



HAL
open science

Qualitative modelling of functional relationships in marine benthic communities

Nikolaos Alexandridis, Jeffrey M. Dambacher, Fred Jean, Nicolas Desroy,
Cédric Bacher

► **To cite this version:**

Nikolaos Alexandridis, Jeffrey M. Dambacher, Fred Jean, Nicolas Desroy, Cédric Bacher. Qualitative modelling of functional relationships in marine benthic communities. *Ecological Modelling*, 2017, 360, pp.300-312. 10.1016/j.ecolmodel.2017.07.021 . hal-02571120

HAL Id: hal-02571120

<https://hal.science/hal-02571120v1>

Submitted on 19 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Qualitative modelling of functional relationships in marine benthic communities

Alexandridis Nikolaos ^{1,*}, Dambacher Jeffrey M. ², Jean Fred ³, Desroy Nicolas ⁴, Bacher Cedric ¹

¹ IFREMER, Centre de Bretagne, DYNECO-LEBCO, CS 10070, 29280 Plouzané, France

² CSIRO, GPO Box 1538, Hobart, Tasmania 7001, Australia

³ Université de Brest, UBO, CNRS, IRD, Institut Universitaire Européen de la Mer, LEMAR, 29280 Plouzané, France

⁴ IFREMER, Laboratoire Environnement et Ressources de Bretagne Nord, BP 70134, 35801 Dinard, France

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

Abstract :

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

Highlights

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

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

39 Introduction

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).

119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177

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)).

178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221
222
223
224
225
226
227
228
229
230
231
232
233
234
235
236

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

237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295

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

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

123
124 2

296
297
298
299
300
301
302
303
304
305
306
307
308
309
310
311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354

125 Methods

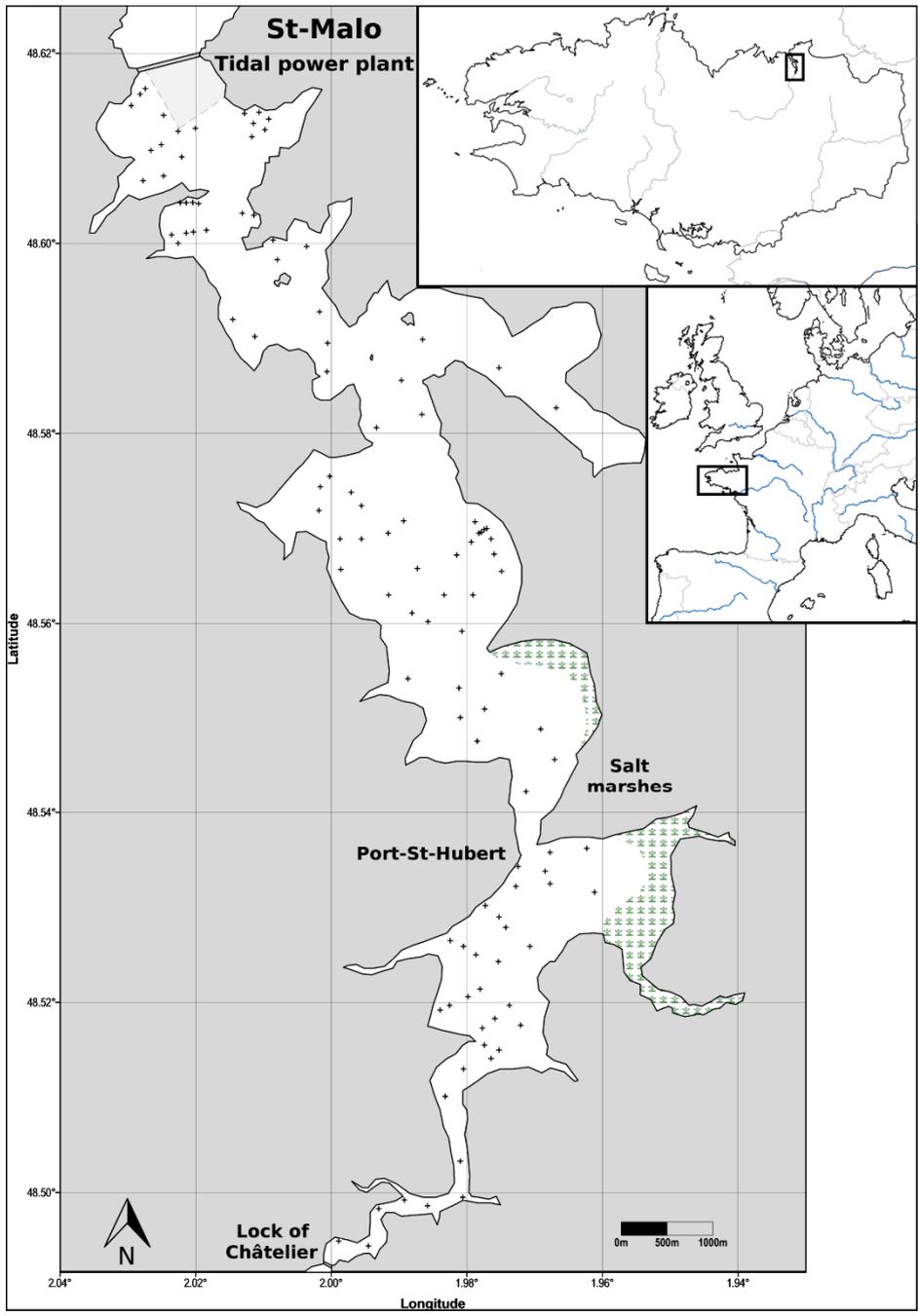
126 2.1

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).

148



149

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

154

155 2.2

156 Functional groups

414
415
416 157 For the representation of the primary functional components of benthic
417
418 158 macroinvertebrate communities in the Rance estuary, we employed 20 functional
419
420 159 groups, previously built on the basis of biological trait information for the 240 species
421
422 160 of the system in 1995 (Alexandridis et al., 2017). The collected abundance data set
423
424 161 allowed each of the groups to be assigned with a representative species along with a
425
426 162 value for each of the 14 biological traits (Table 1). The traits are expected to describe
427
428 163 the role of benthic algae/detritus feeders and predators/scavengers in 7 important
429
430 164 community assembly mechanisms (Table 2). The list of mechanisms was mostly
431
432 165 adopted from the framework developed by Boulangeat et al. (2012) for dynamic
433
434 166 models of terrestrial vegetation. A few adjustments were made to the original
435
436 167 framework, in order to adapt it to marine benthic systems (Alexandridis et al., 2017).
437
438
439
440 168

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

172

173

514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539
540
541
542
543
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558
559
560
561
562
563
564
565
566
567
568
569
570
571
572

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.

573
574
575
576
577
578
579
580
581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630
631

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.

178

179

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.

632
633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651
652
653
654
655
656
657
658
659
660
661
662
663
664
665
666
667
668
669
670
671
672
673
674
675
676
677
678
679
680
681
682
683
684
685
686
687
688
689
690

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).

206

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.

219

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

691
692
693
694
695
696
697
698
699
700
701
702
703
704
705
706
707
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724
725
726
727
728
729
730
731
732
733
734
735
736
737
738
739
740
741
742
743
744
745
746
747
748
749

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.

