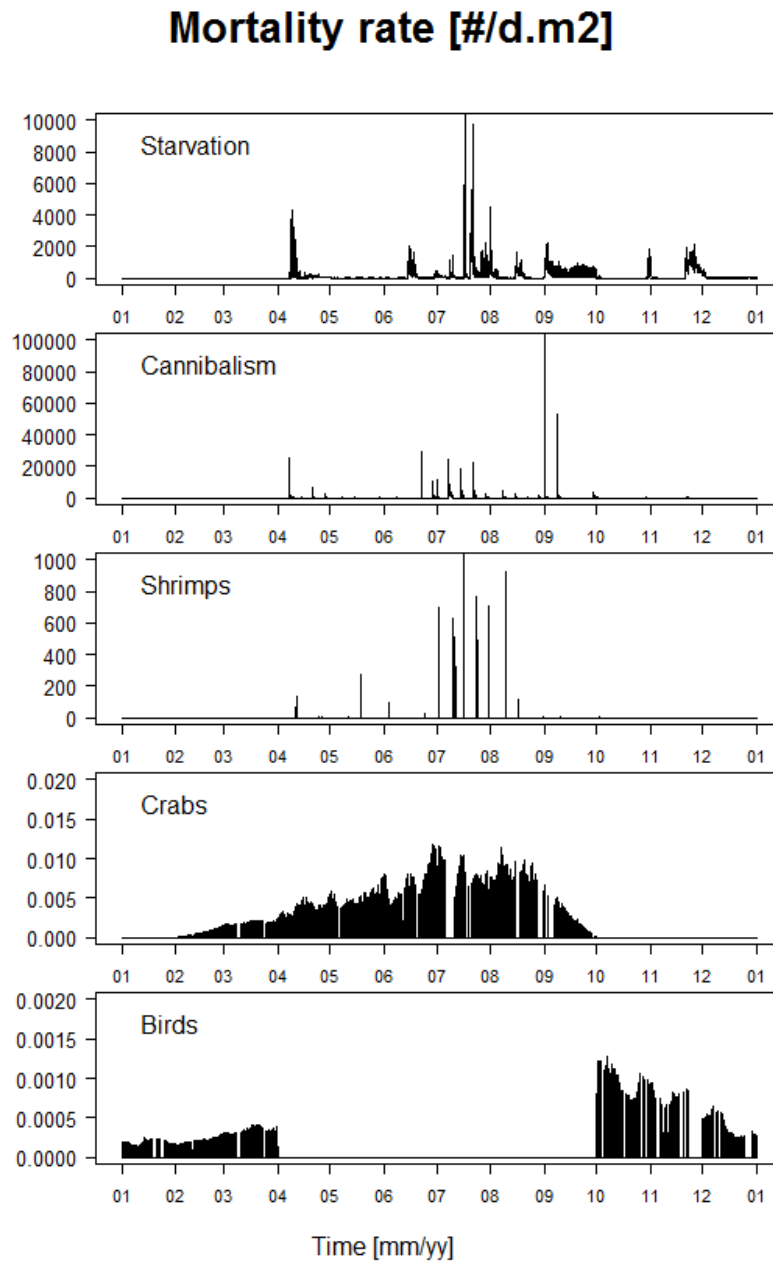


Fig. 6.16. Starvation, cannibalism, shrimps, crabs and birds instantaneously mortality rate in the population (sum of all the cohorts) during 2009, in mussel bed M05.

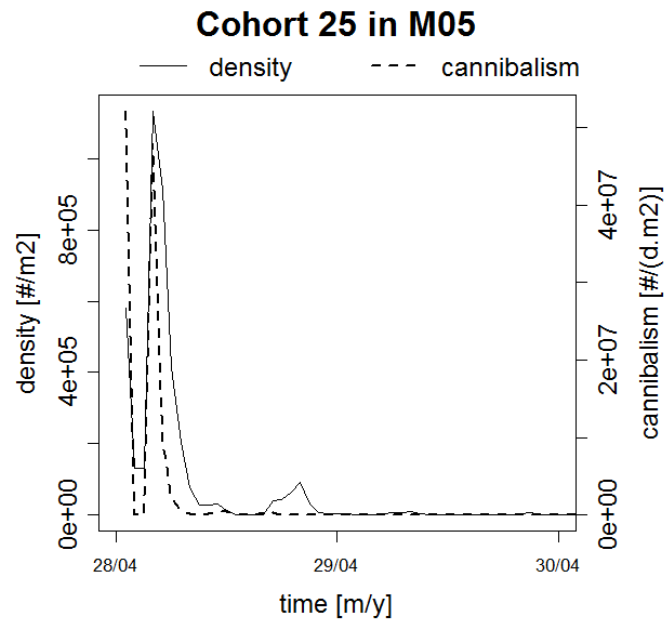


Fig. 6.17. Bivalves total density and cannibalism rate in cohort 25, in mussel bed M05.

Bivalve's effect on ecosystem dynamics

In order to estimate the total influence of the mussel beds over biogeochemical processes in the Balgzand, model results were compared with a scenario without mussel beds (Fig. 6.18). In general, phytoplankton concentration is lower in the presence of bivalves as a result of mussel filtration, and nutrients concentrations are higher, due to mussels' excretions as well as an increase in the particulate organic matter mineralization. In a hypothetical scenario without mussels, the output flux of phytoplankton over one year would be about 15% more than the input flux, implying that the Balgzand is an area of intense primary production, that even exports biomass, certainly by consuming nutrients (Fig.6.19). A net consumption of phosphorus is present in both scenarios, although more intense in the scenario without mussels. However, in the case of ammonia, model results indicate an export in both scenarios. This result suggests that the recycling of ammonia, by mineralization of organic matter is an important process in the system. Ammonia regeneration is responsible to fuel primary production and even to export about 40% more than the input flux.

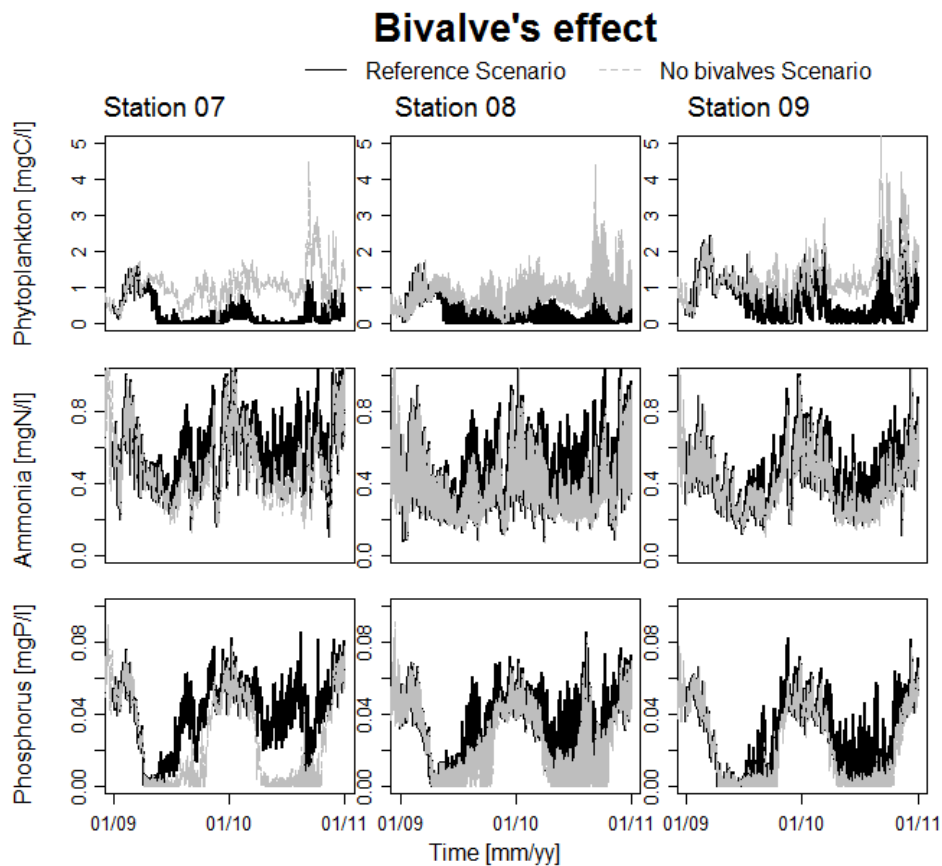


Fig. 6.18. Bivalve's effect on phytoplankton, ammonia and inorganic phosphorus dynamics, in stations 07 (mussel bed), 08 (Balgzand) and 09 (Amsteldiep).

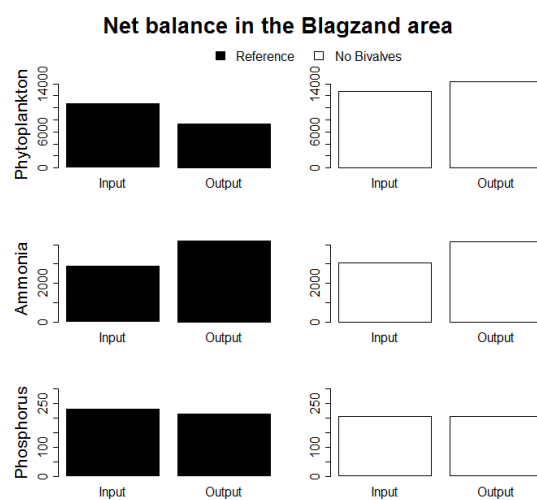


Fig. 6.19. Net balance of phytoplankton, ammonia and inorganic phosphorus in the Balgzand: reference scenario and scenario without bivalves.

