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## **Cross-taxon congruence in the rarity of subtidal rocky marine assemblages: No taxonomic shortcut for conservation monitoring**

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1           **Cross-taxon congruence in the rarity of subtidal rocky marine**  
2           **assemblages: no taxonomic shortcut for conservation monitoring**

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22 **Abstract**

23 The implementation of protection strategies such as the European Marine Strategy Framework  
24 Directive (2008/56/EC) is impeded for subtidal rock bottom habitats because of high sampling  
25 costs due to a very wide taxonomic diversity, and a lack of suitable evaluation tools to estimate  
26 their conservation importance. In this study, we seek to provide an evaluation procedure by (1)  
27 investigating the distribution of rarity among subtidal rock bottom phyla; (2) searching for  
28 potential surrogate phyla with a cross-taxon congruence approach based on their rarity; (3)  
29 proposing an appropriate multi-phyla indicator to evaluate the importance of subtidal rocky  
30 habitats for conservation. We analysed the distribution of 548 species belonging to 8 phyla  
31 sampled in 137 assemblages in subtidal rocky areas located around Brittany, Western France.  
32 We applied the Index of Relative Rarity, a flexible method which fits rarity weights to species  
33 depending on their respective phyla. We found only weak congruence in rarity patterns among  
34 phyla, which prevented any attempt to identify surrogate phyla. This finding has important  
35 implications for the conservation of subtidal rocky habitats as it means that there is no shortcut  
36 to monitor their rarity: working on a subset of phyla would imply a biased evaluation of  
37 biodiversity. Consequently, we propose a multi-phyla Index of Relative Rarity combining all  
38 phyla which allowed us to successfully describe rarity patterns across all sampled sites.

39

40 **Key-words**

41 Occurrence-based rarity, subtidal conservation, rare species, Brittany

42

## 43 **1 Introduction**

44 To mitigate the ongoing loss of marine biodiversity, the European Union has successively  
45 adopted several directives aiming at protecting and conserving marine habitats, ecosystems and  
46 biological diversity: the OSPAR convention (1998), the habitat directive (HD, 92/43/EEC, 1992),  
47 the Natura 2000 network, and more recently the Marine Strategy Framework Directive (MSFD;  
48 2008/56/EC) (2010). Effectively preserving marine biodiversity requires the evaluation and  
49 monitoring of the diversity of different marine taxonomic groups and habitats. With respect to  
50 benthic subtidal habitats, much of the literature has focused on subtidal soft bottom habitats for  
51 which a plethora of tools is available (van Rein et al., 2009). On the other hand, rocky subtidal  
52 habitats remain poorly evaluated because of the difficulties and costs of sampling these  
53 diversified habitats. This lack of consideration impedes their inclusion in the implementation of  
54 European directives, in spite of their high taxonomic diversity and functional role. Consequently,  
55 researchers need to both optimise sampling procedures (Gallon et al., 2013) and identify  
56 potential surrogates that could be used to describe biodiversity based on a reduced set of data.  
57 In this study, we seek to identify biodiversity surrogates as one facet of the importance of  
58 subtidal rocky habitats for conservation, hereby not focusing on other equally important facets  
59 such as ecosystem functioning.

60 The concept of biodiversity surrogates has been extensively explored in the conservation  
61 literature and needs to be refined to be relevant to rocky subtidal habitats. Biodiversity  
62 surrogates fall in two main categories (Grantham et al., 2010): environmental surrogates, which  
63 use a combination of physical and biological data to estimate or predict biodiversity, and  
64 taxonomic surrogates, predominantly based on the use of one or several taxonomic groups to  
65 estimate biodiversity. We focus here on the second category, i.e. the identification of surrogate  
66 phyla by cross-taxon congruence, since it has been advocated as appropriate to predict patterns  
67 of marine biodiversity for conservation purposes when data are scarce (Mellin et al., 2011). The  
68 identification of surrogate taxa in marine habitats has mostly been based on species richness  
69 (Mellin et al., 2011) and, to a lesser extent, on multivariate patterns of assemblage structure  
70 (e.g., Hirst 2008, Smale 2010, Sutcliffe et al. 2012). However, it has been suggested that species  
71 richness is not appropriate because of high spatial and taxonomic variability (Su et al., 2004).  
72 More importantly, species richness is not a good enough indicator for biodiversity conservation  
73 as it does not take the identity of species into account or their varying degrees of vulnerability to  
74 extinction (e.g., Orme et al. 2005). Alternatively, surrogacy across taxa can be assessed by  
75 studying congruency of rarity across assemblages of species, an appropriate approach for taxa  
76 with limited data availability (Leroy et al., 2013, 2012). The choice of rarity as a criterion is  
77 based on the greater extinction risk of rare species relative to ecologically similar common  
78 species (Flather and Sieg, 2007; Gaston, 1994; Roberts and Hawkins, 1999), because they are  
79 appropriate indicators for other species of conservation concern (Larsen et al., 2007; Lawler et  
80 al., 2003), and because they have been shown to sometime support unique ecosystem functions  
81 unsupported by other species (Mouillot et al., 2013).

