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Models of general community assembly mechanisms simulating the spatial and temporal dynamics of benthic biodiversity

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Résumé détaillé

Les macroinvertébrés benthiques entretiennent un ensemble complexe d'interactions avec leur environnement abiotique, leurs ressources et entre eux. Les échelles spatiales et temporelles des processus formant la base de ces interactions ont traditionnellement limité leur étude empirique et le développement de modèles statistiques. Les modèles mécanistes, n'ayant aucune contrainte logistique, offrent un outil alternatif pour étudier de potentiels mécanismes d'assemblage des communautés. Leur développement est toutefois limité par un manque de connaissances des mécanismes structurant les communautés benthiques. Dans le cadre de cette thèse, le premier chapitre du manuscrit tente une revue des outils de modélisation statistique et mécaniste utilisés dans l'étude des macroinvertébrés marins benthiques. Le but est d'identifier une technique permettant d'étudier la dynamique et le comportement de la biodiversité benthique d'une manière spatialement explicite, en utilisant des données déjà existantes.

Même si l'implémentation d'un modèle mécaniste semble s'ajuster aux communautés benthiques, son utilisation nécessite la création d'un nombre limité d'entités avec un rôle fonctionnel clair. Le second chapitre du manuscrit utilise l'hypothèse des groupes émergents, afin de faire ça via une procédure objective et testable. Ce travail combine un jeu de données d'abondance de macroinvertébrés benthiques issu de l'estuaire de la Rance et une matrice de traits biologiques qui décrit le rôle de 240 espèces dans 7 mécanismes généraux d'assemblage des communautés. L'agrégation en 20 groupes fonctionnels est testée face aux postulats de l'hypothèse des groupes émergents. Les résultats généralement positifs supportent la capacité du groupement à reproduire la diversité fonctionnelle dans l'estuaire de la Rance. Un regard rapide sur les groupes renseigne également sur le rôle de quelques mécanismes dans le contrôle des communautés benthiques.

Le manque de connaissances dans l'attribution des relations entre les composantes fonctionnelles dérivées précédemment reste important. Le troisième chapitre du manuscrit s'inscrit dans ce besoin, basé sur des théories écologiques qui prévoient l'existence de trade-offs fonctionnels opérant à grande et petite échelle. Les premiers représentent des processus de type filtre environnemental, alors que les deuxièmes impliquent des trade-offs dans les traits d'histoire de vie. Les associations de traits observées semblent en accord avec ces prédictions, appuyant la capacité de ces processus à façonner les communautés benthiques de l'estuaire de la Rance. Dans un premier temps, des éléments de théorie écologique sont associés à des dires d'experts et incorporées dans 2 modèles qualitatifs des 20 groupes fonctionnels. La stabilité de ces modèles illustre leur potentiel à constituer une représentation plausible du monde naturel. Leur structure pourrait offrir des indices sur la direction potentiellement prise par le système en réponse à des perturbations.

Malgré l'intérêt du développement et de l'analyse de modèles qualitatifs, le but d'étudier la dynamique et le comportement spatialement explicite de la biodiversité ne peut être atteint que par un modèle avec ces mêmes caractéristiques. Le quatrième chapitre du manuscrit présente l'architecture d'un modèle individu-centré, en mettant l'accent sur le transfert des règles d'interactions des modèles qualitatifs vers un cadre dynamique et spatialement explicite. C'est la première version d'un modèle qui permet le changement d'échelle du niveau de l'individu vers celui de l'estuaire de la Rance. L'analyse de sensibilité des résultats de ce modèle permet d'identifier les processus clés qui gouvernent la dynamique spatiale et temporelle de la biodiversité benthique. Ces résultats sont discutés du point de vue d'un cadre générique de modélisation et de son applicabilité à d'autres sites pour évaluer le fonctionnement et la réponse des écosystèmes benthiques à des perturbations.

Extended abstract

Benthic macroinvertebrates are part of a complex network of interactions with their abiotic environment, their resources and with each other. The spatial and temporal scales of the processes that form the basis for these interactions have traditionally restricted their empirical study through the development of statistical models. Mechanistic models, being free of logistical limitations, offer an alternative tool for the study of potential community assembly mechanisms. Their development is, however, restricted by a lack of knowledge on the mechanisms that structure benthic communities. In the context of this thesis, the first chapter of the manuscript attempts a review of the statistical and mechanistic modelling tools that have been applied to marine benthic macroinvertebrates. The objective is to identify a technique that would allow the study of the dynamic behaviour of benthic biodiversity in a spatially explicit way based on existing datasets.

The implementation of a mechanistic modelling framework seems fitting, but it requires the derivation of a limited number of model entities with a clear functional role. The second chapter of the manuscript employs the emergent group hypothesis in order to do that in a way that is objective and testable. It combines an abundance dataset of benthic macroinvertebrate species from the Rance estuary collected in 1995 with a matrix of biological traits that describe the role of 240 species in 7 general community assembly mechanisms. The resulting aggregation into 20 functional groups is tested against the assumptions of the emergent group hypothesis. The generally positive results support the ability of the grouping to represent functional diversity in the Rance estuary. A first look at the emergent groups also provides some insight into the potential role of a few general mechanisms in shaping benthic communities.

The lack of quantitative knowledge for the attribution of relationships among the previously derived functional components is still important. The third chapter of the manuscript addresses this issue based on ecological theories that predict the existence of functional trade-offs operating at both large and small spatial scales. The former represent processes of environmental filtering, while the latter involve trade-offs with respect to life history characteristics. Observed trait associations appear to agree with these predictions, in support of the potential of the respective processes to shape benthic communities in the Rance estuary. In a first inception of the system, elements of ecological theory and expert knowledge are incorporated in the form of general rules of interaction into 2 qualitative models of the 20 functional groups. The general stability of these models illustrates their potential to constitute a plausible representation of the natural world. Their structure could offer clues to the direction that the system might take in response to perturbations.

In spite of the interest in developing and analysing qualitative mathematical models, the goal of studying the dynamic and spatially explicit behaviour of benthic biodiversity can only be reached by a model with the same characteristics. The fourth chapter of the manuscript presents the architecture of an individual-based model, primarily transferring the rules of interaction from the qualitative models to a dynamic and spatially explicit framework. It is the first version of a model that allows the transition from the level of individuals to that of the Rance estuary. The sensitivity analysis of the model can identify the key processes controlling the spatial and temporal behaviour of benthic biodiversity. These results are discussed in the context of the development of a general modelling framework and its transferability to other sites with the goal of assessing the functioning and potential response of benthic ecosystems to perturbations.

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Chapter I: Introduction

I.1 Quantitative models of benthic biodiversity

Biological communities, at the interface between species populations and ecosystems, are linked to some of the greatest challenges facing ecologists today (Sutherland et al., 2013). Their study in marine systems of benthic macroinvertebrates has traditionally relied on the output of observational or experimental research aimed at revealing the drivers of biodiversity (Klok, 2009). The complexity of the processes involved and the spatial and temporal scales at which they typically take place have set a limit to their empirical investigation and the potential to predict future biodiversity patterns (Cardinale et al., 2012). These limitations have made the creation of quantitative models essential for the development and evaluation of ecological theories, along with their synthesis toward the reliable prediction of the state of marine systems dominated by benthic macroinvertebrates (Constable, 1999).

I.1.1 Overview of modelling approaches

Modelling techniques can be primarily differentiated on the basis of their underlying assumptions and the generated output. Both elements are characterised by a set of basic properties. Central among them is their level of biological organisation, whether that is individual, population, community or ecosystem. Typically, a model constitutes a transition from assumptions made at a lower level to output generated at a higher level of biological organisation. This process involves additional properties of model assumptions and output, most notably their scales with respect to space and time. This up-scaling can be achieved in the context of a model through various methodological frameworks. Quantitative models can, therefore, be distinguished on the basis of the level of biological organisation and the spatiotemporal scales of their assumptions and output, along with the modelling methods that allow a transition from the one to the other (Fig. I.1).

Species distribution models (SDMs) are typically developed for key members of benthic communities. They are based on the concept of niche, which describes the environmental requirements of a species' individuals (Hutchinson, 1957) and can be considered to include elements of both abiotic and biotic nature (Araújo and Guisan, 2006). Observed associations between environmental variables and the distribution of organisms are assumed to be a demonstration of these requirements (Austin, 1985). Various tools can be employed to quantify an organism's niche within gradients of environmental conditions (ter Braak and Prentice, 2004). This knowledge can be then combined with information on the concomitant or distinct distribution of the same conditions, interpolating or extrapolating, respectively, the distribution of a species' populations in space or time (Guisan and Zimmermann, 2000).

The various SDMs that have been developed for the marine benthos mostly differ with respect to the tools employed for the quantification of the species' niche. In order to predict the occurrence probability of macrofauna species from a set of abiotic variables in the North Sea, Reiss et al. (2011) used 9 different SDM methods. Statistical approaches, including generalised linear models (GLM), multivariate adaptive regression splines (MARS), random forests (RF), bioclimatic envelope (BIOCLIM) and maximum entropy models (MAXENT), were applied alongside machine learning approaches, including genetic algorithms for rule-set prediction (GARP) and support vector machines (SVM), as well as generalised boosting models (GBM) and mixture discriminant analysis (MDA) that combine statistics with machine learning. The performance of most models was good but not constant across species while their output differed markedly.

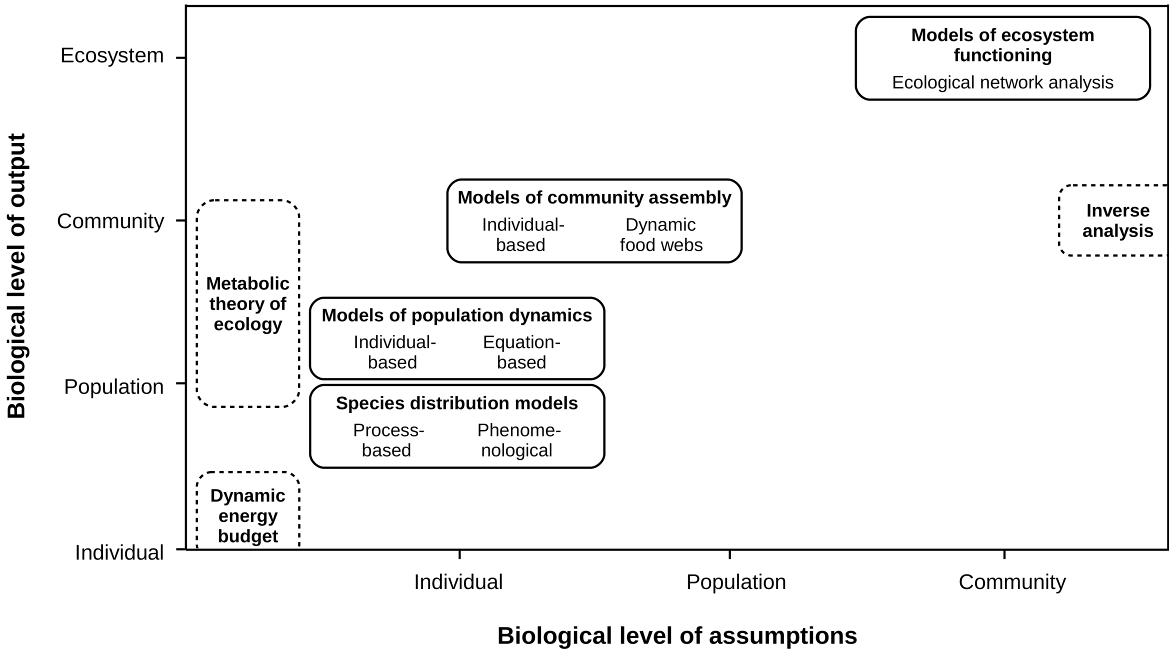

Fig. I.1 General approaches for quantitative modelling of benthic biodiversity, positioned according to the level of biological organisation of their assumptions and output. The dashed lines indicate frameworks complimenting the main modelling approaches, which are enclosed by solid lines. See text for details

The same conclusion was reached by Bučas et al. (2013), who used generalised additive models (GAM), MARS, RF and MAXENT to predict the occurrence and abundance of benthic species in the Baltic Sea. Their study demonstrates the dependence of statistical modelling approaches on the quality of the available data. Models that are based on machine learning are generally more efficient at deriving relationships between environmental variables and species distribution from heterogeneous data sets. However, the black-box nature of these models can put the causality of relationships into question and limit the interpretability of their results. All these approaches are based on correlations and do not explicitly represent important community assembly mechanisms. This can limit their predictive ability in novel or non-equilibrium contexts and does not help advance understanding of biodiversity drivers (Kearney and Porter, 2009).

The limitations of correlative SDMs have prompted the explicit representation of ecophysiological processes through models whose assumptions are made at the sub-individual level. The law of energy conservation allows the mechanistic derivation of an organism's niche from individual bioenergetics along with data of abiotic conditions and food supply. For example, Savina and Ménesguen (2007) combined a biogeochemical model of the water column with a bivalve growth model in order to calculate the organism's scope for growth, then used this quantity to study the bivalve's spatial distribution in the English Channel. The main drawback of such approaches lies in the need to develop a bioenergetics model for each species, often with case-specific functional forms and parameters. In a similar study, Le Goff et al. (2017) used dynamic energy budget theory for a more generic representation of individual bioenergetics.

Models of population dynamics aim to recreate the evolution of species abundance within ecological time scales. Much like SDMs, their output is based on assumptions about the behaviour of individual organisms or the metabolic processes that control individual behaviour. These assumptions can be expressed in the form of rates representing average characteristics of a population. The reproduction of population dynamics is achieved through the use of general difference or differential equations, whose parameters describe species-specific demographic rates (Yodzis and Innes, 1992). The represented population is usually not homogeneous, but structured on the basis of age or size, while individual variability can also be added to the model's parameters. Ananthasubramaniam et al. (2010) studied the stabilising effect of stochastic variability added to the growth rate of their size-structured model of water flea population dynamics.

Various processes affecting population dynamics can be formulated mathematically and included in equation-based models. For example, Roughgarden et al. (1985) represented the settlement of larvae in their age-structured model of barnacle population dynamics. Larval dispersal, a particularly important aspect of the recruitment of benthic macroinvertebrates, has also been the focus of such models. They typically represent it in a spatially implicit manner, by modelling distinct populations of a species as a set of meta-populations linked by the dispersal of planktonic larvae. Quinn et al. (1993) built a meta-population model of a sea urchin, to reveal the importance of harvest refugia for the sustainable exploitation of its populations. Whitlatch et al. (1998) further distinguished the colonization potential of three life stages of an annelid worm, in order to study the demographic consequences of patchy disturbance.

Published literature, experiments and statistical analysis of observations can be used separately or in combination in order to parameterise models of population dynamics. Still, data requirements and the need to mathematically formulate diverse ecological processes often restrict the development of equation-based models. Instead of this average representation, the behaviour of individuals can be modelled separately through simple algorithmic rules and then summed to recreate the dynamics of the entire population. Individual-based models (IBMs) are very flexible and can explicitly represent stochasticity, but are computationally demanding and less tractable than mathematical equations. Similar to mechanistic SDMs, the use of principles from the dynamic energy budget theory for the derivation of rules of individual behaviour can greatly facilitate the development of IBMs and increase their generality (Martin et al., 2012).

Models of community assembly reproduce important community assembly mechanisms, in order to predict the abundance distribution of co-occurring organisms. Assumptions about the nature of these mechanisms are made at the level of individuals or populations and have been traditionally linked to one of two theoretical frameworks. Niche theory is based on differences in the environmental requirements of organisms and their impact on the environment (Leibold, 1995), while neutral theory assumes that all members of a community are functionally equivalent (Hubbell, 1979). The two frameworks were initially considered to be mutually exclusive, but it is now clear that both niche and neutral processes contribute to the assembly of biological communities (Leibold and McPeek, 2006). The relative importance of stochastic vs. deterministic processes remains a central question of community ecology (Sutherland et al., 2013).

The assumption of trophic niche differences has dominated benthic ecological research and has given rise to some of the most widely applied modelling approaches. Food web models quantify trophic interactions among members of a community in the form of interaction strengths. These quantities can be compiled into a community matrix, whose analysis with tools of matrix algebra allows projections of the community's steady state abundance distribution (Levins, 1968). Alternatively, one can abandon the tedious quest for interaction strengths and represent only the sign and direction of trophic interactions (Puccia and Levins, 1985). This qualitative approach focuses on the structure of the food web and its link to basic properties of the system and has proved well-suited to poorly studied marine benthos. For example, Ortiz and Wolff (2002a) applied it to a benthic system in Chile in order to inform its management strategy.

Much more commonly, interaction strengths are incorporated in systems of partial differential equations that reproduce the population dynamics of the community members. The predictive ability of such approaches has made them very popular, particularly for the management of marine fisheries. This has led to the development of dedicated modelling environments, most notably Ecopath with Ecosim (EwE) (Walters et al., 1997). Dynamic simulations performed with EwE are based on a mass-balanced snapshot of the system's trophic structure, represented at the level of species or functional groups. In EwE models of fisheries, marine benthos has been at best represented by a few functional groups. On the other hand, Ortiz and Wolff (2002b) included 23 species and functional groups in their benthic EwE model. Ecospace, the spatially explicit version of EwE, can additionally simulate meta-population dynamics (Walters et al., 1999).

Just like the models of population dynamics that form their basis, dynamic food web models need vast amounts of data and biological knowledge in order to get fully determined. Time series of community composition could be used to statistically infer parameter values that cannot be derived experimentally (Turchin and Taylor, 1992), but most observations comprise only snapshots of the investigated systems. Brey (2010) used artificial neural networks to estimate respiration rates of benthic macroinvertebrates from their biological characteristics and environmental conditions. The use of ecological theories has also shown great potential at specifying community properties. Optimal foraging theory has efficiently predicted trophic structure (Petchey et al., 2008), while physiological allometries from the metabolic theory of ecology have been successful at constraining the parameter space of food web models (Hudson and Reuman, 2013).

Models of biological communities can also take the form of IBMs and OSMOSE is another example that is primarily targeted at the management of fisheries (Shin and Cury, 2001). This spatially explicit framework models the behaviour of age- and size-structured groups, whose diets emerge from size-based rules and their relative position in space and time. The computational demands of community IBMs can be prohibitive to the inclusion of numerous assembly mechanisms. Instead, models of distinct processes can be loosely combined, as has been done with the use of Bayesian networks (Borsuk et al., 2004), or firmly integrated into hybrid models (Gallien et al., 2010). The former may lack for predictive ability, while the amounts of data and knowledge that are typically required by the latter can limit hybrid models to the representation of only well-studied species or the prediction of coarse diversity patterns (Cheung et al., 2008).

Models of ecosystem functioning assume a constant community composition or even a steady state with respect to the abundance distribution of the community members. They represent elements of the ecosystem that are external to benthic communities but can affect the system's functioning. This term refers to "some state or trajectory of the system under consideration and to the sum of those processes that sustain the system" (Jax, 2005). Since the focus is placed on function, the representation of functional groups is usually preferred over taxonomic classifications. Flows of matter and energy, representing trophic relationships among these functional components, are assumed to account for the numerous processes that influence the structure of the system. Information about stocks and flows can be collected from the field, estimated from experiments or derived from distinct models of the system's components.

The Ecopath modelling environment allows the development of the static mass-balanced food webs that form the basis of EwE models (Christensen and Pauly, 1992). Its combination with methods of ecological network analysis can offer insights into many important properties of a system (Ulanowicz, 2004). Ecopath has significantly contributed to the adoption of an ecosystem approach to fisheries that includes benthic communities (Pauly et al., 2000) but it has also been separately applied to the latter to reveal aspects of their functioning (Ortiz and Wolff, 2002c). The common lack of data and knowledge for the marine benthos has often necessitated the application of inverse analysis for the estimation of unknown quantities (Vézina and Platt, 1988). This method has been successfully applied to benthic systems from the level of intertidal mudflats (Leguerrier et al., 2003) to that of sea basins (Garcia et al., 2011).

I.1.2 Modelling biotic interactions

The causality of the correlations that form the basis for statistical and machine learning models presents a major challenge to the key issue of representing biotic interactions in a rapidly changing world (Guisan and Thuiller, 2005). This is usually tackled by including predictor variables that describe the impact of organisms on their environment as a component of their niche. Yet, in most data sets the effects of abiotic conditions are confounded with those of community members, making inferences about the relative importance of jointly fitted predictors problematic, especially in cases where novel combinations of organisms are likely to occur (Elith and Leathwick, 2009). Mechanistic models have the potential to address this issue by explicitly representing biotic interactions (Kearney and Porter, 2009), but they have been characterised by a disproportionate emphasis on trophic networks (Ings et al., 2009).

The inclusion of non-trophic interactions in mechanistic models of community assembly is particularly important for marine benthic macroinvertebrates. 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 rendered classic groupings of macrofauna irrelevant (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.

Modelling of benthic macroinvertebrate communities has been largely based on the assumption that individual growth is limited by space in hard substrates and food in soft ones, in spite of evidence that supports a combined role of the two resources in shaping marine benthos (Svensson and Marshall, 2015; Tamaki et al., 2008). Apart from predation, marine benthic community models have accordingly focused on the representation of competitive interactions over space (Benedetti-Cecchi, 2000) and food (Cugier et al., 2010), with the notable addition of biogenic habitat modification (Pearson, 2001). Most other biotic interactions have, however, been modelled in isolation, with the goal of answering specific research questions. Their combination into ecosystem-level models that mechanistically link the components of biodiversity has only been attempted within qualitative modelling frameworks (Marzloff et al., 2011).

The use of biological traits to embed biotic interactions in the organisms' abiotic environment holds great promise for the combination of distinct areas of research and their modelling tools (McGill et al., 2006). Trait-based representation of interaction networks has been indicated as a "fruitful avenue" for future models of ecological systems (Ings et al., 2009). Biological traits have been extensively employed in the study of marine benthic communities to, primarily, make the link between biodiversity and ecosystem functioning (Bremner, 2008) and, to a lesser extent, describe the emergence of biodiversity patterns (Rigolet et al., 2014). This is a field where individual-based modelling has shown great potential (DeAngelis and Mooij, 2005), by reproducing community assembly mechanisms, in order to predict the response of terrestrial plant (Boulangeat et al., 2014) and animal systems (Scherer et al., 2016) to environmental change.

I.1.3 A general framework for models of biodiversity

The provision of support by more or less hard surfaces is a feature of benthic communities with a profound impact on their structure and functioning. It is also a feature shared with terrestrial systems, which results in marine benthos having a more similar trophic structure with them than with pelagic communities (Brose et al., 2006). Benthic macroinvertebrates and terrestrial vegetation are additionally characterised by competition for basic resources often taking the form of competition for a limited amount of space. This begins with the organisms' initial settlement and continues, sometimes through shifts in competitive hierarchy, over their life cycle. Technical issues involved in the development of marine benthic biodiversity models have likely been already addressed in the terrestrial environment, either combined or in isolation, through different approaches that may vary in their potential to be transferred to the marine benthos.

The framework developed by Boulangeat et al. (2012; 2014) for models of terrestrial plant structure and diversity appears to be well suited to benthic macrofauna systems. It specifically addresses the need for a dynamic and spatially explicit modelling approach, which represents a system's primary functional components in interactions and is able to account for the main drivers of biodiversity. The use of biological traits allows the representation of the organisms' role in various community assembly mechanisms. Theoretical and empirical knowledge on these mechanisms can be flexibly synthesised through individual-based modelling. An issue that could hinder the transfer of this framework to the marine benthos is the level of understanding with respect to the processes that shape marine benthic communities and the quality of the available information regarding biological traits and observed patterns of biodiversity.

The development of models on the basis of general ecological principles can facilitate the transfer of conceptual and methodological knowledge across disciplines. It could allow the representation of systems and processes whose modelling has been restricted by relatively low levels of empirical quantification. Still, readily available datasets remain important, from the definition of a model's entities and the mathematical or algorithmic formulation of its interactions, to its analysis and validation. Models of community assembly, whose output is the most relevant for the prediction of biodiversity patterns, typically make assumptions at the level of populations. Information on species abundance is, therefore, essential to quantitative models of biodiversity, along with information on the abiotic and biotic drivers of abundance patterns. Models that make assumptions at the individual level would also benefit from data on specific biological traits.

For an effective use in models of community assembly, data of species abundance need to clearly illustrate the role of processes that shape marine benthic communities. Ecological theory could be employed when data is missing, at the same time increasing model generality, but risking a reduction of its realism. The diversity of the processes that helped form the observed abundance patterns would largely dictate the exploratory and predictive scope of the model. The extent and resolution of efforts to sample biodiversity and its main drivers should be able to reveal the influence of processes that often operate at distinct spatial and temporal scales. Biological trait information should adequately represent the complex role of organisms in these processes. These requirements to a great extent drove the process of selecting a marine benthic site on which a general framework for models of benthic biodiversity could be developed.

I.2 Modelling biodiversity in the Rance estuary

I.2.1 Objectives of the thesis

This study aims to develop a general modelling framework that is able to reproduce observed spatial and temporal patterns of benthic biodiversity. For this goal to be achieved, a system will first have to be aggregated in a functionally informative way. The components of this system representation will have to be connected in accordance with available knowledge about the processes that control benthic biodiversity. These processes could be driven by factors that are internal or external to benthic communities and could operate at various spatial and temporal scales. The explicit representation of the stochasticity of the modelled processes would increase the framework's realism along with its exploratory scope. The ultimate goal of this approach is the development of modelling tools that will allow the generation of reliable predictions about future patterns of biodiversity, especially in response to projected scenarios of environmental change.

Before reliable predictions can be made, the analysis of the generated framework can address fundamental issues of ecological research, reducing the need for costly or impractical experimental work. These issues include the minimum level of aggregation and complexity that is required for an adequate representation of a system's functioning. The relative importance of different biodiversity drivers could be evaluated, along with the degree to which communities are shaped by internal vs. external or deterministic vs. stochastic processes. Models of different spatiotemporal scales can reveal the level at which a system should be averaged to efficiently represent its impact on higher-level systems and the way it is, in turn, affected by them. Answering these questions requires a degree of model realism that can only be achieved by developing the framework on the basis of data collected from a natural system; in this case, the Rance estuary.

I.2.2 General characteristics of the study site

The Rance estuary is situated in the southern part of the English Channel, in Brittany, France (Fig. I.2). It is a ria-type estuary, flowing into the sea between Dinard and St-Malo. The estuary is 20 km long and has a surface of 22 km^2. Maximum water depth is 17 m at low tide, but the main part is 5–6 m deep. Two areas of different salinity regimes can be identified: the marine reservoir, with salinities constantly higher than 30, and the area upstream of Port St-Jean with brackish water of varying salinity. The drainage basin is dominated by granite geology, except for some calcareous sections downstream. The sea floor immediately adjacent to the estuary is mainly exposed bedrock, sand and gravel. The average annual temperature in the area is 9.5°C and the rainfall 750 mm, while the average river discharge is 7 m^3/s. Intensive farming and agro-industrial activities comprise the main land uses in the drainage basin (Bernez et al., 2004).

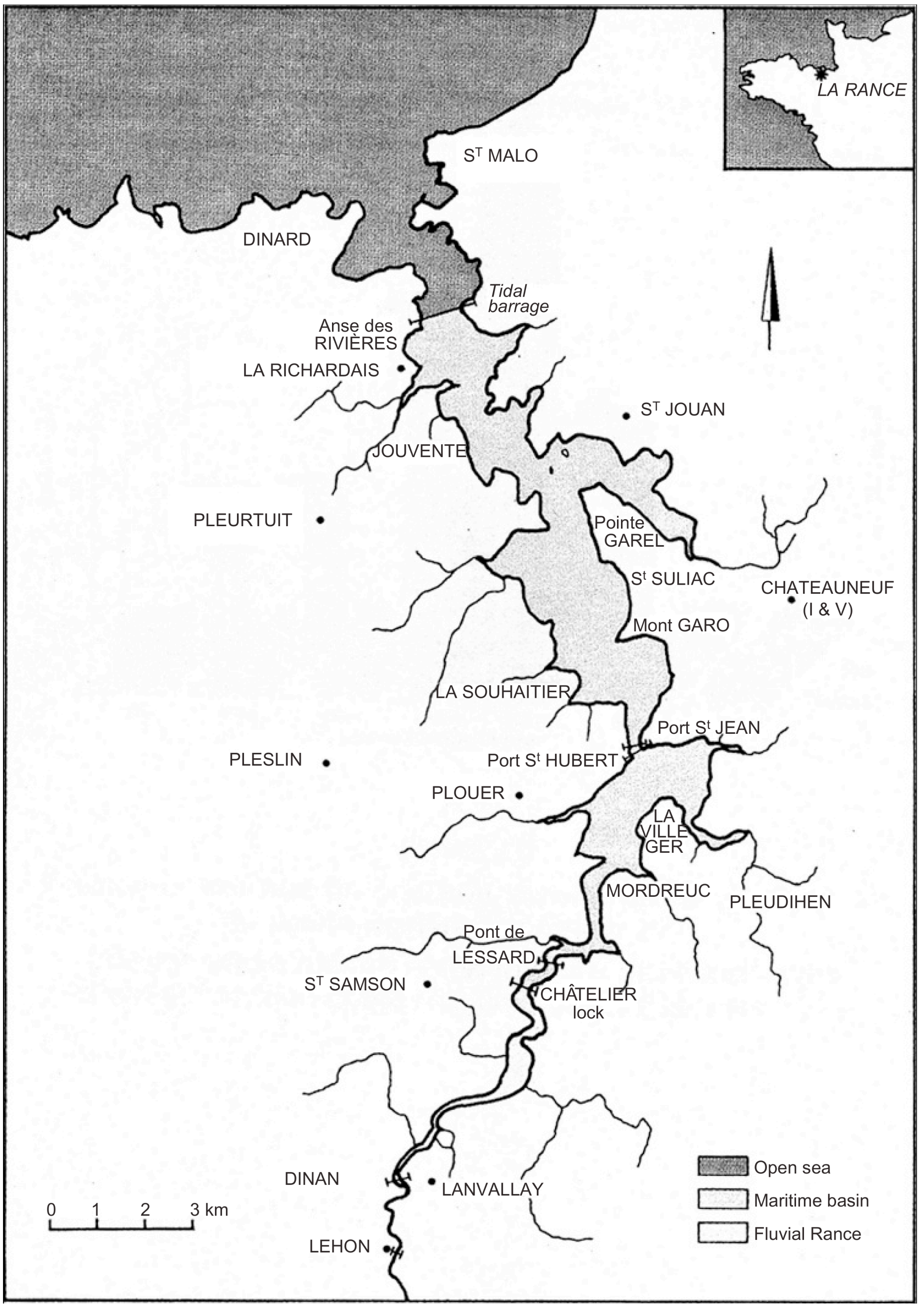

Fig. I.2 Map of the Rance estuary basin within Brittany, France (from Kirby and Retière (2009))

The most distinctive characteristic of the Rance estuary and one of the reasons for its selection as the site of this study is the presence of a tidal power plant close to the estuary entrance. The structure, standing on the granite bed of the estuary over a length of 750 m, comprises, from the left to the right bank, a lock, the actual power plant with 24 bulb sets, a riprap general dam section and a sluiceway dam section with six gates. The bulb sets can operate as pumps from the sea to the storage basin, turbines in either flow direction or orifices for maximisation of water input or discharge. Operation is planned with the goal of maximising profit under variable tides and energy costs (Andre, 1978). The power plant was built between 1963 and 1966 by blocking the entrance of the estuary. During this period river flow was discharged, but the estuary was transformed into a non-tidal, more or less stagnant freshwater system (Kirby and Retière, 2009).

The estuary was re-opened in 1966, with its hydrodynamic regime significantly altered due to the power plant's operation (Fig. I.3). Mean water level was raised by 2.5 m, while the tidal range was reduced by 40% and the water exchanged with the sea by 30%. Tidal range is now 7–8 m on springs and 2.5 m on neaps. The brackish section of the estuary was reduced, moving its junction with the marine reservoir 5 km upstream. Similarly, the intertidal zone corresponds today to 50% of the total surface of the estuary, compared to 70% before 1963. The tidal current regime has become more moderate and benign, except for the immediate vicinity of the power plant. Slack water periods have increased significantly, while turbidity has decreased to values that do not exceed 10 mg/l. The strength of ebb tides has decreased to levels that do not suffice to evacuate sediment brought in by the rising tide (Kirby and Retière, 2009).

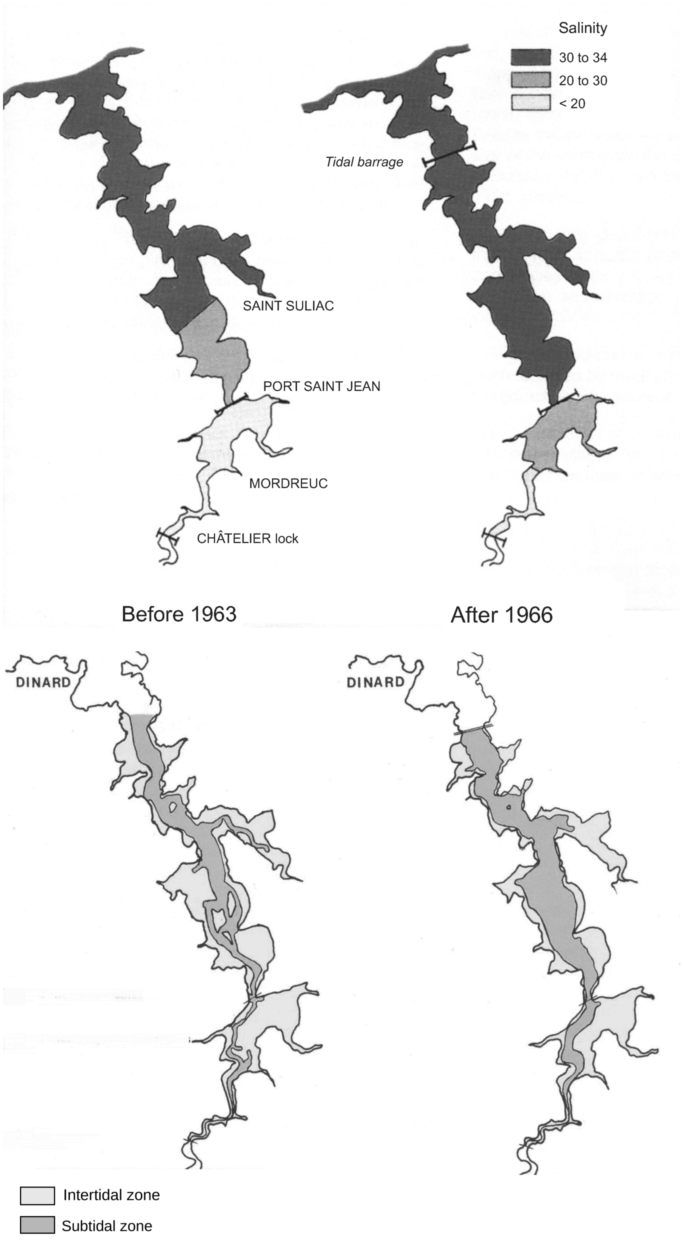

Fig. I.3 Distribution of salinity (upper panel) and extent of the intertidal and subtidal zones (lower panel) in the Rance estuary before (left) and after (right) the construction of the power plant (modified from Kirby and Retière (2009))

More or less detailed depictions of sediment distribution in the Rance estuary from 1883 to 1994 demonstrate the degree to which the riverbed has been altered by the operation of the power plant (Bonnot-Courtois, 1997) (Fig. I.4). Big sections of the former intertidal have been permanently submerged, thus increasing the diversity of the subtidal zone, which was previously dominated by clean sands. The mud content of the sediments has increased in both the subtidal and the intertidal. Increased siltation rates have turned large areas with mobile sands into much more hydraulically stable muddy sands or sandy muds. Strong currents from the gates and bulb sets have eroded parts of the riverbed, replacing sandbanks near the power plant with gravel. In general, particle size tends to decrease and mud content to increase from downstream to upstream of the estuary, with a similar trend observed from the central channel to the banks.

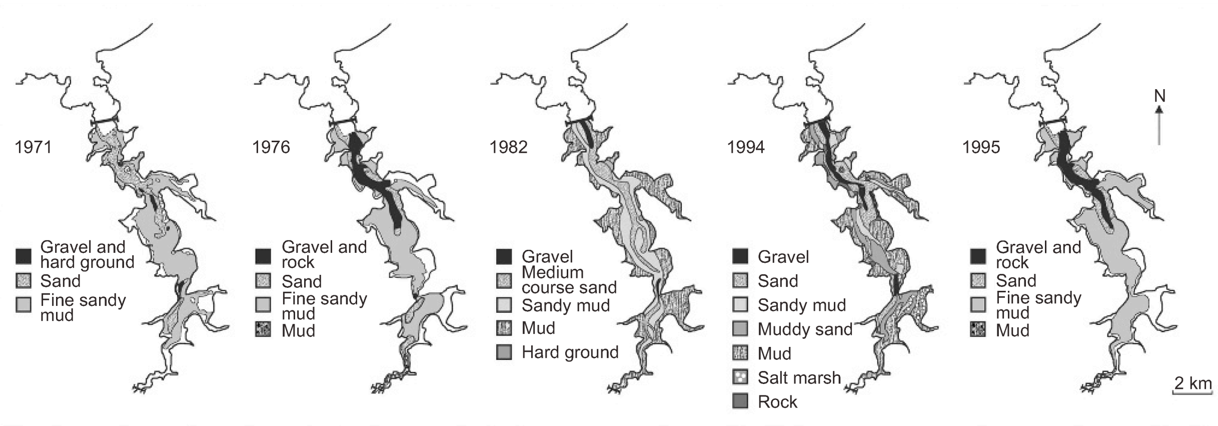

Fig. I.4 Distribution of substrate types in the Rance estuary within 30 years from the construction of the power plant (from Kirby and Retière (2009))

Very little is known about benthic biodiversity patterns before and immediately after the construction of the power plant. It is clear that most marine species were eliminated while the estuary was blocked, getting only partially replaced by freshwater organisms. After the estuary was re-opened, macrobenthic community composition was sampled semi-quantitatively in 1971 and quantitatively in 1976 (Retière, 1979) and 1995 (Desroy, 1998). The last sampling was spatially more comprehensive, while effort was made to render it repetitive with respect to stations previously sampled. These surveys comprise numerous samples of the upper sediment layers, each within an area in the order of 10^{-1} m^2, aimed at capturing a snapshot of the spatial diversity of macrobenthos throughout the system. Samples contain information on the abundance of macroinvertebrate species along with the water depth and sediment type of each station.

It appears that species richness increased quickly after 1966 through the estuary's re-colonization by marine organisms. Within ten years, it was more or less stable around levels similar to those observed before 1963. Higher diversity of the subtidal environment has led to increased biodiversity and abundance in this previously impoverished zone. The introduction of the slipper limpet *Crepidula fornicata* during the 1970's has also contributed by increasing the heterogeneity of the substrate. The carrying capacity of the intertidal zone has significantly increased, probably due to the stabilization of the sediment. Benthic productivity appears to have increased in general, and now stands higher than adjacent estuaries. A rise in nutrient runoff is only partly responsible for that, but has led to higher abundances of green algae. Fish and bird communities have, likewise, benefited from the higher productivity of the system (Kirby and Retière, 2009).

I.2.3 Development of general modelling framework

The abrupt transformation of the Rance estuary into a freshwater system and its gradual transition to its current state constitute a unique natural experiment. The whole process has been the subject of continuous research, with the goal of assessing the impact of the construction and operation of the tidal power plant on the system's biological commnunities. The estuary appears to have returned to a more or less natural state through a re-colonization process that is particularly relevant for marine systems recovering from disturbance. A detailed understanding of the processes involved would help anticipate and direct the response of benthic communities to many types of potential perturbation. The fact that equilibrium has been reached with respect to species richness could indicate that the system is also stabilising with respect to species abundance, but the changes caused by the introduction of the slipper limpet suggest otherwise.

The main reason for the selection of the Rance estuary as the site of this study is the repeated sampling of its macroinvertebrate communities. With 240 benthic species observed in 1995, the Rance estuary is neither extremely rich nor poor, offering a reasonable background for the development of the modelling approach. The extent and resolution of each system snapshot is expected to efficiently capture the environment's control over community composition. The assessment of this role is facilitated by the availability of information of water depth and sediment type along with expert knowledge on the system's species and functioning. Data of biological traits, especially intra-specific trait variability, are sure to be lacking at least for some of the species. Still, the western coast of Europe and the English Channel, in particular, are among the best studied regions regarding their benthos, with collected data being easily accessible.

Considerable variation in species abundance can be observed both within and among the stations sampled in 1995. The former can be explained either by stochastic processes or through niche apportionment, but it is difficult to distinguish between the two (McGill et al., 2007). Part of the latter shows spatial structure, which is only partly explained by environmental variables. The predictive power of these variables with respect to community composition appears to be very limited. The function of benthic communities would be better illustrated by information on the dynamics of species abundance and the distribution of organisms within the samples, but such data is rarely collected in samplings of this scale. What cannot be explained is often uniformly treated as noise. The assessment of the role of stochastic and deterministic processes in shaping communities remains a key challenge of ecological research (Sutherland et al., 2013).

The benthos of the Rance estuary appears not to be limited by the supply of food, while the majority of its recruits are expected to originate from its own populations. Other factors, such as extremely cold winters or wave action, are expected to have an impact that may vary from local to global but is difficult to quantify. The statistical analysis of system snapshots (Desroy, 1998) can reveal the role of the abiotic environment in shaping benthic communities. A more detailed investigation of important processes, such as recruitment (Desroy and Retière, 2001) and predation (Desroy and Retière, 2003), can enhance the mechanistic understanding of community assembly. Still, the complexity of ecological systems often restricts the predictive potential of large-scale observational and small-scale experimental studies. A synthesis of available knowledge within a quantitative framework is essential to predict patterns of biodiversity.

I.2.4 Work plan

The first step of the framework (Fig. I.5) consists in defining the principal functional components of the system through a rigorous and testable procedure (Chapter II). Next, the causal relationships of these components with their environment and with each other are specified through a systematic investigation of traits–environment associations. The simplest representation of these relationships can be produced by qualitative models, which focus on network structure and its impact on fundamental properties of the system (Chapter III). Predictions about the response of the system's components to perturbations can also be generated, but their study requires the comparison of model predictions with observed patterns of community composition (Annex A). Finally, processes that operate at distinct spatiotemporal scales are combined in dynamic and spatially explicit agent-based models of benthic biodiversity (Chapter IV).

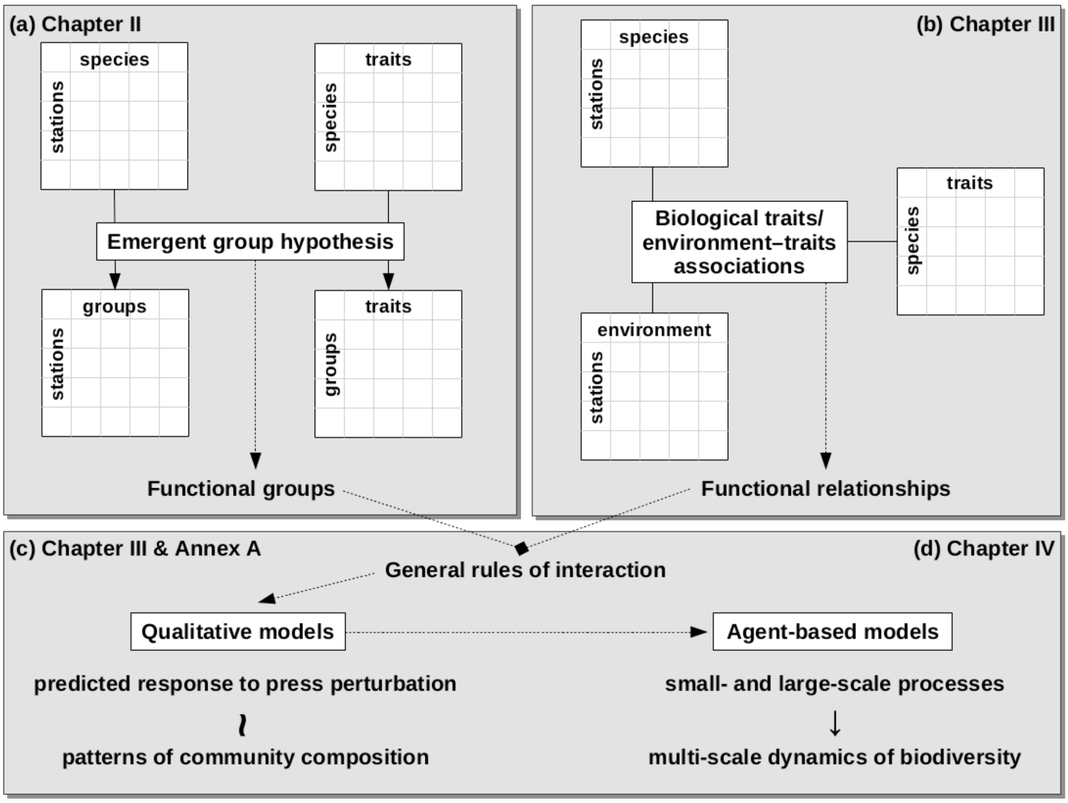

Fig. I.5 Schematic representation of the four main components of the modelling approach and the thesis sections where they are presented. The dotted lines show the central direction that was followed in the study. a) Data of species abundance in different stations and information on the species' traits led to the emergence of functional groups with their own trait values. b) Observed associations among traits and between traits and abiotic conditions allowed the derivation of a set of functional relationships. c) These relationships were expressed in the form of general rules of interaction among the functional groups and were incorporated in qualitative models of benthic communities. A novel approach was employed for the comparison of predicted responses to press perturbations with observed patterns of community composition. d) Agent-based modelling allowed the representation of both small- and large-scale processes in a dynamic and spatially explicit model of benthic biodiversity

I.3 References

Ananthasubramaniam, B., Nisbet, R.M., Nelson, W.A., McCauley, E., Gurney, W.S.C., 2010. Stochastic growth reduces population fluctuations in Daphnia–algal systems. Ecology 92, 362-372.

Andre, H., 1978. Ten years of experience at the "La Rance" tidal power plant. Ocean Manage 4, 165-178.

Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. J Biogeogr 33, 1677-1688.

Austin, M.P., 1985. Continuum Concept, Ordination Methods, and Niche Theory. Annu Rev Ecol Syst 16, 39-61.

Benedetti-Cecchi, L., 2000. Predicting direct and indirect interactions during succession in a mid‐littoral rocky shore assemblage. Ecol Monogr 70, 45-72.

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.

Bernez, I., Daniel, H., Haury, J., Ferreira, M.T., 2004. Combined effects of environmental factors and regulation on macrophyte vegetation along three rivers in western France. River Res Appl 20, 43-59.

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.

Borsuk, M.E., Stow, C.A., Reckhow, K.H., 2004. A Bayesian network of eutrophication models for synthesis, prediction, and uncertainty analysis. Ecol Model 173, 219-239.

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.

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. J Exp Mar Biol Ecol 366, 37-47.

Brey, T., 2010. An empirical model for estimating aquatic invertebrate respiration. Methods Ecol Evol 1, 92-101.

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., 2006. Consumer-resource body-size relationships in natural food webs. Ecology 87, 2411-2417.

Bučas, M., Bergström, U., Downie, A.-L., Sundblad, G., Gullström, M., von Numers, M., Šiaulys, A., Lindegarth, M., 2013. Empirical modelling of benthic species distribution, abundance, and diversity in the Baltic Sea: evaluating the scope for predictive mapping using different modelling approaches. ICES J Mar Sci 70, 1233-1243.

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.

Cheung, W.W., Lam, V.W., Pauly, D., 2008. Dynamic bioclimate envelope model to predict climate-induced changes in distribution of marine fishes and invertebrates. Modelling present and climate-shifted distributions of marine fishes and invertebrates. Fisheries Centre Research Reports 16, 5-50.

Christensen, V., Pauly, D., 1992. ECOPATH II — a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model 61, 169-185.

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.

Cugier, P., Struski, C., Blanchard, M., Mazurié, J., Pouvreau, S., Olivier, F., Trigui, J.R., Thiébaut, E., 2010. Assessing the role of benthic filter feeders on phytoplankton production in a shellfish farming site: Mont Saint Michel Bay, France. J Marine Syst 82, 21-34.

DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. Annu Rev Ecol Evol S 36, 147-168.

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 dissertation, Université de Rennes 1, Rennes, France.

Desroy, N., Retière, C., 2001. Long-term changes in muddy fine sand community of the Rance Basin: role of recruitment. J Mar Biol Assoc UK 81, 553-564.

Desroy, N., Retière, C., 2003. The influence of structure and dynamics of infaunal predator populations on predatory activity: the example of *Nephtys hombergii*. Estuar Coast Shelf S 58, 445-453.

Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu Rev Ecol Evol S 40, 677-697.

Gallien, L., Münkemüller, T., Albert, C.H., Boulangeat, I., Thuiller, W., 2010. Predicting potential distributions of invasive species: where to go from here? Divers Distrib 16, 331-342.

Garcia, C., Chardy, P., Dewarumez, J.-M., Dauvin, J.-C., 2011. Assessment of benthic ecosystem functioning through trophic web modelling: the example of the eastern basin of the English Channel and the Southern Bight of the North Sea. Mar Ecol 32, 72-86.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol Lett 8, 993-1009.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol Model 135, 147-186.

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

Hubbell, S.P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203, 1299-1309.

Hudson, L.N., Reuman, D.C., 2013. A cure for the plague of parameters: constraining models of complex population dynamics with allometries. Proc Biol Sci 280, 20131901.

Hutchinson, G.E., 1957. Concluding Remarks. Cold Spring Harb Sym 22, 415-427.

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.

Jax, K., 2005. Function and “functioning” in ecology: what does it mean? Oikos 111, 641-648.

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

Kirby, R., Retière, C., 2009. Comparing environmental effects of Rance and Severn barrages. P I Civil Eng-Mar En 162, 11-26.

Klok, C., 2009. Model instruments for marine biodiversity policy. A quick scan. Statutory Research Tasks Unit for Nature & the Environment, Wageningen, Netherlands.

Le Goff, C., Lavaud, R., Cugier, P., Jean, F., Flye-Sainte-Marie, J., Foucher, E., Desroy, N., Fifas, S., Foveau, A., 2017. A coupled biophysical model for the distribution of the great scallop Pecten maximus in the English Channel. J Marine Syst 167, 55-67.

Leguerrier, D., Niquil, N., Boileau, N., Rzeznik, J., Sauriau, P.-G., Le Moine, O., Bacher, C., 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Mar Ecol Prog Ser 246, 17-37.

Leibold, M.A., 1995. The Niche Concept Revisited: Mechanistic Models and Community Context. Ecology 76, 1371-1382.

Leibold, M.A., McPeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399-1410.

Levins, R., 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, USA.

Martin, B.T., Zimmer, E.I., Grimm, V., Jager, T., 2012. Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation. Methods Ecol Evol 3, 445-449.

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.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol Evol 21, 178-185.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., White, E.P., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecol Lett 10, 995-1015.

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.

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

Ortiz, M., Wolff, M., 2002b. Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios. Ecol Model 148, 277-291.

Ortiz, M., Wolff, M., 2002c. Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and preliminary assessment of management strategies. J Exp Mar Biol Ecol 268, 205-235.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci 57, 697-706.

Pearson, T.H., 2001. Functional group ecology in soft-sediment marine benthos: The role of bioturbation. Oceanogr Mar Biol 39, 233-267.

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.

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

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

Quinn, J.F., Wing, S.R., Botsford, L.W., 1993. Harvest Refugia in Marine Invertebrate Fisheries: Models and Applications to the Red Sea Urchin, *Strongylocentrotus franciscanus*. Am Zool 33, 537-550.

Reiss, H., Cunze, S., König, K., Neumann, H., Kröncke, I., 2011. Species distribution modelling of marine benthos: a North Sea case study. Mar Ecol Prog Ser 442, 71-86.

Retière, C., 1979. Contribution à la connaissance des peuplements benthiques du golfe Normano-Breton. PhD dissertation, Université de Rennes 1, Rennes.

Rigolet, C., Dubois, S.F., Thiébaut, E., 2014. Benthic control freaks: Effects of the tubiculous amphipod Haploops nirae on the specific diversity and functional structure of benthic communities. J Sea Res 85, 413-427.

Roughgarden, J., Iwasa, Y., Baxter, C., 1985. Demographic Theory for an Open Marine Population with Space-Limited Recruitment. Ecology 66, 54-67.

Savina, M., Ménesguen, A., 2007. The growth of the banded carpet shell (Paphia rhomboïdes) in a contrasted region, the English Channel (Western Europe): A modelling study. Ecol Model 205, 39-51.

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.

Shin, Y.-J., Cury, P., 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquat Living Resour 14, 65-80.

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

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.

Tamaki, A., Nakaoka, A., Maekawa, H., Yamada, F., 2008. Spatial partitioning between species of the phytoplankton-feeding guild on an estuarine intertidal sand flat and its implication on habitat carrying capacity. Estuar Coast Shelf S 78, 727-738.

ter Braak, C.J., Prentice, I.C., 2004. A theory of gradient analysis. Adv Ecol Res 34, 235-282.

Turchin, P., Taylor, A.D., 1992. Complex Dynamics in Ecological Time Series. Ecology 73, 289-305.

Ulanowicz, R.E., 2004. Quantitative methods for ecological network analysis. Comput Biol Chem 28, 321-339.

Vézina, A.F., Platt, T., 1988. Food web dynamics in the ocean. 1. Best-estimates of flow networks using inverse methods. Mar Ecol Prog Ser 42, 269-287.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev Fish Biol Fisher 7, 139-172.

Walters, C., Pauly, D., Christensen, V., 1999. Ecospace: Prediction of Mesoscale Spatial Patterns in Trophic Relationships of Exploited Ecosystems, with Emphasis on the Impacts of Marine Protected Areas. Ecosystems 2, 539-554.

Whitlatch, R.B., Lohrer, A.M., Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., Zajac, R.N., 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. Proceedings of the 32nd European Marine Biology Symposium, 16–22 August, Lysekil, Sweden.

Yodzis, P., Innes, S., 1992. Body Size and Consumer-Resource Dynamics. Am Nat 139, 1151-1175.

Chapter II: Building functional groups of marine benthic macroinvertebrates on the basis of general community assembly mechanisms

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Abstract

The accurate reproduction of the spatial and temporal dynamics of marine benthic biodiversity requires the development of mechanistic models, based on the processes that shape macroinvertebrate communities. The modelled entities should, accordingly, be able to adequately represent the many functional roles that are performed by benthic organisms. With this goal in mind, we applied the emergent group hypothesis (EGH), which assumes functional equivalence within and functional divergence between groups of species. The first step of the grouping involved the selection of 14 biological traits that describe the role of benthic macroinvertebrates in 7 important community assembly mechanisms. A matrix of trait values for the 240 species that occurred in the Rance estuary (Brittany, France) in 1995 formed the basis for a hierarchical classification that generated 20 functional groups, each with its own trait values. The functional groups were first evaluated based on their ability to represent observed patterns of biodiversity. The two main assumptions of the EGH were then tested, by assessing the preservation of niche attributes among the groups and the neutrality of functional differences within them. The generally positive results give us confidence in the ability of the grouping to recreate functional diversity in the Rance estuary. A first look at the emergent groups provides insights into the potential role of community assembly mechanisms in shaping biodiversity patterns. Our next steps include the derivation of general rules of interaction and their incorporation, along with the functional groups, into mechanistic models of benthic biodiversity.

II.1 Introduction

Biological communities (i.e. sets of co-occurring species) are at the heart of some of the most challenging issues currently raised in the field of ecology. These issues include the degree to which communities are shaped by stochastic versus deterministic processes, the potential for species traits to predict the structure and dynamics of communities and the role of environmental variability in space and time (Sutherland et al., 2013). The elucidation of the mechanisms of community assembly would not only enhance our fundamental understanding of ecological processes. It is also expected to increase our ability to conserve biodiversity and ecosystem function.

Function here refers to the second of the meanings assigned to the term by Jax (2005). It is associated with questions, such as “how is the whole sustained” or “what do specific parts contribute to this”. Answering these questions is important, because we value the services provided by a functioning whole. Yet, in view of the current rate of environmental change and its potential impacts on biodiversity (Bellard et al., 2012), we cannot reliably answer them without first addressing the questions that Jax (2005) linked to the functioning of the specific parts, such as “which processes occur” or “how do organisms interact with each other and with their environment”.