231
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

750
751
752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773
774
775
776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804
805
806
807
808

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

254 2.3.4

255 Use of space

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

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

271 2.3.5

272 Food–space competition trade-off

273 In order to better represent differences in the functional roles of benthic
274 organisms in a way that is consistent with the general trade-offs that are expected to

809
810
811 275 characterize these functional roles, we resorted again to the trait of maximum size
812
813 276 (T7). Higher levels of this trait are expected to confer a competitive advantage for
814
815 277 limited food resources, due to a larger area that can be searched for food or distance
816
817 278 from the substrate, which enhances the availability of food from the water column
818
819 279 (McLean and Lasker, 2013). On the other hand, maximum size (T7) appears to be
820
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
824
825 282 Material). Higher values of the latter trait should confer a competitive disadvantage
826
827 283 for limited available space (Tilman 1980). We, thus, assumed that larger maximum
828
829 284 size (T7) represents a competitive advantage for food and disadvantage for space.
830
831

832 285 Based on this assumption, we divided the functional groups of each signed
833
834 286 digraph that consume the basic food resource in two categories, the small and the
835
836 287 big. We did so, by making sure that groups with similar sizes are placed in the same
837
838 288 category and that there are more small than large groups (Blackburn and Gaston,
839
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
843
844 291 levels of the resource for which they are competitively superior. This set of
845
846 292 interactions was represented by an alteration of the existing resource consumption
847
848 293 interactions, so that a functional group receives a positive effect from its limiting
849
850 294 resource, while having a negative effect on the resource that it can efficiently reduce
851
852 295 (Fig. 2e, 3e). This rule was not applied to any groups that would otherwise appear not
853
854 296 to be limited by any of the basic resources, along with group H2 in SD1, whose
855
856 297 relationship with space represents its bulldozing effect on macroinvertebrate recruits.
857
858
859

860 298
861
862 299 2.3.6
863
864
865
866
867

868
869
870
871
872
873
874
875
876
877
878
879
880
881
882
883
884
885
886
887
888
889
890
891
892
893
894
895
896
897
898
899
900
901
902
903
904
905
906
907
908
909
910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926

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
930
931 326 basibiotic organisms being alive or not (Wahl and Mark, 1999). The provision of hard
932
933 327 substrate by the single functional group that is described as basibiont (group H4) was
934
935 328 represented by a positive effect on all algae/detritus feeders of the system and the
936
937 329 sessile predator/scavenger group C5 (Fig. 2g).

939
940 330 Substrate preferences among the organisms of SD2 (T6) appear to match their
941
942 331 effect on the sediment (T14) (see section S2 in the Supplementary Material), in
943
944 332 support of the mobility mode hypothesis and, hence, the separation of organisms into
945
946 333 stabilizers and destabilizers (Posey, 1987). Sediment destabilization in the form of
947
948 334 bioturbation should constitute the main mechanism of sediment engineering in
949
950 335 estuarine soft bottoms (Meadows et al., 2012). Due to its high dispersal potential (T2,
951
952 336 T3 and T4) and its role as a sediment destabilizer (T14), group H10 is expected to be
953
954 337 mostly responsible for it. This group was, therefore, allowed to reduce the available
955
956 338 space for stabilizing organisms of the interface and have a direct negative impact on
957
958 339 infaunal stabilizers (groups H6 and H12). On the other hand, the ensuing bioirrigation
959
960 340 is expected to generate favourable conditions for infaunal destabilizers and was
961
962 341 depicted as a positive effect on group H5 (Fig. 3g).

965 342

967 343 2.3.8

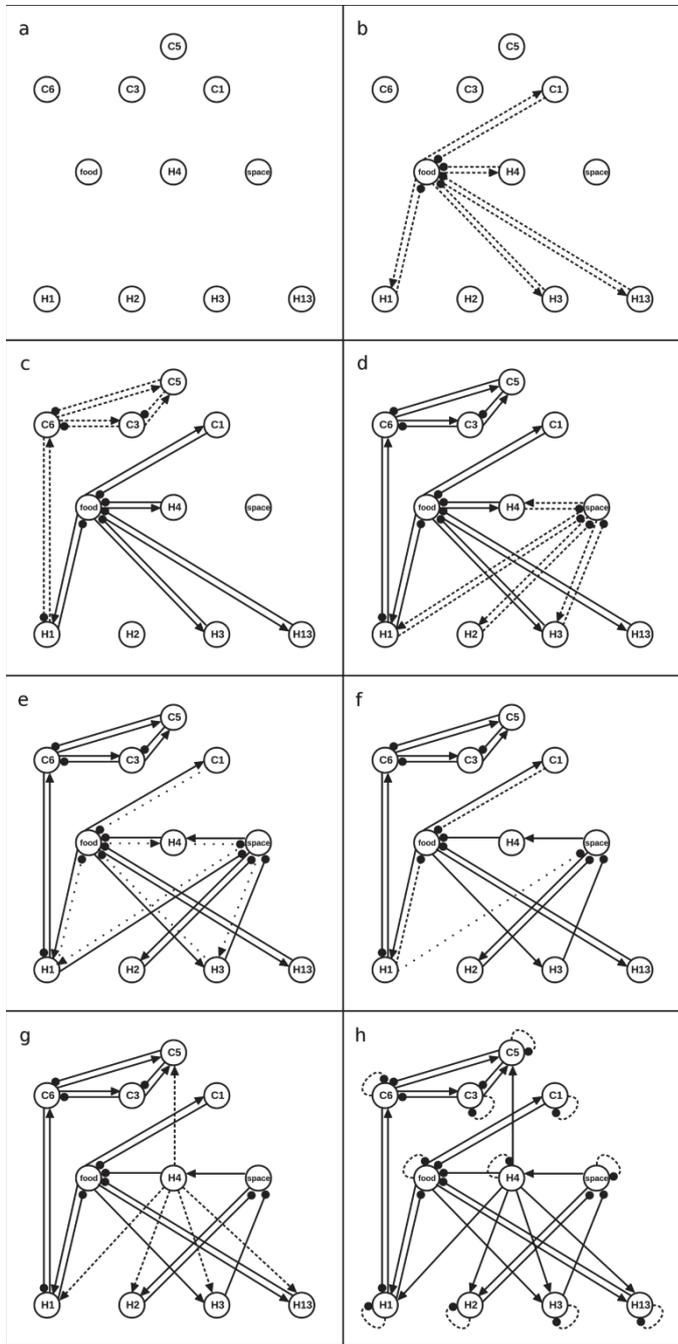
969 344 Intra-group inhibition

971
972 345 Negative self-effects were added to all variables of SD1 and SD2, representing
973
974 346 a variety of processes (Fig. 2h, 3h). In the case of the two basic resources, negative
975
976 347 self-effects are mostly indicative of the existence of intrinsic limitations in the amounts
977
978 348 that are available to their consumers. Negative self-effects for the rest of the variables
979
980 349 can be the result of, among other things, crowding, behavioural inhibition of

986
987
988
989
990
991
992
993
994
995
996
997
998
999
1000
1001
1002
1003
1004
1005
1006
1007
1008
1009
1010
1011
1012
1013
1014
1015
1016
1017
1018
1019
1020
1021
1022
1023
1024
1025
1026
1027
1028
1029
1030
1031
1032
1033
1034
1035
1036
1037
1038
1039
1040
1041
1042
1043
1044

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).

