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Modeling dispersal and spatial connectivity of macro-invertebrates in Danish waters: An agent-based approach

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ABSTRACT

Marine organisms with planktonic life stages are subjected to extensive transport that results from the interactions between ocean currents and their behavioral responses to environmental changes in the course of their life. Questions remain on the identification of key drivers of dispersal and connectivity in marine populations as they can have multiple uses in the conservation and management of marine ecosystems. Here we investigate whether the open Kattegat, at the entrance to Baltic Sea, is the main source of recruitment to the benthos in associated estuaries and coastal sites through export of planktonic invertebrate larvae. We couple a 3D hydrodynamic ocean model (MIKE3FM) to an agent-based model and simulate the dispersal of macro-invertebrate populations in Danish waters. We use characteristic dispersal traits of the larval community (pelagic larval duration, spawning season, and settling behavior) and simulate dispersal processes within the muddy bottom habitats to derive recruitment rates and potential donor populations leading to population connectivity patterns on each site, one bay and two Danish fjords. We then use our recruitment results in the bay to compare them with field data on species diversity in the same area. A total of 48 different combinations of pelagic larval durations and spawning seasons of macro-invertebrates are simulated in two years 2004 and 2010. From these results, we conclude that the central and southern parts of the Danish waters are identified as important spawning grounds whereas the Kattegat does not seem to be the main provider of larvae into the selected sites. The model also predicts higher abundance and recruitment rates of macro-invertebrate larvae in 2010 compared to 2004. These results are supported by comparable species distribution data collected in the study area. Our results show the importance of an integrated modeling tool combining ocean circulation and biological traits to obtain a detailed description of dispersal and connectivity of macro-invertebrate community in the area, which can provide a more accurate baseline to manage marine biodiversity.

1. Introduction

The life cycle of most of the benthic invertebrate fauna is characterized by a planktonic larval stage that can be transported by ocean currents leading to potential dispersal over broad geographic regions (Sala et al., 2013). This planktonic larval stage (referred here as pelagic larval duration or PLD) can last from few days to several months and it plays an important role in the connectivity of marine populations, contributing to meta-population structuring in several regions (Pineda et al., 2010; Bendtsen and Hansen, 2013; Valanko et al., 2015). Planktonic dispersal includes several phases such as spawning, larval transport and the subsequent behavior of settling larvae that eventually recruit to the benthos (Pineda et al., 2007). Altogether, these phases determine population connectivity, which can be defined as the exchange of individuals between geographically separated regions (Cowen and Sponaugle, 2009). Connectivity between separated regions can, in turn, regulate populations' demography by affecting growth and survival of the individuals (Pineda et al., 2007; Cowen and Sponaugle, 2009).

A popular method to address questions related to larval dispersal and connectivity is the use of 3D hydrodynamic models coupled with agent-based models (ABMs). ABMs can simulate populations composed by individual organisms, or groups of organisms, each of them characterized by specific biological traits and which can

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interact with the environment using a unique set of behavioral rules (DeAngelis and Mooij, 2005; Macal and North, 2006). Interest in larval dispersal using ABMs has been growing since the 1980s, with most of the earliest work focusing on larval behavior and dynamics of invertebrates (Obrebski, 1979; McKinney and McKinney, 1993; Palmer et al., 1996; Satuito et al., 1997) and fish (Dight et al., 1990; Paris et al., 2007; Staaterman and Paris, 2013) with the idea that larval supply was the key to determine the adult population dynamics (Levin, 2006).

Recent studies investigate the dispersal of commercially valuable species in the Baltic and North Sea (Pacariz et al., 2014; Daewel et al., 2015; Huwer et al., 2016). Pacariz et al., in 2014 highlight the importance of the Kattegat as a main spawning and nursery area for Atlantic cod (*Gadus morhua*) and other fish, such as plaice (Pleuronectes platessa), sole (*Solea solea*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*). Huwer et al., in 2016 analyze the connectivity of cod larvae in the transition area between the Baltic Sea and the North Sea and identify a general drift of larvae towards the north, from the spawning areas located in the Kattegat, the Sound and the Great Belt, and a high retention for the spawning area in Kiel Bay and Mecklenburg Bay. Finally, connectivity of macro-invertebrates has also been assessed in this transition region by Bendtsen et al., in 2013 with a Eulerian approach. They discover a large connectivity between habitats in the northern and southern part of this transition area but also that self-recruitment is sufficient to sustain the two populations independently.

