Ecological Modelling
September 2017, Volume 360 Pages 300-312
http://dx.doi.org/10.1016/j.ecolmodel.2017.07.021
http://archimer.ifremer.fr/doc/00394/50587/

Qualitative modelling of functional relationships in marine benthic communities

Alexandridis Nikolaos [1, *], Dambacher Jeffrey M. [2], Jean Fred [3], Desroy Nicolas [4], Bacher Cedric [1]

[1] IFREMER, Centre de Bretagne, DYNECO-LEBCO, CS 10070, 29280 Plouzané, France
[2] CSIRO, GPO Box 1538, Hobart, Tasmania 7001, Australia
[3] Université de Brest, UBO, CNRS, IRD, Institut Universitaire Européen de la Mer, LEMAR, 29280 Plouzané, France
[4] IFREMER, Laboratoire Environnement et Ressources de Bretagne Nord, BP 70134, 35801 Dinard, France

* Corresponding author : Nikolaos Alexandridis, email address : nikolaos.alexandridis@ifremer.fr

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.

Highlights

► We derived first principles on the role of benthic organisms in community assembly. ► These principles dictated functional relationships among groups of benthic species. ► Groups and functional relationships comprised qualitative models of benthic systems. ► Stability analysis supported the models' potential to represent benthic communities. ► Model structure offered insight into the role of some community assembly mechanisms.

Keywords : Benthic macroinvertebrates, Biological traits, Biotic interactions, Community assembly, Functional groups, Qualitative modelling

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 (Petchey and Gaston, 2006). Next, a mechanistic description of the way these components interact with their environment and among themselves is necessary. These 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; Halnes 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 (Hérault, 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).

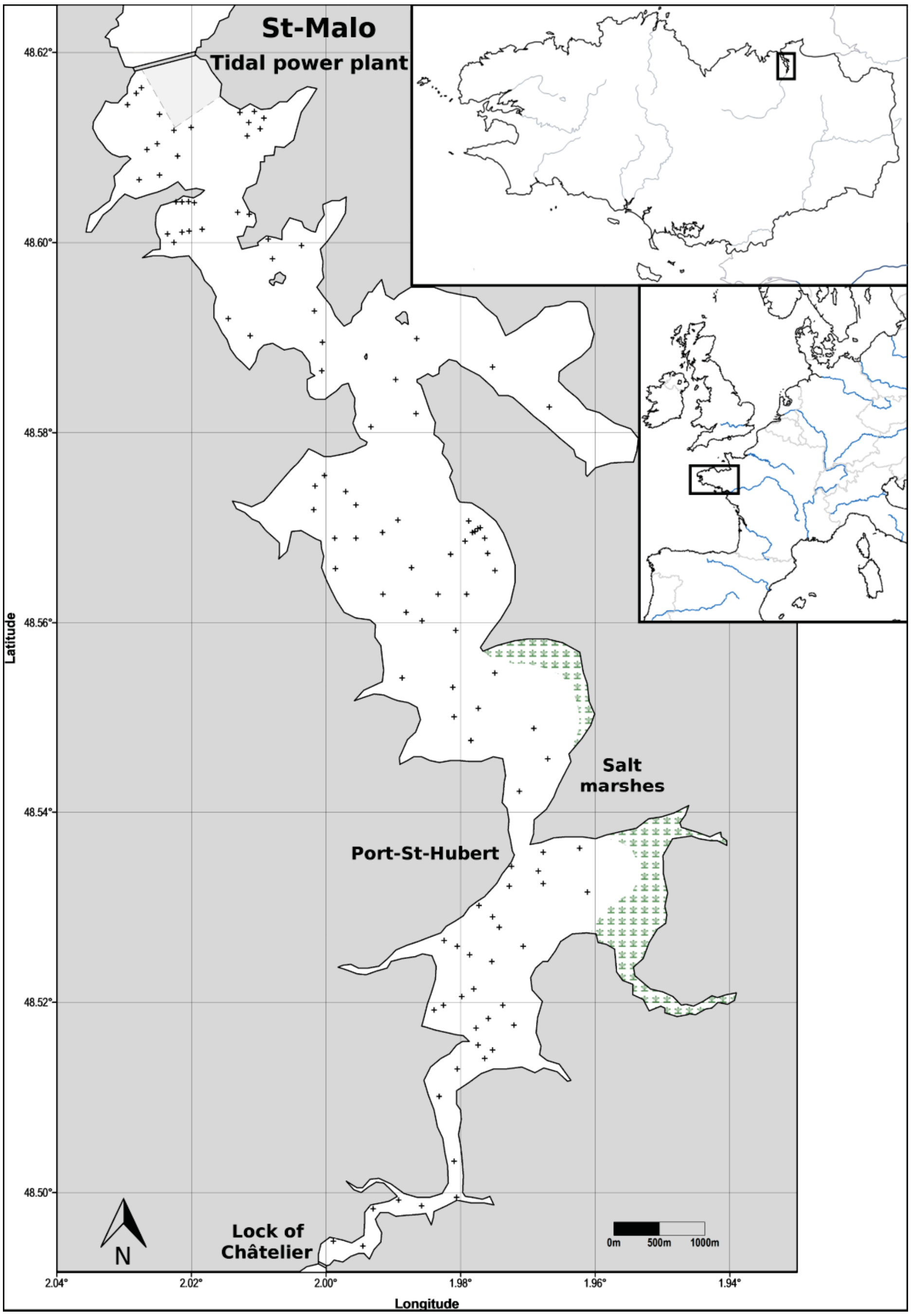

Fig. 1. Map of the study site. The Rance estuary is situated on the northern coast of Brittany, France. Crosses indicate the location of the 113 stations that were sampled in the spring of 1995. The tidal power plant is located at the mouth of the estuary, south of the city of St-Malo

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).

Table 1. Functional groups with their assigned representative species and biological trait values (Alexandridis et al., 2017). For details about the biological traits, see Table 2. Group names starting with ‘H’ correspond to groups of algae/detritus feeders and those starting with ‘C’ correspond to groups of predators/scavengers

Groups	Representative species	T1. temperature	T2. development	T3. dispersal	T4. fecundity	T5. tide/salinity	T6. substrate	T7. size (cm)	T8. area	T9. position	T10. mobility	T11. growth rate	T12. lifespan (yr)	T13. epibiosis	T14. engineering
H1	*Morchellium argus*	eurythermal	brooded	short	low	stenohaline	rock	3.3	0.1	epifauna	sessile	2.6	1.7	epibiont	neutral
H2	*Lepidochitona cinerea*	stenothermal	planktonic	short	high	stenohaline	rock	10.8	4.1	epifauna	mobile	0.9	11.6	epibiont	neutral
H3	*Balanus crenatus*	eurythermal	planktonic	long	high	euryhaline	rock	2.0	0.8	epifauna	sessile	2.5	2.0	epibiont	neutral
H4	*Crepidula fornicata*	stenothermal	planktonic	long	high	stenohaline	rock	7.6	0.0	epifauna	sessile	1.9	11.2	basibiont	neutral
H5	Oligochaeta	stenothermal	laid	short	low	emersed	muddy sand	4.5	5.0	infauna	mobile	3.4	2.0	neutral	destabilizer
H6	*Thyasira flexuosa*	eurythermal	planktonic	short	low	stenohaline	mud	3.6	0.8	infauna	mobile	1.0	10.0	neutral	stabilizer
H7	*Melinna palmata*	stenothermal	brooded	short	low	stenohaline	mud	7.5	0.3	interface	sessile	2.6	3.6	neutral	stabilizer
H8	*Notomastus latericeus*	stenothermal	brooded	short	low	stenohaline	muddy sand	6.0	2.9	interface	mobile	2.6	1.9	neutral	destabilizer
H9	*Hediste diversicolor*	eurythermal	laid	short	high	emersed	muddy sand	12.8	0.2	interface	mobile	2.1	3.4	neutral	destabilizer
H10	*Malacoceros fuliginosus*	eurythermal	planktonic	long	high	euryhaline	mud	8.5	1.9	interface	mobile	2.5	2.7	neutral	destabilizer
H11	*Galathowenia oculata*	eurythermal	planktonic	long	high	euryhaline	mud	11.1	0.0	interface	sessile	2.7	4.4	neutral	stabilizer
H12	*Glycymeris glycymeris*	stenothermal	planktonic	short	high	stenohaline	muddy gravel	8.0	1.4	infauna	mobile	0.8	15.0	neutral	stabilizer
H13	*Anapagurus hyndmanni*	stenothermal	planktonic	long	high	stenohaline	gravel	10.0	0.1	epifauna	mobile	0.6	10.0	neutral	neutral
H14	*Cerastoderma edule*	stenothermal	planktonic	long	high	emersed	muddy sand	8.6	0.5	interface	mobile	0.7	8.9	neutral	stabilizer
C1	*Sphaerosyllis bulbosa*	stenothermal	brooded	short	low	stenohaline	gravel	1.3	0.5	epifauna	mobile	4.7	1.9	neutral	neutral
C2	*Marphysa bellii*	stenothermal	planktonic	short	high	stenohaline	muddy sand	23.3	0.3	interface	mobile	1.1	4.7	neutral	neutral
C3	*Nephtys hombergii*	stenothermal	planktonic	long	high	stenohaline	gravel	10.5	0.3	interface	mobile	2.2	7.3	neutral	neutral
C4	*Myrianida edwardsi*	stenothermal	planktonic	long	low	stenohaline	mud	1.4	3.1	interface	mobile	5.8	1.9	neutral	neutral
C5	*Urticina felina*	eurythermal	planktonic	short	high	euryhaline	rock	16.7	10.3	epifauna	sessile	1.1	14.0	epibiont	neutral
C6	*Syllis cornuta*	stenothermal	planktonic	long	low	stenohaline	rock	7.4	5.2	epifauna	mobile	2.3	2.3	epibiont	neutral