352



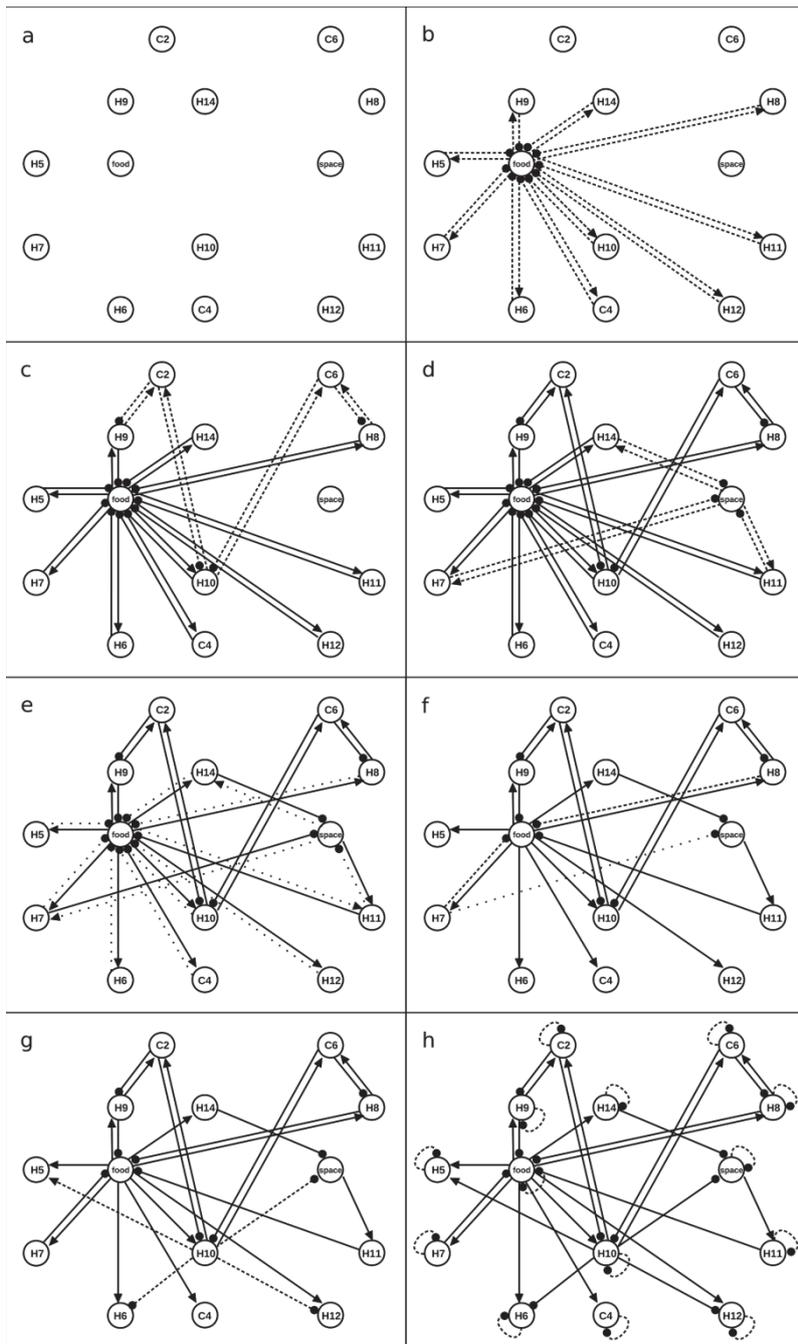
353

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

1045
 1046
 1047
 1048
 1049
 1050
 1051
 1052
 1053
 1054
 1055
 1056
 1057
 1058
 1059
 1060
 1061
 1062
 1063
 1064
 1065
 1066
 1067
 1068
 1069
 1070
 1071
 1072
 1073
 1074
 1075
 1076
 1077
 1078
 1079
 1080
 1081
 1082
 1083
 1084
 1085
 1086
 1087
 1088
 1089
 1090
 1091
 1092
 1093
 1094
 1095
 1096
 1097
 1098
 1099
 1100
 1101
 1102
 1103

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

362



363

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,

1104
1105
1106
1107
1108
1109
1110
1111
1112
1113
1114
1115
1116
1117
1118
1119
1120
1121
1122
1123
1124
1125
1126
1127
1128
1129
1130
1131
1132
1133
1134
1135
1136
1137
1138
1139
1140
1141
1142
1143
1144
1145
1146
1147
1148
1149
1150
1151
1152
1153
1154
1155
1156
1157
1158
1159
1160
1161
1162

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
1166
1167 392 leads to oscillations, due to feedback at higher levels in a system overwhelming
1168
1169 393 feedback at lower levels. The latter case can be assessed by measuring the relative
1170
1171
1172 394 balance of feedback at different system levels.

1173
1174 395 Most biological systems appear to be represented by class I models and their
1175
1176 396 potential for stability is determined by their maximum weighted feedback (Dambacher
1177
1178 397 et al., 2003). This metric is calculated by counting all feedback cycles (both positive
1179
1180 398 and negative) at the highest level of a system and computing the ratio of their net to
1181
1182 399 absolute sums. It portrays the contribution of negative and positive feedback cycles to
1183
1184 400 the overall system feedback. Values that tend toward -1 indicate a high potential for
1185
1186 401 the variables of a system in equilibrium to converge toward their original levels
1187
1188
1189 402 following a pulse perturbation. Values that tend toward 1 indicate a high potential for
1190
1191 403 post-perturbation divergence from these levels. Values near 0 show high ambiguity
1192
1193 404 with respect to the system's stability potential.

1194
1195 405 The classification of the models and the calculation of the stability metrics were
1196
1197 406 based on qualitatively specified community matrices, which are equivalent to signed
1198
1199 407 digraphs as a representation of a system. With the help of tools specifically designed
1200
1201 408 for their analysis (Dambacher et al., 2002), we assigned the qualitative models to one
1202
1203 409 of the two stability classes. Based on this classification, we calculated the metric that
1204
1205 410 quantifies each model's potential for stability.

1206
1207
1208 411
1209
1210 412 Signed digraphs were drawn, and from them qualitatively specified community
1211
1212 413 matrices were derived using the digraph editor software PowerPlay version 2.0
1213
1214 414 (Westfahl et al., 2002). The stability analysis of the qualitative mathematical models
1215
1216 415 was performed with a program for the qualitative and symbolic analysis of community
1217
1218
1219
1220
1221

1222
1223
1224 416 matrices (esapubs.org/archive/ecol/E083/022) using the technical computing
1225
1226 417 software Maple version 18.0 (Maplesoft, 2014).
1227
1228
1229 418
1230
1231 419 3
1232
1233 420 Results
1234
1235 421 3.1
1236
1237 422 Signed digraphs
1238
1239 423 Building the signed digraphs of benthic macroinvertebrate communities in the
1240
1241 424 Rance estuary left the epifaunal SD1 with 9 functional groups and the infaunal SD2
1242
1243 425 with 12, as group C6 participates in both models. In spite of having fewer groups,
1244
1245 426 SD1 has 3 of them acting as predators, compared to only 2 predatory groups in SD2.
1246
1247 427 Only 5 groups interact with algae/detritus in SD1 and 10 groups in SD2, while 3
1248
1249 428 groups interact with the basic resource of space in both models. The representation
1250
1251 429 of the trade-off in competitive ability for food and space appears to have a deeper
1252
1253 430 impact on the structure of the models than the trade-off between early survival and
1254
1255 431 colonization potential. Incorporating the latter often resulted in a reversal of changes
1256
1257 432 made to the models to represent the former. Biogenic habitat modification is of
1258
1259 433 facilitating nature in SD1, taking the form of epibiosis, and of mostly inhibiting nature
1260
1261 434 in SD2, where it represents bioturbation.
1262
1263
1264 435 The qualitatively specified community matrices that correspond to SD1 (Table 3)
1265
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
1269
1270 438 in SD2, only 36 occur in the former model and 41 in the latter. As a measure of
1271
1272 439 system complexity, the proportion of possible interactions among each system's
1273
1274 440 variables that are actually realized is equal to 0.29 in SD1 and 0.21 in SD2. SD1
1275
1276
1277
1278
1279
1280

