



# Qualitative modelling of functional relationships in marine benthic communities



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## ABSTRACT

In order to better understand and predict the dynamics of benthic macroinvertebrate communities, we need to first define the functional components of benthic biodiversity and then provide a mechanistic description of how they interact with their abiotic environment, their basic resources and each other. These interactions should be largely controlled by readily available biological traits, making trait-based modelling an ideal framework for the synthesis of relevant hypotheses from ecological theory and expert knowledge. With the help of benthic species traits, we derived a set of first principles regarding the role of organisms in processes of environmental filtering, consumption of algae/detritus, predation, use of space, biogenic habitat modification and trade-offs in the utilization and allocation of resources. These principles were incorporated into qualitative models in the form of functional relationships linking groups of benthic organisms in the Rance estuary (Brittany, France). The general stability of these models illustrates their potential to persist in time and to constitute a plausible representation of the natural world. Their structure provides insight into the role of various community assembly mechanisms and the direction that the system might take in response to perturbations. The results are expected to inform the development of quantitative models reproducing the spatial and temporal dynamics of marine benthic biodiversity in the Rance estuary.

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## 1. Introduction

Reliable prediction of biodiversity responses to environmental change remains a key challenge of ecological research (Sutherland et al., 2013). Because it involves combinations of species and environmental gradients that have not been observed yet, it requires a mechanistic understanding of the processes that shape biological communities (Kearney and Porter, 2009). Ecological theory has generated many hypotheses about the maintenance of species diversity (Chesson, 2000). However, empirical investigation of these hypotheses has been mostly performed by studies of relatively small spatial and temporal scales (Cardinale et al., 2012). This has limited the potential of their findings to be extrapolated to larger scales and has added uncertainty to projected trends of biodiversity (Pereira et al., 2010).

In ecological systems where observation and experimentation fall short of fully revealing the drivers of biodiversity, the analysis of mechanistic models has been suggested as an alternative way of identifying the most likely community assembly mechanisms (Amarasekare, 2003). Since the role of organisms in the functioning of ecosystems is defined by their traits, the development of trait-based modelling approaches has been suggested as a fruitful avenue for models of ecological systems (Ings et al., 2009). Limited understanding of specific mechanisms should not exclude them from the modelling procedure (Queirós et al., 2015). Instead, awareness about the assumptions that are made at each step should allow models to test alternative hypotheses, elucidate domains of uncertainty and identify critical areas for research.

The development of mechanistic models of biodiversity can be considered to be subject to two main conditions. First, the functional components of biodiversity need to be defined through rigorous and testable procedures (Petchev and Gaston, 2006). Next, a mechanistic description of the way these components interact with their environment and among themselves is necessary. These

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issues have traditionally been addressed in the context of food web modelling. Organisms are typically separated into groups according to their food sources, and interactions among them are assumed to represent their trophic behaviour (Yodzis and Innes, 1992). In lack of empirical information to help formulate these models, various methods have been developed for the construction of food webs, based on principles of community (e.g., Cohen and Newman, 1985; Williams and Martinez, 2000; Cattin et al., 2004) or ecosystem ecology (e.g., Fath, 2004; Morris et al., 2005; Halmes et al., 2007). Still, a disproportionate focus on trophic interactions has restricted the scope of most modelling efforts (but see Kéfi et al. (2012)).

Predicting biodiversity patterns is particularly challenging for communities of marine benthic macroinvertebrates (Constable, 1999). The study of these systems has long suffered from a lack of empirical information (Solan et al., 2003), while non-trophic interactions often play a central role. Many of these organisms can alter the physical or chemical properties of their environment in ways that significantly impact other members of their communities (Meadows et al., 2012). These effects appear to be non-linear and form intricate feedback cycles (Herman et al., 1999), while they can greatly vary among different life stages (Pineda et al., 2009). Along with the prevalence of omnivory and facultative feeding modes, this has reduced the pertinence of classic trophic groupings of benthic macrofauna (Snelgrove and Butman, 1994). Moreover, theoretically derived allometries that have facilitated the quantification of trophic interactions appear to be less efficient for their non-trophic counterparts (Berlow et al., 2009; Petchey et al., 2008), in support of a more mechanistic representation of the latter.