Discussion

The Balgzand model setup was based on a downscaling approach using sub-model nesting. A larger area (Marsdiep domain) was simulated with a coarse resolution. The boundaries were located where data was available, in order to produce reliable and more detailed boundary conditions to a fine resolution sub-model, focusing only on the Balgzand (Balgzand domain). The underlying assumption is that the sub-model is influenced by the father model but, the sub-model does not affect the father model. The use of sub-model nesting was a viable option because: (a) Balgzand presents particular environmental conditions as a consequence of its complex morphology and that it does not affect significantly other areas of the Wadden Sea; (b) comparisons at station 08, using the Marsdiep model and the Balgzand model confirms that the resolution of the model can be important to capture the high variability of the properties (Fig.6.8). The use of a sub-model was thus, a good approach to increase the spatial resolution of the Balgzand domain, enabling a better discretization of the narrow channels and intertidal areas, without increasing too much the computational time. It is important to notice that this setup benefited from previous modelling studies, at the scale of the Wadden Sea and the North Sea (Duran-Matute et al., 2014; Philippart and Hendriks, 2005), that provided high quality boundary conditions for the Marsdiep model.

Hydrodynamic results are only briefly presented, since that was not the main focus of this study. Validation is not detailed but the good agreement between model results and field observations, on water level and temperature, suggests that the current velocities and overall transport is well simulated. The differences found in salinity and TSM concentrations are a result of the simplifications made for this particular setup, namely the use of a depth integrated approach. The sediment transport model, directly linked with particulate matter dynamics, used a simplified version of the processes. It considers only one type of fine sediments, so parameters such as settling velocity ($1 \times 10^{-4} \text{ ms}^{-1}$), critical shear stress for erosion (0.75 Nm^{-2}) and deposition (0.3 Nm^{-2}) to occur and reference erosion rate ($5 \times 10^{-5} \text{ Kgm}^{-2}\text{s}^{-1}$) were estimated by model calibration, within a range of values found in literature, and maintained constant for all simulations. Initial conditions for water column sediment concentrations and fine sediment distribution deposited in the bottom, were estimated by the model. Starting from a homogeneous distribution, sediment transport dynamics was simulated for several months, until a more realistic depiction of the sediments spatial variability was achieved, by identifying erosion and deposition areas. These results were then used to feed the full model simulations as initial conditions. Bottom shear stresses control a great deal of the erosion and deposition processes and in shallow areas such as the Balgzand, wind waves, on top of currents, play an important role. The used wave model is based on wind velocity, direction and fetch. Although with limitations and despite being used in the Marsdiep domain where a part of the North Sea is simulated, it was deemed appropriate to simulate an area like the Balgzand. Wave results in the North Sea area of the Marsdiep model domain have to be considered with caution, as waves in this area are

a product of regional propagation and local generation. However, a model sensitivity analysis was performed and variations on the wave parametrization were not relevant for wave and sediment transport dynamics in the Balgzand, as in addition to being a very shallow area, the Balgzand is shadowed from waves propagating from the North Sea. The wave model has additional restrictions in wind fetch calculations as it does not consider the effect of intertidal areas. Nevertheless, the assumptions are considered valid in line with the aim of the study and the results are in good agreement with the observations.

In general, the Balgzand is an autotrophic and exporting system, i.e. there is biomass net production. Due to its shallowness, temperature, one of the main driving forces for biological processes, is extremely dependent on the heat balance with the atmosphere. In spring and summer, temperature is usually higher in the Balgzand compared to the Marsdiep domain, which triggers the extension of biogeochemical processes. As a result, phytoplankton and nutrients concentrations are also higher. Phytoplankton is high because primary production is intensified by temperature and light. Nutrients concentrations are higher, despite the high uptake by primary producers, because mineralization of organic matter and regeneration of nutrients due to bivalve's activity is also intensified. This study used a basic version of the pelagic biogeochemical processes model. It considers only one group of phytoplankton and zooplankton, it assumes a constant composition of biomass and includes a simple decay model for the particulate organic matter mineralization in the deposited sediments. However, the results proved that the model is able to capture the main seasonal patterns observed in terms of phytoplankton and nutrients. Phytoplankton concentrations are very well reproduced in the two field data stations, but nutrients seem to be systematically higher in the model, although in the same order of magnitude. This suggests that primary production is well simulated and that the differences found in the nutrient concentrations can be a result of the parametrization used for the mineralization of organic matter in the water column and/or in the sediment. In addition, the assumption of constant biomass composition can have an effect on the availability of the nutrients in the water column. Differences are more important in inorganic phosphorus concentrations in station 08, in the Balgzand. This station is located in a channel, close to the Oostoever discharge and as a result it is very influenced by the conditions imposed by this discharge. Because no specific information was found for both Helseur and Oostoever discharges, data from the Den Oever discharge was assumed (except for flow, temperature and salinity), which is possibly not very precise. This can be the main reason why concentrations on inorganic phosphorus are much lower than the observations.

Mussels have an important effect in overall biogeochemical dynamics in the Balgzand. They globally intensify seasonal patterns, particularly in areas close to the mussel beds. This effect was quantified by comparing the reference scenario with a scenario without mussels. Phytoplankton concentration is lower in the presence of mussels, as a result of mussels' filtration, and nutrients concentrations are higher, due to bivalves' excretions, as well as an increase in the particulate organic matter mineralization. Nevertheless, mussels' density in the Balgzand

mussel beds is not very high and their effect is mainly local, thus the overall spatial distribution of constituents is not greatly altered.

The model results indicate that the mussel spawning season in the Balgzand is long. The first spawning event starts when the temperature rises above the threshold imposed in the model, which in 2009 happens in early spring. Because the variability of the environmental conditions inside the system is relatively high, the individuals in each mussel bed have very different conditions, meaning that their reproduction buffer content is also variable. For that reason, spawning events are almost continuous, through the whole period when the temperature is above the threshold. After spawning, the mussel larvae take about 2/3 weeks to reach the settlement size (0.026 cm), which is in agreement with field observations (de Vooy, 1999, e.g.). Dispersion is quite important and larvae are transported through the entire domain. This would suggest that open boundaries should be extended until the maximum area of dispersion. However, that would also imply the imposition of a larvae concentration at the open boundary, and observations are not available. For that reason and because the aim of the study is to focus only on the Balgzand area and to understand mussel beds dynamics in this area, a compromise solution was designed. Because larvae concentration at the open boundary is not known, it is initially considered to be null, meaning that only larvae generated inside the Balgzand domain are accounted for, and no external larvae are computed. When water exits the domain during ebb, it transports the larvae concentration calculated near the open boundary, but when it enters back it should not bring a null value of larvae concentration, as some of the water coming back in is in fact the same water that has left in first place. Thus, a time decay open boundary condition was used. This method computes the open boundary condition based on a reference value (null concentration) and on inner boundary concentration over a time scale. In this study a value of 3 hours was used, which roughly accounts for half a of tide phase (ebb/flood), meaning the open boundary condition depends on the larvae concentrations values calculated at the boundary over the previous 3 hours of simulation. This minimizes the effect of placing the open boundary where larvae concentrations are still high and avoids extending the domain boundaries, increasing computational efforts. This methodology also guarantees that larvae generated inside the domain will leave when crossing the open boundary but return to the Balgzand, depending on currents and fluxes at the boundary, but with a slightly lower concentration, that mimics the dilution/mixing outside the domain.

Larvae are subject to transport but also to cannibalism by adult mussels when they transit through a mussel bed and to starvation, to some extent. Cannibalism is, in fact, according to the model, a very important process. Although it is only responsible for less than 0.01% loss in the initial biomass, its instantaneous mortality rate in number of mussels can be very high and it happens during a very important life stage. The effects on the population dynamics are quite significant. For the two simulated years, most new cohorts die within the first month. When a new cohort does survive cannibalism, it still has to cope with the intense shrimp predation that occurs after reaching the shrimp minimum predation size. The start of shrimp predation coin-

cides with the settlement, meaning that individuals are not transported any more and thus easily predated. In this way, the intense effect of cannibalism associated with the shrimps predation, can result in the extinction of most new cohorts in the existing mussel beds and the tendency is that new mussel beds are formed. The cohorts that were able to persist, were generated either in the beginning of the spawning season (early spring) or in the end (autumn), when the abundance of shrimps is not very high. Thus, the mortality processes at the beginning of their life cycle have an extreme importance and they can control the population dynamics at a particular location even if it does not represent the main mortality cause in an overall analysis. Starvation is the main cause of loss in terms of biomass and predation, either by adult bivalves or by other predators (shrimps, crabs and birds) is responsible for only about 0.1% of the total biomass loss. However, starvation it is not responsible (in the reference scenario) for the death of the whole cohort and consequently not directly responsible for the cohorts' extinction, only for the reduction of their density. It is important to notice that the uptake by predators and their abundance is imposed in the model as a forcing function meaning that there is no direct feedback, only indirectly considered by the input data. This assumption means that the time scale of the feedback on the predators equals the frequency of the data. Perhaps for birds and even for crabs this is a valid assumption, but it possible that this time scale its too high for the shrimps because their growth rate is higher. This can be a model limitation if in the future one aims to simulate or predict the variability of prey-predators dynamics dependent on environmental changes. Future developments and improvements can be implemented in the model regarding this topic. As an exercise, in order to quantify the effect of predation in the mussel spatial distribution, two additional short scenarios (April to January) were performed: (1) with predators (shrimps, crabs and birds) and (2) without predators (Fig. 6.20). Both simulations used the same the initial condition and the same set of parameters: the simulation starts with a constant spatial distribution of larvae with high concentration (1×10^6 #/m²) and it assumes a settlement probability of 100%. The non predators area represents an optimal area for the mussels to establish based only on food availability. The presence of predators reduced the optimal area, meaning that they can also influence the spatial distribution of the mussel beds.