82 It has been established repeatedly that a large proportion of intertidal and subtidal marine  
83 benthic species exhibit narrow geographic ranges (see for instance Sanderson 1996, Chapman  
84 1999). Therefore the frequency distributions of benthic marine species range size are typically  
85 strongly right-skewed with a large number of low occurrence species at local or regional scales  
86 (Ellingsen et al., 2007) similar to terrestrial taxa (Gaston, 1994; Gaston and Blackburn, 2000).  
87 Hence, testing the ability of the rarity of surrogate taxa to capture the rarity of other taxa may

88 help to substantially reduce the cost of sampling protocols to evaluate the rarity of subtidal  
89 assemblages.

90 The methods used to measure rarity in species assemblages must be chosen carefully, because  
91 several methods have been proven to provide inappropriate results under particular conditions  
92 (Leroy et al., 2012). Hence, Leroy et al. (2012) proposed a new, flexible method to assess the  
93 rarity of species assemblages (the Index of Relative Rarity) with respect to the considered phyla.  
94 The rationale of this method is that rarity should be defined according to the taxon considered;  
95 therefore an inflexible method may bias the analysis toward a particular phylum. Indeed, the  
96 threshold of geographic range size below which species are considered rare is generally defined  
97 specifically for each particular phylum because of the large differences in range size among  
98 phyla (Grenyer et al., 2006). This rationale is especially important for subtidal rocky habitats  
99 because the diversity of their phyla may result in very different rarity patterns among phyla.

100 We aimed to investigate patterns of rarity and cross-taxon congruency among sessile and low-  
101 mobility animal phyla of subtidal rocky areas, based on the Index of Relative Rarity developed by  
102 Leroy et al. (2012). The opportunity for such an approach was offered by the compilation of a  
103 database from 137 inventories of assemblages of subtidal rocky habitats around the Brittany  
104 (western France) coast. These inventories were sampled between 1993 and 1998 by biologist  
105 scuba divers of the “Association pour la Découverte du Monde Marin” (Girard-Descatoire et al.,  
106 2000, 1999, 1998, 1997, 1996a, 1996b, 1996c, 1995, 1993; L’Hardy-Halos et al., 2001; L’Hardy-  
107 Halos and Castric-Fey, 2000a, 2000b, 2001) in addition to samples by our diving team from 2005  
108 to 2009. Because this database was initially not designed for such analyses, it may contain biases  
109 that could have a negative impact on the outcomes of our study (Pearman et al., 2006). Hence,  
110 we applied a completeness metric to assess sampling quality across sites and phyla (Soberón et  
111 al., 2007), and improved our database by applying appropriate corrections.

112 The objectives of this study are to (1) investigate the distribution of rarity among the sampled  
113 phyla, in order to calculate appropriate rarity metrics for each phylum; (2) search for potential  
114 surrogate phyla with a cross-taxon congruence approach on the rarity of assemblages of species;  
115 (3) propose a multi-phyla indicator and discuss its potential use to evaluate the importance of  
116 monitored subtidal rocky habitats for conservation.

117

## 118 **2 Material and Methods**

### 119 *2.1 Database compilation*

120 We compiled a database on the biodiversity of benthic assemblages of species of subtidal rocky  
121 habitats around Brittany based on 122 inventories sampled between 1993 and 1998 by biologist  
122 scuba divers (Girard-Descatoire et al., 2000, 1999, 1998, 1997, 1996a, 1996b, 1996c, 1995,  
123 1993; L'Hardy-Halos et al., 2001; L'Hardy-Halos and Castric-Fey, 2000a, 2000b, 2001), and 15  
124 inventories sampled by our diving team from 2005 to 2009.

125 The inventories were grouped into 13 major sites around the Brittany coast, with 4 to 20  
126 inventories per site. The 13 sites span the range of conditions around Brittany: estuaries and  
127 inland seas (Morbihan gulf, Etel ria, Brest bay, Rance estuary), open bays (Lannion bay, St Malo  
128 bay, Morlaix bay, Iroise sea), coastal sites (Granite rose coast, Crozon peninsula, Cape Sizun) and  
129 islands (Sept-Îles archipelago, Ushant island). These inventories of species presence-absence  
130 focused on benthic rocky communities between the infralittoral fringe and the nearest  
131 circalittoral, and were limited to depths of 30 m.