The effort to answer these questions in the marine benthos has been dominated by statistical methods of multivariate analysis (Clarke, 1993; Legendre and Gauthier, 2014). These methods rely on data from temporal and/or spatial sampling schemes, aimed at capturing the species abundance patterns of a system’s macro-, meio- or microbenthic compartment. They often use correlations between environmental variables and community composition with the goal of explaining variations in the latter (ter Braak and Prentice, 2004). With the addition of tools for the analysis of spatial and temporal patterns (Dray et al., 2006; Blanchet et al., 2008) multivariate analysis has become a very efficient exploratory technique. However, its correlative nature, along with its difficulty to account for key ecological phenomena, has restricted its ability to reveal the role of community shaping processes (James and McCulloch, 1990).

In response to the limitations of statistical modelling, efforts have been made to adopt a more mechanistic approach, mostly in the form of dynamic food web models (Yodzis and Innes, 1992) and static trophic network analyses (Ulanowicz, 2004). The amounts of data and knowledge that are typically required by such approaches, along with issues of model complexity and tractability, have set a limit to the number of modelled entities. In spite of efforts to address these issues through the application of tools, such as Ecopath with Ecosim (Ortiz and Wolff, 2002) or the inverse method (Garcia et al., 2011), mechanistic models tend to lack the level of detail that is needed to account for the functioning of benthic communities. The host of biotic interactions that are responsible for shaping these systems is hardly limited to what can be represented by a food web (Menge, 1995). In spite of recent attempts to integrate non-trophic interactions into food web models (Kéfi et al., 2012), the majority of community assembly mechanisms are seldom included in models of marine benthos.

Trait-based approaches have been suggested as an alternative to food web models (Ings et al., 2009). Biological traits have been increasingly employed in the analysis of the functional composition of benthic communities (Bremner, 2008). The emergence of the concept of functional diversity has raised questions, such as “what types of traits”, “which traits” or “how many traits” should be considered. Petchey et al. (2006) argue that the answers depend on the scope of each study, emphasizing the potential for functional classifications of organisms to be nested and the need to treat each classification as a testable hypothesis. Bremner et al. (2006b) suggest including as many traits as possible in biological traits analyses, with recent studies following suit (e.g. Darr et al., 2014; Jimenez et al., 2016). Trait-based modelling approaches have, on the other hand, focused on the most studied processes in the marine benthos: feeding behaviour and substrate modification (Pearson, 2001). The representation of these mechanisms offers valuable information on the contribution of existing communities to the functioning of the system, but it provides very little insight into future trajectories following natural or anthropogenic environmental change.

A variety of ecological theories pertaining to environmental filtering, trophic interactions, resource partitioning, life history trade-offs and response to disturbance have been successfully employed to explain observations of benthic communities. They could be used to generate reliable predictions of benthic biodiversity, if they took the form of mathematical formulations linking a system’s primary functional components. The latter should be generated through a systematic and testable procedure and possess a clear role in various community assembly mechanisms. The framework developed by Boulangeat et al., (2012) for communities of terrestrial vegetation is particularly well-suited for this purpose. It employs the emergent group hypothesis (EGH), which assumes functional equivalence within (neutrality) and functional divergence between (niche differentiation) groups of species (Hérault, 2007). Its application is based on a matrix of species traits that represent their role in important community assembly mechanisms. Group emergence results from correlations among the traits, which are indicative of adaptive responses and evolutionary constraints (Lavorel et al., 1997).

The aggregation of ecosystems through the construction of functional groups is based on the concept of functional redundancy, which is central to theories relating biodiversity variations to ecosystem function (Rosenfeld, 2002). Although the exact nature of this relationship has been subject to debate (Grime, 1997), its existence is beyond dispute (Srivastava and Vellend, 2005). This is why the level of functional redundancy with regard to the assembly of communities, the engines of biodiversity, is particularly important for the conservation of ecosystem function. This level can be demonstrated as the acceptable level of ecological aggregation, i.e. the minimum number of groups that can adequately represent community function. It appears to vary in predictable ways (Hairston and Hairston, 1993), but its accurate assessment requires a good understanding of assembly mechanisms (Walker, 1992).

In spite of recent advances in the quantification of functional redundancy (Muntadas et al., 2016; van der Linden et al., 2016), its assessment remains highly prone to subjectivity, especially with regard to the number of biological traits (Jax, 2005). The framework of Boulangeat et al. (2012) addresses this issue, by defining a specific number of important community assembly mechanisms that need to be explicitly represented. Trait categorization is generally lacking among functional studies of benthic communities. Even when traits are explicitly assigned to a set of general functions (e.g. Törnroos and Bonsdorff, 2012), this is done in order to rather interpret the results of the study than guide the process of biological traits selection. The framework also allows the nesting of finer functional differences within broader ones. This is achieved through the separation of organisms into broad groups with a common resource base, whose consumption is further differentiated based on finer group dissimilarities. Finally, putting the emergent grouping to the test is central to the framework and allows defining the acceptable level of ecological aggregation as the minimum number of groups for which the assumptions of the EGH are supported by observations. Boulangeat et al. (2012) tested the niche constituent of the EGH, by comparing its assumptions with what could be observed in their system. Here, we take their approach one step forward, by investigating the second constituent of the EGH, concerning the neutral behaviour of species within each functional group.

In this study, we revisit a benthic macroinvertebrates abundance data set from the Rance estuary (Brittany, France), previously explored with the use of traditional multivariate analyses (Desroy, 1998). We combine it with a matrix of biological traits, with the goal of aggregating the system through the construction of functional groups. We investigate both niche and neutral attributes of the emergent grouping, gaining insights into the components of functional diversity and redundancy in benthic communities. In doing so, we integrate statistical tools and ecological mechanisms into a quantitative approach toward defining the acceptable level of ecological aggregation. The present study is a first step toward the development of models of benthic community assembly mechanisms, with the generated functional groups as their entities. The application of this generic modelling approach to the Rance estuary is expected to describe the stability characteristics of macroinvertebrate communities as well as their responses to well-documented perturbations, such as the occurrence of particularly cold winters or the introduction of invasive species (Desroy, 1998).

II.2 Methods

II.2.1 Study site

The framework for the construction of functional groups was applied to the Rance estuary (Brittany, France), in the southern part of the English Channel (Fig. II.1). The site is characterized by the presence of a tidal power plant at its mouth, comprising a lock, the generating station proper, a rock dike and a 115 m wide removable dam made up of 6 sluice gates. The system was fundamentally altered during the construction of the plant (1963-1966), after which it was allowed to gradually return to a more natural state (Kirby and Retière, 2009).

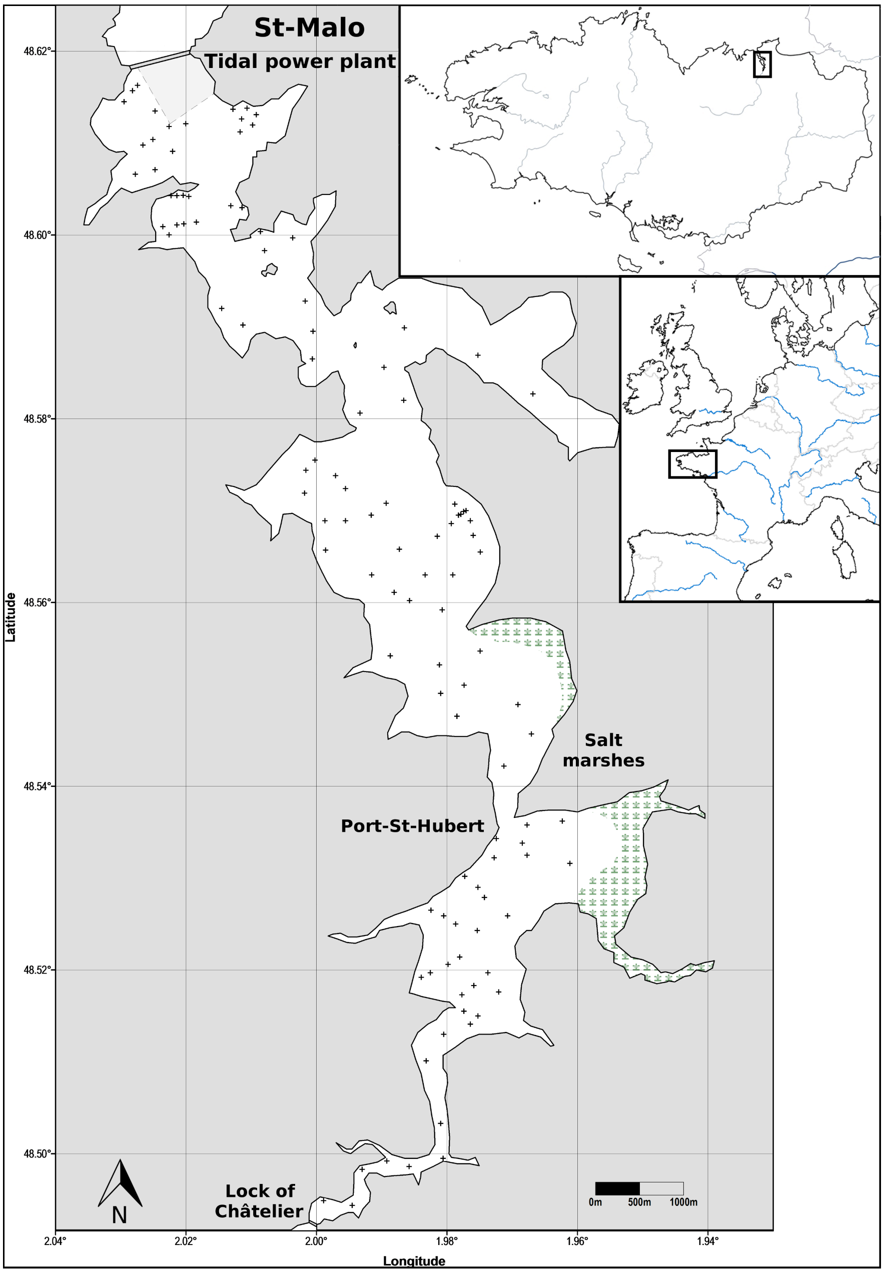


Fig. II.1 Map of the study site. The Rance estuary is situated on the northern coast of Brittany, France. Crosses indicate the location of the 113 stations that were sampled in the spring of 1995. The tidal power plant is located at the mouth of the estuary, south of the city of St-Malo

The operating constraints of the installation impose highly specific "tidal" conditions on the estuary: (1) mean water level is elevated by approximately 2.5 m, (2) slack water periods are particularly long (up to 5 h), (3) emersion time may be half that of the open sea and (4) the tidal range varies between 4.0 m and 5.5 m compared to 9.5 m (mean value) in the open sea, depending on which direction the turbines are operating (Retière, 1994). Reduction in tidal range is correlated with a reduction in the surface area of the intertidal zone; the exposed zone accounts today for 50% of the total surface of the Rance estuary, compared to 70% before the construction of the plant. Maximum water depth is 17 m at low tide, but the main part of the basin is 5-6 m deep. Two areas of differing salinities can be identified: the marine reservoir, in which deep-water salinity remains higher than 30, and the upstream estuary of brackish water (Retière, 1994). The junction between brackish and marine waters has moved about 5 km upstream since the scheme was built.

The strong sluice and turbine currents have eroded parts of the riverbed. Sandbanks closest to the dam have shifted and the bed is more or less covered with gravel or pebbles (Retière, 1994). Meanwhile, 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, beyond Port-St-Hubert. A similar sequence is observable from the central channel to the banks. Natural silting is presumed to have increased since operation of the tidal power plant started. In the upstream part of the estuary, sedimentation rate increased from 0.5 cm y^{-1} before the scheme to 2.7 cm y^{-1} after (Bonnot-Courtois, Ecole Pratique des Hautes Etudes, Dinard, France, personal communication).

II.2.2 Sampling methods

A grid of 113 stations was sampled in April 1995, prior to the spring recruitment (Fig. II.1). Two replicate samples were collected at each of 103 submerged stations using a 0.1 m^2 Smith Mac-Intyre grab, while 10 emerged stations were sampled using a hand corer (5 replicates; replicate area of 1/55 m^2) to a depth of 20 cm. The number of replicates is assumed to be sufficient to characterize the assemblage of species that can be found at each station. Although densities of organisms were extrapolated to a standard surface area, some bias was unavoidably introduced, due to the different characteristics of the sampling gears. All samples were gently washed in situ through a 1 mm sieve and preserved in 4.5% formalin before being sorted, identified and counted in the laboratory. Macroinvertebrates retained on the mesh were determined at species level when possible. A total of 240 species or higher taxonomic groups belonging to 9 phyla were thus identified.

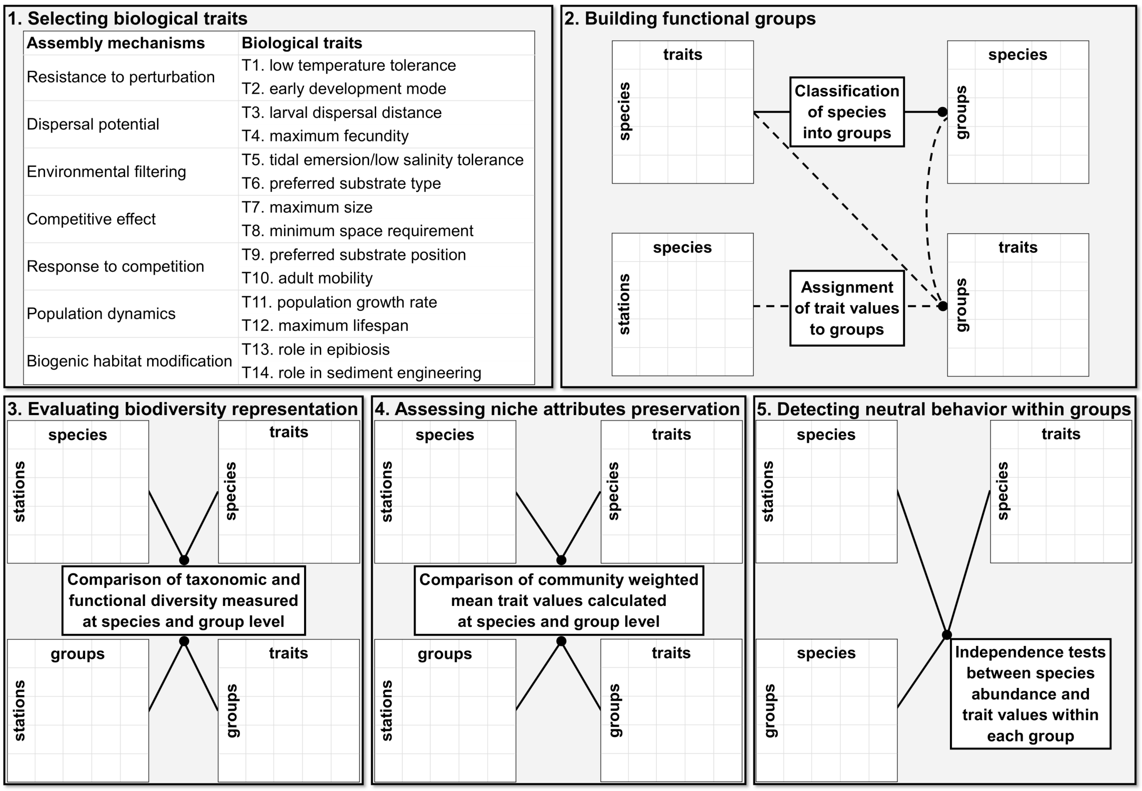
II.2.3 Design and application

Our approach draws on the work of Boulangeat et al. (2012), who employed the EGH for the classification of terrestrial plant species into groups with similar ecological strategies. Much like their approach, our own is divided into five steps (Fig. II.2), with the respective ecological assumptions and methodological framework presented below.

Step 1: selecting biological traits

The objective of this step was to select species characteristics that describe the role of the average individual of each species in the most important community assembly mechanisms. The list of mechanisms was mostly adopted from the framework of Boulangeat et al. (2012), with a few adjustments, in order to adapt it to the special attributes of estuarine benthic systems. The choice of the traits was made based on both the nature of the community assembly mechanisms and the quality of the data that could be found for each of the traits.

Since community assembly mechanisms include competition for a limited amount of resources, we first identified food and space as the basic resources for which benthic organisms compete. Space was assumed to be two-dimensional, while food was defined with the goal of dividing species into groups with a common resource base. The wide-spread adoption of facultative feeding modes only allowed for a distinction between species that feed on algae and detritus on the one hand and those characterized as predators and scavengers on the other.



Assembly mechanisms	Biological traits
Resistance to perturbation	T1. low temperature tolerance
	T2. early development mode
Dispersal potential	T3. larval dispersal distance
	T4. maximum fecundity
Environmental filtering	T5. tidal emersion/low salinity tolerance
	T6. preferred substrate type
Competitive effect	T7. maximum size
	T8. minimum space requirement
Response to competition	T9. preferred substrate position
	T10. adult mobility
Population dynamics	T11. population growth rate
	T12. maximum lifespan
Biogenic habitat modification	T13. role in epibiosis
	T14. role in sediment engineering

Fig. II.2 Schematic representation of the 5 steps that comprise the methodology of functional grouping. In step 1, 14 biological traits were selected, representing 7 community assembly mechanisms. For details, see Table II.1. In step 2, a matrix of species trait values formed the basis for the classification of species into functional groups (solid line). The two matrices, combined with data of species abundance, allowed the assignment of trait values to the functional groups (dashed lines). In step 3, taxonomic diversity and functional divergence were measured for each station at the level of species and functional groups. Measures at the two levels were then compared, in order to evaluate the representation of biodiversity by the functional groups. In step 4, community weighted mean trait values were calculated for each station at the level of species and functional groups. Calculations at the two levels were then compared, in order to assess the preservation of niche attributes by the functional groups. In step 5, the independence between species abundance at each station and their trait values was tested within each functional group and the rejection proportion for every trait was used as an indication of departures from neutrality

Table II.1 List of community assembly mechanisms, biological traits that represent the species' role in them, trait values and comments about their assignment to species

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 enhances food availability (McLean and Lasker, 2013)
	T8. minimum space requirement	0.003/0.1/49.5 (min./median/max.) Values do not represent absolute, but 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 do not represent absolute, but 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

The rest of the biological traits represent seven community assembly mechanisms. The initial goal was for each mechanism to be represented by two traits, so that one set of traits could be used for the species classification and the other for the cross-validation of the resulting grouping. The lack of redundancy in the content of the two sets of traits obliged us to abandon this goal and use all fourteen traits for the classification of the species into groups. The seven community assembly mechanisms are: (1) resistance to perturbation, (2) dispersal potential, (3) environmental filtering, (4) competitive effect, (5) response to competition, (6) population dynamics and (7) biogenic habitat modification. Details about the selected biological traits and the assignment of trait values to the system's species can be found in Table II.1.

The vast majority of the information that was required for the assignment of trait values to the species of the system was provided by the following online databases: *eol.org*, *genustraithandbook.org.uk*, *marinespecies.org*, *marlin.ac.uk* and *species-identification.org*. The remainder was acquired from consultation with experts on the field. Very often the lack of appropriate information for a particular species obliged us to look for data at higher taxonomic levels. The quality of the available information for the ensemble of species and biological traits dictated the resolution of the values that were assigned to them (for details, see Table B.1 in Annex B).

Step 2: building functional groups

This step aims at reducing a community of benthic macroinvertebrates to its principal functional components, by identifying emergent groups of species (Hérault, 2007). It was applied separately for consumers of algae/detritus and predators/scavengers, because the concept of functional equivalence, which is central to the EGH, is defined for trophically similar sympatric species (Hubbell, 2005). The first task involved calculating a distance matrix for both groups of species, based on the rest of the biological traits. Since our list included continuous, ordinal, nominal and binary traits, we opted for the Gower distance (Gower, 1971). These matrices formed the basis for the application of an agglomerative hierarchical clustering technique, the unweighted pair group method with arithmetic mean (Sokal and Michener, 1958). The two generated dendrograms were consecutively pruned at 0.4 and 0.3 distance levels, without, for practical reasons, allowing the formation of groups with only one species.

In order to be able to treat the newly formed groups as independent functional components, we needed to attribute trait values to them. We did that by employing the mass ratio hypothesis (Grime, 1998), which predicts that the functional identity of a group of species is determined by the trait values of the dominant abundance contributors. We measured the abundance contribution of each species in its group, by calculating its median abundance at the stations where it was present. For the ordinal, nominal and binary traits, a group's trait value was defined as the dominant value, as far as the abundance contribution of its species was concerned. For the continuous traits, a group's trait value was defined as the mean trait value of all the species in the group, weighted by their abundance contribution. Each group was, finally, assigned a representative species, which was the one with the highest abundance contribution in the group. In case of ties or close calls, the species with the highest body mass was chosen to represent the group.

Step 3: evaluating biodiversity representation

Once functional groups were built, we had to assess their efficiency at representing natural biodiversity patterns. This need stems from the loss of information that is inherent to the process of classifying a number of species into a much smaller number of groups. We in fact wanted to know if this loss of information lay within acceptable limits, or if, instead, it severely impaired the ecological pertinence of the imposed grouping. If we assume that information at the species level provides an adequate representation of biodiversity, we could reach our goal by comparing biodiversity measurements at this level with the same measurements made at the level of functional groups. Since the role of the groups as functional components of the system was what we were especially interested in, we did not want to be limited to measures of taxonomic diversity, but we wanted to include measures of functional diversity as well.

One framework that offers this possibility is Rao's quadratic entropy, *Q* (Botta-Dukát, 2005). For an assemblage of *T* taxa characterized by the relative abundance vector **p** = ($p_1, p_2, ..., p_T$), it is defined as

$$Q=\sum_{i=1}^{T-1}\sum_{j=i+1}^{T} d_{ij}p_i p_j$$

where d_{ij} is the functional distance between the *i*-th and *j*-th taxa ($d_{ij} = d_{ji}$ and $d_{ii} = 0$). Assuming functional equidistance among taxa ($d_{ij} = 1$), it equals the complement of the Simpson dominance index, thus expressing the probability that two individuals taken at random from an assemblage belong to different taxa. When combined with a functional distance matrix for the taxa in question, like the one previously calculated with the help of the Gower distance, the same index becomes a measure of functional divergence. In this case, Rao's quadratic entropy expresses the average functional distance between two randomly selected individuals of an assemblage. We calculated both versions of the index for all 113 assemblages. If the species-level measures of diversity showed a high correlation with the same measures calculated at the level of functional groups, we could say that the transition from the former level to the latter entailed an acceptable amount of information loss.

Step 4: assessing niche attributes preservation

Niche theory predicts that the dynamics of species populations are controlled by their characteristics (Hutchinson, 1957). Species with divergent trait values exhibit differential responses to dissimilar environments, thus generating the observed distribution patterns of not only the species, but the respective traits as well. The EGH, through its niche constituent, assumes that the same holds true for the emergent groups of species (Hérault, 2007). The interaction of the environment with the organisms through the relevant biological traits should now take place at the level of functional groups, but the resulting trait distribution should not deviate from the one observed at the species level. One way to assess the validity of this assumption is by comparing the functional identity of dominant taxa in an assemblage measured at the species level, with the same metric measured at the level of functional groups.

An indicator of the functional identity of dominant taxa in an assemblage is the community weighted mean (Garnier et al., 2004), which represents the expected trait value for a random community sample. For the ordinal, nominal and binary traits, the community weighted mean was defined as the dominant trait value, as far as taxa abundance is concerned. For the continuous traits, the same measure was defined as the mean trait value of all the taxa in an assemblage, weighted by their relative abundance. The comparison of community weighted means calculated at species and group level for the ordinal, nominal and binary traits was made by deriving the proportion of the assemblages for which the two calculations agreed. For the continuous traits, we examined the correlation between the values calculated at the levels of species and functional groups. High proportions of agreement or correlation coefficients would indicate that the representation of the system at the level of functional groups preserved the niche characteristics of the original one.

Step 5: detecting neutral behaviour within groups

The second major assumption of the EGH is that the organisms that belong to the same functional group are ecologically equivalent (Hérault, 2007). This means that any differences in trait values that the organisms of a group might exhibit, should be random and, therefore, not associated with differences in their abundance (Hubbell, 2005). If this is not the case, the dynamics within the groups could not be considered as neutral, but rather controlled by the values of the trait. Since we only had information on inter-specific trait variation, we could examine this assumption, by checking for high levels of covariation between the abundance of a group's species in an assemblage and the respective trait values.

For the ordinal, nominal and binary traits, this could be done by performing the Kruskal-Wallis independence test (Kruskal and Wallis, 1952), while for the continuous traits, we opted for Hoeffding's test (Hoeffding, 1948). They both test for independence between the abundance of a group's species in an assemblage and the respective trait values and were repeated for each of the functional groups and assemblages. The proportion of rejection of these tests over all groups and assemblages was calculated for each of the traits and was considered as a measure of departure from neutrality for the within-group dynamics, with regard to the respective trait. A high value for a trait would indicate that high covariation between species abundance and trait values occurred more often than expected by chance and would thus challenge the assumption of ecological equivalence among the species of a group, as far as this particular trait is concerned.

All analyses were performed using the statistical software R version 3.2.2 (R Core Team, 2015) with the packages cluster (Maechler et al., 2013), FD (Laliberté et al., 2014), ade4 (Dray and Dufour, 2007) and Hmisc (Harrell and Dupont, 2015).

II.3 Results

II.3.1 Building functional groups

The dendrograms displaying functional distance among the species of the two feeding groups were pruned at 0.4 and 0.3 distance levels, thus allowing the emergence of 7 intermediate and 20 final groups, respectively. Unlike the transition from 7 to 20 functional groups, further classification into 30 groups did not result in improved agreement of observations with theoretical assumptions and it was, therefore, dismissed. The abundance contribution and the trait values of all 20 groups' constituent species determined the representative species and the values which were assigned to the functional groups for each of the 14 biological traits (Table II.2). The trait values of the representative species may not always correspond to those of the functional groups, since all of a group's species contributed to the definition of the latter. The representative species for now only serve to communicate the results of the grouping to experts with knowledge of the system and its species.

The emergent functional groups demonstrate a variety of combinations with regard to their assigned trait values, with a few conspicuous patterns. 4 groups of algae/detritus feeders, represented by an ascidian (h1i), a chiton (h1ii), a barnacle (h1iii) and a slipper limpet (h1iv), and 2 groups of predators/scavengers, represented by a sea anemone (c3i) and an errant polychaete (c3ii), are considered as members of the epifauna of rocky substrates. They are, accordingly, all characterized as epibionts, with the exception of group h1iv, whose members can also provide substrate for epibiotic organisms through their living or dead shells. 1 group of algae/detritus feeders, represented by a hermit crab (h4iii), and 2 groups of predators/scavengers, represented by errant polychaetes (c1i, c2ii), prefer gravelly substrates and do not play a prominent role in either epibiosis or sediment engineering.

Table II.2 Representative species and biological trait values assigned to functional groups of species. For details about the biological traits, see Table II.1. Group names denote the hierarchical classification of species in, successively, consumers of algae/detritus (h) or predators/scavengers (c), 7 intermediate groups (numerals) and 20 final groups (roman numerals)

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
h1i	*Morchellium argus*	eurythermal	brooded	short	low	stenohaline	rock	3.3	0.1	epifauna	sessile	2.6	1.7	epibiont	neutral
h1ii	*Lepidochitona cinerea*	stenothermal	planktonic	short	high	stenohaline	rock	10.8	4.1	epifauna	mobile	0.9	11.6	epibiont	neutral
h1iii	*Balanus crenatus*	eurythermal	planktonic	long	high	euryhaline	rock	2.0	0.8	epifauna	sessile	2.5	2.0	epibiont	neutral
h1iv	*Crepidula fornicata*	stenothermal	planktonic	long	high	stenohaline	rock	7.6	0.0	epifauna	sessile	1.9	11.2	basibiont	neutral
h2i	*Oligochaeta*	stenothermal	laid	short	low	emersed	muddy sand	4.5	5.0	infauna	mobile	3.4	2.0	neutral	destabilizer
h2ii	*Thyasira flexuosa*	eurythermal	planktonic	short	low	stenohaline	mud	3.6	0.8	infauna	mobile	1.0	10.0	neutral	stabilizer
h2iii	*Melinna palmata*	stenothermal	brooded	short	low	stenohaline	mud	7.5	0.3	interface	sessile	2.6	3.6	neutral	stabilizer
h2iv	*Notomastus latericeus*	stenothermal	brooded	short	low	stenohaline	muddy sand	6.0	2.9	interface	mobile	2.6	1.9	neutral	destabilizer
h3i	*Hediste diversicolor*	eurythermal	laid	short	high	emersed	muddy sand	12.8	0.2	interface	mobile	2.1	3.4	neutral	destabilizer
h3ii	*Malacoceros fuliginosus*	eurythermal	planktonic	long	high	euryhaline	mud	8.5	1.9	interface	mobile	2.5	2.7	neutral	destabilizer
h4i	*Galathowenia oculata*	eurythermal	planktonic	long	high	euryhaline	mud	11.1	0.0	interface	sessile	2.7	4.4	neutral	stabilizer
h4ii	*Glycymeris glycymeris*	stenothermal	planktonic	short	high	stenohaline	muddy gravel	8.0	1.4	infauna	mobile	0.8	15.0	neutral	stabilizer
h4iii	*Anapagurus hyndmanni*	stenothermal	planktonic	long	high	stenohaline	gravel	10.0	0.1	epifauna	mobile	0.6	10.0	neutral	neutral
h4iv	*Cerastoderma edule*	stenothermal	planktonic	long	high	emersed	muddy sand	8.6	0.5	interface	mobile	0.7	8.9	neutral	stabilizer
c1i	*Sphaerosyllis bulbosa*	stenothermal	brooded	short	low	stenohaline	gravel	1.3	0.5	epifauna	mobile	4.7	1.9	neutral	neutral
c2i	*Marphysa bellii*	stenothermal	planktonic	short	high	stenohaline	muddy sand	23.3	0.3	interface	mobile	1.1	4.7	neutral	neutral
c2ii	*Nephtys hombergii*	stenothermal	planktonic	long	high	stenohaline	gravel	10.5	0.3	interface	mobile	2.2	7.3	neutral	neutral
c2iii	*Myrianida edwardsi*	stenothermal	planktonic	long	low	stenohaline	mud	1.4	3.1	interface	mobile	5.8	1.9	neutral	neutral
c3i	*Urticina felina*	eurythermal	planktonic	short	high	euryhaline	rock	16.7	10.3	epifauna	sessile	1.1	14.0	epibiont	neutral
c3ii	*Syllis cornuta*	stenothermal	planktonic	long	low	stenohaline	rock	7.4	5.2	epifauna	mobile	2.3	2.3	epibiont	neutral

Finally, the majority of functional groups, 9 of them being algae/detritus feeders and 2 predators/scavengers, prefer muddy or sandy substrates and can be found in the sediment or at the water/sediment interface. The values assigned to them for the qualitative traits show a wide variety of combinations and they consistently feature the lowest and highest values for all quantitative traits. They are represented by oligochaetes (h2i), bivalves (h2ii, h4ii, h4iv) and sedentary (h2iii, h2iv, h3ii, h4i) or errant (h3i, c2i, c2iii) polychaetes, and most of them play a distinct engineering role, either as sediment stabilizers or sediment destabilizers.

II.3.2 Evaluating biodiversity representation

Taxonomic diversity measured at the species level correlates strongly with the same measure calculated at the level of functional groups (Fig. II.3a), an indication of acceptable levels of information loss with regard to general biodiversity patterns. A few extreme deviations from the expected straight line are positioned well below it. Information on functional divergence also appears to be preserved through the transition from species to functional groups (Fig. II.3b), denoting an adequate description of the system's functional components by this reduced representation. Deviations from the expected straight line are in this case positioned on both of its sides, with extreme outliers being mostly positioned above it.

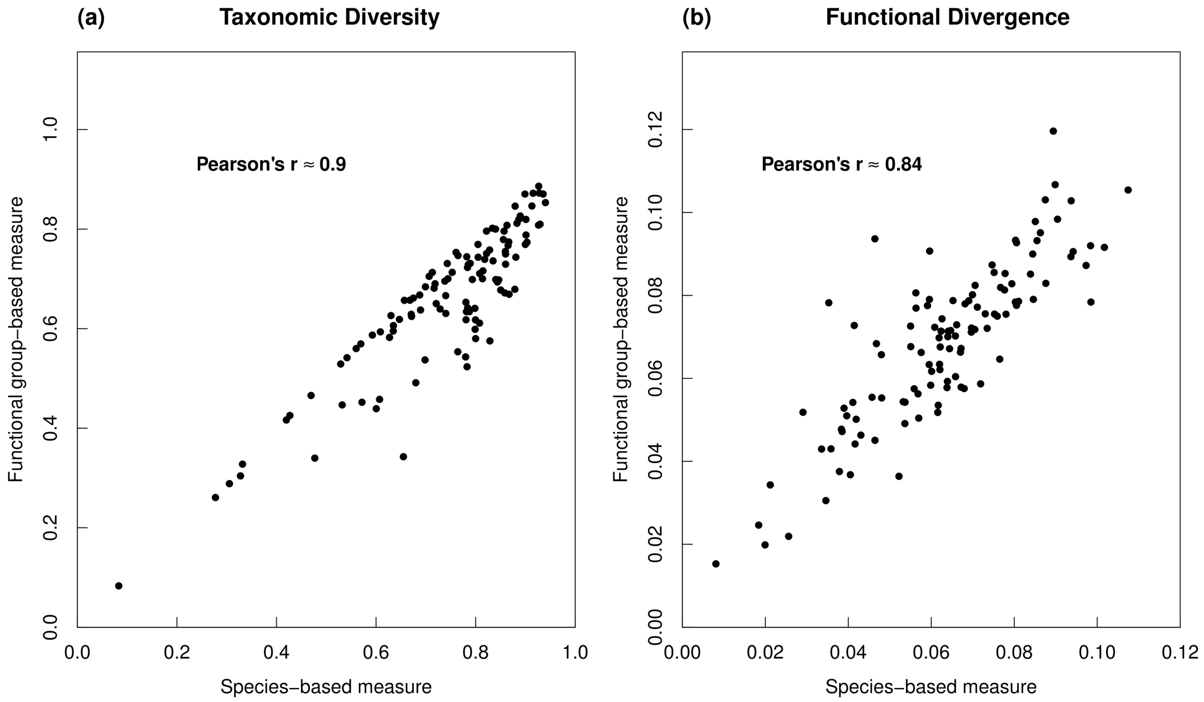
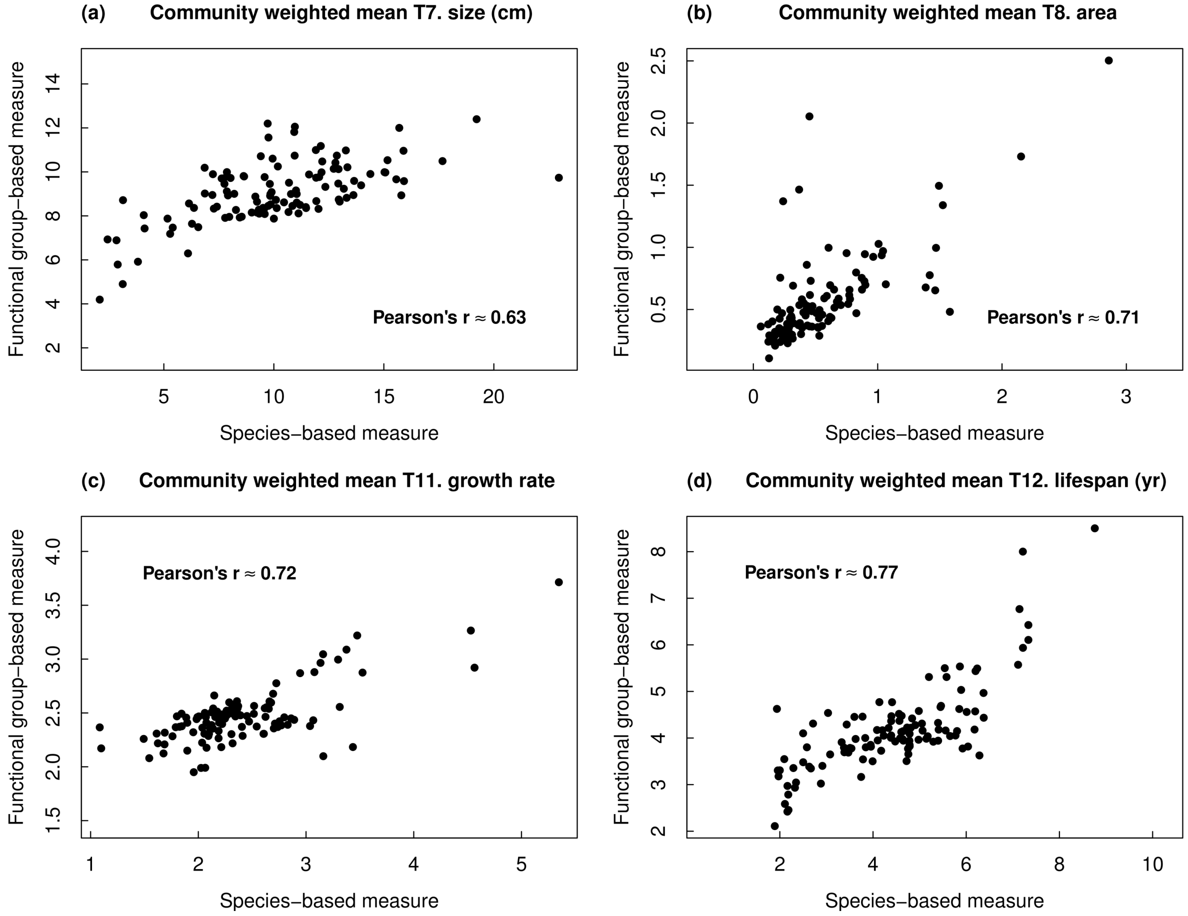


Fig. II.3 Comparison of species-based and functional group-based measurements of a) taxonomic diversity and b) functional divergence for all assemblages. Both quantities were measured as Rao's quadratic entropy based on taxa abundance, by assuming functional equidistance among taxa in the former case, while employing a functional distance matrix in the latter. Pearson's correlation coefficient was calculated as a measure of the linear correlation between measurements made at the two levels of organisation

II.3.3 Assessing niche attributes preservation

The functional identity of assemblages appears in general to be conserved through the transition from species to functional groups, as community weighted means for most biological traits show high levels of agreement or strong correlations, when calculated at the two levels of organisation (Table II.3 and Fig. II.4). Among all biological traits, early development mode, maximum fecundity (Table II.3), and maximum size (Fig. II.4a) show the lowest levels of agreement or correlation. For maximum size, the transition from one level of organisation to the other appears also to be biased, since community weighted means calculated at the species level tend to be higher than those calculated at the level of functional groups.



(a) Community weighted mean T7. size (cm)

(b) Community weighted mean T8. area

(c) Community weighted mean T11. growth rate

(d) Community weighted mean T12. lifespan (yr)

Fig. II.4 Comparison of species-based and functional group-based calculations of community weighted mean trait values for all assemblages. For details about the biological traits (a-d), see Table II.1. Pearson's correlation coefficient was calculated as a measure of the linear correlation between calculations made at the two levels of organisation

II.3.4 Detecting neutral behaviour within groups

The proportion at which tests of independence between the abundance of a group's species in an assemblage and the respective trait values were rejected, is less than 0.1 for most biological traits (Table II.4), supporting the assumption that trait variation within functional groups is mostly random and not associated with observed abundance patterns. The two traits for which this limit is exceeded (early development mode and adult mobility), show proportions of rejection of the independence tests just over the value of 0.1. The comparison of these results with the results of the same independence tests performed at the levels of 2 feeding and 7 intermediate groups reveals a strong tendency toward a reduced proportion of rejection as the resolution of the grouping increases (see Table II.A in the Appendix).

Table II.3 Proportion of agreement between species-based and functional group-based calculations of community weighted mean trait values for all assemblages. For details about the biological traits, see Table II.1

Biological traits	Agreement proportion
T1. low temperature tolerance	0.81
T2. early development mode	0.61
T3. larval dispersal distance	0.96
T4. maximum fecundity	0.62
T5. tidal emersion/low salinity tolerance	0.72
T6. preferred substrate type	0.71
T9. preferred substrate position	0.98
T10. adult mobility	0.92
T13. role in epibiosis	1
T14. role in sediment engineering	0.87

Table II.4 Proportion of rejection of independence tests between the abundance of a group's species in an assemblage and the respective trait values over all functional groups and assemblages. Hoeffding's test was performed in the case of continuous biological traits (denoted by an asterisk), while Kruskal-Wallis independence test was performed in all other cases. For details about the biological traits, see Table II.1

Biological traits	Test rejection proportion
T1. low temperature tolerance	0.02
T2. early development mode	0.11
T3. larval dispersal distance	0.02
T4. maximum fecundity	0.08
T5. tidal emersion/low salinity tolerance	0.08
T6. preferred substrate type	0.05
T7. maximum size	0.08
T8. minimum space requirement*	0
T9. preferred substrate position	0.01
T10. adult mobility	0.12
T11. population growth rate*	0
T12. maximum lifespan	0.05
T13. role in epibiosis	0
T14. role in sediment engineering	0.07

II.4 Discussion

II.4.1 Selecting biological traits

The combination of biological trait information describing the functional role of 240 species in their communities with a conventional species abundance data set from the Rance estuary in 1995, led to the emergence of 20 groups of benthic macroinvertebrates. Like Boulangeat et al. (2012), we selected our set of traits with the goal of representing the role of organisms in the following community assembly mechanisms: resistance to perturbation, dispersal potential, environmental filtering, competitive effect, response to competition and population dynamics. We added the mechanism of biogenic habitat modification, as this is expected to be an important factor shaping benthic communities. Unlike the species abundance data set, which is spatially and temporally restricted to the system in question, the collected information on the functional role of species is highly general and could be readily employed for an application of the approach to a system with similar composition. The represented community assembly mechanisms would be probably retained during a transfer of the approach, but changes in specific biological traits could be well anticipated.

The transferability of each biological trait is likely to depend on a system's similarity to the Rance estuary in 1995, regarding its abiotic and biotic environment. In lack of significant anthropogenic impacts, following a normalization period in the power plant's operation during its first five years, we considered exceptionally cold winters as a source of perturbation. Disturbances, however, tend to be case-specific and their nature, whether anthropogenic or natural, would dictate the identity of the respective traits. For some systems, oxygen could be added to the list of limiting resources (Ferguson et al., 2013), which currently consists of only food and space. Different resources, such as irradiance or nutrients, would have to be considered as limiting for the members of algae-dominated systems (Alexandridis et al., 2012). A new set of resources would require a re-evaluation of the traits that represent the mechanisms of competitive effect and response to competition. Traits that describe allelopathic (Woodin et al., 1993) or symbiotic relationships (Reiss et al., 2003) should also be included, if these are mechanisms with an important role in the system.

We expect the selected mechanisms to largely control processes of community assembly but we cannot be certain that the role of each species is defined in its entirety by the selected biological traits. The use of two traits for the description of the species' role in each mechanism is expected to mitigate the effect of this uncertainty. The lack of cross-validation that it entails, precludes a full examination of the methodology's robustness, which could, however, be explored through various re-sampling techniques. The process of testing the main assumptions of the EGH provides the ultimate validation of the ecological relevance of each biological trait. The replacement or more realistic depiction of the biological traits for which the aggregation of the system results in departures from theoretical assumptions will eventually lead to the most accurate representation of the selected mechanisms. This process is for now limited to the Rance estuary as it was observed in 1995 and it will have to be repeated for the ecological aggregation of any different system. After the approach has been applied to a sufficient number of systems and once persistent patterns in the traits of the emergent groups have been investigated, we will be able to define more general biological traits and groups of benthic macroinvertebrates.

We used 14 biological traits for our functional grouping: 4 binary, 6 nominal, 2 ordinal and 2 continuous. We applied the classification procedure separately for the two feeding groups, similar to the separation of plants into 3 life form groups that Boulangeat et al. (2012) imposed, before building their own functional groups. The resolution of our traits is indicative of the uncertainty encountered during the collection of information, with binary traits showing the highest level of uncertainty and ordinal the lowest. Continuous traits are an exception, because almost all of the species biomass data from which they were derived were calculated from length-weight relationships of questionable generality (Robinson et al., 2010). Trait information of better quality would increase their resolution and the grouping's accuracy, keep us from resorting to higher taxonomic levels to attribute trait values to species and allow us to use species biomass instead of their abundance for the assignment of trait values to the groups. The latter was dismissed at this point, because the abundance data set was considered much more reliable. Its detriment is expected to be largely alleviated by the reduced within-group biomass variation. In what would be a major improvement to the approach, information uncertainty could be addressed through the use of fuzzy coding (Chevenet et al., 1994), which can also account for spatial and temporal intra-specific trait variability (Cardeccia et al., 2016).

II.4.2 Building functional groups

The EGH is based on the assumption of random dynamics within each group (Hérault, 2007). The resulting ecological aggregation reduces the system by specifically subtracting an important component of what is most of the times uniformly considered as stochastic. The assignment of trait values to the emergent groups allows a functional representation of the system and an examination of the role of trait-based interactions in the regulation of system dynamics. Trophic interactions are central to the emergence of these dynamics and, besides the distinction between algae/detritus feeders and predators/scavengers, we expect the relative size of organisms to play an important role in their definition (Brose et al., 2006). The position of organisms and the mobility of their adults should dictate the partitioning of resources through a different use of space (Herman et al., 1999). Well-established ecological theory can help us define competitive interactions among functional groups, based on trade-offs in the consumption of multiple resources and in their allocation strategies (Tilman, 1990). The occurrence of exceptionally cold winters would lead to distinct response patterns, based on the low temperature tolerance of each group (Beukema et al., 2000). The representative species that were assigned to the emergent groups could play a complementary role, by allowing modifications of these interactions on the basis of expert knowledge that is often hard to express in terms of biological traits and ecological theories.

A simple review of the trait values of the emergent functional groups indicates a clear distinction among benthic macroinvertebrate organisms. On the one hand, groups that prefer rocky substrates along with those that prefer gravelly ones can be considered as representative of organisms that belong to the epifauna and depend on the existence of hard structure on the sediment surface. Since hard structure of abiotic origin is very restricted in the Rance estuary, the occurrence of these groups should, to a large extent, be linked to basibiotic organisms, whose living or dead shells provide them with their preferred substrate. On the other hand, groups that prefer muddy or sandy substrates represent organisms that are buried deep in the sediment or at the water/sediment interface. The larger number of algae/detritus feeding groups that can be found in this category compared to the previous one may be associated with the higher occurrence of their preferred habitat near and within the Rance estuary. Epifaunal organisms are contrarily represented by more groups of predators/scavengers, possibly due to the higher structural complexity of their habitat, which in turn allows a larger diversification of predatory strategies.

II.4.3 Evaluating biodiversity representation

The loss of biodiversity information that the transition from species to functional groups entails, appears to be acceptable at both the taxonomic and functional level. In the case of taxonomic diversity, there is a clear pattern of departures from the expected straight line that are positioned below it, in agreement with the expected direction of information loss. Points that are positioned well below this line represent assemblages that consist of the most species rich groups, hence the sharp drop in taxonomic diversity when moving from species to functional groups. In the case of functional divergence, deviations can be observed on both sides of the expected straight line. This pattern is caused by the unavoidable misrepresentation of some species by their functional groups with regard to specific biological traits, which results in functional divergence shifting in either direction. The fact that extreme outliers are mostly positioned above this line is a direct result of the process of functional grouping. Functional divergence is an indicator of niche differentiation (Mason et al., 2005), which is expected to be maximized by a process that reduces the number of components based on their niche differences (Pavoine et al., 2005).

II.4.4 Assessing niche attributes preservation

The functional characteristics of the community, as these can be observed at the species level, appear to be preserved in the representation of the system by functional groups. The clear tendency of community weighted mean values of maximum size to be lower at the level of functional groups than at the level of species is due to the strong negative association of this trait with species abundance and the utilization of the latter for the assignment of trait values to the groups. The low levels of agreement between community weighted mean values of early development mode and maximum fecundity calculated at the level of species and functional groups show that these two biological traits are the ones for which species are the most misrepresented by their assigned groups. The fact that both traits address aspects of reproductive strategy could be a reflection of our low level of understanding with regard to the reproduction of most benthic macroinvertebrates (Tyler et al., 2012). Since these traits belong to two different community assembly mechanisms, they should be considered along with their partner traits for the representation of resistance to perturbation and dispersal potential, respectively.

II.4.5 Detecting neutral behaviour within groups

In addition to the tests originally performed by Boulangeat et al. (2012), we also investigated the second main assumption of the EGH, concerning the neutral behaviour of species within each group. This was done by following one of the three approaches recommended by Hérault (2007) for the validation of his hypothesis. The fact that within group abundance patterns tend to become independent of trait variation as the resolution of the grouping increases, is consistent with the assumption for a transition from trait-controlled to neutral abundance variation during the emergence of the groups. Early development mode is again one of the biological traits for which theoretical assumptions are the least supported by the results, calling for a better description of reproductive strategies. Species are also occasionally misrepresented by their functional groups with regard to the trait of adult mobility. These deviations are still only observed at an acceptably low rate. More frequent deviations could be addressed by the application of weighting during the classification procedure, aimed at increasing the contribution of the biological traits for which the grouping appears to be the most problematic.

II.5 Conclusions

The main contribution of the EGH (Hérault, 2007) and the framework developed by Boulangeat et al. (2012) to the study of functional redundancy and the aggregation of biological communities lies in the mechanistic nature of their approach. Although statistical tools are indispensable to its implementation, they are used in support of decisions made on purely mechanistic grounds. Most notably, the acceptable level of ecological aggregation, which is a direct reflection of functional redundancy, is defined as the minimum number of groups for which the assumptions of the EGH are supported by observations. The crucial process of selecting biological traits is constrained by the requirement to produce the best possible representation of a list of general community assembly mechanisms. It therefore addresses the persisting issue of subjectivity in the assessment of functional redundancy (Jax, 2005). The empirical testing of the grouping against theoretical assumptions, which lies at the heart of the approach, provides a framework for the critical synthesis of mechanisms that ecological theory considers as the drivers of community dynamics.

The approach focuses on the assembly of biological communities, as the driver of benthic biodiversity. This is, however, only one of the ways in which ecosystem properties are influenced by benthic organisms. Processes associated with energy and elemental cycling, habitat/refugia provision and modification of physical properties are among the most widely recognised aspects of ecosystem functioning (Frid et al., 2008). Although the approach was not designed to address these issues, links with them can be drawn at any stage, either during the construction of functional groups or during the development and analysis of models. Most of the traits that we assumed to directly represent community assembly mechanisms (with the exception of resistance to perturbation and environmental filtering) are commonly used in biological traits analyses as indirect indicators of the previously mentioned ecosystem functions (Bremner et al., 2006a). Observed trait associations and ecological theory could facilitate the collection of information that this approach lacks.

The consideration of our list of general community assembly mechanisms in conjunction with the attributes of the functional groups allowed a mechanistic interpretation of a few broad patterns of biodiversity. Our next goal is to employ ecological theory and observed trait associations, in order to inform the definition of rules of interaction among functional groups or between them and the environment. Similar efforts in the terrestrial environment have led to the development of dynamic and spatially explicit trait-based models of plant (Boulangeat et al., 2014) and animal communities (Scherer et al., 2015). By reproducing the assembly mechanisms of the respective systems, these studies were able to predict biodiversity responses to projected climatic and land use change. Our first objective is to answer questions regarding the stability of the system and its potential response to perturbations. Ultimately, we hope to create modelling tools reproducing the emergence of biodiversity patterns under different scenarios of environmental change. By explicitly reproducing the mechanisms that are responsible for these patterns, we expect to shed some light on their role in shaping communities of benthic macroinvertebrates.

II.6 References

Alexandridis, N., Oschlies, A., Wahl, M., 2012. Modeling the effects of abiotic and biotic factors on the depth distribution of *Fucus vesiculosus* in the Baltic Sea. Mar Ecol Prog Ser 463, 59-72.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol Lett 15, 365-377.

Beukema, J.J., Essink, K., Dekker, R., 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator–prey interactions. J Anim Ecol 69, 31-44.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Modelling directional spatial processes in ecological data. Ecol Model 215, 325-336.

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

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16, 533-540.

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.

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. J Exp Mar Biol Ecol 366, 37-47.

Bremner, J., Paramor, O.A.L., Frid, C.L.J., 2006a. Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0-12 nautical mile zone. A report to English Nature from University of Liverpool, Liverpool, UK.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006b. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol Indic 6, 609-622.

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., 2006. Consumer-resource body-size relationships in natural food webs. Ecology 87, 2411-2417.

Cardeccia, A., Marchini, A., Occhipinti-Ambrogi, A., Galil, B., Gollasch, S., Minchin, D., Narščius, A., Olenin, S., Ojaveer, H., 2016. Assessing biological invasions in European Seas: biological traits of the most widespread non-indigenous species. Estuar Coast Shelf S, in press.

Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwater Biol 31, 295-309.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18, 117-143.

Darr, A., Gogina, M., Zettler, M.L., 2014. Functional changes in benthic communities along a salinity gradient– a western Baltic case study. J Sea Res 85, 315-324.

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 dissertation, Université de Rennes 1, Rennes, France.

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

Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Model 196, 483-493.

Ferguson, N., White, C.R., Marshall, D.J., 2013. Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen. Ecology 94, 126-135.

Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas. Hydrobiologia 606, 69-79.

Garcia, C., Chardy, P., Dewarumez, J.-M., Dauvin, J.-C., 2011. Assessment of benthic ecosystem functioning through trophic web modelling: the example of the eastern basin of the English Channel and the Southern Bight of the North Sea. Mar Ecol 32, 72-86.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630-2637.

Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometrics 27, 857-871.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86, 902-910.

Grime, J.P., 1997. Biodiversity and ecosystem function: the debate deepens. Science 277, 1260-1261.

Hairston, N.G.Jr., Hairston, N.G.Sr., 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. Am Nat 142, 379-411.

Harrell, F.E.Jr., Dupont, C., 2015. Hmisc: Harrell Miscellaneous. R package version 3.15-0.

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.

Hoeffding, W., 1948. A non-parametric test of independence. Ann Math Stat 19, 546-557

Hubbell SP 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Funct Ecol 19, 166-172.

Hutchinson, G.E., 1957. Concluding Remarks. Cold Spring Harb Sym 22, 415-427.

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. Review: ecological networks – beyond food webs. J Anim Ecol 78, 253-269.

James, F.C., McCulloch, C.E., 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annu Rev Ecol Syst 21, 129-166.

Jax, K., 2005. Function and "functioning" in ecology: what does it mean? Oikos 111, 641-648.

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

Jimenez, H., Dumas, P., Mouillot, D., Bigot, L., Ferraris, J., 2015. Harvesting effects on functional structure and composition of tropical invertebrate assemblages. ICES J Mar Sci 73, 420-428.

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.

Kirby, R., Retière, C., 2009. Comparing environmental effects of Rance and Severn barrages. P I Civil Eng-Mar En 162, 11-26.

Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. J Am Stat Assoc 47, 583-621.

Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol Evol 12, 474-478.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Legendre, P., Gauthier, O., 2014. Statistical methods for temporal and space–time analysis of community composition data. Proc R Soc B 281, 20132728.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2013. cluster: cluster analysis basics and extensions. R package version 1.14.4.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112-118.

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.

Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol Monogr 65, 21-74.

Muntadas, A., de Juan, S., Demestre, M., 2016. Assessing functional redundancy in chronically trawled benthic communities. Ecol Indic 61, 882-892.

Ortiz, M., Wolff, M., 2002. Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios. Ecol Model 148, 277-291.

Pavoine, S., Ollier, S., Pontier, D., 2005. Measuring diversity from dissimilarities with Rao’s quadratic entropy: are any dissimilarities suitable? Theor Popul Biol 67, 231-239.

Pearson, T.H., 2001. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. Oceanogr Mar Biol 39, 233-267.

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

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.