In this work, we model dispersal patterns of planktonic macro-invertebrate larvae within the transition zone between the Baltic Sea and the North Sea (Fig. 1) to study the connectivity of macro-invertebrate populations. The area is characterized by strong gradients in the biodiversity of the benthic macro-invertebrate community related to environmental gradients, and possibly population connectivity constraint as suggested by Josefson and Hansen (2004). Special emphasis is on the existence of meta-population within coastal areas and fjords that is sustained by recruitment from planktonic larvae originating from donor population in the more open part of Kattegat. To quantify the connectivity, we use a 3D hydrodynamic ocean model coupled with an ABM model. The model describes the macro-invertebrate community using relevant dispersal traits: pelagic larval duration, spawning season, and substrate preference. We believe this trait-based approach which has been used in other ecological studies (Petchey and Gaston, 2002; Litchman et al., 2010; Moksnes et al., 2014) can be useful to identify whether the Kattegat is the main provider for larval recruitment in three selected sites. Therefore, we identify 7 major water bodies and bays within the study area and determine the potential donor population of benthic macro-invertebrate populations in Aarhus Bay, Vejle Fiord and Flensborg Fiord (referred to as ‘focus sites’) together with the connectivity between these 7 areas. Finally, we compare some of the results with data on macro-invertebrate species diversity collected in one of the sites.

2. Methods

2.1. Study area

The area of study is located in the transition area between the North Sea and the Eastern Baltic Sea, covering the Kattegat, the Danish Straits (Great belt and little belt) and some parts of Western Baltic Sea (Kiel and Mecklenburg Bay) (Fig. 1). The hydrography can be characterized by a large scale estuarine circulation pattern maintained by freshwater outflow from the Baltic Sea (Leppäranta and Myrberg, 2009). Throughout the area there is a persistent halocline at about 14–17 m separating a surface layer of outflowing brackish Baltic Sea water from a layer of euhaline bottom water flowing towards the Baltic Sea (EEA, 2002). Surface salinity ranges from >30 in the northernmost part of Kattegat to about 10 in the western Baltic Sea. The surface velocity is dominated by currents generated by local winds which are frequently eastward and influenced by the North Atlantic Oscillation (Møller and Hansen, 1994; Lehmann and Post, 2015). We assess the macro-invertebrate larvae dispersal and connectivity within the 7 water bodies defined in this transition region (Fig. 1) with a focus on settlement in Aarhus Bay Vejle Fiord and Flensborg Fiord.

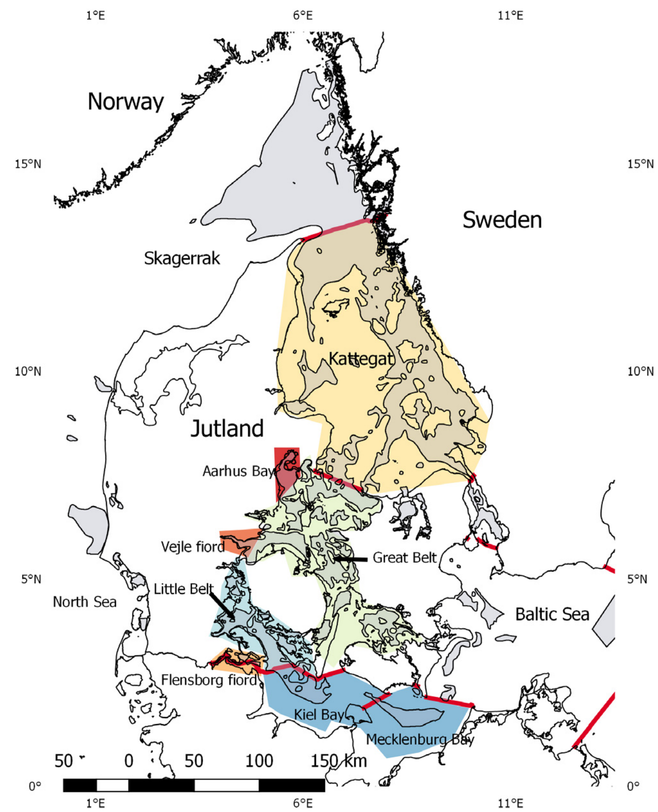

Fig. 1. Map of the study area covering the inner Danish waters. Muddy substrate is represented in gray patches in the area. Red lines indicate HELCOM subbasin divisions. The water bodies considered are: Aarhus Bay, Vejle Fiord, Flensborg Fiord, Kattegat, Great Belt, Little Belt and Kiel & Mecklenburg Bay. For a color representation of the water bodies in the figure, please refer to the online version. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Dispersal traits and choice of parameters

Data on pelagic larval duration, spawning season, substrate preference and depth distribution of the macro-invertebrate community in the Kattegat–Skagerrak area, were extracted from literature for 80 different larval taxa and stages of invertebrate larvae (Table B.1) (data from the Swedish Institute for the Marine Environment Report No 2014:2 by Moksnes et al., in 2014). Due to the extreme variability of the data among taxonomic groups and geographical areas, we summarize the characteristic dispersal traits spanning across species that might account for the specific regional factors and allow us to predict community composition and diversity. Our review suggests that the PLD is typically a period ranging from 11 to 60 days and, in the model, we use eight values within this range introducing week intervals between releases. The spawning season is simulated every month, from April until September, with four releases, one per week. For the