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Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: Role of hydroclimatic processes on the sustainability of biogenic reefs

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ABSTRACT

The honeycomb worm *Sabellaria alveolata* forms biogenic reefs which constitute diversity hotspots on tidal flats. The largest known reefs in Europe, located in the Bay of Mont-Saint-Michel (English Channel), are suffering increasing anthropogenic disturbances which raise the question of their sustainability. As the ability to recover depends partly on the recolonization of damaged reefs by larval supply, evaluating larval dispersal and the connectivity between distant reefs is a major challenge for their conservation. In the present study, we used a 3D biophysical model to simulate larval dispersal under realistic hydroclimatic conditions and estimate larval retention and exchanges among the two reefs of different sizes within the bay. The model takes into account fine-scale hydrodynamic circulation ($800 \times 800\,m^2$), advection–diffusion larval transport, and gregarious settlement behaviour. According to the field data, larval dispersal was simulated for a minimal planktonic larval duration ranging from 4 to 8 weeks and the larval mortality was set to $0.09\,d^{-1}$. The results highlighted the role played by a coastal eddy on larval retention within the bay, as suggested by previous *in situ* observations. Very different dispersal patterns were revealed depending on the spawning reef location, although the two reefs were located only 15 km apart. The settlement success of the larvae released from the smallest reef was mainly related to tidal conditions at spawning, with the highest settlement success for releases at neap tide. The settlement success of the larvae from the biggest reef was more dependent on meteorological conditions: favourable W and SW winds may promote a ten-fold increase in settlement success. Strong year-to-year variability was observed in settlers' numbers, with favourable environmental windows not always coinciding with the main reproductive periods of *Sabellaria*. Settlement kinetics indicated that the ability to delay metamorphosis could significantly improve the settlement success. Although bidirectional exchanges occurred between the two reefs, the highest settlers' numbers originated from the biggest reef because of its stronger reproductive output. Because of the recent decline of this reef due to increasing anthropogenic disturbances larval supply in the bay may not be sufficient enough to ensure the sustainability of the remarkable habitat formed by *Sabellaria alveolata* reefs.

1. Introduction

In coastal temperate regions, reef-building organisms including polychaetes (e.g., sabellariids, serpulids) and bivalves (e.g., mytilids, ostreids) act as ecosystem engineers by physically creating, modifying and maintaining habitats (Jones et al., 1997). By adding micro-scale topographic complexity to the environment, biogenic reefs offer shelters for a large number of marine species and form local hotspots of biodiversity. Although the direct positive effects of the structures built by ecosystem engineers can last longer than the lifetime of the engineer itself, sheltered species diversity tends to decline with the degradation of the reef (Hastings et al., 2007). Thus, the protection of such habitats constitute a major challenge for the biodiversity conservation as they are increasingly threatened by both climate changes and anthropogenic disturbances, such as pollution, overfishing of reef-associated species, or physical degradation of the reefs (Vorberg, 1995; Dubois et al., 2002, 2006). To inventory, preserve and restore the biogenic reefs, action plans have been recently proposed like the European Habitats Directive ("Council

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Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora") whose Annexure I lists the biogenic reefs of open seas and tidal areas among the "natural habitat types of community interest whose conservation requires the designation of special areas of conservation" (Holt et al., 1998). Nevertheless, more research is generally needed to evaluate the extinction risk of those reefs and to propose specific protection management.

Like most marine benthic invertebrates, reef-building organisms exhibit a bentho-pelagic life cycle including a planktonic larval stage of development and two sedentary benthic juvenile and adult stages. For those organisms, successful settlement requires that larvae reach a suitable habitat within a competence period at the end of larval development. It depends on numerous factors involved in larval dispersal and results either from the local retention of larvae or from the connectivity among spatially isolated populations (Caley et al., 1996). Since they drive planktonic larvae, oceanographic processes (e.g., tidal residual currents, wind-induced currents, upwellings, river plumes or gyres) and their variability on time and space scales relevant to the life history of the organism greatly control larval dispersal. On the other hand, dispersal abilities also depend on the interactions between hydrodynamics and biological properties, like spawning period, larval stage duration or larval behaviour. Larval dispersal and connectivity (i.e., the exchange of individuals among geographically isolated marine populations) play then a major role in marine population and metapopulation dynamics in the face of habitat fragmentation (Kinlan et al., 2005; Hastings and Botsford, 2006). A marine metapopulation is defined as a system of discrete local populations which are strongly dependent upon local demographic processes but are also influenced by external supply for population replenishment (Kritzer and Sale, 2003). The metapopulation concept, which has been dramatically developed in marine ecology during the last decade, has become crucial for the maintenance of local adult populations, their ability to recover from natural and anthropogenic disturbances or the implementation of marine conservation and management strategies (Botsford et al., 2001; Hastings and Botsford, 2006). Spatially explicit models highlight the importance of the size and location of discrete local populations and of the spatial scales of dispersal and connectivity in the metapopulation dynamics (Botsford et al., 1994; Gaines et al., 2003; Gerber et al., 2003).

