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## Qualitative modelling of functional relationships in marine benthic communities

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### Abstract :

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

### Highlights

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

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

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

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

61 The development of mechanistic models of biodiversity can be considered to be  
62 subject to two main conditions. First, the functional components of biodiversity need  
63 to be defined through rigorous and testable procedures (Petchey and Gaston, 2006).  
64 Next, a mechanistic description of the way these components interact with their  
65 environment and among themselves is necessary. These issues have traditionally  
66 been addressed in the context of food web modelling. Organisms are typically  
67 separated into groups according to their food sources, and interactions among them  
68 are assumed to represent their trophic behaviour (Yodzis and Innes, 1992). In lack of  
69 empirical information to help formulate these models, various methods have been  
70 developed for the construction of food webs, based on principles of community (e.g.,  
71 Cohen and Newman, 1985; Williams and Martinez, 2000; Cattin et al., 2004) or  
72 ecosystem ecology (e.g., Fath, 2004; Morris et al., 2005; Halnes et al., 2007). Still, a  
73 disproportionate focus on trophic interactions has restricted the scope of most  
74 modelling efforts (but see Kéfi et al. (2012)).

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

89 Quite independent of mechanistic modelling, an increased interest in the  
90 functioning of marine benthic communities has led to the compilation of large data  
91 bases of species traits. At the same time, theoretical and expert knowledge about  
92 potential trait associations is being continuously generated. Particularly lacking is a  
93 systematic procedure for the assignment of functional groupings and inter-group  
94 relationships on the basis of such readily available information. Recent work in the  
95 terrestrial environment led to the development of a trait-based method for the  
96 construction of functional groups for models of plant diversity (Boulangeat et al.,  
97 2012). The conceptual and methodological framework was provided by the emergent  
98 group hypothesis, which assumes functional equivalence within and functional  
99 divergence among emergent groups of species (Hérault, 2007). The adaptation of

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239 100 this framework to the benthic macroinvertebrate communities of the Rance estuary  
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241 101 (Brittany, France) can provide the functional components for a mechanistic  
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243 102 representation of the system (Alexandridis et al., 2017). Here we implement these  
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245 103 components in a demonstration of a systematic procedure for the assignment of  
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247 104 functional relationships between them. In a first conception of the system, we are  
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249 105 restricted to the qualitative nature of the relationships.

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252 106 The objective of our study is to use mechanistic models of benthic macrofauna,  
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254 107 in order to assess the role of different processes in shaping biodiversity patterns in  
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256 108 the Rance estuary. To this end, we represented benthic macroinvertebrate  
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258 109 communities through signed-directed graph (or signed digraph) models. The  
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260 110 previously defined groups of species comprised the functional components of the  
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262 111 system and were assigned to sub-systems based on rules of environmental filtering.  
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264 112 In each of these sub-systems, groups were linked by functional relationships that  
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266 113 were largely derived from ecological theory and expert knowledge regarding general  
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268 114 community assembly mechanisms. This procedure was dictated by each group's  
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270 115 assigned trait values and representative species. The stability analysis of the signed  
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272 116 digraphs demonstrated the potential of the respective systems to persist in time and,  
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274 117 therefore, to constitute a plausible representation of the natural world. The structure  
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276 118 of the models gave some insight into the role of different community assembly  
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278 119 mechanisms, as well as the direction of the system's response to potential  
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280 120 perturbations. This work serves as a first step toward quantitative mechanistic models  
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282 121 that will be able to reproduce the spatial and temporal dynamics of benthic  
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284 122 biodiversity in the Rance estuary (Alexandridis, 2017).