Quite independent of mechanistic modelling, an increased interest in the functioning of marine benthic communities has led to the compilation of large data bases of species traits. At the same time, theoretical and expert knowledge about potential trait associations is being continuously generated. Particularly lacking is a systematic procedure for the assignment of functional groupings and inter-group relationships on the basis of such readily available information. Recent work in the terrestrial environment led to the development of a trait-based method for the construction of functional groups for models of plant diversity (Boulangeat et al., 2012). The conceptual and methodological framework was provided by the emergent group hypothesis, which assumes functional equivalence within and functional divergence among emergent groups of species (Héroult, 2007). The adaptation of this framework to the benthic macroinvertebrate communities of the Rance estuary (Brittany, France) can provide the functional components for a mechanistic representation of the system (Alexandridis et al., 2017). Here we implement these components in a demonstration of a systematic procedure for the assignment of functional relationships between them. In a first conception of the system, we are restricted to the qualitative nature of the relationships.

The objective of our study is to use mechanistic models of benthic macrofauna, in order to assess the role of different processes in shaping biodiversity patterns in the Rance estuary. To this end, we represented benthic macroinvertebrate communities through signed-directed graph (or signed digraph) models. The previously defined groups of species comprised the functional components of the system and were assigned to sub-systems based on rules of environmental filtering. In each of these sub-systems, groups were linked by functional relationships that were largely derived from ecological theory and expert knowledge regarding general community assembly mechanisms. This procedure was dictated by each group's assigned trait values and representative species. The stability analysis of the signed digraphs demonstrated the potential of the respective systems to persist in time and, therefore, to constitute a plausible representation of the natural world. The structure of the models gave some insight into the role of different community assembly mechanisms, as well as the direction of the system's

response to potential perturbations. This work serves as a first step toward quantitative mechanistic models that will be able to reproduce the spatial and temporal dynamics of benthic biodiversity in the Rance estuary (Alexandridis, 2017).

## 2. Methods

### 2.1. Study site

The Rance estuary (Brittany, France) is situated in the southern part of the English Channel (Fig. 1). The site is characterized by the presence of a tidal power plant at its mouth. The operating constraints of the installation have reduced the tidal range in the estuary compared to the open sea. The intertidal zone has shifted from 70% of the total surface of the estuary before the construction of the power plant, to 50% after. Maximum water depth is 17 m at low tide, but the main part of the basin is 5–6 m deep. The sluice and turbine currents from the power plant have eroded parts of the riverbed. Sandbanks closest to the dam have shifted and the bed is predominantly covered with gravel or pebbles (Retière, 1994). At the same time, long periods of slack water have promoted the deposition of fine particles in coves and bays (Bonnot-Courtois and Lafond, 1991). From downstream to upstream of the estuary, pebbles and coarse sands are replaced by medium and fine sands, muddy sands and finally muds upstream of Port-St-Hubert. A similar sequence is observable from the central channel of the estuary to its banks.

Sediment samples were collected from 113 stations on the bed of the Rance estuary in April 1995, prior to the spring recruitment (Fig. 1). The sampled stations are expected to represent the variability of benthic communities in the system. A total of 240 macroinvertebrate (i.e., retained by a 1 mm sieve) species or higher taxonomic groups belonging to 9 phyla were identified in the samples and their abundances in each station were measured (Desroy, 1998).

### 2.2. Functional groups

For the representation of the primary functional components of benthic macroinvertebrate communities in the Rance estuary, we employed 20 functional groups, previously built on the basis of biological trait information for the 240 species of the system in 1995 (Alexandridis et al., 2017). The collected abundance data set allowed each of the groups to be assigned with a representative species along with a value for each of the 14 biological traits (Table 1). The traits are expected to describe the role of benthic algae/detritus feeders and predators/scavengers in 7 important community assembly mechanisms (Table 2). The list of mechanisms was mostly adopted from the framework developed by Boulangeat et al. (2012) for dynamic models of terrestrial vegetation. A few adjustments were made to the original framework, in order to adapt it to marine benthic systems (Alexandridis et al., 2017).

### 2.3. Signed digraphs

The structure of the system was represented by signed digraphs (networks of interactions that portray the interactions' direction and sign but not their strength) (Levins, 1998). The functional groups and the basic resources of food (algae/detritus) and space were depicted as nodes and the signs of the direct effects among them were represented by directed links between the nodes. A link ending in an arrow signified a positive direct effect, such as births produced through the consumption of prey, whereas a link ending in a filled circle signified a negative one, such as deaths from pre-

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