Reiss, H., Knäuper, S., Kröncke, I., 2003. Invertebrate associations with gastropod shells inhabited by *Pagurus bernhardus* (Paguridae) – secondary hard substrate increasing biodiversity in North Sea soft ‐ bottom communities. Sarsia 88, 404-415.

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

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.

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156-162.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., Charno, 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.

Sokal, R.R., Michener, C.D., 1958. A statistical method for evaluating systematic relationships. Univ Kans Sci Bull 28, 1409-1438.

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.

Srivastava, D.S., Vellend, M., 2005. Biodiversity-ecosystem function research: is it relevant to conservation? Annu Rev Ecol Evol S 36, 267-294.

ter Braak, C.J., Prentice, I.C., 2004. A theory of gradient analysis. Adv Ecol Res 34, 235-282.

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.

Törnroos, A., Bonsdorff, E., 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. Ecol Appl 22, 2221-2236.

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.

Ulanowicz, R.E., 2004. Quantitative methods for ecological network analysis. Comput Biol Chem 28, 321-339.

van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H., Marques, J.C., 2016. The performance of trait-based indices in an estuarine environment. Ecol Indic 61, 378-389.

Walker, B.H., 1992. Biodiversity and Ecological Redundancy. Conserv Biol 6, 18-23.

Woodin, S., Marinelli, R., Lincoln, D., 1993. Allelochemical inhibition of recruitment in a sedimentary assemblage. J Chem Ecol 19, 517-530.

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

II.7 Appendix

Table II.A Proportion of rejection of independence tests between the abundance of a group's species in an assemblage and the respective trait values over all functional groups and assemblages. The tests were first performed at the level of 2 feeding groups, then at the level of 7 intermediate groups and finally at the level of 20 final groups. Hoeffding's test was performed in the case of continuous biological traits (denoted by an asterisk), while Kruskal-Wallis independence test was performed in all other cases. For details about the biological traits, see Table II.1

Biological traits	**Test rejection proportion**		
	within herbivores/carnivores	**within 7 intermediate groups**	**within 20 final groups**
T1. low temperature tolerance	0.02	0.02	0.02
T2. early development mode	0.25	0.15	0.11
T3. larval dispersal distance	0.04	0.01	0.02
T4. maximum fecundity	0.05	0.11	0.08
T5. tidal emersion/low salinity tolerance	0.39	0.17	0.08
T6. preferred substrate type	0.32	0.11	0.05
T7. maximum size	0.11	0.12	0.08
T8. minimum space requirement*	0.01	0	0
T9. preferred substrate position	0.10	0.05	0.01
T10. adult mobility	0.15	0.15	0.12
T11. population growth rate*	0.01	0	0
T12. maximum lifespan	0.16	0.10	0.05
T13. role in epibiosis	0.02	0.02	0
T14. role in sediment engineering	0.23	0.20	0.07

Chapter III: Moving from biological traits to functional relationships for use in dynamic models of 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 are expected to be largely controlled by readily available biological traits, thus making trait-based modeling an ideal framework for the synthesis of relevant hypotheses from ecological theory and expert knowledge. Here, we employ a set of theories that predict the existence of functional trade-offs, operating at both large and small spatial scales. The former represent processes of environmental filtering, while the latter involve life history trade-offs that are associated with biogenic habitat modification and differential efficiencies of resource utilization or patterns of resource allocation. Observed trait associations in the Rance estuary (Brittany, France) appear to agree with these predictions, in support of the potential of the respective processes to shape benthic communities. In a first inception of the system, elements of the aforementioned theories together with expert knowledge are incorporated in the form of general rules of interaction into qualitative models of a set of benthic functional groups. 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 could offer clues to the direction that the system might take in response to perturbations and inform the development of quantitative models reproducing the spatial and temporal dynamics of benthic biodiversity in the Rance estuary.

III.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 their ecosystems is defined by their traits, the development of trait-based modeling 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 modeling 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 benthic biodiversity can be considered to be subject to two principal 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. While there is much information on species traits and general theories on how they should be associated, particularly lacking is a systematic procedure of attributing functional groupings and inter- or intra-group relationships to communities of benthic macroinvertebrates.

Recent work in the terrestrial environment has led to the development of a framework for the construction of functional groups for dynamic models of plant biodiversity (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 case of marine benthic macroinvertebrates satisfies the first condition for the development of mechanistic models of benthic biodiversity (Alexandridis et al., 2017). Here we implement the generated functional groups in a demonstration of a systematic procedure for the attribution of functional relationships between them. As a first inception of the system, we limit ourselves to describing only the qualitative nature of these relationships.

We chose the Rance estuary (Brittany, France) for our study of benthic macroinvertebrates, due to the unique circumstances associated with the construction of a tidal power plant at its mouth between 1963 and 1966. The system was fundamentally altered during this period, after which it was allowed to gradually return to a more natural state. We have a good understanding of specific processes involved in this transition and of present-day aspects of the system's functioning. Still, our predictive ability is very restricted. Extensive investigation of the site has been conducted on three occasions over the last decades (Kirby and Retière, 2009). The most recent one dates back to 1995 and shows high levels of α-(local) and β-diversity (regional) (Desroy, 1998). This pattern is indicative of the existence of functional trade-offs among the species of the system that operate at both small and large spatial scales (Kneitel and Chase, 2004).

Environmental filtering has been recognized as an important community assembly mechanism in the Rance estuary (Desroy, 1998). In principle, it can be manifested in the form of associations between species traits and environmental conditions. It represents large-scale trade-offs that allow species to coexist regionally, as a result of habitat partitioning (Chase and Leibold, 2003), or locally, as a result of source-sink dynamics (Mouquet et al., 2003). Local coexistence is, however, most often associated with life history trade-offs that operate at small spatial scales (Amarasekare, 2003). One set of heuristically valuable, albeit insufficiently tested (Miller et al., 2005), trade-off-related hypotheses, is associated with differential efficiencies of resource utilization and patterns of resource allocation (Tilman, 1990). In the particular case of soft bottom systems, the mobility-mode hypothesis describes trade-offs that are expected to play an important role in the assembly of benthic communities (Posey, 1987).

The objective of our study is to combine hypotheses from ecological theory and expert knowledge into a mechanistic representation of benthic macroinvertebrate communities in the

Rance estuary. In a first step, we examined whether the principles that will form the basis for this representation are supported by observed trait associations. We started by identifying the biological traits that describe the functional role of the system's species (Fig. III.1a). We then investigated the spatial distribution of species traits and environmental variables in 1995, looking for associations between biological traits and abiotic conditions that are indicative of environmental filtering (Fig. III.1b). The existence of life history trade-offs was assessed next. Each of the trade-off related hypotheses makes explicit predictions about the species' role in the respective community assembly mechanisms. We proceeded with the investigation of our set of species traits, seeking trait associations that are indicative of these roles (Fig. III.1c).

The second step aimed at the representation of benthic macroinvertebrate communities by signed-directed graph (or signed digraph) models (Fig. III.1d). The previously defined groups of species represented 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 rules of interaction derived from ecological theory and expert knowledge. The entire procedure was driven by each group's assigned trait values and representative species. The feedback analysis of the signed digraph models demonstrated the potential of the respective systems to persist in time and, therefore, to constitute a plausible representation of the natural world. It also gave some information on the direction of the system's response to perturbations (Fig. III.1e). Our work serves as a first step toward quantitative mechanistic models of benthic biodiversity that are able to reproduce its spatial and temporal dynamics in the Rance estuary.

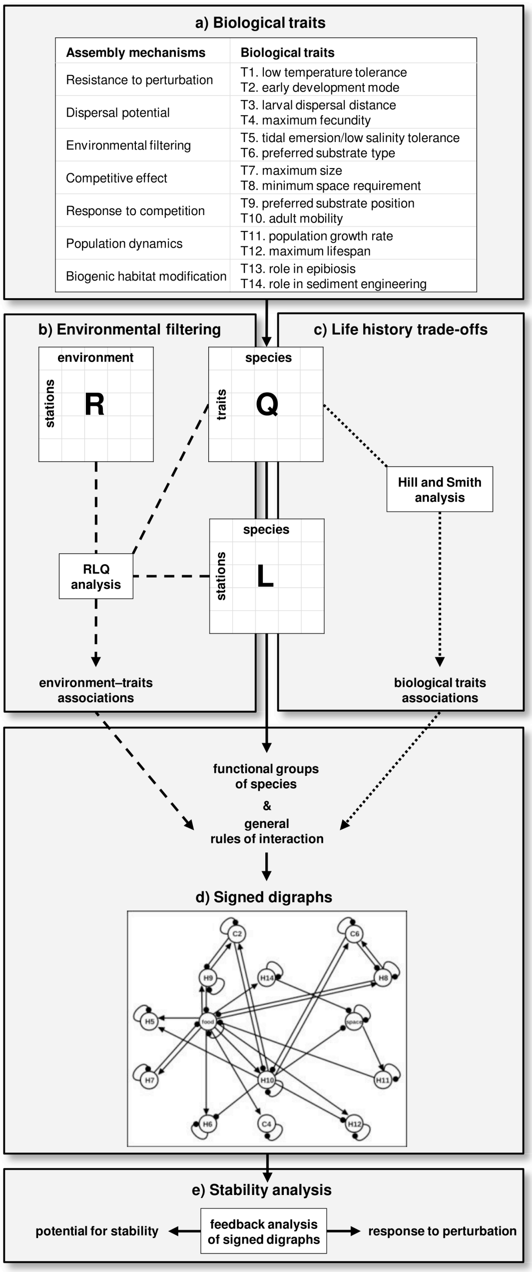


Fig. III.1 Schematic representation of the five steps that comprise the methodology for the mechanistic representation of marine benthos. a) Seven important community assembly mechanisms were selected, each represented by two biological traits that describe the functional role of macroinvertebrate species. For details about the traits, see Table III.1. b) RLQ analysis employed a table of environmental variables (R) and a table of species traits (Q), with a link expressed by a table of species abundances (L), in order to reveal environment–traits associations that support rules of environmental filtering (dashed lines). c) Hill and Smith analysis produced an orthogonal transformation of the table of species traits, in order to reveal biological traits associations that support rules of life history trade-offs (dotted lines). d) The tables of species traits (Q) and abundances (L) were previously combined to build functional groups of species (solid lines). These groups were combined with a set of general rules of interaction for the drawing of signed digraphs, representing functional relationships among benthic organisms. e) The stability analysis of the digraphs illustrated their potential to persist in time and, thus, represent systems that can be found in nature. Further feedback analysis provided insights into the direction in which some of the system's components would respond as a result of perturbations

III.2 Methods

III.2.1 Study site

The Rance estuary (Brittany, France), in the southern part of the English Channel, is characterised by the presence of a tidal power plant situated at its mouth (Fig. III.2). 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 more or less 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, beyond Port-St-Hubert. A similar sequence is observable from the central channel to the banks.

III.2.2 Data collection

A grid of 113 stations was sampled in April 1995, prior to the spring recruitment (Fig. III.2). Sediment samples were washed through a 1 mm sieve and macroinvertebrates retained on the mesh were determined at species level, when possible, and counted. A total of 240 species or higher taxonomic groups belonging to 9 phyla were thus identified (Desroy, 1998). Each station sampled in 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).

III.2.3 Biological traits

The selection of biological traits was made with the goal of identifying characteristics that describe the functional role of the average individual of each species in the most important community assembly mechanisms. The list of mechanisms was mostly adopted from the framework developed by Boulangeat et al. (2012) for the construction of functional groups of terrestrial vegetation. A few adjustments were made to the original framework, in order to adapt it to the special attributes of estuarine benthic systems (Alexandridis et al., 2017).

Since resource competition is included in these mechanisms, we identified food and space as the basic resources for which benthic organisms compete. Space was assumed to be two-dimensional, while food was defined with the goal of dividing species into groups with a homogeneous resource base. The wide-spread adoption of facultative feeding modes among benthic macroinvertebrates only allowed for a distinction between species that feed on algae and detritus on the one hand and those characterized as predators and scavengers on the other.

The remaining 14 traits were divided into 7 categories, each representative of one community assembly mechanism: (1) resistance to perturbation, (2) dispersal potential, (3) environmental filtering, (4) competitive effect, (5) response to competition, (6) population dynamics and (7) biogenic habitat modification. Details about the selected biological traits and the assignment of trait values to the species can be found in Table III.1.

The vast majority of the biological traits information was provided by the following online databases: *eol.org*, *genustraithandbook.org.uk*, *marinespecies.org*, *marlin.ac.uk* and *species-identification.org*. The remainder was acquired from expert knowledge. The quality of the available information for all species and biological traits dictated the resolution of the values that were assigned to them. Lack of information at the species level often obliged us to employ data from higher taxa. The assignment of trait values to the species was done independently for each biological trait. Since, however, we often resorted to higher taxonomic levels, some phylogenetic autocorrelation in trait values among species was unavoidably introduced (for details, see Table B.1 in Annex B).

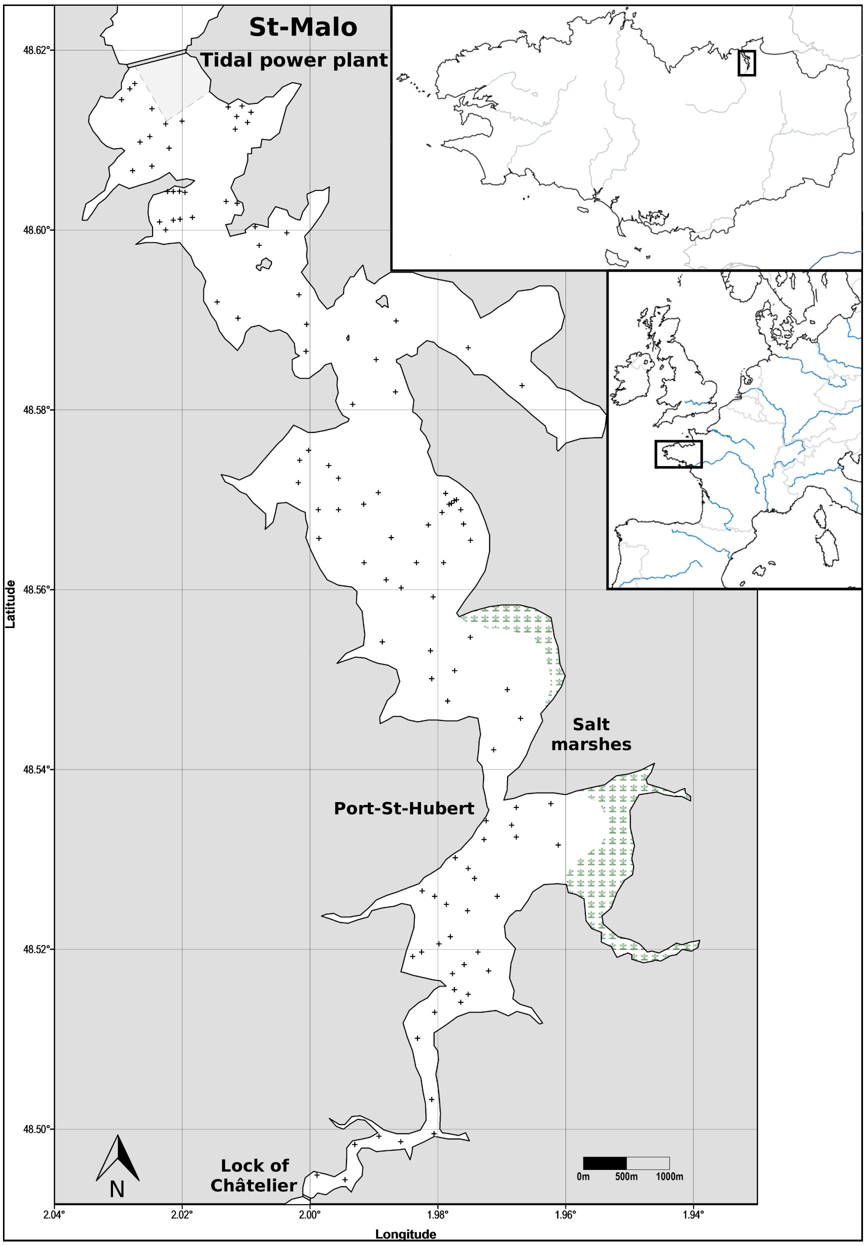


Fig. III.2 Map of the study site. The Rance estuary is situated on the northern coast of Brittany, France. Crosses indicate the location of the 113 stations that were sampled in the spring of 1995. The tidal power plant is located at the mouth of the estuary, south of the city of St-Malo

Table III.1 List of community assembly mechanisms, biological traits that represent the species' role in them, trait values and comments about their assignment to species

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 enhances food availability (McLean and Lasker, 2013)
	T8. minimum space requirement	0.003/0.1/49.5 (min./median/max.) Values do not represent absolute, but 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 do not represent absolute, but 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

III.2.4 Environmental filtering

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 the species of the system (Desroy, 1998). If this is indeed the case, biological traits that describe species preference for abiotic conditions should show high degrees of covariation with the respective environmental variables. Other biological traits that might correlate with the 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 that can be found in 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. This is made possible by the fact that the rows of L correspond to the rows of R and the columns of L correspond to the rows of Q. The end 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.

III.2.5 Life history trade-offs

Our set of biological traits allows the representation of life history 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 favorable to its own members and detrimental to those of the opposite group, sediment preferences (T6) among stabilizers and destabilizers should follow their respective effects on the substrate (T14).

Because trait values were assigned to 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. Hill and Smith analysis is a multivariate statistical procedure that allows 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). Depending on the amount of variance that each of these variables represents, as indicated by the eigenvalues decomposition that forms the basis of the analysis, the projection of the initial variables on the first few axes of the transformed multivariate space can provide insights into the most important associations among biological traits.

III.2.6 Signed digraphs

For the representation of benthic macroinvertebrate communities and their assembly mechanisms, we shifted our focus away from species, toward 20 previously built functional groups (Alexandridis et al., 2017). These groups of species have been assigned with trait values and representative species (Table III.2) and have been found to adequately represent biodiversity in the Rance estuary. Our goal was to incorporate them, along with general rules, into a mechanistic representation of the system. The general rules represented processes of environmental filtering, food consumption, use of space, resource competition and partitioning, reproduction and dispersal, epibiosis, sediment engineering and self-inhibition.

We represented the structure of the system through signed digraphs, in which the functional groups and their basic resources 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 by 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 the aforementioned general rules and the expected role of each functional group in the respective community assembly mechanisms. This role was defined by the group's assigned trait values and representative species.

III.2.7 Stability analysis

We assessed the potential for stability of the generated 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 system stability, classified conditionally stable models accordingly and developed metrics of stability for each model class. Their work was based on the concept of system feedback, which can be defined at different levels of a system, depending on the number of interactions that form a feedback cycle (i.e. feedback cycles at level 1 are self effects, at level 2 they result from pair-wise interactions such as predator–prey, with the highest level of feedback involving *n* number of links for a model with *n* variables). In general terms, negative feedback cycles provide stability and positive feedback cycles act to destabilize a system (Puccia and Levins, 1985). The stability of class I models is jeopardized by positive feedback dominating feedback at the highest level of the system. Instability in class II models is characterized by overcompensation, which leads to oscillations, due to feedback at higher levels in the system overwhelming feedback at lower levels.

Table III.2 Functional groups of species with their assigned representative species and biological trait values (Alexandridis et al., 2017). For details about the biological traits, see Table III.1. 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

The classification of the models and the calculation of the stability metrics were based on qualitatively specified community matrices, which are equivalent to the signed digraphs as a representation of the model system. The potential for stability of class I models is determined by the maximum weighted feedback, which is calculated by counting all feedback cycles (both positive and negative) at the highest level of the system and computing the ratio of their net to absolute sums. Stability of class II models is analyzed by assessing the relative balance of system feedback at higher versus lower levels. With the help of tools specifically designed for the analysis of qualitatively specified community matrices (Dambacher et al., 2002), we assigned our models to one of the two classes. Based on this classification, we calculated the metric that quantifies each model's potential for stability.

All analyses of environmental filtering and life history trade-offs were performed using the statistical software R version 3.2.2 (R Core Team, 2015) with the package ade4 (Dray and Dufour, 2007). 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 qualitative and symbolic analysis of the community matrix (*esapubs.org/archive/ecol/E083/022*) using the technical computing software Maple version 18.0 (Maplesoft, 2014).

III.3 Results

III.3.1 Environmental filtering

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. III.3a) and biological traits (Fig. III.3b) on the first two dimensions of the common co-inertia space reveals one conspicuous pattern: coarse sediment types are strongly associated with trait levels 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 levels, 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 solid elements of abiotic or biotic origin. Increasing water depth is further associated with a transition from organisms that can sustain tidal exposure to those that can only tolerate high salinity levels (T5).

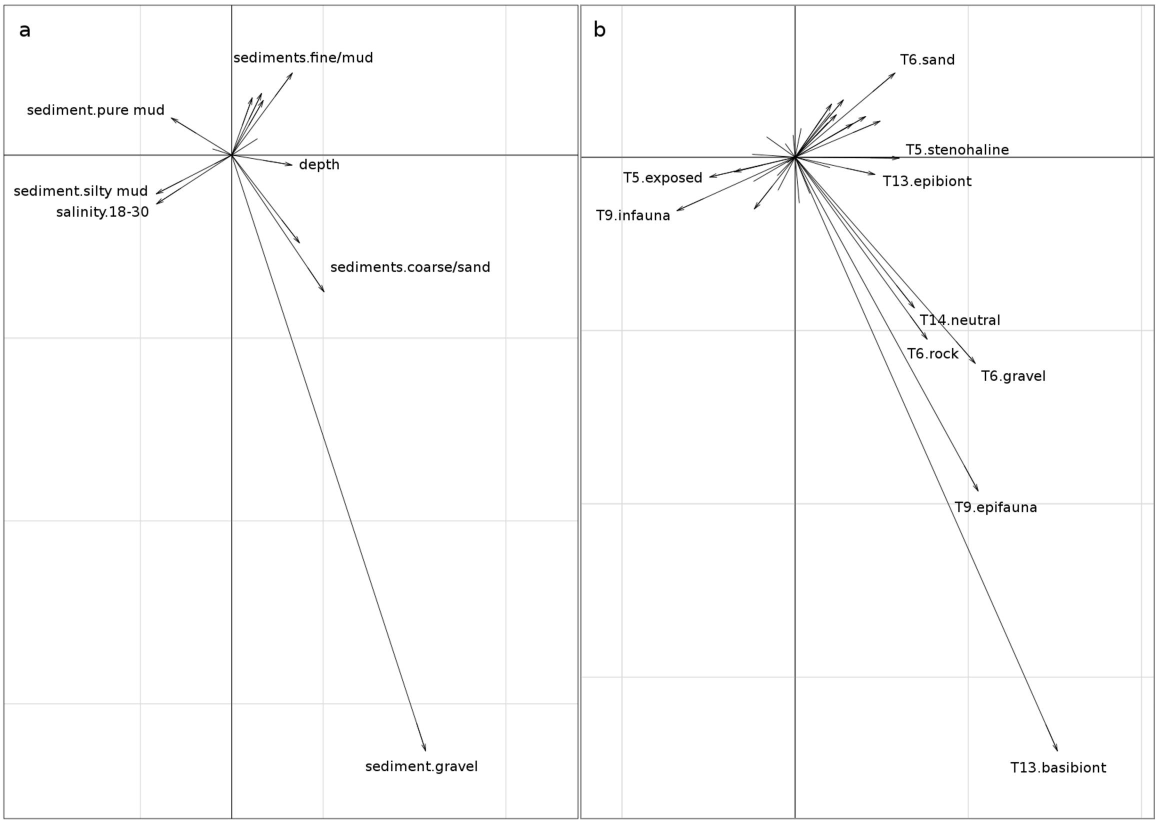


Fig. III.3 Projection of a) environmental variables and b) biological traits on the first two dimensions of the common co-inertia space of the RLQ analysis. In both graphs the horizontal axis represents the first dimension and the vertical the second. In the case of continuous and ordinal variables, 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 closely associated. For details about the traits, see Table III.1

III.3.2 Life history trade-offs

The eigenvalues decomposition of the separate Hill and Smith analysis of 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. III.4a), 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. III.4a), 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 survival rates.

The second axis of the Hill and Smith ordination (Fig. III.4a) 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. III.4a) together with the third and fourth axes of the ordination (Fig. III.4b). 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).

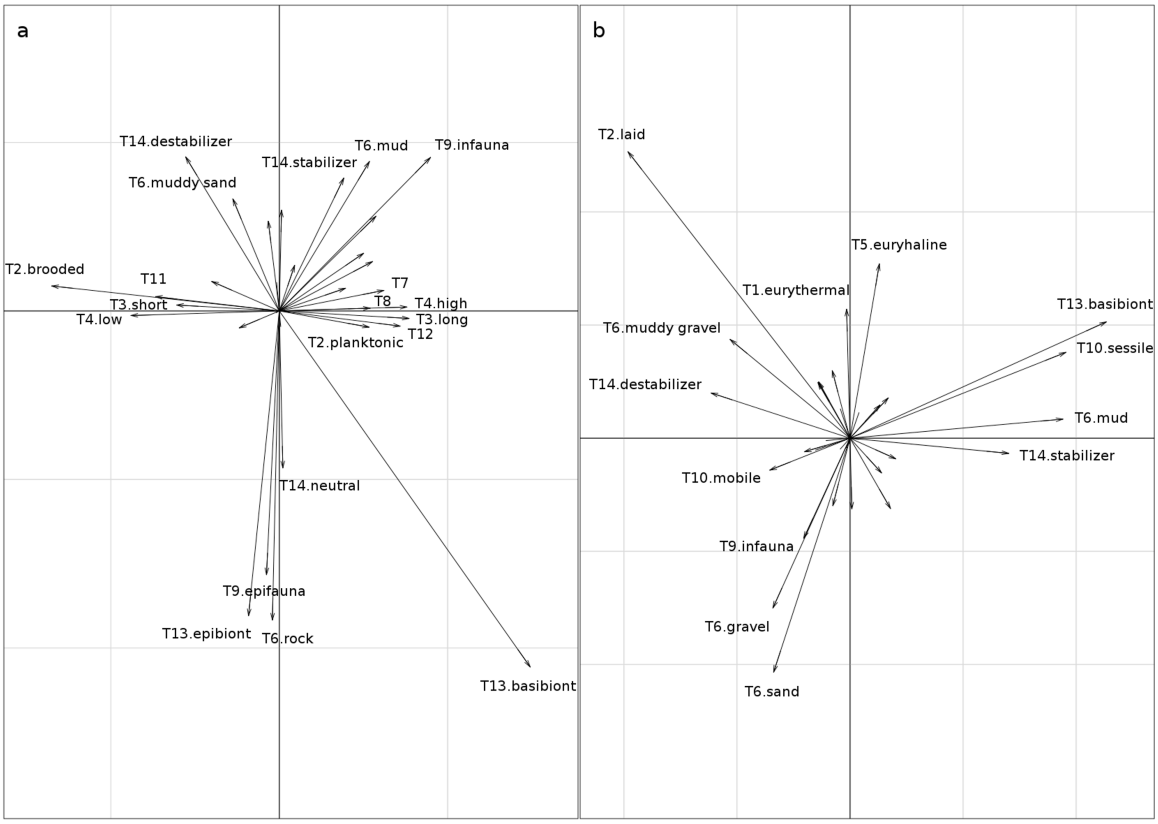


Fig. III.4 Projection of biological traits on a) the first and second and b) the third and fourth dimensions of the transformed multivariate space of the Hill and Smith analysis. In both graphs the horizontal axis represents the lower dimension and the vertical the higher. In the case of continuous and 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 III.1

III.3.3 Signed digraphs

Each node of the signed digraphs represents a functional group, except for the nodes that correspond to the two basic resources, food and space. The clear distinction of epifaunal (T9) organisms with a preference for rock or gravel (T6) from infaunal or interface-positioned organisms (T9) that prefer finer sediment types (T6) (Alexandridis et al., 2017) led us to the drawing of two separate signed digraph models for the sub-systems of these two groups of organisms, signed digraph 1 (SD1) (Fig. III.5a) and signed digraph 2 (SD2) (Fig. III.6a), respectively. 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. Fish and bird predation are not included, because the former plays a restricted role in the Rance estuary, while the latter is highly seasonal and mostly focused on the intertidal zone.

The first set of interactions is related to food consumption. 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 is represented by a negative effect on food and a positive effect on consumers (Fig. III.5b, III.6b). Group H2 in SD1 is excluded from the consumption of the basic food resource, because of the grazing behavior of its representative species. Their continual disturbance activity, which is expected to deprive other organisms of the free use of space (Pascual, 1997), is represented by a consumption interaction with this basic resource.

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). On the other hand, 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, with the energetic costs of prey capture and consumption possibly setting a limit to the predator–prey size difference (Brose et al., 2006a). These general observations led us to assume that groups of predators/scavengers (except for the smallest groups C1 and C4) feed on groups that are smaller or similar in maximum size (T7), but no smaller than 1/3 of the maximum size of the predator/scavenger groups themselves. This interaction is represented by a negative effect on prey and a positive effect on predators (Fig. III.5c, III.6c). 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 are considered as its potential prey. Since the position with respect to the substrate (T9) of all predator/scavenger groups characterizes them as epifauna or interface-related, 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) are excluded from predator–prey interactions.

Just like food, space is assumed to be a basic resource that is “consumed” or used by groups of algae/detritus feeders. Predators/scavengers are 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 “consumption” or use of space by these organisms is represented by a negative effect on space and a positive effect on its consumers (Fig. III.5d, III.6d).

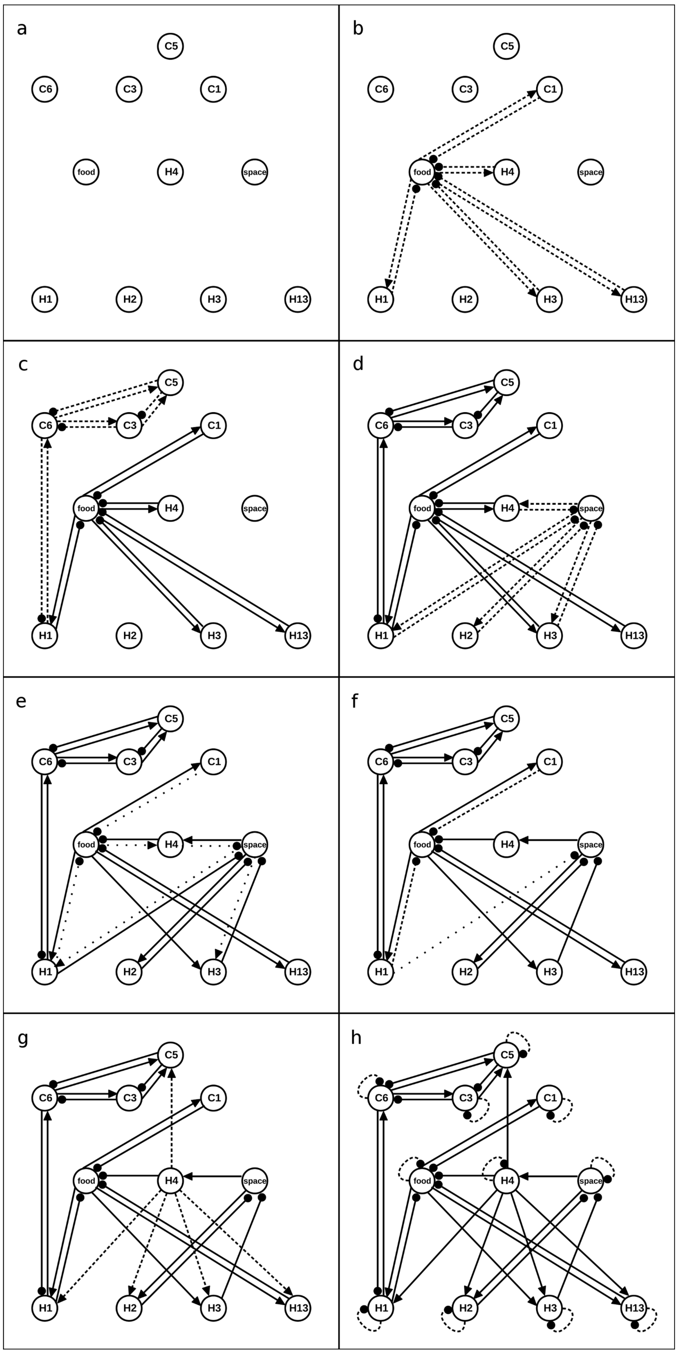


Fig. III.5 Stepwise drawing of signed digraph 1 (SD1). The steps represent processes of a) environmental filtering, b) consumption of algae/detritus, c) predation, d) use of space, e) food–space reduction efficiency trade-off, f) survival–colonization trade-off, g) epibiosis and h) self-inhibition. The nodes represent functional groups (see Table III.2) 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 the links that are added or removed, respectively, at each step. See text for details

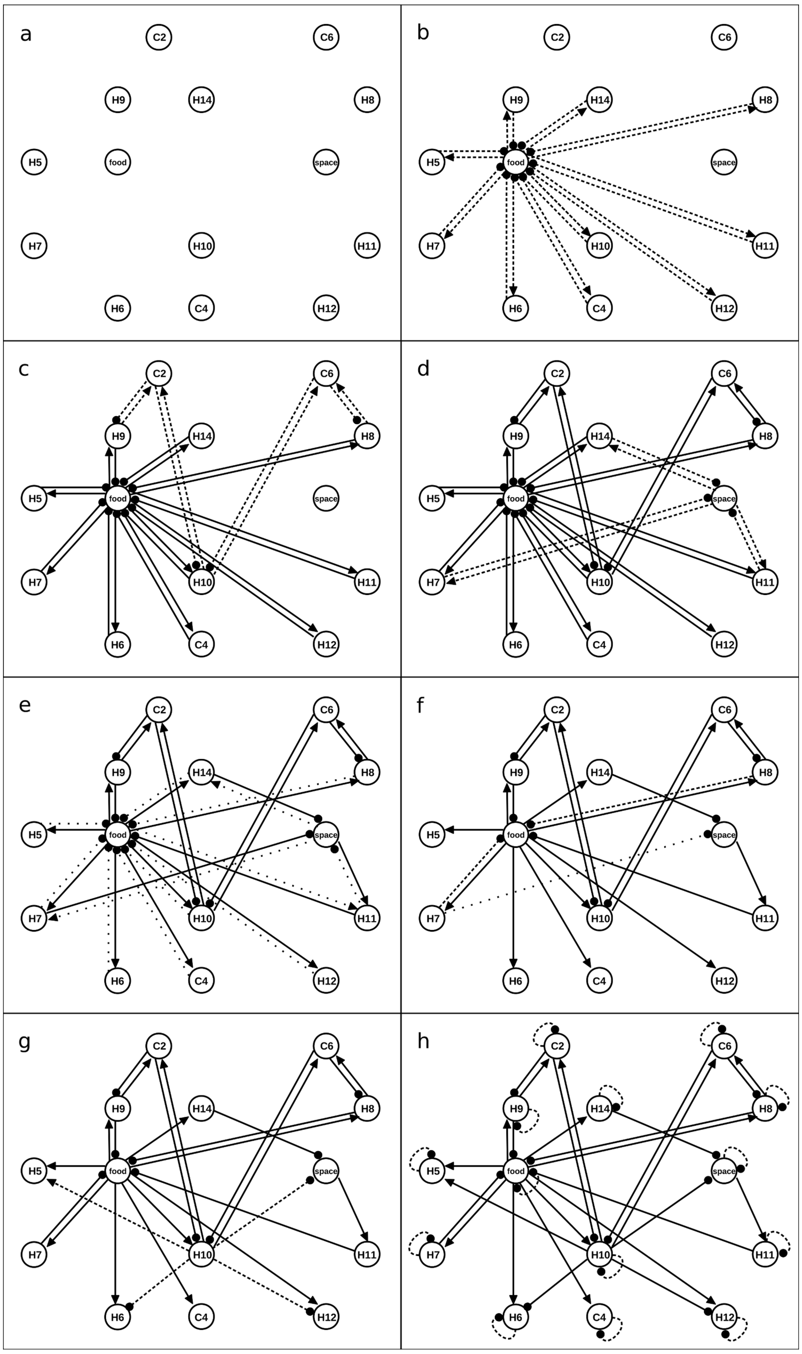


Fig. III.6 Stepwise drawing of signed digraph 2 (SD2). The steps represent processes of a) environmental filtering, b) consumption of algae/detritus, c) predation, d) use of space, e) food–space reduction efficiency trade-off, f) survival–colonization trade-off, g) sediment engineering and h) self-inhibition. The nodes represent functional groups (see Table III.2) 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 the links that are added or removed, respectively, at each step. See text for details

In order to better represent the differences in the functional role of benthic organisms in a way that is consistent with the general trade-offs that are assumed to characterize these functional roles, we resort again to the trait of maximum size (T7). Higher levels of this trait are expected to confer a competitive advantage over food but a disadvantage in the use of space. We, therefore, divide the functional groups of each signed digraph that consume the basic food resource in two categories, the small and the big. We do 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 is 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. III.5e, III.6e). This rule does not apply 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.

We use a combination of three traits to represent the trade-off in the allocation of resources toward early survival versus colonization potential: early development mode (T2), larval dispersal distance (T3) and maximum fecundity (T4). Only functional groups with planktonic early development, long dispersal distance and high fecundity are expected to effectively interact with space, because of their high dispersal potential. The mobility of group H2 in SD1 and its special relationship with space again exclude it from this rule. On the other hand, functional groups with brooded early development are expected to be able to resist a variety of perturbations and, at least locally, reach high levels of abundance. They are, therefore, shown to reduce the basic resource of food, even if their size does not qualify them to do so (Fig. III.5f, III.6f).

The role that organisms play in the phenomenon of epibiosis (T13) is expected to be central to the assembly of the community represented by SD1. The provision of essential structure by the single functional group that is characterized as basibiont (group H4) is represented by a positive effect on all the algae/detritus feeders of the system and the sessile predator/scavenger group C5 (Fig. III.5g). For the system represented by SD2, bioturbation should constitute the main mechanism of biogenic habitat modification (Meadows et al., 2012). Due to its high dispersal potential (T2, T3 and T4) and its role in the phenomenon of sediment engineering (T14) as a destabilizer, group H10 is expected to be mostly responsible for this mechanism. As a result, this functional group is shown to reduce the available space for stabilizing organisms of the interface (basic resource of space) and to have a direct negative impact on infaunal stabilizers (groups H6 and H12). On the other hand, the resulting bioirrigation is expected to create favorable conditions for infaunal destabilizers and is represented by a positive effect on group H5 (Fig. III.6g).

Negative self-effects are added to all the variables of both SD1 and SD2, and represent a variety of processes (Fig. III.5h, III.6h). 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, behavioral inhibition of reproduction, territoriality or accumulation of waste products (Levins, 1998). These or similar processes appear to be widespread in ecological systems (Connell, 1983).

III.3.4 Stability analysis

The results of the stability analysis for the qualitative mathematical models that correspond to SD1 and SD2 are shown in Table III.3. The pattern of increasing weighted feedback with increasing system level in both SD1 and SD2 confirms that they are class I models. We, therefore, used maximum weighted feedback as an indication of their potential for stability. Both models have values for this metric that are well below 0. Maximum weighted feedback equals -0.5 for SD1 and -0.33 for SD2, indicating a high potential for stability for the former model system and a moderate potential for stability for the latter (Dambacher et al., 2003).

Table III.3 Results of the stability analysis for the models that correspond to signed digraphs 1 and 2 (SD1 and SD2). 'wF' represents weighted feedback calculated at the system level that is indicated by the ensuing number. Both models belong to class I (sensu Dambacher et al. (2003)), so their potential for stability is determined by the maximum weighted feedback, i.e. the weighted feedback calculated at the highest system level (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 two basic resources are part of positive feedback cycles of length four (Fig. III.7). External forces acting on the system through one of the basic resources would tend to push the other variables of the cycles in opposite directions (Marzloff et al., 2011). In the case of SD1, the positive feedback cycle is formed by group H3 being enhanced by food while reducing space. Group H4 has the opposite role in the cycle, i.e. it is enhanced by space and reduces food. In the case of SD2, there are two equivalent positive feedback cycles. The role of reducing space while being enhanced by food is played by either group H10 or H14. In both cycles the opposite role is played by group H11, which is enhanced by space and reduces food.

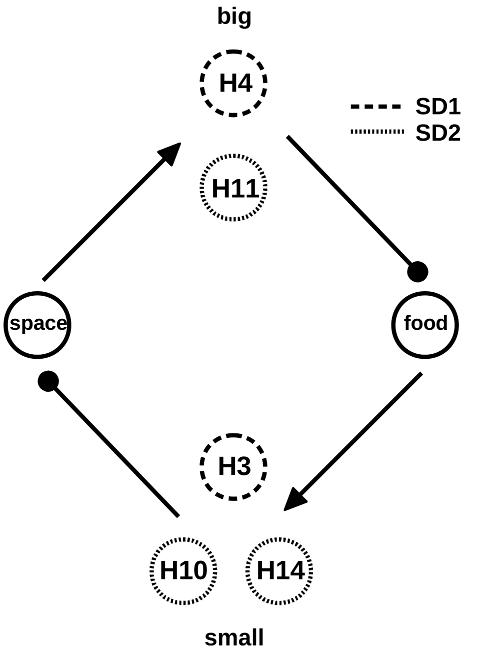


Fig. III.7 Positive feedback cycles involving the basic resources of food and space and a set of big (upper side) and small (lower side) functional groups from signed digraphs 1 (SD1) and 2 (SD2)

III.4 Discussion

III.4.1 Environmental filtering

The common structure between environmental variables and biological traits represents a considerable portion of their independent structures, in support of the importance of observed variable associations across the two data sets. However, the comparison of correlation values between sites and species scores from the RLQ analysis with the same values from the correspondence analysis of the species abundance table shows that a considerable portion of biodiversity patterns remains unexplained by traits–environment associations. These observations are in accordance with the results of statistical analyses of benthic biodiversity previously performed in the Rance estuary, which showed that the assignment of macroinvertebrate species to distinct communities can be a statistically significant but not particularly effective predictor of their spatial distribution (Desroy, 1998).

It appears that niche differences among macroinvertebrate species in the Rance estuary are mostly related to characteristics of the seabed. A similar conclusion was reached by the assignment of these species to functional groups, which clearly distinguished between organisms that occupy the sediment surface supported by hard structures and those that are buried deep in the sediment or at the water/sediment interface (Alexandridis et al., 2017). The occurrence of the former groups was mainly attributed to the living or dead shells of basibiotic organisms, but source-sink dynamics (Mouquet et al., 2003) within the Rance estuary or the southern part of the English Channel should not be excluded. Contrary to expectations, salinity does not appear to play a significant role as an environmental filter, but tidal exposure does, even if only secondary to substrate type.

III.4.2 Life history trade-offs

The proportion of total variation in species traits that is represented by the first four axes of the Hill and Smith analysis is rather small. It should be noted, however, that traits were selected and their values attributed with the goal of representing the role of 240 species in a variety of community assembly mechanisms. To reduce this level of variability to four independent variables is especially difficult, unless we have some idea about the relative importance of each represented mechanism, which would allow the application of weights to the respective biological traits. This is, however, not the case, which is also why we opted for a qualitative modeling approach.

The observed association between traits conferring a competitive advantage for food and a competitive disadvantage for space indicates the existence of a trade-off among benthic organisms in their ability to compete over limited amounts of these two resources (Tilman, 1980). Food (Ingels et al., 2014) and space (Lord and Whitlatch, 2015) have been shown to play a central role in competitive interactions within the marine benthos. Recent work suggests that their combined representation as limiting resources can significantly increase our understanding and predictability of marine benthic systems (Svensson and Marshall, 2015).

The negative association between biological traits linked to high survival rates on the one hand and high colonization potential on the other suggests that a survival–colonization trade-off is effective among benthic organisms (Tilman, 1990). Resistance to disturbance (Schratzberger and Larcombe, 2014) and colonization potential (Limberger and Wickham, 2011) have been involved in trade-offs with competitive ability in the marine benthos. Our results support both scenarios, while the deconstruction of competitive ability into two constituents, one for each of the limiting resources, might be able to explain inconsistencies in previous studies.

The survival–colonization trade-off represents community assembly mechanisms that operate during the early life stages of benthic macroinvertebrates. The previous functional grouping of the same species indicated that reproductive strategies might be under-represented in our set of biological traits, due to the lack of information for most of the organisms (Alexandridis et al., 2017). A more detailed representation of recruitment-related mechanisms would allow the evaluation and modeling 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 clear distinction of organisms that occupy the sediment surface supported by solid structures is a reiteration of the main findings of the RLQ analysis. It represents the benefits involved in an epibiotic life cycle (Wahl, 1989), regardless of whether the basibiotic organisms are still alive or not (Wahl and Mark, 1999). Among the rest of the species, their substrate preferences appear to match their effect on the sediment, thus supporting the separation of benthic macroinvertebrates into groups of sediment stabilizers and destabilizers (Posey, 1987). This tenet of the mobility-mode hypothesis has been empirically upheld and shown to have cascading and long-lasting effects on marine benthic communities (Volkenborn et al., 2009).

III.4.3 Signed digraphs

The fact that assemblages of organisms that occupy the surface of the sediment and those that are buried in it are adequately divergent in function, to the point of being independently represented in studies of marine benthos, has been previously recognized (Reiss et al., 2010). The trait values of epibenthic organisms indicate their preference for settlement on hard substrate. In a site like the Rance estuary, where soft bottoms dominate, their system, represented by SD1, should at least in part owe its existence to the phenomenon of epibiosis. The shared group C6 is an obvious but probably not the only way in which the two systems might interact.

Benthic species were separated in two feeding groups in order to preserve the homogeneity of their resource base (Alexandridis et al., 2017). It is a requirement of the neutral constituent of the emergent group hypothesis, which formed the basis for their functional grouping (Hérault, 2007). This choice might appear to ignore important differentiations in the feeding habits of these organisms. It has been, however, shown that feeding behavior in the marine benthos is highly facultative and categorizations, like the one between suspension- and deposit-feeders, are not always valid (Snelgrove and Butman, 1994).

Instead, modifications of the basic network of trophic interactions through expert knowledge are expected to increase its realism, while the use of allometric scaling should enhance the systems' stability (Brose et al., 2006b). The role of recruitment in the assembly of benthic communities could still be under-represented. Biological traits related to species' reproductive strategies were found to deviate the most from the theoretical assumptions that allowed the construction of functional groups (Alexandridis et al., 2017). We tried to address this issue by employing three different traits for the representation of the survival–colonization trade-off.

Qualitative mathematical modeling is characterized by its ability to represent and combine interactions of sometimes disparate nature. This is obvious in the simultaneous representation of the use of food and space along with biogenic habitat modification, which would be particularly challenging in a quantitative framework (but see Kéfi et al. (2012)). Epibiosis has increased in significance in the Rance estuary since the introduction in the 1970's of the slipper limpet, *Crepidula fornicata*, whose living and dead shells can alter the characteristics of the seabed (Desroy, 1998). Sediment engineering should also play an important role, but this might be contingent on the density of engineering organisms reaching some threshold values (Posey, 1987).

III.4.4 Stability analysis

The qualitative mathematical models developed in this work have a moderate to high potential for stability, which accords well with the view that benthic communities in the Rance estuary have been more or less stable since the end of the 1970's (Desroy, 1998). These results demonstrate the potential of the models to represent systems that actually exist in nature.

Populations of benthic macroinvertebrates in the Rance estuary are still expected to respond to forces external to the system, but in a way that could be attributed to the structure of the respective model. 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 to a potential system-wide change in algae or detritus. 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 of the 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).

III.5 Conclusions

Qualitative mathematical modeling has been successfully employed for the study of both soft- (Ortiz and Wolff, 2002) and hard-bottom (Marzloff et al., 2011) marine communities. Its properties make it particularly well-suited for the integration of ecological and socio-economic systems (Dambacher et al., 2007). Benthic macroinvertebrates are often represented by a few nodes in qualitatively specified food-web models, in which only a few species of interest are explicitly depicted, while all other are lumped based on simplifying assumptions that might restrict the generality of the generated conclusions (e.g. Carey et al., 2014; Reum et al., 2015).

Our approach primarily differs from previous work in the way organisms are represented and interactions are attributed between them. The functional groups that comprise the core of our models were built with the goal of efficiently reproducing functional diversity in the Rance estuary and were rigorously assessed against that goal (Alexandridis et al., 2017). The wide functional scope of the biological traits that formed the basis for this grouping and the multivariate analyses hereby performed, allowed us to represent not just trophic interactions, but the majority of the mechanisms that are expected to shape marine benthic communities in many parts of the world. This was done through a systematic procedure that can be readily applied to similar systems, where empirical investigation and the mechanistic understanding that comes with it have been traditionally restricted.

One of the main advantages of qualitative mathematical models lies in their ability to change with minimum time cost. When there is uncertainty in the model components or interactions, alternative model configurations can be generated and assessed with respect to the system's functioning. We plan to use this property of qualitative mathematical modeling, in order to inform the structure of dynamic and spatially explicit models of the same systems. Their quantification should help us produce precise predictions about both short- and long-term changes of benthic biodiversity in the Rance estuary in response to potential perturbations.

III.6 References

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.

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

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.

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., 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.

Chase, J.M., Leibold, M.A., 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, USA.

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

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.

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 dissertation. 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.

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

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

Ingels, J., Dashfield, S.L., Somerfield, P.J., Widdicombe, S., Austen, M.C., 2014. Interactions between multiple large macrofauna species and nematode communities – Mechanisms for indirect impacts of trawling disturbance. J Exp Mar Biol Ecol 456, 41-49.

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.

Kirby, R., Retière, C., 2009. Comparing environmental effects of Rance and Severn barrages. P I Civil Eng-Mar En 162, 11-26.

Kneitel, J.M., Chase, J.M., 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol Lett 7, 69-80.

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

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

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.

Lord, J., Whitlatch, R., 2015. Predicting competitive shifts and responses to climate change based on latitudinal distributions of species assemblages. Ecology 96, 1264-1274.

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.

Miller, T.E., Burns, J.H., Munguia, P., Walters, E.L., Kneitel, J.M., Richards, P.M., Mouquet, N., Buckley, H.L., 2005. A critical review of twenty years' use of the resource-ratio theory. Am Nat 165, 439-448.

Mouquet, N., Loreau, M., 2003. Community patterns in source-sink metacommunities. Am Nat 162, 544-557.

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

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.

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

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.

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.

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., 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.

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., 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Mar Ecol Prog Ser 58, 175-189.

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.

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.

Chapter IV: Agent-based modelling of the multi-scale dynamics of marine benthic communities

Abstract

Modelling marine benthic biodiversity for exploratory or predictive purposes requires the representation of community assembly mechanisms that operate at distinct spatial and temporal scales. Analytical research has offered insights into the nature of these processes. However, their synthesis in a quantitative framework cannot be easily achieved through traditional modelling techniques. Previous work in the Rance estuary (Brittany, France) revealed the principal functional components of its benthic macroinvertebrate communities and derived a set of relationships of the organisms with their environment and with each other. These elements are combined here for the development of a dynamic and spatially explicit agent-based model that operates at two spatial scales. At the small scale, the model represents trophic and non-trophic interactions among individual organisms. The large scale model uses information on community composition and abiotic conditions to reproduce the organisms' dispersal and the filtering effect of their environment. The dynamic integration of the two models recreates the combined effect of disparate processes on both local and regional patterns of benthic biodiversity. The predictive scope of the model is restricted by the lack of detailed information on important biological traits, but the approach shows potential for the investigation of fundamental ecological questions.

IV.1 Introduction

The investigation and, ultimately, prediction of biodiversity patterns in the marine benthos can be greatly facilitated by the development of mechanistic models of community assembly. Abundance patterns in communities of marine benthic macroinvertebrates result from the interplay of many mechanisms. Some of them, like environmental filtering, may operate at time scales that render them practically constant for the external observer. Other mechanisms, like disturbance due to extreme weather events, may have similar effects throughout a system's spatial extent. Modelling these mechanisms of community assembly would require the reproduction only of their spatial or temporal characteristics. However, most of the mechanisms of community assembly involve processes that may vary both in space and in time, the same holding true for the ways in which they interact. Mechanistic modelling of marine benthic macroinvertebrates would, accordingly, have to be implemented in a dynamic and spatially explicit framework, if it was to reveal the role of these mechanisms in shaping marine benthic communities.

The modelled entities of this framework would ideally represent individual organisms, since this is the level at which biotic interactions that lie behind community assembly mechanisms naturally take place. The role of these entities in the selected mechanisms of community assembly is expected to be largely controlled by biological traits that have been long collected and studied for species of benthic macroinvertebrates. Representing individuals of different species in a way that is consistent with known inter-specific trait differences appears, therefore, to be a suitable framework for a dynamic model of marine benthic communities. The observed levels of species richness would render the development of such a model particularly demanding and itself analytically intractable. The use, instead, of only a few dominant or representative species could solve this problem, but it might restrict the generality of the generated conclusions.

Similar concerns in the development of mechanistic models of terrestrial vegetation led to the development of a framework for the construction of plant functional groups (Boulangeat et al., 2012) on the conceptual basis of the emergent group hypothesis (Hérault, 2007). The emergence of the groups is the result of correlations among biological traits that represent the species' role in a set of important community assembly mechanisms. The adaptation of this framework to communities of marine benthic macroinvertebrates and the assessment of its assumptions against observations from the Rance estuary (Brittany, France) in 1995 allowed the definition of the system's principal functional components (Alexandridis et al., 2017). The trait values that were assigned to the functional groups during this systematic and testable procedure are expected to effectively represent their role in the selected set of community assembly mechanisms.

Competition for a limited amount of resources is central among these mechanisms, with food and space as two obvious candidates (Ingels et al., 2014; Lord and Whitlatch, 2015). Benthic macroinvertebrates in the Rance estuary appear to be differentiated with regard to their use of space between those that are buried in the sediment and those that occupy its surface supported by hard substrate (Chapter III). The dominance of soft bottoms indicates that the latter, at least partly, occur due to the phenomenon of epibiosis. Trophic groupings like the one between suspension- and deposit-feeders seem invalid in view of the highly facultative feeding behaviour of benthic organisms (Snelgrove and Butman, 1994). The requirement for a grouping that preserves the homogeneity of the groups' trophic base (Hubbell, 2005) justifies the separation of benthic organisms into algae/detritus feeders and predators/scavengers. The generated basic network of trophic interactions can be modified through expert knowledge and theoretically anticipated allometries, thus increasing its realism and its potential for stability (Brose et al., 2006b).

The majority of predators appear to be larger than their prey and predator size tends to increase with prey size (Cohen et al., 1993). On the other hand, predator–prey body-size ratios are generally the lowest, just over 2 on average, for marine invertebrates, compared to other taxonomic groups and habitat types. It is possible that the energetic costs of prey capture and consumption set a limit to predator–prey size gaps (Brose et al., 2006a). In the Rance estuary, fish predation of benthic macroinvertebrates is rather restricted and predation by birds is highly seasonal and mostly focused on the intertidal zone (Nicolas Desroy, *personal communication*). The mortality that is caused by predatory macroinvertebrates, although very difficult to estimate, appears likewise to be limited in magnitude, as far as adult prey is concerned. This is due partly to the greater impact of predation on juvenile individuals and partly to the partial ingestion of adults and the regenerative properties of many macroinvertebrate species. The predation rate that is experienced by a species appears to be dictated by its relative abundance (Desroy, 1998).

Post-settlement mortality of juvenile individuals is one of the many abiotic and biotic factors that influence the recruitment of benthic macroinvertebrates (Olafsson et al., 1994). It shows high levels of both intra- and inter-specific variation (Hunt and Scheibling, 1997). Information at the former level indicates that small initial increments in body size lead to significant increases in survival rates in the face of predation (Gosselin and Qian, 1997).

The supply of larvae and the settlement of juveniles are still prerequisites for post-settlement processes to occur, but their complexity often makes simplifications particularly difficult (Pineda et al., 2009). The settlement probabilities of different species are expected to be influenced by the traits of fecundity, dispersal distance and early development mode, which form trait combinations indicative of trade-offs between early survival and colonization potential (Kupriyanova et al., 2001). The abiotic environment is also expected to influence the successful settlement of juveniles. Apart from the direct effect of environmental filtering due to tidal exposure or the existence of suitable substrate, benthic organisms are also known to modify their habitat through sediment stabilization and destabilization, thus modulating the settlement probabilities of new recruits (Posey, 1987).

