



Modelling benthic invasion by the colonial gastropod *Crepidula fornicata* and its competition with the bivalve *Pecten maximus*. 1. A new 0D model for population dynamics of colony-forming species

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ABSTRACT

The north-American marine gastropod *Crepidula fornicata* (Linné 1758), commonly called slipper limpet, has been introduced accidentally in Great Britain, along with American oysters (*Crassostrea virginica*) at the end of the 19th century. Its spreading, enhanced by oyster transport and international shipping, turned into invasion of a lot of benthic grounds along the North-European coasts. When local conditions are favorable to larval confinement and adult growth, the invasion by very dense populations may deeply change initially sandy or muddy benthic communities into similar “slipper limpet communities”. Competition for space eliminates several species of native infauna, and hampers the survival of some epibenthic bivalves such as the scallop *Pecten maximus*. As the clogging of dredges by superabundant slipper limpets drastically limits scallop fishing, some insight in the future distribution and abundance of both species (*Crepidula* and *Pecten*) seems necessary, especially in the English Channel where the scallop is intensively harvested. An original model, storing in a “intraspecific matching matrix” the numbers of pairs of aged animals present in the slipper limpet chains, has been developed to take into account the year-class association and stack formation specific to *Crepidula fornicata*. Then, an “interspecific matching matrix” component has been added to that “intraspecific matching matrix” in order to describe the simple year-class structure of the scallop along with the age distribution of slipper limpets stuck on scallop shells and forming the base of chains. Such a model can explore the dynamics of both populations at a secular time scale. This first part of work details the 0D-behavior of the populations, alone or together, on 1 m² benthic area. As far as the scallop is concerned, the fact that class 1 cannot recruit in dense populations until the death of old animals has freed some place induces a limit-cycle, with a 11 years period, and a large amplitude. On the contrary, in the case of the slipper limpet, because of the constant possibility for class 1 to recruit on the top of existing colonies, even if the bottom coverage is total, the population reaches a stable steady state abundance, without significant oscillations. Competition for space between the two species does not alter significantly the slipper limpet, whereas it lowers the mean abundance and alters (by damping and slowing down) the limit cycle of the scallop.

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1. Introduction

The benthic, marine gastropod *Crepidula fornicata* (Linné 1758), belonging to the family Calyptraeidae and commonly called slipper limpet, is native of the North-American Atlantic coast, but has been introduced accidentally in Great Britain, along with American oysters (*Crassostrea virginica*) at the end of the 19th century. Oyster

transport between different farms and the increase of international shipping over recent decades have spread this initial inoculate throughout the northern hemisphere. Blanchard (1996) shows in his historic compilation that, since the first observation on oyster beds in Liverpool Bay in 1872, the species has become an “oyster pest” along the coasts of the southern half of the UK, western France, Belgium and the Netherlands. In the English Channel, colonization moved westward, from Portsmouth in 1913 to Start Point (Devon) in 1960. But the Thames estuary also has been heavily infested since the 70's. On the Belgian and Dutch coasts, the slipper limpet was observed since the 20's, but remained confined in sheltered harbours, as Ostende or in estuaries as the Scheldt one. The closure of Lake Grevelingen in 1971 gave a formidable opportunity to

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the gastropod colonies to invade the benthos of this confined area. In France, whereas only rare specimens were observed before the World War II in the oyster beds of the northern half of the bay of Biscay, more and more specimens were collected at the end of the 40's, on mussel beds in Normandy, on scallops in the bay of Brest. This sudden introduction in several places was caused by animals fouling the hulls during Allied shipping operations, coming either from Great-Britain or directly from the USA (Blanchard, 1995). The subsequent spread along the Atlantic coast was facilitated by oyster transfers (Marteil, 1963, 1965), but these Atlantic populations seem to have rapidly reached an equilibrium, e.g. around 5000 tons in Marennes-Oléron bay (Sauriau et al., 1998). On the contrary, the populations occupying the western French side of the English Channel may continue their spreading since the 250,000 tons assessed in the bay of Saint-Brieuc by Hamon and Blanchard (1994) and the 214,000 tons recorded in the bay of Mont-Saint Michel by Ehrhold et al. (1998).

The invasive character of this species is commonly linked to some of its biological characteristics. Individuals are protandric hermaphrodites, and build stable colonies by stacking successive age-classes, with the youngest male on top and the oldest female at the base of the colony. These quasi-motionless piles can totally cover the bottom, and ensure their growth by filtering plankton in the water bottom layer. Even if such assemblages can provide refuge to a well diversified benthic community, they cause a progressive standardization of the benthic communities (Hamon et al., 2002). Potential predators sampled within limpet beds (crabs, flatfishes, asterids, drilling gastropods) do not seem to feed intensively on the colonies. The question then arises about the ultimate capacity of this gastropod to invade a large part of the European coastal zone and deeply modify its various benthic assemblages.

