

Modelling benthic invasion by the colonial gastropod *Crepidula fornicata* and its competition with the bivalve *Pecten maximus*. 2. Coupling the 0D model of colony-forming species to a connectivity matrix for a realistic distributed simulation of benthic invasion

Alain Ménesguen*, Aloïs Hachet, Thomas Grégoris

Ifremer, Centre de Bretagne, Unité DYNECO/Laboratoire LEBCO, 29280 Plouzané, France

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ABSTRACT

The anthropogenic introduction in U.K. waters of the north-American marine gastropod *Crepidula fornicata* (Linné, 1758), commonly called slipper limpet, and its consecutive spreading has led in less than a century to the invasion of a part of benthic grounds along the North-European coasts. Competition for space has hampered the maintenance of the native scallop *Pecten maximus*, whereas dredge clogging has drastically limited scallop fishing, especially in the Western English Channel. In order to assess the possible future distribution and abundance of both species (*Crepidula* and *Pecten*), an original model of slipper limpet chains joined to a simple year-class model of the scallop (Ménésguen and Grégoris, 2017) has been coupled to a connectivity matrix summarizing the annual dispersion of emitted larvae in a realistic marine domain. This distributed model can explore the dynamics of both populations at the century scale and has been applied at two different geographical scales: a local one (the bays of Brest and Douarnenez, Western Brittany, France) and a regional one (Bay of Biscay and English Channel). First eigenvectors of the connectivity matrix are used to delineate the main retention areas. For each species taken alone, simulations starting with a few animals in different spots do converge in less than a century towards the same geographic distribution, compatible with the actual field distribution. This suggests that hydrodynamic patterns of larval drift create a strong attractor for these populations; it is reached by different routes of colonization, depending on the initial inoculation. The non-linear interaction created by the lack of space when the populations have filled the benthic area seems to be stronger for scallop populations than for slipper limpets, because of the permanent capacity of *Crepidula* beds to fix some larvae on the top of existing colonies. Whereas the scallop abundance experiences a rather large limit-cycle, with a dominant 11 years period and a lot of harmonics, the slipper limpet has commonly a stable steady state abundance. Competition between both populations tends to lower the mean scallop abundance and to lengthen and damp its fundamental period of oscillations. Simulated distributions can be locally improved by linking the larval survival to a distributed environmental stressor, as the salinity for scallop or a metallic contamination for the slipper limpet in the case of the bay of Brest.

1. Introduction

Since its first observation on oyster beds in Liverpool Bay in 1872, the marine gastropod *Crepidula fornicata* has invaded a lot of coastal benthic ecosystems along the coasts of the southern half of the UK, on the French side of the English Channel, along Belgium and the Netherlands. Its northward progression seems to be stopped by the too cold temperatures (Thieltges et al., 2004). Several papers have reported new sites of colonization, and some have attempted a global compilation of the sites where the species has been observed in the North-East

Atlantic (Blanchard, 1997, Fig. 1). The most extended populations present along the French coasts have been observed first in the Golfe Normand-Breton (Quiniou and Blanchard, 1987), especially the bay of Saint-Brieuc (Hamon and Blanchard, 1994), and secondly, in the bay of Seine (Leblanc et al., 2011). The abundances observed in the bay of Saint-Brieuc (Blanchard et al., 2001) are around 3000 ind. m⁻² in dense beds (coverage > 70%), and around 1000 ind. m⁻² in more sparse populations (40% < coverage < 70%); but Blanchard (2005) found up to 4000 ind. m⁻² in the bay of Mont Saint-Michel and Quiniou and Blanchard (1987) 9000 ind. m⁻² around the Chaussey Islands, in the

* Corresponding author at: Ifremer, Centre de Bretagne, Unité DYNECO/Laboratoire LEBCO, Z.I. de la Pointe du Diable, CS 10070, 29280 Plouzané, France.
E-mail address: amenesg@ifremer.fr (A. Ménesguen).

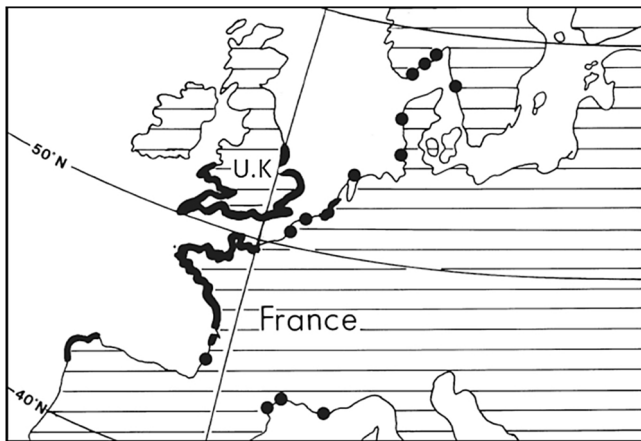


Fig. 1. Observed general distribution of the slipper limpet on the NW European coasts (from Blanchard, 1997).