Large year-to-year fluctuations of adult abundances of a polychaete species in the English channel were found not to be related to larval supply, an indication of the significance of post-settlement processes (Ellien et al., 2000). Besides juvenile and adult predation mortality, competition for food and space is expected to be central among them. The effect of these two resources on benthic macroinvertebrates can be quite variable, depending on abiotic factors and the life stage of organisms, and can be additionally confounded by potential resource interactions (Svensson and Marshall, 2015). In general, it appears that the trait of adult body size plays a crucial role in the definition of competitive hierarchies. Smaller species are expected to show higher growth rates and to be better competitors for limited amounts of space, while larger species can occupy larger areas and should be competitively superior in face of food limitation (Chapter III). Intra-specific competition for food and space can also affect individual growth rates (Côté et al., 1994).

The spatial scales at which pre- and post-settlement processes take place are not expected to overlap, as pre-settlement processes should operate at much larger scales than post-settlement ones (Fraschetti et al., 2002). Exchanges across scales are mainly the result of larval dispersal; immigration and emigration of adults can in most cases be considered as unimportant for the population dynamics of benthic species (Eckman, 1996).

This set of ecological principles provided the conceptual and methodological framework for the construction of a dynamic and spatially explicit agent-based model (ABM) of benthic macroinvertebrates in the Rance estuary. The model combines two spatial scales, one at the level of a sampling area and one at the level of the whole system. The former, small-scale model represents processes of sediment engineering, epibiosis, settlement of juveniles, post-settlement mortality, competition for food and space, predation and mortality due to ageing. Its entities are juvenile and adult individuals that belong to one of 20 functional groups. Their role in the aforementioned processes was defined by their set of biological traits. The latter, large-scale model represents processes of environmental filtering due to tidal exposure and larval dispersal and employs the output of the small-scale model in each time step of one year. Its output, along with information on the tidal regime, is in turn used as input by the small-scale model during each year's representation of juveniles' settlement. The goal is to explore, through the process of model verification, the feasibility of representing a system of benthic macroinvertebrates within the specified conceptual and methodological framework. The modelling effort is far from being concluded, as there remain many possibilities for refinement and expansion.

IV.2 Methods

The model consists of two spatially nested sub-models (Fig. IV.1). The small-scale model represents the level of a sampling area and the large-scale model represents the Rance estuary. In both models space is two-dimensional and each time step corresponds to one year. The small-scale model represents space occupation by individual macroinvertebrates that belong to one of 20 functional groups (Alexandridis et al., 2017). These individuals start as juvenile settlers and grow into adults, with the goal of avoiding death due to competition and predation and reaching their full lifespan. The rules that define the interaction of individuals with their environment represent important elements of their life history and are dictated by the trait values of the functional group to which each individual belongs (Table IV.1). The combination of these trait values among the functional groups is representative of large-scale (environmental filtering) and small-scale (life history) trade-offs that are expected to control the assembly of marine benthic communities (Chapter III). The large-scale model represents the distinction between the subtidal and the intertidal zone and the interaction of metapopulations of the 20 functional groups through larval dispersal. Each spatial entity of the large-scale model is represented by one realization of the small-scale model. These realizations are separated into those of the subtidal and the intertidal zone, each category being represented by a distinct small-scale model. All model realizations interact in space and time through the large-scale model.

Agent-based modelling allows the emergence of intricate patterns from simple rules of interaction, providing an intuitive framework for the representation of complex ecological systems (DeAngelis and Mooij, 2005). However, it is these characteristics that often render model analysis particularly burdensome. Difficulties in the evaluation of ABMs due to their documentation motivated the development of the ODD (Overview, Design concepts and Details) protocol (Grimm et al., 2006). The authors proposed a standard structure for the documentation of ABMs, with the goal of facilitating reading and writing model descriptions (Grimm et al., 2010). The description of the small-scale model, which is relatively complex, follows the ODD protocol, while the much simpler large-scale model is described in short.

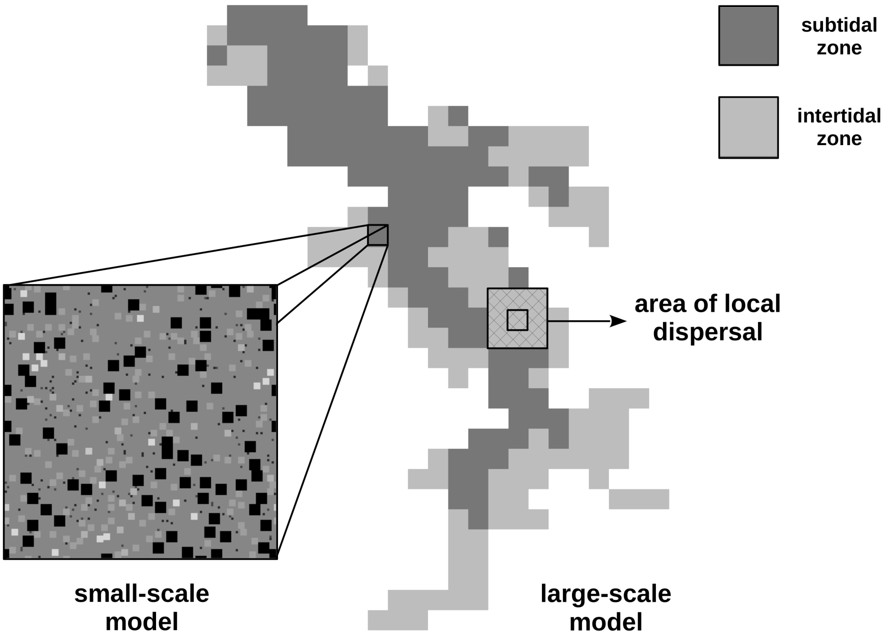


Fig. IV.1 Graphical representation of the large-scale model of the Rance estuary, divided into the subtidal and the intertidal zone. Each patch of the two tidal zones is represented by one realization of the respective small-scale model. This model has approximately the dimensions of a sampling area and represents the space that is occupied by individuals of different functional groups (illustrated as squares of different sizes and colours). The realizations of the small-scale model interact in each time step through local larval dispersal. During this process, the contribution of each functional group to the spawner pool that is employed in each small-scale model is defined as the relative abundances of the groups within the area comprised of the respective patch of the large-scale model and its 8 immediate neighbours (cross hatched square)

Table IV.1 Functional groups of species with their assigned representative species and biological trait values (Alexandridis et al., 2017). Group names starting with ‘FG’ and ‘FGP’ correspond to algae/detritus feeders and predators/scavengers, respectively

Groups	Representative species	Temperature	Development	Dispersal	Fecundity	Tide/salinity	Substrate	Size (cm)	Area	Position	Mobility	Growth rate	Lifespan (yr)	Epibiosis	Engineering
FG1	*Myrianida edwardsi*	stenothermal	planktonic	long	low	stenohaline	mud	1.4	3.1	interface	mobile	5.8	1.9	neutral	neutral
FG2	*Thyasira flexuosa*	eurythermal	planktonic	short	low	stenohaline	mud	3.6	0.8	infauna	mobile	1.0	10.0	neutral	stabilizer
FG3	*Oligochaeta*	stenothermal	laid	short	low	emersed	muddy sand	4.5	5.0	infauna	mobile	3.4	2.0	neutral	destabilizer
FG4	*Notomastus latericeus*	stenothermal	brooded	short	low	stenohaline	muddy sand	6.0	2.9	interface	mobile	2.6	1.9	neutral	destabilizer
FG5	*Melinna palmata*	stenothermal	brooded	short	low	stenohaline	mud	7.5	0.3	interface	sessile	2.6	3.6	neutral	stabilizer
FG6	*Glycymeris glycymeris*	stenothermal	planktonic	short	high	stenohaline	muddy gravel	8.0	1.4	infauna	mobile	0.8	15.0	neutral	stabilizer
FG7	*Malacoceros fuliginosus*	eurythermal	planktonic	long	high	euryhaline	mud	8.5	1.9	interface	mobile	2.5	2.7	neutral	destabilizer
FG8	*Cerastoderma edule*	stenothermal	planktonic	long	high	emersed	muddy sand	8.6	0.5	interface	mobile	0.7	8.9	neutral	stabilizer
FG9	*Crepidula fornicata*	stenothermal	planktonic	long	high	stenohaline	rock	7.6	0.0	epifauna	sessile	1.9	11.2	basibiont	neutral
FG10	*Galathowenia oculata*	eurythermal	planktonic	long	high	euryhaline	mud	11.1	0.0	interface	sessile	2.7	4.4	neutral	stabilizer
FG11	*Hediste diversicolor*	eurythermal	laid	short	high	emersed	muddy sand	12.8	0.2	interface	mobile	2.1	3.4	neutral	destabilizer
FG12	*Sphaerosyllis bulbosa*	stenothermal	brooded	short	low	stenohaline	gravel	1.3	0.5	epifauna	mobile	4.7	1.9	neutral	neutral
FG13	*Balanus crenatus*	eurythermal	planktonic	long	high	euryhaline	rock	2.0	0.8	epifauna	sessile	2.5	2.0	epibiont	neutral
FG14	*Morchellium argus*	eurythermal	brooded	short	low	stenohaline	rock	3.3	0.1	epifauna	sessile	2.6	1.7	epibiont	neutral
FG15	*Anapagurus hyndmanni*	stenothermal	planktonic	long	high	stenohaline	gravel	10.0	0.1	epifauna	mobile	0.6	10.0	neutral	neutral
FG16	*Lepidochitona cinerea*	stenothermal	planktonic	short	high	stenohaline	rock	10.8	4.1	epifauna	mobile	0.9	11.6	epibiont	neutral
FGP1	*Syllis cornuta*	stenothermal	planktonic	long	low	stenohaline	rock	7.4	5.2	epifauna	mobile	2.3	2.3	epibiont	neutral
FGP2	*Marphysa bellii*	stenothermal	planktonic	short	high	stenohaline	muddy sand	23.3	0.3	interface	mobile	1.1	4.7	neutral	neutral
FGP3	*Nephtys hombergii*	stenothermal	planktonic	long	high	stenohaline	gravel	10.5	0.3	interface	mobile	2.2	7.3	neutral	neutral
FGP4	*Urticina felina*	eurythermal	planktonic	short	high	euryhaline	rock	16.7	10.3	epifauna	sessile	1.1	14.0	epibiont	neutral

IV.2.1 Small-scale model

IV.2.1.1 Purpose

The model was designed to explore the potential of reproducing observed patterns of abundance distribution for functional groups of benthic macroinvertebrates, using simple rules related to inter- and intra-group competition for food and space, sediment engineering and epibiosis. It is in this sense a model of α-diversity and a general framework that can incorporate many additional community assembly mechanisms and a quantitatively more realistic representation of the system.

IV.2.1.2 Entities, state variables and scales

The model's only entities, its patches, make up a square grid, with dimensions of 60 × 60 patches. In order to avoid edge effects, the grid wraps both horizontally and vertically into a torus. Each patch has two sets of state variables, one for the infauna and one for the epifauna. One variable in each set indicates whether a patch is occupied and by a member of which functional group (sp/ep). There are twenty functional groups. Ten of them belong to the infauna (FG1-8, FG10-11), five groups belong to the epifauna (FG12-16), one can be part of both the infauna and the epifauna (FG9) and four groups represent predator/scavenger organisms (FGP1-4). The infauna consists of four small groups (FG1-4), which can occupy one patch, five intermediate groups (FG5-9), which start at one patch and can occupy its eight immediate neighbours during their growth, and two large groups (FG10-11), which can, through the same procedure, occupy one patch and its twenty-four closest neighbours. The infaunal group that also belongs to the epifauna (FG9) represents basibiotic organisms that are intermediate in size. It is on patches occupied by this group that epifauna, including individuals of the same group but staying small in size, can settle and grow. In total, the epifauna consists of four small groups (FG9, FG12-14), which can occupy one patch, and two intermediate groups (FG15-16), which start at one patch and can occupy its eight immediate neighbours during their growth. The other two variables of each set are used for the central patch of individuals (g/a, h/ag). The first one identifies those among the individuals of intermediate and large groups that grow in spite of competition and the second one gives the age of the individuals of all groups that survive at the end of each year. One global variable for each functional group of the infauna and the epifauna describes the respective group abundances (g1-16). One additional variable gives the same number only for the infaunal individuals of the basibiotic functional group (ba). One global variable for each functional group of the infauna and the epifauna represents the contribution of each group to the respective spawner pool, for use in the recruitment process at the start of each year (fg1-16). Two global variables give the number of sediment stabilizing and destabilizing individuals (es, ed), while another one gives the x and y coordinates of the site (xy), employed during exporting and importing the model's current status. Five more variables keep track of the central patches of the individuals of small, intermediate and large infaunal and epifaunal groups that survive at the end of each year (s/m/l, sm/la). Finally, one global variable for each predator/scavenger group describes their respective abundance at the end of each year (p1-4). Patch size corresponds to the area exclusively occupied by an individual that belongs to one of the small functional groups. The dimensions of the grid represent an arbitrary sampling area of the real system. One time step corresponds to one year, starting right before the spring dispersal.

IV.2.1.3 Process overview and scheduling

Every time step starts by moving time one step forward. The first of the model's actions represents the process of recruitment. First, the contribution of each group of the infauna and the epifauna to the respective spawner pool is defined as the group's contribution to the total abundance of the respective set of groups during the previous time step within an area defined in the large-scale model. Then juveniles of the eleven infaunal groups settle randomly on empty patches, with settlement probabilities defined by the contribution of each group to the spawner pool, their fecundity, dispersal distance, early development mode, role in sediment engineering and position in the sediment and the relative abundance of sediment stabilizing and destabilizing functional groups during the previous time step. The juveniles experience post-settlement mortality with rates that are dictated by each group's adult size and those that die are removed from the system. Next, juveniles of the six epifaunal groups settle randomly on patches that are occupied by infaunal adults of the basibiotic functional group and are empty of any epibiotic groups, with settlement probabilities defined by the contribution of each group to the spawner pool, their fecundity, dispersal distance and early development mode. The juveniles experience post-settlement mortality with rates that are dictated by each group's adult size and those that die are removed from the system. The second action represents the growth in terms of occupied patches of individuals of intermediate and large size and the process of inter- and intra-group competition that it entails. First, the newly settled individuals of intermediate infaunal groups, then the infaunal individuals of the basibiotic group and finally the individuals of large infaunal groups grow in random order to their final size based on the competition submodel. The individuals of the two intermediate epifaunal groups are the next to grow, first those of the group that is associated with hard substrate and then those of the group that is associated with gravel. The third action represents the process of ageing by one year of all individuals that survived the previous time step. During the fourth and final action, all individuals that could not grow to their full predefined size or were overgrown, those that reached their lifespan during the current time step or were epibionts of deceased basibionts, die and vacate their previously occupied patches. Basibiotic individuals that die of ageing and have epibionts of the same group, take the age of their oldest epibiotic basibiont and retain the rest of their epibionts. Individuals of the prey groups die and are removed in decreasing order of their predators' size. This process starts with each predator's most abundant prey and, if this is less abundant than the selected number, individuals from its next most abundant prey are removed, until the total of removed individuals is the closest possible to the selected number. Finally, all global variables and the model's grid display are updated and functional group abundances are printed out.

IV.2.1.4 Design concepts

Basic principles

The model aims to reproduce the mechanisms of inter- and intra-group competition assumed to take place primarily for food and space within benthic macroinvertebrate communities. It also includes a very basic representation of predator–prey relationships and the mechanisms of sediment engineering and epibiosis. The last two mechanisms are represented through the process of recruitment. The former is expressed by the effect of the dominance of stabilizing or destabilizing groups on each group's settlement probability and the latter by the settlement of epifaunal groups on space occupied by the basibiotic functional group. Only intermediate and large groups are assumed to contribute to the pools of sediment destabilizers and stabilizers. The benefits of epibiosis are illustrated by the fact that individuals do not need to occupy as much space in order to survive, so large groups are treated as intermediate and intermediate as small. Small groups retain their original space occupation. After the random settlement of juveniles, competition is demonstrated through the process of somatic growth toward each group's predefined body size, assuming that bigger individuals occupy more space. Competition between members of different functional groups is characterized by trade-offs, associated with their main attribute, their body size. Individuals with small size do not need to grow at all to occupy their space. Individuals with intermediate size are better competitors for food, so they can grow over small individuals. Individuals with large size are assumed to grow slower, so they are the last to do so, but are better competitors for food. They can, therefore, grow over both small and intermediate individuals. A competitive advantage of purely infaunal groups over the basibiotic group, on the one hand, and the groups associated with rock over those associated with gravel, on the other, is expressed by the fact that individuals of the latter groups are in both cases the last to grow. The special requirements of the basibiotic functional group is expressed by the fact that its members can only grow if their potential occupied area neighbours that of adult members of the group. Individuals that do not grow to their predefined size or are even partially overgrown, are assumed to be the most susceptible to mortality caused by a number of factors and are removed from the system. Post-settlement mortality is also assumed to be controlled by adult body size, with intermediate groups suffering from higher mortality than large groups and lower mortality than small groups. The body size of groups also dictates the existence of predator–prey interactions, additionally influenced by the predators' mobility and the preys' defensive mechanisms and position in the sediment. Among their prey groups, predators start with those that are the most abundant, with prey individuals being removed from the system in decreasing order of their predators' size.

Emergence

The main output of the model consists of the abundance distribution of functional groups over time. Differences among the groups can be attributed to their different settlement substrates, fecundity, dispersal distance, early development mode, role in sediment engineering, position in the sediment, post-settlement mortality, the order and manner in which their members grow after their successful settlement and their differential mortality due to restricted growth, overgrowth by larger individuals, ageing, loss of basibiotic substrate and susceptibility to predation.

Adaptation

Individuals adapt their settlement, growth and lifespan to their biotic environment, namely, the contribution of their functional group to the spawner pool, the dominance of sediment stabilizers or destibilizers, the availability of suitable substrate, the individuals in their potential occupation area, their basibionts or epibionts, the relative abundance of their group compared to the abundance of other prey groups and the abundance of their predator groups, as shaped by the system's history.

Objectives

The rules of recruitment, competition and mortality are derived from ecological theory and expert knowledge, so objectives are not explicitly modelled. It is, however, implied that the ability to outgrow other individuals and reach the maximum lifespan conveys fitness to each phenotype.

Prediction

Because outgrowing other individuals and reaching the maximum lifespan are assumed a priori to be the objectives of individual organisms, prediction is not modelled.

Sensing

There is no sensing in the model. Interactions among individuals are controlled by rules of recruitment, competition and mortality representing processes of inter- and intra-group competition for food and space, sediment engineering and epibiosis.

Interaction

One set of interactions among individuals is based on processes of exploitative competition for space and food. The former is modelled explicitly, with individuals competing for a limited number of patches, while the latter is implied in the modelled functional trade-offs that lead to the death of individuals that do not grow to their predefined size. Space competition among infaunal and epifaunal individuals is first demonstrated during the settlement of juveniles on unoccupied patches. Intra-group competition for space and food takes place among members of not only the same functional group but also different groups with the same size, by keeping them from growing over each other. Inter-group competition for the same resources takes place among individuals of different sizes and involves taking over patches that were previously occupied by other individuals. Another set of interactions is associated with the phenomenon of epibiosis. Individuals of the basibiotic functional group provide the patches on which individuals of epifaunal groups can settle. Additionally, the oldest epifaunal basibiont of an infaunal basibiont that dies of ageing, takes its place as infaunal basibiont. Adult infaunal basibionts also allow the growth of infaunal basibiotic juveniles in their immediate neighbourhood. Apart from these direct interactions, individuals also interact indirectly, through their contribution to the spawner pool, the pools of sediment stabilizers and destabilizers and the relative abundance of prey groups.

Stochasticity

Settlement of juveniles during recruitment is represented by a stochastic process, in which each empty patch is randomly attributed a juvenile that belongs to one of the potential settling groups. Settlement probabilities are determined by each group's fecundity, dispersal distance, early development mode, role in sediment engineering, position in the sediment and contribution to the spawner pool along with the relative abundance of sediment stabilizing and destabilizing functional groups during the previous step. Post-settlement mortality is also stochastic, as the identity of the juveniles to be removed is selected at random and based on the adult body size of each functional group. Stochasticity is added to the process of competition through the order in which individuals of the same competitive ability grow. Finally, the process by which prey individuals among each predator's preferred prey groups are removed from the system is random.

Collectives

The formation of collectives is imposed on the model through the assignment of values for the functional group variables to each empty patch during the recruitment process. The behaviour of members of different functional groups is differentiated through their initial settlement probabilities, their post-settlement mortality rates, the order and manner in which individuals of different groups grow, through their lifespan, their role in the phenomena of sediment engineering and epibiosis and their role as potential prey of the predator groups.

Observation

The contribution of infaunal and epifaunal functional groups to the respective spawner pools are printed out after their definition for testing purposes. The output that is most relevant to the purpose of the model is the abundance distribution of the functional groups at the end of each time step. For this to be derived, the area covered by each functional group is divided by the number of patches that corresponds to the occupied area of an individual of each group. This is done separately for the infaunal and epifaunal individuals of the basibiotic group, as the two differ in size. The former is assigned to a separate variable and then the two numbers are added to produce the group's total abundance. The abundance of the predator groups is derived from the abundance of their potential prey. All this output is printed out at the end of each time step. It is also plotted at the beginning of each step in the form of a histogram of functional group abundances and a new point in a graph that illustrates their evolution through time.

IV.2.1.5 Initialization

The model's initialization starts by randomly attributing a value that corresponds to one of the eleven infaunal functional groups to the respective variable of every patch on the grid, thus representing the settlement of infaunal juveniles. In this process, the chances for the juveniles of each group to be attributed to a patch are defined by the fecundity, dispersal distance and early development mode of the group. Newly settled juveniles experience mortality with rates defined by each group’s body size and those that die are removed from the system. Patches occupied by purely infaunal groups of intermediate size in random order turn the functional group variable of their eight immediate neighbours into their own value, unless any of their neighbours is occupied by a functional group of the same size, in which case nothing happens. The process is repeated for patches occupied by the basibiotic functional group, on the additional condition that at least another patch within each patch's twenty-four closest neighbours is occupied by a member of the same group. Patches occupied by groups of large size in random order turn the functional group variable of their twenty-four immediate neighbours into their own value, unless any of these neighbours is occupied by a functional group of the same size, in which case nothing happens. Patches occupied by small groups that were not overgrown, along with those occupied by intermediate and large groups that grew to their full predefined size and were also not overgrown are attributed to the respective set of patches and their age is set to one year. These patches and the patches into which they grew are then excluded from a process that changes the infaunal functional group variable of all other patches into a value that signifies that they are not occupied. Patches that are occupied by infaunal individuals of the basibiotic functional group are randomly attributed a value that corresponds to one of the six epifaunal groups, thus representing the settlement of epifaunal juveniles. The chances of the groups to be attributed to each patch are defined by the fecundity, dispersal distance and early development mode of each group. Newly settled juveniles experience mortality with rates defined by each group’s body size and those that die are removed from the system. First, patches occupied by intermediate groups associated with rock and then those occupied by intermediate groups associated with gravel in random order turn the functional group variable of their eight immediate neighbours into their own value, unless any of their neighbours is occupied by an epifaunal individual of the same size, in which case nothing happens (epifaunal basibiotic individuals do not participate, since they stay small in size). Patches occupied by small groups that were not overgrown, along with those occupied by intermediate groups that grew to their full predefined size, are attributed to the respective set of patches and their age is set to one year. These patches and the patches into which they grew are then excluded from a process that changes the epifaunal functional group variable of all other patches into a value that signifies that they are not occupied. Finally, the variables that calculate the abundance of each functional group, along with those calculating the abundance of sediment stabilizers and destabilizers, are updated, colours are given to the patches based, first, on their infaunal and then on their epifaunal variables of functional group occupation and the count of time steps is reset, thus also updating the graph areas.

IV.2.1.6 Input data

The abiotic environment is assumed to be constant in space and time. The contribution of each group of the infauna and the epifauna to the respective spawner pool is imported in each time step from the large-scale model.

IV.2.1.7 Submodels

The recruitment submodel starts by defining the contribution of infaunal and epifaunal functional groups to the respective spawner pool as each group’s contribution to the total abundance of the respective set of groups during the previous time step within an area defined in the large-scale model. In a process representing the settlement of infaunal juveniles, the variable of infaunal group occupation of every patch that is not occupied by an infaunal group is randomly attributed a value that corresponds to one of the eleven infaunal groups. In this process, the chances of each group's juveniles to be attributed to an empty patch are defined by the relative abundance of sediment stabilizing and destabilizing groups, along with the fecundity, dispersal distance, early development mode, role in sediment engineering, position in the sediment and contribution of each group to the infaunal spawner pool. Newly settled juveniles experience mortality with rates defined by each group’s body size and those that die are removed from the system. In a process representing the settlement of epifaunal juveniles, the variable of epifaunal group occupation of patches that are occupied by adult infaunal individuals of the basibiotic functional group and are empty of epifaunal groups, are randomly attributed a value that corresponds to one of the six epifaunal groups. In this process, the chances of each group's juveniles to be attributed to an empty patch are defined by the fecundity, dispersal distance, early development mode and contribution of each group to the epifaunal spawner pool. Newly settled juveniles experience mortality with rates defined by each group’s body size and those that die are removed from the system.

The competition submodel starts with the growth of the newly settled infaunal individuals. Patches occupied by juveniles of purely infaunal groups of intermediate size, in random order turn the functional group variable of their eight immediate neighbours into their own value, unless any of their neighbours is occupied by a functional group of the same size or an adult of a large group, in which case nothing happens. The process is repeated for patches occupied by juveniles of the basibiotic group, on the additional condition that at least another patch within each patch's twenty-four closest neighbours is occupied by an adult member of the same group. Patches occupied by juveniles of large groups in random order turn the functional group variable of their twenty-four immediate neighbours into their own value, unless any of these neighbours is occupied by a functional group of the same size, in which case nothing happens. The growth of newly settled epifaunal individuals comes next. Patches occupied by juveniles of, first, intermediate groups associated with rock and then intermediate groups associated with gravel, in random order turn the functional group variable of their eight immediate neighbours into their own value, unless any of their neighbours is occupied by an epifaunal individual of the same size, in which case nothing happens (epifaunal basibiotic individuals do not participate, since they stay small in size).

The ageing submodel adds one year to the age of individuals that survived the previous time step.

The mortality submodel starts with infaunal individuals. Juveniles of small groups that were not overgrown are attributed to the respective set and their age is set to one year. The same is applied to juveniles of intermediate groups that grew to their full predefined size and were not overgrown, along with juveniles of large groups that grew to their full predefined size and adults of intermediate groups that were not overgrown, except that the latter retain their age. All individuals that did not grow to their full predefined size or were even partially overgrown are then removed from the system. The same happens to individuals of purely infaunal small and intermediate groups that reached their lifespan. Juveniles of small epifaunal groups have their age set to one year, while adults of the same groups that reached their lifespan are removed from the system. Infaunal individuals of the basibiotic functional group that reached their lifespan are removed from the system, along with their epibiotic individuals, unless any of the epibionts is member of their group, in which case the older among them takes their place and keeps the rest of the epibionts. Juveniles of intermediate epifaunal groups that grew to their full predefined size, have their age set to one year, while those that did not, along with adults of the same groups that reached their lifespan are removed from the system. Large infaunal individuals that reached their lifespan are the last to be removed. In a process representing predation, the largest predator starts with the most abundant group among its potential prey and removes individuals at random, until the selected number has been removed (all abundances calculated at the end of the previous time step). If this number is not reached, it moves to the next group of its potential prey and repeats the process. The same is applied to the second and third largest predators. Individuals of large, intermediate and small groups that survived are attributed to the respective sets. The abundance of the predators is derived from the abundance of their potential prey groups. Finally, the variables that calculate the abundance of each functional group, along with those calculating the abundance of sediment stabilizers and destabilizers, are updated, colours are given to the patches based, first, on their infaunal and then on their epifaunal variables of functional group occupation and the abundances of all functional groups are printed out.

IV.2.2 Large-scale model

The grid of the large-scale model represents the Rance estuary, with patch size corresponding to an area of approximately 0.2 km^2. The model starts by attributing a sediment type to each patch, based on a sedimentary map of the Rance estuary from 1994 (Bonnot-Courtois, 1997). The patches are then assigned to the subtidal or intertidal zone, based on their sediment type. Areas covered by gravel, coarse sand, intermediate/coarse sand, fine/intermediate sand, muddy sand and sandy mud are assigned to the subtidal zone. Areas covered by silty mud, mud, pure mud and salt marshes are assigned to the intertidal zone. The small-scale model of the subtidal is then loaded and the patches of the subtidal zone, in random order, ask it to initialize and export the generated instance in a file named after their own x and y coordinates. At the same time, the patches of the subtidal zone are attributed with the generated group abundances, which are printed out, and a colour on the grid, which indicates whether these abundances are dominated by sediment stabilizers or destabilizers. The same procedure is then applied to the small-scale model of the intertidal and the patches of the intertidal zone.

One time step corresponds to one year, starting right before spring dispersal. First, the patches of the subtidal zone in random order ask the small-scale model of the subtidal to import the model instance that was generated for them during the previous time step and set each infaunal and epifaunal functional group’s contribution to the respective spawner pool equal to the median abundance of each group within the patches themselves and their eight immediate neighbours that are part of the system. Within the same procedure, the patches ask the small-scale model to move one step forward and export the generated instance in a file named after their own x and y coordinates. At the same time the patches are attributed with the generated group abundances, which are printed out, and a colour on the grid, which indicates whether the generated group abundances are dominated by sediment stabilizers or destabilizers. The same procedure is then applied to the patches of the intertidal zone and the respective small-scale model.

IV.2.3 Parameterization

An overview of the model's parameterization is given in Table IV.2.

IV.2.3.1 Settlement probability

Small-scale model of the subtidal

The settlement probabilities of all infaunal and epifaunal functional groups that are employed during the model's initialization are defined by each group's fecundity, dispersal distance and early development mode. Specifically, groups with brooded early development mode (FG4, FG5, FG12, FG14) and groups with long dispersal distance and high fecundity (FG7, FG8, FG9, FG10, FG13, FG15), along with groups with any of these trait levels and a laid early development mode (FG11) have settlement probabilities that are three times as high as the settlement probabilities of groups with none of the aforementioned trait levels (FG2). The latter have settlement probabilities that are half the settlement probabilities of functional groups with planktonic early development mode and either long dispersal distance (FG1) or high fecundity (FG6, FG16) along with groups with short dispersal distance, low fecundity and laid early development mode (FG3).

The settlement probabilities of epifaunal functional groups that are employed during the model's recruitment submodel are derived from the settlement probabilities that are employed during the model's initialization, by making them proportional to each group's contribution to the epifaunal spawner pool. The settlement probabilities of infaunal functional groups are additionally determined by each group's role in sediment engineering and position in the sediment, along with the relative abundance of sediment stabilizing and destabilizing groups, before each group's contribution to the infaunal spawner pool is factored in, following the same procedure as above. The former elements represent the mechanism of sediment engineering, which is imposed by first dividing the settlement probabilities of mobile stabilizers and groups that live deep in the sediment (FG2, FG3, FG6, FG8) by 2. The rest of the rules apply only on the remaining infaunal groups. If the effective sediment stabilizers (intermediate and large sessile stabilizers FG5 and FG10) outnumber the effective destabilizers (intermediate and large destabilizers FG7 and FG11), the settlement probabilities of the stabilizers (FG5, FG10) and the basibiotic group FG9 are multiplied by 2 and those of the destabilizers (FG4, FG7, FG11) are divided by 2. Otherwise, the settlement probabilities of the stabilizers (FG5, FG10) and the basibiotic group FG9 are divided by 2 and those of the destabilizers (FG4, FG7, FG11) are multiplied by 2. The infaunal group that is neutral with respect to both epibiosis and sediment engineering (FG1) does not have its settlement probability modified during this process.

Small-scale model of the intertidal

The settlement probabilities of all infaunal and epifaunal functional groups that are employed during the model's initialization are defined by each group's fecundity, dispersal distance, early development mode and tolerance to low salinity/tidal exposure. The three former processes are represented by using the same settlement probabilities as those employed in the initialization of the small-scale model of the subtidal. The latter process of environmental filtering is imposed by altering these settlement probabilities. Specifically, the settlement probabilities of all stenohaline groups (FG1, FG2, FG4, FG5, FG6, FG9, FG12, FG14, FG15, FG16) are divided by 2.

The settlement probabilities of epifaunal functional groups that are employed during the model's recruitment submodel are derived from the settlement probabilities that are employed during the model's initialization, by making them proportional to each group's contribution to the epifaunal spawner pool. The settlement probabilities of infaunal functional groups are additionally determined by each group's role in sediment engineering and the relative abundance of sediment stabilizing and destabilizing groups, before each group's contribution to the infaunal spawner pool is factored in, following the same procedure as above. The former elements represent the mechanism of sediment engineering, which is imposed by altering the settlement probabilities of all euryhaline and emersed groups (FG3, FG7, FG8, FG10, FG11). If the effective sediment stabilizers (intermediate and large stabilizers FG8 and FG10) outnumber the effective destabilizers (intermediate and large destabilizers FG7 and FG11), the settlement probabilities of stabilizer groups (FG8, FG10) are multiplied by 2 and those of destabilizer groups (FG3, FG7, FG11) are divided by 2. Otherwise, the settlement probabilities of the stabilizers (FG8, FG10) are divided by 2 and those of the destabilizers (FG3, FG7, FG11) are multiplied by 2.

IV.2.3.2 Post-settlement mortality

The mortality rates experienced by juveniles of all functional groups after their settlement on the seabed is assumed to be controlled by each group's body size, with values representing extreme and intermediate levels observed in nature. 90% of juveniles of small functional groups, 50% of intermediate groups and 10% of juveniles of large groups are removed from the system following their settlement.

IV.2.3.3 Predation

The potential prey of the predator groups consists of groups that are smaller or similar in size but no smaller than 1/3 of their own size, are not buried deep in the sediment and their representative species are not protected by plates, shells or tubes. Specifically, FGP1 has groups FG4 and FG7 as its potential prey, while the potential prey of FGP2 consists of FG7 and FG11. The sessile predator group FGP4 is additionally limited to mobile epifaunal organisms and can, therefore, feed on groups FGP1 and FGP3. The availability of precise information on the diet of the representative species of predator group FGP3 in the Rance estuary allows the assignment of groups FG4 and FG5 as its potential prey. The abundance of predator groups at each time step in the subtidal and intertidal models is assumed to be equal to 1/10 of the total abundance of their potential prey and 1/10 of the abundance of the most abundant group among the potential prey, respectively, during the previous time step. The number of individuals of the potential prey groups that die due to predation and are removed from the system at each time step is equal to the abundance of their respective predators.

IV.2.4 Model analysis

The lack of detailed knowledge on a number of important ecological processes allowed only their very basic, often semi-quantitative, representation. Accordingly, the model's analysis focused on its structural characteristics and theoretical background, rather than its parameterization. The goal was to explore the potential of developing a dynamic and spatially explicit model of benthic macroinvertebrates within the specified conceptual and methodological framework, so no attempts were made at model validation.

First, a 10-year simulation of the standard version of the model was replicated 3 times. The choice of 10 years was made because the possibility of all sites in the Rance estuary to stay undisturbed and evolve concurrently should decrease significantly as the number of time steps increases. The number of replicates was chosen for practical reasons. The simulation that resulted in the higher level of beta diversity (see below) was singled out (hereafter, the "benchmark simulation") and the abundances of all functional groups in each patch of the large-scale model were mapped for each of the 10 time steps.

Table IV.2 Parameterization of the subtidal and the intertidal small-scale models during their initialization and their subsequent simulation in the case that they are dominated by sediment stabilizing or destabilizing functional groups

Groups	**Size**	**Position in substrate**	**Subtidal initial settlement probability multiplier**	**Intertidal initial settlement probability multiplier**	**Subtidal stabilizer-dominated settlement probability multiplier**	**Subtidal destabilizer-dominated settlement probability multiplier**	**Intertidal stabilizer-dominated settlement probability multiplier**	**Intertidal destabilizer-dominated settlement probability multiplier**	**Post-settlement mortality rate (%)**	**Potential prey groups**	**Subtidal habitat modification role**	**Intertidal habitat modification role**
FG1	S	infauna	2/3	1/3	1	1	1	1	90	-	-	-
FG2	S	infauna	1/3	1/6	1/2	1/2	1	1	90	-	-	-
FG3	S	infauna	2/3	2/3	1/2	1/2	1/2	2	90	-	-	-
FG4	S	infauna	1	1/2	1/2	2	1	1	90	-	-	-
FG5	M	infauna	1	1/2	2	1/2	1	1	50	-	stabilizer	-
FG6	M	infauna	2/3	1/3	1/2	1/2	1	1	50	-	-	-
FG7	M	infauna	1	1	1/2	2	1/2	2	50	-	destabilizer	destabilizer
FG8	M	infauna	1	1	1/2	1/2	2	1/2	50	-	-	stabilizer
FG9	M	infauna/epifauna	1	1/2	2	1/2	1	1	50	-	basibiont	basibiont
FG10	L	infauna	1	1	2	1/2	2	1/2	10	-	stabilizer	stabilizer
FG11	L	infauna	1	1	1/2	2	1/2	2	10	-	destabilizer	destabilizer
FG12	S	epifauna	1	1/2	-	-	-	-	90	-	-	-
FG13	S	epifauna	1	1	-	-	-	-	90	-	-	-
FG14	S	epifauna	1	1/2	-	-	-	-	90	-	-	-
FG15	L	epifauna	1	1/2	-	-	-	-	10	-	-	-
FG16	L	epifauna	2/3	1/3	-	-	-	-	10	-	-	-
FGP1	-	-	-	-	-	-	-	-	-	FG4, FG7	-	-
FGP2	-	-	-	-	-	-	-	-	-	FG7, FG11	-	-
FGP3	-	-	-	-	-	-	-	-	-	FG4, FG5	-	-
FGP4	-	-	-	-	-	-	-	-	-	FGP1, FGP3	-	-

IV.2.4.1 Spatial resolution

The influence of spatial resolution on the model's behaviour was investigated by separately increasing the resolution of the large- and the small-scale models. The resolution of the small-scale models was set to 120 × 120 patches and the area represented by a patch of the large-scale model to approximately 0.05 km^2. In the latter, the calculation of each infaunal and epifaunal group's contribution to the respective spawner pool in a patch of the large-scale model was based on the patch and its 24 closest neighbours that are part of the system. The goal was to conserve the dispersal distance of the low-resolution model.

This high-resolution version of the large-scale model was first combined with the low-resolution version of the small-scale models (HL-LS configuration). Then the low-resolution version of the large-scale model was combined with the high-resolution version of the small-scale models (LL-HS configuration). A 10-year simulation of each model configuration (standard, HL-LS, LL-HS) was replicated 3 times. The output of interest consisted in the evolution through time of the minimum, median and maximum number of functional groups per patch of the large-scale model over all of its patches. The goal was to illustrate the rate at which the system moves toward equilibrium, following an initial state where all functional groups are present in most patches of the system.

IV.2.4.2 Sensitivity analysis

Sensitivity analysis was performed on the basis of the low-resolution version of both the small- and the large-scale model. First, the role of the dispersal distance was examined by using all of the system's patches for the calculation of each infaunal and epifaunal group's contribution to the respective spawner pool in each patch of the large-scale model. Then the role of post-settlement mortality was examined by completely removing it from the small-scale models. The role of sediment engineering was examined by removing its effect on the settlement probabilities of the small-scale model. Finally, the role of predation was examined by removing predation mortality from the small-scale model. Each model configuration was simulated for 10 years and replicated 3 times.

The effect on the model's behaviour was investigated by demonstrating the evolution of beta diversity through time and comparing it with the levels that were observed at the level of functional groups in the Rance estuary in 1995. Beta diversity was in all cases quantified as the variance of the Hellinger-transformed table of group abundances in different sites (Legendre and De Cáceres, 2013). In the case of the observations, this table consisted of functional group abundances in the 113 sites (71 subtidal, 42 intertidal) that were sampled in the Rance estuary in 1995. In the case of the output of the different model configurations, the table consisted of functional group abundances in 113 patches (71 subtidal, 42 intertidal) that were selected out of the 230 patches of the large-scale model, in order to represent the areas of the Rance estuary that were sampled in 1995.

IV.2.4.3 Group accumulation

Group accumulation curves illustrate the accumulation of functional groups as the number of sites increases. At samples consisting of one site, they depict the average number of groups per site and, as the number of sites increases, the curves can be extrapolated to produce an estimate of the total number of groups in an area larger than the one sampled. The combined depiction of the confidence interval (± 2 standard errors) demonstrates the degree of variation. The group accumulation curves and their variance were calculated by using an analytical expression (Ugland et al., 2003). Curves were produced for the 113 macroinvertebrate samples from the Rance estuary in 1995 and for 113 patches that were selected as described above out of the 230 patches of the large-scale model output in the 1st, 2nd, 3rd and 10th year of the benchmark simulation. These years were selected because it is when the qualitatively biggest changes were observed.

IV.2.4.4 Spatial correlation

Mantel correlograms were used to assess the level of spatial correlation in the multivariate domain of functional group abundances. They consist of the normalized Mantel statistic between a multivariate dissimilarity matrix among sites and an equivalent dissimilarity matrix derived by attributing the value 0 to pairs of sites that belong to the same distance class and the value 1 to all other pairs of sites. The process is repeated for each distance class and each value of the Mantel statistic can be tested by permutations. Mantel correlograms were produced for the 113 macroinvertebrate samples from the Rance estuary in 1995 and for 113 patches that were selected as described above out of the 230 patches of the large-scale model output in the 1st, 2nd, 3rd and 10th year of the benchmark simulation. Distances for the model output were calculated between the centres of symmetry of each patch of the large-scale model, by assuming patch dimensions of 450 m × 450 m. The tables of functional group abundances were Hellinger-transformed and Holm’s correction for multiple testing was applied to the permutation tests. The number of distance classes was calculated using Sturge’s rule and the correlograms were limited to distance classes that include all sites (Borcard et al., 2011).

IV.2.4.5 Correspondence analysis

Correspondence analysis (Legendre and Legendre, 1998) was first performed on the table of functional group abundances in the 113 sites that were sampled in the Rance estuary in 1995. It was then performed on the table of functional group abundances in 113 out of the 230 patches of the large-scale model output in the 1st, 2nd, 3rd and 10th year of the benchmark simulation. The patches correspond to the areas of the Rance estuary that were sampled in 1995, while these years are the time steps when the qualitatively biggest changes were observed. The goal was to compare patterns in the relative frequencies of functional groups along the different sites, so scaling 2 was selected for the projection of groups on the first two axes of the reduced multivariate space (Borcard et al., 2011).

IV.2.5 Software

Simulations of both the small- and the large-scale models were implemented in the multi-agent modelling environment NetLogo version 5.3.1 (Wilensky, 1999). Interactions between the two scales were realized through the NetLogo extension LevelSpace (Hjorth et al., 2015). The source code of the subtidal/intertidal small-scale models and the large-scale model can be found in Annex C. All model analyses were performed using the statistical software R version 3.2.2 (R Core Team, 2015) with the packages vegan (Oksanen et al., 2015) and raster (Hijmans, 2016) and the function beta.div (Legendre and De Cáceres, 2013, Appendix S4).

IV.3 Results

A common pattern of all model simulations was the initial presence of all functional groups in most patches of the large-scale model and the gradual dominance of some of them in some patches and others in some other patches (see Fig. IV.A-IV.J in the Appendix). The general trend was for the whole system to be covered by stabilizer-dominated patches. Pockets of resistance to this trend were, however, formed by destabilizer-dominated patches of the subtidal and the intertidal, within which the opposite trend could be observed. The small-scale models can also be run independently, by setting each group’s contribution to the spawner pool equal to its abundance in the same models. The output depends on the model's initialization but otherwise appears to be constant.

If at the model's initialization the subtidal model is dominated by stabilizers, groups FG2, FG5 and FG10 persist along with the predators FGP3 and FGP4 (see Fig. IV.K in the Appendix), whereas the dominance of stabilizers in the intertidal model leads to the persistence of groups FG2, FG8 and FG10 (see Fig. IV.L in the Appendix). In both cases, besides being characterised by random noise, the functional group abundances appear to follow periodic orbits. The dominance of destabilizers at the model's initialization results in the persistence of groups FG4, FG7 and FG11 in the subtidal (see Fig. IV.M in the Appendix) and groups FG3, FG7 and FG11 in the intertidal model (see Fig. IV.N in the Appendix). All four predator groups persist in the former case, while predators FGP1, FGP2 and FGP4 persist in the latter. An equilibrium point, featuring stochastic variability, is reached in both cases.

IV.3.1 Spatial resolution

The shift of the model's large- and small-scale components to a higher spatial resolution (HL-LS and LL-HS configurations, respectively) generated output that was qualitatively similar to that of the standard model. The analysis of these high-resolution configurations was, therefore, focused on the rate at which the system moved away from its initial conditions (Fig. IV.2). The maximum number of groups per patch of the large-scale model moved from 20 at initialization to 16 or 17 after 10 years of simulation in all model configurations. The rate of decrease of the minimum number of groups was, likewise, the same in all three model configurations. It started at 17 and reached the value of 4 after 10 years in the standard and the HL-LS model configurations. The use of the high-resolution small-scale models (LL-HS) generally increased the minimum number of groups, which started at 19 and reached the value of 6 after 10 years. The median number of groups appears to decrease slower in the HL-LS and LL-HS model configurations, reaching the value of 12 or 13 after 10 years, compared to 11 groups in the standard model.

IV.3.2 Sensitivity analysis

The evolution of beta diversity during 10-year simulations of the standard model shows a clear increasing trend during the first nine years, followed by a slight decrease (Fig. IV.3a). The levels reached in the ninth year were, at least in one of the three replicates (0.35), quite close to those observed in the Rance estuary (0.38). The replacement of the neighbourhood dispersal by its global counterpart drastically changed beta diversity in the modelled system (Fig. IV.3b). The generated values remained rather stable just under 0.1 throughout most of the 10 year simulations, showing a slight decrease at the end. The removal of post-settlement mortality also influenced the levels of beta diversity, which reached their peak (just under 0.3) in the sixth year and had a general declining tendency afterwards (Fig. IV.3c). The effect on beta diversity of removing the role of sediment engineering in defining the groups' settlement probabilities was two-fold (Fig. IV.3d). First, variability among the three simulations was reduced to a minimum. Additionally, levels of beta diversity increased very slowly, reaching values just over 0.1 in the tenth year. The removal of predation mortality had a minimal effect on beta diversity (Fig. IV.3e). The levels that were reached in all three simulations were similar to those of the standard model, except for the lack of any decline toward the end.

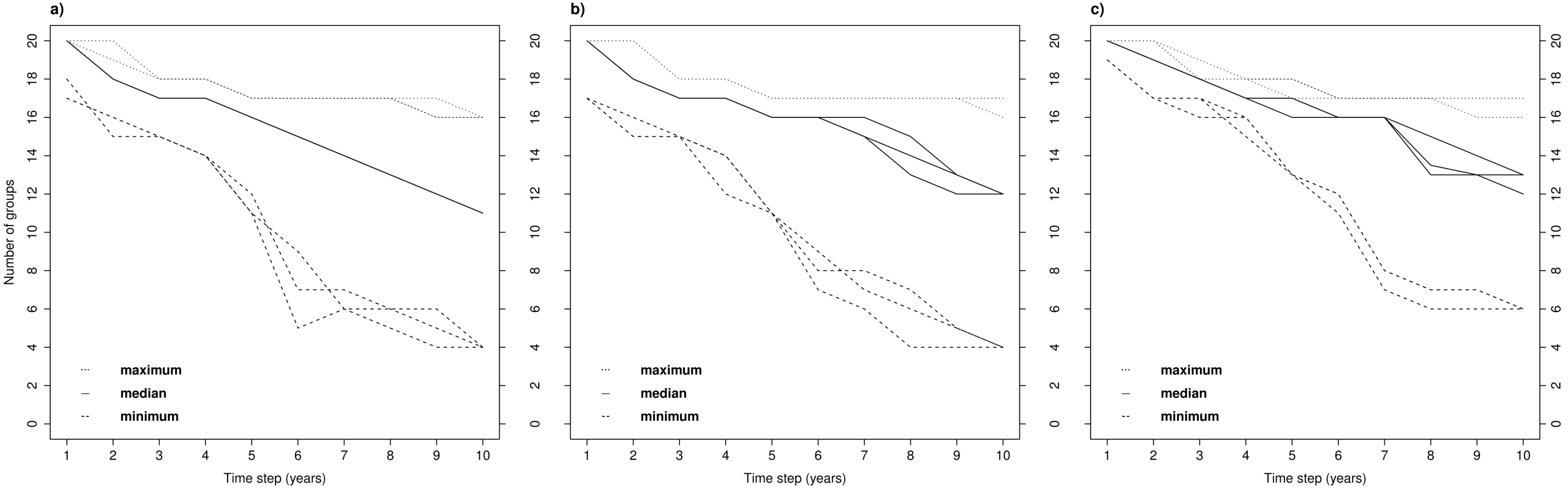


Fig. IV.2 Evolution of the minimum (dashed line), median (solid line) and maximum (dotted line) number of functional groups per patch of the large-scale model in three 10-year simulations of a) the standard model configuration, b) the one with the high-resolution large-scale model (HL-LS) and c) the one with the high-resolution small-scale models (LL-HS)

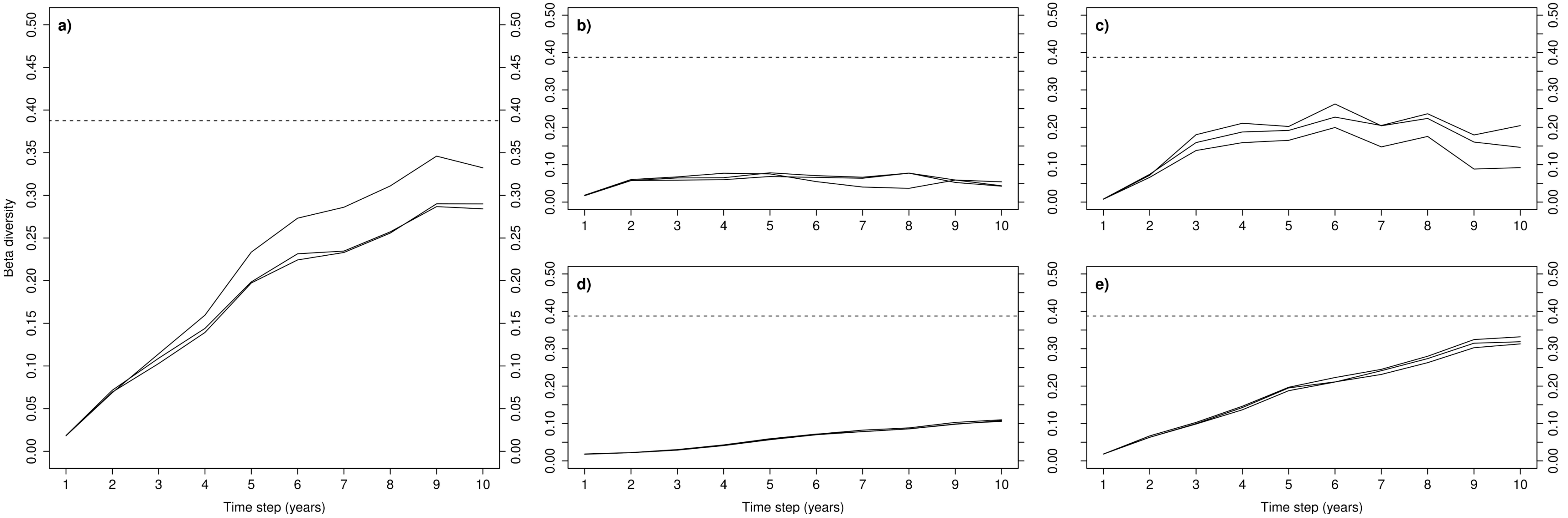


Fig. IV.3 Evolution of beta diversity in three 10-year simulations of a) the standard model configuration, b) the one with global dispersal, c) the one without post-settlement mortality, d) the one without sediment engineering and e) the one without predation mortality. The dotted line indicates the observed level of beta diversity in the Rance estuary in 1995

IV.3.3 Group accumulation

The group accumulation curve from the sampling of the Rance stuary illustrates high variation at small samples that gradually goes down as the sample increases (Fig. IV.4a). It appears that the average number of groups per site is about 11. The evolution of the group accumulation curve over a 10-year simulation of the standard model (Fig. IV.4b-e) started with almost all sites having all 20 functional groups. Some of them were gradually excluded from some sites and others from all of them, leading to increased variation and a total number of 17 functional groups in the 10th year. The average number of groups per site appears to drop through to the 10th year, when it reached levels similar to those of the observations. Still, variation was below the levels that were observed in the Rance estuary.

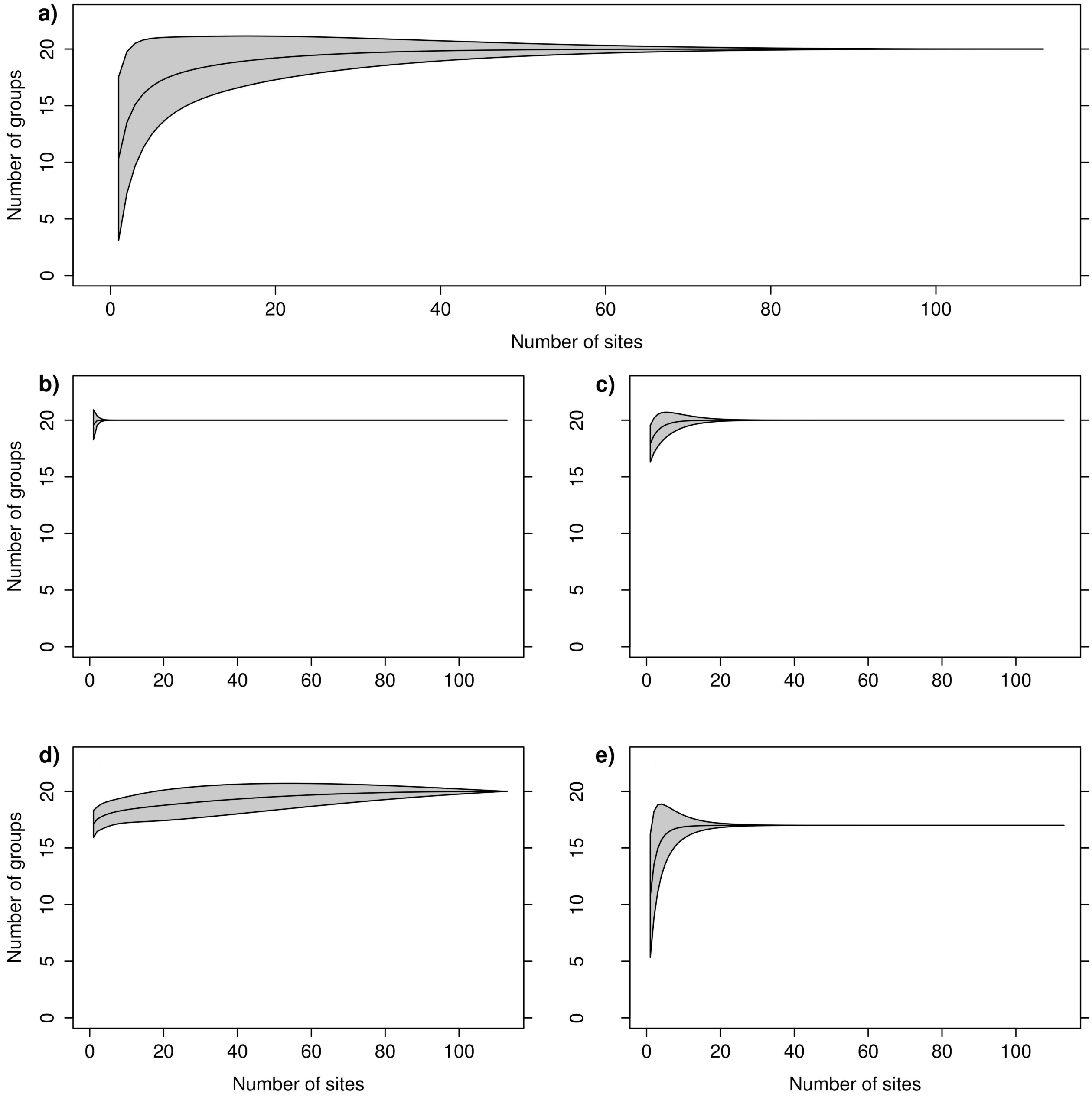


Fig. IV.4 Group accumulation curves with confidence intervals illustrated as shaded areas for a) the 113 sites that were sampled in the Rance estuary in 1995 and 113 sites selected from b) the 1st, c) the 2nd, d) the 3rd and e) the 10th year of the benchmark simulation

IV.3.4 Spatial correlation

The Mantel correlogram of the observed functional group abundances shows a significantly positive spatial correlation just over 0.1 and 0.05 in the first two distance classes (0.5 km and 1.5 km) and a significantly negative correlation of about -0.05 in the fourth (3.5 km) and eighth (7.5 km) distance classes (Fig. IV.5a). Spatial correlation in the 1st year of the model output was demonstrated as statistically significant values -0.06 and -0.04 in the fifth and sixth distance classes (5 km and 6 km) (Fig. IV.5b). Significantly negative spatial correlation of the same magnitude occurred in the third and fourth distance classes (3 km and 4 km) in the 2nd (Fig. IV.5c) and the 3rd year (Fig. IV.5d), accompanied by the same level of significantly positive correlation in the first distance class (1 km). The latter was retained in the 10th year (Fig. IV.5e), when it reached values just under 0.15, along with a significant spatial correlation of almost -0.1 in the third distance class (3000 m). Significantly negative correlations of similar magnitude occurred also in the seventh and eighth distance classes (7 km and 8 km) of the 10th year.