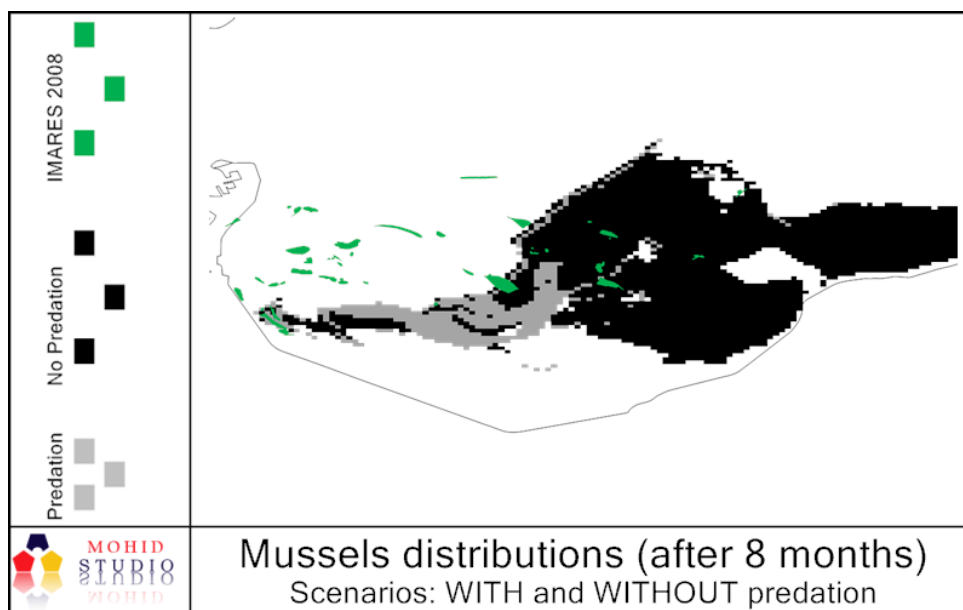


Fig. 6.20. Mussel distribution obtained with and without predators.

Results on bivalves do not deviate from the observations but it was also not possible to exactly quantify agreement with measurements. The distribution of mussel beds can be after controlled by predation but it is, in the model, primarily controlled by the settlement probability, which was assumed as dependent on the amount of shells in the bottom. Therefore, most of the new mussel beds are formed in adjacent areas of existing mussel beds or former mussel beds. To avoid a complete restriction of mussel bed establishment, a minimum value of 0.1 was used for this parameter, and that explains why some of the new cohorts settled far from existing mussel beds, next or inside some of the channels. The channels, that in the Balgzand are not very deep would be, theoretically, perfect spots for new mussel beds because the intense water flow would guarantee food availability. However, strong velocities are also responsible for the detachment of individuals, and those will eventually die. This mortality process is responsible for designing the pattern of the 'mussel bed lines' (Fig.6.11) that do not correspond with observations. New parametrization could be tested in order to obtain a pattern more consistent with the observations but perhaps a more realistic approach would be to use bottom shear stress to limit the individuals' settlement, rather than velocity. In this way the effect of waves and short storm events would also be taken into account.

An attempt at validating model results regarding to mussel distribution, density and biomass was made using some of the existing data. In terms of spatial distribution, the comparison with the contours estimated by IMARES for the spring 2009 indicates the presence of some small new mussel beds and only a few are actually predicted by the model. But only a few are also detected in the SIBES program, probably because the aim of the monitoring programs is different and/or the sampling timing and methodology is also different. Model results indicate, as well as the observations, that most of the initial mussel beds persist and some of them increase in

terms of area. It is important to notice that spring 2009 is only a few months after the start of the simulation and although the spawning season has already started, the mussel model properties are still very dependent on the initial conditions. More realistic results could perhaps be found using a longer bivalve model spin-up and longer runs, but this was not possible yet as more input data would be needed. The comparison in terms of densities, in the monitored mussel beds is also difficult to interpret, because field data is sparse and there is high variability between different cells within the same mussel bed. However, the model and the observed densities are, for most mussel beds, in the same order of magnitude, which is considered to be a good agreement at this stage. Observations in terms of biomass are always more challenging to predict because they depend on a higher number of factors. Additionally, the initial condition for bivalves, in this setup, was established based on their densities and length, and the correspondent biomass was not consistent with the measurements. This issue can also be subject of improvements in future implementations.

Finally, it is important to notice that the current study does not take into account other macrofauna existing in the system. New configurations of the model including other important species in the area (e.g. cockles) can be performed. The model is prepared for that and the only limitation would be the availability of data.

Conclusions

The process oriented modelling tool that results from the coupling between an individual-based population model for bivalves (based on the Dynamic Energy Budgets theory, DEB) and a hydrodynamic and biogeochemical model (MOHID Water Modelling System) was tested, for the first time, in a real system – The Balgzand (Wadden Sea, The Netherlands). The model proved to be able to respond properly to the environmental conditions dynamics and the agreement with the observations are generally good, particularly regarding hydrodynamics and water properties distribution (temperature, phytoplankton, nutrients). The analysis of the reference scenario results concludes that early stage mortality (top-down) can control the persistence of the new cohorts, in particular cannibalism and shrimp predation, although starvation (bottom-up) is the main process responsible for bivalve loss over the year in terms of biomass. It strengthens that there is no single mortality factor responsible for the population dynamics regulation. The validation on mussel bed properties is hampered by the detailed model results that need to be synthesized and summarized to be comparable with the observations, which are usually sparse. The current study used many data sources from previous projects, studies and entities. A validation attempt was made and possible explanations for the deviations were identified. Performing scenarios is also a useful way of using the model. This study uses a scenario considering the nonexistence of mussel beds in the Balgzand to test and quantify their effect over local biogeochemical processes. More scenarios could be performed to provide insight in the relative

importance of a process. As an example, it could be interesting to test the influence of oysters and cockles on mussel growth; test the influence of temperature in prey-predators relations between mussels and shrimps; estimate possible locations for artificial mussel beds or characterize ecosystem response to different environmental scenarios. To our knowledge, this was the first integrated modelling study that focuses on mussel beds in the Balgzand. The complexity of the presented model is already high, but it is not yet limiting its implementation in real systems. In fact, the study suggests that some of the features could even be improved by including a more detailed description of some of the processes. The first step was taken, but only more tests, implementations and improvements will give the model, and the scientific community using it, the desired experience to serve as an effective and reliable management tool.

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7. General Discussion

The aim of this thesis was to study and quantify the dynamics of bivalve communities and their influence on the pelagic system. To achieve this, an individual-based population model for bivalves (based on the Dynamic Energy Budget theory), was developed and coupled to a hydrodynamic and biogeochemical model (MOHID Water Modelling System). The result is a process oriented modelling tool that integrates physical, biogeochemical, ecological and physiological factors governing bivalve populated marine ecosystems, by describing and quantifying mass and energy fluxes between all the actors involved. The different chapters of the thesis correspond to the successive steps where specific processes were described, modelled, and where the model results were as much as possible tested and validated against data. In Chapter 6 the model was applied to a real ecosystem (Balgzand, Wadden Sea, The Netherlands) to study the bivalves population dynamics and to quantify the influence of mussel communities on the pelagic system, in terms of phytoplankton and nutrients.

The model development was not straightforward. Many choices and assumptions were made at the individual, population and ecosystem level. Decisions were made based on a balance between knowledge, simplicity, technical issues and time limitation. This last chapter discusses those decisions, their consequences, enumerate other possible ways and sketch future perspectives. Following the thesis structure, this discussion will go from the individual up to the population and the environment.

From the environment to the individual

The activity of an individual bivalve depends on its physiological condition and also on environmental factors. Environmental factors are usually not constant over time or space. Individuals react to those changes, and they may do this in different ways. Yet, the individual model built in this study describes the reaction of an 'average individual' to changes in the environmental conditions, assuming that the number of individuals is big enough to minimize the effect of individuality. So, in the present model individuals only change through grow and development. Besides, the possibility that individuals may change either through phenotypic flexibility or genetic adaptations is not considered.

DEB theory was used to build a model to simulate metabolic processes in a bivalve individual, in relation to environmental conditions. The reasons for choosing DEB theory have been presented earlier but it is worth to point out that DEB is not just a model, but a theory based on a mechanistic view of an organism's metabolic processes, including growth, maturation and reproduction. The basic principles and formulations are valid for all different stages of the individual, meaning that the same set of equations can be used to simulate their complete life cycle. The set of equations and the principles behind them are not simple and not easy to understand, but they are for sure simpler than reality. So far, models based on DEB theory have been able to simulate a wide range of processes in a wide range of species, see <http://www.bio.vu.nl/thb/deb/>.

The standard DEB model does include the main features of an individual, but specific processes can and should be added to simulate particular features of the target species, considered important for the aim of a particular study. Following this idea, a novel mechanistic description of the bivalves feeding process was developed (Chapter 2). Both quantity and quality of suspended particulate matter in estuaries and coastal systems fluctuate strongly and there was a lack of a mechanistic description that could deal with those fluctuations. In the feeding processes model, filtration, ingestion and assimilation are assumed as three different steps and pseudofaeces production is computed as the difference between filtered and ingested fluxes. The concept of Synthesizing Units described by the DEB theory was used to develop generic formulations to account for different types of food, with type-specific ingestion and assimilation efficiencies. Necessary parameters were estimated and the model performance was evaluated by comparison with literature data for the blue mussel, for a wide range of experimental conditions. The lack of data and of detailed information on the experimental setup adds some uncertainty to the parameters estimation. Nevertheless, the model results are in good agreement with observations. DEB models suffer, not only from the fact that they require a high number of parameters, but also that most of them cannot be measured directly and/or do not have a simple relation with measurable quantities. The same happens with the state variables. This implies that parameter estimation procedures are complex by necessity. During this project many developments occurred in this field and a new estimation procedure was established – the covariation method, described in Lika et al. (2011). The underlying idea is that the set of parameters should be estimated in one step, using all the data available and also by introducing a set of physiological constraints that does not allow the parameters (or functions of the parameters) to deviate too much from what it is assumed as realistic. Chapter 3 describes one of the first implementations of this method, where a new parameter set for the blue mussel is estimated. The paper discusses in detail the applicability and limitations of the method. It is important to notice that the parameter set will change if further modifications are included in the model or if more data become available. The datasets used to estimate the parameters were as much as possible independent and correspond to data obtained in different sites under different conditions. But they refer to a limited number of individuals, using different sampling/measure methods, and most likely do not cover all possible conditions. Thus, it is still probable that the best mussel parameter set has not yet been found. However, for the present model configuration and for the tested datasets, the study concludes that the parameter set obtained by the covariation method leads to a better fit between model and observations, and is therefore potentially more consistent and robust. The individual model and the parameters were tested by comparing model predictions against field observations obtained at four different locations in the North Sea – Wadden Sea, Sean Gas Field(UK), Oyster Grounds and North of Dogger Bank (UK), as described in Chapter 4. At these locations, labelled mussels (*Mytilus edulis*) were kept under natural conditions, some of them for several years. Shell length was measured for each mussel repeatedly during the experiment and dry weight was determined at the end of the experiment for some mussels. Tempera-

ture, salinity, chlorophyll concentration and Secchi-depth were measured next to the experiment sites. This experimental setup was good for the validation of almost all model features. Results were explored and the individual model was able to reproduce perfectly the pattern and reasonably the average growth of the mussels at the four places. This result implies that the main metabolic processes at the individual level are well described by the model. Nevertheless, the experiment was not really prepared with the purpose of model validation and for that reason some model features were not properly validated. Although the model is able to deal with different types of particles, chlorophyll was used as a proxy for food concentration, meaning that the different sources of food were not known and only one type of food was assumed. Results do not indicate that a different food source was needed to explain the results, but this part of the model was not validated. It was however possible to test and conclude that inorganic particles can have an important effect on the individual performances, and that variability in sediment concentration can even be more important than seasonal changes in food composition. An important suggestion for future experiments and field monitoring programs is thus that they should always include measurements of total suspended matter in the water column and not only on food (or food proxy).

