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A coupled biophysical model for the distribution of the great scallop *Pecten maximus* in the English Channel

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ABSTRACT

In this paper we used a modelling approach integrating both physical and biological constraints to understand the biogeographical distribution of the great scallop *Pecten maximus* in the English Channel during its whole life cycle. A 3D bio-hydrodynamical model (ECO-MARS3D) providing environmental conditions was coupled to (i) a population dynamics model and (ii) an individual ecophysiological model (Dynamic Energy Budget model). We performed the coupling sequentially, which underlined the respective role of biological and physical factors in defining *P. maximus* distribution in the English Channel. Results show that larval dispersion by hydrodynamics explains most of the scallop distribution and enlighten the main known hotspots for the population, basically corresponding to the main fishing areas. The mechanistic description of individual bioenergetics shows that food availability and temperature control growth and reproduction and explain how populations may maintain themselves in particular locations. This last coupling leads to more realistic densities and distributions of adults in the English Channel. The results of this study improves our knowledge on the stock and distribution dynamics of *P. maximus*, and provides grounds for useful tools to support management strategies.

1. Introduction

The great scallop *Pecten maximus* is exploited all along its distribution range, from Norway to Portugal. Fisheries are mostly located in the English Channel, where *P. maximus* is the most abundantly harvested species in terms of landings (in biomass and in value) for the French inshore fleet. Considering its broad distribution and its high economic value, several studies have been conducted on the biology and life history traits of this species (Mason, 1957; Antoine, 1979; Le Pennec et al., 2003; Brand, 2006; Cragg, 2006; Thompson and MacDonald, 2006).

The great scallop is a meroplanktonic hermaphrodite species, spending a small part of its development in the water column (as larvae) and the major part of its life on the sea floor. The mechanisms providing suitable environmental conditions for the settlement and the development of *P. maximus* have yet to be considered simultaneously to determine the potential for survival and growth of individuals in a given habitat. As they are difficult to carry out, numerical models dealing with the whole life cycle of species are uncommon (Possingham and Roughgarden, 1990; Dekshenieks et al., 2000; Klinck et al., 2002; Savina and Ménesguen, 2008). Studies focus either on the larval dispersion modelling (for example: Young et al., 1998; Ellien et al., 2004; Condie et al., 2006; Bidegain et al., 2013; Nicolle et al., 2013), or on the population dynamics of the benthic stage (McArdle et al., 1997; Solidoro et al., 2003; Gangnery et al., 2004). Distribution of benthic marine species is driven by numerous abiotic (hydrodynamics, sediment type, *etc.*) and biotic (individual physiology characteristics, ecological interactions) factors. If growth, fecundity and mortality are known to be related to physiological state and food availability, they also depend on predation, trophic competition and physiological stress. Coupling the environment (temperature, hydrodynamics, food availability) to the entire life cycle of *P. maximus* is essential to correctly understand the bio-geographical distribution of the species.

The present study is based on the use and coupling of three models: 1) the hydrodynamic MARS3D model (Model for Applications at Regional Scale, Lazure and Dumas, 2008) used to compute the physical characteristics prevailing in the English Channel (temperature, salinity, tide, current velocities) was coupled to a NPZD (Nutrient-Phytoplankton-Zooplankton-Detritus) primary production model (giving the ECO-MARS3D model) in order to simulate the biological properties of

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the ecosystem (particularly chlorophyll-*a* as a food proxy for scallops); 2) a population dynamic model developed for *P. maximus*, describing the whole life cycle (planktonic and benthic stages) using a mechanistic approach (based on Savina and Ménesguen, 2008) and 3) an ecophysiological model based on the Dynamic Energy Budget (DEB) theory (Kooijman, 2010) adapted to *P. maximus* (Lavaud et al., 2014) to simulate individual growth, fecundity and physiological status. The present paper describes the coupling of these models to describe the biogeography of the great scallop in the English Channel. The simulated spatialized abundances are discussed regarding *in situ* data, which are limited to presence of *P. maximus* and landings from French and UK fleets in the English Channel.

2. Materials and methods

2.1. General description of the study area

The English Channel is part of the Northwest European Continental shelf and separates the Atlantic Ocean from the North Sea. Its western boundary is approximately represented by the longitudinal line crossing the Scilly Islands seaward from the Cornish coast in the UK and the eastern boundary is defined by the Strait of Dover (Fig. 1). The Channel is characterized by a macrotidal regime, which leads to strong tidal currents and a high tidal range, a complex gyre system around the Islands of Jersey and Guernsey (Normand-Breton gulf) and a general residual circulation from west to east, driving water from the Atlantic to the North Sea (Salomon and Breton, 1993). The eastern part of the Channel receives strong fresh water input, mainly coming from the Seine River (mean flow about 500 $m^3 s^{-1}$). The Seine River brings nutrients to the Bay of Seine and more generally the eastern Channel, occasionally leading to eutrophic conditions resulting in phytoplankton proliferation, toxic blooms, *etc.* (Cugier et al., 2005; Romero et al., 2013; Passy et al., 2016).