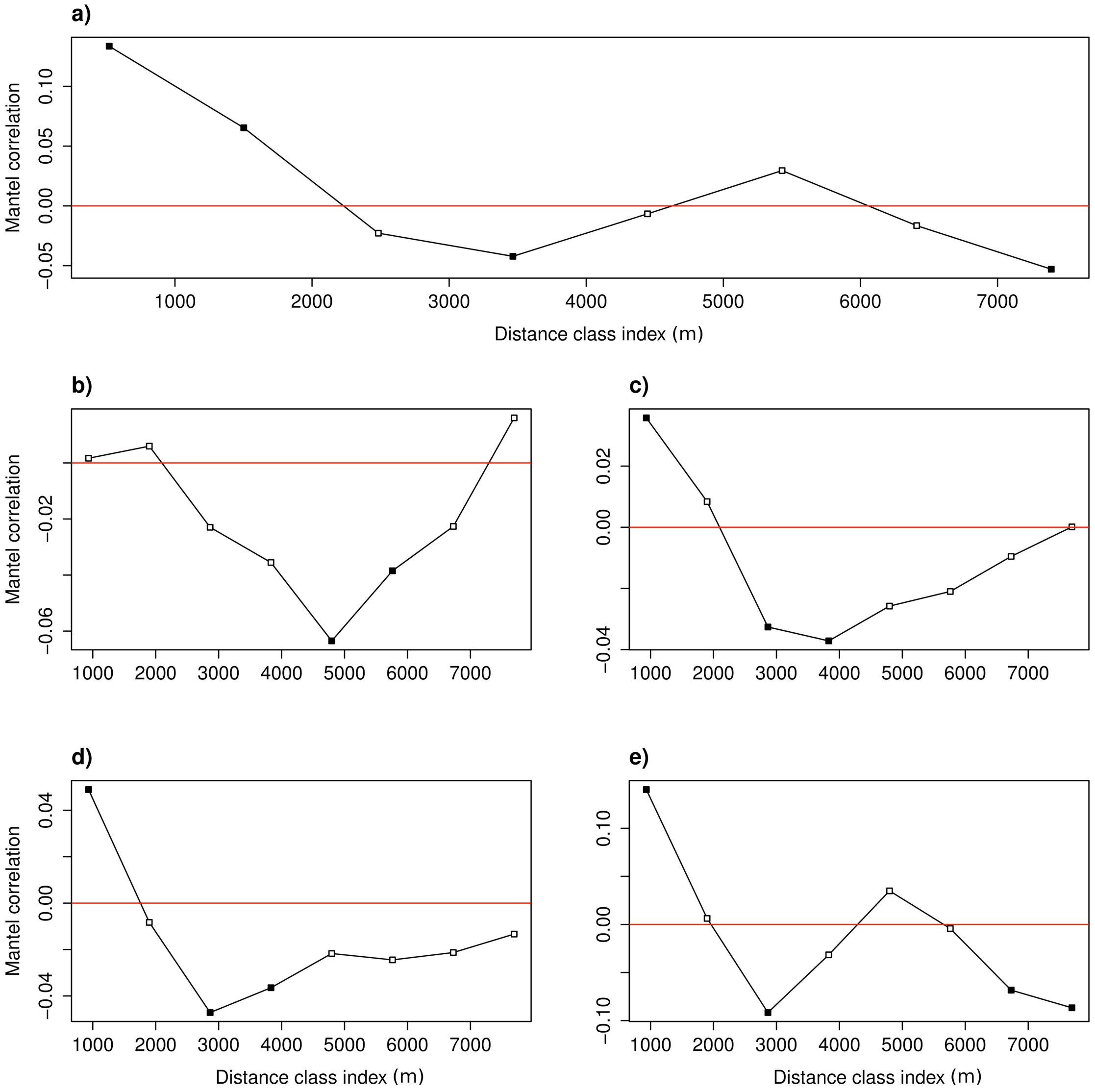


Fig. IV.5 Correlograms of the Mantel statistic in different distance classes for a) the observations from the Rance estuary in 1995 and the model output in b) the 1st, c) the 2nd, d) the 3rd and e) the 10th year of the benchmark simulation. Filled squares indicate statistically significant values at 0.05 level

IV.3.5 Correspondence analysis

The relative position of functional groups as they are projected on the first two axes of the reduced multivariate space illustrates their similarity with regard to their relative frequencies along the sites (Fig. IV.6). It should be noted that the first two axes of the correspondence analysis that is performed on the observed group abundances represent only about 32% of the total variation, whereas the same value for the output of the 1st, the 2nd, the 3rd and the 10th simulated year is equal to 72%, 84%, 79% and 73%, respectively.

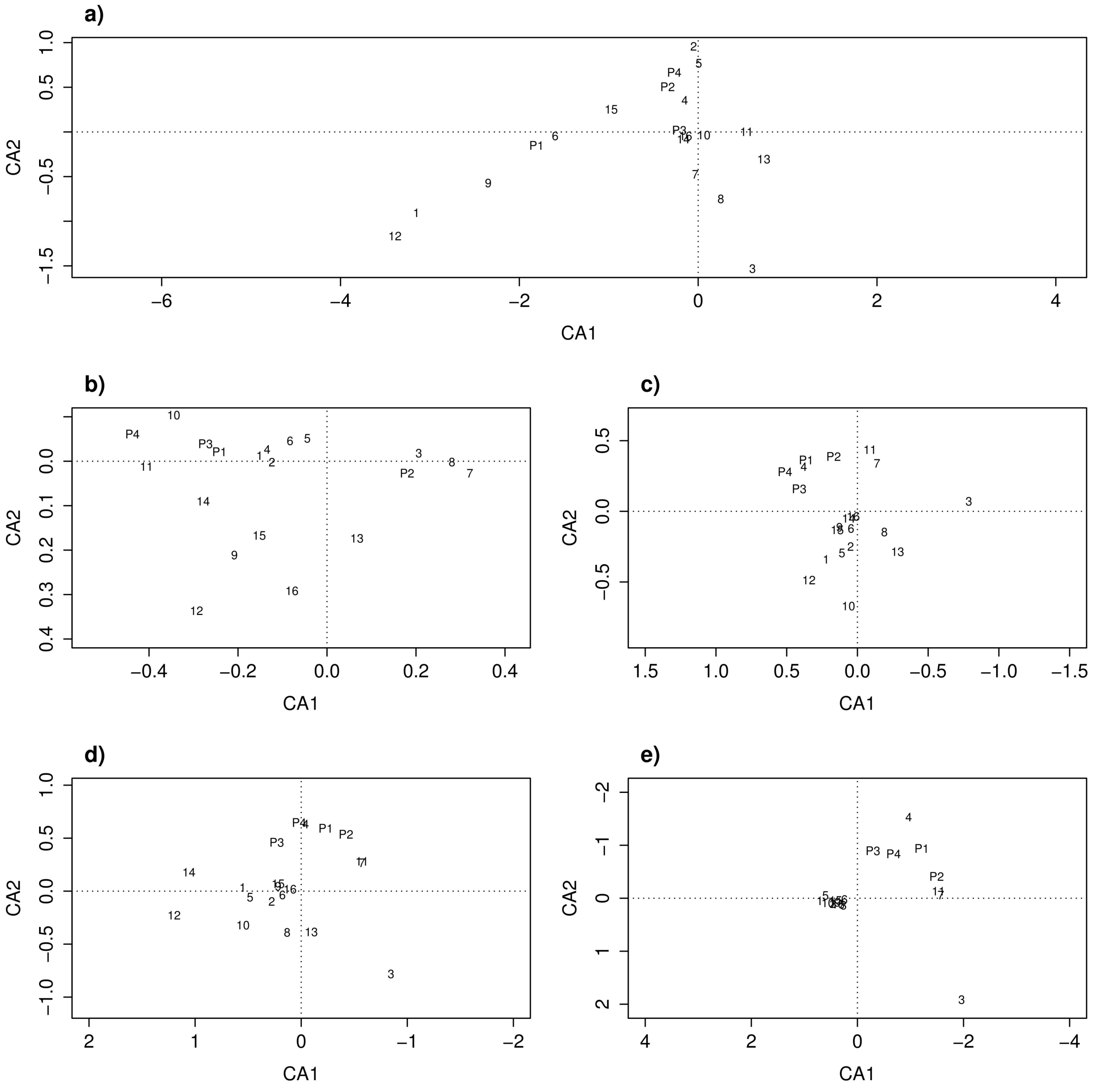


Fig. IV.6 Projection of functional groups on the first two axes of the correspondence analysis of group abundances a) from the Rance estuary in 1995 and b) from the 1st, c) the 2nd, d) the 3rd and e) the 10th year of the benchmark simulation

Some of the patterns that can be seen in the observed group associations are also evident in the results of the simulations. The observed separation of groups FG12 and FG1 can be seen after the 1st year of the simulation. The same holds true for the separation of group FG3 along with groups FG8 and FG13. Groups FG12 and FG13 gradually get eliminated and group FG8 converges toward the majority of the groups but the separation of group FG3 remains a constant pattern through time. The association between groups FG4, FGP2, FGP3 and FGP4 is also a common pattern of the observations and the entire simulation period after the initialization, whereas their initial association with groups FG5 and FG2 quickly recedes. The close and constant association of groups FG7 and FG11 throughout the simulation period can to some extent also be seen in the observations. In the 10th year of the simulation groups FG3, FG4, FG7 and FG11 are clearly separated from the rest of the groups along the first axis, themselves being separated along the second one. Predatory groups FGP1, FGP3 and FGP4 on the one hand and FGP2 on the other are also separated from the majority of the groups and to a lesser degree among themselves, as the former are mostly associated with group FG4 and the latter with groups FG7 and FG11.

IV.4 Discussion

The output of the model represents the dynamics of functional diversity in benthic macroinvertebrate communities at two spatial scales. The first one corresponds to the output of the small-scale model and can be considered to represent α-diversity. Abundance patterns at this scale were characterised by the gradual dominance of a few functional groups. This is an inherent property of the small-scale model and represents the process of competitive exclusion. Abundance patterns at the level of the large-scale model were complicated by the diversity among its patches and the process of local dispersal. The turnover of functional group abundance in the large-scale model can be considered to represent β-diversity. The generated abundance patterns were largely controlled by the distinction between the subtidal and the intertidal zone and the dominance of sediment stabilizers or destabilizers in each patch. The few areas of destabilizer-dominated patches that were left after 10 years of simulation did not seem able to resist the general trend of patches becoming dominated by sediment stabilizers. This trend could be the result of overestimating the effect of sediment engineering, particularly sediment stabilization, which might be contingent on the respective functional groups reaching certain density levels.

IV.4.1 Spatial resolution

The evolution of the minimum, median and maximum number of functional groups per patch of the large-scale model illustrates the rate at which the model moves away from its initial conditions. All three model configurations started with a small gap between the minimum and maximum values, which then increased as patches diverged in their community composition. This gap was constantly smaller in the configuration with the high-resolution small-scale model. This is the result of lower levels of stochastic variability in the small-scale model, although there is no reason to believe that this is more realistic than the other model configurations. An important consequence of lower levels of stochastic variability was slower competitive exclusion, which is expected to slow down the model's evolution toward a state of equilibrium. This state should be characterised by a reduction of the gap between the minimum and maximum values, probably at the level of 3 and 5 functional groups per patch, based on the output of the independent simulations of the intertidal and subtidal small-scale models, respectively. The general trend thus appears to be one of initially high α-diversity and low β-diversity, followed by a decrease in α-diversity and an increase in β-diversity, before both α- and β-diversity stabilize at their lowest levels.

IV.4.2 Sensitivity analysis

The model was able to generate levels of β-diversity that were not far from those observed in the Rance estuary in 1995, but would probably fail at sustaining them. The results of the sensitivity analysis identify local dispersal and sediment engineering as the most important drivers of β-diversity. No clusters of patches that were dominated by sediment stabilizers or destabilizers were formed in the case of global dispersal. The low levels of β-diversity that were reached are the result of stochasticity in the small-scale model's initialization and the distinction between the subtidal and the intertidal zone; they themselves decreased toward the end of the simulation. Without sediment engineering this initialization effect was removed, so that all three simulations had almost identical output. β-diversity increased at a very slow rate, as differences in community composition were gradually amplified through local dispersal, but did not really take off during the 10-year simulations. The removal of post-settlement mortality allowed small functional groups to overwhelmingly dominate the small-scale models. This accelerated the model's evolution and restricted the potential for differentiation. The small impact of removing predation mortality is in line with the limited role that was attributed to it in the small-scale models.

IV.4.3 Group accumulation

The evolution of the accumulation curve illustrates the transition from a rather homogeneous system to a more heterogeneous one. During this transition, three obligate epibiotic functional groups (FG12-14) were eliminated from the system. This could indicate that epibiosis cannot by itself sustain observed levels of epifaunal diversity, making the representation of different substrate types necessary. In the 10th year of the simulation the average number of functional groups per site was similar to what could be observed in the Rance estuary but the variation around this value was lower. This becomes evident as the sample size increases and variation in the model output becomes zero, compared to its sustained high levels in the observations. The latter appears to be akin to the picture seen in the 3rd year of the simulation, when the soon-to-disappear epibiotic functional groups became particularly rare. The rareness of functional groups appears to be an element of the observations that is underrepresented in the model output of the 10th year. It could be an inherent property of the sampling scheme that was applied to the Rance estuary, requiring a large-scale model of a much higher resolution for its recreation. Still, it could also be recreated by a collection of sites that are at different stages of ecological evolution.

IV.4.4 Spatial correlation

Mantel correlograms, like the one constructed for the observations from the Rance estuary in 1995, typically constitute a representation of environmental filtering. They demonstrate significantly positive correlation in small distance classes, due to habitat similarity that drives similar community composition, and significantly negative correlation in large distance classes, where habitat and community composition become increasingly dissimilar. The distances represented by each class and the specific patterns of spatial correlation are characteristic of each ecological system. The similarity of the correlogram that was generated for the 10th year of the benchmark simulation with the one that was generated for the observations from the Rance estuary, demonstrates the potential of the model to recreate observed patterns of multivariate spatial correlation based primarily on local dispersal and sediment engineering. The spatial patterns in the model output appear in general to lag behind in distance compared to the respective patterns in the observations. This trend might be associated with the particularly localised representation of dispersal. It is not clear to which degree the observed spatial patterns are caused by abiotic environmental filtering or biogenic habitat modification or how the two can interact.

IV.4.5 Correspondence analysis

The results of the correspondence analysis that was separately performed on the observed group abundances and the model output shows that the first two axes of the former represent a much smaller proportion of the total variation compared to the first two axes of the latter. This is not surprising, since the model aims to reproduce only a fraction of the ecological processes that are expected to take place. The fact that some of the observed functional group associations can also be seen in the correspondence analysis of the model output indicates that some of the most important processes were represented efficiently and others less so. The separation of functional groups that are associated with the intertidal zone in the fourth quadrant of the observed group projection is more or less visible in the group projection of the model output throughout the simulated period. The same holds true for the association of group FG4 with the majority of predatory groups in the second quadrant of the observed group projection. The placement of the basibiotic group FG9 in the third quadrant of the projections that correspond to the initial time steps, before epibiosis is largely eliminated, corresponds well with its placement in the observed group projection, along with the gravel-associated groups FG6, FG12 and FG15.

IV.4.6 Limitations and potential improvements

Among the many assumptions made during the development of the model, those associated with the representation of space are central and could significantly affect its potential to recreate observed patterns of benthic biodiversity. Although epibiosis can be seen as a third dimension of the small-scale model and the impact of sediment engineering is defined by considering each functional group's preferred position in the sediment, the representation of space occupation in the model is 2-dimensional, both for the infauna and the epifauna. The transition from the small-scale to the large-scale model is based on the assumption that each patch of the latter can be represented by a realization of the former. The validity of this assumption depends on the ability of the large-scale model's resolution to represent spatial variability in the Rance estuary. Patterns of spatial correlation in the model output were similar to observations and increased model resolution led to qualitatively similar results, supporting the transition between scales, at least for the scales of interest. Still, it appears that model resolution could affect temporal patterns, with increased resolution, especially of the small-scale model, increasing the rate at which the model moves away from its initial conditions and toward equilibrium.

The representation of time in the model is likewise limited to the reproduction of annual patterns of benthic biodiversity, ignoring any seasonal variability. Differences among functional groups regarding the order in which they grow constitute an implicit representation of differences in competitive ability rather than sequential processes in time. Furthermore, all patches of the large-scale model are assumed to initialize together and run concurrently over the simulated period. This assumption should become increasingly unrealistic as the number of time steps increases, since disturbances, such as extremely low temperatures or sediment destabilization, impacting all or a subset of the patches are expected to be common. The addition of a realistic disturbance regime could additionally prevent the model from reaching a state of equilibrium and allow it to sustain high diversity levels. Simulations of 10 years were not long enough for the model to reach such a state, but the model's behaviour makes it possible to guess what it might look like. It is reasonable to assume that subtidal and intertidal patches of the large-scale model would eventually be dominated by stabilizing functional groups, possibly the same that dominate in the independent simulations of the subtidal and the intertidal small-scale models, respectively.

The ability of the 20 functional groups to represent functional diversity as observed in the Rance estuary in 1995 (Alexandridis et al., 2017) supports the pertinence of the applied level of ecological aggregation and the assigned values of biological traits. This does not rule out any potential benefits of a more detailed representation of the existing functional roles or the inclusion of new ones. In this regard, the common food resource of algae/detritus could be differentiated based on the nutritional value of its main constituents. This distinction along with the explicit representation of individuals' mobility and position in the sediment could allow the consideration of biogeochemical processes that are expected to play a central role in the assembly of marine benthic communities (Herman et al., 1999). The explicit representation of movement would also be a prerequisite for a more realistic reproduction of predation. Dispersal, on the other hand, would probably increase in realism if its distance was not kept constant for all functional groups, but differed based on each group's maximum dispersal distance. Furthermore, the model could include some general information on patterns of water movement or even be coupled to a hydrodynamic model of the Rance estuary, thus significantly improving the representation of larval dispersal.

The addition of information on the hydrodynamics of the Rance estuary would create new opportunities for the representation of food availability for individual organisms. Food has been shown to become less available within the boundary layer as distance from its main sources increases (Fréchette et al., 1989), while renewal rate from the water column depends on flow velocity and turbulent mixing (Butman et al., 1994). Differences in food availability in different parts of the Rance estuary could be represented by adjusting the space that is required for the survival of individual organisms in the respective small-scale models. Another form of large-scale environmental variability that could significantly increase the ecological pertinence of the model is the distinction of different substrate types, as the characteristics of the seabed are known to shape benthic macroinvertebrate communities in the Rance estuary (Desroy, 1998). The model's representation of sediment engineering could to a large extent mimic the actual environmental filtering effect of substrate, although how the two might interact is not clear. Sediment engineering was thus able to generate realistic patterns of diversity but could probably not sustain them, a task at which more or less permanent environmental filtering could be much more effective.

IV.5 References

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.

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.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer, New York, USA.

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.

Butman, C.A., Fréchette, M., Geyer, W.R., Starczak, V.R., 1994. Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. Limnol Oceanogr 39, 1755-1768.

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.

Côté, J., Himmelman, J.H., Claereboudt, M.R., 1994. Separating effects of limited food and space on growth of the giant scallop *Placopecten magellanicus* in suspended culture. Mar Ecol Prog Ser 106, 85-91.

DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. Annu Rev Ecol Evol S 36, 147-168.

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 Dissertation, Université de Rennes 1, Rennes, France.

Ellien, C., Thiebaut, É., Barnay, A.-S., Dauvin, J.-C., Gentil, F., Salomon, J.-C., 2000. The influence of variability in larval dispersal on the dynamics of a marine metapopulation in the eastern Channel. Oceanol Acta 23, 423-442.

Fraschetti, S., Giangrande, A., Terlizzi, A., Boero, F., 2002. Pre- and post-settlement events in benthic community dynamics. Oceanol Acta 25, 285-295.

Fréchette, M., Butman, C.A., Geyer, W.R., 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol Oceanogr 34, 19-36.

Gosselin, L.A., Qian, P.Y., 1997. Juvenile mortality in benthic marine invertebrates. Mar Ecol Prog Ser 146, 265-282.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol Model 198, 115-126.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecol Model 221, 2760-2768.

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.

Hijmans, R.J., 2016. raster: Geographic Data Analysis and Modeling. http://cran.r-project.org/package=raster. R package version 2.5-8.

Hjorth, A., Head, B., Wilensky, U., 2015. LevelSpace NetLogo extension. http://ccl.northwestern.edu/rp/levelspace/index.shtml. Center for Connected Learning and Computer Based Modeling, Northwestern University, Evanston, USA.

Hubbell, S.P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Funct Ecol 19, 166-172.

Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155, 269-301.

Ingels, J., Dashfield, S.L., Somerfield, P.J., Widdicombe, S., Austen, M.C., 2014. Interactions between multiple large macrofauna species and nematode communities – mechanisms for indirect impacts of trawling disturbance. J Exp Mar Biol Ecol 456, 41-49.

Kupriyanova, E.K., Nishi, E., Ten Hove, H.A., Rzhavsky, A.V., 2001. Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. Taylor & Francis Ltd, London, UK.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol Lett 16, 951-963.

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

Lord, J., Whitlatch, R., 2015. Predicting competitive shifts and responses to climate change based on latitudinal distributions of species assemblages. Ecology 96, 1264-1274.

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. vegan: Community Ecology Package. https://github.com/vegandevs/vegan. R package version 2.2-1.

Olafsson, E.B., Peterson, C.H., Ambrose, W.G., 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments – the relative significance of presettlement and postsettlement processes. Oceanogr Mar Biol 32, 65-109.

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.

R Core Team, 2015. R: a language and environment for statistical computing. http://www.R-project.org/. R Foundation for Statistical Computing, Vienna, Austria.

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

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.

Ugland, K.I., Gray, J.S., Ellingsen, K.E., 2003. The species–accumulation curve and estimation of species richness. J Anim Ecol 72, 888-897.

Wilensky, U., 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, USA.

IV.6 Appendix

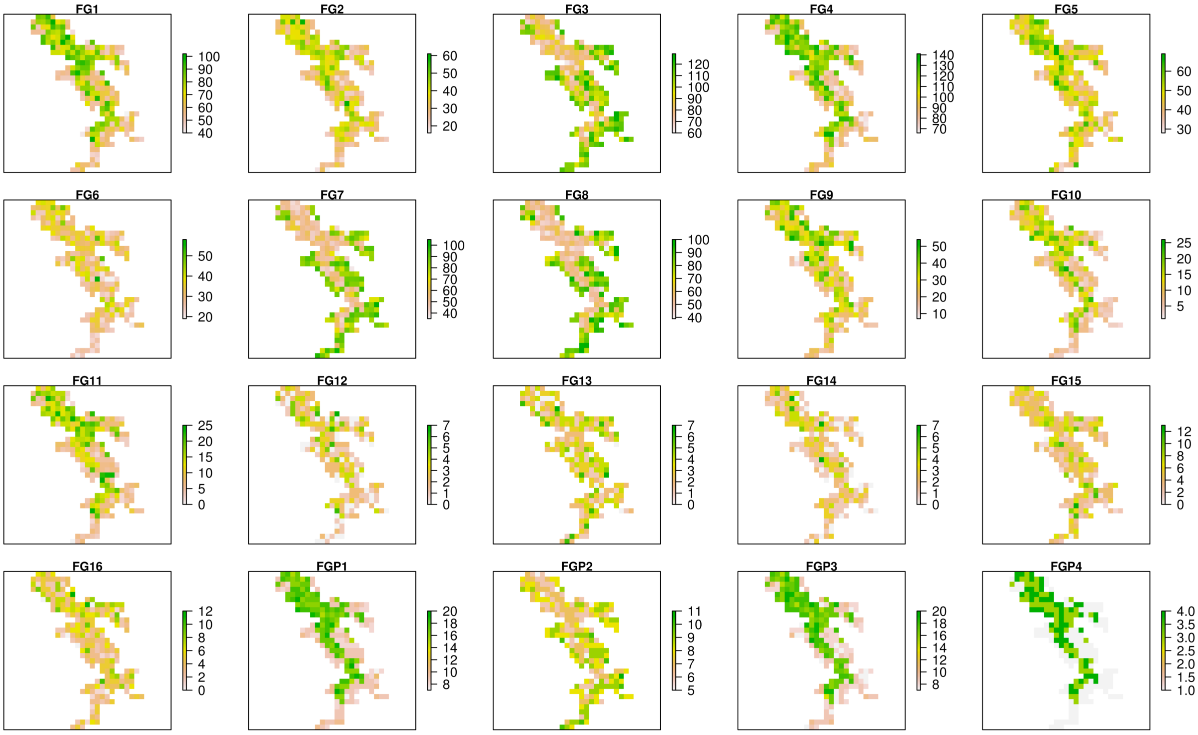


Fig. IV.A Functional group abundances in the 1st year of the benchmark simulation

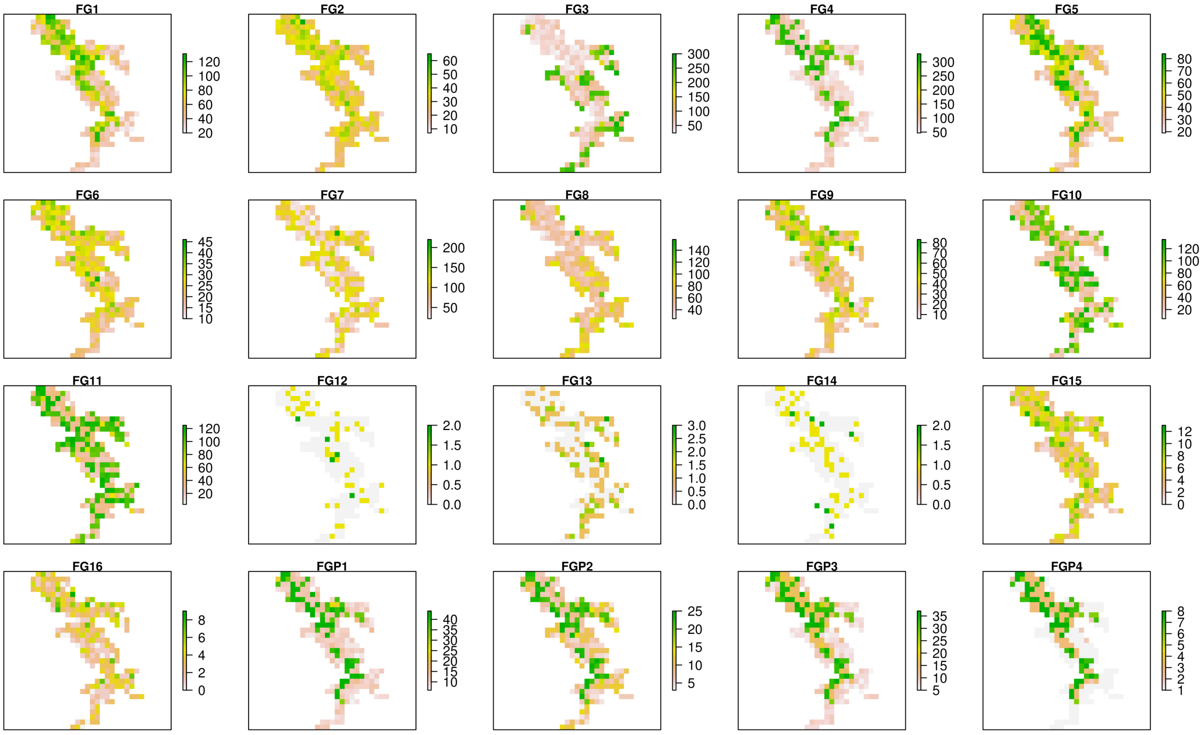


Fig. IV.B Functional group abundances in the 2nd year of the benchmark simulation

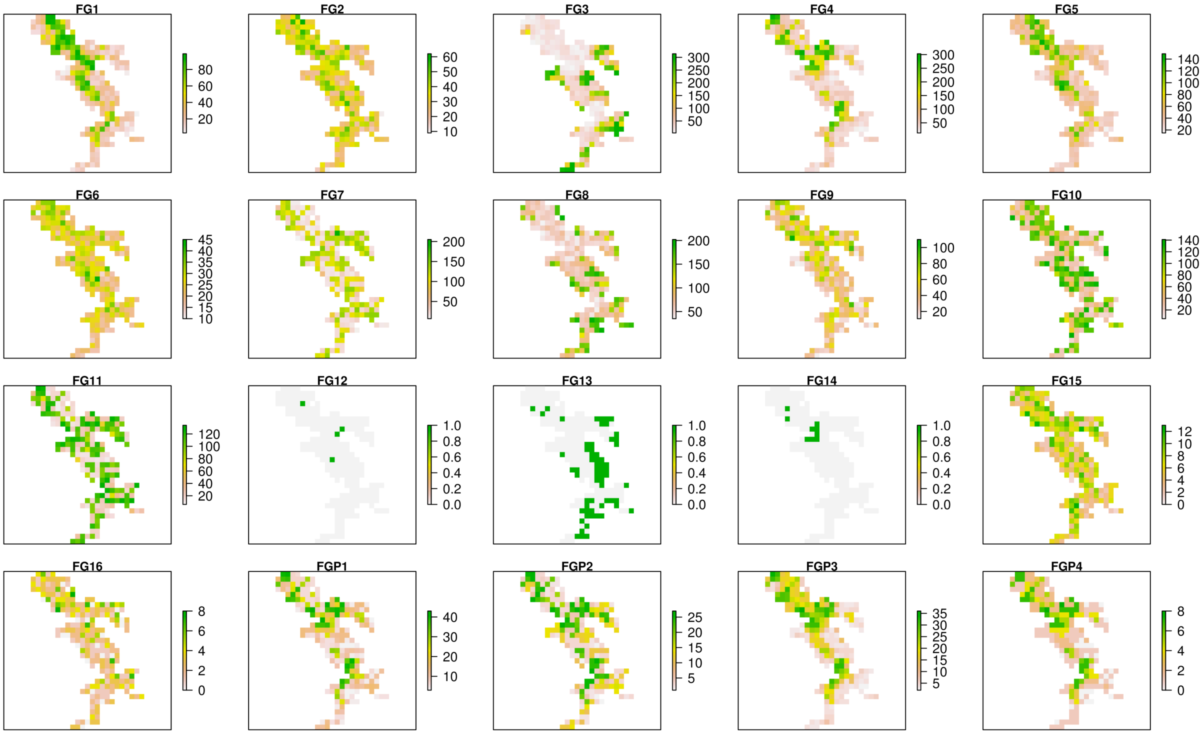
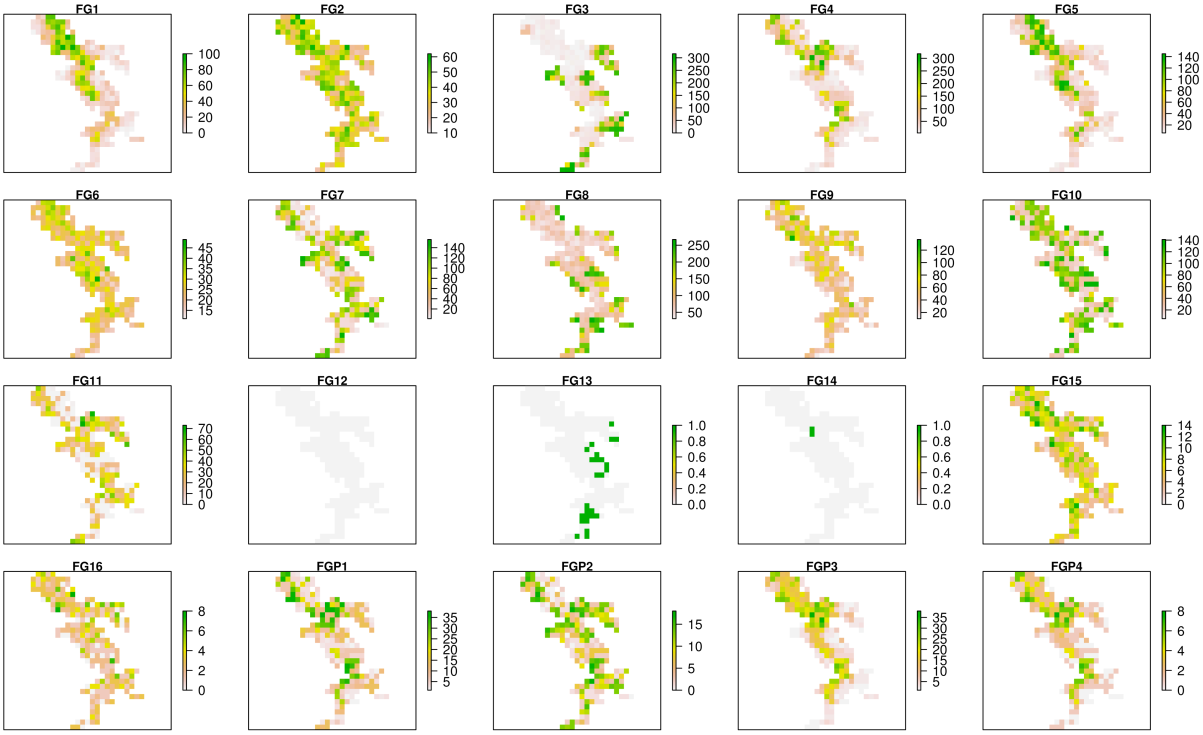


Fig. IV.C Functional group abundances in the 3rd year of the benchmark simulation



. **Fig. IV.D** Functional group abundances in the 4th year of the benchmark simulation

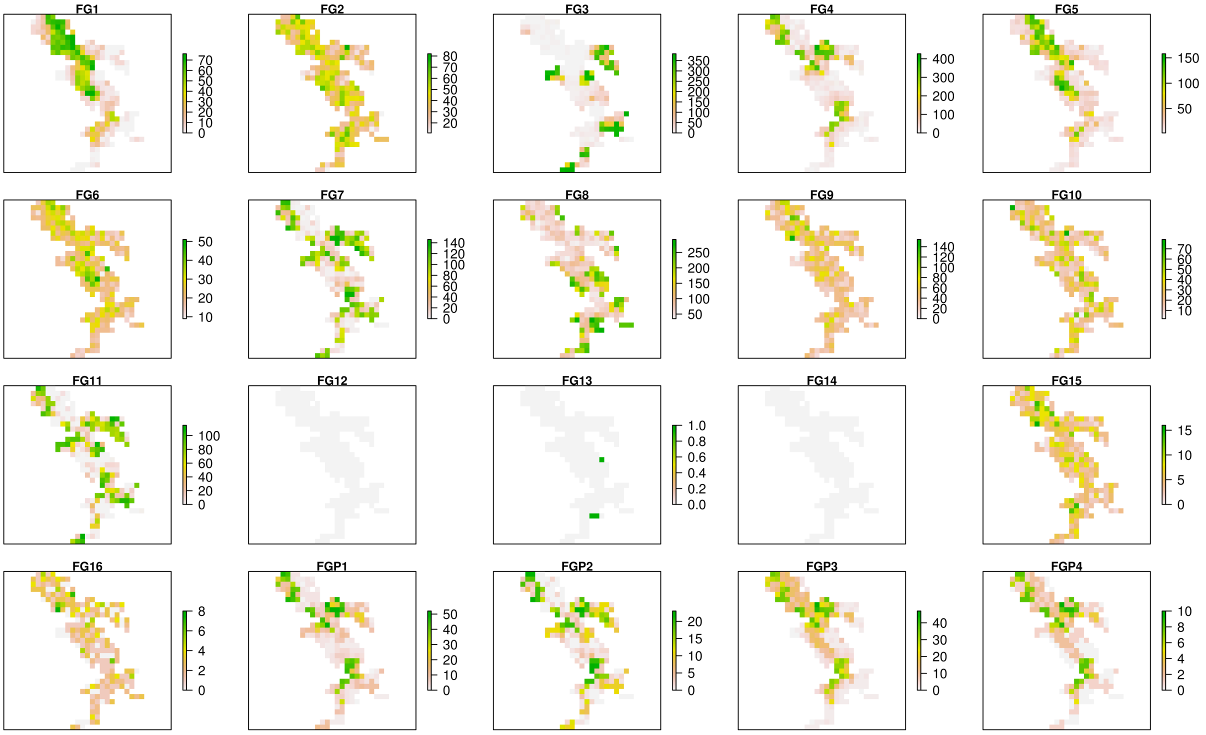


Fig. IV.E Functional group abundances in the 5th year of the benchmark simulation

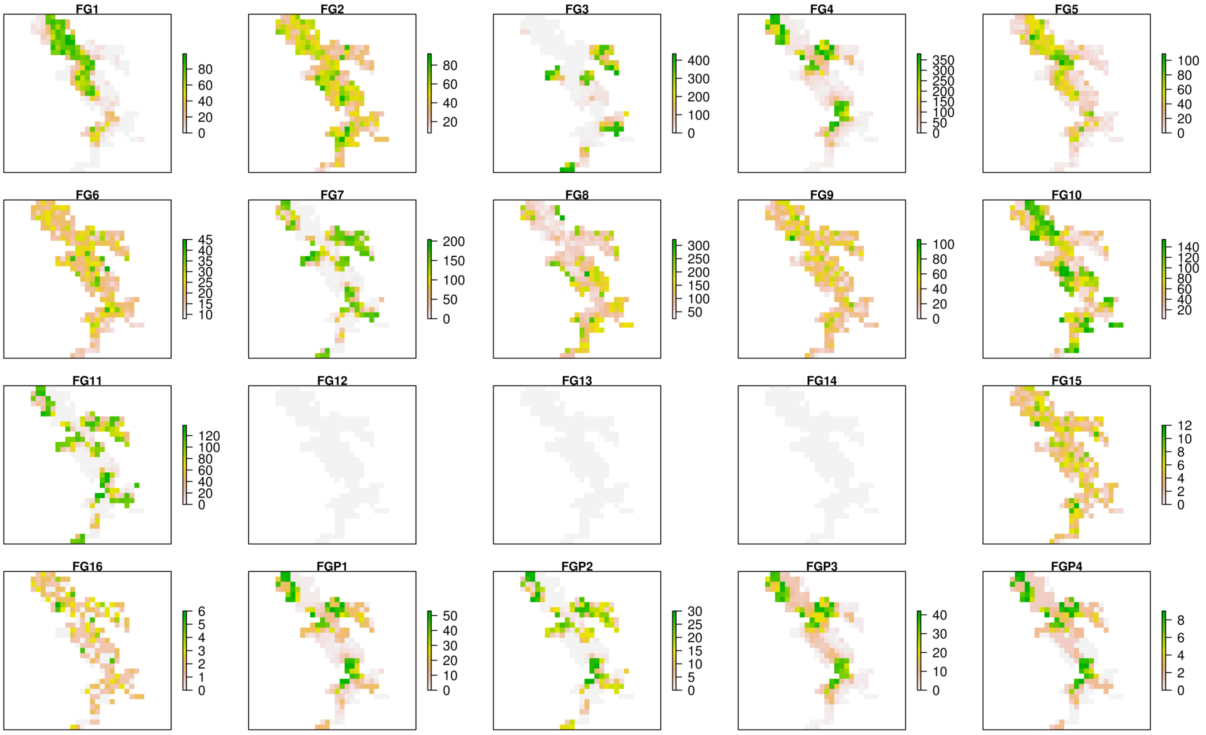


Fig. IV.F Functional group abundances in the 6th year of the benchmark simulation

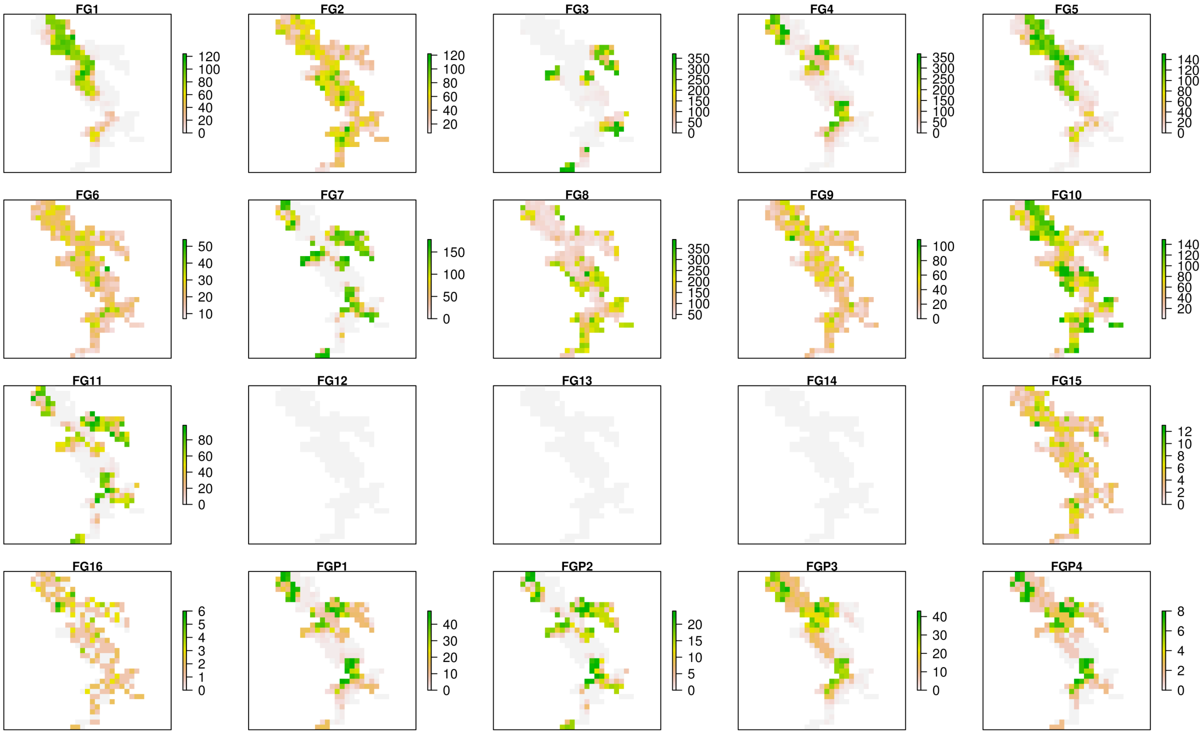


Fig. IV.G Functional group abundances in the 7th year of the benchmark simulation

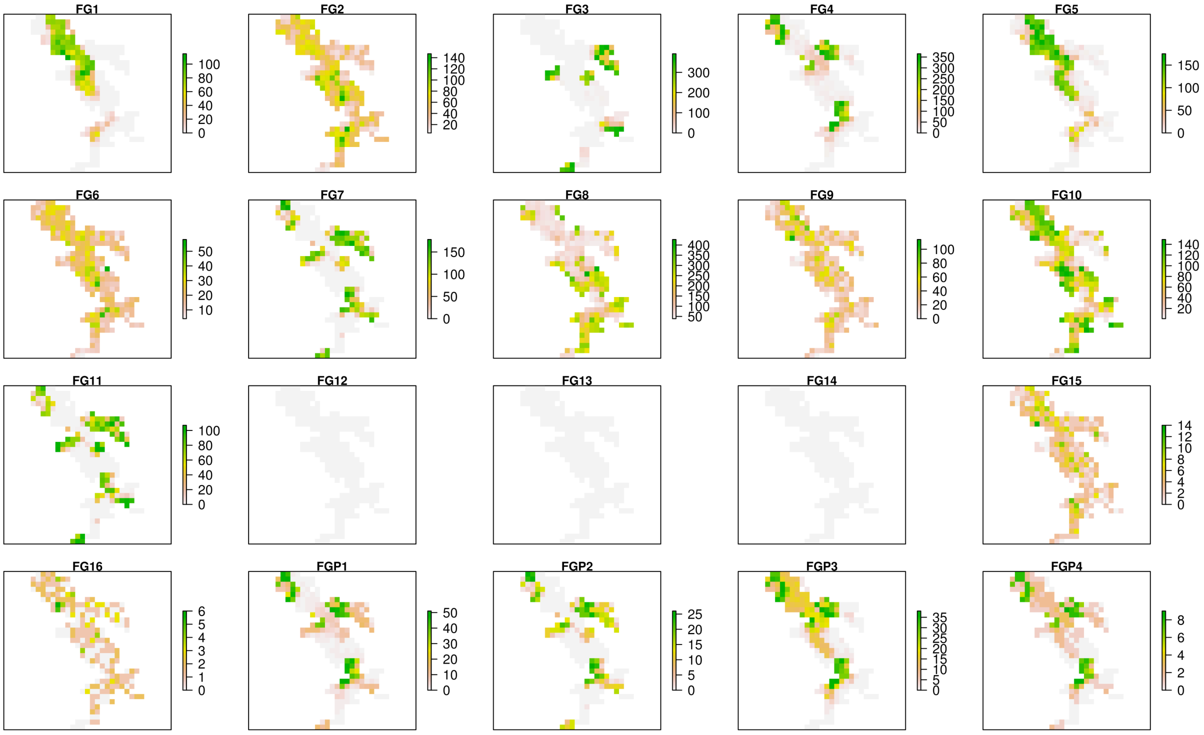


Fig. IV.H Functional group abundances in the 8th year of the benchmark simulation

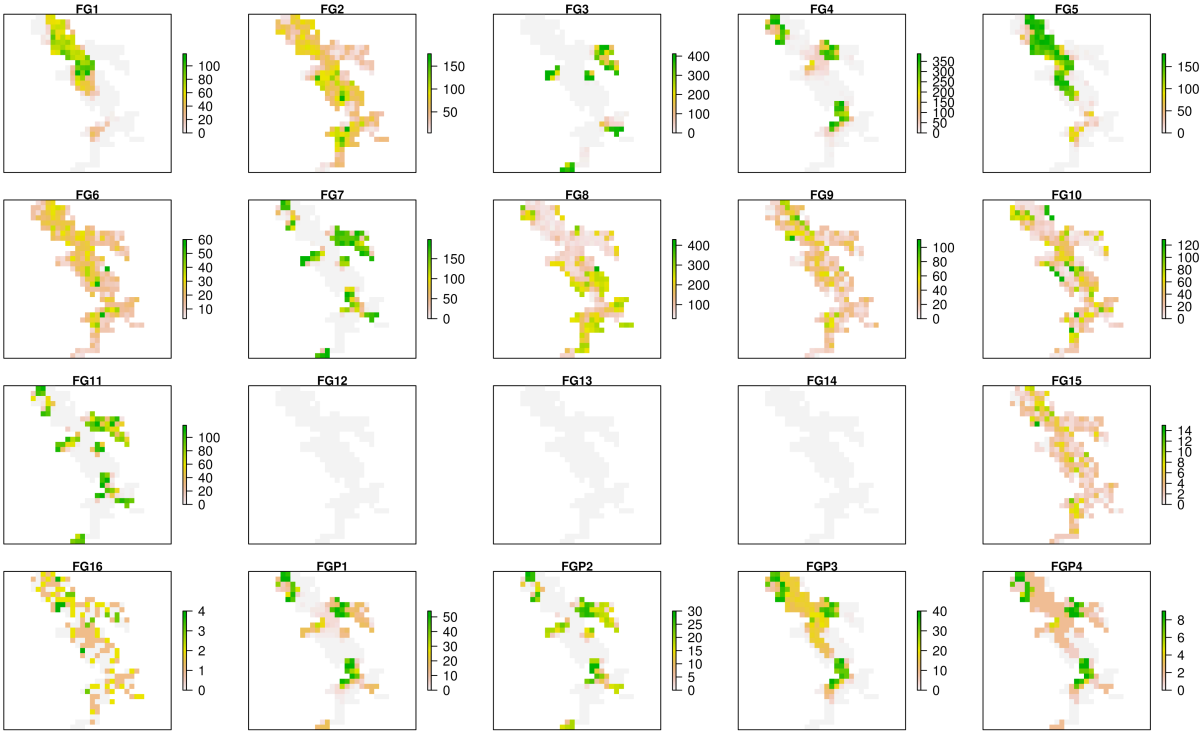
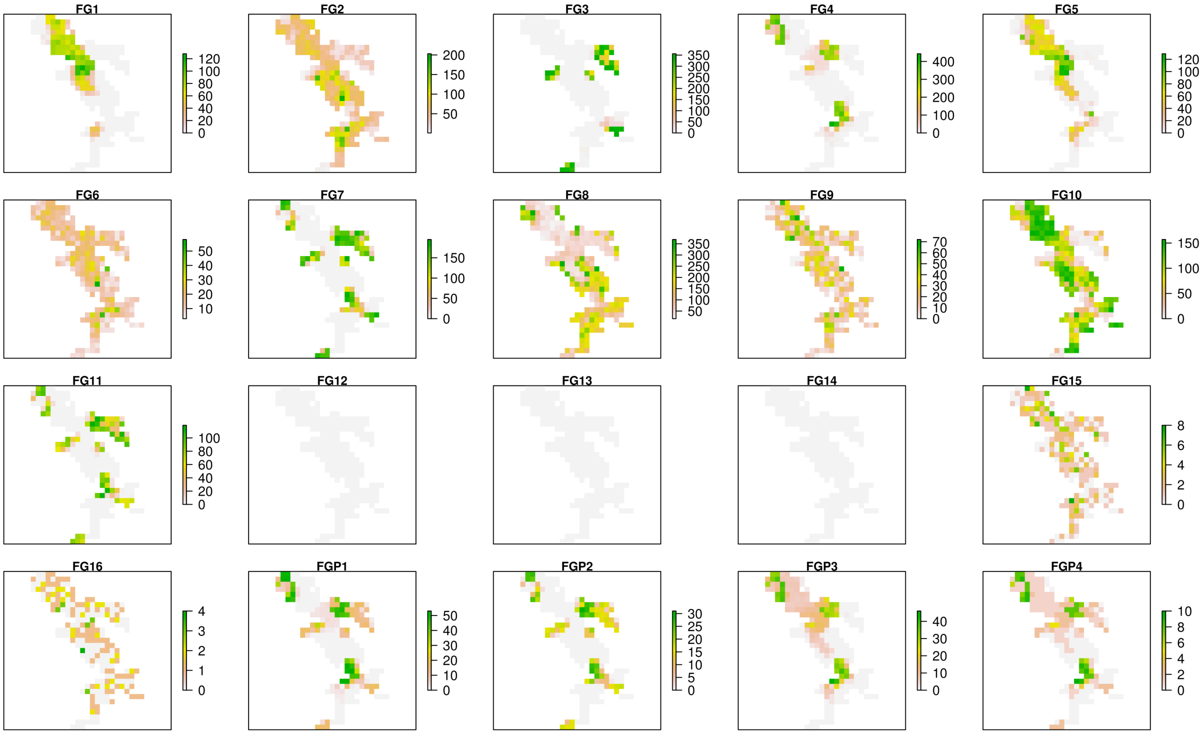


Fig. IV.I Functional group abundances in the 9th year of the benchmark simulation



. **Fig. IV.J** Functional group abundances in the 10th year of the benchmark simulation

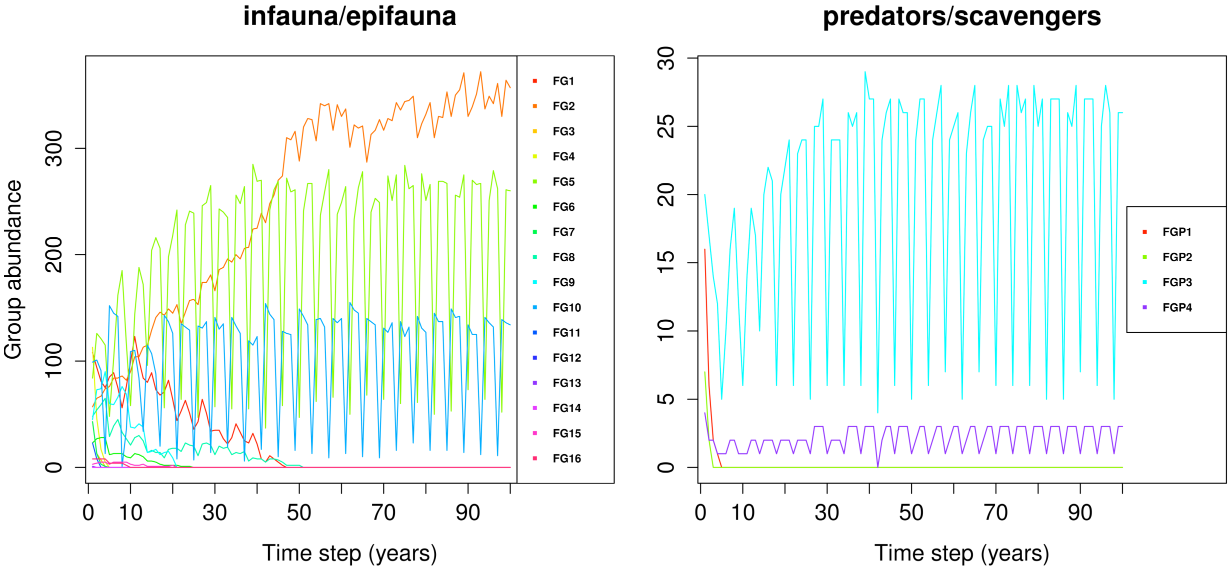


Fig. IV.K Evolution of functional group abundances in an independent simulation of the subtidal small-scale model that is dominated by sediment stabilizers

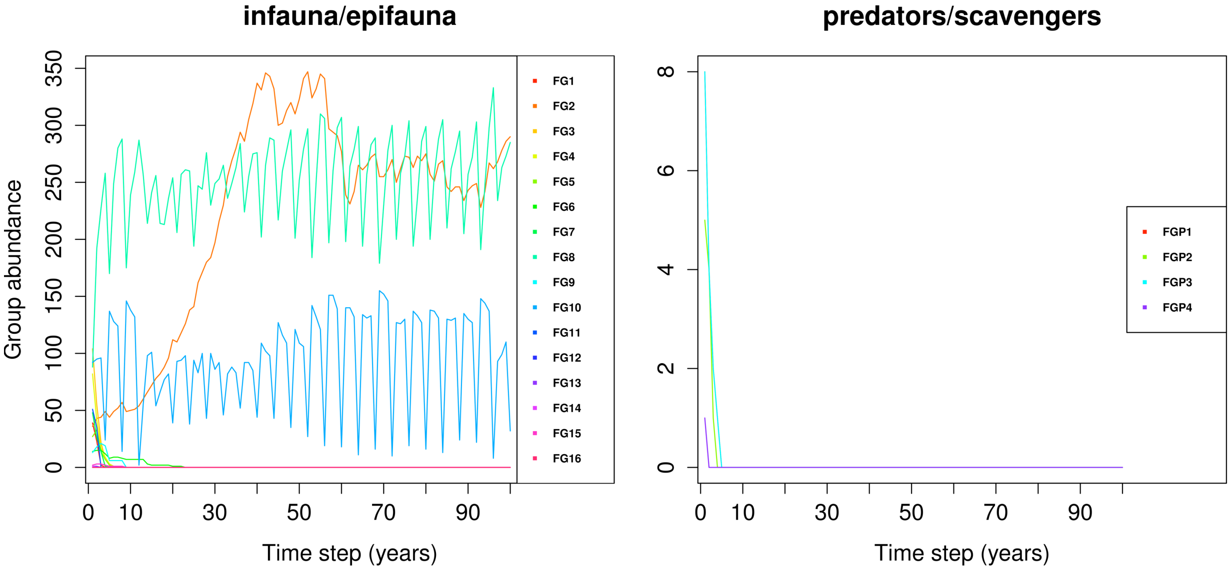


Fig. IV.L Evolution of functional group abundances in an independent simulation of the intertidal small-scale model that is dominated by sediment stabilizers

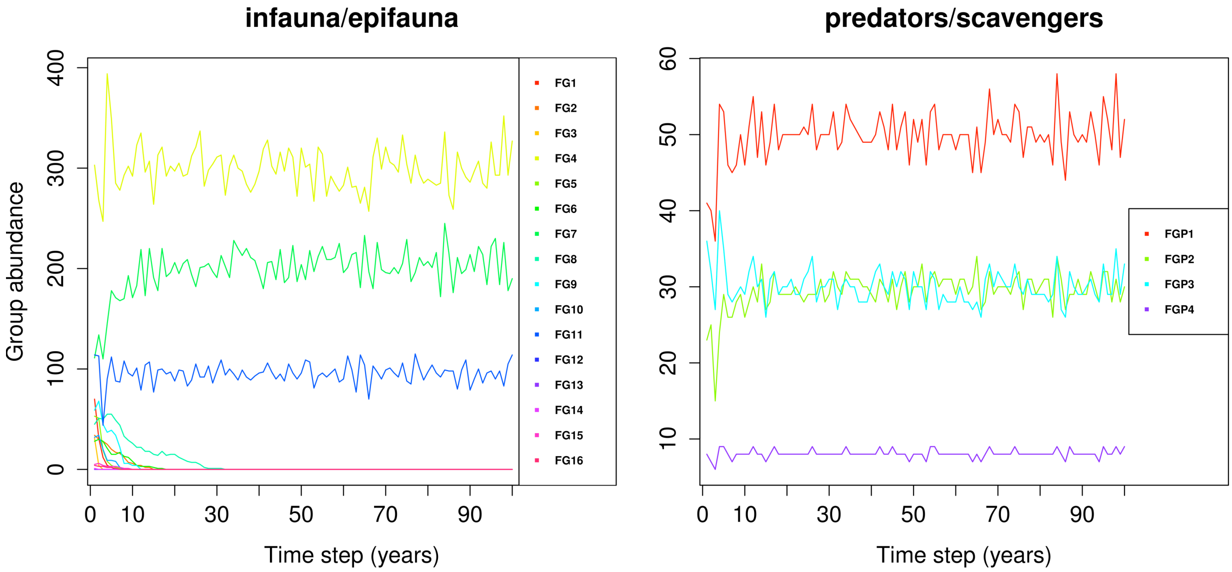


Fig. IV.M Evolution of functional group abundances in an independent simulation of the subtidal small-scale model that is dominated by sediment destabilizers

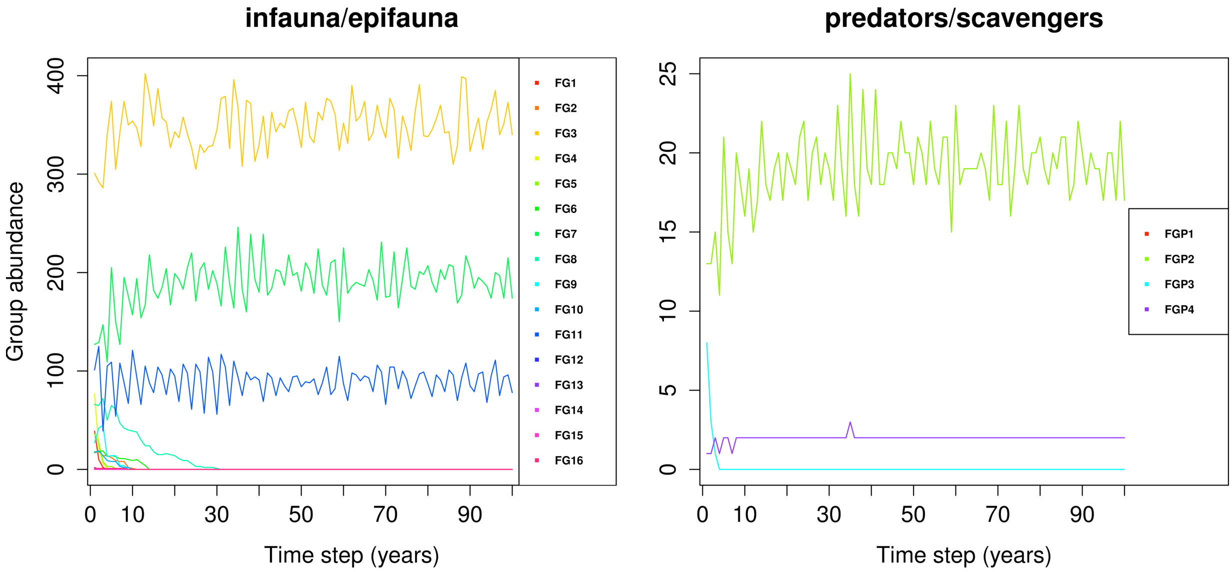


Fig. IV.N Evolution of functional group abundances in an independent simulation of the intertidal small-scale model that is dominated by sediment destabilizers

Chapter V: Conclusions

V.1 Study site

The Rance estuary occupies a central place in the studies presented here, as it provided the data set from which the system's primary functional components were derived (Alexandridis et al., 2017). The grouping procedure confirmed that both niche and neutral processes are at play, shaping benthic communities in the Rance estuary. Among the former, the filtering role of substrate type, its biogenic modification and the organisms' trophic behaviour stand out in their impact on the functional characteristics of the groups. The evaluation of the grouping against its theoretical assumptions made it clear that processes linked to divergent reproductive strategies could not be adequately represented, due to the quality of the available trait information. Still, the resulting level of ecological aggregation provides an objective and testable measure of the level of functional redundancy in benthic communities of the Rance estuary.