132 In this substantial inventory, eight animal taxa (conveniently called “phyla” in this paper) were  
133 kept for our analyses: Porifera, Cnidaria, Annelida, Mollusca, Arthropoda, Bryozoa,  
134 Echinodermata and Chordata, for a total of 548 species. This choice focused on only sessile and  
135 low-mobility species to minimise bias in scuba-diving surveys throughout the 13 investigated  
136 sites. The systematic nomenclature of the database was checked following the World Register of  
137 Marine Species (WoRMS Editorial Board, 2016) to avoid both orthographic mistakes and  
138 synonymies (Costello et al., 2001).

### 139 *2.2 Database robustness and occurrence estimation*

140 We first analysed the robustness of the database to assess and mitigate potential biases in  
141 sampling efforts, which could lead to an uneven representation of species diversity and  
142 occurrence among sites. Our analysis was divided into a three step process based on a  
143 completeness index (Soberón et al., 2007). The completeness index assesses the completeness of  
144 a set of samples by dividing the observed richness by the total estimated species richness on the  
145 basis of a richness estimator (Soberón et al., 2007). We calculated three richness estimators  
146 (Chao2, ICE and Jack1) (Hortal et al., 2006; Soberón et al., 2007) which yielded similar results;  
147 we included average values across the three estimators in the main text, and values for all three  
148 indicators in Appendix A.

149 Firstly, we analysed the completeness of the whole database. Secondly, all phyla pooled together,  
150 we analysed the completeness of each site in order to identify and remove under-sampled sites  
151 with a completeness threshold (see below). Thirdly, we analysed the completeness of each  
152 phylum in each site. Then we calculated the average completeness of each phylum across all  
153 sites in order to remove phyla that were on average insufficiently sampled across all sites. We  
154 applied a conservative rule to remove phyla and sites based on a threshold of completeness that  
155 we defined at 75%, i.e. when the observed richness did not reach 75% of estimated richness for  
156 a particular site or phylum and for at least two richness estimators, this site or phylum was  
157 removed.

158 The number of sampled stations differed between sites, from 4 to 20 sampled stations (Table 1).  
159 This difference introduced a bias if the occurrence was calculated from the number of sampled  
160 stations: a species occurring in all stations of a particular site would receive a higher occurrence

161 if the site had 20 sampled stations than if the site had 4 sampled stations. Hence, this would  
 162 result in an artificial “commonness” for better-sampled sites, versus an artificial rarity for less-  
 163 sampled sites. Therefore, to remove this bias, we estimated the frequency of occurrence of each  
 164 species in each site with the following formula:

$$165 \quad Q_{ij} = \frac{q_{ij}}{N_j}$$

166 where:  $Q_{ij}$  is the frequency of occurrence of species  $i$  in site  $j$ ;  $N_j$  is the number of stations  
 167 sampled in the site  $j$ , and  $q_{ij}$  is the number of stations of site  $j$  in which species  $i$  has been found.  
 168 The total occurrence ( $Q_i$ ) of each species  $i$  is then calculated as the sum of its occurrence in all  
 169 sites:  $Q_i = \sum Q_{ij}$ .

### 170 *2.3 Species rarity and calculation of rarity weights*

171 We first analysed the frequency distribution of species occurrences to demonstrate differences  
 172 in the distribution of rarity among phyla. Then, we calculated rarity weights for each species on  
 173 the basis of a method that could be adjusted according to a user-chosen rarity cut-off point  
 174 (Leroy et al., 2013, 2012). With this method, rare species receive rarity weights that increase  
 175 exponentially when their occurrence falls below a rarity cut-off point. Thus, weights of rare  
 176 species (with occurrence lower than the cut-off) are amplified, whereas weights of common  
 177 species (with occurrence higher than the rarity cut-off) tend to zero. At the cut-off point, species  
 178 weight is always equal to 5% of the weight of the rarest species (Leroy et al., 2013). The rarity  
 179 cut-off point should be defined specifically for each phylum rather than choosing a general cut-  
 180 off for all phyla, especially when phyla have different life histories (Flather and Sieg, 2007).