Table 2. List of community assembly mechanisms, biological traits that represent the organisms’ role in them, potential trait values and comments about their assignment to the system’s species, which formed the basis for the construction of the 20 functional groups (Alexandridis et al., 2017)

Mechanisms	Biological traits	Trait values	Comments
Resistance to perturbation	T1. low temperature tolerance	eurythermal/stenothermal	Species that can tolerate continued exposure to single-digit temperatures (eurythermal) were distinguished from those that cannot (stenothermal).
	T2. early development mode	planktonic/laid/brooded	Trait values should define a gradient of increasing ability to cope with perturbations during the early life stages, due to increasing investment in early offspring survival.
Dispersal potential	T3. larval dispersal distance	short/long	Species were separated in two groups based on their maximum observed dispersal distance, with a distance of 10 km used as the breaking point.
	T4. maximum fecundity	low/high	Species were separated in two groups, with the number of 1000 eggs produced by a female of each species per year used as the breaking point.
Environmental filtering	T5. tidal emersion/ low salinity tolerance	emersed/euryhaline/ stenohaline	Soft bottom species that can tolerate long tidal exposure should be able to tolerate low salinity (emersed). Immersed species either can tolerate salinities that differ greatly from those of the open sea (euryhaline) or cannot (stenohaline).
	T6. preferred substrate type	mud/muddy sand/ sand/muddy gravel/ gravel/rock	The assignment of one value to each species represented its greatest substrate affinity, but was often too restrictive.
Competitive effect	T7. maximum size	1 cm/2 cm/10 cm/20 cm/ 40 cm	Trait values should define a gradient of increasing area that can be searched for food or distance from the substrate, which should enhance food availability (McLean and Lasker, 2013).
	T8. minimum space requirement	0.003/0.1/49.5 (min./median/max.) Values are not absolute, but rather relative levels.	Species with the lowest trait value should compete best for space (Tilman, 1980). Trait values were derived from data on body mass (Robinson et al., 2010) and use of an exponent of ¾ from the metabolic theory of ecology (Jetz et al., 2004).
Response to competition	T9. preferred substrate position	infauna/interface/epifauna	Living deep in the sediment (infauna), at its upper layer (interface) or on its surface (epifauna) should allow species co-existence in spite of established competitive hierarchies.
	T10. adult mobility	mobile/sessile	Differences in the ability of species to move should lead to resource partitioning and avoidance of competition.
Population dynamics	T11. population growth rate	0.27/2.14/6.95 (min./median/max.) Values are not absolute, but rather relative levels.	Trait values were derived from data on body mass (Robinson et al., 2010) and use of an exponent of -¼ from the metabolic theory of ecology (Savage et al., 2004).
	T12. maximum lifespan	1 yr/2 yr/10 yr/20 yr	Different trait values should reflect differentiations in species population dynamics.

Biogenic habitat modification	T13. role in epibiosis	basibiont/epibiont/neutral	Species that can grow on other organisms (epibiont) were distinguished from those that also provide biotic substrate (basibiont). Neutral species do not participate in epibiosis.
	T14. role in sediment engineering	stabilizer/destabilizer/ neutral	Sediment destabilizing species should inhibit sessile, tube building species (stabilizers) and vice versa (Posey, 1987). Neutral species do not participate in sediment engineering.

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 predation. A self-effect, as in self-thinning, was depicted as a link that starts and ends at the same node.

Links were drawn based on functional relationships representing general community assembly mechanisms and the expected role of each group in them. This role was defined by the groups' assigned trait values and representative species (Table 1). The functional relationships encompass processes of 1) environmental filtering, 2) consumption of algae/detritus, 3) predation, 4) use of space, 5) food–space competition trade-off, 6) early survival–colonization trade-off, 7) biogenic habitat modification and 8) intra-group inhibition. Predation of benthos by fish and birds was not included, because the former plays a limited role in the Rance estuary, while the latter is highly seasonal and mostly restricted to the intertidal zone.

In addition to the explicit representation of space as a basic resource (see section 2.3.4), implicit spatial considerations were required for the representation of a few other processes (see sections 2.3.5–2.3.7). The modelled functional relationships represent interactions among populations of functional groups within an area that is adequately large for the processes that shape these inter-group interactions to occur. Intra-group spatial interactions were addressed independently (see section 2.3.8).

2.3.1

Environmental filtering

Epifaunal (T9) organisms with a preference for rock or gravel (T6) are clearly distinguished from infaunal or interface-positioned organisms (T9) that prefer finer sediment types (T6), with respect to both their functional characteristics (Alexandridis et al., 2017) and their distribution patterns in the Rance estuary (see section S1 in the Supplementary Material). This observation led to the drawing of two separate signed digraphs for these two groups of organisms, signed digraph 1 (SD1) for the former, epifaunal (Fig. 2a) and signed digraph 2 (SD2) for the latter, infaunal (Fig. 3a). Only group C6 is part of both models, because of the high mobility (T10) and ambiguous substrate preference (T6) of its species. The two sub-systems might co-occur but the way in which they interact is not addressed here.

2.3.2

Consumption of algae/detritus

Algae/detritus feeders along with predators/scavengers with the smallest maximum size (T7) among all functional groups (groups C1 in SD1 and C4 in SD2) are assumed to consume the basic food resource, either from the water column or through deposit feeding. This interaction was represented by a negative effect on food and a positive effect on consumers (Fig. 2b, 3b). Group H2 in SD1 was excluded from the consumption of the basic food resource, because of the grazing behaviour of its representative species. The bulldozing effect of this behaviour, which is expected to deprive other organisms of the free use of space (Pascual, 1997), was represented by a consumption interaction with this resource.

2.3.3

Predation

The majority of predators appear to be larger than their prey, and predator size generally increases with the size of prey (Cohen et al., 1993). This general observation formed the assumption that groups of predators/scavengers (except for the smallest groups C1 and C4) can only feed on groups that are smaller or similar in maximum size (T7). Prey groups were, still, not allowed to be smaller than 1/3 of the maximum size of the predator/scavenger groups themselves. The reason is that predator–prey body-size ratios are generally the lowest, just over 2 on average, for marine invertebrate predators, compared to predators of other taxonomic groups and habitat types, probably due to the energetic costs of prey capture and consumption (Brose et al., 2006a).

Predation was represented by a negative effect on prey and a positive effect on predators (Fig. 2c, 3c). The predator/scavenger group C5 in SD1 is represented by a sea anemone and its adult mobility (T10) is restricted, hence, only mobile functional groups were considered as its potential prey. Since all predator/scavenger groups are characterized as epifauna or interface-related (T9), infaunal functional groups (groups H5, H6 and H12 in SD2) along with groups whose representative species are protected by plates (groups H2 and H3 in SD1), shells (groups H4, H13 in SD1 and H14 in SD2) or tubes (groups H7 and H11 in SD2) were excluded from predator–prey interactions.

2.3.4

Use of space

Just like food, space is assumed to be a basic resource that is “consumed” or used by groups of algae/detritus feeders. Predators/scavengers (including sessile group C5) are, instead, expected to only have their prey as their basic resource. In addition to the aforementioned group H2, space in SD1 is also used by algae/detritus feeders that are characterized as sessile (T10), since mobile organisms probably do not have such a strong interaction with space.

In SD2, we expect the role of organisms in sediment engineering (T14) to play a central role in their interaction with space, with sediment stabilizers being primarily limited by it. Organisms are also assumed to partition space, by occupying different positions with respect to the substrate (T9). Since the two-dimensional nature of the interface renders space particularly limiting for organisms that occupy this position, we set space as a resource only for stabilizing groups of the interface. The use of space by these organisms was represented by a negative effect on space and a positive effect on its consumers (Fig. 2d, 3d).

2.3.5

Food–space competition trade-off

In order to better represent differences in the functional roles of benthic organisms in a way that is consistent with the general trade-offs that are expected to characterize these functional roles, we resorted again to the trait of maximum size (T7). Higher levels of this trait are expected to confer a competitive advantage for limited food resources, due to a larger area that can be searched for food or distance from the substrate, which enhances the availability of food from the water column (McLean and Lasker, 2013). On the other hand, maximum size (T7) appears to be positively associated with the trait of minimum space requirement (T8) among benthic macroinvertebrates of the Rance estuary (see section S2 in the Supplementary Material). Higher values of the latter trait should confer a competitive disadvantage for limited available space (Tilman 1980). We, thus, assumed that larger maximum size (T7) represents a competitive advantage for food and disadvantage for space.

Based on this assumption, we divided the functional groups of each signed digraph that consume the basic food resource in two categories, the small and the big. We did so, by making sure that groups with similar sizes are placed in the same category and that there are more small than large groups (Blackburn and Gaston, 1994). The members of each category are expected to be limited by the resource for which they have a competitive disadvantage, while being able to efficiently reduce the levels of the resource for which they are competitively superior. This set of interactions was represented by an alteration of the existing resource consumption interactions, so that a functional group receives a positive effect from its limiting resource, while having a negative effect on the resource that it can efficiently reduce (Fig. 2e, 3e). This rule was not applied to any groups that would otherwise appear not to be limited by any of the basic resources, along with group H2 in SD1, whose relationship with space represents its bulldozing effect on macroinvertebrate recruits.