The primary data contained information on spatial patterns of community composition, which along with the ecological context in which they were collected (Desroy, 1998) allowed the use of the theoretical frameworks that formed the basis of the two modelling approaches (Chapter III, IV). The generated models may not be adequately validated for the formulation of reliable predictions about the Rance estuary, but they appear to highlight the role of disturbance in shaping its benthic communities. However, this work is not so much about the Rance estuary as it is about the first principles that were used for the formation of functional groups and their incorporation in models of community assembly. Specifically, the work explores the feasibility of a dynamic and spatially explicit representation of macroinvertebrate diversity, based on a snapshot of the system and a set of theoretical assumptions.

V.2 Empirical research

V.2.1 Single scale

Data sets like the one employed here, constituting no more than a snapshot of the system's biotic component and information on a few important abiotic variables, are not a rare occurrence among coastal benthic systems. They are typically analysed with the use of an array of multivariate statistical techniques that can reveal spatial patterns of community composition and relate them to a set of abiotic conditions (Borcard et al., 2011). Little information beyond abiotic niche requirements and potential drivers of spatial autocorrelation can be offered by this approach. Specifically, only guesses can be made about the dynamic behaviour of the system that led to the observed biodiversity patterns or its temporal and spatial response to a perturbation. Data on the organisms' biological traits can provide a more mechanistic understanding of biodiversity patterns (Dray et al., 2014), but does not significantly improve their predictability.

The use of long-term monitoring data can reveal some aspects of the dynamics that underlie the biodiversity patterns usually observed in a system snapshot. Observations of the abundance of 3 polychaete species collected over a period of 3 decades in the Wadden Sea revealed top-down cascading effects of severe winters, along with recovery cycles over the following years (Beukema et al., 2000). Monitoring efforts of this scale are, however, very rare, while the effects of perturbations may be much weaker and somewhat confounded by their propagation through feedback cycles connecting the community members of more diverse systems. The short-term investigation of spatial and temporal patterns of 11 macrobenthic species conducted in the Schelde estuary in the same period detected the spatial effect of environmental variables, but showed little evidence of temporal structure (Ysebaert and Herman, 2002).

V.2.2 Multiple scales

The study of Ysebaert and Herman (2002) was very effective at revealing the spatial scales of macroinvertebrate diversity patterns, along with important factors that lie behind them. Most of the differences in species abundance were observed at the scale of 10^2 m and half of the spatial structure could be explained by environmental variables, namely salinity, mud content, chlorophyll a and bed level height. However, some species showed significantly different abundance levels at distances over 10^3 m. This pattern could not be explained by environmental factors but had a significant component that interacted with the factor year, indicating synchronous development driven by the short-distance dispersal of adults or larvae. The large proportion of unexplained spatial structure demonstrates the limitations of studies focused on large-scale niche differences as the main mechanism of community assembly (Amarasekare, 2003).

The combination of large-scale (10^2 m) observations of abundance patterns with small-scale (10^0 m) experiments on adult–juvenile interactions in Manukau Harbour revealed the combined role of large-scale abiotic variability and small-scale biotic interactions in shaping observed biodiversity patterns (Thrush et al., 1997). Dauwe et al. (1998) used a diagenetic model to represent the small-scale effect of bioturbation on the vertical distribution of food. By combining the output of this model with information on the relative quality of organic matter in distant sites of the North Sea, they were able to explain the trophic structure of their benthic communities. The experimental investigation of a community's composition during its recovery from hypoxia in the Westerschelde estuary revealed complex successional dynamics, related to resource availability, natural variation and a host of biological traits (Van Colen et al., 2008).

This small sample of studies combining the output of observational, experimental and modelling research illustrates the potential of investigating benthic biodiversity patterns across spatial and temporal scales. It also serves as a demonstration of the challenges involved in any attempt to model the wide array of mechanisms that shape benthic communities at different scales. Constable (1999) remarked on the extreme complexity of the processes that would need to be included in such a model. He indicated recruitment, environmental filtering, biogenic habitat modification, competition for food and space, predation, extrinsic perturbations and natural variability in space and time as the main elements that would need to be represented. He also identified the emergence of large-scale diversity patterns from processes at the level of individual organisms as the factor presenting the greatest methodological challenges.

V.3 Modelling macrobenthos

V.3.1 Functional groups

Faced with the multitude and complexity of the processes that can shape benthic macroinvertebrate communities, most modelling efforts have either concentrated on single or related species or represented one or two mechanisms that are expected to primarily control community assembly at a single scale. The first step taken here toward a more comprehensive model of macrobenthos aimed at the reduction of its components through a systematic and testable procedure that retains sufficient information on their role in the most important community assembly mechanisms (Alexandridis et al., 2017). 20 functional groups were found to efficiently represent taxonomic and functional diversity patterns observed at the level of their 240 constituent species. This process of ecological aggregation preserves trait-controlled abundance patterns, by building groups of species with neutral variation of trait values (Hérault, 2007).

The transition from species to functional groups was essential for the development of the following modelling approaches. A reduction of the number of modelled entities can lead to lower complexity and higher tractability, significantly facilitating model analysis. The practice of representing only common or representative species usually ignores 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 grouping procedure that was employed here uses a wide array of biological traits, putting the emphasis on the species' functional role instead of their abundance, which is used only secondarily for the assignment of trait values to each functional group.

V.3.2 Functional relationships

The evaluation of the functional grouping against its theoretical assumptions suggested that, for most biological traits, species abundances depend, at least to some extent, on the trait values that were assigned to the species (Alexandridis et al., 2017). The nature of this relationship was further elucidated through the investigation of associations of biological traits with environmental variables and among themselves (Chapter III). The former indicated substrate type and tidal exposure as the factors that mostly influence community composition based on large-scale trade-offs among species caused by environmental filtering. The latter indicated the existence of small-scale trade-offs due to different efficiencies of food and space utilization, differences in survival rates and colonization potential or differences in the species' impact and response with regard to biogenic habitat modification.

These results allowed the application of the respective theoretical frameworks for the definition of functional relationships of the previously built groups with their basic resources and with each other (Chapter III). Each of the community assembly mechanisms that are represented by these relationships encompasses a variety of processes that could potentially be represented in a more detailed way. Similar to the assignment of trait values to each species, where the available information with the lowest resolution dictated the resolution of each biological trait, the level at which each mechanism was represented was restricted 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 represented at a relatively high level of biological organization.

For instance, the biogeochemical nature of sediment engineering was not explicitly addressed, as the distinction between sediment stabilizers and destabilizers (Posey, 1987) was the best that could be done with the available information at the species level. Still, the ecological relevance of representing biogenic habitat modification at this level has been experimentally upheld (Volkenborn et al., 2009). Similarly, the complex set of processes that comprise the phenomenon of competition was only represented through the use of each group's body 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 were found to play a central role in the successional dynamics of benthic communities, with the functional role of organisms being largely defined by their adult body size (Van Colen et al., 2008).

V.3.3 Qualitative models

Ecological theories that predict the existence of functional trade-offs were combined with expert knowledge on the functioning of benthic communities for the construction of qualitative models of the system in the Rance estuary (Chapter III). This allowed quantifying the system's potential for stability and predicting the direction of its components' response to press perturbations. Initial results regarding the system's response to altered food input and the effect of severe winters appear to agree with empirical evidence from similar systems. The approach for the comparison of model predictions with abundance observations allows the use of a single snapshot of the system for the elucidation of the ecological processes that can shape it through time. It, therefore, addresses a common issue of the statistical approaches that have been traditionally employed for the analysis of data sets of this nature.

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). Their flexibility allows the rapid assessment of alternative assumptions about system structure, based on their impact on the generated model predictions (Dambacher et al., 2002). They can, therefore, direct the initial steps of more quantitative modelling approaches, before investment in model development has rendered structural changes too costly. Still, the distinct role of processes that take place at different spatial scales cannot be explicitly represented by qualitative models, which limits their understanding and the potential to make predictions about spatially structured drivers. Transient dynamics can, likewise, not be easily addressed; they are, however, known to be a common feature of marine benthic systems (Beukema et al., 2000).

V.3.4 Agent-based models

V.3.4.1 Scales of mechanisms

The need for a spatially and temporally explicit representation of marine benthic communities led to the development of a modelling approach on the basis of the aforementioned ecological principles (Chapter IV). Among them, environmental filtering and differences in dispersal potential appear to operate at relatively large spatial scales (Ysebaert and Herman, 2002). On the other hand, biotic interactions, characterised by trade-offs in the efficiency of food and space utilization, differences in early survival rate and the effects of biogenic habitat modification, can be considered to take place at much smaller spatial scales (Van Colen et al., 2008). Community assembly mechanisms operating at different scales are very common in ecological systems and are typically demonstrated as high levels of both local and regional diversity (Kneitel and Chase, 2004), similar to patterns observed in the Rance estuary.

The distinction between small- and large-scale community assembly mechanisms led to the adoption of a multi-scale modelling approach. Biotic interactions were represented at the level of individuals, forming spatially distinct assemblages, whose composition drove patterns of larval dispersal and was shaped by the effect of tidal regime. The representation of biotic interactions at the individual level allows the combination of various ecological processes that have not yet or could not have been adequately analysed to permit their representation through mathematical formulations. In spite of recent attempts to address this issue by integrating non-trophic interactions into food web models (Kéfi et al., 2012), most biotic interactions are still significantly underrepresented. First principles about the way individuals interact can, instead, be derived from ecological theory or expert knowledge and represented by simple algorithms.

V.3.4.2 Individual-based models

The explicit representation of individual variation is an important advantage of individual-based models (IBMs) compared to differential or difference equation approaches (DeAngelis and Mooij, 2005). Combined with the confirmed removal of functionally equivalent variability that resulted from the process of species grouping, this characteristic of IBMs allowed the explicit representation of the role of stochastic but functionally consequential system variation. On the other hand, the taxing procedure of statistical analysis that IBMs typically have to undergo illustrates the benefits of analytically tractable mathematical formulations. Still, the amount of data and knowledge that are required by the latter, very often forces classical modelling approaches to rely on potentially unrealistic assumptions about the dynamics of the system, most notably their proximity to steady state or transition to it at a rate that is adequately low compared to the rates of the modelled processes (Jean, 1994).

IBMs are themselves not free of assumptions, but these do not involve the dynamics of the modelled system, as patterns emerge from how individuals interact with their environment and with each other. Ideally, the rules of interaction are formulated in terms of fitness maximization by individual organisms, providing a basis for predictions that is more general and reliable than commonly applied empirical relationships (Stillman et al., 2015). The use of ecophysiological models can significantly facilitate this task. Martin et al. (2013) used dynamic energy budget theory, in order to represent evolved metabolic trade-offs within individual organisms and reproduce the population dynamics of a water flea. In cases where the members of entire communities and their complex webs of interactions need to be represented, the required load of information and the level of model complexity are prohibitive to the application of such approaches.

IBMs in the marine benthos have been mostly employed with the goal of reproducing small-scale distribution patterns of one or two related species, driven by the availability of basic resources and the colonization of empty space. Special focus has been placed on the most well-studied benthic organisms, with coralline (Sleeman et al., 2005), macroalgal (Yñiguez et al., 2008) and bivalve growth and dispersal (Liu et al., 2014) successfully represented at the individual level. The development of IBMs of biological communities or entire ecosystems and the associated array of ecological processes still lags significantly behind the level that has been reached in the terrestrial environment. The explicit representation of terrestrial plant (Boulangeat et al., 2014) and animal community assembly mechanisms (Scherer et al., 2016) has improved predictions about biodiversity responses to projected climatic and land use change.

In order to recreate the dynamics of biological communities, IBMs have had to settle for an implicit representation of fitness maximization, since this is not explicitly modelled as the goal of individual organisms. The rules of interaction are, instead, phenomenological, representing the role of individuals in empirically derived community assembly mechanisms. The latter may take the form of ecological theories that use fitness maximization as a first principle, but do not allow behaviours to directly emerge from it. This has rendered IBMs an ideal framework for not only the synthesis but also the assessment and advancement of classical ecological theory (Evans et al., 2013). Also, expert knowledge on the way individual organisms interact, which is widely available but hard to formulate mathematically, can be used to complement or modify algorithms that describe theoretically expected biotic interactions.

In the small-scale IBM, the – common among trophic models – principle of mass conservation was replaced by the conservation of total space. The representation of pre-emptive competition for space is explicit, while exploitative competition for food is implicit in the represented overgrowth competition. The body size of each functional group is central to the definition of its individuals' role in competition, additionally controlling predatory interactions and the post-settlement mortality of juveniles. Settlement probabilities are controlled primarily by the groups' trait values with respect to reproductive strategies and secondarily by the traits of sediment position and mobility. Epibiosis is modelled through the settlement of organisms on basibionts, while sediment engineering is governed by the relative abundance of stabilizers and destabilizers and the modification of settlement probabilities based on each group's preferences.

The way that the control of biological traits over the individuals' role in the respective ecological processes was translated into algorithmic rules of interaction is of highly qualitative nature, in the sense that it often represents the extreme cases of a continuum of potential options. The large-scale representation of tidal regime and larval dispersal is much simpler in its essence but maintains the same characteristics. Better quantification of the modelled processes would be essential, if the goal was to make predictions about the Rance estuary. Since, however, this work is limited to exploring the potential of a dynamic and spatially explicit representation of benthic biodiversity, aspects of model structure and function are much more pertinent. Among those, the concurrent representation of community assembly mechanisms at different spatial scales appears to be conceptually and methodologically the most challenging issue.

V.3.4.3 Inter-scale modelling

One way of representing spatially structured processes that take place at distinct scales is the reduction of the small-scale component to a mean-field representation, which is then integrated into the large-scale model. This technique is very common among cases where both scales are represented through mathematical formulations of system dynamics and many methods have been developed to accommodate various ecological assumptions (Morozov and Poggiale, 2012). Less often, analytic representations have been combined with agent-based simulations in a variety of model configurations (Swinerd and McNaught, 2012). In those closer to the case of multi-scale modelling with large-scale patterns emerging from biotic interactions that occur at the level of individual organisms, analytic models are used to bound an aggregate measure of agent-based models or the latter is used to influence a parameter of analytic models.

The transfer of knowledge from the level of individual organisms, where most experiments are performed and theories are developed, to the level at which biodiversity patterns are typically observed is one of the central problems in ecology (Denny and Benedetti-Cecchi, 2012). However, the issue of up-scaling IBMs in order to combine them with agent-based models of large-scale processes has not been adequately addressed. The nonparametric up-scaling approach of Cipriotti et al. (2015) was designed to fill this gap. The important state variables of the small-scale model define a state space, which is divided into a finite number of discrete states. Simulation runs of the small-scale model, covering the entire range of pertinent initial conditions, states and external drivers, define transition matrices that are used by the large-scale model. This link is not dynamic and its conclusions are restricted to the range of the simulations.

The representation of the dynamic link between processes that operate at different scales is important for the reproduction of the effects of cross-scale interactions. Those include nonlinear dynamics with thresholds that result from pattern–process relationships changing across scales (Peters et al., 2007). This study identified transfer processes and spatial heterogeneity at intermediate scales as important components of the link between small- and large-scale patterns and processes. Similar to these conclusions, the model presented here consists of two spatially distinct representations that are dynamically linked by larval dispersal and sediment engineering. This link is formed at the level of biological assemblages that represent larger areas assumed to have homogeneous composition. It is implemented through aggregate community measures fed into the ecosystem model, whose spatial patterns influence assembly parameters.

V.3.4.4 Model validation

This multi-scale agent-based modelling approach appears to be well-suited for the evaluation of alternative hypotheses about community assembly mechanisms operating at different spatial scales. Before the model can be safely applied for this purpose, it has to be thoroughly validated. Kubicek et al. (2015) developed a validation approach specifically aimed at ecological IBMs. The whole process is organised in relation to the hierarchical structure of the model and is oriented toward its context. A variety of techniques can assist its application to this model, including expert knowledge about the model's assumptions, visual inspection of small-scale abundance distributions or large-scale spatial patterns, statistical comparison of model output with comparable but independent observations, comparison of aggregated model results with patterns observed at higher system levels or experimental evaluation of model-generated hypotheses.

V.3.4.5 Data sets

It is obvious that the model's validation would benefit from the use of independent data of benthic macroinvertebrates abundance from the Rance estuary. This role could be played by the available data sets of '71 and '76, with the former possibly used for the model's initialisation. Due to the model's stochastic nature, the analysis of aggregated temporal and spatial properties, akin to the Mantel correlogram, would probably constitute the most effective use of such data in the context of the aforementioned validation approach. These data sets could also be used for the assessment of the consistency of the functional grouping over time or for the formation of new, more consistent groups. If, however, the goal is the derivation of general functional groups of marine benthic macroinvertebrates, data from other sites would be much more useful, with the range of sampled systems dictating the generality of the groups.

V.3.4.6 Minor adjustments

The transition to more general functional groups would require considering not only a new set of species but also new ecological processes, along with the respective biological traits. Yet, at this stage, improving the representation of community assembly mechanisms in the Rance estuary is probably more important than making the functional groups and the model more general. The addition of two elements is expected to significantly increase the model's realism. First, spatial heterogeneity with regard to substrate type is known to control community composition in the Rance estuary (Desroy, 1998). Second, physical disturbance in the form of substrate destabilization or severe winters can be reasonably assumed to be a shaping factor of most estuarine benthic systems. These two factors can be added to the current version of the model through small adjustments to its large-scale spatial features and small-scale rules of interaction.

Minor improvements to the model, such as those mentioned above, might change its dynamic behaviour in important ways. Most notably, they could help sustain high levels of β-diversity, by either increasing spatial variability of the abiotic environment or keeping the system away from an equilibrium point. If the latter took the form of a constant initialisation of a subset of the sites, it could also promote the persistence of rare functional groups. However, if the model fails at reproducing important aspects of observed biodiversity patterns, changes should be made to the basic assumptions on which it was built. First, simplifications that were employed for the representation of community assembly mechanisms at a specific level of biological organisation could be revised toward a more detailed description. Second, fundamental elements of the way space and time are depicted could be altered to become more realistic.

V.3.4.7 Major changes

Community assembly mechanisms

Improving the representation of community assembly mechanisms should probably centre on trophic interactions. At this point, predation is implicitly considered to contribute to the mortality of individuals that are left most vulnerable due to overgrowth competition. Explicit predation mortality plays only a minor role. The distinct depiction of mortality due to lack of resources would allow predation mortality to be modelled explicitly in its entirety. The former could be achieved by translating known relations between community structure and organic fluxes (Herman et al., 1999) into IBM-oriented rules of interaction. This task would require further differentiation of trophic strategies, e.g. by distinguishing between suspension and deposit feeders. The use of fuzzy coding is expected to greatly facilitate the assignment of ambiguous trait values. Data of hydrodynamics and primary production would help define organic matter deposition fluxes.

Information regarding the abiotic and biotic characteristics of the water column could be derived from observations of the system or the output of models. Its incorporation into the IBM could be achieved by adjusting the minimum space that is required by individual organisms. Data of hydrodynamics in the Rance estuary would also allow a more explicit representation of larval dispersal, especially if it was combined with a distinct contribution of each functional group based on their fecundity and dispersal potential. If necessary, the representation of space and time could be altered more fundamentally. Instead of implicitly letting the organisms' position influence their functional role, at least two layers of sediment could be distinguished, with space occupation represented separately. Likewise, time steps could be reduced below the current level of one year. This would allow the seasonal depiction of productivity, reproduction and disturbance.

Ecosystem functions

Modelling marine benthic diversity largely owes its importance to the well-established but only poorly understood link between biodiversity and ecosystem functioning (Srivastava and Vellend, 2005). The study of this link requires biodiversity patterns to be explicitly associated with ecosystem functions, such as energy and elemental cycling, the provision of habitat or the modification of physical properties of the system (Frid et al., 2008). These functions have long been the subject of statistical analyses based on many of the biological traits that are here assumed to represent the organisms' role in community assembly mechanisms (Bremner et al., 2006). The use of these traits as indicators of ecosystem functions can be extended to associate the latter with modelled biodiversity. This task can be assisted by theoretically (Brown et al., 2004) and empirically (Brey, 2010) derived links between traits and ecosystem functions.

Modelling tools

As new features are added and the complexity of the model increases, the use of Netlogo (Wilensky, 1999) as the programming environment may soon become restrictive. It is the highest-level among widely used agent-based modelling platforms, placing special emphasis on ease of learning, using and sharing. The result is a tool that favours rapid model development at the expense of direct control and customizability. Execution speed is not its strong point, but it appears to be on a par with similar platforms (Railsback et al., 2006). Repast (North et al., 2013) may be the tool of choice, if speed is a high priority, but its extensive use is hampered by the lack of generic yet simple tools (Drogoul et al., 2013).

GAMA (Grignard et al., 2013), on the other hand, appears to be well-positioned along the usability–performance continuum. Its advanced environment representations and dynamic multi-level support make it ideal for this approach.

V.3.4.8 Model generalisation

The changes mentioned above have the immediate goal of improving the representation of community assembly mechanisms in the Rance estuary. Still, their nature is also expected to make the transfer of the modelling approach to other systems easier. This would result from representing the modelled processes even more explicitly. Changes to the model aiming at its application to similar systems would mostly involve subtracting elements that are not relevant or modifying them, by changing a few parameters. This should be facilitated by the suggested changes, since the model's elements would be more directly linked to the respective mechanisms. It appears that the greatest challenge with respect to the transfer of the approach to other sites is presented by the collection of reliable data of community composition, biological traits and important environmental variables over a considerable extent of space and time.

The best strategy for a long-term investment in this approach would probably start with its transfer to a few sites, whose differences from the Rance estuary would be dictated by the envisioned modelling scope. The sites should be chosen based on the availability of species abundance data sets that are representative of the system's spatial and, if possible, temporal variability. The same holds true for the environmental conditions of tidal regime and substrate type, along with any variables that might be selected for addition to the framework. The availability of databases of biological traits for the system's species is also a prerequisite, along with some degree of expert knowledge on its functioning. The definition of general functional groups of marine benthic macroinvertebrates should follow, based on the sum of community assembly mechanisms that are employed for the application of the approach in the selected sites.

V.4 References

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.

Beukema, J.J., Essink, K., Dekker, R., 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator–prey interactions. J Anim Ecol 69, 31-44.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer, New York, USA.

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.

Bremner, J., Paramor, O., Frid, C., 2006. Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0-12 nautical mile zone. A report to English Nature from University of Liverpool, Liverpool, UK.

Brey, T., 2010. An empirical model for estimating aquatic invertebrate respiration. Methods Ecol Evol 1, 92-101.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771-1789.

Cipriotti, P.A., Wiegand, T., Pütz, S., Bartoloni, N.J., Paruelo, J.M., 2015. Nonparametric upscaling of stochastic simulation models using transition matrices. Methods Ecol Evol 7, 313-322.

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.

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

Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar Ecol Prog Ser 173, 67-83.

DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. Annu Rev Ecol Evol S 36, 147-168.

Denny, M., Benedetti-Cecchi, L., 2012. Scaling Up in Ecology: Mechanistic Approaches. Annu Rev Ecol Evol S 43, 1-22.

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 dissertation, Université de Rennes 1, Rennes, France.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95, 14-21.

Drogoul, A., Amouroux, E., Caillou, P., Gaudou, B., Grignard, A., Marilleau, N., Taillandier, P., Vavasseur, M., Vo, D.-A., Zucker, J.-D., 2013. GAMA: multi-level and complex environment for agent-based models and simulations. Proceedings of the 2013 international conference on Autonomous agents and multi-agent systems, St. Paul, USA.

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., De Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., 2013. Do simple models lead to generality in ecology? Trends Ecol Evol 28, 578-583.

Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas. Hydrobiologia 606, 69-79.

Grignard, A., Taillandier, P., Gaudou, B., Vo, D.A., Huynh, N.Q., Drogoul, A., 2013. GAMA 1.6: Advancing the Art of Complex Agent-Based Modeling and Simulation. PRIMA 2013: Principles and Practice of Multi-Agent Systems: 16th International Conference, December 1-6, Dunedin, New Zealand.

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.

Jean, F., 1994. Modélisation à l'état stable des transferts de Carbone dans le réseau trophique benthique de la rade de Brest (France). PhD dissertation, Université de Brest, Brest, France.

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.

Kneitel, J.M., Chase, J.M., 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol Lett 7, 69-80.

Kubicek, A., Jopp, F., Breckling, B., Lange, C., Reuter, H., 2015. Context-oriented model validation of individual-based models in ecology: A hierarchically structured approach to validate qualitative, compositional and quantitative characteristics. Ecol Complex 22, 178-191.

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

Liu, Q.-X., Herman, P.M.J., Mooij, W.M., Huisman, J., Scheffer, M., Olff, H., van de Koppel, J., 2014. Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. Nat Commun 5, 5234.

Lyons, K.G., Brigham, C.A., Traut, B.H., Schwartz, M.W., 2005. Rare Species and Ecosystem Functioning. Conserv Biol 19, 1019-1024.

Martin, B.T., Jager, T., Nisbet, R.M., Preuss, T.G., Grimm, V., 2013. Predicting Population Dynamics from the Properties of Individuals: A Cross-Level Test of Dynamic Energy Budget Theory. Am Nat 181, 506-519.

Morozov, A., Poggiale, J.-C., 2012. From spatially explicit ecological models to mean-field dynamics: The state of the art and perspectives. Ecol Complex 10, 1-11.

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.

North, M.J., Collier, N.T., Ozik, J., Tatara, E.R., Macal, C.M., Bragen, M., Sydelko, P., 2013. Complex adaptive systems modeling with Repast Simphony. Com Adap Sy Model 1, 3.

Peters, D.P.C., Bestelmeyer, B.T., Turner, M.G., 2007. Cross–Scale Interactions and Changing Pattern–Process Relationships: Consequences for System Dynamics. Ecosystems 10, 790-796.

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

Railsback, S.F., Lytinen, S.L., Jackson, S.K., 2006. Agent-based simulation platforms: Review and development recommendations. Simulation 82, 609-623.

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.

Sleeman, J.C., Boggs, G.S., Radford, B.C., Kendrick, G.A., 2005. Using Agent ‐ Based Models to Aid Reef Restoration: Enhancing Coral Cover and Topographic Complexity through the Spatial Arrangement of Coral Transplants. Restor Ecol 13, 685-694.

Srivastava, D.S., Vellend, M., 2005. Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation? Annu Rev Ecol Evol S 36, 267-294.

Stillman, R.A., Railsback, S.F., Giske, J., Berger, U., Grimm, V., 2015. Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. BioScience 65, 140-150.

Swinerd, C., McNaught, K.R., 2012. Design classes for hybrid simulations involving agent-based and system dynamics models. Simul Model Pract Th 25, 118-133.

Thrush, S.F., Cummings, V.J., Dayton, P.K., Ford, R., Grant, J., Hewitt, J.E., Hines, A.H., Lawrie, S.M., Pridmore, R.D., Legendre, P., McArdle, B.H., Schneider, D.C., Turner, S.J., Whitlatch, R.B., Wilkinson, M.R., 1997. Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult/juvenile interactions. J Exp Mar Biol Ecol 216, 153-169.

Tilman, D., 1980. Resources: A Graphical-Mechanistic Approach to Competition and Predation. Am Nat 116, 362-393.

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. Helgol Mar Res 63, 27-35.

Wilensky, U., 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, USA.

Yñiguez, A.T., McManus, J.W., DeAngelis, D.L., 2008. Allowing macroalgae growth forms to emerge: Use of an agent-based model to understand the growth and spread of macroalgae in Florida coral reefs, with emphasis on Halimeda tuna. Ecol Model 216, 60-74.

Ysebaert, T., Herman, P.M., 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. Mar Ecol Prog Ser 244, 105-124.

Annex A: Comparing qualitative predictions of benthic responses to perturbations with observed patterns of functional diversity

A.1 Introduction

Understanding functional aspects of biodiversity often relies on a limited number of observations, offering no more than a snapshot of the investigated system. The Rance estuary (Brittany, France) is a typical example, with only two comprehensive samplings of benthic macroinvertebrate abundance (1976, 1995), separated by almost twenty years (Kirby and Retiere, 2009). The result is a high degree of difficulty in understanding the dynamics that have structured these communities. All the more so, when the ultimate goal is to provide testable predictions about the system's response to potential perturbations.

Qualitative mathematical models can generate rigorous predictions, albeit sacrificing the element of precision (Levins, 1998). Still, testing these predictions against observations of the previously described nature is not easy. Samples of community composition are often collected after a perturbation, without much knowledge on the prior state of the system. This holds true for the 1995 macroinvertebrate sampling of the Rance estuary, restricting the testability of qualitative models (Chapter III) that were built around a set of previously formed functional groups (Alexandridis et al., 2017).

This study presents an approach that allows the comparison of qualitative modelling predictions with post-perturbation biodiversity patterns. The approach employs a matrix of observed functional group abundances and a matrix that describes the system's predicted response to potential perturbations affecting at least one of its components. It was applied to data of macroinvertebrate community composition collected after the extremely cold winter of 1994 (Desroy, 1998) and the predictions of qualitative mathematical models that are expected to represent the mechanisms that shape benthic communities in this system.

A.2 Methods

A.2.1 Community composition

Samples of the upper sediment layers were collected in 113 sites of the subtidal and the intertidal zone in April 1995, prior to the spring recruitment. Invertebrate organisms larger than 1 mm were counted and determined at species level, when possible (Desroy, 1998). A set of 14 biological traits describing the role of the 240 macroinvertebrate species in 7 important community assembly mechanisms allowed the application of the emergent group hypothesis (Hérault, 2007) for the construction of 20 functional groups. The groups were assigned their own trait values and were found to adequately represent functional diversity in the Rance estuary (Alexandridis et al., 2017). Two separate matrices of functional community composition in the 113 sampled sites, $\mathbf{C_1}$ and $\mathbf{C_2}$, were produced for the epifaunal and the infaunal groups, respectively.

A.2.2 Qualitative models

Observed trait associations at the species level were found to agree with ecological theories that predict the existence of functional trade-offs among benthic organisms. Elements of these theories along with expert knowledge were incorporated in the form of general rules of interaction into two signed-directed graph (or signed digraph) models of the previously built functional groups, one for epifaunal organisms with a preference for rock or gravel (SD_1) and one for infaunal or interface-positioned organisms that prefer finer sediment types (SD_2) (Fig. A.1). Qualitatively specified community matrices $\mathbf{A_1}$ and $\mathbf{A_2}$ were produced as an equivalent representation of SD_1 and SD_2, respectively (Dambacher and Rossignol, 2001). The stability analysis of the two models revealed a moderate to high potential for stability (Chapter III).

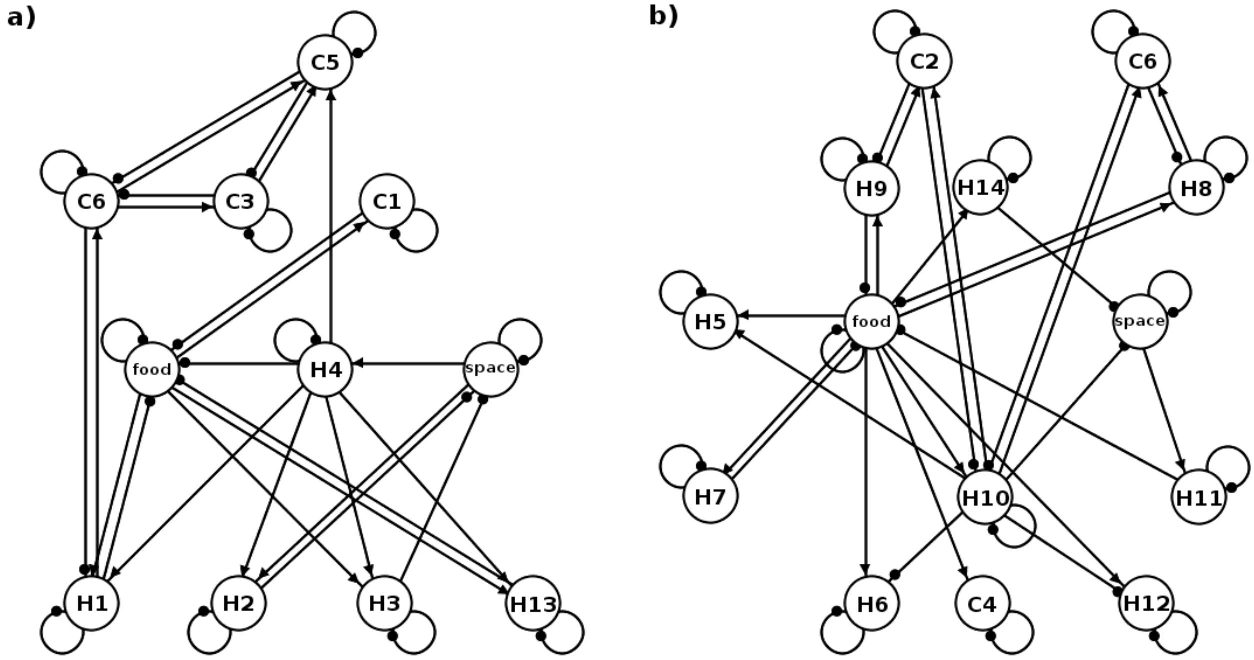


Fig. A.1 Signed digraphs a) SD_1 and b) SD_2, representing the mechanisms that shape epifaunal and infaunal benthic macroinvertebrate communities, respectively. The nodes represent functional groups or the basic resources of food and space. Links ending in arrows and filled circles represent positive and negative direct effects, respectively. For details, see Chapter III

A.2.3 Qualitative predictions

Assuming that the modelled system is stable, the adjoint of the negative community matrix predicts the direction of the equilibrium response of community members following a press perturbation to the system (Dambacher et al., 2002). It represents the relative strength of complementary feedback contributing to each member's response to sustained input and it was found to correspond well with quantitative predictions of response strength (Dambacher et al., 2003). The adjoint was calculated for both $\mathbf{A_1}$ and $\mathbf{A_2}$, producing matrices $\mathbf{B_1}$ and $\mathbf{B_2}$, respectively. The rows of each matrix describe the predicted response of each model's functional groups. The groups' response to positive input to a group or one of the food/space resources can be read along each matrix's columns. The response of the two basic resources was removed as impertinent.

A.2.4 Theoretical framework

Given a community matrix **A**, Eq. 1 predicts the difference between the community member i's equilibrium abundance (N_i*) before and after sustained input to parameter h (p_h)

of community member j's growth rate function (f_j). The sign of this difference is defined by the first term of the expression, as the other two terms constitute a positive scalar in stable systems. This property of the adjoint matrix can be employed in predicting the direction of the system's response to press perturbations, if the community matrix is only qualitatively specified. If the pre-perturbation abundance distribution of each community member is unknown, the assumption that it shows random variation within an adequately small range would allow the comparison of post-perturbation patterns of relative abundance with the predictions of the adjoint matrix.

$$dN_i^* = \underbrace{N_i{}^*{}_{\mathrm{new}}}_{\substack{\text{observed}\\ \text{abundance}}} - \underbrace{N_i{}^*{}_{\mathrm{old}}}_{\substack{\text{unknown}\\ \text{abundance}}} = \underbrace{\mathrm{adj}(-\mathbf{A})_i}_{\substack{\text{complementary}\\ \text{feedback}}} \times \underbrace{\frac{1}{\det(-\mathbf{A})}}_{\substack{\text{overall}\\ \text{feedback}}} \times \underbrace{\frac{\partial f_j}{\partial p_h} d p_h}_{\substack{\text{strength}\\ \text{of input}}} \tag{1}$$

A.2.5 General assumptions

The comparison of observations with model predictions is based on the assumption that the system is near or has reached a new equilibrium following a perturbation. The processes represented in the models should occur at spatial and temporal scales that would allow this state to be reached within the spatial resolution of the sampling and within the time since the perturbation. If this is the case, the epifauna and the infauna that were sampled in each site can be considered to be an independent realization of the respective qualitative model. If it is further assumed that perturbation is demonstrated throughout the system as varying input to mainly one of its variables, patterns of predicted response of the community's members along the respective column of the adjoint matrix should agree with observed patterns of relative abundance distribution.

A.2.6 Data transformation

In order to standardize functional group abundances by site productivity and group dominance level, the values of matrices $\mathbf{C_1}$ and $\mathbf{C_2}$ were divided first by each site's total abundance and then by each group's maximum frequency. Square root transformation was applied to the results, in order to reduce the importance of observations with very high values. Euclidean distances between the functional groups were derived from the output of the transformation. They are expected to quantify the groups' dissimilarity with respect to their relative abundance distribution. Euclidean distances between the functional groups were also derived from each column of matrices $\mathbf{B_1}$ and $\mathbf{B_2}$. These are expected to quantify the groups' dissimilarity with respect to their predicted response to input added to the system through the respective model variable.

A.2.7 Congruence analysis

The agreement between patterns of relative abundance distribution and predicted responses to press perturbation was evaluated by comparing the respective functional group distance matrices. Those that were derived from the transformed $\mathbf{C_1}$ and $\mathbf{C_2}$ were compared in turn with those that were derived from each column of $\mathbf{B_1}$ and $\mathbf{B_2}$, respectively. The agreement between each pair was quantified by calculating Kendall's W coefficient of concordance and testing its significance through a permutation test (9999 permutations with Holm correction for multiple testing) (Campbell et al., 2009). The extremely cold winter of 1994 is expected to have affected all sites, albeit with varying intensity. Functional groups should also differ with regard to their sensitivity to perturbation and their potential impact on community dynamics.

A.3 Results

The permutation tests of Kendall's *W* assigned statistical significance to the two highest coefficients of concordance (Table A.1). The observed patterns of relative abundance distribution appear to agree with the predicted response to input added through group C3 in the epifaunal (SD_1) system ($W = 0.76$) and group H7 in the infaunal (SD_2) system ($W = 0.67$). This means that sustained positive or negative change to these two functional groups is predicted to result in response patterns that are significantly consistent with the observed patterns of relative abundance in their respective systems.

Table A.1 Kendall's *W* coefficient of concordance between functional group distance matrices derived from the transformed $\mathbf{C_1}$ ($\mathbf{C_2}$) matrix and a column of the $\mathbf{B_1}$ ($\mathbf{B_2}$) matrix that corresponds to one of the SD_1 (SD_2) variables. Subscripts 1 and 2 indicate members of epifaunal and infaunal communities, respectively. The transformed $\mathbf{C_1}$ and $\mathbf{C_2}$ matrices represent observed patterns of functional group abundance distribution. Each column of the $\mathbf{B_1}$ and $\mathbf{B_2}$ matrices represents the predicted response of functional groups to sustained input added to the system through the respective system variable. Coefficients of concordance that are statistically significant at 0.05 level are indicated with an asterisk

SD_1 variable	Kendall's *W*	SD_2 variable	Kendall's *W*
Food	0.41	Food	0.49
Space	0.49	Space	0.49
H1	0.37	H5	0.57
H2	0.46	H6	0.48
H3	0.57	H7	0.67 *
H4	0.56	H8	0.56
H13	0.31	H9	0.64
C1	0.38	H10	0.58
C3	0.76 *	H11	0.49
C5	0.65	H12	0.44
C6	0.40	H14	0.45
-	-	C2	0.51
-	-	C4	0.44
-	-	C6	0.43

A.4 Discussion

Predictions of qualitative models have been previously compared with observations of systems where the responses of community members strongly correlate with alternative states, leading to well-documented regime shifts (Dambacher and Ramos-Jiliberto, 2007; Marzloff et al., 2011). This approach has the potential to reveal the impact of perturbations in cases where, like most ecological systems, predictions are ambiguous and responses are confounded by complex networks of interaction, while observations are at best limited.

It is very likely that the Rance estuary system, as represented by the community composition dataset and the two qualitative models, fails to meet all the assumptions of this approach. It is not, however, clear to what degree that happens or how robust the approach might be to violations of each assumption. This application should, therefore, be viewed as demonstrative rather than an attempt to validate the two qualitative models.

The cold winter of 1994 is expected to have shaped benthic macroinvertebrate communities, as they were observed in 1995 (Desroy, 1998). Functional groups C3 and H7 were both assigned a stenothermal trait value, meaning that they would be negatively affected by single-digit temperatures (Alexandridis et al., 2017). They are not the only groups to be assigned this trait value, but they are among the most dominant groups in terms of abundance. This would make their impact on community dynamics stronger compared to other groups that might have been affected in a similar way (Grime, 1998).

In this application, all sites were assumed to have been more or less affected by the same perturbation. If it is, instead, expected that sites would be affected in different ways, they should be grouped and analysed separately. It was also assumed that perturbation is demonstrated as input through primarily one variable of the system. This allowed each column of the adjoint matrix to be independently compared with the observed patterns of relative abundance distribution. If community members are known to be affected in a similar way, the system's response to their combined input can be used instead, by adding or subtracting the respective columns of the adjoint matrix (Dambacher et al., 2002).

A.5 References

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.

Campbell, V., Legendre, P., Lapointe, F.-J., 2009. Assessing congruence among ultrametric distance matrices. J Classif 26, 103-117.

Dambacher, J.M., Rossignol, P.A., 2001. The golden rule of complementary feedback. ACM SIGSAM Bulletin 35, 1-9.

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., Li, H.W., Rossignol, P.A., 2003. Qualitative predictions in model ecosystems. Ecol Model 161, 79-93.

Dambacher, J.M., Ramos-Jiliberto, R., 2007. Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. Q Rev Biol 82, 227-250.

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 Dissertation, Université de Rennes 1, Rennes, France.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86, 902-910.

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

Kirby, R., Retière, C., 2009. Comparing environmental effects of Rance and Severn barrages. P I Civil Eng-Mar En 162, 11-26.

Levins, R., 1998. Qualitative mathematics for understanding, prediction, and intervention in complex ecosystems. Ecosyst Health, 178-204.