From this moment on, in this project, the individual model and the parameters were fixed, assuming that no more developments were needed.

From the individual to the population

Many choices can be made when upgrading from the individual to the population model and some were already discussed in Chapter 5. In this study, an individual based population model (based on DEB) was built, meaning that the population dynamics is represented by several cohorts' trajectories. Each cohort consists of identical individuals born at the same time and showing identical properties (e.g. size, biomass) throughout their life. The population model is thus responsible for the book-keeping of the information generated by the individual model over time, one for each cohort. Each cohort is simulated as an independent entity which can interact with other cohorts through food competition. Other population processes included are initial egg mortality, background mortality, and predation (including cannibalism).

At the individual level, validation is relatively easy using experimental data or field measurements of the relevant environmental data. At the population level challenges arise, because it is, in fact, an intermediate level. It is much more demanding to separate and be in control of all the involved processes, without stepping into the ecosystem level. For instance, the feedback loop with the food should be included, but in practice food conditions depend upon so many other factors than only grazing. The same happens with the predators. Compromises have to be made and these feedbacks were, in this study, only partially considered, using data instead.

A simple schematic implementation of the model for a mussel bed located in the intertidal area

of the Balgzand (Chapter 5) was possible by making use of several years of data on one particular mussel bed. We also used a vast number of studies available on mussels and their predators and on environmental and food conditions that have been monitored for several years at a nearby location. Major simplifications were made on the loss of larvae by dispersion, the tide effect, and the already mentioned feedbacks to lower and upper trophic levels. The loss of larvae by dispersion was simulated by increasing a unique constant parameter (initial egg mortality rate). Food supply to the mussels was simulated using a very simple approach. It was assumed that flooding occurs instantaneously, meaning an input of water with Wadden Sea properties (food and temperature) to the mussel bed; high tide is maintained for a fixed number of hours, and during this period mussels filter (and re-filter) the water, depleting food concentration; ebb also occurs instantaneously and during the low tide the mussels are outside the water, meaning that they are not able to feed; after 5 hours of low tide, flood occurs and brings again water with more particles and food, completing the tidal cycle. So feedback to the food only occurs during one high tide, and at the start of each new tide, new food is delivered. Without the effect of food depletion during high tide, the individuals in the mussel bed would not be limited by food and the population would increase indefinitely. This result implies that the time scale of the feedback processes are lower than the frequency of the food data, which was about one month. The tide effect imposed in the model reduced it to the time scale of a tidal cycle. On the other hand, the study assumes for the predators, that the feedback from the mussels is already included in the imposed data, meaning that the time scale of these processes is higher than for the food and equals the frequency of the data.

Besides the great amount of data, important information on predators' diet is still missing, namely on what fraction of the predators diet consists of mussels. As the role of predation is an important question, multiple scenarios were explored, with simple variations of the predation parameters. This resulted in thousands of model simulations. Criteria were then developed to select well fitting results, narrowing the parameters combinations. The selected modelling scenarios were able to reproduce the timing of some peaks in mussel abundances. They also produced similar size distributions, but the absolute number of individuals was not well predicted. Possible causes were identified and suggestions were made to overcome the discrepancy. A better description of food availability and larvae/food dispersion might be the way forward. We did however not pursue this course any further. The population model was considered as an intermediate step and the time and effort spending on improving it by including new, perhaps complex, configurations would deviate from the initial aim of building the integrated modelling tool. Nevertheless, it had been an important step that provided useful information for the next step in the project.

From the population to the ecosystem

Populations directly affect the trophic levels below and above them. But indirectly they will also affect the food of their food, or the predators of their predators. Hence, the first step when upgrading from a population model to the ecosystem is to establish the main actors (properties, species, or groups of species), where a balance must be found between what it is known and what can reasonably be simulated. In the case of the Balgzand, described in Chapter 6, it is assumed that the main actors are phytoplankton, zooplankton, mussels and bacteria (implicitly simulated by including the mineralization of organic matter, in the sediment and water column). The activity of other macrofauna species, e.g. the cockles, is neglected. This option seems reasonable for a first implementation, taking into account the information available for the model input. The model is however prepared to deal with different species, as long as data and parameters are available.

All the actors live in the changing environment of the Balgzand intertidal area that has strong tidal effects and some dependence on fresh water discharges. The MOHID Water Modelling System was the ecosystem model chosen to be coupled with the DEB bivalve population model. MOHID is a three dimensional (3D) water modelling system based on the finite volume concept and besides the hydrodynamic model it couples several modules responsible for computing turbulence, eulerian and lagrangian transport, sediment transport, biogeochemical/ecological processes and water quality. The coupling philosophy assumes that the biogeochemical processes are solved separately, but consistently, from the advection and diffusion, which allows the desired model flexibility to be implemented in any type of grid (1D, 2D, 3D). Biogeochemical modules can be seen as a zero-dimensional model, where external forcing conditions are provided (ex: light, temperature, salinity) and mass fluxes between state variables (e.g. phytoplankton, ammonia, bivalve) are computed for each control volume using only the *sinks and sources* term of equations. In the current study a new Module Bivalve was developed under this methodology. The module computes the time evolution of bivalve properties (e.g. reserves, structure, length) for each cohort in each grid cell, as well as the correspondent effect on other water properties concentrations (e.g. phytoplankton, ammonia) due to their activity. In this way, the feedback of each bivalve cohort activity in the ecosystem, including food depletion, is naturally simulated in each time step and the effect of tide on the food supply is simulated by the advection-diffusion processes between grid cells. The hydrodynamics and the biogeochemical models included in the MOHID system have been extensively implemented in several ecosystems and in several configurations with a wide range of aims, with good results. The pelagic biogeochemical processes can be simulated using three different modules with different complexities. The least complex module was chosen to perform the simulations in the Balgzand, although the bivalve population model is actually prepared to deal with all the options. The main features of the model are: nitrogen and phosphorous cycles are simulated explicitly; constant C:N:P ratios are assumed for organic matter and plankton; and the main state variables are one group of phy-

toplankton, one group of zooplankton, dissolved nutrients and dissolved and particulate phases of organic matter. This module (and others included in MOHID) was not built under the DEB theory and the differences between the two approaches have never been tested. Can this be a problem? It is not completely clear if this fact will actually have any reflection in the results. When compared with observations (obtained from chlorophyll-*a* measurements), the current model is able to simulate well the seasonal patterns of phytoplankton at different locations in the domain, at least in the reference scenario (2009/2010), as shown in Chapter 6. Thus, the use of a DEB model would probably not improve significantly the predictions in terms of the seasonal pattern, but it could allow the prediction of detailed information on food composition, possibly with an effect on bivalves' activity. More detail in the food composition would be an improvement but it could also add more complexity. Would it then be reasonable to have only one unique group of phytoplankton? Would it not be better to simulate different species, with different DEB parameters? But how many? And in addition, do we have DEB parameters for all of them? Do we have enough detail in the observations to be compared with the model results? All these options are quite reasonable, although the complexity and consequently the computational effort would obviously increase. At this stage, and in line with the aim of studying bivalves' dynamics and effect in the system, the good prediction of the seasonal pattern in the average food conditions (concentration and composition) for the bivalves seems already a good achievement. Suggestion is made that before increasing the complexity of the biogeochemical model, more, longer and more detailed validations should be made at the bivalve level. Additional scenarios could also be performed in order to test if the deviations from the average food composition would imply deviations in the results.

The analysis of the reference scenario suggests that early stage mortality can control the persistence of the new cohorts, in particular cannibalism followed by shrimp predation. Cannibalism is included in the model as the filtration of larvae by adult mussels. Larvae are, for the mussels, like any other food source. Its filtration depends on the individual clearance rate, which depends on their size and the amount of particulate properties in the water column. It is assumed that there is no preference in filtration for any specific properties and that selection is made after filtration, before ingestion. Larvae filtration, i.e. cannibalism by adult mussels, is intense because larvae concentration is high. The importance of shrimp predation for new cohorts to persist in the population was noticed already in Chapter 5 and more clearly in Chapter 6. In the model results, the persistence of some cohorts was only possible when spawning events happened in early spring and/or late autumn, when abundance of shrimps was low. The model also considered one extra parameter to account for the fraction of mussels included in the shrimps diet, which was crucial for population persistence. The reason behind this parameter is that the shrimps uptake rate reported in literature is relatively high (Campos et al., 2009; Andresen and van der Meer, 2010, e.g.), suggesting that the actual values could be lower. A rough estimation of this parameter was found in Chapter 5 and used in Chapter 6, because no information was available for that. Although many studies are available for the shrimp's life cycle and size

prey preferences, there is still a lack of knowledge on their diet. Perhaps it is only related with the concentration of food items, as assumed for the mussel. But that is still unknown. Also from the model point of view, the shrimps abundance and size is imposed, meaning that there is no growth along the season and there is no change on their size prey preference. Because the prey-predators dynamics is sensible to these relations, and the effect of shrimps seems to be so strong, perhaps their life cycle should be simulated in more detail, with a DEB model and using the already available first estimates of DEB parameters presented by Campos et al. (2009). The effect of the other predators were not found to be as intense, but it is possible that the simulations would have to be longer.