2.3.6

Early survival–colonization trade-off

We used three traits to represent life history trade-offs: early development mode (T2), larval dispersal distance (T3) and maximum fecundity (T4). High levels for the last two traits appear to be associated with planktonic early development (T2) among benthic organisms in the Rance estuary, whereas low levels are associated with brooded early development (T2) and high population growth rates (T11) (see section S2 in the Supplementary Material). The former trait associations are expected to result in higher colonization potential, whereas the latter can be linked to higher early survival rates. The distinction between these groups of trait values represents a trade-off among benthic organisms in the allocation of resources toward early survival versus colonization potential (Tilman, 1990).

Functional groups with planktonic early development, long dispersal distance and high fecundity are the only groups expected to effectively interact with the resource of space, because of their high dispersal potential. The mobility of group H2 in SD1 and its special relationship with space again excluded it from this rule. On the other hand, functional groups with brooded early development should be able to resist a variety of perturbations and, at least locally, reach high levels of abundance. They were, therefore, depicted as able to reduce the resource of food, even if their size did not qualify them to do so (Fig. 2f, 3f).

2.3.7

Biogenic habitat modification

The organisms that are represented by SD1 are distinguished from the rest by their epifaunal position (T9) and requirement for hard substrate (T6) (see section S2 in the Supplementary Material). Their occurrence in the Rance estuary can be at least partly attributed to the phenomenon of epibiosis (T13), regardless of the basibiotic organisms being alive or not (Wahl and Mark, 1999). The provision of hard substrate by the single functional group that is described as basibiont (group H4) was represented by a positive effect on all algae/detritus feeders of the system and the sessile predator/scavenger group C5 (Fig. 2g).

Substrate preferences among the organisms of SD2 (T6) appear to match their effect on the sediment (T14) (see section S2 in the Supplementary Material), in support of the mobility mode hypothesis and, hence, the separation of organisms into stabilizers and destabilizers (Posey, 1987). Sediment destabilization in the form of bioturbation should constitute the main mechanism of sediment engineering in estuarine soft bottoms (Meadows et al., 2012). Due to its high dispersal potential (T2, T3 and T4) and its role as a sediment destabilizer (T14), group H10 is expected to be mostly responsible for it. This group was, therefore, allowed to reduce the available space for stabilizing organisms of the interface and have a direct negative impact on infaunal stabilizers (groups H6 and H12). On the other hand, the ensuing bioirrigation is expected to generate favourable conditions for infaunal destabilizers and was depicted as a positive effect on group H5 (Fig. 3g).

2.3.8

Intra-group inhibition

Negative self-effects were added to all variables of SD1 and SD2, representing a variety of processes (Fig. 2h, 3h). In the case of the two basic resources, negative self-effects are mostly indicative of the existence of intrinsic limitations in the amounts that are available to their consumers. Negative self-effects for the rest of the variables can be the result of, among other things, crowding, behavioural inhibition of reproduction, territoriality or accumulation of waste products (Levins, 1998). These or similar processes appear to be wide-spread in ecological systems (Connell, 1983).

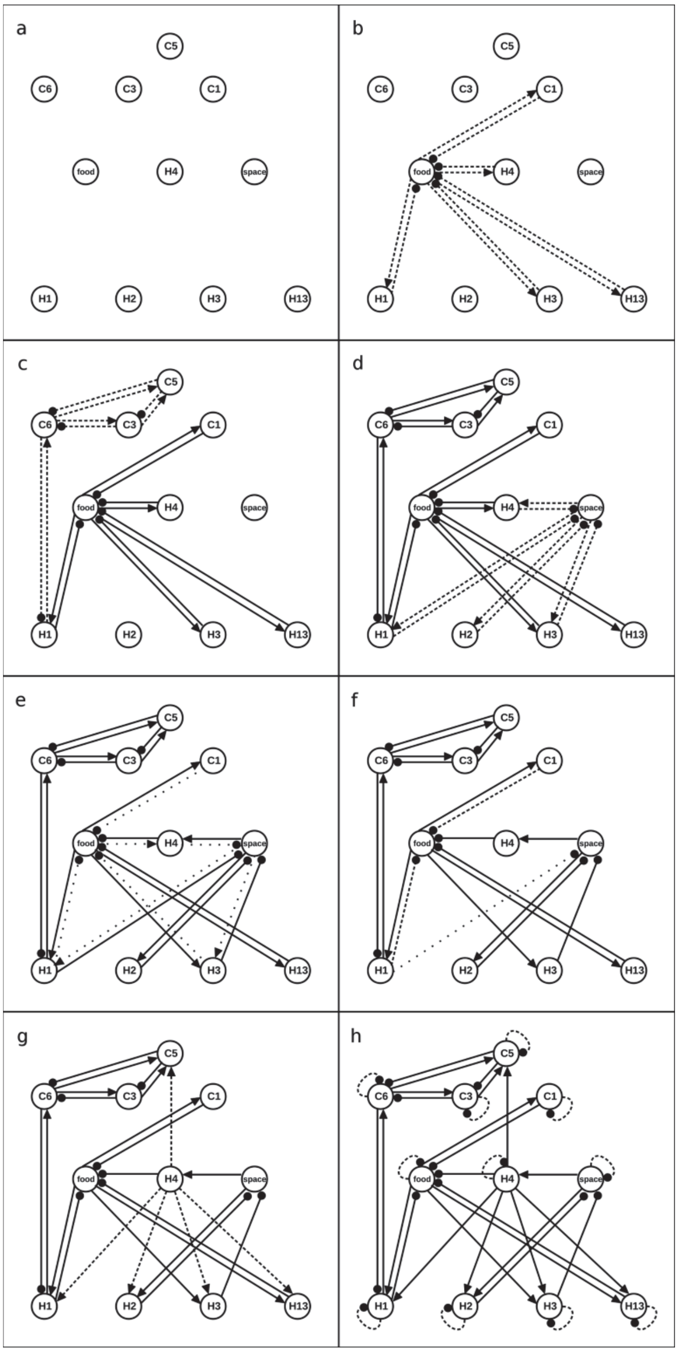

Fig. 2. Stepwise drawing of signed digraph 1 (SD1, epifauna). The steps represent processes of a) environmental filtering, b) consumption of algae/detritus, c) predation, d) use of space, e) food–space competition trade-off, f) early survival–colonization trade-off, g) epibiosis and h) intra-group inhibition. The nodes represent functional

groups (see Table 1) or the basic resources of food and space. Links ending in arrows and filled circles represent positive and negative direct effects, respectively. Dashed and dotted lines represent links that are added and removed, respectively, at each step. See text for details

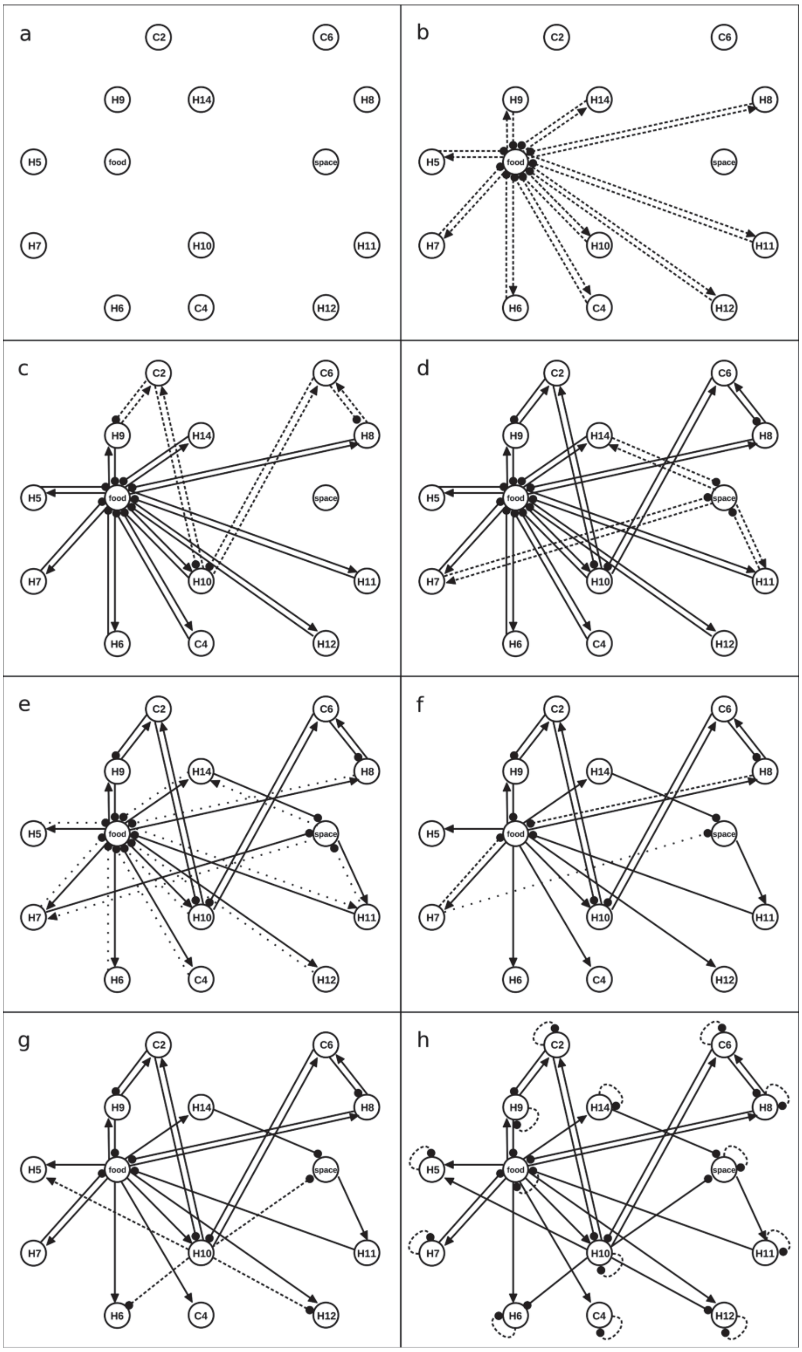

Fig. 3. Stepwise drawing of signed digraph 2 (SD2, infauna). The steps represent processes of a) environmental filtering, b) consumption of algae/detritus, c) predation,

d) use of space, e) food–space competition trade-off, f) early survival–colonization trade-off, g) sediment engineering and h) intra-group inhibition. The nodes represent functional groups (see Table 1) or the basic resources of food and space. Links ending in arrows and filled circles represent positive and negative direct effects, respectively. Dashed and dotted lines represent links that are added and removed, respectively, at each step. See text for details