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125 Methods

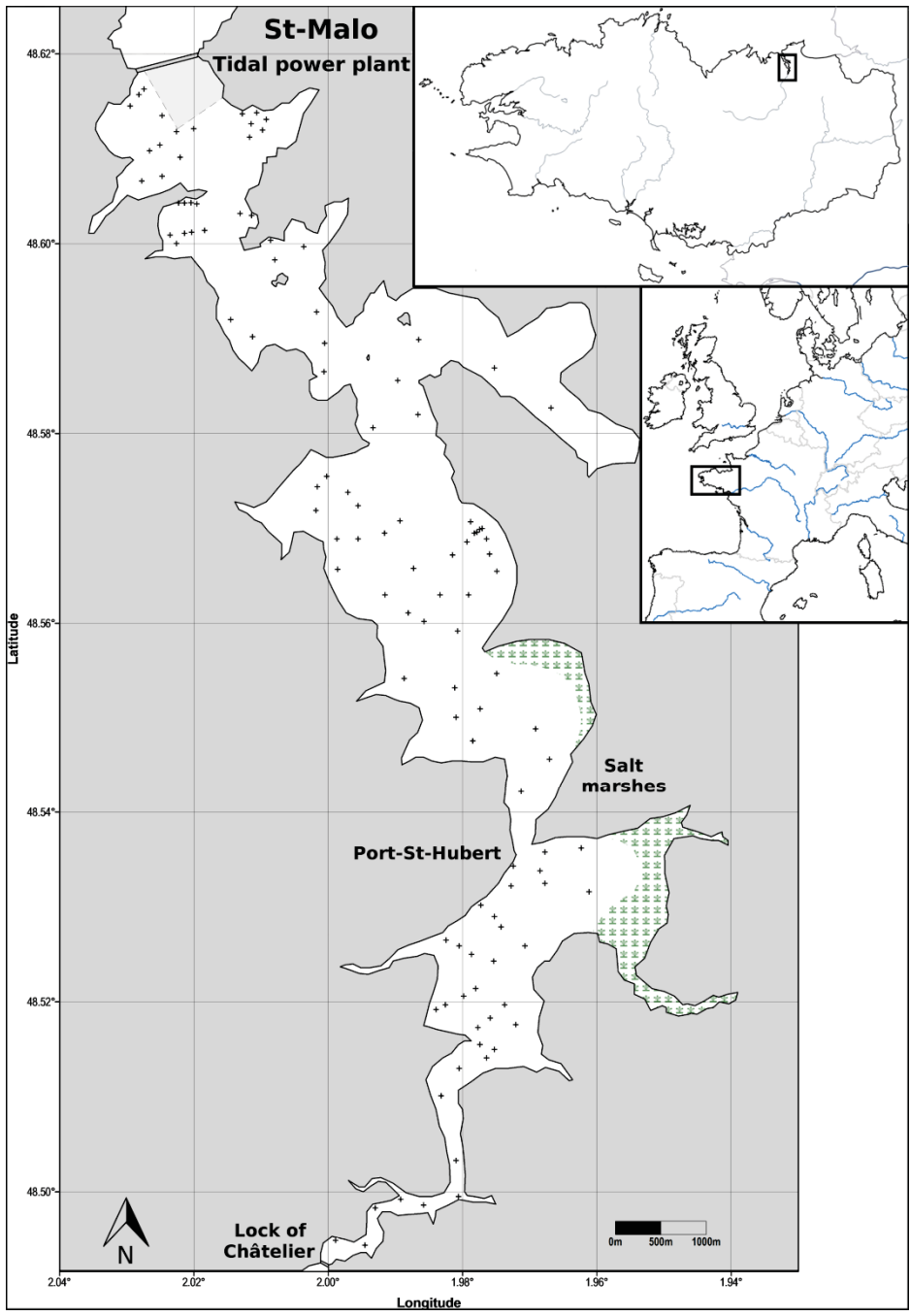
126 2.1

127 Study site

128 The Rance estuary (Brittany, France) is situated in the southern part of the  
129 English Channel (Fig. 1). The site is characterized by the presence of a tidal power  
130 plant at its mouth. The operating constraints of the installation have reduced the tidal  
131 range in the estuary compared to the open sea. The intertidal zone has shifted from  
132 70% of the total surface of the estuary before the construction of the power plant, to  
133 50% after. Maximum water depth is 17 m at low tide, but the main part of the basin is  
134 5-6 m deep. The sluice and turbine currents from the power plant have eroded parts  
135 of the riverbed. Sandbanks closest to the dam have shifted and the bed is  
136 predominantly covered with gravel or pebbles (Retière, 1994). At the same time, long  
137 periods of slack water have promoted the deposition of fine particles in coves and  
138 bays (Bonnot-Courtois and Lafond, 1991). From downstream to upstream of the  
139 estuary, pebbles and coarse sands are replaced by medium and fine sands, muddy  
140 sands and finally muds upstream of Port-St-Hubert. A similar sequence is observable  
141 from the central channel of the estuary to its banks.

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

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

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155 2.2

156 Functional groups



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416 157 For the representation of the primary functional components of benthic  
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418 158 macroinvertebrate communities in the Rance estuary, we employed 20 functional  
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420 159 groups, previously built on the basis of biological trait information for the 240 species  
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422 160 of the system in 1995 (Alexandridis et al., 2017). The collected abundance data set  
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424 161 allowed each of the groups to be assigned with a representative species along with a  
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426 162 value for each of the 14 biological traits (Table 1). The traits are expected to describe  
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428 163 the role of benthic algae/detritus feeders and predators/scavengers in 7 important  
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430 164 community assembly mechanisms (Table 2). The list of mechanisms was mostly  
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432 165 adopted from the framework developed by Boulangeat et al. (2012) for dynamic  
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434 166 models of terrestrial vegetation. A few adjustments were made to the original  
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436 167 framework, in order to adapt it to marine benthic systems (Alexandridis et al., 2017).  
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169 Table 1. Functional groups with their assigned representative species and biological trait values (Alexandridis et al., 2017). For  
 170 details about the biological traits, see Table 2. Group names starting with 'H' correspond to groups of algae/detritus feeders and  
 171 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	<i>Morchellium argus</i>	eurythermal	brooded	short	low	stenohaline	rock	3.3	0.1	epifauna	sessile	2.6	1.7	epibiont	neutral
H2	<i>Lepidochitona cinerea</i>	stenothermal	planktonic	short	high	stenohaline	rock	10.8	4.1	epifauna	mobile	0.9	11.6	epibiont	neutral
H3	<i>Balanus crenatus</i>	eurythermal	planktonic	long	high	euryhaline	rock	2.0	0.8	epifauna	sessile	2.5	2.0	epibiont	neutral
H4	<i>Crepidula fornicata</i>	stenothermal	planktonic	long	high	stenohaline	rock	7.6	0.0	epifauna	sessile	1.9	11.2	basibiont	neutral
H5	<i>Oligochaeta</i>	stenothermal	laid	short	low	emersed	muddy sand	4.5	5.0	infauna	mobile	3.4	2.0	neutral	destabilizer
H6	<i>Thyasira flexuosa</i>	eurythermal	planktonic	short	low	stenohaline	mud	3.6	0.8	infauna	mobile	1.0	10.0	neutral	stabilizer
H7	<i>Melinna palmata</i>	stenothermal	brooded	short	low	stenohaline	mud	7.5	0.3	interface	sessile	2.6	3.6	neutral	stabilizer
H8	<i>Notomastus latericeus</i>	stenothermal	brooded	short	low	stenohaline	muddy sand	6.0	2.9	interface	mobile	2.6	1.9	neutral	destabilizer
H9	<i>Hediste diversicolor</i>	eurythermal	laid	short	high	emersed	muddy sand	12.8	0.2	interface	mobile	2.1	3.4	neutral	destabilizer
H10	<i>Malacoceros fuliginosus</i>	eurythermal	planktonic	long	high	euryhaline	mud	8.5	1.9	interface	mobile	2.5	2.7	neutral	destabilizer
H11	<i>Galathowenia oculata</i>	eurythermal	planktonic	long	high	euryhaline	mud	11.1	0.0	interface	sessile	2.7	4.4	neutral	stabilizer
H12	<i>Glycymeris glycymeris</i>	stenothermal	planktonic	short	high	stenohaline	muddy gravel	8.0	1.4	infauna	mobile	0.8	15.0	neutral	stabilizer
H13	<i>Anapagurus hyndmanni</i>	stenothermal	planktonic	long	high	stenohaline	gravel	10.0	0.1	epifauna	mobile	0.6	10.0	neutral	neutral
H14	<i>Cerastoderma edule</i>	stenothermal	planktonic	long	high	emersed	muddy sand	8.6	0.5	interface	mobile	0.7	8.9	neutral	stabilizer
C1	<i>Sphaerosyllis bulbosa</i>	stenothermal	brooded	short	low	stenohaline	gravel	1.3	0.5	epifauna	mobile	4.7	1.9	neutral	neutral
C2	<i>Marphysa bellii</i>	stenothermal	planktonic	short	high	stenohaline	muddy sand	23.3	0.3	interface	mobile	1.1	4.7	neutral	neutral
C3	<i>Nephtys hombergii</i>	stenothermal	planktonic	long	high	stenohaline	gravel	10.5	0.3	interface	mobile	2.2	7.3	neutral	neutral
C4	<i>Myrianida edwardsi</i>	stenothermal	planktonic	long	low	stenohaline	mud	1.4	3.1	interface	mobile	5.8	1.9	neutral	neutral
C5	<i>Urticina felina</i>	eurythermal	planktonic	short	high	euryhaline	rock	16.7	10.3	epifauna	sessile	1.1	14.0	epibiont	neutral
C6	<i>Syllis cornuta</i>	stenothermal	planktonic	long	low	stenohaline	rock	7.4	5.2	epifauna	mobile	2.3	2.3	epibiont	neutral