181 The rarity weight  $w_i$  of each species  $i$  was calculated with the following formula (Leroy et al.,  
 182 2013):

$$183 \quad w_i = \exp \left( - \left( \frac{Q_i - Q_{\min}}{r \times Q_{\max} - Q_{\min}} \times 0.97 + 1.05 \right)^2 \right) \quad (1)$$

184 Where all parameters were defined for the considered phylum:  $Q_i$  is the occurrence of species  $i$ ;  
 185  $Q_{\min}$  and  $Q_{\max}$ , minimum and maximum occurrences, respectively, of the considered phylum; and  
 186  $r$ , chosen rarity cut-off point (as a percentage of maximum occurrence) for the considered  
 187 phylum.

188 To select a rarity cut-off point for each phylum, we followed Gaston’s recommendations (1994):  
 189 the rarity cut-off was the first quartile of the frequency distribution of species occurrences (i.e.  
 190 rare species are the 25% species with the lowest occurrence). We analysed the effect of this cut-  
 191 off choice on our analyses with a sensitivity analysis (Appendix B).

### 192 *2.4 Index of Relative Rarity*

193 The  $I_{RR}$  of an assemblage of species is calculated as the average weight of rarity of all the species  
 194 of the assemblage. The  $I_{RR}$  is subsequently normalised between 0 and 1:

$$195 \quad I_{RR} = \frac{\sum_{i=1}^S w_i - w_{\min}}{w_{\max} - w_{\min}} \quad (2)$$

196 Where:  $w_i$  is the weight of the  $i^{\text{th}}$  species of the assemblage;  $S$ , species richness; and  $w_{\min}$  and  
197  $w_{\max}$ , minimum and maximum possible weights, respectively. The  $I_{\text{RR}}$  ranges from 0 (all species  
198 of the assemblage have the minimum weight, i.e. ubiquitous species) to 1 (all species of the  
199 assemblage have the maximum weight, i.e. very rare species).

200

## 201 *2.5 Analyses*

202 For each of the 133 inventories of our database, we calculated phylum-specific  $I_{\text{RR}}$  for each of the  
203 8 phyla. To search for potential surrogate phyla, we analysed the congruence between each pair  
204 of phyla with the phylum-specific  $I_{\text{RR}}$ . Given the nested nature of the sampling design, we could  
205 not directly analyse the correlation among the 133 inventories. We therefore analysed the  
206 correlations at two levels: between sites and within sites. For the between sites level, we tested  
207 for cross-phyla correlations using mean  $I_{\text{RR}}$  values for each site. For the within sites level, we  
208 tested for cross-phyla correlations within each site and reported the average within-site  
209 correlation, as well as the percentage of sites for which a significant correlation was detected.  
210 Our expectations were that a good surrogate phylum should be correlated to other phyla within  
211 each site and between sites as well. The congruence was measured with the rank-based  
212 correlation coefficient of Spearman. We finally constructed and analysed a multi-phyla index of  
213 rarity with phylum-specific rarity cut-offs (see Appendix C).

214 All data analyses were performed using R (R Core Team, 2016); completeness analyses were  
215 done with the “fossil” package (Vavrek, 2011), rarity analyses with the “Rarity” package (Leroy,  
216 2015), correlation analyses with the “psych” package (Revelle, 2016) and graphics with  
217 “ggplot2” (Wickham, 2009), all available on the Comprehensive R Archive Network.



218 **3 Results**

219 *3.1 Database analysis*

220 The completeness of the whole database was very high with 93% of the estimated total species  
 221 richness sampled (Table 1). On average, 265±54 (mean±sd) species were sampled per site, with  
 222 an average estimated species richness of 314±56. The completeness of almost all sites was  
 223 relatively high with an average completeness value of 0.84±0.08). The only under-sampled site  
 224 was the Rance estuary, with an estimated completeness of 0.60 and 4 sampled sites. Hence, the  
 225 Rance estuary was removed for the calculation of species occurrence and cross-taxon  
 226 congruence analyses. Interestingly, the heterogeneity in sampling intensities across sites did not  
 227 lead to significant differences in completeness indices (observed richness vs. sampling effort:  
 228 Pearson’s  $r = -0.09$ ,  $df = 10$ ,  $p = 0.78$ ; completeness vs. sampling effort: Pearson’s  $r = 0.53$ ,  
 229  $df = 10$ ,  $p = 0.07$ ).

**Table 1.** Sampling completeness of the different sites of the database. Averaged estimated richness is the average richness based on three estimators: Chao2, ICE and Jack1 (all values in Appendix A). Completeness index: species richness divided by estimated species richness. Sampling intensity: number of inventories.