1281
1282
1283
1284
1285
1286
1287
1288
1289
1290
1291
1292
1293
1294
1295
1296
1297
1298
1299
1300
1301
1302
1303
1304
1305
1306
1307
1308
1309
1310
1311
1312
1313
1314
1315
1316
1317
1318
1319
1320
1321
1322
1323
1324
1325
1326
1327
1328
1329
1330
1331
1332
1333
1334
1335
1336
1337
1338
1339

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

1340
1341
1342
1343
1344
1345
1346
1347
1348
1349
1350
1351
1352
1353
1354
1355
1356
1357
1358
1359
1360
1361
1362
1363
1364
1365
1366
1367
1368
1369
1370
1371
1372
1373
1374
1375
1376
1377
1378
1379
1380
1381
1382
1383
1384
1385
1386
1387
1388
1389
1390
1391
1392
1393
1394
1395
1396
1397
1398

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	-

454

455

456 3.2

457 Feedback analysis

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

1399
 1400
 1401
 1402
 1403
 1404
 1405
 1406
 1407
 1408
 1409
 1410
 1411
 1412
 1413
 1414
 1415
 1416
 1417
 1418
 1419
 1420
 1421
 1422
 1423
 1424
 1425
 1426
 1427
 1428
 1429
 1430
 1431
 1432
 1433
 1434
 1435
 1436
 1437
 1438
 1439
 1440
 1441
 1442
 1443
 1444
 1445
 1446
 1447
 1448
 1449
 1450
 1451
 1452
 1453
 1454
 1455
 1456
 1457

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.

469
 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*

474
 475
 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.

487

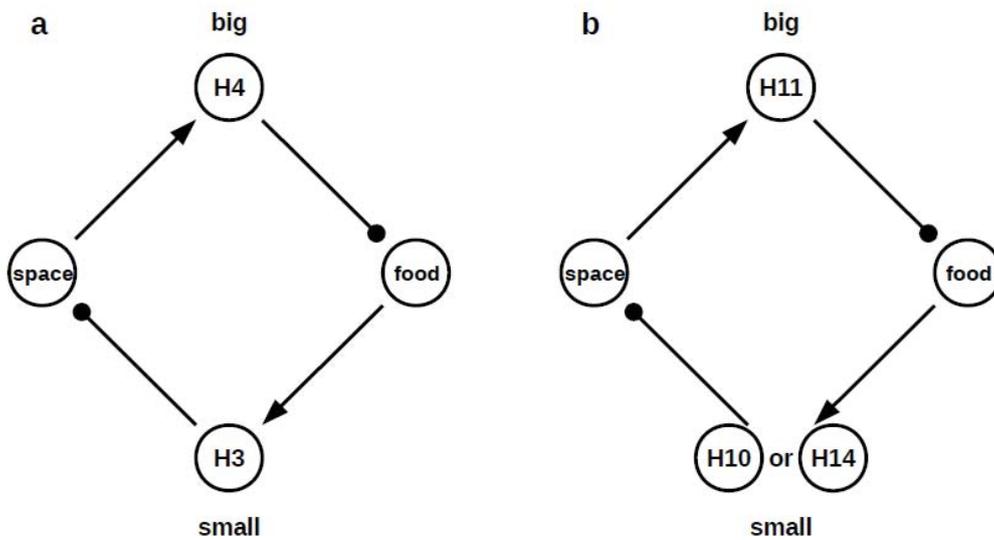


Fig. 4. Positive feedback cycles from a) SD1 (see Fig. 2) and b) SD2 (see Fig. 3). Each feedback cycle links the basic resources of food and space with one big and one small functional group. Links ending in arrows and filled circles represent positive and negative direct effects, respectively

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

1517
1518
1519
1520
1521
1522
1523
1524
1525
1526
1527
1528
1529
1530
1531
1532
1533
1534
1535
1536
1537
1538
1539
1540
1541
1542
1543
1544
1545
1546
1547
1548
1549
1550
1551
1552
1553
1554
1555
1556
1557
1558
1559
1560
1561
1562
1563
1564
1565
1566
1567
1568
1569
1570
1571
1572
1573
1574
1575

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,

1576
1577
1578 529 biological traits were used as proxies for the role of functional groups in a set of
1579
1580 530 theoretically expected community assembly mechanisms that were illustrated through
1581
1582 531 a highly abstract representation of the system.
1583

1584 532 For instance, the biogeochemical aspects of sediment engineering were not
1585
1586 533 explicitly represented, as the distinction between sediment stabilizers and
1587
1588 534 destabilizers (Posey, 1987) was the best possible representation, given the available
1589
1590 535 information at the species level. Still, this tenet of the mobility-mode hypothesis has
1591
1592 536 been empirically upheld and shown to have cascading and long-lasting effects on
1593
1594 537 benthic communities (Volkenborn et al., 2009). Similarly, the complex set of
1595
1596 538 processes that comprise the phenomenon of resource competition was only
1597
1598 539 represented through the use of each group's maximum size in the context of the
1600
1601 540 concentration reduction hypothesis for space and food (Tilman, 1980). Space
1602
1603 541 limitation due to adult–juvenile interactions and exploitative competition for food have
1604
1605 542 been shown to play a central role in the successional dynamics of benthic
1606
1607 543 communities, with the functional role of organisms largely defined by their size (Van
1608
1609 544 Colen et al., 2008). The combined representation of food and space as limiting
1610
1611 545 resources can significantly increase our understanding and predictability of marine
1612
1613 546 benthic systems (Svensson and Marshall, 2015).

1614 547 The separation of benthic macroinvertebrates into algae/detritus feeders and
1615
1616 548 predators/scavengers aimed to preserve the homogeneity of their resource base, so
1617
1618 549 that theoretically expected community assembly mechanisms could be implemented.
1619
1620 550 This choice might appear to ignore important differentiations in the feeding habits of
1621
1622 551 these organisms, such as the distinction between suspension- and deposit-feeders. It
1623
1624 552 has been, however, shown that feeding behaviour in the marine benthos is highly
1625
1626 553 facultative and similar categorizations are not always valid (Snelgrove and Butman,
1627
1628
1629
1630
1631
1632
1633
1634

1635
1636
1637
1638
1639
1640
1641
1642
1643
1644
1645
1646
1647
1648
1649
1650
1651
1652
1653
1654
1655
1656
1657
1658
1659
1660
1661
1662
1663
1664
1665
1666
1667
1668
1669
1670
1671
1672
1673
1674
1675
1676
1677
1678
1679
1680
1681
1682
1683
1684
1685
1686
1687
1688
1689
1690
1691
1692
1693

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,

1694
1695
1696
1697
1698
1699
1700
1701
1702
1703
1704
1705
1706
1707
1708
1709
1710
1711
1712
1713
1714
1715
1716
1717
1718
1719
1720
1721
1722
1723
1724
1725
1726
1727
1728
1729
1730
1731
1732
1733
1734
1735
1736
1737
1738
1739
1740
1741
1742
1743
1744
1745
1746
1747
1748
1749
1750
1751
1752

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).

590
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.

1753
1754
1755
1756
1757
1758
1759
1760
1761
1762
1763
1764
1765
1766
1767
1768
1769
1770
1771
1772
1773
1774
1775
1776
1777
1778
1779
1780
1781
1782
1783
1784
1785
1786
1787
1788
1789
1790
1791
1792
1793
1794
1795
1796
1797
1798
1799
1800
1801
1802
1803
1804
1805
1806
1807
1808
1809
1810
1811

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).