The current study was able to confirm, by comparing the model results in different scenarios, that bivalves do have the potential to influence ecosystem functioning due to their role in nutrient cycling. The Balgzand acts as a sink of phytoplankton, due to bivalves' filtration. Without bivalves it would export phytoplankton. The results also show that it acts as a source of ammonia, exporting about 40% more than the input flux, suggesting that ammonia regeneration in the system is very significant. The bivalves' activity intensifies the seasonal patterns of phytoplankton and nutrients in the areas close to the mussel beds, but they do not change their overall spatial distribution.

From the theory to numerical modelling

Once the processes and their formulations are established, programming the model is, in theory, relatively straightforward. But ecosystem models are big. The set of equations and especially the algorithms that solve these equations can be very complex. Processes that occur simultaneously in nature have to be translated into a sequence in the code. During the development a predefined structure has to be maintained. This is especially true when the number of programmers working on a code is high, like in MOHID, that has several hundreds of thousands code lines. MOHID's structure is therefore highly organized, making it relatively easy to follow and at the same time very flexible. The incorporation of the individual based population model complied with MOHID rules and benefited from some of its advanced programming features. For example, the bivalves model is programmed using an object oriented approach, which allows the definition of several different bivalve species, each one with the same functional organization but with a different set of parameters. Each species is defined by one or more cohorts and each cohort is simulated independently with its own set of processes. All cohorts share the same set of equations. The development of the population model posed some challenges, namely the dynamic allocation of newborn cohorts and deallocation of dead cohorts. Typically in a sequential code, there is a construction phase (memory allocation), a computing phase (solving the algorithms) and a deconstruction phase (memory release). In this project, it was possible to implement a run time dynamic allocation/deallocation of memory which is triggered

by population processes, from which it is not a priori known when they will occur. MOHID uses a property list, which includes all the constituents that are simulated (e.g. phytoplankton, ammonia, sediments, mussel reserves, number of mussels, etc). This list is created at the beginning of a new simulation based on a configuration file. Now, new properties can be added or removed from the list with no limitations during run time. For example when a new cohort from a certain species is created by a spawning event simulated by the model, 6 new properties are added to the list, namely number of individuals, length, reserves, structure, maturity and reproduction buffers. These properties are then ready to enter the computational cycle with no need for additional modifications.

Cohort properties are simulated in an Eulerian approach, using a computational grid. In each grid cell, a transport equation is solved for each property, simulating advection and turbulent mixing (when at a larvae stage) and physiological processes. During most of their life cycle, bivalves' have a fixed position, thus the advection and diffusion term is null. Individuals from the same cohort located in the different locations can develop differently (e.g. grow faster or slower) if environmental conditions are unequal at these locations. During the larvae stage, advection and turbulent mixing are important as they are responsible for the actual transport of individuals. The activation of these processes in run time is also new, as well as its deactivation once the individuals reach the juvenile stage and settle. Larvae from the same cohort are subject to different environmental conditions during their initial period of life, and they will grow differently. When they are mixed due to transport, the model takes their concentrations and mass fluxes into account to perform a weighted average of the cohort properties. This is especially important to assure a correct methodology of the highly interdependent cohort properties. Thus, the Eulerian approach introduces some limitations due to 'numerical diffusion' generated in the case of larvae transport when solving the advection term of the transport equation. This is mostly caused by high gradients between larvae concentrations (from a specific cohort) with the ambient water and it can be minimized by the use of fine computational grids and small integration time steps. Different approaches could be followed, namely using a Lagrangian scheme that allows the elimination of the advection term. However, this would create other difficulties regarding information exchange between the Lagrangian and Eulerian model properties, and possibly increase the computational efforts. The computational time is actually one of the main challenges in the current model. It can increase significantly depending on how many cohorts are generated and how much time they remain as larvae. For that reason, the model is able to aggregate spawning events by including a minimum time between them, which is set as a parameter. The detail with which the exact birth date of a new cohort is simulated depends on the aim of the study. In addition, the model is able to be coupled with the simplest (Module Water Quality) or the more complex (Module Life) model options to compute the pelagic biogeochemical processes, thus allowing control over the computational efforts necessary to simulate them. One final important note is that although the model is very complex, and computationally demanding, it was built in a very flexible way, meaning that almost all the processes and options

can be switched on or off. Thus, the complexity of the model is entirely defined by the user, which will have to make decisions depending on the aim and time of the study.

From the model to the environment

The time scale of estuarine ecology depends on the time scales of ecological processes and on the time scale of the forcing functions. For that reason, the ecological model must run for time periods much longer than those involved on hydrodynamics, nevertheless requiring similar resolutions for explicitly simulating the transport processes. Fine grid resolution should imply better results and model boundaries should be set far from the study area, but these options do have some costs in terms of increased computational time. There is thus a compromise between the model resolution, the overall simulated area and time, besides with what detail should processes be simulated and the number of state variables necessary to do so. In addition, boundaries require data which should be more detailed and precise as they are closer from the study area. The sub-model approach used to simulate the Balgzand area, and presented in Chapter 6, can be a good compromise. In this approach a larger area is simulated with a coarse resolution, with boundaries located where data is available. This model will produce better and more reliable boundary conditions to a fine resolution sub-model, with focus in the study area. The underlying assumption is that the sub-model properties are influenced by the father model conditions but the sub-model does not influence the properties in the father model, for now. Maybe in the near future a 'two-way' system could be implemented in MOHID. This approach would make it possible to increase the resolution in the Balgzand domain and capture the high variability without increasing too much the computational time. It is important to notice that the current setup benefited from previous modelling studies that produced good results which were used as boundary conditions in the Marsdiep model (Duran-Matute et al., 2014; Philippart and Hendriks, 2005), and helped confining the model domains directly close to the study area. Nevertheless, the model's computational effort is quite demanding, in terms of computer memory, computational time and management of the generated information (in the order of tenths of gigabytes per year of simulation). The amount of data necessary to run and to validate the model is quite high. The reference scenario (2009 and 2010) was chosen because it was the period with more information available. A two years period was assumed as the minimum possible time interval to perform analysis and draw conclusions on the dynamics of biogeochemical cycles and bivalves properties. In terms of phytoplankton and nutrients the simulation period was found adequate. After a two year spin-up run to establish initial conditions, this properties revealed a stable seasonal pattern during the two year simulation scenario and results were very satisfactory. However, for bivalves processes the simulation time could be extended to better identify the pattern in the densities in the mussel beds. The validation on mussel bed properties is hampered by the detailed model results that need to be synthesized and summarized to be

comparable with the observations, which are usually sparse. The current study used many data sources from previous projects, studies and entities. A validation attempt was made and possible explanations for the deviations were identified. More data is and probably will be available in the future and the model would benefit from new comparisons.

Performing scenarios is also a useful way of using the model. This study uses a scenario considering the nonexistence of mussel beds in the Balgzand to test and quantify their effect over local biogeochemical processes. More scenarios could be performed in many different topics to give insight of the processes relative importance in the system. As an example, it could be interesting to test the influence of oysters and cockles on mussel growth; test the influence of temperature in prey-predators relations between mussels and shrimps; estimate possible locations for artificial mussel beds or characterize ecosystem response to different environmental scenarios. Moreover, the tool can be potentially used to simulate human engineered ecosystems (e.g. mussel farms in built structures such as beds, rafts or long lines), and study its efficiency, productivity rates and sustainability.

The first step was taken, but only more tests, implementations and improvements will give the model, and the scientific community using it, the desired experience to serve as an effective and reliable management tool.

Concluding remarks

The originality of this work lies, among others, in the integration of several fields of knowledge to achieve a better understanding of the relative importance of the processes that describe the role of mussels (and bivalves) in their ecosystem. Complexity can only be understood by following many diverse approaches and methods in different directions. Mathematical modelling is a strong direction. By modelling the main processes and the complex set of relations, whereby suspension-feeding shellfish interact with ecosystem processes, one can realistically hope to simulate their population dynamics and their environmental impact. This will naturally increase the model complexity, although it would be still too simple compared with reality. In fact, the presented model is only relatively complex, when compared with very complex end-to-end type of models. These models attempt to represent the entire ecological system and the associated abiotic environment, usually in the context of fisheries, global climate changes and exploitation (Cury et al., 2008; Fulton, 2010; Rose, 2012). As stated by Fulton et al. (2003), too much complexity leads to too much uncertainty and problems with interpretation of the model's dynamics and predictions, while too little detail results in models that cannot produce realistic behaviour. No single 'best' model is possible to develop and one crucial property for an useful tool is flexibility (Fulton, 2010). Flexibility in the main actors, in the processes and in the spatial and temporal resolution, to enable different model configurations depending on

the particular aim. Also, the validation process has to be beyond the comparison of the point data towards testing whether the models capture the main features of ecosystem structure (Hannah et al., 2010). The potential of complex models relies also in the possibility of performing different management scenarios as a guide to possible impacts and to explore implications of alternative broad policies (Fulton et al., 2003). The present work follows this philosophy. Models are suitably complex if all critical processes, drivers and components under scrutiny are captured (Fulton, 2010), which can be difficult to access. Perhaps one way of obtaining the minimum model complexity possible, concerning a particular aim, is to perform an iterative procedure on the modelling approach. In this procedure, the model should be successively improved and tested against observations (or patterns) in careful and small steps, analysing strengths and weaknesses. Individual processes can and should be identified, isolated and described as much as possible, in order to understand their place in the overall picture. Simpler models can be built to explain particular observations. If we are able to successfully design and implement those models, there is no reason to think why they cannot succeed in an integrated way. If the integration does not 'work', it will only mean that either the simpler models were not representative enough or we are still missing something and thus, the whole model structure should be rethought.