2.4

Feedback analysis

The concept of feedback in qualitatively specified systems, such as signed digraphs, can be defined at different levels of a system, depending on the number of interactions that are considered to participate in feedback cycles (i.e., closed paths of interactions linking a subset of a system's variables without crossing any of them twice). Feedback cycles at level 1 are self effects, at level 2 they comprise pair-wise interactions, such as predator–prey, with the highest level of feedback involving *n* interactions in a model with *n* variables. A cycle can consist of positive and negative interactions and the product of their signs sets the overall sign of the cycle. In general terms, negative feedback cycles provide stability and positive feedback cycles act to destabilize a system (Puccia and Levins, 1985).

We assessed the potential for stability of our qualitative models as an indication of the likelihood of the respective systems to exist in nature. To this end, we followed the approach of Dambacher et al. (2003), who derived two criteria for the stability of qualitative models, classified conditionally stable models accordingly and developed stability metrics for each of the two model classes. The stability of class I models is jeopardized by positive feedback dominating feedback at the highest level of a system. Instability in class II models is characterized by overcompensation, which leads to oscillations, due to feedback at higher levels in a system overwhelming feedback at lower levels. The latter case can be assessed by measuring the relative balance of feedback at different system levels.

Most biological systems appear to be represented by class I models and their potential for stability is determined by their maximum weighted feedback (Dambacher et al., 2003). This metric is calculated by counting all feedback cycles (both positive and negative) at the highest level of a system and computing the ratio of their net to absolute sums. It portrays the contribution of negative and positive feedback cycles to the overall system feedback. Values that tend toward -1 indicate a high potential for the variables of a system in equilibrium to converge toward their original levels following a pulse perturbation. Values that tend toward 1 indicate a high potential for post-perturbation divergence from these levels. Values near 0 show high ambiguity with respect to the system’s stability potential.

The classification of the models and the calculation of the stability metrics were based on qualitatively specified community matrices, which are equivalent to signed digraphs as a representation of a system. With the help of tools specifically designed for their analysis (Dambacher et al., 2002), we assigned the qualitative models to one of the two stability classes. Based on this classification, we calculated the metric that quantifies each model's potential for stability.

Signed digraphs were drawn, and from them qualitatively specified community matrices were derived using the digraph editor software PowerPlay version 2.0 (Westfahl et al., 2002). The stability analysis of the qualitative mathematical models was performed with a program for the qualitative and symbolic analysis of community matrices (*esapubs.org/archive/ecol/E083/022*) using the technical computing software Maple version 18.0 (Maplesoft, 2014).

3

Results

3.1

Signed digraphs

Building the signed digraphs of benthic macroinvertebrate communities in the Rance estuary left the epifaunal SD1 with 9 functional groups and the infaunal SD2 with 12, as group C6 participates in both models. In spite of having fewer groups, SD1 has 3 of them acting as predators, compared to only 2 predatory groups in SD2. Only 5 groups interact with algae/detritus in SD1 and 10 groups in SD2, while 3 groups interact with the basic resource of space in both models. The representation of the trade-off in competitive ability for food and space appears to have a deeper impact on the structure of the models than the trade-off between early survival and colonization potential. Incorporating the latter often resulted in a reversal of changes made to the models to represent the former. Biogenic habitat modification is of facilitating nature in SD1, taking the form of epibiosis, and of mostly inhibiting nature in SD2, where it represents bioturbation.

The qualitatively specified community matrices that correspond to SD1 (Table 3) and SD2 (Table 4) offer a detailed description of the interactions that comprise the two models. Of the 121 possible interactions in SD1 and the 196 possible interactions in SD2, only 36 occur in the former model and 41 in the latter. As a measure of system complexity, the proportion of possible interactions among each system's variables that are actually realized is equal to 0.29 in SD1 and 0.21 in SD2. SD1 comprises 21 negative and 15 positive interactions, while SD2 has the same number of positive interactions as SD1 and 26 negative.

Table 3. Qualitatively specified community matrix corresponding to SD1 (see Fig. 2). Values along each column indicate negative (-), positive (+) or absent (0) direct effects of the respective variable on the variables of the rows. The variables represent functional groups (see Table 1) or the basic resources of food and space

	food	space	H1	H2	H3	H4	H13	C1	C3	C6	C5
food	-	0	-	0	0	-	-	-	0	0	0
space	0	-	0	-	-	0	0	0	0	0	0
H1	+	0	-	0	0	+	0	0	0	-	0
H2	0	+	0	-	0	+	0	0	0	0	0
H3	+	0	0	0	-	+	0	0	0	0	0
H4	0	+	0	0	0	-	0	0	0	0	0
H13	+	0	0	0	0	+	-	0	0	0	0
C1	+	0	0	0	0	0	0	-	0	0	0
C3	0	0	0	0	0	0	0	0	-	+	-
C6	0	0	+	0	0	0	0	0	-	-	-
C5	0	0	0	0	0	+	0	0	+	+	-

Table 4. Qualitatively specified community matrix corresponding to SD2 (see Fig. 3). Values along each column indicate negative (-), positive (+) or absent (0) direct effects of the respective variable on the variables of the rows. The variables represent functional groups (see Table 1) or the basic resources of food and space

	food	space	H5	H9	H14	H8	C2	C6	H6	H7	H10	H11	H12	C4
food	-	0	0	-	0	-	0	0	0	-	0	-	0	0

space	0	-	0	0	-	0	0	0	0	0	-	0	0	0
H5	+	0	-	0	0	0	0	0	0	0	+	0	0	0
H9	+	0	0	-	0	0	-	0	0	0	0	0	0	0
H14	+	0	0	0	-	0	0	0	0	0	0	0	0	0
H8	+	0	0	0	0	-	0	-	0	0	0	0	0	0
C2	0	0	0	+	0	0	-	0	0	0	+	0	0	0
C6	0	0	0	0	0	+	0	-	0	0	+	0	0	0
H6	+	0	0	0	0	0	0	0	-	0	-	0	0	0
H7	+	0	0	0	0	0	0	0	0	-	0	0	0	0
H10	+	0	0	0	0	0	-	-	0	0	-	0	0	0
H11	0	+	0	0	0	0	0	0	0	0	0	-	0	0
H12	+	0	0	0	0	0	0	0	0	0	-	0	-	0
C4	+	0	0	0	0	0	0	0	0	0	0	0	0	-

3.2

Feedback analysis

The results of the stability analysis for the qualitatively specified community matrices that correspond to SD1 and SD2 are shown in Table 5. The pattern of increasing weighted feedback with increasing system level for both models indicates that their stability could be compromised by positive feedback dominating feedback at the highest level of the system rather than by overcompensation; SD1 and SD2 are, therefore, class I models (sensu Dambacher et al. (2003)). Consequently, their potential for stability is determined by their maximum weighted feedback, which quantifies the contribution of negative and positive feedback cycles to the overall system feedback. This metric is well below 0 for both models, indicating the dominance of negative feedback cycles over positive ones, along with a moderate level of ambiguity with respect to the stability potential of the system.

Table 5. Results of the stability analysis for the systems represented by SD1 (see Fig. 2) and SD2 (see Fig. 3). Values along each row correspond to weighted feedback (wF) calculated at the system level that is indicated by the ensuing number. The value of maximum weighted feedback for each model is indicated by an asterisk

	wF1	wF2	wF3	wF4	wF5	wF6	wF7	wF8	wF9	wF10	wF11	wF12	wF13	wF14
SD1	-1	-1	-0.99	-0.97	-0.94	-0.9	-0.83	-0.75	-0.66	-0.57	-0.5*	-	-	-
SD2	-1	-1	-1	-0.99	-0.98	-0.95	-0.9	-0.84	-0.77	-0.69	-0.6	-0.51	-0.42	-0.33*

In both SD1 and SD2, the basic resources of food and space are part of positive feedback cycles of length four. In the case of SD1, the positive feedback cycle is formed with groups H3 and H4 (Fig. 4a). The former, being small, is enhanced by food and reduces space, while the latter, being big, plays the opposite role. In SD2 there are two equivalent positive feedback cycles (Fig. 4b). Each of them is formed with one of the small groups H10 and H14, which are enhanced by food and reduce space, along with big group H11, which plays the opposite role. Due to the self-enhancing nature of positive feedback cycles, variables are likely to respond to long-term perturbations in a correlated manner. Food quantity and the abundances of small groups H3, H10 and H14 would shift in the same direction, opposite to the amount of available space and the abundances of big groups H4 and H11.