616
617 5

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

1812
1813
1814
1815
1816
1817
1818
1819
1820
1821
1822
1823
1824
1825
1826
1827
1828
1829
1830
1831
1832
1833
1834
1835
1836
1837
1838
1839
1840
1841
1842
1843
1844
1845
1846
1847
1848
1849
1850
1851
1852
1853
1854
1855
1856
1857
1858
1859
1860
1861
1862
1863
1864
1865
1866
1867
1868
1869
1870

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 (Boulangéat 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
648 Acknowledgments: We thank Claire Chevalier, Stanislas F. Dubois, Antoine Carlier
649 and Patrick Le Mao for sharing their knowledge of the system and assisting in the
650 collection of biological traits information. We are also grateful to the editor and

1871
1872
1873 651 anonymous reviewers for comments that substantially improved the manuscript. This
1874
1875 652 work was supported by LabexMer French project (ANR-10-LABX-19-01).
1876
1877 653
1878
1879 654 References
1880
1881 655 Alexandridis, N., 2017. Models of general community assembly mechanisms
1882
1883 656 simulating the spatial and temporal dynamics of benthic biodiversity. PhD
1884
1885 657 Thesis. Université de Bretagne Occidentale, Brest, France.
1886
1887 658 <http://archimer.ifremer.fr/doc/00383/49481/>
1888
1889
1890 659 Alexandridis, N., Bacher, C., Desroy, N., Jean, F., 2017. Building functional groups of
1891
1892 660 marine benthic macroinvertebrates on the basis of general community assembly
1893
1894 661 mechanisms. J. Sea Res. 121, 59-70.
1895
1896 662 Amarasekare, P., 2003. Competitive coexistence in spatially structured environments:
1897
1898 663 a synthesis. Ecol. Lett. 6, 1109-1122.
1899
1900 664 Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J., Brose, U., 2009.
1901
1902 665 Simple prediction of interaction strengths in complex food webs. P. Natl. Acad.
1903
1904 666 Sci. USA 106, 187-191.
1905
1906 667 Blackburn, T.M., Gaston, K.J., 1994. Animal body size distributions: patterns,
1907
1908 668 mechanisms and implications. Trends Ecol. Evol. 9, 471-474.
1909
1910 669 Bonnot-Courtois, C., Lafond, L.R., 1991. Caractérisation et comportement des vases
1911
1912 670 dans l'estuaire de la Rance. Rapport EDF. EPHE, Dinard, France.
1913
1914 671 Boulangeat, I., Georges, D., Thuiller, W., 2014. FATE-HD: a spatially and temporally
1915
1916 672 explicit integrated model for predicting vegetation structure and diversity at
1917
1918 673 regional scale. Glob. Change Biol. 20, 2368-2378.
1919
1920 674 Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne, S.,
1921
1922 675 Lavorel, S., van Es, J., Vittoz, P., Thuiller, W., 2012. Improving plant functional
1923
1924
1925
1926
1927
1928
1929

1930
1931
1932 676 groups for dynamic models of biodiversity: at the crossroads between functional
1933
1934 677 and community ecology. *Glob. Change Biol.* 18, 3464-3475.
1935
1936 678 Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F.,
1937
1938
1939 679 Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L.,
1940
1941 680 Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E.,
1942
1943 681 Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner,
1944
1945 682 T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G.,
1946
1947 683 Cohen, J.E., 2006a. Consumer-resource body-size relationships in natural food
1948
1949 684 webs. *Ecology* 87, 2411-2417.
1950
1951 685 Brose, U., Williams, R.J., Martinez, N.D., 2006b. Allometric scaling enhances stability
1952
1953 686 in complex food webs. *Ecol. Lett.* 9, 1228-1236.
1954
1955 687 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P.,
1956
1957 688 Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C.,
1958
1959 689 Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012.
1960
1961 690 Biodiversity loss and its impact on humanity. *Nature* 486, 59-67.
1962
1963
1964 691 Carey, M.P., Levin, P.S., Townsend, H., Minello, T.J., Sutton, G.R., Francis, T.B.,
1965
1966 692 Harvey, C.J., Toft, J.E., Arkema, K.K., Burke, J.L., Kim, C.K., Guerry, A.D.,
1967
1968 693 Plummer, M., Spiridonov, G., Ruckelshaus, M., 2014. Characterizing coastal
1969
1970 694 foodwebs with qualitative links to bridge the gap between the theory and the
1971
1972 695 practice of ecosystem-based management. *ICES J. Mar. Sci.* 71, 713-724.
1973
1974
1975 696 Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R., Gabriel, J.P.,
1976
1977 697 2004. Phylogenetic constraints and adaptation explain food-web structure.
1978
1979 698 *Nature* 427, 835-839.
1980
1981 699 Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev.*
1982
1983 700 *Ecol. Syst.* 31, 343-366.
1984
1985
1986
1987
1988

1989
1990
1991 701 Cohen, J.E., Newman, C.M., 1985. A stochastic theory of community food webs. I.
1992
1993 702 Models and aggregated data. Proc. R. Soc. Lond. Ser. B 224, 421-448.
1994
1995 703 Cohen, J.E., Pimm, S.L., Yodzis, P., Saldaña, J., 1993. Body sizes of animal
1996 704 predators and animal prey in food webs. J. Anim. Ecol. 62, 67-78.
1997
1998 705 Connell, J.H., 1983. On the prevalence and relative importance of interspecific
1999 706 competition: evidence from field experiments. Am. Nat. 122, 661-696.
2000
2001 707 Constable, A.J., 1999. Ecology of benthic macro-invertebrates in soft-sediment
2002 708 environments: A review of progress towards quantitative models and
2003 709 predictions. Aust. J. Ecol. 24, 452-476.
2004
2005 710 Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg,
2006 711 K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt,
2007 712 M., 1998. The value of the world's ecosystem services: putting the issues in
2008 713 perspective. Ecol. Econ. 25, 67-72.
2009
2010 714 Dambacher, J.M., Brewer, D.T., Dennis, D.M., Macintyre, M., Foale, S., 2007.
2011 715 Qualitative modelling of gold mine impacts on Lihir island's socioeconomic
2012 716 system and reef-edge fish community. Environ. Sci. Technol. 41, 555-562.
2013
2014 717 Dambacher, J.M., Li, H.W., Rossignol, P.A., 2002. Relevance of community structure
2015 718 in assessing indeterminacy of ecological predictions. Ecology 83, 1372-1385.
2016
2017 719 Dambacher, J.M., Luh, H.K., Li, H.W., Rossignol, P.A., 2003. Qualitative stability and
2018 720 ambiguity in model ecosystems. Am. Nat. 161, 876-888.
2019
2020 721 Desroy, N., 1998. Les peuplements benthiques de substrats meubles du bassin
2021 722 maritime de la Rance. Évolution de la biodiversité et effets de l'activité
2022 723 prédatrice de *Nephtys hombergii* (Annélide Polychète). PhD Thesis. Université
2023 724 de Rennes 1, Rennes, France.
2024
2025
2026
2027
2028
2029
2030
2031
2032
2033
2034
2035
2036
2037
2038
2039
2040
2041
2042
2043
2044
2045
2046
2047