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Summary

Modelling bivalves in estuaries and coastal areas

The ability to predict the dynamics of bivalve populations in response to environmental change, natural or human induced, is quite useful for the management of coastal ecosystems, either with the purpose of commercial exploitation optimization, environmental impact assessment, climate changes implications or assessing the impact of exotic species introduction. Mathematical models have been used to address some of these questions. Current models that couple complex descriptions of both ecological and physical processes still lack the simulation of reproduction and recruitment success, as well as the size distribution of the population, which can be important for its dynamics.

The aim of this thesis was to study and quantify the dynamics of bivalve communities and their influence on the pelagic system. To achieve this, an individual-based population model for bivalves (based on the Dynamic Energy Budget theory), was developed and coupled to a hydrodynamic and biogeochemical model (MOHID Water Modelling System). The result is a process oriented modelling tool that integrates physical, biogeochemical, ecological and physiological factors governing bivalve populated marine ecosystems. The originality of this work lies, among others, in the integration of several fields of knowledge to achieve a better understanding of the relative importance of the processes. The integrated modelling tool was successively tested throughout its development and it was implemented in a real ecosystem (Balgzand, Wadden Sea, The Netherlands). The structure of the thesis mirrors the steps towards the final goal of building and implementing the integrating modelling tool.

Chapter 2 deals with detailing feeding processes in bivalves, particularly on blue mussel *Mytilus edulis*. A new mechanistic description of bivalves feeding was developed as an extension of the standard DEB model. Filtration, ingestion and assimilation are assumed as three different steps and pseudofaeces production is computed as the difference between filtered and ingested fluxes. The concept of Synthesizing Units described by the DEB theory was used to develop generic formulations to account for different types of food, with type-specific ingestion and assimilation efficiencies. Necessary parameters were estimated and the model performance was evaluated by comparison with literature data for the blue mussel for a wide range of experimental conditions, with good results.

A new set of DEB parameters for the blue mussel is presented in Chapter 3. The new estimate is based on the covariation method that consists of a simultaneous minimization of the weighted sum of squared deviations between data sets and model predictions in one single procedure. Different data sets, obtained from the literature, were used in the estimation procedure. For the present model configuration and for the tested datasets, the study concludes that the parameter set obtained by the covariation method leads to a better fit between model and observations, and is therefore potentially more consistent and robust.

In Chapter 4, the individual model, including the feeding model extension presented in Chapter 2, and the new parameter set presented in Chapter 3, was tested against field observations. At four locations in the North Sea, labelled mussels were kept under natural condition. Shell length and dry weight was determined for some mussels and environmental properties were measured close to the experimental sites. Results revealed that the individual model was able to reproduce perfectly the pattern and reasonably the average growth of the mussels in the four places. This result implies that the main metabolic processes at the individual level are well described by the model. By performing different model scenarios we conclude that inorganic particles can have an important effect in the individual performances, even more than seasonal changes in food composition.

The upgrading of the generic individual model from Chapter 4 into a population model is de-

scribed in Chapter 5. An individual based population model (based on DEB) was built, meaning that the population dynamics is represented by several cohorts' trajectories. Each cohort consists of identical individuals born at the same time and showing identical properties throughout their life and that interact with other cohorts through food competition. Other population processes included are initial egg mortality, background mortality, and predation (including cannibalism). Model properties were studied through the analysis of theoretical scenarios. Next, the model was used to schematically simulate a mussel bed located in the intertidal area of the Balgzand. Major simplifications were made on the loss of larvae by dispersion, the tide effect, and the feedbacks to lower and upper trophic levels. Besides the great amount of available data, important information on predators' diet is still missing, namely on what fraction of the predators diet consists of mussels. As the role of predation is an important question, multiple scenarios were explored, with simple variations of the predation parameters. Criteria were then developed to select well fitting results, narrowing the parameters combinations. The selected modelling scenarios were able to reproduce the timing of some peaks in mussel abundances. They also produced similar size distributions, but the absolute number of individuals was not well predicted. Possible causes were identified and suggestions were made to overcome the discrepancy, including a better description of food availability and larvae/food dispersion potentially given by an ecosystem model.

Chapter 6 firstly describes the main features of the model and the concepts used in coupling the individual based population model with MOHID Water Modelling System. This is followed by a fully integrated implementation in the Balgzand area, The Netherlands. The model simulates, in a fine resolution domain, hydrodynamics (currents and water elevations), waves, heat, salt and sediment transport, biogeochemical cycle of nutrients, primary production and bivalve population dynamics. It is initialized and forced by an extensive observation data set during a period of two years (2009/2010). Model results for a reference scenario are in good agreement with observations, and provide a consistent quantitative description of local hydrodynamics and biogeochemical cycles. The mussel spawning season in the Balgzand is long and almost continuous and larvae dispersion is quite important. The study strengthens that there is no single mortality factor responsible for the population dynamics regulation. Early stage mortality (top-down) can control the persistence of new cohorts, in particular cannibalism and shrimp predation, although starvation (bottom-up) is the main process responsible for bivalve loss over the year in terms of biomass. By performing a scenario considering the nonexistence of mussel beds the study shows that in general bivalves' activity intensifies the seasonal patterns of phytoplankton and nutrients in areas close to the mussel beds, but they do not change their overall spatial distribution. The Balgzand acts as a sink of phytoplankton, due to bivalves' filtration. Without bivalves it would export phytoplankton. It also acts as a source of ammonia, exporting about 40% more than the input flux, suggesting high ammonia regeneration. Thus, the study confirms and quantifies that bivalves do have the potential to influence ecosystem functioning due to their role in nutrient cycling.

As future work, more scenarios could be performed to provide insight in the relative importance of a process. As an example, it could be interesting to test the influence of oysters and cockles on mussel growth; test the influence of temperature in prey-predators relations between mussels and shrimps; or estimate possible locations for artificial mussel beds. As the first integrated modelling study that focus on the mussel' beds in the Balgzand, the main difficulties in model design, setup and analysis were overcome and it can now be further used, tested and improved. The model is general enough to allow its application to any ecosystem with similar processes

and multiple species. The first step was taken, but only more tests, implementations and improvements will give the model, and the scientific community using it, the desired experience to serve as an effective and reliable management tool in estuaries and coastal areas.

Sumário

Modelação de bivalves em estuários e zonas costeiras

A capacidade de previsão da dinâmica de população de bivalves, em resposta de alterações ambientais, naturais ou antropogénicas, é muito útil na gestão do ecossistema, seja com o objectivo de optimização da exploração comercial, quantificação de impacte ambiental, implicações das alterações climáticas ou análise de impacte na introdução de novas espécies. Algumas destas questões têm sido analisadas com recurso a modelos matemáticos. Os modelos actuais, que incluem descrições detalhadas tanto de processos ecológicos como de processos físicos, carecem ainda da simulação da reprodução, do sucesso no recrutamento de novos indivíduos e ainda da simulação da distribuição por tamanho dos indivíduos, que podem ser importantes para a dinâmica da população.

O objectivo desta tese é o estudo e quantificação da dinâmica das comunidades de bivalves e a sua influência no sistema pelágico. Neste sentido, foi desenvolvido um modelo de população baseado no indivíduo (usando a teoria Dynamic Energy Budgets) e posteriormente acoplado a um modelo hidrodinâmico/biogeoquímico (MOHID Water Modelling System). O resultado é uma ferramenta de modelação orientada por processos que integra o efeito de factores físicos, biogeoquímicos e fisiológicos determinantes na dinâmica de população de bivalves, descrevendo e quantificando os fluxos de massa/energia entre todos os componentes. A originalidade deste trabalho encontra-se na integração de vários campos do conhecimento para alcançar uma melhor compreensão sobre a importância relativa dos processos.

A ferramenta de modelação integrada foi testada sucessivamente ao longo do seu desenvolvimento. Os diferentes capítulos da tese correspondem a etapas importantes do estudo, onde processos ou particularidades do modelo foram desenvolvidos e/ou analisados em maior detalhe e, tanto quanto possível, testados e validados através da comparação com dados.

O Capítulo 2 foca o processo de aquisição de alimento nos bivalves, em particular nos mexilhões (*Mytilus edulis*). As flutuações na quantidade e qualidade de material particulado em suspensão em estuários e sistemas costeiros são uma das suas principais características. A falta de uma descrição mecanicista dos processos de filtração de bivalves capaz de lidar com estas variações motivou o desenvolvimento de um módulo adicional que pode ser utilizado com uma extensão do modelo standard DEB. A filtração, ingestão e assimilação são considerados, neste módulo, como três processos distintos, sequenciais e a produção de pseudofaeces é o resultado da diferença entre o material filtrado e ingerido. O conceito de Unidades de Síntese (Synthesizing Units) definido pela teoria DEB foi usado para desenvolver formulações genéricas que permitem considerar diferentes tipos de partículas com taxas de ingestão e eficiências de assimilação específicas. Os parâmetros necessários para este modelo foram estimados e o seu desempenho foi avaliado, com bons resultados, através da comparação com dados existentes na literatura relativa ao mexilhão, para uma ampla gama de condições experimentais.

No Capítulo 3 é apresentado um novo conjunto de parâmetros DEB para o mexilhão. A nova estimativa baseia-se no método de covariação recentemente desenvolvido, que consiste na aplicação em simultâneo do método dos mínimos quadrados dos desvios entre os diversos conjuntos de dados e as previsões do modelo num procedimento único. O método inclui ainda uma série

de restrições fisiológicas, introduzindo o conceito de pseudo-dados. Foram usados neste procedimento, diferentes conjuntos de dados, obtidos a partir de literatura. Os resultados do modelo usando os novos parâmetros e os anteriores foram então comparados com as observações. Concluiu-se que para a configuração actual do modelo e para os conjuntos de dados testados, os parâmetros obtidos pelo método de covariação leva a um melhor ajuste entre o modelo e as observações, e é, portanto, potencialmente mais consistente e robusto.