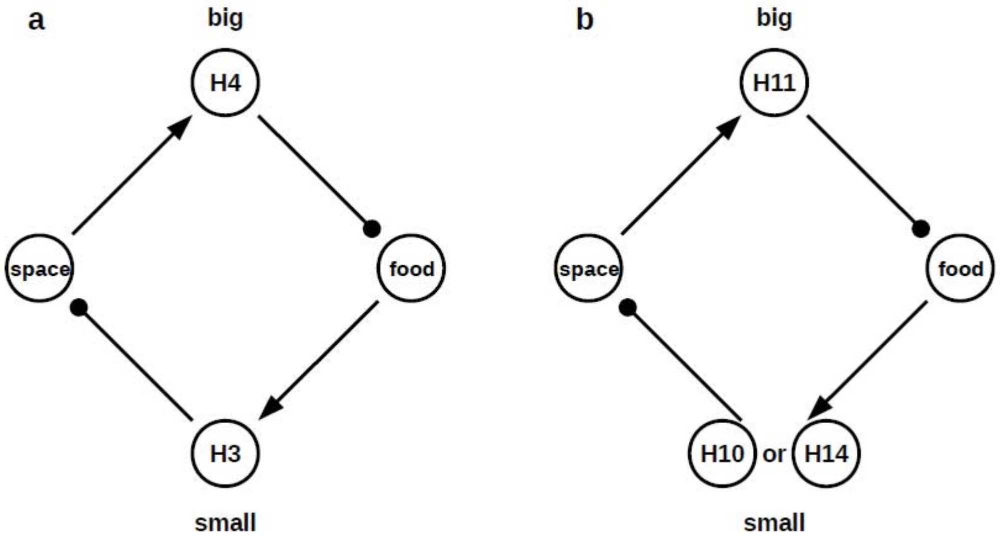

Fig. 4. Positive feedback cycles from a) SD1 (see Fig. 2) and b) SD2 (see Fig. 3). Each feedback cycle links the basic resources of food and space with one big and one small functional group. Links ending in arrows and filled circles represent positive and negative direct effects, respectively

4

Discussion

4.1

Functional groups

Qualitatively specified food-web models often represent only a few dominant species of marine benthic macroinvertebrates, while other community members may be grouped into broad trophic categories (e.g., Carey et al., 2014; Reum et al., 2015). This practice cannot explicitly account for key non-trophic interactions and tends to ignore the rarest members of a community, in spite of evidence for their significant contribution to ecosystem functioning (Lyons et al., 2005). This contribution can be disproportionate to their abundance, as species with the most distinct combinations of traits have been shown to be rarer than expected by chance (Mouillot et al., 2013).

The variables of the models developed here were built through a procedure that places emphasis on the species' functional role instead of their abundance; the latter is used only secondarily for the assignment of trait values to each group (Alexandridis et al., 2017). The wide functional scope of the traits that formed the basis for the grouping allowed the representation of not just trophic interactions, but the majority of the mechanisms that are expected to shape benthic communities in many parts of the world. Trait variation within the groups was found to be largely neutral, allowing a system representation that is free of functionally equivalent variability (Hérault, 2007).

4.2

Signed digraphs

The evaluation of the functional grouping against its theoretical assumptions suggested that species abundances in the Rance estuary depend, at least to some extent, on species trait values (Alexandridis et al., 2017). The nature of this relationship was further elucidated through the investigation of associations of biological traits with environmental variables and with each other (see Supplementary Material). These results were combined with theoretical expectations and expert knowledge to define functional relationships between the groups and their basic resources.

Each of the community assembly mechanisms that are represented by these relationships encompasses a variety of processes that could potentially be represented much more explicitly. The level at which each mechanism was actually represented was dictated by the available trait and environmental information. Hence, biological traits were used as proxies for the role of functional groups in a set of theoretically expected community assembly mechanisms that were illustrated through a highly abstract representation of the system.

For instance, the biogeochemical aspects of sediment engineering were not explicitly represented, as the distinction between sediment stabilizers and destabilizers (Posey, 1987) was the best possible representation, given the available information at the species level. Still, this tenet of the mobility-mode hypothesis has been empirically upheld and shown to have cascading and long-lasting effects on benthic communities (Volkenborn et al., 2009). Similarly, the complex set of processes that comprise the phenomenon of resource competition was only represented through the use of each group’s maximum size in the context of the concentration reduction hypothesis for space and food (Tilman, 1980). Space limitation due to adult–juvenile interactions and exploitative competition for food have been shown to play a central role in the successional dynamics of benthic communities, with the functional role of organisms largely defined by their size (Van Colen et al., 2008). The combined representation of food and space as limiting resources can significantly increase our understanding and predictability of marine benthic systems (Svensson and Marshall, 2015).

The separation of benthic macroinvertebrates into algae/detritus feeders and predators/scavengers aimed to preserve the homogeneity of their resource base, so that theoretically expected community assembly mechanisms could be implemented. This choice might appear to ignore important differentiations in the feeding habits of these organisms, such as the distinction between suspension- and deposit-feeders. It has been, however, shown that feeding behaviour in the marine benthos is highly facultative and similar categorizations are not always valid (Snelgrove and Butman, 1994). Instead, the modification of networks of trophic interactions through expert knowledge is expected to increase their realism, while the use of allometric scaling should enhance their stability (Brose et al., 2006b).

Survival rates (Schratzberger and Larcombe, 2014) and colonization potential (Limberger and Wickham, 2011) have been separately involved in trade-offs with the competitive ability of benthic organisms. Our assumptions allow for both scenarios, while the deconstruction of competitive ability into two constituents, for the basic resources of food and space, could resolve inconsistencies in previous findings.

The role of recruitment in the assembly of benthic communities may still be under-represented. Biological traits related to species' reproductive strategy were found to deviate the most from the theoretical assumptions that allowed the construction of the functional groups (Alexandridis et al., 2017). Relevant trait information is, however, consistently lacking (Tyler et al., 2012). A more accurate depiction of recruitment-related processes would allow the explicit representation of trade-offs that have been shown to play a significant role in the assembly of benthic communities (Lindquist and Hay, 1996; Marshall and Steinberg, 2014).

The functional divergence between organisms that occupy the surface of the sediment (epifauna) and those that are buried in it (infauna) has been previously recognized in the study of marine benthos (Reiss et al., 2010). In the Rance estuary, the epifauna (SD1) features a lower functional diversity of algae/detritus feeders and a higher functional diversity of predators/scavengers, compared to the infauna (SD2). Additionally, a much higher number of groups ended up interacting with algae/detritus in SD2 compared to SD1. The complex diagenetic processes that affect the basic food resource within the sediment of the seafloor (Herman et al., 1999) could be responsible for the diversity of infaunal organisms that feed on it. On the other hand, the high structural complexity of the habitat occupied by epifaunal organisms may result in a higher diversity of predatory strategies. Trophic differences could be associated with a variety of biological traits, leading to observed patterns of functional diversity. The epifaunal system also appears to be more complex, with a higher proportion of possible interactions realized compared to the infaunal system. This is primarily caused by an under-representation of positive interactions in the latter system. The qualitatively antithetical role of biogenic habitat modification in the two systems (facilitating in SD1, mostly inhibiting in SD2) contributes partly to these differences. Its impact may extend to productivity patterns, as epifauna-dominated systems (seagrass/algae beds) seem in general to be more productive than infauna-dominated (estuaries) (Costanza et al., 1998).

4.3

Feedback analysis

The results of the stability analysis suggest that the models developed in this work have a moderate to high potential for stability. This demonstrates the likelihood of the system to persist in time in spite of perturbations. These perturbations can take various forms, from local sediment re-suspension due to wave action, to system-wide reduction of secondary production during extremely cold winters (Desroy, 1998). Despite the impact of such pulse perturbations on spatial and temporal distribution patterns of benthic macroinvertebrates, the composition of their communities has been mostly stable in the Rance estuary since late 1970's. The agreement between observed stability levels and the predictions of feedback analysis can be considered as partial validation of the generated models.

Populations of benthic macroinvertebrates in the Rance estuary are still expected to change in response to constant or press perturbations, but in a way that can be attributed to the structure of the qualitative models. For instance, the participation of the basic resource of food in positive feedback cycles in both SD1 and SD2 allows the formulation of predictions about the direction in which the other variables in these cycles would respond as a result of system-wide persistent changes in primary production. Within these cycles, which constitute a qualitative representation of Tilman's (1980) concentration reduction hypothesis, a decrease in the amount of available food is expected, in general, to lead to less smaller and more larger individuals, with a concomitant increase in the amount of available space. Similar patterns have been observed as a result of bathymetric decreases in nutrient input (Rex and Etter, 1998) and can have profound impacts on the functioning of ecological systems (Woodward et al., 2005).

5

Conclusions

Qualitative mathematical models have been successfully employed for the study of both soft- (Ortiz and Wolff, 2002) and hard-bottom (Marzloff et al., 2011) marine benthos. The properties of these models make them particularly well-suited for the integration of systems that comprise processes of disparate nature (Dambacher et al., 2007). Our approach primarily differs from previous work in the way organisms are represented and interactions are attributed between them. This is done through a systematic procedure that employs theoretical and expert knowledge from a wide range of sources. It can be applied, with adjustments of various degrees, for the mechanistic representation of many ecological systems for which empirical information is limited.

Qualitative models sacrifice the element of precision, in order to produce a general and realistic representation of the causal relationships that shape a system (Levins, 1966). When there is uncertainty in the model components or interactions, alternative model configurations can be easily generated and assessed with respect to the functioning of the system (Dambacher et al., 2002). Qualitative modelling can, therefore, direct the initial steps of more quantitative approaches, before investment in model development has rendered structural changes too costly. We plan to use this property to inform the structure of dynamic and spatially explicit trait-based models of marine benthic communities in the Rance estuary (Alexandridis, 2017).