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

Annex B: Species traits and functional groups

Table B.1 List of benthic macroinvertebrate species that were found in the Rance estuary in 1995 along with the functional group to which they belong and the value that was assigned to them for each of the 14 biological traits. Group names correspond to the alternative nomenclatures employed in Chapters II/III

Groups	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
h2iv/H8	*Abludomelita gladiosa*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h2iv/H8	*Abludomelita obtusata*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h3ii/H10	*Abra alba*	stenothermal	planktonic	long	high	exposed	muddy sand	2	0.5	interface	mobile	1.3	2	neutral	destabilizer
h3ii/H10	*Abra nitida*	eurythermal	planktonic	long	high	euryhaline	mud	2	0.5	interface	mobile	1.2	2	neutral	destabilizer
h3ii/H10	*Abra prismatica*	stenothermal	planktonic	long	high	stenohaline	sand	2	0.3	interface	mobile	1.5	2	neutral	destabilizer
h3ii/H10	*Abra tenuis*	stenothermal	planktonic	long	high	exposed	mud	2	0.6	interface	mobile	1.2	2	neutral	destabilizer
h4iv/H14	*Acanthocardia tuberculata*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	6.0	interface	mobile	0.5	20	neutral	stabilizer
h1ii/H2	*Acanthochitona discrepans*	stenothermal	planktonic	short	high	stenohaline	rock	2	0.5	epifauna	mobile	1.2	10	epibiont	neutral
c3ii/C6	*Achelia echinata*	stenothermal	planktonic	short	low	stenohaline	rock	1	0.2	epifauna	mobile	1.7	2	epibiont	neutral
h4iv/H14	*Acrocnida brachiata*	stenothermal	planktonic	long	high	stenohaline	sand	2	0.8	interface	mobile	1.1	10	neutral	stabilizer
h2iii/H7	*Ampelisca brevicornis*	stenothermal	brooded	short	low	stenohaline	muddy sand	2	0.1	interface	sessile	2.1	2	neutral	stabilizer
h2iii/H7	*Ampelisca diadema*	stenothermal	brooded	short	low	euryhaline	muddy gravel	1	0.0	interface	sessile	3.5	2	neutral	stabilizer
h2iv/H8	*Ampelisca tenuicornis*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h2iv/H8	*Ampelisca typica*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h3i/H9	*Ampharete acutifrons*	eurythermal	laid	short	high	exposed	muddy sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h4i/H11	*Amphicteis gunneri*	eurythermal	planktonic	short	high	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	10	neutral	stabilizer
h4i/H11	*Amphiglena mediterranea*	stenothermal	planktonic	short	high	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h2iv/H8	*Amphilochus spencebatei*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h2ii/H6	*Amphipholis squamata*	eurythermal	brooded	short	low	stenohaline	gravel	10	3.5	interface	mobile	0.7	10	neutral	stabilizer
h4iii/H13	*Anapagurus hyndmanni*	stenothermal	planktonic	long	high	stenohaline	gravel	10	20.0	epifauna	mobile	0.4	10	neutral	neutral
h2iv/H8	*Animoceradocus semiserratus*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	1	neutral	destabilizer
c2i/C2	*Antalis vulgaris*	stenothermal	planktonic	short	high	stenohaline	muddy sand	10	0.7	infauna	mobile	1.1	2	neutral	destabilizer
h2iii/H7	*Aonides oxycephala*	stenothermal	planktonic	short	low	stenohaline	gravel	10	0.1	interface	sessile	2.4	1	neutral	stabilizer
h2iii/H7	*Aora typica*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	2	neutral	stabilizer
h3i/H9	*Aphelochaeta marioni*	eurythermal	laid	short	high	euryhaline	muddy sand	10	0.1	interface	mobile	2.4	10	neutral	destabilizer
c1i/C1	*Apherusa bispinosa*	eurythermal	brooded	short	low	euryhaline	muddy sand	1	0.0	epifauna	mobile	3.5	2	neutral	neutral

c2i/C2	*Aphrodita aculeata*	eurythermal	planktonic	short	high	stenohaline	muddy sand	20	49.5	interface	mobile	0.3	10	neutral	neutral
h4i/H11	*Aponuphis bilineata*	stenothermal	planktonic	long	high	stenohaline	sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h2iii/H7	*Apseudopsis latreillii*	stenothermal	brooded	short	low	exposed	muddy sand	1	0.0	interface	sessile	4.4	2	neutral	stabilizer
h3i/H9	*Arenicola marina*	eurythermal	laid	short	high	exposed	muddy sand	20	0.9	interface	mobile	1.1	10	neutral	destabilizer
h3i/H9	*Aricidea (Acmira) cerrutii*	eurythermal	laid	short	high	stenohaline	sand	10	0.1	interface	mobile	2.4	10	neutral	destabilizer
h2iv/H8	*Astacilla longicornis*	eurythermal	brooded	short	low	stenohaline	muddy sand	2	0.0	epifauna	mobile	3.0	2	neutral	neutral
h1iii/H3	*Balanus crenatus*	eurythermal	planktonic	long	high	euryhaline	rock	2	0.4	epifauna	sessile	1.4	2	epibiont	neutral
c2ii/C3	*Bela nebula*	stenothermal	planktonic	long	high	stenohaline	sand	10	1.6	epifauna	mobile	0.9	20	neutral	neutral
h4ii/H12	*Calliostoma zizyphinum*	stenothermal	laid	short	high	stenohaline	muddy gravel	2	1.0	epifauna	mobile	1.0	10	neutral	neutral
c3ii/C6	*Callipallene emaciata*	stenothermal	planktonic	short	low	stenohaline	rock	1	0.2	epifauna	mobile	1.7	2	epibiont	neutral
h1ii/H2	*Calyptraea chinensis*	stenothermal	laid	short	high	euryhaline	rock	2	0.8	epifauna	sessile	1.1	10	epibiont	neutral
h3i/H9	*Capitella capitata*	eurythermal	laid	short	high	exposed	muddy sand	10	0.1	interface	mobile	2.4	2	neutral	destabilizer
c3ii/C6	*Carcinus maenas*	stenothermal	planktonic	long	high	exposed	rock	10	6.2	epifauna	mobile	0.5	10	epibiont	neutral
h2iii/H7	*Caulleriella alata*	stenothermal	brooded	short	high	stenohaline	mud	2	0.0	interface	sessile	3.8	10	neutral	stabilizer
h4iv/H14	*Cerastoderma edule*	stenothermal	planktonic	long	high	exposed	muddy sand	10	6.0	interface	mobile	0.5	10	neutral	stabilizer
h4iv/H14	*Cerastoderma glaucum*	stenothermal	planktonic	long	high	exposed	muddy sand	10	6.0	interface	mobile	0.5	10	neutral	stabilizer
h1ii/H2	*Cereus pedunculatus*	stenothermal	brooded	short	high	stenohaline	rock	20	7.5	epifauna	sessile	0.5	20	epibiont	neutral
c2ii/C3	*Cerianthus lloydii*	eurythermal	planktonic	long	high	euryhaline	mud	20	7.5	interface	sessile	0.5	20	neutral	stabilizer
h3i/H9	*Chaetozone setosa*	eurythermal	laid	short	high	euryhaline	muddy gravel	2	0.0	interface	mobile	3.8	2	neutral	destabilizer
h2iv/H8	*Cheirocratus intermedius*	stenothermal	brooded	short	low	stenohaline	sand	2	0.1	interface	mobile	2.1	1	neutral	destabilizer
h2iv/H8	*Cheirocratus sundevalli*	stenothermal	brooded	short	low	stenohaline	gravel	2	0.1	interface	mobile	2.1	1	neutral	destabilizer
h3i/H9	*Cirratulus cirratus*	eurythermal	laid	short	high	euryhaline	muddy gravel	40	3.3	interface	mobile	0.7	10	neutral	destabilizer
h3ii/H10	*Cirriformia tentaculata*	stenothermal	planktonic	long	high	stenohaline	muddy gravel	20	0.9	interface	mobile	1.1	10	neutral	destabilizer
h2iv/H8	*Corophium volutator*	stenothermal	brooded	short	low	exposed	muddy sand	2	0.1	interface	mobile	2.1	1	neutral	destabilizer
c2ii/C3	*Crangon crangon*	stenothermal	planktonic	long	high	exposed	muddy sand	10	0.6	epifauna	mobile	1.2	10	neutral	neutral
h1iv/H4	*Crepidula fornicata*	stenothermal	planktonic	long	high	exposed	rock	10	3.6	epifauna	sessile	0.7	10	basibiont	neutral
c1i/C1	*Cyathura carinata*	stenothermal	brooded	short	low	exposed	muddy sand	2	0.3	epifauna	mobile	1.5	2	neutral	neutral
c1i/C1	*Cymodoce truncata*	stenothermal	brooded	short	low	stenohaline	muddy sand	2	0.3	epifauna	mobile	1.5	2	neutral	neutral
h2iv/H8	*Deflexilodes tuberculatus*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h1i/H1	*Dendrodoa grossularia*	eurythermal	planktonic	short	low	euryhaline	rock	2	0.4	epifauna	sessile	1.4	2	epibiont	neutral
h2iv/H8	*Dexamine spinosa*	stenothermal	brooded	short	low	euryhaline	muddy sand	2	0.1	interface	mobile	2.1	2	neutral	neutral
h2iv/H8	*Diastylis bradyi*	eurythermal	brooded	short	low	stenohaline	muddy sand	2	0.3	epifauna	mobile	1.5	1	neutral	neutral
h1ii/H2	*Diodora graeca*	stenothermal	laid	short	high	stenohaline	rock	10	7.1	epifauna	mobile	0.5	20	epibiont	neutral
h3ii/H10	*Diplocirrus glaucus*	eurythermal	planktonic	long	high	stenohaline	muddy sand	2	0.0	interface	mobile	3.8	2	neutral	destabilizer
h1iv/H4	*Dodecaceria concharum*	stenothermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	sessile	2.4	10	epibiont	neutral
c2ii/C3	*Ebalia tuberosa*	stenothermal	planktonic	long	high	stenohaline	gravel	2	1.2	interface	mobile	0.9	2	neutral	neutral

c2ii/C3	*Edwardsia claparedii*	stenothermal	planktonic	long	high	stenohaline	mud	10	0.3	interface	mobile	1.5	10	neutral	stabilizer
h2iii/H7	*Ericthonius punctatus*	stenothermal	brooded	short	low	stenohaline	muddy sand	2	0.1	interface	sessile	2.1	1	neutral	stabilizer
c2ii/C3	*Eteone longa*	eurythermal	planktonic	long	high	euryhaline	muddy gravel	10	0.1	interface	mobile	2.4	2	neutral	neutral
h2iii/H7	*Euclymene oerstedi*	stenothermal	brooded	short	low	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	10	neutral	stabilizer
h2iv/H8	*Eudorella truncatula*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	4.4	2	neutral	neutral
c3ii/C6	*Eulalia viridis*	eurythermal	planktonic	long	low	euryhaline	rock	10	0.1	epifauna	mobile	2.4	10	epibiont	neutral
c2ii/C3	*Eumida punctifera*	stenothermal	planktonic	long	high	stenohaline	gravel	10	0.1	interface	mobile	2.4	2	neutral	neutral
c2ii/C3	*Eumida sanguinea*	stenothermal	planktonic	long	high	stenohaline	gravel	10	0.1	interface	mobile	2.4	2	neutral	neutral
h4i/H11	*Eunereis longissima*	eurythermal	planktonic	long	high	euryhaline	muddy sand	40	3.3	interface	sessile	0.7	2	neutral	stabilizer
h4i/H11	*Eupolymnia nebulosa*	eurythermal	planktonic	short	high	stenohaline	gravel	20	0.9	interface	sessile	1.1	2	neutral	stabilizer
c2ii/C3	*Eurysyllis tuberculata*	stenothermal	planktonic	long	high	stenohaline	muddy gravel	1	0.0	interface	mobile	7.0	2	neutral	neutral
c3ii/C6	*Eusyllis blomstrandi*	eurythermal	planktonic	short	high	stenohaline	rock	2	0.0	interface	mobile	3.8	1	epibiont	neutral
c1i/C1	*Exogone (Exogone) naidina*	eurythermal	brooded	short	low	stenohaline	gravel	1	0.0	epifauna	mobile	7.0	2	neutral	neutral
h4iii/H13	*Galathea intermedia*	stenothermal	brooded	long	low	stenohaline	gravel	10	2.6	epifauna	mobile	0.7	10	neutral	neutral
h4i/H11	*Galathowenia oculata*	eurythermal	planktonic	long	high	euryhaline	mud	10	0.1	interface	sessile	2.4	10	neutral	stabilizer
h2iv/H8	*Gammarus locusta*	eurythermal	brooded	short	low	euryhaline	muddy gravel	2	0.1	epifauna	mobile	2.1	1	neutral	neutral
h2iv/H8	*Gammarus salinus*	stenothermal	brooded	short	low	exposed	muddy gravel	2	0.1	epifauna	mobile	2.1	1	neutral	neutral
h4ii/H12	*Gibbula magus*	stenothermal	planktonic	short	high	stenohaline	muddy gravel	10	7.1	interface	mobile	0.5	10	neutral	neutral
c2ii/C3	*Glycera alba*	stenothermal	planktonic	long	high	euryhaline	muddy sand	10	0.1	interface	mobile	2.4	10	neutral	neutral
c2ii/C3	*Glycera tridactyla*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	0.1	interface	mobile	2.4	10	neutral	neutral
h4ii/H12	*Glycymeris glycymeris*	stenothermal	planktonic	short	high	stenohaline	muddy gravel	10	2.1	infauna	mobile	0.8	20	neutral	stabilizer
h2i/H5	*Golfingia (Golfingia) vulgaris vulgaris*	eurythermal	planktonic	long	low	stenohaline	muddy sand	10	0.1	infauna	mobile	2.4	2	neutral	destabilizer
c2ii/C3	*Goniada emerita*	stenothermal	planktonic	long	high	stenohaline	sand	10	0.1	interface	mobile	2.4	2	neutral	neutral
h4iv/H14	*Goodallia triangularis*	stenothermal	planktonic	short	high	stenohaline	sand	1	0.1	interface	mobile	2.1	10	neutral	stabilizer
c2ii/C3	*Haminoea navicula*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	6.8	interface	mobile	0.5	10	neutral	neutral
c3ii/C6	*Haplosyllis spongicola*	stenothermal	laid	short	low	stenohaline	rock	2	0.0	epifauna	mobile	3.8	2	epibiont	neutral
h3i/H9	*Hediste diversicolor*	stenothermal	laid	short	high	exposed	muddy sand	20	0.9	interface	mobile	1.1	2	neutral	destabilizer
c2iii/C4	*Hesionura elongata*	stenothermal	planktonic	long	low	stenohaline	sand	2	0.0	infauna	mobile	3.8	1	neutral	destabilizer
h4i/H11	*Heteromastus filiformis*	eurythermal	planktonic	long	low	exposed	muddy sand	20	0.9	interface	sessile	1.1	2	neutral	stabilizer
c2i/C2	*Hilbigneris gracilis*	eurythermal	laid	short	low	stenohaline	muddy sand	10	0.1	interface	mobile	2.4	10	neutral	neutral
h3ii/H10	Holothuriidae	eurythermal	planktonic	long	high	stenohaline	sand	40	15.7	interface	mobile	0.4	10	neutral	destabilizer
h1i/H1	*Idotea granulosa*	stenothermal	brooded	short	low	stenohaline	rock	2	0.3	epifauna	mobile	1.5	2	epibiont	neutral
c3ii/C6	*Iphimedia obesa*	stenothermal	brooded	short	low	stenohaline	rock	2	0.3	epifauna	mobile	1.5	1	epibiont	neutral
h2iv/H8	*Iphinoe tenella*	stenothermal	planktonic	short	low	euryhaline	muddy sand	2	0.3	interface	mobile	1.5	2	neutral	destabilizer
h1i/H1	*Janira maculosa*	eurythermal	brooded	short	low	stenohaline	rock	1	0.0	epifauna	mobile	4.4	2	epibiont	neutral
h1i/H1	*Jasmineira elegans*	eurythermal	planktonic	short	low	stenohaline	rock	2	0.0	epifauna	sessile	3.8	2	epibiont	neutral

h1i/H1	*Jassa falcata*	eurythermal	brooded	short	low	stenohaline	rock	2	0.1	epifauna	sessile	2.1	1	epibiont	neutral
h4iv/H14	*Kurtiella bidentata*	stenothermal	planktonic	long	low	euryhaline	muddy sand	2	0.5	infauna	mobile	1.2	10	neutral	stabilizer
h4i/H11	*Lanice conchilega*	eurythermal	planktonic	long	high	euryhaline	mud	40	3.3	interface	sessile	0.7	2	neutral	stabilizer
h4i/H11	*Leiochone leiopygos*	eurythermal	planktonic	long	high	stenohaline	mud	20	0.9	interface	sessile	1.1	2	neutral	stabilizer
h4i/H11	*Leonnates glauca*	eurythermal	planktonic	long	high	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	10	neutral	stabilizer
h1ii/H2	*Lepidochitona (Lepidochitona) cinerea*	stenothermal	planktonic	short	high	stenohaline	rock	2	0.5	epifauna	mobile	1.2	10	epibiont	neutral
c2ii/C3	*Lepidonotus squamatus*	eurythermal	planktonic	long	high	euryhaline	gravel	10	0.1	epifauna	mobile	2.4	2	neutral	neutral
h2iv/H8	*Leptocheirus hirsutimanus*	stenothermal	brooded	short	low	stenohaline	gravel	1	0.0	interface	mobile	3.5	1	neutral	destabilizer
h2iii/H7	*Leptochelia dubia*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	4.4	2	neutral	stabilizer
h1i/H1	*Leucothoe incisa*	stenothermal	brooded	short	low	stenohaline	rock	1	0.0	epifauna	mobile	3.5	1	epibiont	neutral
h1i/H1	*Leucothoe spinicarpa*	eurythermal	brooded	short	low	stenohaline	rock	2	0.1	epifauna	mobile	2.1	1	epibiont	neutral
h2iii/H7	*Liljeborgia pallida*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer
c2ii/C3	*Liocarcinus navigator*	stenothermal	planktonic	long	high	euryhaline	muddy sand	10	5.7	interface	mobile	0.6	10	neutral	neutral
h4iv/H14	*Lucinoma borealis*	stenothermal	planktonic	long	high	stenohaline	sand	10	7.6	interface	mobile	0.5	10	neutral	stabilizer
c2i/C2	*Lumbrineris japonica*	stenothermal	laid	short	low	stenohaline	gravel	40	3.3	interface	mobile	0.7	10	neutral	neutral
h4iv/H14	*Lyonsia norwegica*	stenothermal	planktonic	long	low	stenohaline	sand	10	5.2	interface	mobile	0.6	10	neutral	stabilizer
c3ii/C6	*Lysianassa ceratina*	stenothermal	brooded	short	low	stenohaline	rock	2	0.1	interface	mobile	2.1	1	epibiont	neutral
c3ii/C6	*Lysianassa insperata*	eurythermal	brooded	short	low	stenohaline	rock	2	0.1	interface	mobile	2.1	1	epibiont	neutral
c2i/C2	*Lysidice ninetta*	stenothermal	laid	short	high	stenohaline	muddy sand	20	0.9	interface	mobile	1.1	2	neutral	neutral
c2i/C2	*Lysidice unicornis*	stenothermal	laid	short	high	stenohaline	muddy sand	20	0.9	interface	mobile	1.1	2	neutral	neutral
h4iv/H14	*Macoma balthica*	eurythermal	planktonic	long	high	exposed	mud	2	0.5	infauna	mobile	1.2	10	neutral	stabilizer
c3ii/C6	*Macropodia rostrata*	stenothermal	planktonic	long	low	stenohaline	rock	2	1.9	epifauna	mobile	0.8	10	epibiont	neutral
h2iii/H7	*Maera grossimana*	stenothermal	brooded	short	low	stenohaline	muddy sand	2	0.1	interface	sessile	2.1	2	neutral	stabilizer
h3ii/H10	*Malacoceros fuliginosus*	eurythermal	planktonic	long	high	euryhaline	mud	10	0.1	interface	mobile	2.4	2	neutral	destabilizer
c3ii/C6	*Malmgreniella ljungmani*	stenothermal	planktonic	long	low	stenohaline	rock	2	0.0	interface	mobile	3.8	2	epibiont	neutral
c3ii/C6	*Malmgreniella lunulata*	stenothermal	planktonic	long	low	stenohaline	rock	2	0.0	interface	mobile	3.8	2	epibiont	neutral
h4i/H11	*Manayunkia aestuarina*	stenothermal	planktonic	long	high	exposed	mud	1	0.0	interface	sessile	7.0	2	neutral	stabilizer
c2i/C2	*Marphysa bellii*	stenothermal	planktonic	short	high	stenohaline	muddy sand	20	0.9	interface	mobile	1.1	2	neutral	neutral
c2i/C2	*Marphysa sanguinea*	stenothermal	planktonic	short	high	stenohaline	muddy sand	40	3.3	interface	mobile	0.7	2	neutral	neutral
h2i/H5	*Mediomastus fragilis*	stenothermal	planktonic	short	low	exposed	mud	10	0.1	infauna	mobile	2.4	2	neutral	destabilizer
h2iii/H7	*Megalomma vesiculosum*	stenothermal	planktonic	short	low	stenohaline	mud	20	0.9	interface	sessile	1.1	2	neutral	stabilizer
h2iii/H7	*Melinna palmata*	stenothermal	laid	short	high	stenohaline	mud	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h2iii/H7	*Microdeutopus anomalus*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer
h2iii/H7	*Microdeutopus damnoniensis*	stenothermal	brooded	short	low	euryhaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer
h2iii/H7	*Microdeutopus gryllotalpa*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer
h2iii/H7	*Microdeutopus versiculatus*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer

h1iv/H4	*Mimachlamys varia*	eurythermal	planktonic	long	high	stenohaline	rock	10	4.1	epifauna	sessile	0.6	10	basibiont	neutral
h2iii/H7	*Monocorophium acherusicum*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer
h2iii/H7	*Monocorophium sextonae*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	sessile	3.5	1	neutral	stabilizer
c1i/C1	*Monoculodes carinatus*	stenothermal	brooded	short	low	stenohaline	sand	1	0.0	interface	mobile	3.5	1	neutral	neutral
h1i/H1	*Morchellium argus*	stenothermal	planktonic	short	low	euryhaline	rock	10	1.3	epifauna	sessile	0.9	2	epibiont	neutral
h2iv/H8	Munnidae	eurythermal	brooded	short	low	stenohaline	gravel	1	0.0	interface	mobile	4.4	2	neutral	destabilizer
c2iii/C4	*Myrianida edwardsi*	stenothermal	planktonic	long	low	stenohaline	gravel	2	0.0	epifauna	mobile	3.8	2	neutral	neutral
h2iv/H8	Mysidae	eurythermal	brooded	short	low	euryhaline	muddy sand	2	0.3	epifauna	mobile	1.5	1	neutral	neutral
h1iv/H4	*Mytilus edulis*	eurythermal	planktonic	long	high	exposed	rock	10	3.9	epifauna	sessile	0.6	20	basibiont	neutral
h4i/H11	*Myxicola infundibulum*	eurythermal	planktonic	short	high	euryhaline	muddy sand	20	0.9	interface	sessile	1.1	2	neutral	stabilizer
c2ii/C3	*Nassarius pygmaeus*	stenothermal	planktonic	long	high	stenohaline	muddy sand	2	0.8	interface	mobile	1.1	20	neutral	neutral
c2ii/C3	*Nassarius reticulatus*	stenothermal	planktonic	long	high	euryhaline	muddy gravel	10	4.2	interface	mobile	0.6	20	neutral	neutral
c2i/C2	Nemertea	stenothermal	planktonic	short	low	stenohaline	mud	20	0.9	interface	mobile	1.1	2	neutral	neutral
c2ii/C3	*Nephtys caeca*	eurythermal	planktonic	long	high	euryhaline	muddy sand	20	0.9	interface	mobile	1.1	10	neutral	neutral
c2ii/C3	*Nephtys cirrosa*	stenothermal	planktonic	long	high	exposed	sand	10	0.1	interface	mobile	2.4	10	neutral	neutral
c2ii/C3	*Nephtys hombergii*	stenothermal	planktonic	long	high	exposed	mud	20	0.9	interface	mobile	1.1	10	neutral	neutral
h4i/H11	*Nicolea venustula*	stenothermal	planktonic	long	high	stenohaline	muddy gravel	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h2iv/H8	*Notomastus latericeus*	eurythermal	planktonic	short	low	euryhaline	muddy sand	40	3.3	interface	mobile	0.7	2	neutral	destabilizer
h2iv/H8	*Nototropis vedlomensis*	eurythermal	brooded	short	low	stenohaline	sand	1	0.0	interface	mobile	3.5	1	neutral	destabilizer
h2iv/H8	*Nucula nucleus*	stenothermal	planktonic	short	low	stenohaline	sand	2	1.0	interface	mobile	1.0	10	neutral	destabilizer
h2iv/H8	*Nucula turgida*	stenothermal	planktonic	short	low	stenohaline	muddy sand	2	1.0	interface	mobile	1.0	10	neutral	destabilizer
c3ii/C6	Nudibranchia	stenothermal	laid	short	low	stenohaline	rock	10	3.1	epifauna	mobile	0.7	1	epibiont	neutral
c3ii/C6	*Nymphon brevirostre*	eurythermal	planktonic	short	low	stenohaline	rock	1	0.2	epifauna	mobile	1.7	2	epibiont	neutral
c3ii/C6	*Odontosyllis ctenostoma*	stenothermal	planktonic	short	high	stenohaline	rock	2	0.0	interface	mobile	3.8	2	epibiont	neutral
c3ii/C6	*Odontosyllis gibba*	stenothermal	planktonic	short	high	stenohaline	rock	2	0.0	interface	mobile	3.8	2	epibiont	neutral
h2i/H5	Oligochaeta	stenothermal	laid	short	low	exposed	muddy sand	2	0.0	infauna	mobile	3.8	2	neutral	destabilizer
h2iv/H8	*Ophelina acuminata*	eurythermal	planktonic	short	low	euryhaline	muddy sand	10	0.1	infauna	mobile	2.4	2	neutral	destabilizer
h3ii/H10	*Orbinia sertulata*	eurythermal	planktonic	short	high	stenohaline	muddy sand	40	3.3	interface	mobile	0.7	2	neutral	destabilizer
h1i/H1	*Oridia armandi*	stenothermal	planktonic	short	low	stenohaline	rock	1	0.0	epifauna	sessile	7.0	2	epibiont	neutral
h1iv/H4	*Ostrea edulis*	stenothermal	planktonic	long	high	euryhaline	rock	10	2.5	epifauna	sessile	0.7	10	basibiont	neutral
h2iv/H8	*Othomaera othonis*	stenothermal	brooded	short	low	stenohaline	muddy sand	2	0.1	interface	mobile	2.1	1	neutral	destabilizer
c2ii/C3	*Oxydromus flexuosus*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	0.1	epifauna	mobile	2.4	2	neutral	neutral
h4iii/H13	*Pagurus bernhardus*	stenothermal	planktonic	long	high	euryhaline	sand	10	2.6	epifauna	mobile	0.7	10	neutral	neutral
c3ii/C6	*Palaemon serratus*	stenothermal	planktonic	long	high	exposed	rock	10	0.5	epifauna	mobile	1.2	10	epibiont	neutral
h4iv/H14	*Pandora albida*	eurythermal	planktonic	long	low	euryhaline	sand	10	5.2	interface	mobile	0.6	10	neutral	stabilizer
h3ii/H10	*Paradoneis armata*	stenothermal	planktonic	short	high	stenohaline	sand	10	0.1	interface	mobile	2.4	2	neutral	destabilizer

h3ii/H10	*Paradoneis lyra*	eurythermal	planktonic	short	high	stenohaline	mud	2	0.0	interface	mobile	3.8	2	neutral	destabilizer
h2iv/H8	*Pariambus typicus*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	1	neutral	destabilizer
h4iv/H14	*Parvicardium exiguum*	stenothermal	planktonic	long	high	euryhaline	muddy sand	2	0.9	interface	mobile	1.0	10	neutral	stabilizer
h4iv/H14	*Parvicardium scabrum*	stenothermal	planktonic	long	high	stenohaline	sand	2	0.9	interface	mobile	1.0	10	neutral	stabilizer
c3ii/C6	*Perinereis cultrifera*	stenothermal	planktonic	long	high	stenohaline	rock	20	0.9	interface	mobile	1.1	2	epibiont	neutral
h3ii/H10	*Peringia ulvae*	stenothermal	planktonic	long	low	exposed	mud	1	0.1	interface	mobile	2.3	2	neutral	destabilizer
h2iv/H8	*Perioculodes longimanus*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	1	neutral	destabilizer
h2iv/H8	*Phascolion (Phascolion) strombus strombus*	eurythermal	planktonic	short	low	euryhaline	muddy sand	10	0.1	interface	mobile	2.4	2	neutral	destabilizer
c2ii/C3	*Pholoe minuta*	eurythermal	planktonic	long	high	euryhaline	muddy sand	2	0.0	interface	mobile	3.8	10	neutral	neutral
h2iii/H7	*Phoronis psammophila*	stenothermal	planktonic	short	low	stenohaline	sand	10	0.3	interface	sessile	1.5	2	neutral	stabilizer
c3ii/C6	*Phtisica marina*	stenothermal	brooded	short	low	euryhaline	rock	2	0.1	epifauna	mobile	2.1	1	epibiont	neutral
c3ii/C6	*Phyllodoce laminosa*	stenothermal	planktonic	long	high	stenohaline	rock	40	3.3	interface	mobile	0.7	2	epibiont	neutral
c2ii/C3	*Phyllodoce longipes*	eurythermal	planktonic	long	high	stenohaline	gravel	10	0.1	interface	mobile	2.4	2	neutral	neutral
c2ii/C3	*Phyllodoce mucosa*	eurythermal	planktonic	long	high	euryhaline	muddy sand	20	0.9	interface	mobile	1.1	2	neutral	neutral
h1ii/H2	*Pisidia longicornis*	stenothermal	planktonic	long	low	stenohaline	rock	2	1.9	epifauna	mobile	0.8	10	epibiont	neutral
h4i/H11	*Pista cristata*	eurythermal	planktonic	short	high	euryhaline	muddy sand	10	0.1	interface	sessile	2.4	10	neutral	stabilizer
c3i/C5	*Platynereis dumerilii*	stenothermal	planktonic	short	high	euryhaline	rock	10	0.1	epifauna	sessile	2.4	2	epibiont	neutral
h4i/H11	*Poecilochaetus serpens*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	10	neutral	stabilizer
h4iv/H14	*Polititapes aureus*	stenothermal	planktonic	long	high	exposed	muddy sand	10	8.9	interface	mobile	0.5	10	neutral	stabilizer
h4iv/H14	*Polititapes rhomboides*	stenothermal	planktonic	long	high	stenohaline	sand	10	8.9	interface	mobile	0.5	10	neutral	stabilizer
h1iv/H4	*Polycirrus aurantiacus*	stenothermal	planktonic	short	low	euryhaline	rock	10	0.1	interface	sessile	2.4	10	epibiont	stabilizer
h1iii/H3	*Polydora ciliata*	eurythermal	planktonic	long	high	euryhaline	rock	2	0.0	interface	sessile	3.8	2	epibiont	stabilizer
h2iv/H8	*Pontocrates arenarius*	stenothermal	brooded	short	low	stenohaline	sand	1	0.0	interface	mobile	3.5	1	neutral	destabilizer
h1i/H1	*Potamilla torelli*	stenothermal	planktonic	short	low	stenohaline	rock	10	0.1	epifauna	sessile	2.4	2	epibiont	neutral
h4i/H11	*Prionospio fallax*	eurythermal	planktonic	long	low	stenohaline	mud	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
c3ii/C6	*Proceraea aurantiaca*	stenothermal	planktonic	long	low	euryhaline	rock	2	0.0	interface	mobile	3.8	2	epibiont	neutral
c2ii/C3	*Protodorvillea kefersteini*	eurythermal	planktonic	long	high	stenohaline	gravel	2	0.0	interface	mobile	3.8	2	neutral	neutral
h2iv/H8	*Pseudocuma (Pseudocuma) longicorne*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	4.4	2	neutral	destabilizer
h4i/H11	*Pseudopolydora antennata*	eurythermal	planktonic	long	high	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h4i/H11	*Pseudopolydora pulchra*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
c3ii/C6	*Pseudoprotella phasma*	stenothermal	brooded	short	low	stenohaline	rock	2	0.1	epifauna	mobile	2.1	1	epibiont	neutral
h4i/H11	*Pygospio elegans*	stenothermal	planktonic	long	high	exposed	mud	2	0.0	interface	sessile	3.8	2	neutral	stabilizer
h1ii/H2	*Sabella pavonina*	stenothermal	planktonic	short	high	exposed	rock	40	3.3	epifauna	sessile	0.7	2	epibiont	neutral
h3ii/H10	*Saccocirrus papillocercus*	stenothermal	planktonic	short	high	stenohaline	gravel	2	0.0	interface	mobile	3.8	2	neutral	destabilizer
h2iv/H8	*Scalibregma celticum*	stenothermal	planktonic	short	low	euryhaline	muddy sand	2	0.0	interface	mobile	3.8	1	neutral	destabilizer
h3i/H9	*Scoloplos (Scoloplos) armiger*	eurythermal	laid	short	high	euryhaline	muddy sand	20	0.9	interface	mobile	1.1	10	neutral	destabilizer

h4iv/H14	*Scrobicularia plana*	stenothermal	planktonic	long	high	exposed	mud	10	4.6	infauna	mobile	0.6	2	neutral	stabilizer
h4iv/H14	*Solen marginatus*	stenothermal	planktonic	long	high	stenohaline	sand	20	20.2	infauna	mobile	0.4	10	neutral	stabilizer
c1i/C1	*Sphaerosyllis bulbosa*	stenothermal	brooded	short	low	stenohaline	gravel	1	0.0	interface	mobile	7.0	2	neutral	neutral
c1i/C1	*Sphaerosyllis hystrix*	eurythermal	brooded	short	low	stenohaline	gravel	1	0.0	interface	mobile	7.0	2	neutral	neutral
h4i/H11	*Spio filicornis*	eurythermal	planktonic	long	low	euryhaline	muddy sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h4i/H11	*Spio martinensis*	stenothermal	planktonic	long	high	stenohaline	sand	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h1iv/H4	*Spirobranchus lamarcki*	stenothermal	planktonic	long	low	stenohaline	rock	2	0.0	epifauna	sessile	3.8	10	basibiont	neutral
h4iv/H14	*Spisula elliptica*	eurythermal	planktonic	long	high	euryhaline	muddy sand	10	4.6	infauna	mobile	0.6	10	neutral	stabilizer
h4iv/H14	*Spisula solida*	stenothermal	planktonic	long	high	euryhaline	sand	10	3.2	infauna	mobile	0.7	10	neutral	stabilizer
c2ii/C3	*Sthenelais boa*	eurythermal	planktonic	long	high	stenohaline	muddy sand	20	0.9	interface	mobile	1.1	10	neutral	neutral
h4i/H11	*Streblospio shrubsolii*	stenothermal	planktonic	short	high	euryhaline	mud	1	0.0	interface	sessile	7.0	2	neutral	stabilizer
c2iii/C4	*Streptodonta pterochaeta*	stenothermal	planktonic	long	low	stenohaline	mud	1	0.0	interface	mobile	7.0	2	neutral	neutral
c2iii/C4	*Syllides longocirratus*	stenothermal	planktonic	long	low	stenohaline	muddy sand	1	0.0	interface	mobile	7.0	2	neutral	neutral
c2iii/C4	*Syllidia armata*	eurythermal	planktonic	long	low	stenohaline	muddy sand	1	0.0	interface	mobile	7.0	2	neutral	neutral
c3ii/C6	*Syllis armillaris*	eurythermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	mobile	2.4	2	epibiont	neutral
c3ii/C6	*Syllis cornuta*	eurythermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	mobile	2.4	2	epibiont	neutral
c3ii/C6	*Syllis gracilis*	stenothermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	mobile	2.4	2	epibiont	neutral
c3ii/C6	*Syllis hyalina*	eurythermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	mobile	2.4	2	epibiont	neutral
c3ii/C6	*Syllis prolifera*	stenothermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	mobile	2.4	2	epibiont	neutral
c3ii/C6	*Syllis variegata*	eurythermal	planktonic	long	high	stenohaline	rock	10	0.1	epifauna	mobile	2.4	2	epibiont	neutral
h1ii/H2	*Tectura virginea*	stenothermal	planktonic	long	high	stenohaline	rock	2	1.0	interface	mobile	1.0	10	epibiont	neutral
h4i/H11	*Terebellides stroemii*	eurythermal	planktonic	short	high	euryhaline	mud	10	0.1	interface	sessile	2.4	2	neutral	stabilizer
h3i/H9	*Tharyx* sp	eurythermal	laid	short	low	euryhaline	muddy sand	10	0.1	interface	mobile	2.4	10	neutral	destabilizer
c2ii/C3	*Thia scutellata*	stenothermal	planktonic	long	high	stenohaline	sand	2	1.3	interface	mobile	0.9	10	neutral	neutral
h2ii/H6	*Thyasira flexuosa*	eurythermal	planktonic	short	low	stenohaline	mud	2	0.8	infauna	mobile	1.1	10	neutral	stabilizer
h1ii/H2	*Tricolia pullus*	stenothermal	planktonic	short	high	stenohaline	rock	2	1.0	epifauna	mobile	1.0	10	epibiont	neutral
c3ii/C6	*Trypanosyllis (Trypanosyllis) coeliaca*	stenothermal	planktonic	short	low	stenohaline	rock	2	0.0	epifauna	mobile	3.8	2	epibiont	neutral
c2i/C2	*Tubulanus polymorphus*	stenothermal	planktonic	short	low	stenohaline	sand	40	3.3	interface	mobile	0.7	2	neutral	neutral
h4iv/H14	*Upogebia deltaura*	stenothermal	planktonic	long	high	stenohaline	muddy sand	10	0.7	infauna	mobile	1.1	10	neutral	stabilizer
h2iv/H8	*Urothoe elegans*	eurythermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
h2iv/H8	*Urothoe pulchella*	stenothermal	brooded	short	low	stenohaline	muddy sand	1	0.0	interface	mobile	3.5	2	neutral	destabilizer
c3i/C5	*Urticina felina*	eurythermal	planktonic	short	high	euryhaline	rock	20	7.5	epifauna	sessile	0.5	20	epibiont	neutral
h4iv/H14	*Venerupis corrugata*	stenothermal	planktonic	long	high	euryhaline	muddy gravel	10	8.9	infauna	mobile	0.5	10	neutral	stabilizer
h4iv/H14	*Venus verrucosa*	stenothermal	planktonic	long	high	stenohaline	gravel	10	8.9	infauna	mobile	0.5	10	neutral	stabilizer

Annex C: Source code of NetLogo models

C.1 Subtidal small-scale model

```
globals [es ed s m l sm la xy n p1 p2 p3 p4 g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 ba fg1 fg2 fg3 fg4 fg5 fg6 fg7 fg8 fg9 fg10 fg11 fg12 fg13 fg14 fg15
fg16] ; define variables of abundances of sediment stabilizing (es) and destabilizing (ed) groups, central patches of the individuals of small (s), intermediate (m), large (l)
infaunal and small (sm), intermediate (la) epifaunal groups that survive at the end of each year, IBM name according to x-y coordinates of respective Rance patch (xy),
number of functional groups in the system (n), abundances of 4 predatory groups (p1-p4), abundances of 16 infaunal/epifaunal groups (g1-g16), abundance of infaunal
individuals of basibiotic group (ba) and contributions of infaunal/epifaunal groups to the respective spawner pool (fg1-fg16)
patches-own [sp ep g h a ag] ; define patch variables of infaunal (sp) and epifaunal (ep) group occupation, central patches of intermediate and large infaunal (g) and
intermediate epifaunal (h) individuals that grow in spite of competition and age of infaunal (a) and epifaunal (ag) individuals that survive at the end of a year

to make-movie ; make movie of model interface during initialization plus 9 time steps
  user-message "First, save your new movie file (choose a name ending with .mov)"
  let path user-new-file
  if not is-string? path [ stop ]
  setup
  movie-start path
  movie-set-frame-rate 1
  movie-grab-interface
  while [ ticks < 10 ]
  [go
    movie-grab-interface ]
  movie-close
  user-message (word "Exported movie to " path)
end

to export ; export all model entities and output to an external file named after the value of the xy variable
  export-world (word xy ".csv")
end

to import ; import all model entities and output from an external file named after the value of the xy variable
  import-world (word xy ".csv")
end

to setup ; initialize the model
  clear-all ; clear all model entities and output
  set s no-patches ; set variable s to an empty patch agentset
  set m no-patches ; set variable m to an empty patch agentset
  set l no-patches ; set variable l to an empty patch agentset
  set sm no-patches ; set variable sm to an empty patch agentset
```

```
 set la no-patches ; set variable la to an empty patch agentset
 ask patches [set sp one-of (list 45 45 55 65 65 75 75 75 85 85 85 95 95 105 105 105 115 115 115 125 125 125 135 135 135 145 145 145)] ; randomly attribute an infaunal group to the infaunal group occupation variable of each patch/the chances of each group to be attributed are defined by its fecundity, dispersal distance and early development mode
 ask n-of ( 0.9 * count patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] ) patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] [ set sp 35 ] ; randomly remove a subset of newly settled infaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
 ask n-of ( 0.5 * count patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125 ] ) patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125 ] [ set sp 35 ]
 ask n-of ( 0.1 * count patches with [ sp = 135 or sp = 145 ] ) patches with [ sp = 135 or sp = 145 ] [ set sp 35 ]
 ask patches with [sp > 80 and sp < 120] [ ; in random order expand patch occupation of surviving juveniles of purely infaunal intermediate groups to 8 immediate neighbors, unless any of them is occupied by an infaunal individual of the same size
   if map [? < 85 or ? > 125] [sp] of neighbors = [true true true true true true true true] [
     ask neighbors [set sp [sp] of myself]
     set g -3 ; assign the value -3 to the central patches variable of purely infaunal intermediate individuals that grew in spite of competition
     ]
   ]
 ask patches with [sp = 125] [ ; in random order expand patch occupation of surviving juveniles of the basibiotic group to 8 immediate neighbors, unless any of them is occupied by an infaunal individual of the same size and provided that at least one patch within each patch's 24 closest neighbors is occupied by an individual of the same group
   if map [? < 85 or ? > 125] [sp] of neighbors = [true true true true true true true true] and count patches in-radius 2.9 with [sp = 125] > 1 [
     ask neighbors [set sp [sp] of myself]
     set g -3 ; assign the value -3 to the central patches variable of basibiotic intermediate individuals that grew in spite of competition
     ]
   ]
 ask patches with [sp > 130] [ ; in random order expand patch occupation of surviving juveniles of infaunal large groups to 24 closest neighbors, unless any of them is occupied by an infaunal individual of the same size
   if map [? < 135] [sp] of other patches in-radius 2.9 = [true true true true true true true true true true true true true true true true true true true true true true true true] [
     ask patches in-radius 2.9 [set sp [sp] of myself]
     set g -5 ; assign the value -5 to the central patches variable of large infaunal individuals that grew in spite of competition
     ]
   ]
 ask patches with [sp > 40 and sp < 80] [set sp (sp - 35) / 10 set g -11 set a 0] ; assign the value -11 to the central patches variable of small infaunal individuals that were not overgrown and set their age to 1 year
 set s (patch-set patches with [g = -11]) ; assign the central patches of small infaunal individuals that were not overgrown to the respective patch set
 ask patches with [g = -3 and sp < 130 and length (filter [? = sp] [sp] of patches in-radius 1.9) = 9] [ask patches in-radius 1.9 [set sp (sp - 35) / 10] set g -7 set a 0] ; assign the value -7 to the central patches variable of intermediate infaunal individuals that grew and were not overgrown and set their age to 1 year
 set m (patch-set patches with [g = -7]) ; assign the central patches of intermediate infaunal individuals that grew and were not overgrown to the respective patch set
 ask patches with [g = -5 and length (filter [? = sp] [sp] of patches in-radius 2.9) = 25] [ask patches in-radius 2.9 [set sp (sp - 35) / 10] set g -9 set a 0] ; assign the value -9 to the central patches variable of large infaunal individuals that grew and were not overgrown and set their age to 1 year
 set l (patch-set patches with [g = -9]) ; assign the central patches of large infaunal individuals that grew and were not overgrown to the respective patch set
 ask patches with [sp > 11] [set sp 35] ; clear the infaunal group occupation variable of patches occupied by infaunal individuals that did not grow or were overgrown

 ask patches with [sp = 9] [set ep one-of (list 165 165 165 175 175 175 185 185 185 195 195 195 205 205 205 215 215)] ; randomly attribute an epifaunal group to the epifaunal group occupation variable of patches occupied by infaunal individuals of the basibiotic group/the chances of each group to be attributed are defined by its fecundity, dispersal distance and early development mode
 ask n-of ( 0.9 * count patches with [ ep = 165 or ep = 175 or ep = 185 ] ) patches with [ ep = 165 or ep = 175 or ep = 185 ] [ set ep 0 ] ; randomly remove a subset of newly settled epifaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
```

```
  ask n-of ( 0.5 * count patches with [ ep = 195 ] ) patches with [ ep = 195 ] [ set ep 0 ]
  ask n-of ( 0.1 * count patches with [ ep = 205 or ep = 215 ] ) patches with [ ep = 205 or ep = 215 ] [ set ep 0 ]
  ask patches with [ep = 215] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with rock to 8 immediate neighbors, unless any of them is occupied by an epifaunal individual of the same size
   if map [? < 200] [ep] of neighbors = [true true true true true true true true] [
    ask neighbors [set ep [ep] of myself]
    set h 3 ; assign the value 3 to the central patches variable of epifaunal intermediate individuals associated with rock that grew in spite of competition
    ]
   ]
  ask patches with [ep = 205] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with gravel to 8 immediate neighbors, unless any of them is occupied by an epifaunal individual of the same size
   if map [? < 200] [ep] of neighbors = [true true true true true true true true] [
    ask neighbors [set ep [ep] of myself]
    set h 3 ; assign the value 3 to the central patches variable of epifaunal intermediate individuals associated with gravel that grew in spite of competition
    ]
   ]
  ask patches with [ep > 160 and ep < 200] [set ep (ep - 35) / 10 set h 5 set ag 0] ; assign the value 5 to the central patches variable of small epifaunal individuals that were not overgrown and set their age to 1 year
  set sm (patch-set patches with [h = 5]) ; assign the central patches of small epifaunal individuals that were not overgrown to the respective patch set
  ask patches with [h = 3 and length (filter [? = ep] [ep] of patches in-radius 1.9) = 9] [ask patches in-radius 1.9 [set ep (ep - 35) / 10] set h 7 set ag 0] ; assign the value 7 to the central patches variable of intermediate epifaunal individuals that grew and were not overgrown and set their age to 1 year
  set la (patch-set patches with [h = 7]) ; assign the central patches of intermediate epifaunal individuals that grew and were not overgrown to the respective patch set
  ask patches with [ep > 18] [set ep 0] ; clear the epifaunal group occupation variable of patches occupied by epifaunal individuals that did not grow

  set g1 count patches with [ sp = 1 ] ; give the small infaunal groups abundance variables values equal to the number of patches occupied by each group
  set g2 count patches with [ sp = 2 ]
  set g3 count patches with [ sp = 3 ]
  set g4 count patches with [ sp = 4 ]
  set g5 count patches with [ sp = 5 ] / 9 ; give the intermediate infaunal groups abundance variables values equal to the number of patches occupied by each group divided by the individually occupied number of patches
  set g6 count patches with [ sp = 6 ] / 9
  set g7 count patches with [ sp = 7 ] / 9
  set g8 count patches with [ sp = 8 ] / 9
  set g9 count patches with [ sp = 9 ] / 9
  set ba g9 ; give the infaunal basibionts abundance variable a value equal to the infaunal abundance of the basibiotic group
  set g10 count patches with [ sp = 10 ] / 25 ; give the large infaunal groups abundance variables values equal to the number of patches occupied by each group divided by the individually occupied number of patches
  set g11 count patches with [ sp = 11 ] / 25
  set p1 round ((g4 + g7) / 10) ; give the predatory groups abundance variables values equal to the sum of their prey groups abundance divided by 10
  set p3 round ((g4 + g5) / 10)
  set p2 round ((g7 + g11) / 10)
  set p4 round ((p1 + p3) / 10)
  set es (g5 + g10) ; give the sediment stabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large sessile stabilizers
  set ed (g7 + g11) ; give the sediment destabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large destabilizers
  ask patches [set pcolor sp] ; color patches according to their infaunal group occupation variable

  set g12 count patches with [ ep = 13 ] ; give the small epifaunal groups abundance variables values equal to the number of patches occupied by each group
```

```
  set g13 count patches with [ ep = 14 ]
  set g14 count patches with [ ep = 15 ]
  set g9 g9 + count patches with [ ep = 16 ] ; give the basibiotic group abundance variable a value equal to the sum of the abundances of the infaunal and epifaunal individuals of the group
  set g15 count patches with [ ep = 17 ] / 9 ; give the intermediate epifaunal groups abundance variables values equal to the number of patches occupied by each group divided by the individually occupied number of patches
  set g16 count patches with [ ep = 18 ] / 9
  ask patches with [ ep > 0 ] [ set pcolor ep ] ; color patches occupied by epifaunal individuals according to their epifaunal group occupation variable

  set n length filter [? > 0] (list g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 p1 p2 p3 p4) ; give the variable of number of functional groups in the system a value equal to the number of groups with abundances larger than 0
  reset-ticks ; set tick counter to zero, set up and update all plots
end

to go ; move the model one step forward
  set-current-plot "Functional group abundance" ; clear the histogram of functional group abundances
  clear-plot
  tick ; advance the tick counter by one and update all plots
  do-recruitment ; run the recruitment submodel
  do-competition ; run the competition submodel
  do-ageing ; run the ageing submodel
  do-mortality ; run the mortality submodel
end

to do-recruitment ; run the recruitment submodel
  output-print " " output-type "f " output-type fg1 output-type " " output-type fg2 output-type " " output-type fg3 output-type " " output-type fg4 output-type " " output-type fg5 output-type " " output-type fg6 output-type " " output-type fg7 output-type " " output-type fg8 output-type " " output-type fg9 output-type " " output-type fg10 output-type " " output-type fg11 output-type " " output-type fg12 output-type " " output-type fg13 output-type " " output-type fg14 output-type " " output-type fg15 output-type " " output-print fg16 ; print out the values of infaunal/epifaunal groups contribution to the respective spawner pool
  let fg ( fg1 + fg2 + fg3 + fg4 + fg5 + fg6 + fg7 + fg8 + fg9 + fg10 + fg11 ) ; define the contribution of infaunal groups to the respective spawner pool as the contribution of each group to the total abundance of the respective set of groups during the previous time step
  ifelse es > ed ; randomly attribute an infaunal group to the infaunal group occupation variable of patches that are not occupied by infauna/the chances of each group to be attributed are defined by its fecundity, dispersal distance, early development mode, role in sediment engineering, position in the sediment, contribution to the infaunal spawner pool and the relative abundance of sediment stabilizing and destabilizing groups
  [ ask patches with [sp = 35] [ set sp one-of (se n-values ((fg1 / fg) * 200) [45] n-values ((fg2 / fg) * 50) [55] n-values ((fg3 / fg) * 100) [65] n-values ((fg4 / fg) * 150) [75] n-values ((fg5 / fg) * 600) [85] n-values ((fg6 / fg) * 100) [95] n-values ((fg7 / fg) * 150) [105] n-values ((fg8 / fg) * 150) [115] n-values ((fg9 / fg) * 600) [125] n-values ((fg10 / fg) * 600) [135] n-values ((fg11 / fg) * 150) [145]) ] ]
  [ ask patches with [sp = 35] [ set sp one-of (se n-values ((fg1 / fg) * 200) [45] n-values ((fg2 / fg) * 50) [55] n-values ((fg3 / fg) * 100) [65] n-values ((fg4 / fg) * 600) [75] n-values ((fg5 / fg) * 150) [85] n-values ((fg6 / fg) * 100) [95] n-values ((fg7 / fg) * 600) [105] n-values ((fg8 / fg) * 150) [115] n-values ((fg9 / fg) * 150) [125] n-values ((fg10 / fg) * 150) [135] n-values ((fg11 / fg) * 600) [145]) ] ]
  ask n-of ( 0.9 * count patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] ) patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] [ set sp 35 ] ; randomly remove a subset of newly settled infaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
  ask n-of ( 0.5 * count patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125 ] ) patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125 ] [ set sp 35 ]
  ask n-of ( 0.1 * count patches with [ sp = 135 or sp = 145 ] ) patches with [ sp = 135 or sp = 145 ] [ set sp 35 ]

let fge ( fg9 + fg12 + fg13 + fg14 + fg15 + fg16 ) ; define the contribution of epifaunal groups to the respective spawner pool as the contribution of each group to the total
```

```
abundance of the respective set of groups during the previous time step
  ask patches with [sp = 9 and ep = 0] [ set ep one-of (se n-values ((fg9 / fge) * 300) [195] n-values ((fg12 / fge) * 300) [165] n-values ((fg13 / fge) * 300) [175] n-values
((fg14 / fge) * 300) [185] n-values ((fg15 / fge) * 300) [205] n-values ((fg16 / fg) * 200) [215] ) ] ; randomly attribute an epifaunal group to the epifaunal group occupation
variable of patches occupied by infaunal individuals of the basibiotic group that are not occupied by epifauna/the chances of each group to be attributed are defined by its
fecundity, dispersal distance, early development mode and contribution to the infaunal spawner pool
  ask n-of ( 0.9 * count patches with [ ep = 165 or ep = 175 or ep = 185 ] ) patches with [ ep = 165 or ep = 175 or ep = 185 ] [ set ep 0 ] ; randomly remove a subset of newly
settled epifaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
  ask n-of ( 0.5 * count patches with [ ep = 195 ] ) patches with [ ep = 195 ] [ set ep 0 ]
  ask n-of ( 0.1 * count patches with [ ep = 205 or ep = 215 ] ) patches with [ ep = 205 or ep = 215 ] [ set ep 0 ]
end

to do-competition ; run the competition submodel
  ask patches with [sp > 80 and sp < 120] [ ; in random order expand patch occupation of surviving juveniles of purely infaunal intermediate groups to 8 immediate
neighbors, unless any of them is occupied by an infaunal individual of the same size
    if map [(? < 5 or ? > 11) and (? < 85 or ? > 125)] [sp] of neighbors = [true true true true true true true true] [
      ask neighbors [set sp [sp] of myself]
      set g 1 / ticks ; assign the value 1/time step to the central patches variable of purely infaunal intermediate individuals that grew in spite of competition
      ]
    ]
  ask patches with [sp = 125] [ ; in random order expand patch occupation of surviving juveniles of the basibiotic group to 8 immediate neighbors, unless any of them is
occupied by an infaunal individual of the same size and provided that at least one patch within each patch's 24 closest neighbors is occupied by an individual of the same
group
    if map [(? < 5 or ? > 11) and (? < 85 or ? > 125)] [sp] of neighbors = [true true true true true true true true] and count patches in-radius 2.9 with [sp = 9] > 0 [
      ask neighbors [set sp [sp] of myself]
      set g 1 / ticks ; assign the value 1/time step to the central patches variable of basibiotic intermediate individuals that grew in spite of competition
      ]
    ]
  ask patches with [sp > 130] [ ; in random order expand patch occupation of surviving juveniles of infaunal large groups to 24 closest neighbors, unless any of them is
occupied by an infaunal individual of the same size
    if map [(? < 10 or ? > 11) and ? < 135] [sp] of other patches in-radius 2.9 = [true true true true true true true true true true true true true true true true true true true true
true true true true] [
      ask patches in-radius 2.9 [set sp [sp] of myself]
      set g 2 * ticks ; assign the value 2xtime step to the central patches variable of large infaunal individuals that grew in spite of competition
      ]
    ]

  ask patches with [ep = 215] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with rock to 8 immediate
neighbors, unless any of them is occupied by an epifaunal individual of the same size
    if map [(? < 17 or ? > 18) and ? < 205] [ep] of neighbors = [true true true true true true true true] [
      ask neighbors [set ep [ep] of myself]
      set h 2 * ticks ; assign the value 2xtime step to the central patches variable of epifaunal intermediate individuals associated with rock that grew in spite of competition
      ]
    ]
  ask patches with [ep = 205] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with gravel to 8 immediate
neighbors, unless any of them is occupied by an epifaunal individual of the same size
    if map [(? < 17 or ? > 18) and ? < 205] [ep] of neighbors = [true true true true true true true true] [
      ask neighbors [set ep [ep] of myself]
```

```
      set h 2 * ticks ; assign the value 2xtime step to the central patches variable of epifaunal intermediate individuals associated with gravel that grew in spite of competition
      ]
    ]
end

to do-ageing ; run the ageing submodel
  ask s [set a a + 1] ; add one year to the age of small infaunal individuals that survived from the previous time step
  ask m [set a a + 1] ; add one year to the age of intermediate infaunal individuals that survived from the previous time step
  ask l [set a a + 1] ; add one year to the age of large infaunal individuals that survived from the previous time step

  ask sm [set ag ag + 1] ; add one year to the age of small epifaunal individuals that survived from the previous time step
  ask la [set ag ag + 1] ; add one year to the age of intermediate epifaunal individuals that survived from the previous time step
end

to do-mortality ; run the mortality submodel
  ask patches with [sp > 40 and sp < 80] [set sp (sp - 35) / 10 set a 0] ; set the age of newly settled small infaunal individuals that were not overgrown to 1 year and
  set s patches with [sp < 5] ; add them to the respective patch set
  ask m with [length (filter [? = sp] [sp] of patches in-radius 1.9) != 9 or sp > 9] [ask patches in-radius 1.9 with [sp < 130] [set sp 35] ask la in-radius 1.9 [set ep 0] ask patches in-radius 1.9 with [ep < 17 or (ep > 160 and ep < 200) or h = 2 * ticks] [set ep 0]] ; clear the infaunal and epifaunal group occupation variable of patches occupied by intermediate infaunal individuals that were overgrown
  set m m with [sp < 10] ; remove the central patches of intermediate infaunal individuals that were overgrown from the respective patch set of individuals that survive at the end of the year
  ask patches with [g = 1 / ticks and sp > 80 and sp < 130 and length (filter [? = sp] [sp] of patches in-radius 1.9) = 9] [ask patches in-radius 1.9 [set sp (sp - 35) / 10] set g -1 / ticks set a 0] ; assign the value -1/time step to the central patches variable of intermediate infaunal individuals that grew and were not overgrown and set their age to 1 year
  set m (patch-set m patches with [g = -1 / ticks]) ; add the central patches of intermediate infaunal individuals that grew and were not overgrown to the respective patch set
  ask patches with [g = 2 * ticks] [ask patches in-radius 2.9 [set sp (sp - 35) / 10] set a 0] ; set the age of newly settled large infaunal individuals that grew to 1 year and
  set l (patch-set l patches with [g = 2 * ticks]) ; add them to the respective patch set
  ask patches with [sp > 11] [set sp 35] ; clear the infaunal group occupation variable of patches occupied by newly settled infaunal individuals that did not grow or were overgrown
  ask s with [sp = 1 and a > 0] [set sp 35] ; clear the infaunal group occupation variable of patches occupied by small infaunal individuals that reached their lifespan
  ask s with [sp = 2 and a > 8] [set sp 35]
  ask s with [sp = 3 and a > 0] [set sp 35]
  ask s with [sp = 4 and a > 0] [set sp 35]
  ask m with [sp = 5 and a > 2] [ask patches in-radius 1.9 [set sp 35]] ; clear the infaunal group occupation variable of patches occupied by intermediate infaunal individuals that reached their lifespan
  ask m with [sp = 6 and a > 13] [ask patches in-radius 1.9 [set sp 35]]
  ask m with [sp = 7 and a > 1] [ask patches in-radius 1.9 [set sp 35]]
  ask m with [sp = 8 and a > 7] [ask patches in-radius 1.9 [set sp 35]]

  ask patches with [ep > 160 and ep < 200] [set ep (ep - 35) / 10 set ag 0] ; set the age of newly settled small epifaunal individuals that were not overgrown to 1 year
  ask sm with [ep = 13 and ag > 0] [set ep 0] ; clear the epifaunal group occupation variable of patches occupied by small epifaunal individuals that reached their lifespan
  ask sm with [ep = 14 and ag > 0] [set ep 0]
  ask sm with [ep = 15 and ag > 0] [set ep 0]
  ask sm with [ep = 16 and ag > 9] [set ep 0]
  ask m with [sp = 9 and a > 9] [ ; ask infaunal individuals of the basibiotic group that reached their lifespan
```

```
   ifelse length (filter [? = 16] [ep] of patches in-radius 1.9) > 0 ; if they have any epibiotic individuals of the same group
   [set a max [ag] of patches in-radius 1.9 with [ep = 16] ask max-one-of patches in-radius 1.9 with [ep = 16] [ag] [set ep 0]] ; to take the age of the oldest one and remove it from the epibionts
   [ask patches in-radius 1.9 [set sp 35 set ep 0]]] ; otherwise clear the infaunal and epifaunal group occupation variable of patches occupied by them
  set sm patches with [ep > 0 and ep < 17] ; add newly settled small epifaunal individuals that were not overgrown to the respective patch set
  ask la with [length (filter [? = ep] [ep] of patches in-radius 1.9) != 9] [ask patches in-radius 1.9 [set ep 0]] ; clear the epifaunal group occupation variable of patches occupied by intermediate epifaunal individuals that are no more epibionts
  ask patches with [h = 2 * ticks and ep > 200] [ask patches in-radius 1.9 [set ep (ep - 35) / 10] set h -2 * ticks set ag 0] ; set the age of newly settled intermediate epifaunal individuals that grew to 1 year and
  set la (patch-set la with [ep > 0] patches with [h = -2 * ticks]) ; add them to the respective patch set
  ask patches with [ep > 18] [set ep 0] ; clear the epifaunal group occupation variable of patches occupied by intermediate epifaunal individuals that did not grow
  ask la with [ep = 17 and ag > 8] [ask patches in-radius 1.9 [set ep 0]] ; clear the epifaunal group occupation variable of patches occupied by intermediate epifaunal individuals that reached their lifespan
  ask la with [ep = 18 and ag > 10] [ask patches in-radius 1.9 [set ep 0]]
  set sm sm with [(ep = 13 and ag < 1) or (ep = 14 and ag < 1) or (ep = 15 and ag < 1) or (ep = 16 and ag < 10)] ; update the patch set of small epifaunal individuals
  set la la with [(ep = 17 and ag < 9) or (ep = 18 and ag < 11)] ; update the patch set of intermediate epifaunal individuals

  ask l with [sp = 10 and a > 2] [ask patches in-radius 2.9 [set sp 35]] ; clear the infaunal group occupation variable of patches occupied by large infaunal individuals that reached their lifespan
  ask l with [sp = 11 and a > 1] [ask patches in-radius 2.9 [set sp 35]]
  let pr4 count s with [sp = 4] ; assign the abundances of prey groups to the potential prey variables
  let pr5 count m with [sp = 5]
  let pr7 count m with [sp = 7]
  let pr11 count l with [sp = 11]
  ifelse pr11 >= pr7 ; if larger prey was more or equally abundant to smaller prey
  [ask n-of min list p2 count l with [sp = 11 and a < 2] l with [sp = 11 and a < 2] [ask patches in-radius 2.9 [set sp 35]]] ; randomly remove as many larger prey individuals as there were large predators
  [ask n-of min list max list 0 (p2 - count m with [sp = 7 and a < 2]) count l with [sp = 11 and a < 2] l with [sp = 11 and a < 2] [ask patches in-radius 2.9 [set sp 35]]] ; otherwise randomly remove as many larger prey individuals as there were large predators minus the abundance of the smaller prey
  set l l with [(sp = 10 and a < 3) or (sp = 11 and a < 2)] ; update the patch set of large epifaunal individuals
  ifelse pr7 > pr11 ; if smaller prey was more abundant than larger prey
  [ask n-of min list p2 count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ; randomly remove as many smaller prey individuals as there were large predators
  [ask n-of min list max list 0 (p2 - count l with [sp = 11 and a < 2]) count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ; otherwise randomly remove as many smaller prey individuals as there were large predators minus the abundance of the larger prey
  ifelse pr5 >= pr4 ; if larger prey was more or equally abundant to smaller prey
  [ask n-of min list p3 count m with [sp = 5 and a < 3] m with [sp = 5 and a < 3] [ask patches in-radius 1.9 [set sp 35]]] ; randomly remove as many larger prey individuals as there were intermediate predators
  [ask n-of min list max list 0 (p3 - count s with [sp = 4 and a < 1]) count m with [sp = 5 and a < 3] m with [sp = 5 and a < 3] [ask patches in-radius 1.9 [set sp 35]]] ; otherwise randomly remove as many larger prey individuals as there were intermediate predators minus the abundance of the smaller prey
  ifelse pr7 >= pr4 ; if larger prey was more or equally abundant to smaller prey
  [ask n-of min list p1 count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ; randomly remove as many larger prey individuals as there were small predators
  [ask n-of min list max list 0 (p1 - count s with [sp = 4 and a < 1]) count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ; otherwise randomly remove as many larger prey individuals as there were small predators minus the abundance of the smaller prey
  set m m with [(sp = 5 and a < 3) or (sp = 6 and a < 14) or (sp = 7 and a < 2) or (sp = 8 and a < 8) or (sp = 9 and a < 10)] ; update the patch set of intermediate epifaunal individuals
```

```
  ifelse pr4 > pr5 ; if smaller prey was more abundant than larger prey
  [ask n-of min list p3 count s with [sp = 4] s with [sp = 4] [set sp 35]] ; randomly remove as many smaller prey individuals as there were intermediate predators
  [ask n-of min list max list 0 (p3 - count m with [sp = 5]) count s with [sp = 4] s with [sp = 4] [set sp 35]] ; otherwise randomly remove as many smaller prey individuals as
there were small predators minus the abundance of the larger prey
  ifelse pr4 > pr7 ; if smaller prey was more abundant than larger prey
  [ask n-of min list p1 count s with [sp = 4] s with [sp = 4] [set sp 35]] ; randomly remove as many smaller prey individuals as there were small predators
  [ask n-of min list max list 0 (p1 - count m with [sp = 7]) count s with [sp = 4] s with [sp = 4] [set sp 35]] ; otherwise randomly remove as many smaller prey individuals as
there were small predators minus the abundance of the larger prey
  set s s with [(sp = 1 and a < 1) or (sp = 2 and a < 9) or (sp = 3 and a < 1) or (sp = 4 and a < 1)] ; update the patch set of small epifaunal individuals
  set g1 count patches with [ sp = 1 ] ; give the small infaunal groups abundance variables values equal to the number of patches occupied by each group
  set g2 count patches with [ sp = 2 ]
  set g3 count patches with [ sp = 3 ]
  set g4 count patches with [ sp = 4 ]
  set g5 count patches with [ sp = 5 ] / 9 ; give the intermediate infaunal groups abundance variables values equal to the number of patches occupied by each group divided
by the individually occupied number of patches
  set g6 count patches with [ sp = 6 ] / 9
  set g7 count patches with [ sp = 7 ] / 9
  set g8 count patches with [ sp = 8 ] / 9
  set g9 count patches with [ sp = 9 ] / 9
  set ba g9 ; give the infaunal basibionts abundance variable a value equal to the infaunal abundance of the basibiotic group
  set g10 count patches with [ sp = 10 ] / 25 ; give the large infaunal groups abundance variables values equal to the number of patches occupied by each group divided by
the individually occupied number of patches
  set g11 count patches with [ sp = 11 ] / 25
  set p1 round ((g4 + g7) / 10) ; give the predatory groups abundance variables values equal to the sum of their prey groups abundance divided by 10
  set p3 round ((g4 + g5) / 10)
  set p2 round ((g7 + g11) / 10)
  set p4 round ((p1 + p3) / 10)
  set es (g5 + g10) ; give the sediment stabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large sessile stabilizers
  set ed (g7 + g11) ; give the sediment destabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large destabilizers
  ask patches [set pcolor sp] ; color patches according to their infaunal group occupation variable

  set g12 count patches with [ ep = 13 ] ; give the small epifaunal groups abundance variables values equal to the number of patches occupied by each group
  set g13 count patches with [ ep = 14 ]
  set g14 count patches with [ ep = 15 ]
  set g9 g9 + count patches with [ ep = 16 ] ; give the basibiotic group abundance variable a value equal to the sum of the abundances of the infaunal and epifaunal
individuals of the group
  set g15 count patches with [ ep = 17 ] / 9 ; give the intermediate epifaunal groups abundance variables values equal to the number of patches occupied by each group
divided by the individually occupied number of patches
  set g16 count patches with [ ep = 18 ] / 9
  ask patches with [ ep > 0 ] [ set pcolor ep ] ; color patches occupied by epifaunal individuals according to their epifaunal group occupation variable

  output-type "g " output-type g1 output-type " " output-type g2 output-type " " output-type g3 output-type " " output-type g4 output-type " " output-type g5 output-type " "
output-type g6 output-type " " output-type g7 output-type " " output-type g8 output-type " " output-type g9 output-type " " output-type g10 output-type " " output-type g11
output-type " " output-type g12 output-type " " output-type g13 output-type " " output-type g14 output-type " " output-type g15 output-type " " output-type g16 output-
type " " output-type p1 output-type " " output-type p2 output-type " " output-type p3 output-type " " output-print p4 ; print out the values of infaunal/epifaunal and
predatory groups abundance
  set n length filter [? > 0] (list g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 p1 p2 p3 p4) ; give the variable of number of functional groups in the system a value
```

```
equal to the number of groups with abundances larger than 0
end
```