Segue-se a implementação e teste do modelo de indivíduo, incluindo a extensão dos processos de filtração apresentada no Capítulo 2, e o novo conjunto de parâmetros apresentado no Capítulo 3. Previsões do modelo foram comparadas com observações de campo obtidas em quatro locais diferentes no mar do Norte, descritos no Capítulo 4. Nestes locais, mexilhões rotulados foram mantidos sob condições naturais, alguns deles durante vários anos. O comprimento da concha foi medido para cada indivíduo repetidamente durante a experiência e no peso seco foi determinado no fim do ensaio para alguns dos indivíduos. Algumas propriedades, tais como temperatura, salinidade, concentração de clorofila e profundidade de Secchi foram medidos em locais próximos da experiência. Os resultados foram explorados e o modelo de indivíduo foi capaz de reproduzir perfeitamente o padrão e razoavelmente a média de crescimento dos mexilhões nos quatro locais. Este resultado implica que os principais processos metabólicos ao nível do indivíduo são bem descritos pelo modelo. Através da simulação de diferentes cenários foi também possível concluir que as partículas inorgânicas podem ter um efeito importante nas performances individuais e que a variabilidade na concentração de sedimentos pode ser mais importante do que as alterações sazonais na composição do alimento. Este resultado sugere que futuras experiências e programas de monitorização deverão, sempre que possível incluir não só medições de quantidade de comida, mas também o total de matéria em suspensão na coluna de água.

A utilização do modelo individual genérico do Capítulo 4 como unidade básica de um modelo de população é descrita no Capítulo 5. O modelo de população de bivalves baseado no indivíduo foi desenhado, construído e testado seguindo uma abordagem 0D, com a finalidade de simular a dinâmica de população de um banco de mexilhão localizado numa área intertidal. O modelo encontra-se organizado por espécies de bivalves e cada espécie pode conter diferentes coortes. Cada coorte é simulada como uma entidade independente, que pode interagir com outros da sua própria espécie ou de espécies diferentes. O modelo inclui ainda a mortalidade inicial de ovos, mortalidade natural, competição por alimento e predação (incluindo canibalismo) como principais processos ao nível da população. As propriedades do modelo foram estudadas através da análise de cenários teóricos e também através de sucessivas simulações, usando diferentes combinações de parâmetros numa configuração realista, em condições ambientais baseadas em observações. Para diminuir as possíveis combinações de parâmetros, as estimativas do modelo foram comparadas com observações de campo obtidas para um banco de mexilhão específico incluído num programa de monitorização de longo prazo. Este capítulo foi um importante passo para o desenvolvimento e implementação do modelo integrado completo apresentado no Capí-

tulo 6.

O Capítulo 6, descreve, em primeiro lugar, as principais características do modelo e os conceitos utilizados no acoplamento ao MOHID Water Modelling System. De seguida, descreve a implementação integrada do modelo completo no Balgzand, uma área intertidal, localizada na parte mais ocidental do Wadden Sea, Holanda. O modelo simula, num domínio de alta resolução, a hidrodinâmica (correntes e elevações de água), ondas, temperatura, salinidade e transporte de sedimentos, ciclo biogeoquímico dos principais nutrientes, produção primária e dinâmica de população de bivalves. A inicialização e o forçamento utiliza um extenso conjunto de dados de campo e resultados de modelos para um período de dois anos (2009/2010) que representam as condições actuais do ecossistema. Os resultados do modelo para o cenário de referência estão de acordo com as observações e fornecem uma descrição quantitativa consistente da hidrodinâmica local e os processos biogeoquímicos. O período anual de reprodução dos mexilhões é bastante longo, quase contínuo, e a dispersão de larvas é significativa. O estudo sugere que não existe um único processo de mortalidade responsável pela regulação da população. A mortalidade intensa nas primeiras fases do ciclo de vida dos indivíduos devido a predação (top-down) controla a persistência de novos coortes, em particular o canibalismo e a predação pelo camarão. No entanto, a mortalidade devido a falta de alimento é o principal processo de mortalidade em termos de perda anual de biomassa. A actividade dos bivalves intensifica os padrões sazonais do fitoplâncton e nutrientes nas zonas próximas dos bancos de mexilhões, embora não altere a sua distribuição espacial global. O Balgzand funciona como consumidor de fitoplâncton, devido à filtração por parte dos bivalves. Sem bivalves o sistema exportaria fitoplâncton. Os resultados demonstram ainda que o Balgzand actua como fonte de amónia, exportando cerca de 40 % do fluxo de entrada, o que sugere que a regeneração de amónia dentro do sistema é muito significativa.

O estudo não só confirma, mas quantifica através da comparação dos resultados do modelo em diferentes cenários, que os bivalves têm o potencial para influenciar o funcionamento do ecossistema devido ao seu papel no ciclo biogeoquímico dos nutrientes. O estudo da importância relativa dos processos pode assim recorrer à simulação de diferentes cenários utilizando diversas configurações do modelo. Como exemplo de trabalho futuro sugere-se o estudo da influência de outras espécies, tais como ostras e berbigão, no crescimento dos mexilhões; o teste da influência da temperatura nas relações predador-presa entre mexilhões e camarão; estimar a possível localização de bancos de mexilhão artificiais ou ainda o estudo das respostas da população a alterações nas condições ambientais.

Tratando-se do primeiro estudo de modelação integrada focado nos bancos de mexilhão no Balgzand, as principais dificuldades no design do modelo, configuração e análise de resultados foram superadas e este poderá agora ser novamente usado, testado e ainda melhorado. O modelo é suficientemente geral para permitir a sua aplicação a qualquer ecossistema com processos semelhantes e várias espécies. Este foi o primeiro passo, mas só mais testes, implementações e melhoramentos poderão dar ao modelo e à comunidade científica a desejável experiência para

que o modelo possa ser utilizado como uma ferramenta efectiva e eficaz e confiável na gestão do ecossistema e na tomada de decisões em estuários e zonas costeiras.

Samenvatting

Het modelleren van tweekleppigen in estuaria en kustgebieden

Het kunnen voorspellen van de manier waarop populaties van tweekleppige schelpdieren reageren op veranderingen in hun omgeving is van groot belang voor een goed beheer van kustecosystemen. Dit geldt zowel voor wilde als voor geëxploiteerde schelpdierpopulaties, voor natuurlijke als voor door de mens veroorzaakte veranderingen, voor klimaatveranderingen als voor veranderingen veroorzaakt door de introductie van nieuwe soorten. Om de effecten van deze veranderingen te beschrijven worden wiskundige modellen gebruikt. De huidige modellen beschrijven weliswaar complexe fysische en ecologische processen, maar houden nog geen rekening met de grootteverdeling van de populatie van tweekleppigen en geven op zijn best een summiere beschrijving van de voortplanting en de rekrutering van de populatie, processen die wel van groot belang zijn voor de dynamica van de populatie.

Het doel van dit proefschrift is het bestuderen en kwantificeren van de dynamica van populaties van tweekleppigen en hun invloed op het pelagische ecosysteem. Om dit doel te bereiken is een individu-gebaseerd populatiemodel voor tweekleppigen opgesteld, dat gebaseerd is op de dynamische-energiebudget (DEB) theorie en is dit model vervolgens gekoppeld aan een hydrodynamisch en biogeochemisch model (MOHID Water Modelling System). Het resultaat is een proces-georiënteerd modelgereedschap dat fysische, biogeochemische, ecologische en fysiologische factoren integreert; factoren, die bepalend zijn voor door tweekleppigen gedomineerde mariene ecosystemen. Het vernieuwende element in dit werk is onder meer de integratie van kennis uit uiteenlopende vakgebieden om zodoende een beter begrip te krijgen van het relatieve belang van alle deelprocessen. Gedurende de ontwikkeling van dit modelgereedschap zijn herhaaldelijk testen uitgevoerd en uiteindelijk is het toegepast op een echt bestaand ecosysteem, het Balgzand in de Nederlandse Waddenzee. De structuur van het proefschrift weerspiegelt de stappen die genomen zijn om dit modelgereedschap te maken.

Hoofdstuk 2 behandelt de manier waarop tweekleppigen, vooral mossels *Mytilus edulis*, hun voedsel vergaren. Het standaard DEB model werd uitgebreid met een nieuwe mechanistische beschrijving van de wijze waarop tweekleppigen voedsel zoeken. Filtratie, opname en assimilatie worden gezien als drie achtereenvolgende stappen en de productie van pseudofaeces wordt berekend als het verschil tussen het uitgefilterde en het opgenomen materiaal. Het concept van de zogeheten Synthesizing Units, een van de bouwstenen van de DEB theorie, werd gebruikt om te komen tot algemene formuleringen waarin onderscheid gemaakt kan worden tussen verschillende soorten voedsel, ieder met zijn specifieke opnamesnelheid en assimilatie-efficiëntie. De benodigde parameters werden geschat en een vergelijking tussen modelvoorspellingen en literatuurgegevens voor uiteenlopende experimentele omstandigheden lieten goede resultaten zien voor de mossel.

Nieuwe schattingen van de DEB parameters voor de mossel worden in hoofdstuk 3 gegeven. De zogeheten covariatiemethode wordt gebruikt, waarin een gewogen som van de gekwadrateerde afwijkingen tussen gegevens en modelvoorspellingen voor meerdere gegevenssets tegelijkertijd in een enkele procedure geminimaliseerd wordt. De op basis van meerdere gegevenssets uit de literatuur verkregen parameterset geeft dus het minimale verschil tussen model en waarnemin-

gen.

In hoofdstuk 4 wordt het individu-model, met daarin opgenomen de voedselvergaringsmodule uit hoofdstuk 2 en met de nieuwe parameterset uit hoofdstuk 3, getest tegen nieuwe veldwaarnemingen. Deze waarnemingen komen van vier plekken op de Noordzee waar uitgezette en individueel gemerkte mossels onder natuurlijke omstandigheden konden opgroeien. Schelpenlengte en drooggewicht werden bepaald en omgevingsvariabelen werden continu gemeten. De resultaten lieten zien dat het individu-model het waargenomen groeipatroon perfect beschreef en dat ook de gemiddelde groeisnelheid redelijk goed beschreven werd op de vier plekken. Blijkbaar worden de belangrijkste metabolische processen van de individuele mossel goed beschreven door het model. Door het bestuderen van meerdere modelscenario's vonden wij dat anorganische deeltjes een groot effect hebben op de groei, zelfs meer dan de seizoenale veranderingen in de voedselsamenstelling.