Similar efforts in terrestrial environments were able to predict the responses of plant (Boulangeat et al., 2014) and animal communities (Scherer et al., 2016) to projected climatic and land use change. They faced issues that are shared by our study, such as the lack of information on important biological traits or the limited potential for validating model predictions with species data. Quite similar to our study, they addressed these issues by using surrogate traits or investigating the plausibility of their findings in view of specific system perturbations. The conclusion of our work should help bridge the gap between terrestrial and marine systems with regard to the formulation of reliable predictions of biodiversity responses to environmental change.

Acknowledgments: We thank Claire Chevalier, Stanislas F. Dubois, Antoine Carlier and Patrick Le Mao for sharing their knowledge of the system and assisting in the collection of biological traits information. We are also grateful to the editor and anonymous reviewers for comments that substantially improved the manuscript. This work was supported by LabexMer French project (ANR-10-LABX-19-01).

References

Alexandridis, N., 2017. Models of general community assembly mechanisms simulating the spatial and temporal dynamics of benthic biodiversity. PhD Thesis. Université de Bretagne Occidentale, Brest, France. http://archimer.ifremer.fr/doc/00383/49481/

Alexandridis, N., Bacher, C., Desroy, N., Jean, F., 2017. Building functional groups of marine benthic macroinvertebrates on the basis of general community assembly mechanisms. J. Sea Res. 121, 59-70.

Amarasekare, P., 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecol. Lett. 6, 1109-1122.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J., Brose, U., 2009. Simple prediction of interaction strengths in complex food webs. P. Natl. Acad. Sci. USA 106, 187-191.

Blackburn, T.M., Gaston, K.J., 1994. Animal body size distributions: patterns, mechanisms and implications. Trends Ecol. Evol. 9, 471-474.

Bonnot-Courtois, C., Lafond, L.R., 1991. Caractérisation et comportement des vases dans l'estuaire de la Rance. Rapport EDF. EPHE, Dinard, France.

Boulangeat, I., Georges, D., Thuiller, W., 2014. FATE-HD: a spatially and temporally explicit integrated model for predicting vegetation structure and diversity at regional scale. Glob. Change Biol. 20, 2368-2378.

Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne, S., Lavorel, S., van Es, J., Vittoz, P., Thuiller, W., 2012. Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. Glob. Change Biol. 18, 3464-3475.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G., Cohen, J.E., 2006a. Consumer-resource body-size relationships in natural food webs. Ecology 87, 2411-2417.

Brose, U., Williams, R.J., Martinez, N.D., 2006b. Allometric scaling enhances stability in complex food webs. Ecol. Lett. 9, 1228-1236.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59-67.

Carey, M.P., Levin, P.S., Townsend, H., Minello, T.J., Sutton, G.R., Francis, T.B., Harvey, C.J., Toft, J.E., Arkema, K.K., Burke, J.L., Kim, C.K., Guerry, A.D., Plummer, M., Spiridonov, G., Ruckelshaus, M., 2014. Characterizing coastal foodwebs with qualitative links to bridge the gap between the theory and the practice of ecosystem-based management. ICES J. Mar. Sci. 71, 713-724.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R., Gabriel, J.P., 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature 427, 835-839.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343-366.

Cohen, J.E., Newman, C.M., 1985. A stochastic theory of community food webs. I. Models and aggregated data. Proc. R. Soc. Lond. Ser. B 224, 421-448.

Cohen, J.E., Pimm, S.L., Yodzis, P., Saldaña, J., 1993. Body sizes of animal predators and animal prey in food webs. J. Anim. Ecol. 62, 67-78.

Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122, 661-696.

Constable, A.J., 1999. Ecology of benthic macro-invertebrates in soft-sediment environments: A review of progress towards quantitative models and predictions. Aust. J. Ecol. 24, 452-476.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1998. The value of the world's ecosystem services: putting the issues in perspective. Ecol. Econ. 25, 67-72.

Dambacher, J.M., Brewer, D.T., Dennis, D.M., Macintyre, M., Foale, S., 2007. Qualitative modelling of gold mine impacts on Lihir island's socioeconomic system and reef-edge fish community. Environ. Sci. Technol. 41, 555-562.

Dambacher, J.M., Li, H.W., Rossignol, P.A., 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. Ecology 83, 1372-1385.

Dambacher, J.M., Luh, H.K., Li, H.W., Rossignol, P.A., 2003. Qualitative stability and ambiguity in model ecosystems. Am. Nat. 161, 876-888.

Desroy, N., 1998. Les peuplements benthiques de substrats meubles du bassin maritime de la Rance. Évolution de la biodiversité et effets de l'activité prédatrice de *Nephtys hombergii* (Annélide Polychète). PhD Thesis. Université de Rennes 1, Rennes, France.

Fath, B.D., 2004. Network analysis applied to large-scale cyber-ecosystems. Ecol. Model. 171, 329–337.

Halnes, G., Fath, B.D., Liljenström, H., 2007. The modified niche model: including detritus in simple structural food web models. Ecol. Model. 208, 9-16.

Hérault, B., 2007. Reconciling niche and neutrality through the Emergent Group approach. Perspect. Plant Ecol. 9, 71-78.

Herman, P., Middelburg, J., Van de Koppel, J., Heip, C., 1999. Ecology of estuarine macrobenthos. Adv. Ecol. Res. 29, 195-240.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H., Woodward, G., 2009. Ecological networks – beyond food webs. J. Anim. Ecol. 78, 253-269.

Jetz, W., Carbone, C., Fulford, J., Brown, J.H., 2004. The scaling of animal space use. Science 306, 266-268.

Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol. Lett. 12, 334-350.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C., Brose, U., 2012. More than a meal… integrating non-feeding interactions into food webs. Ecol. Lett. 15, 291-300.

Levins, R., 1998. Qualitative mathematics for understanding, prediction, and intervention in complex ecosystems. In: Ecosystem Health. Blackwell Science, Oxford, UK.

Levins, R., 1966. The strategy of model building in population biology. Am. Sci. 54, 421-431.

Limberger, R., Wickham, S.A., 2011. Competition–colonization trade-offs in a ciliate model community. Oecologia 167, 723-732.

Lindquist, N., Hay, M.E., 1996. Palatability and chemical defense of marine invertebrate larvae. Ecol. Monogr. 66, 431-450.

Lyons, K.G., Brigham, C.A., Traut, B.H., Schwartz, M.W., 2005. Rare species and ecosystem functioning. Conserv. Biol. 19, 1019-1024.

Maplesoft, 2014. Maple. Waterloo Maple Inc., Waterloo, Canada.

Marshall, D.J., Steinberg, P.D., 2014. Larval size and age affect colonization in a marine invertebrate. J. Exp. Biol. 217, 3981-3987.

Marzloff, M.P., Dambacher, J.M., Johnson, C.R., Little, L.R., Frusher, S.D., 2011. Exploring alternative states in ecological systems with a qualitative analysis of community feedback. Ecol. Model. 222, 2651-2662.

McLean, E.L., Lasker, H.R., 2013. Height matters: position above the substratum influences the growth of two demosponge species. Mar. Ecol. 34, 122-129.

Meadows, P.S., Meadows, A., Murray, J.M.H., 2012. Biological modifiers of marine benthic seascapes: their role as ecosystem engineers. Geomorphology 157-158, 31-48.

Morris, J.T., Christian, R.R., Ulanowicz, R.E., 2005. Analysis of size and complexity of randomly constructed food webs by information theoretic metrics. In: Belgrano, A., Scharler, U.M., Dunne, J., Ulanowicz, R.E. (Eds.), Aquatic food webs: an ecosystem approach. Oxford University Press, Oxford, UK.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, T.C.E., Renaud, J., Thuiller, W., 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLOS Biol. 11, e1001569.

Ortiz, M., Wolff, M., 2002. Application of loop analysis to benthic systems in northern Chile for the elaboration of sustainable management strategies. Mar. Ecol.-Prog. Ser. 242, 15-27.

Pascual, M.S., 1997. Carriage of dwarf males by adult female puelche oysters: the role of chitons. J. Exp. Mar. Biol. Ecol. 212, 173-185.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496-1501.

Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. Size, foraging, and food web structure. P. Natl. Acad. Sci. USA 105, 4191-4196.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741-758.

Pineda, J., Reyns, N.B., Starczak, V.R., 2009. Complexity and simplification in understanding recruitment in benthic populations. Popul. Ecol. 51, 17-32.

Posey, M.H., 1987. Influence of relative mobilities on the composition of bentic communities. Mar. Ecol.-Prog. Ser. 39, 99-104.

Puccia, C.J., Levins, R., 1985. Qualitative modeling of complex systems. Harvard University Press, Cambridge, USA.

Queirós, A.M., Bruggeman, J., Stephens, N., Artioli, Y., Butenschön, M., Blackford, J.C., Widdicombe, S., Allen, J.I., Somerfield, P.J., 2015. Placing biodiversity in ecosystem models without getting lost in translation. J. Sea Res. 98, 83-90.

Reiss, H., Degraer, S., Duineveld, G.C.A., Kröncke, I., Aldridge, J., Craeymeersch, J.A., Eggleton, J.D., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Pohlmann, T., Rachor, E., Robertson, M., Vanden Berghe, E., van Hoey, G., Rees, H.L., 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. ICES J. Mar. Sci. 67, 278-293.

Retière, C., 1994. Tidal power and the aquatic environment of La Rance. Biol. J. Linn. Soc. 51, 25-36.