2048
2049
2050 725 Fath, B.D., 2004. Network analysis applied to large-scale cyber-ecosystems. *Ecol.*
2051
2052 726 *Model.* 171, 329–337.
2053
2054 727 Halnes, G., Fath, B.D., Liljenström, H., 2007. The modified niche model: including
2055
2056 728 detritus in simple structural food web models. *Ecol. Model.* 208, 9-16.
2057
2058
2059 729 Hérault, B., 2007. Reconciling niche and neutrality through the Emergent Group
2060
2061 730 approach. *Perspect. Plant Ecol.* 9, 71-78.
2062
2063 731 Herman, P., Middelburg, J., Van de Koppel, J., Heip, C., 1999. Ecology of estuarine
2064
2065 732 macrobenthos. *Adv. Ecol. Res.* 29, 195-240.
2066
2067 733 Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F.,
2068
2069 734 Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E.,
2070
2071 735 Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H., Woodward, G.,
2072
2073 736 2009. Ecological networks – beyond food webs. *J. Anim. Ecol.* 78, 253-269.
2074
2075
2076 737 Jetz, W., Carbone, C., Fulford, J., Brown, J.H., 2004. The scaling of animal space
2077
2078 738 use. *Science* 306, 266-268.
2079
2080 739 Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological
2081
2082 740 and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334-350.
2083
2084 741 Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit,
2085
2086 742 A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A.,
2087
2088 743 Blanchette, C.A., Iles, A.C., Brose, U., 2012. More than a meal... integrating
2089
2090 744 non-feeding interactions into food webs. *Ecol. Lett.* 15, 291-300.
2091
2092
2093 745 Levins, R., 1998. Qualitative mathematics for understanding, prediction, and
2094
2095 746 intervention in complex ecosystems. In: *Ecosystem Health*. Blackwell Science,
2096
2097 747 Oxford, UK.
2098
2099 748 Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 54,
2100
2101 749 421-431.
2102
2103
2104
2105
2106

2107
2108
2109 750 Limberger, R., Wickham, S.A., 2011. Competition–colonization trade-offs in a ciliate
2110
2111 751 model community. *Oecologia* 167, 723-732.
2112
2113 752 Lindquist, N., Hay, M.E., 1996. Palatability and chemical defense of marine
2114
2115 753 invertebrate larvae. *Ecol. Monogr.* 66, 431-450.
2116
2117
2118 754 Lyons, K.G., Brigham, C.A., Traut, B.H., Schwartz, M.W., 2005. Rare species and
2119
2120 755 ecosystem functioning. *Conserv. Biol.* 19, 1019-1024.
2121
2122 756 Maplesoft, 2014. Maple. Waterloo Maple Inc., Waterloo, Canada.
2123
2124 757 Marshall, D.J., Steinberg, P.D., 2014. Larval size and age affect colonization in a
2125
2126 758 marine invertebrate. *J. Exp. Biol.* 217, 3981-3987.
2127
2128 759 Marzloff, M.P., Dambacher, J.M., Johnson, C.R., Little, L.R., Frusher, S.D., 2011.
2129
2130 760 Exploring alternative states in ecological systems with a qualitative analysis of
2131
2132 761 community feedback. *Ecol. Model.* 222, 2651-2662.
2133
2134 762 McLean, E.L., Lasker, H.R., 2013. Height matters: position above the substratum
2135
2136 763 influences the growth of two demosponge species. *Mar. Ecol.* 34, 122-129.
2137
2138
2139 764 Meadows, P.S., Meadows, A., Murray, J.M.H., 2012. Biological modifiers of marine
2140
2141 765 benthic seascapes: their role as ecosystem engineers. *Geomorphology* 157-
2142
2143 766 158, 31-48.
2144
2145 767 Morris, J.T., Christian, R.R., Ulanowicz, R.E., 2005. Analysis of size and complexity
2146
2147 768 of randomly constructed food webs by information theoretic metrics. In:
2148
2149 769 Belgrano, A., Scharler, U.M., Dunne, J., Ulanowicz, R.E. (Eds.), *Aquatic food*
2150
2151 770 *webs: an ecosystem approach*. Oxford University Press, Oxford, UK.
2152
2153
2154 771 Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M.,
2155
2156 772 Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, T.C.E., Renaud, J.,
2157
2158 773 Thuiller, W., 2013. Rare species support vulnerable functions in high-diversity
2159
2160 774 ecosystems. *PLOS Biol.* 11, e1001569.
2161
2162
2163
2164
2165

2166
2167
2168 775 Ortiz, M., Wolff, M., 2002. Application of loop analysis to benthic systems in northern
2169
2170 776 Chile for the elaboration of sustainable management strategies. *Mar. Ecol.-Prog.*
2171
2172 Ser. 242, 15-27.
2173 777
2174
2175 778 Pascual, M.S., 1997. Carriage of dwarf males by adult female puelche oysters: the
2176
2177 779 role of chitons. *J. Exp. Mar. Biol. Ecol.* 212, 173-185.
2178
2179 780 Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W.,
2180
2181 781 Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung,
2182
2183 782 W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C.,
2184
2185 783 Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P.,
2186
2187 784 Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global
2188
2189 785 biodiversity in the 21st century. *Science* 330, 1496-1501.
2190
2191 786 Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. Size, foraging, and
2192
2193 787 food web structure. *P. Natl. Acad. Sci. USA* 105, 4191-4196.
2194
2195
2196 788 Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking
2197
2198 789 forward. *Ecol. Lett.* 9, 741-758.
2199
2200 790 Pineda, J., Reyns, N.B., Starczak, V.R., 2009. Complexity and simplification in
2201
2202 791 understanding recruitment in benthic populations. *Popul. Ecol.* 51, 17-32.
2203
2204 792 Posey, M.H., 1987. Influence of relative mobilities on the composition of benthic
2205
2206 793 communities. *Mar. Ecol.-Prog. Ser.* 39, 99-104.
2207
2208
2209 794 Puccia, C.J., Levins, R., 1985. Qualitative modeling of complex systems. Harvard
2210
2211 795 University Press, Cambridge, USA.
2212
2213 796 Queirós, A.M., Bruggeman, J., Stephens, N., Artioli, Y., Butenschön, M., Blackford,
2214
2215 797 J.C., Widdicombe, S., Allen, J.I., Somerfield, P.J., 2015. Placing biodiversity in
2216
2217 798 ecosystem models without getting lost in translation. *J. Sea Res.* 98, 83-90.
2218
2219
2220
2221
2222
2223
2224

2225
2226
2227 799 Reiss, H., Degraer, S., Duineveld, G.C.A., Kröncke, I., Aldridge, J., Craeymeersch,
2228
2229 800 J.A., Eggleton, J.D., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Pohlmann, T.,
2230
2231 801 Rachor, E., Robertson, M., Vanden Berghe, E., van Hoey, G., Rees, H.L., 2010.
2232
2233 802 Spatial patterns of infauna, epifauna, and demersal fish communities in the
2234
2235 803 North Sea. ICES J. Mar. Sci. 67, 278-293.
2236
2237
2238 804 Retière, C., 1994. Tidal power and the aquatic environment of La Rance. Biol. J. Linn.
2239
2240 805 Soc. 51, 25-36.
2241
2242 806 Reum, J.C.P., McDonald, P.S., Ferriss, B.E., Farrell, D.M., Harvey, C.J., Levin, P.S.,
2243
2244 807 2015. Qualitative network models in support of ecosystem approaches to
2245
2246 808 bivalve aquaculture. ICES J. Mar. Sci. 72, 2278-2288.
2247
2248
2249 809 Rex, M.A., Etter, R.J., 1998. Bathymetric patterns of body size: implications for deep-
2250
2251 810 sea biodiversity. Deep-Sea Res. Pt. II 45, 103-127.
2252
2253 811 Robinson, L.A., Greenstreet, S.P.R., Reiss, H., Callaway, R., Craeymeersch, J., de
2254
2255 812 Boois, I., Degraer, S., Ehrich, S., Fraser, H.M., Goffin, A., Kröncke, I.,
2256
2257 813 Jorgenson, L.L., Robertson, M.R., Lancaster, J., 2010. Length–weight
2258
2259 814 relationships of 216 North Sea benthic invertebrates and fish. J. Mar. Biol.
2260
2261 815 Assoc. UK 90, 95-104.
2262
2263 816 Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., Charnov, E.L., 2004. Effects of
2264
2265 817 body size and temperature on population growth. Am. Nat. 163, 429-441.
2266
2267
2268 818 Scherer, C., Jeltsch, F., Grimm, V., Blaum, N., 2016. Merging trait-based and
2269
2270 819 individual-based modelling: An animal functional type approach to explore the
2271
2272 820 responses of birds to climatic and land use changes in semi-arid African
2273
2274 821 savannas. Ecol. Model. 326, 75-89.
2275
2276 822 Schratzberger, M., Larcombe, P., 2014. The role of the sedimentary regime in
2277
2278 823 shaping the distribution of subtidal sandbank environments and the associated
2279
2280
2281
2282
2283