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

Mechanisms	Biological traits	Trait values	Comments
Resistance to perturbation	T1. low temperature tolerance	eurythermal/stenothermal	Species that can tolerate continued exposure to single-digit temperatures (eurythermal) were distinguished from those that cannot (stenothermal).
	T2. early development mode	planktonic/laid/brooded	Trait values should define a gradient of increasing ability to cope with perturbations during the early life stages, due to increasing investment in early offspring survival.
Dispersal potential	T3. larval dispersal distance	short/long	Species were separated in two groups based on their maximum observed dispersal distance, with a distance of 10 km used as the breaking point.
	T4. maximum fecundity	low/high	Species were separated in two groups, with the number of 1000 eggs produced by a female of each species per year used as the breaking point.
Environmental filtering	T5. tidal emersion/ low salinity tolerance	emersed/euryhaline/ stenohaline	Soft bottom species that can tolerate long tidal exposure should be able to tolerate low salinity (emersed). Immersed species either can tolerate salinities that differ greatly from those of the open sea (euryhaline) or cannot (stenohaline).
	T6. preferred substrate type	mud/muddy sand/ sand/muddy gravel/ gravel/rock	The assignment of one value to each species represented its greatest substrate affinity, but was often too restrictive.
Competitive effect	T7. maximum size	1 cm/2 cm/10 cm/20 cm/ 40 cm	Trait values should define a gradient of increasing area that can be searched for food or distance from the substrate, which should enhance food availability (McLean and Lasker, 2013).
	T8. minimum space requirement	0.003/0.1/49.5 (min./median/max.) Values are not absolute, but rather relative levels.	Species with the lowest trait value should compete best for space (Tilman, 1980). Trait values were derived from data on body mass (Robinson et al., 2010) and use of an exponent of $\frac{3}{4}$ from the metabolic theory of ecology (Jetz et al., 2004).
Response to competition	T9. preferred substrate position	infauna/interface/epifauna	Living deep in the sediment (infauna), at its upper layer (interface) or on its surface (epifauna) should allow species co-existence in spite of established competitive hierarchies.
	T10. adult mobility	mobile/sessile	Differences in the ability of species to move should lead to resource partitioning and avoidance of competition.
Population dynamics	T11. population growth rate	0.27/2.14/6.95 (min./median/max.) Values are not absolute, but rather relative levels.	Trait values were derived from data on body mass (Robinson et al., 2010) and use of an exponent of $-\frac{1}{4}$ 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.

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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.

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180 2.3

181 Signed digraphs

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

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

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

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### 207 2.3.1

#### 208 Environmental filtering

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

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### 220 2.3.2

#### 221 Consumption of algae/detritus

222 Algae/detritus feeders along with predators/scavengers with the smallest  
223 maximum size (T7) among all functional groups (groups C1 in SD1 and C4 in SD2)  
224 are assumed to consume the basic food resource, either from the water column or

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225 through deposit feeding. This interaction was represented by a negative effect on  
226 food and a positive effect on consumers (Fig. 2b, 3b). Group H2 in SD1 was excluded  
227 from the consumption of the basic food resource, because of the grazing behaviour of  
228 its representative species. The bulldozing effect of this behaviour, which is expected  
229 to deprive other organisms of the free use of space (Pascual, 1997), was represented  
230 by a consumption interaction with this resource.

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232 2.3.3

233 Predation

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

244 Predation was represented by a negative effect on prey and a positive effect on  
245 predators (Fig. 2c, 3c). The predator/scavenger group C5 in SD1 is represented by a  
246 sea anemone and its adult mobility (T10) is restricted, hence, only mobile functional  
247 groups were considered as its potential prey. Since all predator/scavenger groups are  
248 characterized as epifauna or interface-related (T9), infaunal functional groups (groups  
249 H5, H6 and H12 in SD2) along with groups whose representative species are

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752 250 protected by plates (groups H2 and H3 in SD1), shells (groups H4, H13 in SD1 and  
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754 251 H14 in SD2) or tubes (groups H7 and H11 in SD2) were excluded from predator–prey  
755  
756 252 interactions.  
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#### 760 254 2.3.4

#### 762 255 Use of space

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765 256 Just like food, space is assumed to be a basic resource that is “consumed” or  
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767 257 used by groups of algae/detritus feeders. Predators/scavengers (including sessile  
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769 258 group C5) are, instead, expected to only have their prey as their basic resource. In  
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771 259 addition to the aforementioned group H2, space in SD1 is also used by algae/detritus  
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773 260 feeders that are characterized as sessile (T10), since mobile organisms probably do  
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775 261 not have such a strong interaction with space.  
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778 262 In SD2, we expect the role of organisms in sediment engineering (T14) to play a  
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780 263 central role in their interaction with space, with sediment stabilizers being primarily  
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782 264 limited by it. Organisms are also assumed to partition space, by occupying different  
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784 265 positions with respect to the substrate (T9). Since the two-dimensional nature of the  
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786 266 interface renders space particularly limiting for organisms that occupy this position,  
787  
788 267 we set space as a resource only for stabilizing groups of the interface. The use of  
789  
790 268 space by these organisms was represented by a negative effect on space and a  
791  
792 269 positive effect on its consumers (Fig. 2d, 3d).  
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#### 796 271 2.3.5

#### 798 272 Food–space competition trade-off

800  
801 273 In order to better represent differences in the functional roles of benthic  
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803 274 organisms in a way that is consistent with the general trade-offs that are expected to  
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811 275 characterize these functional roles, we resorted again to the trait of maximum size  
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813 276 (T7). Higher levels of this trait are expected to confer a competitive advantage for  
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815 277 limited food resources, due to a larger area that can be searched for food or distance  
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817 278 from the substrate, which enhances the availability of food from the water column  
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819 279 (McLean and Lasker, 2013). On the other hand, maximum size (T7) appears to be  
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821 280 positively associated with the trait of minimum space requirement (T8) among benthic  
822  
823 281 macroinvertebrates of the Rance estuary (see section S2 in the Supplementary  
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825 282 Material). Higher values of the latter trait should confer a competitive disadvantage  
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827 283 for limited available space (Tilman 1980). We, thus, assumed that larger maximum  
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829 284 size (T7) represents a competitive advantage for food and disadvantage for space.  
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832 285       Based on this assumption, we divided the functional groups of each signed  
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834 286 digraph that consume the basic food resource in two categories, the small and the  
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836 287 big. We did so, by making sure that groups with similar sizes are placed in the same  
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838 288 category and that there are more small than large groups (Blackburn and Gaston,  
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840 289 1994). The members of each category are expected to be limited by the resource for  
841  
842 290 which they have a competitive disadvantage, while being able to efficiently reduce the  
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844 291 levels of the resource for which they are competitively superior. This set of  
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846 292 interactions was represented by an alteration of the existing resource consumption  
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848 293 interactions, so that a functional group receives a positive effect from its limiting  
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850 294 resource, while having a negative effect on the resource that it can efficiently reduce  
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852 295 (Fig. 2e, 3e). This rule was not applied to any groups that would otherwise appear not  
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854 296 to be limited by any of the basic resources, along with group H2 in SD1, whose  
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856 297 relationship with space represents its bulldozing effect on macroinvertebrate recruits.  
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860 299 2.3.6  
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### 300 Early survival–colonization trade-off

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

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

319

### 320 2.3.7

#### 321 Biogenic habitat modification

322 The organisms that are represented by SD1 are distinguished from the rest by  
323 their epifaunal position (T9) and requirement for hard substrate (T6) (see section S2  
324 in the Supplementary Material). Their occurrence in the Rance estuary can be at

927  
928  
929 325 least partly attributed to the phenomenon of epibiosis (T13), regardless of the  
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931 326 basibiotic organisms being alive or not (Wahl and Mark, 1999). The provision of hard  
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933 327 substrate by the single functional group that is described as basibiont (group H4) was  
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935 328 represented by a positive effect on all algae/detritus feeders of the system and the  
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937 329 sessile predator/scavenger group C5 (Fig. 2g).