In hoofdstuk 5 wordt het op DEB gestoelde individu-model uit hoofdstuk 4 uitgebreid naar een populatiemodel. Een individu-gebaseerd populatiemodel werd ontwikkeld, waarin de populatiedynamica weergegeven wordt middels de ontwikkeling van meerdere cohorten. Elk cohort bestaat uit identieke individuen die op dezelfde dag geboren zijn en gedurende hun hele leven gelijk aan elkaar blijven. Elk cohort interacteert met andere cohorten alleen via het voedsel. Andere populatie-processen die meegenomen werden zijn een initiële eisterfte, een achtergrondsterfte en predatie (inclusief kannibalisme). De modeleigenschappen werden bestudeerd door middel van de analyse van theoretische scenario's. Vervolgens werd het model gebruikt om op een heel schematische manier een mosselbed op het inteergetijdengebied van het Balgzand te simuleren. Het verlies van larven tengevolge van uitspoelen, het effect van getij en de terugkoppelingen met de hogere en lagere trofische niveau's werden op een sterk vereenvoudigde manier beschreven. Hoewel er redelijk veel informatie aanwezig is, weten wij nog te weinig van het dieet van de belangrijkste predatoren: welk gedeelte bestaat uit mossels? Omdat de rol van predatie wel belangrijk lijkt werden meerdere scenario's getest. De scenario's verschilden in de predatieparameters. Op basis van bepaalde criteria werden modeluitkomsten dan als mogelijk of onmogelijk geclassificeerd, waarbij dus de set van mogelijke parametercombinaties sterk verkleind werd. De geselecteerde modelscenario's waren redelijk in staat om het tijdstip te voorspellen waarop pieken in mosselaantallen voorkomen. Ook de voorspelde grootteverdeling klopte behoorlijk, maar het voorspelde absolute aantal mossels zat ver naast de werkelijkheid. Een betere beschrijving van het voedselaanbod en van het uitspoelen van de larven zou dit probleem wel eens kunnen oplossen: de reden om het populatiemodel te koppelen aan een ecosysteemmodel.

Hoofdstuk 6 beschrijft allereerst de belangrijkste eigenschappen van zo'n model, waarin het individu-gebaseerde populatiemodel gekoppeld wordt met het MOHID systeem. Vervolgens wordt de implementatie voor het Balgzand beschreven. Het model simuleert met een fijne resolutie de hydrodynamica (stromingen en waterstanden), de golven, de warmte, het zout- en sedimenttransport, de biogeochemische kringloop van voedingsstoffen, de primaire productie en

de dynamica van de populatie tweekleppigen. De definitie van de begintoestand en de beschrijving van de omgeving van het modelsysteem gebeurt op basis van een uitvoerige tweejarige dataset (2009/2010). De modelresultaten voor een referentiescenario stemmen goed overeen met waarnemingen aan het systeem op het vlak van de lokale hydrodynamica en de biogeochemische kringloop. Het paaiseizoen van de mossels op het Balgzand is lang volgens het model en ook de verspreiding van larven blijkt belangrijk. De studie wijst er op dat er niet één enkele sterftefactor is die de populatie reguleert. Vroege sterfte door kannibalisme of garnalen (top-down) kan het lot van een cohort bezegelen, maar toch is verhongering (bottom-up) het belangrijkste proces voor het teruglopen van de mosselbiomassa. Het scenario zonder mossels liet zien dat de aanwezigheid van mossels weliswaar het seizoenspatroon van voedingsstoffen en fytoplankton versterkt vlak bij de mosselbedden, maar dat de grote ruimtelijke patronen niet of nauwelijks beïnvloed worden. Door de filtratie van tweekleppigen verdwijnt er op het Balgzand meer fytoplankton dan er geproduceerd wordt. Zonder tweekleppigen zou het Balgzand juist fytoplankton exporteren. Het Balgzand is daarentegen een bron van ammonia en exporteert ongeveer 40% meer dan het importeert, hetgeen een hoge ammoniumregeneratie suggereert. Kortom, de studie laat op een kwantitatieve manier zien dat tweekleppigen de mogelijkheid hebben het functioneren van het ecosysteem te beïnvloeden, juist vanwege hun rol in de kringloop van voedingsstoffen.

Als toekomstig werk zouden meer scenario's getest kunnen worden om verder inzicht te krijgen in het relatieve belang van de deelprocessen. Om wat voorbeelden te noemen: wat is de invloed van oester en kokkels op de groei van mossels; wat is de invloed van temperatuur op de prooi-predator relatie tussen de garnaal en de mossel; wat voor rol speelt de locatiekeuze op de invloed van kunstmatig aangelegde mosselbedden? Als eerste geïntegreerde modelstudie van de mosselbedden op het Balgzand zijn de kinderziektes wat betreft modelontwerp, opzet en analyse achter de rug. Het model kan nu verder gebruikt worden, getest worden en verbeterd worden. Het model is algemeen genoeg om ook als voorbeeld te dienen voor andere ecosystemen waarin vergelijkbare processen en soorten een rol spelen. De eerste stap is nu gezet, maar alleen vervolgtesten, implementaties en verbeteringen zullen de wetenschappelijke gemeenschap die er gebruik van maakt, de benodigde ervaring geven om het model op een effectieve manier in te zetten ten behoeve van het beheer van estuaria en kustgebieden.

Curriculum Vitae



Sofia Saraiva was born on April 17th, 1979 in Covilhã, Portugal. She completed her secondary education at Escola Frei Heitor Pinto in 1996, and continued with an Environmental Engineering 5 year degree at Instituto Superior Técnico (IST), University of Lisbon (UL) in Lisbon. Sofia graduated in 2001, with a final project on the study of primary production dynamics in the Tagus estuary (Portugal) using an ecosystem model. In the same year she started a junior position at the MARETEC (IST) where she worked for several years, on many different projects and topics but always related with ecosystem modelling and biogeochemical cycles of nutrients.

During that period she had the opportunity to learn new modelling techniques and programming languages as well as gain experience on model development and use, to understand particular system dynamics. As a complement to modelling, Sofia was also responsible for the design, implementation and execution of monitoring programs with automatic acquisition systems including the use of probes, GPS and dataloggers to collect information for model validation. In 2005 she concluded the two years MSc project on modelling macroalgae activity in Ria de Aveiro (Portugal). A PhD position brought Sofia to the NIOZ in Texel, The Netherlands, in 2008, to research on bivalves and their interaction with other components of the ecological system. In 2009, Sofia received a PhD grant from the Fundação para a Ciência e a Tecnologia (Portugal) to continue her studies on bivalves, supervised by Prof. Jaap van der Meer (NIOZ), Prof. Bas Kooijman (VU), Prof. Ramiro Neves (IST) and Tânia Sousa (IST). The research goal was to study bivalve population dynamics and quantify their influence on the pelagic system, through the development and use of a modelling tool. This tool is the result of coupling a size-structured population model for bivalves, based on the Dynamic Energy Budgets Theory, with a hydrodynamic and biogeochemical model (MOHID).

Publications

Publications covered in this thesis

- submitted* Saraiva, S., Fernandes, L., van der Meer, J., Neves, R. and Kooijman, S. The role of bivalves in the Balgzand: first steps on an integrated modelling approach. *Ecol. Model.*
- in press* Saraiva, S., van der Meer, J., Kooijman, S., and Ruardij, P. Bivalves: from individual to population modelling. *J. Sea Res.*, DOI: 10.1016/j.seares.2014.06.004.
- 2012 Saraiva, S., van der Meer, J., Kooijman, S., Witbaard, R., Philippart, C., Hippler, D., and Parker, R. Validation of a dynamic energy budget (DEB) model for the blue mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.*, 463:141–158.
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- 2011 Saraiva, S., van der Meer, J., Kooijman, S., and Sousa, T. Modelling feeding processes in bivalves: A mechanistic approach. *Ecol. Model.*, 222:514–523.

Other publications

- 2010 Troost, T.A., Wijsman J.W.M., Saraiva S., Freitas V. Modelling shellfish growth with dynamic energy budget models: and application for cockles and mussels in the Oosterschelde (southwest Netherlands). *Phil. Trans. R. Soc. B.*, 365: 3567–3577.
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The aim of this thesis was to study and quantify the dynamics of bivalve communities and their influence on the pelagic system. An individual-based population model for bivalves (using the Dynamic Energy Budget theory) was developed and coupled to a hydrodynamic and biogeochemical model (MOHID Water Modelling System). The result is a process oriented modelling tool that integrates physical, biogeochemical, ecological and physiological factors governing bivalve populated marine ecosystems. The model includes new techniques to simulate feeding processes using a mechanistic approach and a revised set of parameters is presented for the blue mussel (*Mytilus edulis*). The individual model was validated against observations, further extended to a population model and ultimately coupled to MOHID. A fully integrated modelling study was performed in the Balgzand (The Netherlands). The model simulates, in a fine resolution domain, hydrodynamics (currents and water elevations), waves, heat, salt and sediment transport, biogeochemical cycle of nutrients, primary production and bivalve population dynamics. The study strengthens that there is no single mortality factor responsible for the population dynamics regulation. Early stage mortality (top-down) can control the persistence of new cohorts, in particular cannibalism and shrimp predation, although starvation (bottom-up) is the main process responsible for bivalve loss over the year in terms of biomass. The study also confirms and quantifies that bivalves do have the potential to influence ecosystem functioning due to their role in nutrient cycling. The model is general enough to allow its application to any ecosystem with similar processes and it can simulate multiple species. Such a tool can be further used to characterize ecosystem response to different environmental changes (natural or anthropogenic) and to serve as an effective and reliable management and decision making tool in estuaries and coastal areas.