2284
2285
2286 824 meiofaunal nematode communities: an example from the southern North Sea.
2287
2288 825 PLoS ONE 9, e109445.
2289
2290 826 Snelgrove, P.V.R., Butman, C.A., 1994. Animal-sediment relationships revisited:
2291
2292 cause versus effect. *Oceanogr. Mar. Biol.* 32, 111-177.
2293 827
2294
2295 828 Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D.,
2296
2297 829 Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., Iocco, L.,
2298
2299 830 Valenete, R., Watson, J., Rosenberg, R., 2003. Towards a greater
2300
2301 831 understanding of pattern, scale and process in marine benthic systems: a
2302
2303 832 picture is worth a thousand worms. *J. Exp. Mar. Biol. Ecol.* 285-286, 313-338.
2304
2305 833 Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T.,
2306
2307 834 Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails,
2308
2309 835 R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G.,
2310
2311 836 Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y.,
2312
2313 837 Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves,
2314
2315 838 D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A.,
2316
2317 839 Wardle, D.A., Wiegand, T., 2013. Identification of 100 fundamental ecological
2318
2319 840 questions. *J. Ecol.* 101, 58-67.
2320
2321 841 Svensson, J.R., Marshall, D.J., 2015. Limiting resources in sessile systems: food
2322
2323 842 enhances diversity and growth of suspension feeders despite available space.
2324
2325 843 *Ecology* 96, 819-827.
2326
2327 844
2328
2329 844 Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition
2330
2331 845 and succession. *Oikos* 58, 3-15.
2332
2333 846
2334
2335 847 Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and
2336
2337 predation. *Am. Nat.* 116, 362-393.
2338
2339
2340
2341
2342

2343
2344
2345 848 Tyler, E.H.M., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead,
2346
2347 849 O., Palomares, M.L.D., Webb, T.J., 2012. Extensive gaps and biases in our
2348
2349 850 knowledge of a well-known fauna: implications for integrating biological traits
2350
2351 851 into macroecology. *Global Ecol. Biogeogr.* 21, 922-934.
2352
2353
2354 852 Van Colen, C., Montserrat, F., Vincx, M., Herman, P.M.J., Ysebaert, T., Degraer, S.,
2355
2356 853 2008. Macrobenthic recovery from hypoxia in an estuarine tidal mudflat. *Mar.*
2357
2358 854 *Ecol. Prog. Ser.* 372, 31-42.
2359
2360 855 Volkenborn, N., Robertson, D.M., Reise, K., 2009. Sediment destabilizing and
2361
2362 856 stabilizing bio-engineers on tidal flats: cascading effects of experimental
2363
2364 857 exclusion. *Helgoland Mar. Res.* 63, 27-35.
2365
2366
2367 858 Wahl, M., Mark, O., 1999. The predominantly facultative nature of epibiosis:
2368
2369 859 experimental and observational evidence. *Mar. Ecol.-Prog. Ser.* 187, 59-66.
2370
2371 860 Westfahl, P., Heath, Z., Woodrow, C., 2002. Powerplay Digraph Editor. Loop Group
2372
2373 861 Dev Team, Corvallis, USA.
2374
2375 862 Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. *Nature*
2376
2377 863 404, 180-183.
2378
2379 864 Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido,
2380
2381 865 A., Warren, P.H., 2005. Body size in ecological networks. *Trends Ecol. Evol.* 20,
2382
2383 866 402-409.
2384
2385 867 Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. *Am. Nat.*
2386
2387 868 139, 1151-1175.
2388
2389
2390
2391
2392
2393
2394
2395
2396
2397
2398
2399
2400
2401

2402
2403
2404 **SUPPLEMENTARY MATERIAL**
2405

2406 **S.1 Environmental filtering**

2407 **S.1.1 Methods**
2408

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.
2438

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
2443
2444
2445
2446
2447
2448
2449
2450
2451

2461
2462
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.
2468
2469

2470
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.
2481
2482
2483
2484
2485
2486
2487
2488

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).
2505
2506
2507
2508
2509
2510

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
2515
2516
2517
2518
2519

epifaunal position (T9) and the role of basibionts (T13). These trait values, along with the one that identifies epibiotic organisms (T13) and is associated with increasing water depth, are all characteristic of benthos that occupies the surface of the seabed, supported by structure of abiotic or biotic origin. Increasing water depth is further associated with a transition from organisms that tolerate tidal exposure to those that have to be submerged in high salinity levels (T5).