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939 330 Substrate preferences among the organisms of SD2 (T6) appear to match their  
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941 331 effect on the sediment (T14) (see section S2 in the Supplementary Material), in  
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943 332 support of the mobility mode hypothesis and, hence, the separation of organisms into  
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945 333 stabilizers and destabilizers (Posey, 1987). Sediment destabilization in the form of  
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947 334 bioturbation should constitute the main mechanism of sediment engineering in  
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949 335 estuarine soft bottoms (Meadows et al., 2012). Due to its high dispersal potential (T2,  
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951 336 T3 and T4) and its role as a sediment destabilizer (T14), group H10 is expected to be  
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953 337 mostly responsible for it. This group was, therefore, allowed to reduce the available  
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955 338 space for stabilizing organisms of the interface and have a direct negative impact on  
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957 339 infaunal stabilizers (groups H6 and H12). On the other hand, the ensuing bioirrigation  
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959 340 is expected to generate favourable conditions for infaunal destabilizers and was  
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961 341 depicted as a positive effect on group H5 (Fig. 3g).

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### 966 967 343 2.3.8

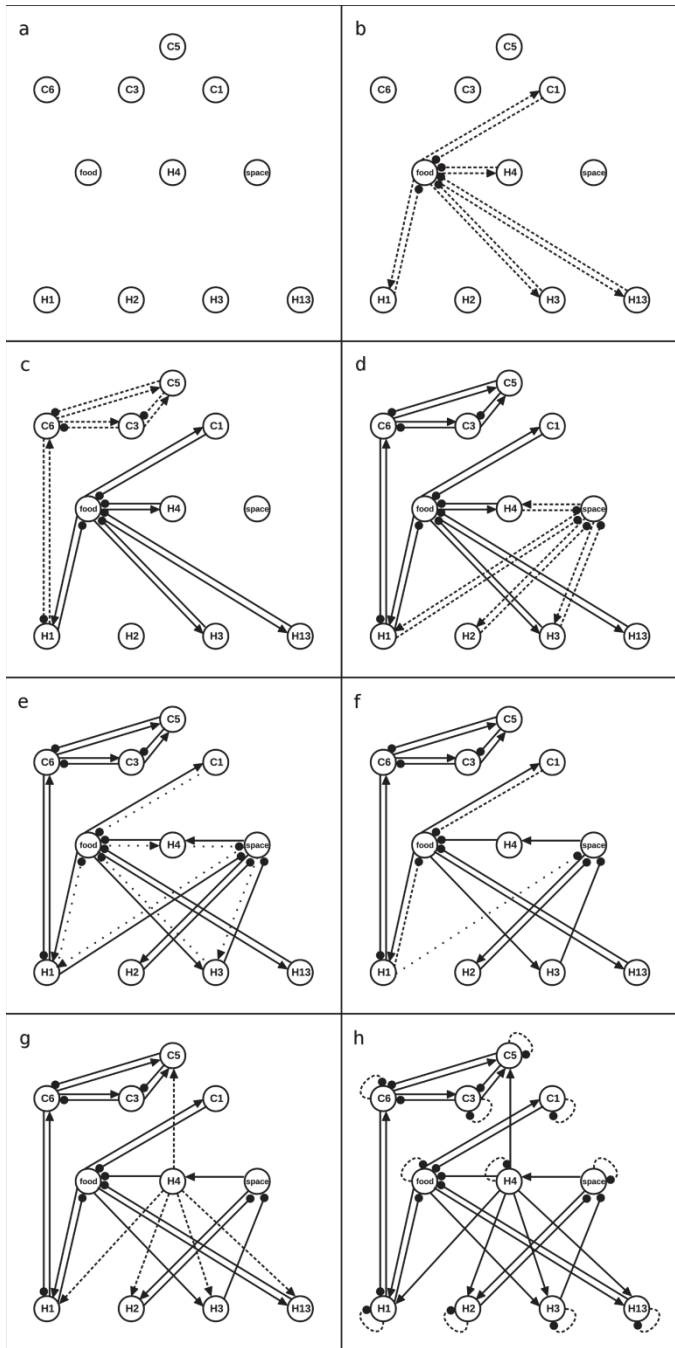
#### 968 969 344 Intra-group inhibition

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971 345 Negative self-effects were added to all variables of SD1 and SD2, representing  
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973 346 a variety of processes (Fig. 2h, 3h). In the case of the two basic resources, negative  
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975 347 self-effects are mostly indicative of the existence of intrinsic limitations in the amounts  
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977 348 that are available to their consumers. Negative self-effects for the rest of the variables  
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979 349 can be the result of, among other things, crowding, behavioural inhibition of

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350 reproduction, territoriality or accumulation of waste products (Levins, 1998). These or  
351 similar processes appear to be wide-spread in ecological systems (Connell, 1983).

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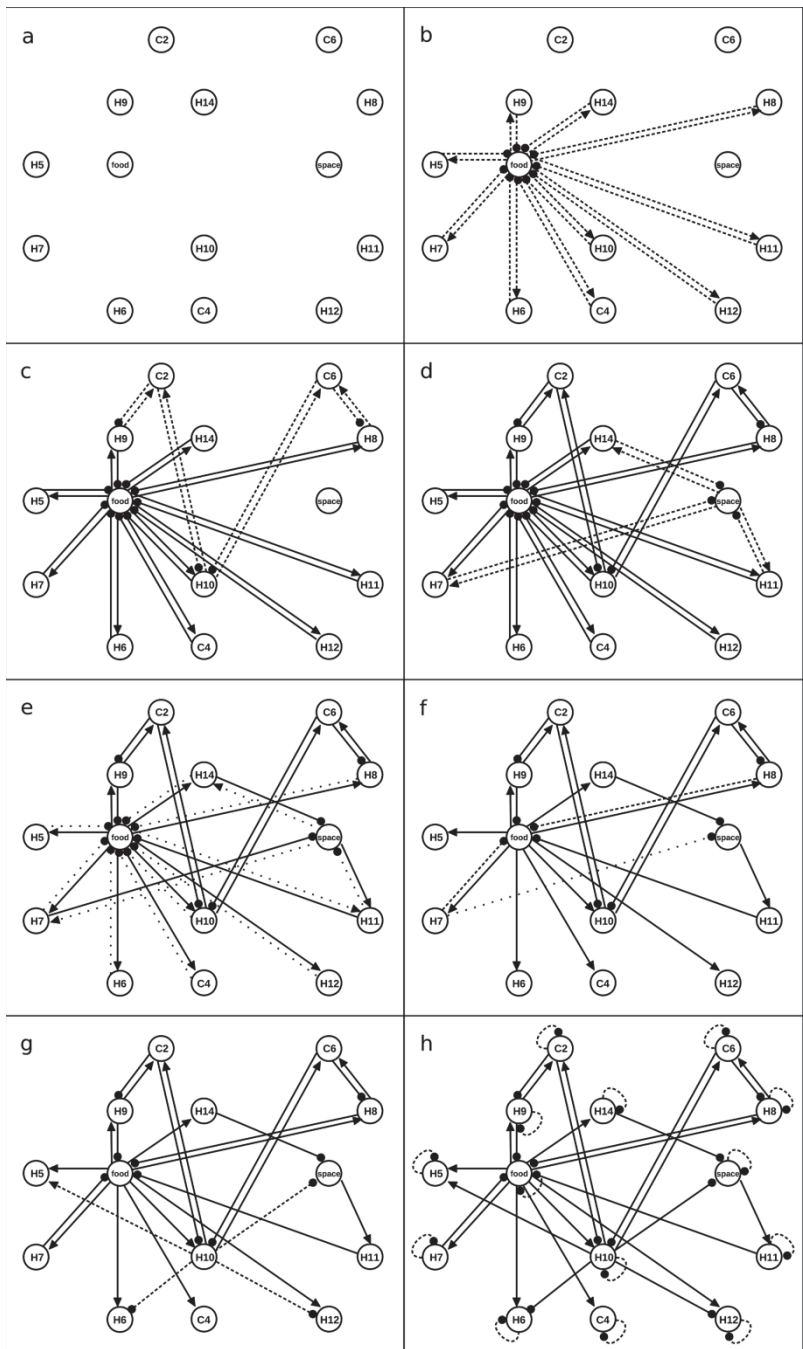
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354 Fig. 2. Stepwise drawing of signed digraph 1 (SD1, epifauna). The steps represent  
355 processes of a) environmental filtering, b) consumption of algae/detritus, c) predation,  
356 d) use of space, e) food–space competition trade-off, f) early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