This article proposes an original approach to colony modelling, and applies it to a 0D problem (i.e. building an assemblage of colonies over a small ground surface). A sensitivity test to the larval input shows the crucial role of this biological parameter in the settlement success. Then, the model is used in its “no colonial” mode and applied to an exploited bivalve, the scallop *Pecten maximus*, which has suffered from the invasion by the slipper limpet. Competition and phoretic cooperation between slipper limpet and scallop is finally tested in a unique, merged model of both species. A second article will distribute this 0D model over the Bay of Biscay-English Channel continental shelf in order to simulate the invasion by slipper limpet and the competition between the two species.

2. Material and methods

2.1. The colony model

2.1.1. The “matching matrix”

Classical population dynamics assumes that individuals belonging to various age-classes are independent from each other, so that they occupy randomly the physical space left available. Topological information in population models appears in two research fields: the simulation of the dynamics of animal swarms (Parrish and Edelstein-Keshet, 1999), and the simulation of the topology of growing plants (Lindenmayer, 1968). Whereas the first domain focuses on emergent properties of a cloud of similar individuals, the L-system approach used by the second domain is fundamentally based on local properties of cell division, not on the age of individual cells. As no model seems to have been built to simulate a non-random static topology of species age-classes, we propose here to tackle with colonies as ordered chains of characters taken among an alphabet of p letters (i.e. the p age classes). As the full determination of all the colony assemblages that can be made by re-assorting N individuals belonging to p age-classes is a very com-

plex combinatorial task, we will limit our description of the colony topology to the only census of all the present pairs of contiguous animals. We then define the “matching matrix” of the population as the $(p + 1) \times (p + 1)$ table (with the rows and the columns numbered from 0 to p) containing in cell (i, j) the number of individuals of age i surmounted by an individual of age j which are to be found in colonies occupying a unit surface of sea bottom. In the case of the slipper limpet, the upper right triangle of the matrix will be empty, because animals cannot surmount individuals younger than themselves. In spite of some observed cases of late individuals of a year class surmounting an early individual of the same year class, we will also admit that animals can only be surmounted by individuals strictly younger than themselves, i.e. that the diagonal terms of the matching matrix remain null. The first row (numbered 0) of the matrix is devoted to animals which rest on the sea bottom, whereas the first column (numbered 0) inventories the animals that are not surmounted by any other individual, i.e. animals located at the top of the colonies; the cell $(1, 0)$ gives the total number of individuals of age 1. An interesting property of such a matching matrix is that the vector containing the sums of the $(p + 1)$ rows is identical to the one containing the sums of the $(p + 1)$ columns. As an example, the “matching matrix” of a population corresponding to a single colony is given in Fig. 1 (left panel). The number of couples appearing in the “matching matrix” depends on the elemental benthic area chosen for this 0D model; here we have chosen 1 m^2 . But as this elemental area stands for a wide region in the field, we allow counts in the “matching matrix” to be real numbers, not exclusively integers; this prevents from a too quick elimination of rare age-classes.

2.1.2. The annual modification of the “matching matrix”

We consider that the colonization of the bottom by the slipper limpet is a first order Markovian process having a time step of one year. Annual changes in the abundance of the p age classes are the result of entrance of pelagic larvae, which transform into benthic first age class animals during the recruitment process, and losses of benthic animals. Because only juvenile males can crawl to a suitable site for attachment, whereas animals of 2 years and more are incapable of further movement (Fretter and Graham, 1981), we have considered adults as quasi-immobile, so that no immigration or emigration of benthic animals is taken into account.

The entrance of young animals by settling of pelagic larvae can be either internal to the system (i.e. larvae come from eggs laid by the animals present in the domain) or external (i.e. larvae come from eggs laid by animals outside of the domain) or both. Despite a large period of spawning spreading from March to September in Brittany (Marteil, 1963), the populations of *Crepidula fornicata* in the bay of Brest have shown during four consecutive years 3–4 peaks of hatching per year, the main one occurring in May or June (Richard et al., 2006). In Wales, Bohn et al. (2012) have also observed the main peak of larvae in water in June. Because of the annual time step of our model, we have gathered the possible successive hatching periods in a single one per year and we have used an allometric power law for fecundity dependence on size (Richard et al., 2006). Class 1 individuals ordinarily recruit on existing colonies (Cahill, 2015). In the simplest version of our model, we allow only one recruit per top animal of an existing colony, whereas in an improved version we allow larvae to fix on existing animals, whatever their position in the colony. But larvae can also fix on another benthic substrates (rocks, shells of dead molluscs. . .). As they prefer settling on living benthic slipper limpets (Bohn et al., 2013), we assign a fitness coefficient $\alpha < 1.0$ to bare grounds for slipper limpets colonization. Whatever its final target, this recruitment process is supposed to have a probability proportional to the fraction of ground area covered by the target area. The recruitment probability on individuals occupying the top position of existing colonies has been set as the ratio (bottom area covered by colonies: total bottom

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