The honeycomb worm *Sabellaria alveolata* is the most common reef-building polychaete along the NE Atlantic coasts, living in the intertidal fringe from the Solway Firth (west Scotland) to the south of the Moroccan coasts (Cunningham et al., 1984). Along the European coasts, the largest reef structures are located in the Bay of Mont-Saint-Michel (English Channel) where they form irregularly shaped, patchy banks that may exceed 1 m high and cover a surface of several hundreds of hectares. The two main formations reported within the bay (i.e., Sainte-Anne reef and Champeaux reef) provide a complex habitat for macrofauna and exhibit high levels of biodiversity that contrast with the surrounding soft-bottom environments (Dubois et al., 2002). If these biodiversity hotspots are a highly dynamic habitat subject to numerous natural perturbations (e.g., storms), they are also increasingly threatened by direct and indirect anthropogenic disturbances including the colonization by mussels and oysters from local aquaculture, the development of ephemeral green algae in response to eutrophication or the physical degradation of the reef through trampling and shellfish farming (Dubois et al., 2002, 2006). These disturbances may cause significant damages to the reef structure and a reduction in density of new recruits has already been reported (Dubois et al., 2006).

According to these damages, the long-term persistence of *Sabellaria alveolata* reefs in the Bay of Mont-Saint-Michel is questionable and would partly depend on sufficient larval supply during the worm life span, which varies between 4 and 5 years and can rarely reach 8–10 years (Wilson, 1971). Larval supply may be all the more important since large year-to-year variations in the recruitment of *Sabellaria alveolata* were commonly reported (Wilson, 1971; Gruet, 1986). Indeed, as a species with a long larval life span (Wilson, 1968b; Cazaux, 1970; Dubois et al., 2007), one speculative possibility to explain recruitment failure would be the lack of larval supply due to circulation conditions flushing larvae away from the reefs (Holt et al., 1998). Conversely, several processes have been proposed to explain local successful settlement and reduced larval losses in this species. First, competent *Sabellaria alveolata* larvae, i.e., larvae that have acquired the ability to settle, exhibit an active habitat selection and are able to delay metamorphosis (Wilson, 1968a; Pawlick, 1988). Second, in the Bay of Mont-Saint-Michel, *Sabellaria alveolata* presents an extended reproductive period with a semi-continuous spawning from April to October (Dubois, 2003; Dubois et al., 2007). This long period of larval occurrence in the water column increases the probability that some larvae match favourable environmental conditions and successfully settle. Third, preliminary field observations on larval distribution carried out within the bay in July 2002 suggested that the tidal residual circulation, especially the occurrence of eddy structures could limit larval horizontal transport and contribute to larval retention for few weeks (Dubois et al., 2007).

While understanding factors that control larval dispersal and larval supply to benthic populations is a fundamental issue in conservation biology, quantifying empirically these parameters and their spatio-temporal variations remains extremely difficult. Nevertheless, recent methodological developments including molecular ecology, geochemical fingerprinting and hydrodynamic modelling provide new powerful tools to study larval dispersal (see the review by Levin, 2006). Numerical simulations constitute a quantitative approach to better understand the role of highly changeable hydrodynamics and biological factors on larval dispersal, and estimate dispersal distance and potential origin of larval supply. Although biophysical models vary a lot in terms of spatial scales and complexity, two main types of model are commonly used to simulate larval dispersal in marine organisms: (1) Eulerian models that solve an advection–diffusion equation and provide the spatial and temporal evolution of larval concentrations at each mesh point and (2) Lagrangian models (also called individual-based models or IBM) that compute individual particle pathways. The latter have been widely used during the last years to follow the trajectories of a large number of larval particles with specific parameters (e.g., larval growth, larval behaviour) in order to simulate the dispersal of different marine invertebrates and fishes (see review by Miller, 2007, and references therein). Conversely, advection–diffusion models allow to save computing time when larval transport is simulated for a long period of time and when no individual specificities are considered, usually because of limited knowledge of biological parameters such as growth conditions or behaviour response to the environment. Although a comprehensive larval dispersal model should account for 3-dimensional (3D) flow regimes, individual larval locomotion and some demographic parameters, dispersal has been successfully modelled as an advection–diffusion process for several invertebrates like polychaetes (Jolly et al., in press), bivalves (Gilg and Hilbish, 2003), echinoderms (Dunstan and Bax, 2007), and corals (Treml et al., 2008). Here, we propose to explore realistic potential dispersal of *Sabellaria alveolata* larvae in an Eulerian framework using a 3D hydrodynamic model of the Bay of Mont-Saint-Michel which predicts tidally and wind-induced currents, and drives an advection–diffusion larval transport model accounting also for larval mortality and settlement. In this context, the aims of our study are (1) to assess the role of