



The role of bivalves in the Balgzand: First steps on an integrated modelling approach



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ABSTRACT

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 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), in particular cannibalism and shrimp predation, can control the persistence of new cohorts in the first month although starvation (bottom-up) represents the main cause of biomass loss in an overall. The tendency is that new mussel beds are formed in areas adjacent to already existing mussel beds and channel edges. 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 also 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 used further, tested and improved in the same or other systems in order to serve as an effective and reliable scientific and management tool.

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1. 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 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 et al., 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 sec-

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ond 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 bivalve production and population dynamics in interaction with an ever changing environment by improving the description of food availability and relevant physical processes, supplied by the ‘physical transport’ type of models. Some examples of this approach can be found in the literature (e.g. Klinck et al., 2002; Hofmann et al., 2006; Goff et al., 2017)

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 (e.g. de Vooy, 1999); (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). Reproduction and recruitment success can not be deterministically predicted 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). Some studies also focus on the dispersal and settlement of the larvae (e.g. Bidegain et al., 2013). However, in those studies the reproduction is detached from the bivalve development stage. In addition, understanding top-down control requires the simulation of the individual size, throughout their main live stages (larvae, juvenile and adult), since predators have size preferences. 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 because the underlying processes are size depended and consequently their relative importance in time and space and that can be done 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. The direct consequence is that the same set of equations can be used to simulate the complete life cycle of a bivalve. This is an advantage in the coupling with 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 (e.g. Fulton et al., 2003; Cury et al., 2008; Hannah et al., 2010), 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).

2. Material and methods

2.1. Model description

2.1.1. 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 is considered 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 organic matter (detritus). 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.

2.1.2. 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), coupled with a feeding processes model,

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