C.2 Intertidal small-scale model

```
globals [es ed s m l sm la xy n p1 p2 p3 p4 g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 ba fg1 fg2 fg3 fg4 fg5 fg6 fg7 fg8 fg9 fg10 fg11 fg12 fg13 fg14 fg15
fg16] ; define variables of abundances of sediment stabilizing (es) and destabilizing (ed) groups, central patches of the individuals of small (s), intermediate (m), large (l)
infaunal and small (sm), intermediate (la) epifaunal groups that survive at the end of each year, IBM name according to x-y coordinates of respective Rance patch (xy),
number of functional groups in the system (n), abundances of 4 predatory groups (p1-p4), abundances of 16 infaunal/epifaunal groups (g1-g16), abundance of infaunal
individuals of basibiotic group (ba) and contributions of infaunal/epifaunal groups to the respective spawner pool (fg1-fg16)
patches-own [sp ep g h a ag] ; define patch variables of infaunal (sp) and epifaunal (ep) group occupation, central patches of intermediate and large infaunal (g) and
intermediate epifaunal (h) individuals that grow in spite of competition and age of infaunal (a) and epifaunal (ag) individuals that survive at the end of a year

to make-movie ; make movie of model interface during initialization plus 9 time steps
  user-message "First, save your new movie file (choose a name ending with .mov)"
  let path user-new-file
  if not is-string? path [ stop ]
  setup
  movie-start path
  movie-set-frame-rate 1
  movie-grab-interface
  while [ ticks < 10 ]
  [go
    movie-grab-interface ]
  movie-close
  user-message (word "Exported movie to " path)
end

to export ; export all model entities and output to an external file named after the value of the xy variable
  export-world (word xy ".csv")
end

to import ; import all model entities and output from an external file named after the value of the xy variable
  import-world (word xy ".csv")
end

to setup ; initialize the model
  clear-all ; clear all model entities and output
  set s no-patches ; set variable s to an empty patch agentset
  set m no-patches ; set variable m to an empty patch agentset
  set l no-patches ; set variable l to an empty patch agentset
  set sm no-patches ; set variable sm to an empty patch agentset
  set la no-patches ; set variable la to an empty patch agentset
  ask patches [set sp one-of (list 45 45 55 65 65 65 65 75 75 75 85 85 85 95 95 105 105 105 105 105 105 115 115 115 115 115 115 125 125 125 135 135 135 135 135 135
```

```
145 145 145 145 145 145)] ; randomly attribute an infaunal group to the infaunal group occupation variable of each patch/the chances of each group to be attributed are
defined by its tolerance of tidal exposure, fecundity, dispersal distance and early development mode
 ask n-of ( 0.9 * count patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] ) patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] [ set sp 35 ] ; randomly remove a
subset of newly settled infaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
 ask n-of ( 0.5 * count patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125] ) patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125] [ set
sp 35 ]
 ask n-of ( 0.1 * count patches with [ sp = 135 or sp = 145 ] ) patches with [ sp = 135 or sp = 145 ] [ set sp 35 ]
 ask patches with [sp > 80 and sp < 120] [ ; in random order expand patch occupation of surviving juveniles of purely infaunal intermediate groups to 8 immediate
neighbors, unless any of them is occupied by an infaunal individual of the same size
   if map [? < 85 or ? > 125] [sp] of neighbors = [true true true true true true true true] [
    ask neighbors [set sp [sp] of myself]
    set g -3 ; assign the value -3 to the central patches variable of purely infaunal intermediate individuals that grew in spite of competition
    ]
   ]
 ask patches with [sp = 125] [ ; in random order expand patch occupation of surviving juveniles of the basibiotic group to 8 immediate neighbors, unless any of them is
occupied by an infaunal individual of the same size and provided that at least one patch within each patch's 24 closest neighbors is occupied by an individual of the same
group
   if map [? < 85 or ? > 125] [sp] of neighbors = [true true true true true true true true] and count patches in-radius 2.9 with [sp = 125] > 1 [
    ask neighbors [set sp [sp] of myself]
    set g -3 ; assign the value -3 to the central patches variable of basibiotic intermediate individuals that grew in spite of competition
    ]
   ]
 ask patches with [sp > 130] [ ; in random order expand patch occupation of surviving juveniles of infaunal large groups to 24 closest neighbors, unless any of them is
occupied by an infaunal individual of the same size
   if map [? < 135] [sp] of other patches in-radius 2.9 = [true true true true true true true true true true true true true true true true true true true true true true true true] [
    ask patches in-radius 2.9 [set sp [sp] of myself]
    set g -5 ; assign the value -5 to the central patches variable of large infaunal individuals that grew in spite of competition
    ]
   ]
 ask patches with [sp > 40 and sp < 80] [set sp (sp - 35) / 10 set g -11 set a 0] ; assign the value -11 to the central patches variable of small infaunal individuals that were
not overgrown and set their age to 1 year
 set s (patch-set patches with [g = -11]) ; assign the central patches of small infaunal individuals that were not overgrown to the respective patch set
 ask patches with [g = -3 and sp < 130 and length (filter [? = sp] [sp] of patches in-radius 1.9) = 9] [ask patches in-radius 1.9 [set sp (sp - 35) / 10] set g -7 set a 0] ; assign
the value -7 to the central patches variable of intermediate infaunal individuals that grew and were not overgrown and set their age to 1 year
 set m (patch-set patches with [g = -7]) ; assign the central patches of intermediate infaunal individuals that grew and were not overgrown to the respective patch set
 ask patches with [g = -5 and length (filter [? = sp] [sp] of patches in-radius 2.9) = 25] [ask patches in-radius 2.9 [set sp (sp - 35) / 10] set g -9 set a 0] ; assign the value -9
to the central patches variable of large infaunal individuals that grew and were not overgrown and set their age to 1 year
 set l (patch-set patches with [g = -9]) ; assign the central patches of large infaunal individuals that grew and were not overgrown to the respective patch set
 ask patches with [sp > 11] [set sp 35] ; clear the infaunal group occupation variable of patches occupied by infaunal individuals that did not grow or were overgrown

 ask patches with [sp = 9] [set ep one-of (list 165 165 165 175 175 175 175 175 175 185 185 185 195 195 195 205 205 205 215 215)] ; randomly attribute an epifaunal
group to the epifaunal group occupation variable of patches occupied by infaunal individuals of the basibiotic group/the chances of each group to be attributed are defined by
its tolerance of tidal exposure, fecundity, dispersal distance and early development mode
 ask n-of ( 0.9 * count patches with [ ep = 165 or ep = 175 or ep = 185 ] ) patches with [ ep = 165 or ep = 175 or ep = 185 ] [ set ep 0 ] ; randomly remove a subset of newly
settled epifaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
 ask n-of ( 0.5 * count patches with [ ep = 195 ] ) patches with [ ep = 195 ] [ set ep 0 ]
 ask n-of ( 0.1 * count patches with [ ep = 205 or ep = 215 ] ) patches with [ ep = 205 or ep = 215 ] [ set ep 0 ]
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  ask patches with [ep = 215] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with rock to 8 immediate neighbors, unless any of them is occupied by an epifaunal individual of the same size
    if map [? < 200] [ep] of neighbors = [true true true true true true true true] [
      ask neighbors [set ep [ep] of myself]
      set h 3 ; assign the value 3 to the central patches variable of epifaunal intermediate individuals associated with rock that grew in spite of competition
      ]
    ]
  ask patches with [ep = 205] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with gravel to 8 immediate neighbors, unless any of them is occupied by an epifaunal individual of the same size
    if map [? < 200] [ep] of neighbors = [true true true true true true true true] [
      ask neighbors [set ep [ep] of myself]
      set h 3 ; assign the value 3 to the central patches variable of epifaunal intermediate individuals associated with gravel that grew in spite of competition
      ]
    ]
  ask patches with [ep > 160 and ep < 200] [set ep (ep - 35) / 10 set h 5 set ag 0] ; assign the value 5 to the central patches variable of small epifaunal individuals that were not overgrown and set their age to 1 year
  set sm (patch-set patches with [h = 5]) ; assign the central patches of small epifaunal individuals that were not overgrown to the respective patch set
  ask patches with [h = 3 and length (filter [? = ep] [ep] of patches in-radius 1.9) = 9] [ask patches in-radius 1.9 [set ep (ep - 35) / 10] set h 7 set ag 0] ; assign the value 7 to the central patches variable of intermediate epifaunal individuals that grew and were not overgrown and set their age to 1 year
  set la (patch-set patches with [h = 7]) ; assign the central patches of intermediate epifaunal individuals that grew and were not overgrown to the respective patch set
  ask patches with [ep > 18] [set ep 0] ; clear the epifaunal group occupation variable of patches occupied by epifaunal individuals that did not grow

  set g1 count patches with [ sp = 1 ] ; give the small infaunal groups abundance variables values equal to the number of patches occupied by each group
  set g2 count patches with [ sp = 2 ]
  set g3 count patches with [ sp = 3 ]
  set g4 count patches with [ sp = 4 ]
  set g5 count patches with [ sp = 5 ] / 9 ; give the intermediate infaunal groups abundance variables values equal to the number of patches occupied by each group divided by the individually occupied number of patches
  set g6 count patches with [ sp = 6 ] / 9
  set g7 count patches with [ sp = 7 ] / 9
  set g8 count patches with [ sp = 8 ] / 9
  set g9 count patches with [ sp = 9 ] / 9
  set ba g9 ; give the infaunal basibionts abundance variable a value equal to the infaunal abundance of the basibiotic group
  set g10 count patches with [ sp = 10 ] / 25 ; give the large infaunal groups abundance variables values equal to the number of patches occupied by each group divided by the individually occupied number of patches
  set g11 count patches with [ sp = 11 ] / 25
  set p1 round ((max list g4 g7) / 10) ; give the predatory groups abundance variables values equal to those of the most abundant of their prey groups divided by 10
  set p3 round ((max list g4 g5) / 10)
  set p2 round ((max list g7 g11) / 10)
  set p4 round ((max list p1 p3) / 10)
  set es (g8 + g10) ; give the sediment stabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large sessile stabilizers that tolerate tidal exposure
  set ed (g7 + g11) ; give the sediment destabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large destabilizers that tolerate tidal exposure
  ask patches [set pcolor sp] ; color patches according to their infaunal group occupation variable

  set g12 count patches with [ ep = 13 ] ; give the small epifaunal groups abundance variables values equal to the number of patches occupied by each group
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  set g13 count patches with [ ep = 14 ]
  set g14 count patches with [ ep = 15 ]
  set g9 g9 + count patches with [ ep = 16 ] ; give the basibiotic group abundance variable a value equal to the sum of the abundances of the infaunal and epifaunal individuals of the group
  set g15 count patches with [ ep = 17 ] / 9 ; give the intermediate epifaunal groups abundance variables values equal to the number of patches occupied by each group divided by the individually occupied number of patches
  set g16 count patches with [ ep = 18 ] / 9
  ask patches with [ ep > 0 ] [ set pcolor ep ] ; color patches occupied by epifaunal individuals according to their epifaunal group occupation variable

  set n length filter [? > 0] (list g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 p1 p2 p3 p4) ; give the variable of number of functional groups in the system a value equal to the number of groups with abundances larger than 0
  reset-ticks ; set tick counter to zero, set up and update all plots
end

to go ; move the model one step forward
  set-current-plot "Functional group abundance" ; clear the histogram of functional group abundances
  clear-plot
  tick ; advance the tick counter by one and update all plots
  do-recruitment ; run the recruitment submodel
  do-competition ; run the competition submodel
  do-ageing ; run the ageing submodel
  do-mortality ; run the mortality submodel
end

to do-recruitment ; run the recruitment submodel
  output-print " " output-type "f " output-type fg1 output-type " " output-type fg2 output-type " " output-type fg3 output-type " " output-type fg4 output-type " " output-type fg5 output-type " " output-type fg6 output-type " " output-type fg7 output-type " " output-type fg8 output-type " " output-type fg9 output-type " " output-type fg10 output-type " " output-type fg11 output-type " " output-type fg12 output-type " " output-type fg13 output-type " " output-type fg14 output-type " " output-type fg15 output-type " " output-print fg16 ; print out the values of infaunal/epifaunal groups contribution to the respective spawner pool
  let fg ( fg1 + fg2 + fg3 + fg4 + fg5 + fg6 + fg7 + fg8 + fg9 + fg10 + fg11 ) ; define the contribution of infaunal groups to the respective spawner pool as the contribution of each group to the total abundance of the respective set of groups during the previous time step
  ifelse es > ed ; randomly attribute an infaunal group to the infaunal group occupation variable of patches that are not occupied by infauna/the chances of each group to be attributed are defined by its tolerance of tidal exposure, fecundity, dispersal distance, early development mode, role in sediment engineering, position in the sediment, contribution to the infaunal spawner pool and the relative abundance of sediment stabilizing and destabilizing groups
  [ ask patches with [sp = 35] [ set sp one-of (se n-values ((fg1 / fg) * 100) [45] n-values ((fg2 / fg) * 50) [55] n-values ((fg3 / fg) * 100) [65] n-values ((fg4 / fg) * 150) [75] n-values ((fg5 / fg) * 150) [85] n-values ((fg6 / fg) * 100) [95] n-values ((fg7 / fg) * 150) [105] n-values ((fg8 / fg) * 600) [115] n-values ((fg9 / fg) * 150) [125] n-values ((fg10 / fg) * 600) [135] n-values ((fg11 / fg) * 150) [145]) ] ]
  [ ask patches with [sp = 35] [ set sp one-of (se n-values ((fg1 / fg) * 100) [45] n-values ((fg2 / fg) * 50) [55] n-values ((fg3 / fg) * 400) [65] n-values ((fg4 / fg) * 150) [75] n-values ((fg5 / fg) * 150) [85] n-values ((fg6 / fg) * 100) [95] n-values ((fg7 / fg) * 600) [105] n-values ((fg8 / fg) * 150) [115] n-values ((fg9 / fg) * 150) [125] n-values ((fg10 / fg) * 150) [135] n-values ((fg11 / fg) * 600) [145]) ] ]
  ask n-of ( 0.9 * count patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] ) patches with [ sp = 45 or sp = 55 or sp = 65 or sp = 75 ] [ set sp 35 ] ; randomly remove a subset of newly settled infaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
  ask n-of ( 0.5 * count patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125 ] ) patches with [ sp = 85 or sp = 95 or sp = 105 or sp = 115 or sp = 125 ] [ set sp 35 ]
  ask n-of ( 0.1 * count patches with [ sp = 135 or sp = 145 ] ) patches with [ sp = 135 or sp = 145 ] [ set sp 35 ]

let fge ( fg9 + fg12 + fg13 + fg14 + fg15 + fg16 ) ; define the contribution of epifaunal groups to the respective spawner pool as the contribution of each group to the total
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abundance of the respective set of groups during the previous time step
  ask patches with [sp = 9 and ep = 0] [ set ep one-of (se n-values ((fg9 / fge) * 300) [195] n-values ((fg12 / fge) * 300) [165] n-values ((fg13 / fge) * 600) [175] n-values
((fg14 / fge) * 300) [185] n-values ((fg15 / fge) * 300) [205] n-values ((fg16 / fg) * 200) [215] ) ] ; randomly attribute an epifaunal group to the epifaunal group occupation
variable of patches occupied by infaunal individuals of the basibiotic group that are not occupied by epifauna/the chances of each group to be attributed are defined by its
tolerance of tidal exposure, fecundity, dispersal distance, early development mode and contribution to the infaunal spawner pool
  ask n-of ( 0.9 * count patches with [ ep = 165 or ep = 175 or ep = 185 ] ) patches with [ ep = 165 or ep = 175 or ep = 185 ] [ set ep 0 ] ; randomly remove a subset of newly
settled epifaunal juveniles of each group from the system/juvenile mortality rates are defined by the body size of each group
  ask n-of ( 0.5 * count patches with [ ep = 195 ] ) patches with [ ep = 195 ] [ set ep 0 ]
  ask n-of ( 0.1 * count patches with [ ep = 205 or ep = 215 ] ) patches with [ ep = 205 or ep = 215 ] [ set ep 0 ]
end

to do-competition ; run the competition submodel
  ask patches with [sp > 80 and sp < 120] [ ; in random order expand patch occupation of surviving juveniles of purely infaunal intermediate groups to 8 immediate
neighbors, unless any of them is occupied by an infaunal individual of the same size
    if map [(? < 5 or ? > 11) and (? < 85 or ? > 125)] [sp] of neighbors = [true true true true true true true true] [
      ask neighbors [set sp [sp] of myself]
      set g 1 / ticks ; assign the value 1/time step to the central patches variable of purely infaunal intermediate individuals that grew in spite of competition
      ]
    ]
  ask patches with [sp = 125] [ ; in random order expand patch occupation of surviving juveniles of the basibiotic group to 8 immediate neighbors, unless any of them is
occupied by an infaunal individual of the same size and provided that at least one patch within each patch's 24 closest neighbors is occupied by an individual of the same
group
    if map [(? < 5 or ? > 11) and (? < 85 or ? > 125)] [sp] of neighbors = [true true true true true true true true] and count patches in-radius 2.9 with [sp = 9] > 0 [
      ask neighbors [set sp [sp] of myself]
      set g 1 / ticks ; assign the value 1/time step to the central patches variable of basibiotic intermediate individuals that grew in spite of competition
      ]
    ]
  ask patches with [sp > 130] [ ; in random order expand patch occupation of surviving juveniles of infaunal large groups to 24 closest neighbors, unless any of them is
occupied by an infaunal individual of the same size
    if map [(? < 10 or ? > 11) and ? < 135] [sp] of other patches in-radius 2.9 = [true true true true true true true true true true true true true true true true true true true true
true true true true] [
      ask patches in-radius 2.9 [set sp [sp] of myself]
      set g 2 * ticks ; assign the value 2xtime step to the central patches variable of large infaunal individuals that grew in spite of competition
      ]
    ]

  ask patches with [ep = 215] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with rock to 8 immediate
neighbors, unless any of them is occupied by an epifaunal individual of the same size
    if map [(? < 17 or ? > 18) and ? < 205] [ep] of neighbors = [true true true true true true true true] [
      ask neighbors [set ep [ep] of myself]
      set h 2 * ticks ; assign the value 2xtime step to the central patches variable of epifaunal intermediate individuals associated with rock that grew in spite of competition
      ]
    ]
  ask patches with [ep = 205] [ ; in random order expand patch occupation of surviving juveniles of epifaunal intermediate groups associated with gravel to 8 immediate
neighbors, unless any of them is occupied by an epifaunal individual of the same size
    if map [(? < 17 or ? > 18) and ? < 205] [ep] of neighbors = [true true true true true true true true] [
      ask neighbors [set ep [ep] of myself]
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   set h 2 * ticks ; assign the value 2xtime step to the central patches variable of epifaunal intermediate individuals associated with gravel that grew in spite of competition
   ]
  ]
end

to do-ageing ; run the ageing submodel
 ask s [set a a + 1] ; add one year to the age of small infaunal individuals that survived from the previous time step
 ask m [set a a + 1] ; add one year to the age of intermediate infaunal individuals that survived from the previous time step
 ask l [set a a + 1] ; add one year to the age of large infaunal individuals that survived from the previous time step

 ask sm [set ag ag + 1] ; add one year to the age of small epifaunal individuals that survived from the previous time step
 ask la [set ag ag + 1] ; add one year to the age of intermediate epifaunal individuals that survived from the previous time step
end

to do-mortality ; run the mortality submodel
 ask patches with [sp > 40 and sp < 80] [set sp (sp - 35) / 10 set a 0] ; set the age of newly settled small infaunal individuals that were not overgrown to 1 year and
 set s patches with [sp < 5] ; add them to the respective patch set
 ask m with [length (filter [? = sp] [sp] of patches in-radius 1.9) != 9 or sp > 9] [ask patches in-radius 1.9 with [sp < 130] [set sp 35] ask la in-radius 1.9 [set ep 0] ask patches in-radius 1.9 with [ep < 17 or (ep > 160 and ep < 200) or h = 2 * ticks] [set ep 0]] ; clear the infaunal and epifaunal group occupation variable of patches occupied by intermediate infaunal individuals that were overgrown
 set m m with [sp < 10] ; remove the central patches of intermediate infaunal individuals that were overgrown from the respective patch set of individuals that survive at the end of the year
 ask patches with [g = 1 / ticks and sp > 80 and sp < 130 and length (filter [? = sp] [sp] of patches in-radius 1.9) = 9] [ask patches in-radius 1.9 [set sp (sp - 35) / 10] set g -1 / ticks set a 0] ; assign the value -1/time step to the central patches variable of intermediate infaunal individuals that grew and were not overgrown and set their age to 1 year
 set m (patch-set m patches with [g = -1 / ticks]) ; add the central patches of intermediate infaunal individuals that grew and were not overgrown to the respective patch set
 ask patches with [g = 2 * ticks] [ask patches in-radius 2.9 [set sp (sp - 35) / 10] set a 0] ; set the age of newly settled large infaunal individuals that grew to 1 year and
 set l (patch-set l patches with [g = 2 * ticks]) ; add them to the respective patch set
 ask patches with [sp > 11] [set sp 35] ; clear the infaunal group occupation variable of patches occupied by newly settled infaunal individuals that did not grow or were overgrown
 ask s with [sp = 1 and a > 0] [set sp 35] ; clear the infaunal group occupation variable of patches occupied by small infaunal individuals that reached their lifespan
 ask s with [sp = 2 and a > 8] [set sp 35]
 ask s with [sp = 3 and a > 0] [set sp 35]
 ask s with [sp = 4 and a > 0] [set sp 35]
 ask m with [sp = 5 and a > 2] [ask patches in-radius 1.9 [set sp 35]] ; clear the infaunal group occupation variable of patches occupied by intermediate infaunal individuals that reached their lifespan
 ask m with [sp = 6 and a > 13] [ask patches in-radius 1.9 [set sp 35]]
 ask m with [sp = 7 and a > 1] [ask patches in-radius 1.9 [set sp 35]]
 ask m with [sp = 8 and a > 7] [ask patches in-radius 1.9 [set sp 35]]

 ask patches with [ep > 160 and ep < 200] [set ep (ep - 35) / 10 set ag 0] ; set the age of newly settled small epifaunal individuals that were not overgrown to 1 year
 ask sm with [ep = 13 and ag > 0] [set ep 0] ; clear the epifaunal group occupation variable of patches occupied by small epifaunal individuals that reached their lifespan
 ask sm with [ep = 14 and ag > 0] [set ep 0]
 ask sm with [ep = 15 and ag > 0] [set ep 0]
 ask sm with [ep = 16 and ag > 9] [set ep 0]
 ask m with [sp = 9 and a > 9] [ ; ask infaunal individuals of the basibiotic group that reached their lifespan
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    ifelse length (filter [? = 16] [ep] of patches in-radius 1.9) > 0 ; if they have any epibiotic individuals of the same group
    [set a max [ag] of patches in-radius 1.9 with [ep = 16] ask max-one-of patches in-radius 1.9 with [ep = 16] [ag] [set ep 0]] ; to take the age of the oldest one and remove
it from the epibionts
    [ask patches in-radius 1.9 [set sp 35 set ep 0]]] ; otherwise clear the infaunal and epifaunal group occupation variable of patches occupied by them
  set sm patches with [ep > 0 and ep < 17] ; add newly settled small epifaunal individuals that were not overgrown to the respective patch set
  ask la with [length (filter [? = ep] [ep] of patches in-radius 1.9) != 9] [ask patches in-radius 1.9 [set ep 0]] ; clear the epifaunal group occupation variable of patches
occupied by intermediate epifaunal individuals that are no more epibionts
  ask patches with [h = 2 * ticks and ep > 200] [ask patches in-radius 1.9 [set ep (ep - 35) / 10] set h -2 * ticks set ag 0] ; set the age of newly settled intermediate epifaunal
individuals that grew to 1 year and
  set la (patch-set la with [ep > 0] patches with [h = -2 * ticks]) ; add them to the respective patch set
  ask patches with [ep > 18] [set ep 0] ; clear the epifaunal group occupation variable of patches occupied by intermediate epifaunal individuals that did not grow
  ask la with [ep = 17 and ag > 8] [ask patches in-radius 1.9 [set ep 0]] ; clear the epifaunal group occupation variable of patches occupied by intermediate epifaunal
individuals that reached their lifespan
  ask la with [ep = 18 and ag > 10] [ask patches in-radius 1.9 [set ep 0]]
  set sm sm with [(ep = 13 and ag < 1) or (ep = 14 and ag < 1) or (ep = 15 and ag < 1) or (ep = 16 and ag < 10)] ; update the patch set of small epifaunal individuals
  set la la with [(ep = 17 and ag < 9) or (ep = 18 and ag < 11)] ; update the patch set of intermediate epifaunal individuals

  ask l with [sp = 10 and a > 2] [ask patches in-radius 2.9 [set sp 35]] ; clear the infaunal group occupation variable of patches occupied by large infaunal individuals that
reached their lifespan
  ask l with [sp = 11 and a > 1] [ask patches in-radius 2.9 [set sp 35]]
  let pr4 count s with [sp = 4] ; assign the abundances of prey groups to the potential prey variables
  let pr5 count m with [sp = 5]
  let pr7 count m with [sp = 7]
  let pr11 count l with [sp = 11]
  ifelse pr11 >= pr7 ; if larger prey was more or equally abundant to smaller prey
  [ask n-of min list p2 count l with [sp = 11 and a < 2] l with [sp = 11 and a < 2] [ask patches in-radius 2.9 [set sp 35]]] ; randomly remove as many larger prey individuals as
there were large predators
  [ask n-of min list max list 0 (p2 - count m with [sp = 7 and a < 2]) count l with [sp = 11 and a < 2] l with [sp = 11 and a < 2] [ask patches in-radius 2.9 [set sp 35]]] ;
otherwise randomly remove as many larger prey individuals as there were large predators minus the abundance of the smaller prey
  set l l with [(sp = 10 and a < 3) or (sp = 11 and a < 2)] ; update the patch set of large epifaunal individuals
  ifelse pr7 > pr11 ; if smaller prey was more abundant than larger prey
  [ask n-of min list p2 count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ; randomly remove as many smaller prey individuals
as there were large predators
  [ask n-of min list max list 0 (p2 - count l with [sp = 11 and a < 2]) count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ;
otherwise randomly remove as many smaller prey individuals as there were large predators minus the abundance of the larger prey
  ifelse pr5 >= pr4 ; if larger prey was more or equally abundant to smaller prey
  [ask n-of min list p3 count m with [sp = 5 and a < 3] m with [sp = 5 and a < 3] [ask patches in-radius 1.9 [set sp 35]]] ; randomly remove as many larger prey individuals as
there were intermediate predators
  [ask n-of min list max list 0 (p3 - count s with [sp = 4 and a < 1]) count m with [sp = 5 and a < 3] m with [sp = 5 and a < 3] [ask patches in-radius 1.9 [set sp 35]]] ;
otherwise randomly remove as many larger prey individuals as there were intermediate predators minus the abundance of the smaller prey
  ifelse pr7 >= pr4 ; if larger prey was more or equally abundant to smaller prey
  [ask n-of min list p1 count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ; randomly remove as many larger prey individuals as
there were small predators
  [ask n-of min list max list 0 (p1 - count s with [sp = 4 and a < 1]) count m with [sp = 7 and a < 2] m with [sp = 7 and a < 2] [ask patches in-radius 1.9 [set sp 35]]] ;
otherwise randomly remove as many larger prey individuals as there were small predators minus the abundance of the smaller prey
  set m m with [(sp = 5 and a < 3) or (sp = 6 and a < 14) or (sp = 7 and a < 2) or (sp = 8 and a < 8) or (sp = 9 and a < 10)] ; update the patch set of intermediate epifaunal
individuals
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  ifelse pr4 > pr5 ; if smaller prey was more abundant than larger prey
  [ask n-of min list p3 count s with [sp = 4] s with [sp = 4] [set sp 35]] ; randomly remove as many smaller prey individuals as there were intermediate predators
  [ask n-of min list max list 0 (p3 - count m with [sp = 5]) count s with [sp = 4] s with [sp = 4] [set sp 35]] ; otherwise randomly remove as many smaller prey individuals as
there were small predators minus the abundance of the larger prey
  ifelse pr4 > pr7 ; if smaller prey was more abundant than larger prey
  [ask n-of min list p1 count s with [sp = 4] s with [sp = 4] [set sp 35]] ; randomly remove as many smaller prey individuals as there were small predators
  [ask n-of min list max list 0 (p1 - count m with [sp = 7]) count s with [sp = 4] s with [sp = 4] [set sp 35]] ; otherwise randomly remove as many smaller prey individuals as
there were small predators minus the abundance of the larger prey
  set s s with [(sp = 1 and a < 1) or (sp = 2 and a < 9) or (sp = 3 and a < 1) or (sp = 4 and a < 1)] ; update the patch set of small epifaunal individuals
  set g1 count patches with [ sp = 1 ] ; give the small infaunal groups abundance variables values equal to the number of patches occupied by each group
  set g2 count patches with [ sp = 2 ]
  set g3 count patches with [ sp = 3 ]
  set g4 count patches with [ sp = 4 ]
  set g5 count patches with [ sp = 5 ] / 9 ; give the intermediate infaunal groups abundance variables values equal to the number of patches occupied by each group divided
by the individually occupied number of patches
  set g6 count patches with [ sp = 6 ] / 9
  set g7 count patches with [ sp = 7 ] / 9
  set g8 count patches with [ sp = 8 ] / 9
  set g9 count patches with [ sp = 9 ] / 9
  set ba g9 ; give the infaunal basibionts abundance variable a value equal to the infaunal abundance of the basibiotic group
  set g10 count patches with [ sp = 10 ] / 25 ; give the large infaunal groups abundance variables values equal to the number of patches occupied by each group divided by
the individually occupied number of patches
  set g11 count patches with [ sp = 11 ] / 25
  set p1 round ((max list g4 g7) / 10) ; give the predatory groups abundance variables values equal to those of the most abundant of their prey groups divided by 10
  set p3 round ((max list g4 g5) / 10)
  set p2 round ((max list g7 g11) / 10)
  set p4 round ((max list p1 p3) / 10)
  set es (g8 + g10) ; give the sediment stabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large sessile stabilizers that
tolerate tidal exposure
  set ed (g7 + g11) ; give the sediment destabilizing groups abundance variable a value equal to the sum of the abundances of intermediate and large destabilizers that
tolerate tidal exposure
  ask patches [set pcolor sp] ; color patches according to their infaunal group occupation variable

  set g12 count patches with [ ep = 13 ] ; give the small epifaunal groups abundance variables values equal to the number of patches occupied by each group
  set g13 count patches with [ ep = 14 ]
  set g14 count patches with [ ep = 15 ]
  set g9 g9 + count patches with [ ep = 16 ] ; give the basibiotic group abundance variable a value equal to the sum of the abundances of the infaunal and epifaunal
individuals of the group
  set g15 count patches with [ ep = 17 ] / 9 ; give the intermediate epifaunal groups abundance variables values equal to the number of patches occupied by each group
divided by the individually occupied number of patches
  set g16 count patches with [ ep = 18 ] / 9
  ask patches with [ ep > 0 ] [ set pcolor ep ] ; color patches occupied by epifaunal individuals according to their epifaunal group occupation variable

  output-type "g " output-type g1 output-type " " output-type g2 output-type " " output-type g3 output-type " " output-type g4 output-type " " output-type g5 output-type " "
output-type g6 output-type " " output-type g7 output-type " " output-type g8 output-type " " output-type g9 output-type " " output-type g10 output-type " " output-type g11
output-type " " output-type g12 output-type " " output-type g13 output-type " " output-type g14 output-type " " output-type g15 output-type " " output-type g16 output-
type " " output-type p1 output-type " " output-type p2 output-type " " output-type p3 output-type " " output-print p4 ; print out the values of infaunal/epifaunal and
```

```
predatory groups abundance
 set n length filter [? > 0] (list g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 p1 p2 p3 p4) ; give the variable of number of functional groups in the system a value equal to the number of groups with abundances larger than 0
end
```

C.3 Large-scale model

```
extensions [ ls gis ] ; load LevelSpace (ls) and GIS (gis) extensions

globals [ Rance ] ; define Rance GIS dataset

patches-own [ sediment sys sp p1 p2 p3 p4 g1 g2 g3 g4 g5 g6 g7 g8 g9 g10 g11 g12 g13 g14 g15 g16 fg1 fg2 fg3 fg4 fg5 fg6 fg7 fg8 fg9 fg10 fg11 fg12 fg13 fg14 fg15 fg16 ba ] ; define patch variables of sediment type (sediment), tidal zone (sys), number of functional groups (sp), abundances of 4 predatory groups (p1-p4), abundances of 16 infaunal/epifaunal groups (g1-g16), interim abundances of 16 infaunal/epifaunal groups (fg1-fg16), abundance of infaunal individuals of basibiotic group (ba)

to setup ; initialize the model
 ca ; clear all model entities and output
 ls:reset ; close down all child models
 set Rance gis:load-dataset <give path and name of ".shp" file> ; load Rance GIS dataset
 gis:apply-coverage Rance "LEG_ORIG" sediment ; copy sediment values from Rance GIS dataset to patch variable of sediment type
 display-sediment ; color Rance patches according to their sediment type
 display-system ; assign Rance patches to the subtidal or intertidal zone and color them accordingly
 ls:load-gui-model <give path and name of ".nlogo" file for the subtidal small-scale nodel> ; load subtidal IBM
 ask patches with [ sys = 1 ] [ ; ask patches of the subtidal zone to
  let pxy (word pxcor "-" pycor) ; take a name according to their x-y coordinates
  ls:ask 0 "setup" ; ask the subtidal IBM to initialize
  (ls:ask 0 "set xy ?" pxy) ; ask the subtidal IBM to take their name
  ls:ask 0 "export" ; ask the subtidal IBM to export all entities and output to an external file with this name
   ifelse "es" ls:of 0 > "ed" ls:of 0 ; take a color according to the dominance in the subtidal IBM of
   [ set pcolor cyan ] ; sediment stabilizers
   [ set pcolor pink ] ; or destabilizers
  set g1 "g1" ls:of 0 ; give the variables of group abundances and number of functional groups the values of the respective variables of the subtidal IBM
  set g2 "g2" ls:of 0
  set g3 "g3" ls:of 0
  set g4 "g4" ls:of 0
  set g5 "g5" ls:of 0
  set g6 "g6" ls:of 0
  set g7 "g7" ls:of 0
  set g8 "g8" ls:of 0
  set g9 "g9" ls:of 0
  set ba "ba" ls:of 0
  set g10 "g10" ls:of 0
  set g11 "g11" ls:of 0
  set g12 "g12" ls:of 0
```

```
    set g13 "g13" ls:of 0
    set g14 "g14" ls:of 0
    set g15 "g15" ls:of 0
    set g16 "g16" ls:of 0
    set p1 "p1" ls:of 0
    set p2 "p2" ls:of 0
    set p3 "p3" ls:of 0
    set p4 "p4" ls:of 0
    set sp "n" ls:of 0
    output-type sys output-type " " output-type pxcor output-type " " output-type pycor output-type " " output-type g1 output-type " " output-type g2 output-type " " output-type g3 output-type " " output-type g4 output-type " " output-type g5 output-type " " output-type g6 output-type " " output-type g7 output-type " " output-type g8 output-type " " output-type g9 output-type " " output-type g10 output-type " " output-type g11 output-type " " output-type g12 output-type " " output-type g13 output-type " " output-type g14 output-type " " output-type g15 output-type " " output-type g16 output-type " " output-type p1 output-type " " output-type p2 output-type " " output-type p3 output-type " " output-type p4 output-type " " output-print ba ; print out the values of tidal zone, x-y coordinates and group abundances variables
  ]
  ls:load-gui-model <give path and name of ".nlogo" file for the intertidal small-scale nodel> ; load intertidal IBM
  ask patches with [ sys = 2 ] [ ; ask patches of the intertidal zone to
    let pxy (word pxcor "-" pycor) ; take a name according to their x-y coordinates
    ls:ask 1 "setup" ; ask the intertidal IBM to initialize
    (ls:ask 1 "set xy ?" pxy) ; ask the intertidal IBM to take their name
    ls:ask 1 "export" ; ask the intertidal IBM to export all entities and output to an external file with this name
      ifelse "es" ls:of 1 > "ed" ls:of 1 ; take a color according to the dominance in the intertidal IBM of
      [ set pcolor sky ] ; sediment stabilizers
      [ set pcolor magenta ] ; or destabilizers
    set g1 "g1" ls:of 1 ; give the variables of group abundances and number of functional groups the values of the respective variables of the intertidal IBM
    set g2 "g2" ls:of 1
    set g3 "g3" ls:of 1
    set g4 "g4" ls:of 1
    set g5 "g5" ls:of 1
    set g6 "g6" ls:of 1
    set g7 "g7" ls:of 1
    set g8 "g8" ls:of 1
    set g9 "g9" ls:of 1
    set ba "ba" ls:of 1
    set g10 "g10" ls:of 1
    set g11 "g11" ls:of 1
    set g12 "g12" ls:of 1
    set g13 "g13" ls:of 1
    set g14 "g14" ls:of 1
    set g15 "g15" ls:of 1
    set g16 "g16" ls:of 1
    set p1 "p1" ls:of 1
    set p2 "p2" ls:of 1
    set p3 "p3" ls:of 1
    set p4 "p4" ls:of 1
    set sp "n" ls:of 1
    output-type sys output-type " " output-type pxcor output-type " " output-type pycor output-type " " output-type g1 output-type " " output-type g2 output-type " " output-
```

```
type g3 output-type " " output-type g4 output-type " " output-type g5 output-type " " output-type g6 output-type " " output-type g7 output-type " " output-type g8 output-type " " output-type g9 output-type " " output-type g10 output-type " " output-type g11 output-type " " output-type g12 output-type " " output-type g13 output-type " " output-type g14 output-type " " output-type g15 output-type " " output-type g16 output-type " " output-type p1 output-type " " output-type p2 output-type " " output-type p3 output-type " " output-type p4 output-type " " output-print ba ; print out the values of tidal zone, x-y coordinates and group abundances variables
  ]
  reset-ticks ; set tick counter to zero, set up and update all plots
end

to go ; move the model one step forward
  set-current-plot "Subtidal functional group abundance" ; clear the plot of subtidal groups abundances
  clear-plot
  set-current-plot "Intertidal functional group abundance" ; clear the plot of intertidal groups abundances
  clear-plot
  tick ; advance the tick counter by one and update all plots
  if ticks > 9 [ stop ] ; stop the model after initialization plus 9 time steps
  ask patches with [ sys = 1 ] [ ; ask patches of the subtidal zone to
    let pxy (word pxcor "-" pycor) ; take a name according to their x-y coordinates
    let f1 median [g1] of patches in-radius 1.9 with [ pcolor > 0 ] ; define the infaunal/epifaunal groups contribution to the respective IBM spawner pool as the median abundance of each group within the patch and its eight immediate neighbors that are part of the system
    let f2 median [g2] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f3 median [g3] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f4 median [g4] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f5 median [g5] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f6 median [g6] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f7 median [g7] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f8 median [g8] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f9 median [g9] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f10 median [g10] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f11 median [g11] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f12 median [g12] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f13 median [g13] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f14 median [g14] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f15 median [g15] of patches in-radius 1.9 with [ pcolor > 0 ]
    let f16 median [g16] of patches in-radius 1.9 with [ pcolor > 0 ]
    (ls:ask 0 "set xy ?" pxy) ; ask the subtidal IBM to take their name
    ls:ask 0 "import" ; ask the subtidal IBM to import all entities and output from an external file with this name
    (ls:ask 0 "set fg1 ?1 set fg2 ?2 set fg3 ?3 set fg4 ?4 set fg5 ?5 set fg6 ?6 set fg7 ?7 set fg8 ?8 set fg9 ?9 set fg10 ?10 set fg11 ?11 set fg12 ?12 set fg13 ?13 set fg14 ?14 set fg15 ?15 set fg16 ?16" f1 f2 f3 f4 f5 f6 f7 f8 f9 f10 f11 f12 f13 f14 f15 f16) ; give the values of the variables of the infaunal/epifaunal groups contribution to the respective spawner pool to the respective variables of the subtidal IBM
    ls:ask 0 "go" ; ask the subtidal IBM to move one step forward
    ls:ask 0 "export" ; ask the subtidal IBM to export all entities and output to an external file with this name
    ifelse "es" ls:of 0 > "ed" ls:of 0 ; take a color according to the dominance in the subtidal IBM of
      [ set pcolor yellow ] ; sediment stabilizers
      [ set pcolor red ] ; or destabilizers
    set sp "n" ls:of 0 ; give the variables of number of functional groups and interim infaunal/epifaunal and predatory group abundances the values of the respective variables of the subtidal IBM
    set fg1 "g1" ls:of 0
```

```
    set fg2 "g2" ls:of 0
    set fg3 "g3" ls:of 0
    set fg4 "g4" ls:of 0
    set fg5 "g5" ls:of 0
    set fg6 "g6" ls:of 0
    set fg7 "g7" ls:of 0
    set fg8 "g8" ls:of 0
    set fg9 "g9" ls:of 0
    set fg10 "g10" ls:of 0
    set fg11 "g11" ls:of 0
    set fg12 "g12" ls:of 0
    set fg13 "g13" ls:of 0
    set fg14 "g14" ls:of 0
    set fg15 "g15" ls:of 0
    set fg16 "g16" ls:of 0
    set p1 "p1" ls:of 0
    set p2 "p2" ls:of 0
    set p3 "p3" ls:of 0
    set p4 "p4" ls:of 0
    output-type sys output-type " " output-type pxcor output-type " " output-type pycor output-type " " output-type fg1 output-type " " output-type fg2 output-type " " output-type fg3 output-type " " output-type fg4 output-type " " output-type fg5 output-type " " output-type fg6 output-type " " output-type fg7 output-type " " output-type fg8 output-type " " output-type fg9 output-type " " output-type fg10 output-type " " output-type fg11 output-type " " output-type fg12 output-type " " output-type fg13 output-type " " output-type fg14 output-type " " output-type fg15 output-type " " output-type fg16 output-type " " output-type p1 output-type " " output-type p2 output-type " " output-type p3 output-type " " output-type p4 output-type " " output-print ba ; print out the values of tidal zone, x-y coordinates and group abundances variables
  ]
  ask patches with [ sys = 1 ] [ ; ask patches of the subtidal zone to give the infaunal/epifaunal group abundances variables the values of the interim infaunal/epifaunal group abundances variables
    set g1 fg1
    set g2 fg2
    set g3 fg3
    set g4 fg4
    set g5 fg5
    set g6 fg6
    set g7 fg7
    set g8 fg8
    set g9 fg9
    set g10 fg10
    set g11 fg11
    set g12 fg12
    set g13 fg13
    set g14 fg14
    set g15 fg15
    set g16 fg16
]
  ask patches with [ sys = 2 ] [ ; ask patches of the intertidal zone to
    let pxy (word pxcor "-" pycor) ; take a name according to their x-y coordinates
    let f1 median [g1] of patches in-radius 1.9 with [ pcolor > 0 ] ; define the infaunal/epifaunal groups contribution to the respective IBM spawner pool as the median
```

```
abundance of each group within the patch and its eight immediate neighbors that are part of the system
  let f2 median [g2] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f3 median [g3] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f4 median [g4] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f5 median [g5] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f6 median [g6] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f7 median [g7] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f8 median [g8] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f9 median [g9] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f10 median [g10] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f11 median [g11] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f12 median [g12] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f13 median [g13] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f14 median [g14] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f15 median [g15] of patches in-radius 1.9 with [ pcolor > 0 ]
  let f16 median [g16] of patches in-radius 1.9 with [ pcolor > 0 ]
  (ls:ask 1 "set xy ?" pxy) ; ask the intertidal IBM to take their name
  ls:ask 1 "import" ; ask the intertidal IBM to import all entities and output from an external file with this name
  (ls:ask 1 "set fg1 ?1 set fg2 ?2 set fg3 ?3 set fg4 ?4 set fg5 ?5 set fg6 ?6 set fg7 ?7 set fg8 ?8 set fg9 ?9 set fg10 ?10 set fg11 ?11 set fg12 ?12 set fg13 ?13 set fg14 ?14
set fg15 ?15 set fg16 ?16" f1 f2 f3 f4 f5 f6 f7 f8 f9 f10 f11 f12 f13 f14 f15 f16) ; give the values of the variables of the infaunal/epifaunal groups contribution to the
respective spawner pool to the respective variables of the intertidal IBM
  ls:ask 1 "go" ; ask the intertidal IBM to move one step forward
  ls:ask 1 "export" ; ask the intertidal IBM to export all entities and output to an external file with this name
  ifelse "es" ls:of 1 > "ed" ls:of 1 ; take a color according to the dominance in the intertidal IBM of
   [ set pcolor green ] ; sediment stabilizers
   [ set pcolor orange ] ; or destabilizers
  set sp "n" ls:of 1 ; give the variables of number of functional groups and interim infaunal/epifaunal and predatory group abundances the values of the respective variables
of the intertidal IBM
  set fg1 "g1" ls:of 1
  set fg2 "g2" ls:of 1
  set fg3 "g3" ls:of 1
  set fg4 "g4" ls:of 1
  set fg5 "g5" ls:of 1
  set fg6 "g6" ls:of 1
  set fg7 "g7" ls:of 1
  set fg8 "g8" ls:of 1
  set fg9 "g9" ls:of 1
  set fg10 "g10" ls:of 1
  set fg11 "g11" ls:of 1
  set fg12 "g12" ls:of 1
  set fg13 "g13" ls:of 1
  set fg14 "g14" ls:of 1
  set fg15 "g15" ls:of 1
  set fg16 "g16" ls:of 1
  set p1 "p1" ls:of 1
  set p2 "p2" ls:of 1
  set p3 "p3" ls:of 1
```

```
    set p4 "p4" ls:of 1
    output-type sys output-type " " output-type pxcor output-type " " output-type pycor output-type " " output-type fg1 output-type " " output-type fg2 output-type " "
output-type fg3 output-type " " output-type fg4 output-type " " output-type fg5 output-type " " output-type fg6 output-type " " output-type fg7 output-type " " output-type
fg8 output-type " " output-type fg9 output-type " " output-type fg10 output-type " " output-type fg11 output-type " " output-type fg12 output-type " " output-type fg13
output-type " " output-type fg14 output-type " " output-type fg15 output-type " " output-type fg16 output-type " " output-type p1 output-type " " output-type p2 output-
type " " output-type p3 output-type " " output-type p4 output-type " " output-print ba ; print out the values of tidal zone, x-y coordinates and group abundances variables
  ]
  ask patches with [ sys = 2 ] [ ; ask patches of the intertidal zone to give the infaunal/epifaunal group abundances variables the values of the interim infaunal/epifaunal
group abundances variables
    set g1 fg1
    set g2 fg2
    set g3 fg3
    set g4 fg4
    set g5 fg5
    set g6 fg6
    set g7 fg7
    set g8 fg8
    set g9 fg9
    set g10 fg10
    set g11 fg11
    set g12 fg12
    set g13 fg13
    set g14 fg14
    set g15 fg15
    set g16 fg16
]
end

to display-sediment ; color Rance patches according to their sediment type and all other patches black
ask patches
  [ ifelse ( is-string? sediment )
    [ set pcolor read-from-string sediment ]
    [ set pcolor black ] ]
end

to display-system ; assign Rance patches to one of two tidal zones according to their sediment type, subtidal (gravel, coarse sand, intermediate/coarse sand,
fine/intermediate sand, muddy sand, sandy mud) or intertidal (silty mud, mud, pure mud, salt marshes) and color them accordingly
  ask patches with [pcolor > 10 and pcolor < 90] [set pcolor 15 set sys 1]
  ask patches with [pcolor > 90 and pcolor < 140] [set pcolor 45 set sys 2]
end
```

Modélisations des mécanismes généraux d'assemblage des communautés pour simuler la dynamique spatio-temporelle de la biodiversité benthique

Résumé

Les macroinvertébrés benthiques entretiennent un ensemble complexe d'interactions. Les échelles spatiales et temporelles des processus formant la base de ces interactions ont traditionnellement limité leur étude empirique. Le premier chapitre du manuscrit tente une revue des outils de modélisation utilisés dans l'étude du benthos marin.

Même si l'implémentation d'un modèle mécaniste semble s'ajuster aux communautés benthiques, son utilisation nécessite la création d'un nombre limité d'entités avec un rôle fonctionnel clair. Le second chapitre du manuscrit utilise l'hypothèse des groupes émergents, afin de faire cela via une procédure objective et testable. Le groupement est testé face aux postulats théoriques et les résultats supportent sa capacité à reproduire la diversité fonctionnelle dans l'estuaire de la Rance.

Le manque de connaissances dans l'attribution des relations entre les composantes fonctionnelles reste important. Le troisième chapitre du manuscrit s'inscrit dans ce besoin, basé sur des théories écologiques qui prévoient l'existence de trade-offs fonctionnels opérant à grande et petite échelle. Dans un premier temps, ces éléments sont incorporées dans des modèles qualitatifs des groupes fonctionnels.

Malgré l'intérêt du développement et de l'analyse de modèles qualitatifs, le but d'étudier la dynamique et le comportement spatialement explicite de la biodiversité ne peut être atteint que par un modèle avec ces mêmes caractéristiques. Le quatrième chapitre du manuscrit présente l'architecture d'un modèle individu-centré, en mettant l'accent sur le transfert des règles d'interactions des modèles qualitatifs vers un cadre dynamique et spatialement explicite.

Mots-clés: assemblage des communautés, estuaire de la Rance, groupes fonctionnels, macrofaune benthique, modélisation de la biodiversité, modélisation orientée agent, modélisation qualitative, trade-offs fonctionnels, traits biologiques

Models of general community assembly mechanisms simulating the spatial and temporal dynamics of benthic biodiversity

Abstract

Benthic macroinvertebrates are part of a complex network of interactions. The spatial and temporal scales of the processes that form the basis for these interactions have traditionally restricted their empirical investigation. The first chapter of the manuscript attempts a review of the modelling tools that have been employed for the study of the marine benthos.

The implementation of a mechanistic modelling framework seems fitting, but it requires the derivation of a few model entities with a clear functional role. The second chapter of the manuscript employs the emergent group hypothesis to do that in a way that is objective and testable. The resulting grouping is tested against theoretical expectations and the results support its ability to represent functional diversity in the Rance estuary.

The lack of knowledge for the attribution of relationships among functional components is still important. The third chapter of the manuscript addresses this issue based on ecological theories that predict the existence of functional trade-offs operating at both large and small spatial scales. In a first inception of the system, these elements are incorporated in the form of general rules of interaction into qualitative models of the functional groups.

In spite of the interest in developing and analysing qualitative models, the goal of studying the dynamic and spatially explicit behaviour of benthic biodiversity can only be reached by a model with the same characteristics. The fourth chapter of the manuscript presents the architecture of an individual-based model, primarily transferring the rules of interaction from the qualitative models to a dynamic and spatially explicit framework.

Key-words: agent-based modelling, benthic macrofauna, biodiversity model, biological traits, community assembly, functional groups, functional trade-offs, qualitative modelling, Rance estuary