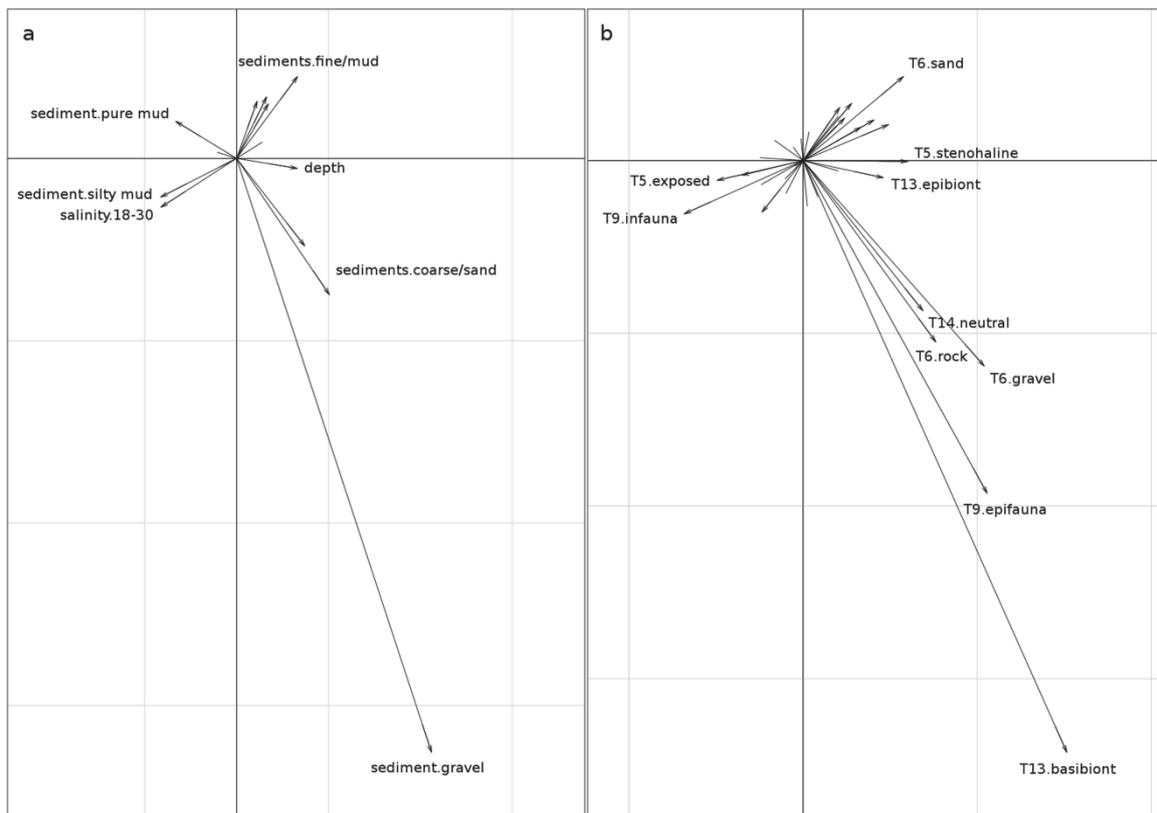


Fig. S1 Projection of a) environmental variables and b) biological traits on the first two dimensions of the common co-inertia space of the RLQ analysis. In both graphs the horizontal axis represents the first dimension and the vertical the second. In the case of continuous and ordinal variables, the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

S.2 Functional trade-offs

S.2.1 Methods

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

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

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

S.2.2 Results

The eigenvalues decomposition of Hill and Smith for the biological traits data set shows that about twice as much variation can be found along each of the first two axes (15% and 14% of total variation) compared to each of the two axes that follow (8% and 7% of total

2638
2639
2640 variation). The first four axes combined represent just over 43% of the total variation of
2641
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
2672
2673 (T10), destabilizing organisms (T14) that have a preference for coarser and mixed sediment
2674
2675 types (T6).
2676
2677
2678
2679
2680
2681
2682
2683
2684
2685
2686
2687
2688
2689
2690
2691
2692
2693
2694
2695
2696

2697
2698
2699
2700
2701
2702
2703
2704
2705
2706
2707
2708
2709
2710
2711
2712
2713
2714
2715
2716
2717
2718
2719
2720
2721
2722
2723
2724
2725
2726
2727
2728
2729
2730
2731
2732
2733
2734
2735
2736
2737
2738
2739
2740
2741
2742
2743
2744
2745
2746
2747
2748
2749
2750
2751
2752
2753
2754
2755

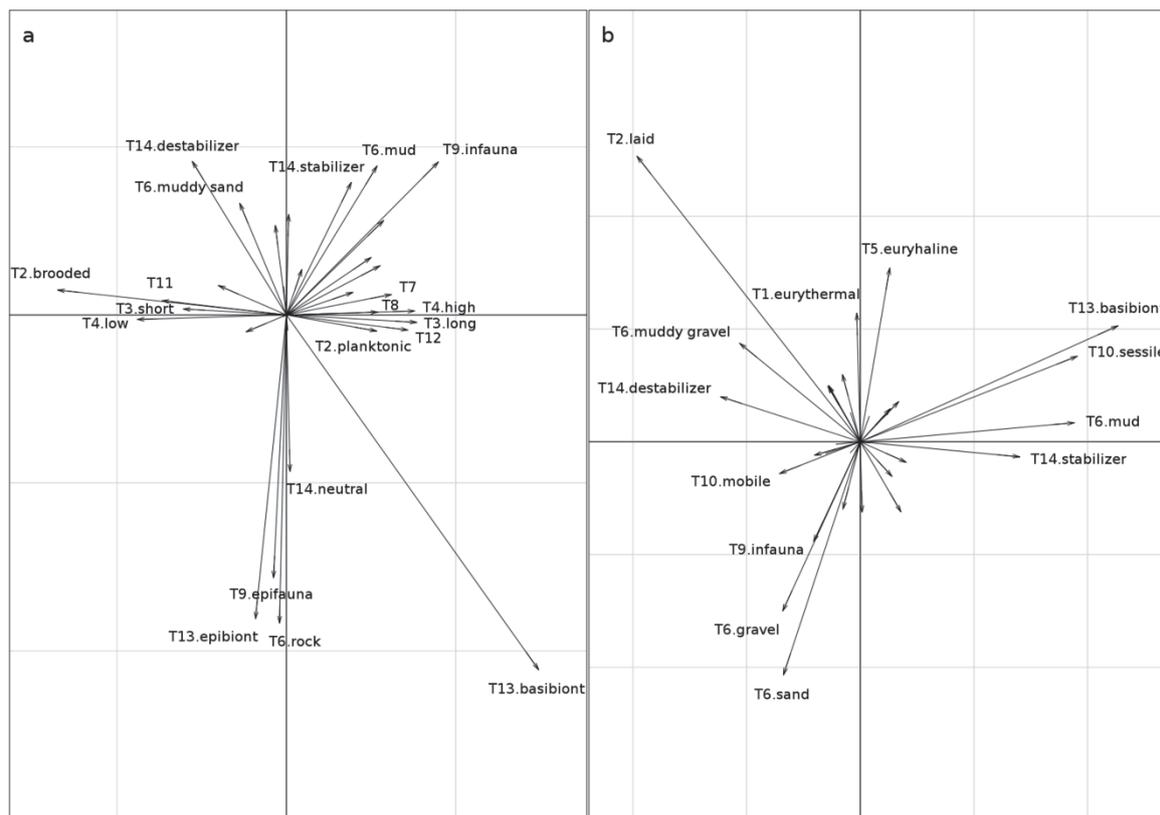


Fig. S2 Projection of biological traits on a) the first and second and b) the third and fourth dimensions of the transformed multivariate space of Hill and Smith analysis. In both graphs the horizontal axis represents the lower dimension and the vertical the higher. In the case of continuous and ordinal 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

2756
2757
2758 **References**
2759

- 2760 Bonnot-Courtois, C., 1997. Evolution de la répartition des sédiments dans l'estuaire de la
2761 Rance, 1883-1994. Atlas Permanent de la Mer et du Littoral 3, 29.
2762
- 2763 Desroy, N., 1998. Les peuplements benthiques de substrats meubles du bassin maritime de la
2764 Rance. Évolution de la biodiversité et effets de l'activité prédatrice de *Nephtys*
2765 *hombergii* (Annélide Polychète). PhD Thesis. Université de Rennes 1, Rennes, France.
2766
- 2767 Dolédec, S., Chessel, D., Ter Braak, C.J.F., Champely, S., 1996. Matching species traits to
2768 environmental variables: a new three-table ordination method. Environ. Ecol. Stat. 3,
2769 143-166.
2770
- 2771 Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for
2772 ecologists. J. Stat. Softw. 22, 1-20.
2773
- 2774 Hill, M.O., Smith, A.J.E., 1976. Principal component analysis of taxonomic data with multi-
2775 state discrete characters. Taxon 25, 249-255.
2776
- 2777 Legendre, P., Legendre, L., 1998. Numerical ecology. Second English edition. Elsevier,
2778 Amsterdam, Netherlands.
2779
- 2780 Posey, M.H., 1987. Influence of relative mobilities on the composition of benthic communities.
2781 Mar. Ecol.-Prog. Ser. 39, 99-104.
2782
- 2783 R Core Team, 2015. R: a language and environment for statistical computing. R Foundation
2784 for Statistical Computing, Vienna, Austria.
2785
- 2786 Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation.
2787 Am. Nat. 116, 362-393.
2788
- 2789 Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and
2790 succession. Oikos 58, 3-15.
2791
2792
2793
2794
2795
2796
2797
2798
2799
2800
2801
2802
2803
2804
2805
2806
2807
2808
2809
2810
2811
2812
2813
2814