Reum, J.C.P., McDonald, P.S., Ferriss, B.E., Farrell, D.M., Harvey, C.J., Levin, P.S., 2015. Qualitative network models in support of ecosystem approaches to bivalve aquaculture. ICES J. Mar. Sci. 72, 2278-2288.

Rex, M.A., Etter, R.J., 1998. Bathymetric patterns of body size: implications for deep-sea biodiversity. Deep-Sea Res. Pt. II 45, 103-127.

Robinson, L.A., Greenstreet, S.P.R., Reiss, H., Callaway, R., Craeymeersch, J., de Boois, I., Degraer, S., Ehrich, S., Fraser, H.M., Goffin, A., Kröncke, I., Jorgenson, L.L., Robertson, M.R., Lancaster, J., 2010. Length–weight relationships of 216 North Sea benthic invertebrates and fish. J. Mar. Biol. Assoc. UK 90, 95-104.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., Charnov, E.L., 2004. Effects of body size and temperature on population growth. Am. Nat. 163, 429-441.

Scherer, C., Jeltsch, F., Grimm, V., Blaum, N., 2016. Merging trait-based and individual-based modelling: An animal functional type approach to explore the responses of birds to climatic and land use changes in semi-arid African savannas. Ecol. Model. 326, 75-89.

Schratzberger, M., Larcombe, P., 2014. The role of the sedimentary regime in shaping the distribution of subtidal sandbank environments and the associated meiofaunal nematode communities: an example from the southern North Sea. PLoS ONE 9, e109445.

Snelgrove, P.V.R., Butman, C.A., 1994. Animal-sediment relationships revisited: cause versus effect. Oceanogr. Mar. Biol. 32, 111-177.

Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D., Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., Iocco, L., Valenete, R., Watson, J., Rosenberg, R., 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. J. Exp. Mar. Biol. Ecol. 285-286, 313-338.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A., Wiegand, T., 2013. Identification of 100 fundamental ecological questions. J. Ecol. 101, 58-67.

Svensson, J.R., Marshall, D.J., 2015. Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. Ecology 96, 819-827.

Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58, 3-15.

Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation. Am. Nat. 116, 362-393.

Tyler, E.H.M., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D., Webb, T.J., 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Global Ecol. Biogeogr. 21, 922-934.

Van Colen, C., Montserrat, F., Vincx, M., Herman, P.M.J., Ysebaert, T., Degraer, S., 2008. Macrobenthic recovery from hypoxia in an estuarine tidal mudflat. Mar. Ecol. Prog. Ser. 372, 31-42.

Volkenborn, N., Robertson, D.M., Reise, K., 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. Helgoland Mar. Res. 63, 27-35.

Wahl, M., Mark, O., 1999. The predominantly facultative nature of epibiosis: experimental and observational evidence. Mar. Ecol.-Prog. Ser. 187, 59-66.

Westfahl, P., Heath, Z., Woodrow, C., 2002. Powerplay Digraph Editor. Loop Group Dev Team, Corvallis, USA.

Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. Nature 404, 180-183.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. Trends Ecol. Evol. 20, 402-409.

Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. Am. Nat. 139, 1151-1175.

SUPPLEMENTARY MATERIAL

S.1 Environmental filtering

S.1.1 Methods

Each station sampled in the spring of 1995 was associated with a particular sediment type (pure mud, mud, silty mud, sandy mud, muddy sand, fine/intermediate sand, intermediate/coarse sand, coarse sand, gravel), based on a sedimentary map established in 1994 (Bonnot-Courtois, 1997). The depth (or elevation) of each station was measured at low tide during the collection of samples. Each station was assigned a salinity regime, depending on which of three sectors of the Rance estuary it was situated in. The innermost part of the estuary, up to Pleudihen-sur-Rance, was subject to high salinity variation, ranging from 0.5 to 30. Beyond this point, downstream to Port-St-Hubert, salinity values ranged between 18 and 30. The rest of the estuary experienced more or less constant salinity levels, over the value of 30, similar to those of the open sea (Desroy, 1998).

Among the 14 biological traits for which the species of the system were assigned with values, we expect the trait of tolerance to tidal emersion and low salinity levels (T5) along with that of preferred substrate type (T6) to adequately represent the most important environmental limitations that are faced by benthic macroinvertebrates in the Rance estuary (Desroy, 1998). If this is indeed the case, these two biological traits, describing species preference for abiotic conditions, should show high degrees of covariation with the respective environmental variables. Other biological traits that might correlate with the two traits in question are also expected to show similar patterns of covariation.

RLQ analysis is a statistical technique that can relate the biological traits of organisms to the characteristics of the environment in which they live (Dolédec et al., 1996). L refers to a table of species abundance at a number of sites and it describes, among other things, the actual habitat utilization of different species. R refers to a table of environmental variables measured at the same sites as species abundance. Q refers to a table of biological traits for all the species of table L. RLQ analysis starts with the separate ordination of table L. It then uses the resulting sites and species weights in the separate ordinations of tables R and Q, respectively. The result is an ordination of the common structure of tables R and Q with a link expressed by table L.

Since environmental variables and biological traits include both qualitative and quantitative information, we opted for Hill and Smith analysis (Hill and Smith, 1976) for the separate ordinations of the 113 sites × 3 environmental variables (R) and the 240 species × 14 biological traits (Q) tables. Correspondence analysis (Legendre and Legendre, 1998) was performed for the separate ordination of the 113 sites × 240 species abundance table (L). The application of correspondence analysis allows RLQ analysis to maximize the covariance between linear combinations of environmental variables and biological traits (Dolédec et al., 1996). This maximized covariance, projected on orthogonal axes of decreasing contribution to the total value, is called co-inertia.

The comparison of this eigenvalues decomposition (RLQ) with the eigenvalues decomposition from the separate ordinations of the environmental variables (R) and biological traits (Q) tables can show what part of the variance of the original data sets is represented in their common structure. The optimal correlation between sites and species scores from the separate ordination of the species abundance table (L) can be compared with the equivalent correlation from the RLQ analysis, in order to illustrate how well the original species abundance patterns are represented by the associations between environmental variables and biological traits. These associations can be best demonstrated by projecting environmental variables and biological traits side-by-side on the same dimensions of the common co-inertia space.

All analyses were performed using the statistical software R version 3.2.2 (R Core Team, 2015) with the package ade4 (Dray and Dufour, 2007).

S.1.2 Results

The eigenvalues decomposition of the RLQ analysis shows that the proportion of the common structure between environmental variables and biological traits that is portrayed along the first axis (73%) is much larger than the proportion that is portrayed along the second one (17%). The first two axes combined represent 90% of the covariance between environmental variables and biological traits. The cumulated amount of variance that is preserved on the first two axes of the RLQ ordination, compared to the equivalent variance from the separate ordinations of the environmental variables (R) and biological traits (Q) tables, is just over 85% in both cases. The correlation values between sites and species scores along the first and second axes of the RLQ analysis are 76% and 60% of the respective correlation values from the separate ordination of the species abundance table (L).

The side-by-side projection of environmental variables (Fig. S1a) and biological traits (Fig. S1b) on the first two dimensions of the common co-inertia space reveals one conspicuous pattern: coarse sediment types are strongly associated with trait values that represent preference for gravel or rock (T6), no role in sediment engineering (T14), an epifaunal position (T9) and the role of basibionts (T13). These trait values, along with the one that identifies epibiotic organisms (T13) and is associated with increasing water depth, are all characteristic of benthos that occupies the surface of the seabed, supported by structure of abiotic or biotic origin. Increasing water depth is further associated with a transition from organisms that tolerate tidal exposure to those that have to be submerged in high salinity levels (T5).