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

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

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

373 2.4

374 Feedback analysis

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

385 We assessed the potential for stability of our qualitative models as an indication  
386 of the likelihood of the respective systems to exist in nature. To this end, we followed  
387 the approach of Dambacher et al. (2003), who derived two criteria for the stability of  
388 qualitative models, classified conditionally stable models accordingly and developed  
389 stability metrics for each of the two model classes. The stability of class I models is  
390 jeopardized by positive feedback dominating feedback at the highest level of a

1163  
1164  
1165 391 system. Instability in class II models is characterized by overcompensation, which  
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1167 392 leads to oscillations, due to feedback at higher levels in a system overwhelming  
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1169 393 feedback at lower levels. The latter case can be assessed by measuring the relative  
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1172 394 balance of feedback at different system levels.

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1174 395 Most biological systems appear to be represented by class I models and their  
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1176 396 potential for stability is determined by their maximum weighted feedback (Dambacher  
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1178 397 et al., 2003). This metric is calculated by counting all feedback cycles (both positive  
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1180 398 and negative) at the highest level of a system and computing the ratio of their net to  
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1182 399 absolute sums. It portrays the contribution of negative and positive feedback cycles to  
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1184 400 the overall system feedback. Values that tend toward -1 indicate a high potential for  
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1186 401 the variables of a system in equilibrium to converge toward their original levels  
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1189 402 following a pulse perturbation. Values that tend toward 1 indicate a high potential for  
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1191 403 post-perturbation divergence from these levels. Values near 0 show high ambiguity  
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1193 404 with respect to the system's stability potential.

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1195 405 The classification of the models and the calculation of the stability metrics were  
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1197 406 based on qualitatively specified community matrices, which are equivalent to signed  
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1199 407 digraphs as a representation of a system. With the help of tools specifically designed  
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1201 408 for their analysis (Dambacher et al., 2002), we assigned the qualitative models to one  
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1203 409 of the two stability classes. Based on this classification, we calculated the metric that  
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1205 410 quantifies each model's potential for stability.

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1208 411  
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1210 412 Signed digraphs were drawn, and from them qualitatively specified community  
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1212 413 matrices were derived using the digraph editor software PowerPlay version 2.0  
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1214 414 (Westfahl et al., 2002). The stability analysis of the qualitative mathematical models  
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1216 415 was performed with a program for the qualitative and symbolic analysis of community  
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1224 416 matrices ([esapubs.org/archive/ecol/E083/022](https://esapubs.org/archive/ecol/E083/022)) using the technical computing  
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1226 417 software Maple version 18.0 (Maplesoft, 2014).  
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1233 420 Results  
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1235 421 3.1  
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1237 422 Signed digraphs  
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1239 423 Building the signed digraphs of benthic macroinvertebrate communities in the  
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1241 424 Rance estuary left the epifaunal SD1 with 9 functional groups and the infaunal SD2  
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1243 425 with 12, as group C6 participates in both models. In spite of having fewer groups,  
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1245 426 SD1 has 3 of them acting as predators, compared to only 2 predatory groups in SD2.  
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1247 427 Only 5 groups interact with algae/detritus in SD1 and 10 groups in SD2, while 3  
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1249 428 groups interact with the basic resource of space in both models. The representation  
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1251 429 of the trade-off in competitive ability for food and space appears to have a deeper  
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1253 430 impact on the structure of the models than the trade-off between early survival and  
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1255 431 colonization potential. Incorporating the latter often resulted in a reversal of changes  
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1257 432 made to the models to represent the former. Biogenic habitat modification is of  
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1259 433 facilitating nature in SD1, taking the form of epibiosis, and of mostly inhibiting nature  
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1261 434 in SD2, where it represents bioturbation.  
1262  
1263  
1264 435 The qualitatively specified community matrices that correspond to SD1 (Table 3)  
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1266 436 and SD2 (Table 4) offer a detailed description of the interactions that comprise the  
1267  
1268 437 two models. Of the 121 possible interactions in SD1 and the 196 possible interactions  
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1270 438 in SD2, only 36 occur in the former model and 41 in the latter. As a measure of  
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1272 439 system complexity, the proportion of possible interactions among each system's  
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1274 440 variables that are actually realized is equal to 0.29 in SD1 and 0.21 in SD2. SD1  
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441 comprises 21 negative and 15 positive interactions, while SD2 has the same number  
442 of positive interactions as SD1 and 26 negative.

443  
444 Table 3. Qualitatively specified community matrix corresponding to SD1 (see Fig. 2).  
445 Values along each column indicate negative (-), positive (+) or absent (0) direct  
446 effects of the respective variable on the variables of the rows. The variables  
447 represent functional groups (see Table 1) or the basic resources of food and space

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

448  
449  
450 Table 4. Qualitatively specified community matrix corresponding to SD2 (see Fig. 3).  
451 Values along each column indicate negative (-), positive (+) or absent (0) direct  
452 effects of the respective variable on the variables of the rows. The variables  
453 represent functional groups (see Table 1) or the basic resources of food and space

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



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

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3.2

### Feedback analysis

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

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467 dominance of negative feedback cycles over positive ones, along with a moderate  
468 level of ambiguity with respect to the stability potential of the system.

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

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

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

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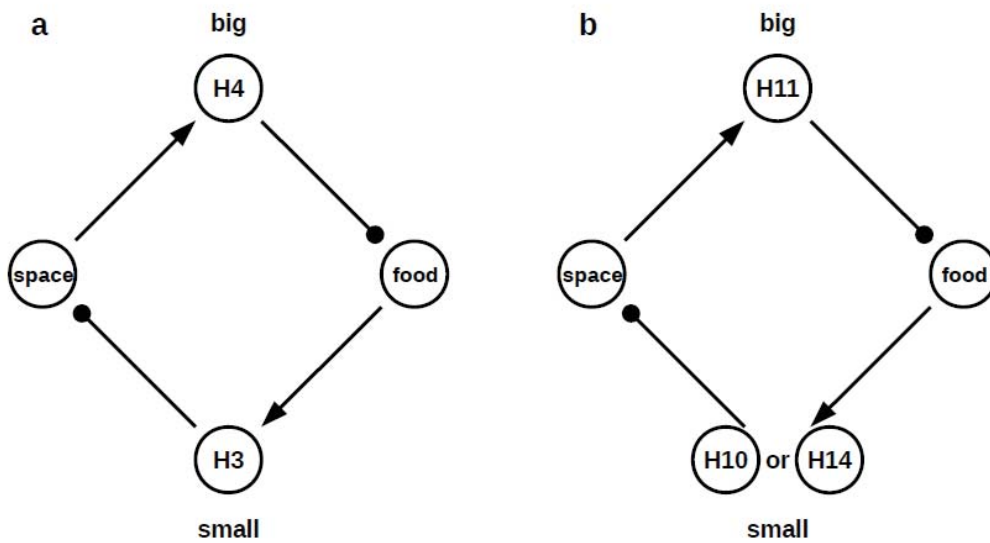