Golfe Normand-Breton. On the Atlantic coast, the main spots are smaller, in the bay of Brest (Guérin, 2004) and the Marennes-Oléron bay (Sauriau et al., 1998). A recent compilation of recorded presences of slipper limpets in historical samples taken in the southern part of the English Channel (Blanchard, 2012) (Fig. 2 upper panel) and the corresponding compilation for the northern part of the English Channel by the National Biodiversity Network's Gateway (Fig. 2, lower panel) ascertain qualitatively the presence of the slipper limpet on the French side of the English Channel, from the bay of Saint-Brieuc up to the Belgian frontier (and its absence in the north-western part of Brittany), as well as its presence in the shallow strip around UK. The apparent lack along the Picardy coast (French side of the Eastern English Channel) mentioned in 1997 has been filled in the 2011 map and confirmed in 2013 by Augris and Clabaux (2013), who recorded dense *Crepidula* beds near the coast of Fécamp and Saint-Valéry en Caux. In the bay of Brest, the distribution observed in the field till the end of the 20th century (Fig. 3, top panel, from Coum, 1979) has regressed during the last decade (Fig. 3, bottom panel, from Carlier, pers. comm.). Assessing from field data the effect of the slipper limpet invasion on the scallop distribution is not easy, because distribution maps of the scallop populations are recent and show more the modified distribution than the pristine one, as well for our local site where scallops are confined in the middle of the bay of Brest (Fig. 4, top panel from Thouzeau et al., 2000) as for our regional site, where distribution of active fishing areas appears to be peripheral (Fig. 4, bottom map, from Le Goff et al., 2017).

Two questions then arise: 1/ has the species reached nowadays its maximum extent (if not, which areas will it invade furthermore?), 2/ can we expect a future regression of the colonized area?

Even if anthropogenic actions (maritime transport, discharge to the sea of dredging wastes...) have had a decisive seminal role, the answer to the first question is now strongly linked to the natural dissemination potential of the larval stage of this species. The hydrodynamical modelling of the coastal seas under concern can then bring a reliable support to this question, by giving the geographic distribution of tracers released from any marine position and transported during the larval phase duration.

The second question depends on many poorly known processes (interspecific competition, infections by viruses and bacteria, toxic effects of chemical pollutants or phytoplanktonic toxins...), so the long term observation is necessary to get plausible answers.

Models which have explored the dissemination/settlement of benthic populations are mainly based on lagrangian simulation of larvae, i.e. they simulate the trajectories of numerous larvae (or batches of larvae) released from single or multiple locations at different dates (Cowen et al., 2000; Ayata et al., 2010; Andutta et al., 2012). A statistical analysis of the trajectories can show the trapping areas, created

by local, bathymetry-driven modifications of the flow field, the so-called “sticky water effect” (Wolanski, 1994). Some models however deal with larvae as eulerian variables (Alexander and Roughgarden, 1996; Bendtsen and Hansen, 2013). Whatever the type of model used (eulerian or lagrangian), the exchanges of larvae between different places in the domain can be computed and gathered in a connectivity matrix. In the growing literature on connectivity, several approaches can be found to analyse the topology of the dispersal network. Whereas Trembl et al. (2008) relied on graph theory, Nilsson Jacobi and Jonsson et al., 2011 used the eigenvalues of the connectivity matrix (and especially the value of the leading one) to assess the persistence of subpopulations thanks to the perturbation method. As the eigenvectors themselves don't seem to have been used until now, we propose in this study their use to map the main retention regions, if the connectivity matrix ensures a complete cover of the discretized area under study. The synthetic 2D model of larval dispersion brought by the connectivity matrix is easily coupled to a previously described 0D model of the chain-forming slipper limpet (Ménesguen and Grégoris, 2017) to simulate the many decades long invasion phase, and to map the climax steady state distribution of this gastropod species. A similar model of the scallop, a non-colonial bivalve, is then run in competition with the slipper limpet one. The unique case of observed strong regression of a dense slipper limpet population (in the southern part of the bay of Brest) is used to test a putative harmful effect of heavy metal pollution on the *Crepidula* larvae.

2. Material and methods

2.1. The connectivity matrix

In order to simulate the larval drift occurring during the pelagic larval phase (i.e. a maximal 40 days duration), as well for the gastropod *Crepidula fornicata* as for the bivalve *Pecten maximus*, a 3D hydrodynamical model of the region of interest has been run from May, 20 to June, 30 of the year 2000. The MARS3D hydrodynamical code (Lazure and Dumas, 2008) has been applied first to the French Atlantic shelf, using a regular grid with 4×4 km meshes and 30 sigma levels and covering the Bay of Biscay, the English Channel and the southern part of the North Sea, up to the Rhine estuary (Fig. 5, left panel). For a more local extent, the same code has been applied to the two bays of Brest and Douarnenez, at the western end of France, using a regular grid with 0.75×0.75 km meshes and 10 sigma levels (Fig. 5, right panel). The connectivity between an emitting mesh and a receiving one of the model grid is defined here as the fraction of a conservative tracer initially placed only in the bottom layer of the emitting mesh which is retrieved 40 days after in the receiving one. The tracer may be a dissolved one, or a particulate one having a settling velocity. The tracer fraction in the receiving meshes may be computed diversely: we can sum up the total tracer present in the receiving water column, or keep only the fraction present in a specific layer, for instance the bottom one. If the model grid contains m water meshes, a $(m + 1) \times (m + 1)$ matrix of connectivity \mathbf{M} will be constructed and then used every year to compute the annual transport of larvae over the domain. For our regional case, $m = 3513$, whereas $m = 814$ in our local case. The first row gives the tracer quantity entering the domain during the simulation duration (i.e. zero in the general case), and the first column gives the tracer quantity which has left the domain at the end of the simulation. Owing to the rapid increase of memory necessary to store during a century the age-class structures of the distributed population model, meshes of the hydrodynamical basic grid have been pooled into square “super-meshes” of 3×3 meshes for the regional model, and 2×2 meshes for the local model. If the “super-mesh” contains only water basic meshes, its initial tracer concentration will be set to 1.0, whereas if it contains w water meshes and t terrestrial meshes, the initial tracer concentration will be set to $w/(w + t)$ only. The coarse grid on which the connectivity matrix has been computed will be referenced as the

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