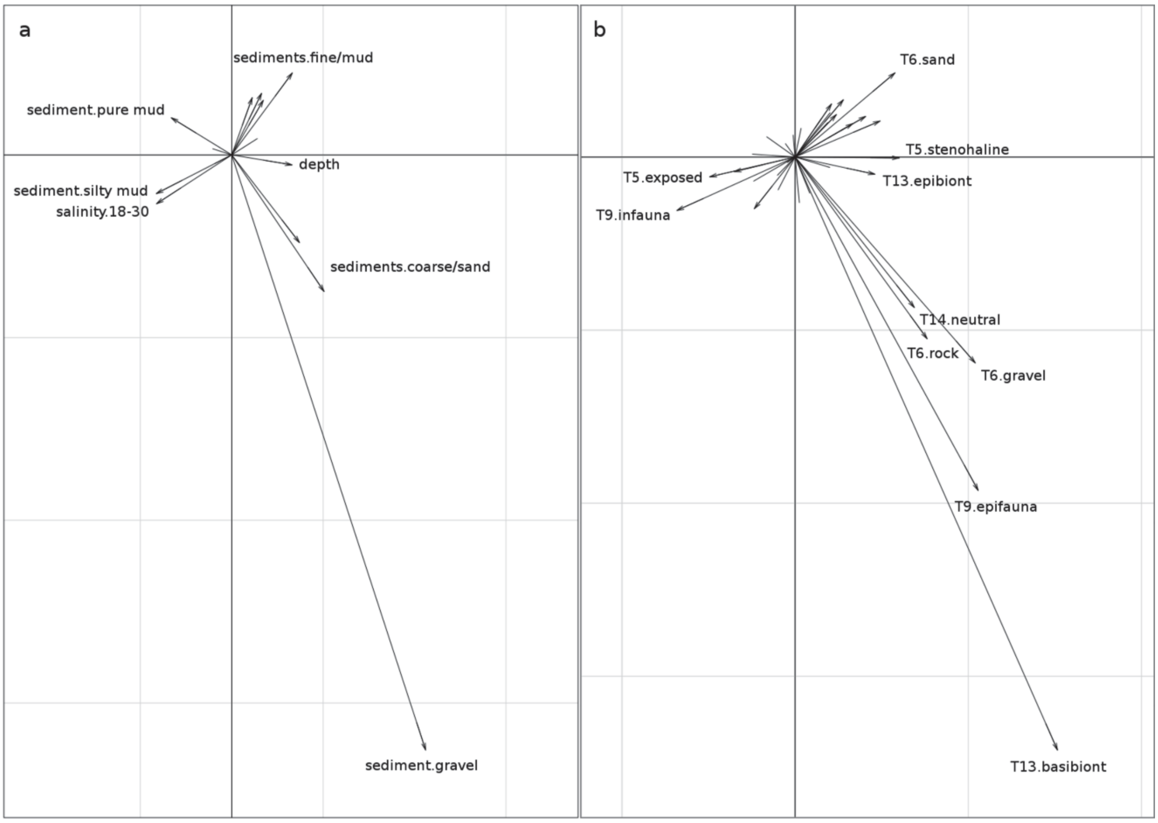

Fig. S1 Projection of a) environmental variables and b) biological traits on the first two dimensions of the common co-inertia space of the RLQ analysis. In both graphs the horizontal axis represents the first dimension and the vertical the second. In the case of continuous and ordinal variables, the arrows indicate the direction of increasing values. In the case of nominal and binary variables, the tips of the arrows indicate the position of the centroids for the respective variable values (shown as variable.value). Plural in the variable names indicates the representation of multiple values that are close in nature and ordination. For details about the traits, see Table 2

S.2 Functional trade-offs

S.2.1 Methods

Our set of 14 biological traits allows the representation of functional trade-offs through specific combinations of trait values. In the case of a trade-off among benthic macroinvertebrates in their utilization efficiency for the two basic resources (food and space) (Tilman, 1980), we would expect trait values that confer a competitive advantage for each resource (greater size (T7) and lower minimum space requirement (T8)) to be negatively associated. A trade-off in the allocation of resources toward early survival versus colonization potential (Tilman, 1990) would result in the survival-enhancing brooded early development mode (T2) being negatively associated with both dispersal distance (T3) and maximum fecundity (T4). Finally, the stabilizers of the mobility-mode hypothesis (Posey, 1987) are expected to bind fine particles, thus leading to the creation of muddy sediments, while destabilizers are expected to disrupt the substrate, resulting in more heterogeneous sediment types. Since each group is assumed to create sediment conditions that are favourable to its own members and detrimental to those of the opposite group, sediment preferences (T6) among stabilizers and destabilizers should correspond to their respective effects on the substrate (T14).

Because values were assigned to the species independently for each biological trait, we can assess the ecological pertinence of each hypothesis, by inspecting the biological traits data set, looking for the respective trait associations. The multivariate ordination technique of Hill and Smith allowed the transformation of the 240 species × 14 biological traits table into a set of orthogonal variables that contain decreasing portions of the table's total variance (Hill and Smith, 1976). The eigenvalues decomposition, on which this technique is based, reveals the amount of variance that each of these variables represents. The projection of the initial trait variables on the first few axes of the transformed multivariate space can provide insights into the most important associations among biological traits.

All analyses were performed using the statistical software R version 3.2.2 (R Core Team, 2015) with the package ade4 (Dray and Dufour, 2007).

S.2.2 Results

The eigenvalues decomposition of Hill and Smith for the biological traits data set shows that about twice as much variation can be found along each of the first two axes (15% and 14% of total variation) compared to each of the two axes that follow (8% and 7% of total variation). The first four axes combined represent just over 43% of the total variation of biological traits among species of benthic macroinvertebrates.

The projection of biological traits on the first four dimensions of the transformed multivariate space reveals the most important biological trait associations. Along the first axis (Fig. S2a), maximum size (T7) is assumed to define a competitive hierarchy for food. Minimum space requirement (T8), in the same direction of the axis, is expected to define an inverse competitive hierarchy for space.

On the positive half of the first axis (Fig. S2a), high levels of maximum fecundity (T4) and dispersal distance (T3) are associated with planktonic early development mode (T2). The combination of these trait values is expected to lead to higher colonization potential among marine benthos. On the negative half of the same axis, low levels of maximum fecundity (T4) and dispersal distance (T3) are associated with brooded early development mode (T2) and high population growth rate (T11), thus forming a trait combination that is assumed to enhance early survival rates.

The second axis of the Hill and Smith ordination (Fig. S2a) mainly serves to distinguish organisms with an epifaunal position (T9) and requirement for hard substrates (T6). Trait differences among the rest of the organisms, which are mostly associated with soft bottoms (T6), are featured along the first (Fig. S2a) together with the third and fourth axes of the ordination (Fig. S2b). It appears that sessile organisms (T10) that prefer mud (T6), stabilize the sediment (T14) and create substrate for epibionts (T13) are distinguished from mobile (T10), destabilizing organisms (T14) that have a preference for coarser and mixed sediment types (T6).

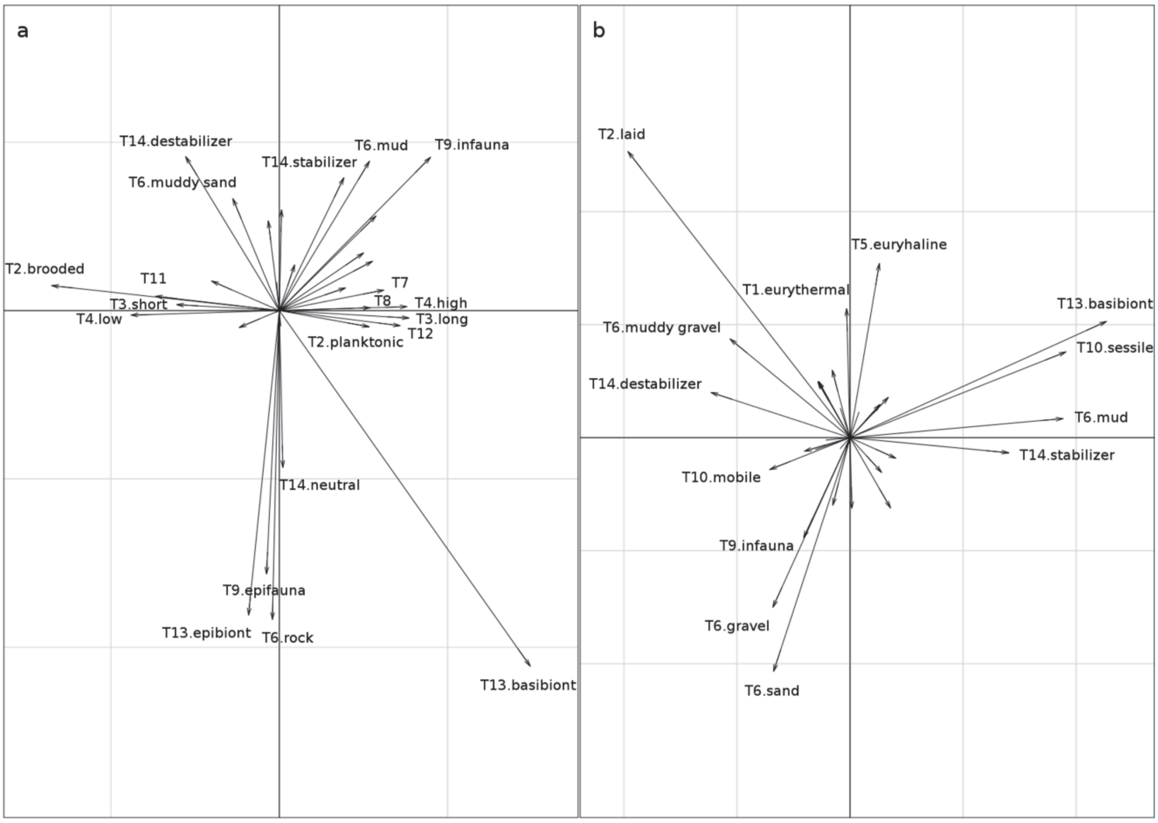

Fig. S2 Projection of biological traits on a) the first and second and b) the third and fourth dimensions of the transformed multivariate space of Hill and Smith analysis. In both graphs the horizontal axis represents the lower dimension and the vertical the higher. In the case of continuous and ordinal traits, the arrows indicate the direction of increasing values. In the case of nominal and binary traits, the tips of the arrows indicate the position of the centroids for the respective trait values (shown as trait.value). For details about the traits, see Table 2

References

Bonnot-Courtois, C., 1997. Evolution de la répartition des sédiments dans l'estuaire de la Rance, 1883-1994. Atlas Permanent de la Mer et du Littoral 3, 29.

Desroy, N., 1998. Les peuplements benthiques de substrats meubles du bassin maritime de la Rance. Évolution de la biodiversité et effets de l'activité prédatrice de *Nephtys hombergii* (Annélide Polychète). PhD Thesis. Université de Rennes 1, Rennes, France.

Dolédec, S., Chessel, D., Ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environ. Ecol. Stat. 3, 143-166.

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1-20.

Hill, M.O., Smith, A.J.E., 1976. Principal component analysis of taxonomic data with multi-state discrete characters. Taxon 25, 249-255.

Legendre, P., Legendre, L., 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam, Netherlands.

Posey, M.H., 1987. Influence of relative mobilities on the composition of bentic communities. Mar. Ecol.-Prog. Ser. 39, 99-104.

R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation. Am. Nat. 116, 362-393.

Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58, 3-15.