Fig. 4. Positive feedback cycles from a) SD1 (see Fig. 2) and b) SD2 (see Fig. 3). Each feedback cycle links the basic resources of food and space with one big and one small functional group. Links ending in arrows and filled circles represent positive and negative direct effects, respectively

#### 4

### Discussion

#### 4.1

#### Functional groups

Qualitatively specified food-web models often represent only a few dominant species of marine benthic macroinvertebrates, while other community members may be grouped into broad trophic categories (e.g., Carey et al., 2014; Reum et al., 2015). This practice cannot explicitly account for key non-trophic interactions and tends to ignore the rarest members of a community, in spite of evidence for their significant contribution to ecosystem functioning (Lyons et al., 2005). This contribution can be

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504 disproportionate to their abundance, as species with the most distinct combinations of  
505 traits have been shown to be rarer than expected by chance (Mouillot et al., 2013).

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

514  
515 4.2

516 Signed digraphs

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

525 Each of the community assembly mechanisms that are represented by these  
526 relationships encompasses a variety of processes that could potentially be  
527 represented much more explicitly. The level at which each mechanism was actually  
528 represented was dictated by the available trait and environmental information. Hence,

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1578 529 biological traits were used as proxies for the role of functional groups in a set of  
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1580 530 theoretically expected community assembly mechanisms that were illustrated through  
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1582 531 a highly abstract representation of the system.

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1584 532 For instance, the biogeochemical aspects of sediment engineering were not  
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1586 533 explicitly represented, as the distinction between sediment stabilizers and  
1587 533 destabilizers (Posey, 1987) was the best possible representation, given the available  
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1589 534 information at the species level. Still, this tenet of the mobility-mode hypothesis has  
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1591 535 been empirically upheld and shown to have cascading and long-lasting effects on  
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1593 536 benthic communities (Volkenborn et al., 2009). Similarly, the complex set of  
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1595 537 processes that comprise the phenomenon of resource competition was only  
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1597 538 represented through the use of each group's maximum size in the context of the  
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1599 539 concentration reduction hypothesis for space and food (Tilman, 1980). Space  
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1601 540 limitation due to adult–juvenile interactions and exploitative competition for food have  
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1603 541 been shown to play a central role in the successional dynamics of benthic  
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1605 542 communities, with the functional role of organisms largely defined by their size (Van  
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1607 543 Colen et al., 2008). The combined representation of food and space as limiting  
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1609 544 resources can significantly increase our understanding and predictability of marine  
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1611 545 benthic systems (Svensson and Marshall, 2015).

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1613 546  
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1615 547 The separation of benthic macroinvertebrates into algae/detritus feeders and  
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1617 548 predators/scavengers aimed to preserve the homogeneity of their resource base, so  
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1619 549 that theoretically expected community assembly mechanisms could be implemented.  
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1621 550 This choice might appear to ignore important differentiations in the feeding habits of  
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1623 551 these organisms, such as the distinction between suspension- and deposit-feeders. It  
1624  
1625 552 has been, however, shown that feeding behaviour in the marine benthos is highly  
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1627 553 facultative and similar categorizations are not always valid (Snelgrove and Butman,  
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554 1994). Instead, the modification of networks of trophic interactions through expert  
555 knowledge is expected to increase their realism, while the use of allometric scaling  
556 should enhance their stability (Brose et al., 2006b).

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

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

570 The functional divergence between organisms that occupy the surface of the  
571 sediment (epifauna) and those that are buried in it (infauna) has been previously  
572 recognized in the study of marine benthos (Reiss et al., 2010). In the Rance estuary,  
573 the epifauna (SD1) features a lower functional diversity of algae/detritus feeders and  
574 a higher functional diversity of predators/scavengers, compared to the infauna (SD2).  
575 Additionally, a much higher number of groups ended up interacting with algae/detritus  
576 in SD2 compared to SD1. The complex diagenetic processes that affect the basic  
577 food resource within the sediment of the seafloor (Herman et al., 1999) could be  
578 responsible for the diversity of infaunal organisms that feed on it. On the other hand,

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579 the high structural complexity of the habitat occupied by epifaunal organisms may  
580 result in a higher diversity of predatory strategies. Trophic differences could be  
581 associated with a variety of biological traits, leading to observed patterns of functional  
582 diversity. The epifaunal system also appears to be more complex, with a higher  
583 proportion of possible interactions realized compared to the infaunal system. This is  
584 primarily caused by an under-representation of positive interactions in the latter  
585 system. The qualitatively antithetical role of biogenic habitat modification in the two  
586 systems (facilitating in SD1, mostly inhibiting in SD2) contributes partly to these  
587 differences. Its impact may extend to productivity patterns, as epifauna-dominated  
588 systems (seagrass/algae beds) seem in general to be more productive than infauna-  
589 dominated (estuaries) (Costanza et al., 1998).

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591 4.3

592 Feedback analysis

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



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

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## 618 Conclusions

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



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627 mechanistic representation of many ecological systems for which empirical  
628 information is limited.

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

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

647  
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2404 **SUPPLEMENTARY MATERIAL**  
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2406 **S.1 Environmental filtering**

2407 **S.1.1 Methods**  
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2409 Each station sampled in the spring of 1995 was associated with a particular sediment  
2410 type (pure mud, mud, silty mud, sandy mud, muddy sand, fine/intermediate sand,  
2411 intermediate/coarse sand, coarse sand, gravel), based on a sedimentary map established in  
2412 1994 (Bonnot-Courtois, 1997). The depth (or elevation) of each station was measured at low  
2413 tide during the collection of samples. Each station was assigned a salinity regime, depending  
2414 on which of three sectors of the Rance estuary it was situated in. The innermost part of the  
2415 estuary, up to Pleudihen-sur-Rance, was subject to high salinity variation, ranging from 0.5 to  
2416 30. Beyond this point, downstream to Port-St-Hubert, salinity values ranged between 18 and  
2417 30. The rest of the estuary experienced more or less constant salinity levels, over the value of  
2418 30, similar to those of the open sea (Desroy, 1998).  
2419

2420 Among the 14 biological traits for which the species of the system were assigned with  
2421 values, we expect the trait of tolerance to tidal emersion and low salinity levels (T5) along  
2422 with that of preferred substrate type (T6) to adequately represent the most important  
2423 environmental limitations that are faced by benthic macroinvertebrates in the Rance estuary  
2424 (Desroy, 1998). If this is indeed the case, these two biological traits, describing species  
2425 preference for abiotic conditions, should show high degrees of covariation with the respective  
2426 environmental variables. Other biological traits that might correlate with the two traits in  
2427 question are also expected to show similar patterns of covariation.  
2428