High species richness and abundance of benthic fauna is encountered in the English Channel (Holme, 1966; Cabioch, 1968; Gentil, 1976; Cabioch et al., 1977; Retière, 1979) that has favored the development of many fisheries including the great scallop. However, precise knowledge of its distribution and abundance in the English Channel is still lacking. Available data are mostly qualitative (Fig. 2), except in the two major areas of the French fishery: the bays of Seine and of Saint-Brieuc (see Fig. 1) where average stock assessments are between 6000 and 8000 tons, respectively, for the year 2012. Nevertheless, observed landing values could give a proxy of the real biomass distribution (Fig. 3). This species is heavily harvested and despite the significance of the great scallop fishery in the English Channel, there is no regulation system at the European level to date (Foucher and Fifas, 2013).

2.2. Models

2.2.1. Hydrodynamical and biogeochemical models

The three-dimensional (3D) hydrodynamic model MARS (Lazure and Dumas, 2008) was used to simulate physical properties in the study area. It is a finite difference, mode splitting model in a sigma-coordinate framework, here applied to the English Channel (from 47.88°N to 51.15°N in latitude and from −7.03°W to 3.00°W in longitude). The study area was divided in 2 by 2 km meshes to form a rectangular grid with a vertical resolution of 10 sigma layers. This hydrodynamic model allows computing current velocity, temperature and salinity fields. It was coupled to a NPZD primary production model used to simulate the dynamics of free-living plankton in the Channel (ECO-MARS3D).

This NPZD model is similar to the one previously developed for the same area by Vanhoutte-Brunier et al. (2008). The model integrates the nutrient cycles of nitrogen, phosphorus and silica and considers three phytoplanktonic compartments: diatoms, dinoflagelates and nanoflagelates expressed in the form of their nitrogen content (Fig. 4). These three variables were converted into a single parameter expressed as chlorophyll-*a* (chl-*a*) concentration and later used as a trophic source proxy for the great scallop (see http://wwz.ifremer.fr/mars3d/Le-modele/Descriptif/ for a complete description of the model and of the different modules).

2.2.2. The population dynamic model

As most bivalve species, *P. maximus* presents a larval planktonic phase. After a dispersal period of approximately one month in the water column, larvae settle on the sea bottom to achieve metamorphosis. Then, great scallops spend the rest of their life in the benthic compartment with limited mobility. The modelling of population dynamics takes into account these two stages and is based on the model developed by Savina and Ménesguen (2008) for *Paphia rhomboïdes* (Fig. 5). All the equations and parameters of the population

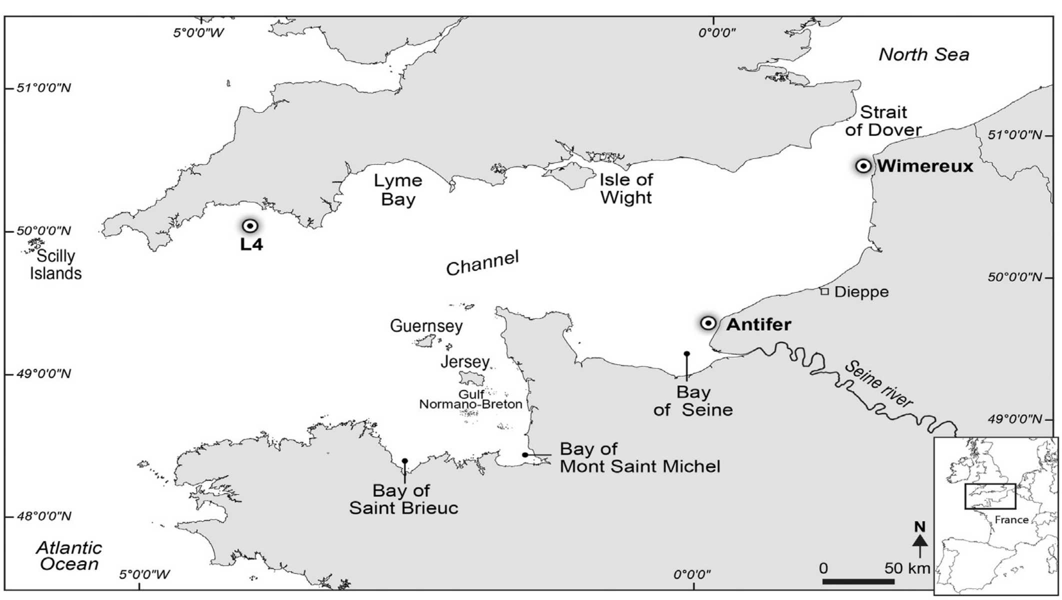

Fig. 1. Studied area in the English Channel (all the locations cited in the text are clearly shown). Locations of time series environmental data for ecosystem model validation (L4, Antifer, Wimereux).