2429 RLQ analysis is a statistical technique that can relate the biological traits of organisms to  
2430 the characteristics of the environment in which they live (Dolédec et al., 1996). L refers to a  
2431 table of species abundance at a number of sites and it describes, among other things, the actual  
2432 habitat utilization of different species. R refers to a table of environmental variables measured  
2433 at the same sites as species abundance. Q refers to a table of biological traits for all the species  
2434 of table L. RLQ analysis starts with the separate ordination of table L. It then uses the  
2435 resulting sites and species weights in the separate ordinations of tables R and Q, respectively.  
2436 The result is an ordination of the common structure of tables R and Q with a link expressed by  
2437 table L.  
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2439 Since environmental variables and biological traits include both qualitative and  
2440 quantitative information, we opted for Hill and Smith analysis (Hill and Smith, 1976) for the  
2441 separate ordinations of the 113 sites  $\times$  3 environmental variables (R) and the 240 species  $\times$  14  
2442 biological traits (Q) tables. Correspondence analysis (Legendre and Legendre, 1998) was  
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2463 performed for the separate ordination of the 113 sites  $\times$  240 species abundance table (L). The  
2464 application of correspondence analysis allows RLQ analysis to maximize the covariance  
2465 between linear combinations of environmental variables and biological traits (Dolédec et al.,  
2466 1996). This maximized covariance, projected on orthogonal axes of decreasing contribution to  
2467 the total value, is called co-inertia.  
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2471 The comparison of this eigenvalues decomposition (RLQ) with the eigenvalues  
2472 decomposition from the separate ordinations of the environmental variables (R) and biological  
2473 traits (Q) tables can show what part of the variance of the original data sets is represented in  
2474 their common structure. The optimal correlation between sites and species scores from the  
2475 separate ordination of the species abundance table (L) can be compared with the equivalent  
2476 correlation from the RLQ analysis, in order to illustrate how well the original species  
2477 abundance patterns are represented by the associations between environmental variables and  
2478 biological traits. These associations can be best demonstrated by projecting environmental  
2479 variables and biological traits side-by-side on the same dimensions of the common co-inertia  
2480 space.  
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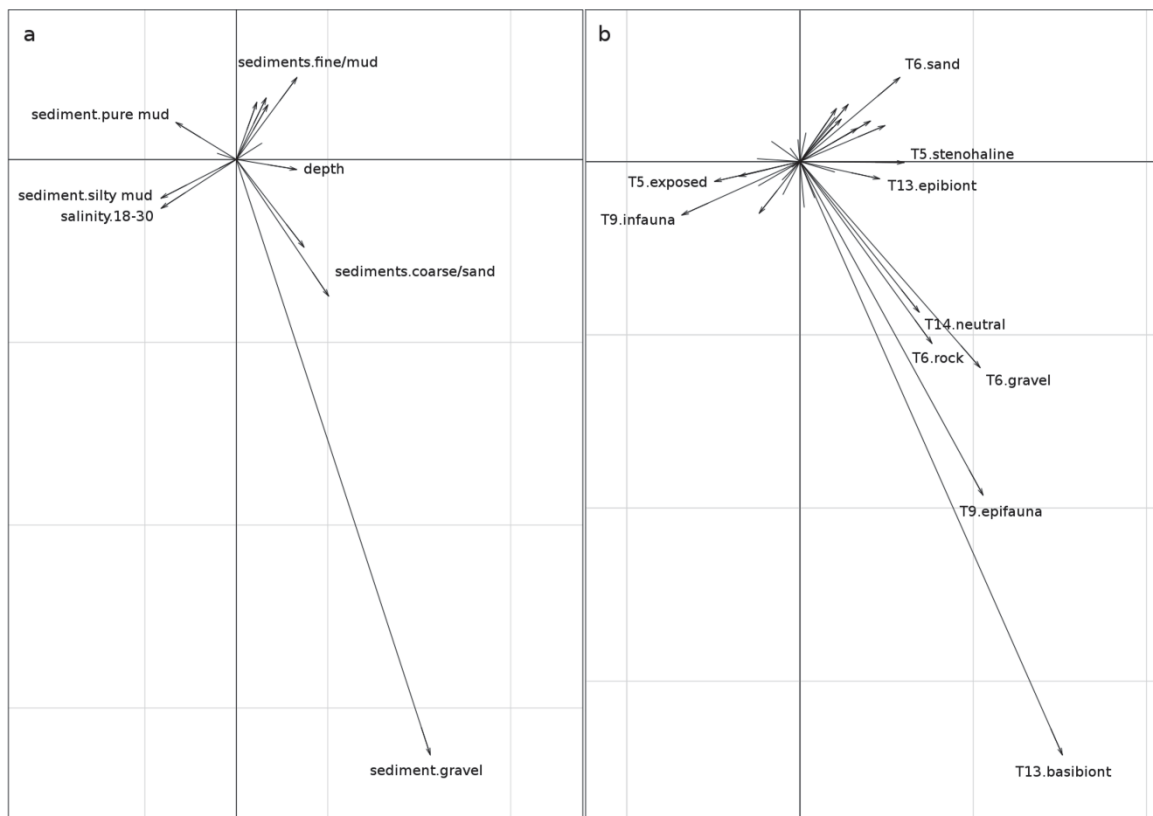
2489 All analyses were performed using the statistical software R version 3.2.2 (R Core  
2490 Team, 2015) with the package ade4 (Dray and Dufour, 2007).  
2491

### 2492 2493 **S.1.2 Results** 2494

2495 The eigenvalues decomposition of the RLQ analysis shows that the proportion of the  
2496 common structure between environmental variables and biological traits that is portrayed  
2497 along the first axis (73%) is much larger than the proportion that is portrayed along the second  
2498 one (17%). The first two axes combined represent 90% of the covariance between  
2499 environmental variables and biological traits. The cumulated amount of variance that is  
2500 preserved on the first two axes of the RLQ ordination, compared to the equivalent variance  
2501 from the separate ordinations of the environmental variables (R) and biological traits (Q)  
2502 tables, is just over 85% in both cases. The correlation values between sites and species scores  
2503 along the first and second axes of the RLQ analysis are 76% and 60% of the respective  
2504 correlation values from the separate ordination of the species abundance table (L).  
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2511 The side-by-side projection of environmental variables (Fig. S1a) and biological traits  
2512 (Fig. S1b) on the first two dimensions of the common co-inertia space reveals one  
2513 conspicuous pattern: coarse sediment types are strongly associated with trait values that  
2514 represent preference for gravel or rock (T6), no role in sediment engineering (T14), an  
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epifaunal position (T9) and the role of basibionts (T13). These trait values, along with the one that identifies epibiotic organisms (T13) and is associated with increasing water depth, are all characteristic of benthos that occupies the surface of the seabed, supported by structure of abiotic or biotic origin. Increasing water depth is further associated with a transition from organisms that tolerate tidal exposure to those that have to be submerged in high salinity levels (T5).



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

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2581 **S.2 Functional trade-offs**  
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2583 **S.2.1 Methods**

2584 Our set of 14 biological traits allows the representation of functional trade-offs through  
2585 specific combinations of trait values. In the case of a trade-off among benthic  
2586 macroinvertebrates in their utilization efficiency for the two basic resources (food and space)  
2587 (Tilman, 1980), we would expect trait values that confer a competitive advantage for each  
2588 resource (greater size (T7) and lower minimum space requirement (T8)) to be negatively  
2589 associated. A trade-off in the allocation of resources toward early survival versus colonization  
2590 potential (Tilman, 1990) would result in the survival-enhancing brooded early development  
2591 mode (T2) being negatively associated with both dispersal distance (T3) and maximum  
2592 fecundity (T4). Finally, the stabilizers of the mobility-mode hypothesis (Posey, 1987) are  
2593 expected to bind fine particles, thus leading to the creation of muddy sediments, while  
2594 destabilizers are expected to disrupt the substrate, resulting in more heterogeneous sediment  
2595 types. Since each group is assumed to create sediment conditions that are favourable to its  
2596 own members and detrimental to those of the opposite group, sediment preferences (T6)  
2597 among stabilizers and destabilizers should correspond to their respective effects on the  
2598 substrate (T14).  
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2608 Because values were assigned to the species independently for each biological trait, we  
2609 can assess the ecological pertinence of each hypothesis, by inspecting the biological traits data  
2610 set, looking for the respective trait associations. The multivariate ordination technique of Hill  
2611 and Smith allowed the transformation of the 240 species  $\times$  14 biological traits table into a set  
2612 of orthogonal variables that contain decreasing portions of the table's total variance (Hill and  
2613 Smith, 1976). The eigenvalues decomposition, on which this technique is based, reveals the  
2614 amount of variance that each of these variables represents. The projection of the initial trait  
2615 variables on the first few axes of the transformed multivariate space can provide insights into  
2616 the most important associations among biological traits.  
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2624 All analyses were performed using the statistical software R version 3.2.2 (R Core  
2625 Team, 2015) with the package ade4 (Dray and Dufour, 2007).  
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2629 **S.2.2 Results**

2630 The eigenvalues decomposition of Hill and Smith for the biological traits data set shows  
2631 that about twice as much variation can be found along each of the first two axes (15% and  
2632 14% of total variation) compared to each of the two axes that follow (8% and 7% of total  
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2640 variation). The first four axes combined represent just over 43% of the total variation of  
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2642 biological traits among species of benthic macroinvertebrates.

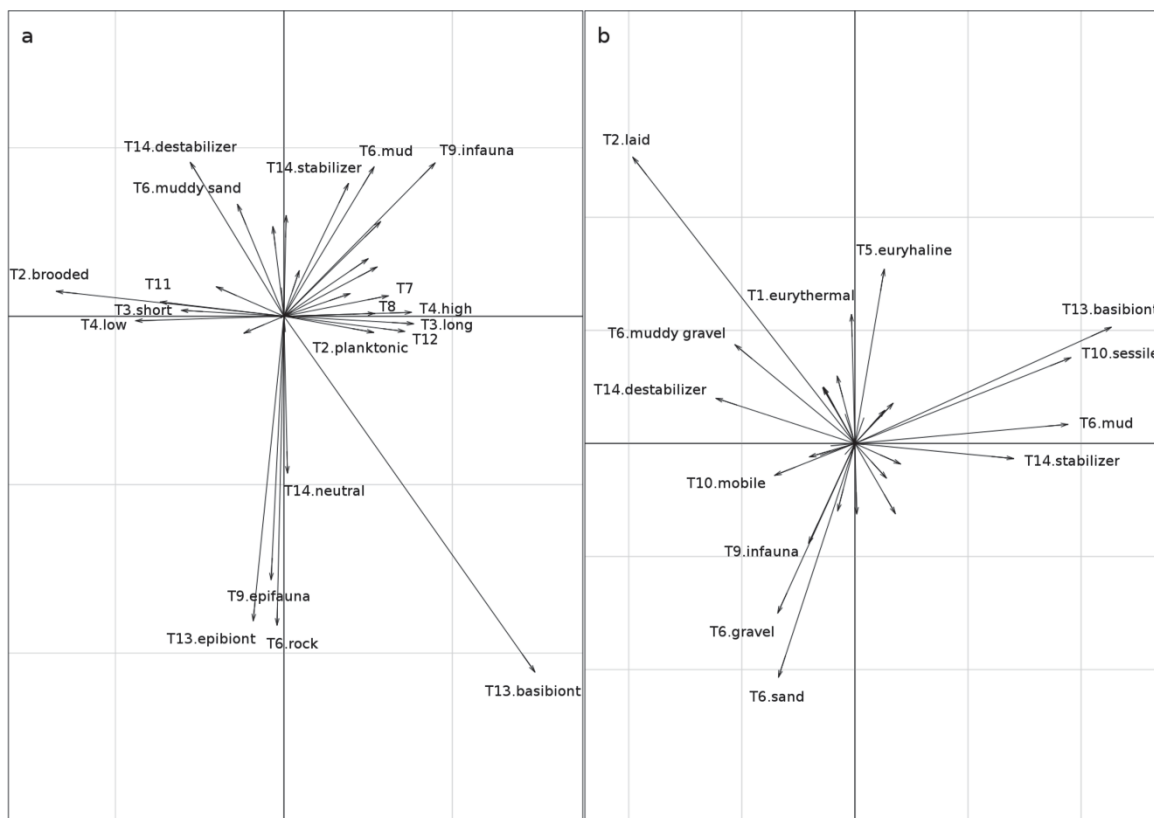
2643 The projection of biological traits on the first four dimensions of the transformed  
2644 multivariate space reveals the most important biological trait associations. Along the first axis  
2645 (Fig. S2a), maximum size (T7) is assumed to define a competitive hierarchy for food.  
2646  
2647 Minimum space requirement (T8), in the same direction of the axis, is expected to define an  
2648  
2649 inverse competitive hierarchy for space.  
2650

2651 On the positive half of the first axis (Fig. S2a), high levels of maximum fecundity (T4)  
2652 and dispersal distance (T3) are associated with planktonic early development mode (T2). The  
2653 combination of these trait values is expected to lead to higher colonization potential among  
2654  
2655 marine benthos. On the negative half of the same axis, low levels of maximum fecundity (T4)  
2656  
2657 and dispersal distance (T3) are associated with brooded early development mode (T2) and  
2658  
2659 high population growth rate (T11), thus forming a trait combination that is assumed to  
2660  
2661 enhance early survival rates.  
2662

2663 The second axis of the Hill and Smith ordination (Fig. S2a) mainly serves to distinguish  
2664 organisms with an epifaunal position (T9) and requirement for hard substrates (T6). Trait  
2665 differences among the rest of the organisms, which are mostly associated with soft bottoms  
2666  
2667 (T6), are featured along the first (Fig. S2a) together with the third and fourth axes of the  
2668  
2669 ordination (Fig. S2b). It appears that sessile organisms (T10) that prefer mud (T6), stabilize  
2670  
2671 the sediment (T14) and create substrate for epibionts (T13) are distinguished from mobile  
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2673 (T10), destabilizing organisms (T14) that have a preference for coarser and mixed sediment  
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2675 types (T6).  
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**Fig. S2** Projection of biological traits on a) the first and second and b) the third and fourth dimensions of the transformed multivariate space of Hill and Smith analysis. In both graphs the horizontal axis represents the lower dimension and the vertical the higher. In the case of continuous and ordinal traits, the arrows indicate the direction of increasing values. In the case of nominal and binary traits, the tips of the arrows indicate the position of the centroids for the respective trait values (shown as trait.value). For details about the traits, see Table 2

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