	Species richness	Average estimated richness	Completeness index	Sampling intensity
Database	540	574	0.94	137
Rance estuary	204	343	0.60	4
St Malo bay	309	354	0.87	10
Granite rose coast	310	341	0.91	16
Sept Îles archipelago	355	409	0.87	12
Lannion bay	323	363	0.89	13
Morlaix bay	246	304	0.81	4
Brest sea	256	282	0.91	11
Brest bay	275	320	0.86	12
Crozon peninsula	168	194	0.87	13
Cape Sizun	218	263	0.83	10
Ushant island	217	253	0.86	20
Morbihan gulf	299	337	0.89	6
Etel ria	265	311	0.85	6
Mean values	265	314	0.84	11

230

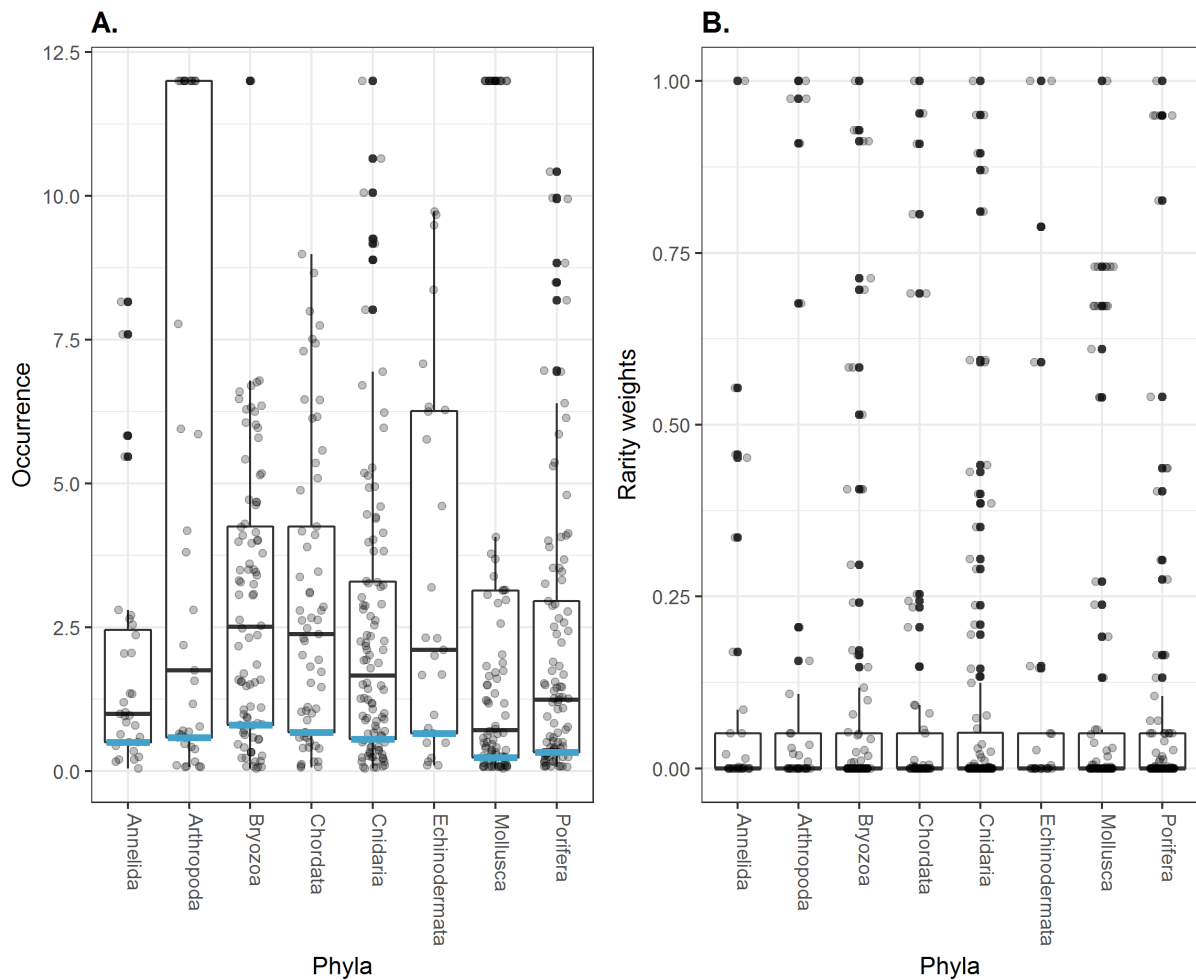
231 The average completeness per site of phyla ranged from 0.81 to 0.91, indicating that all these  
 232 phyla were sampled with similar intensities for the 13 sites (Table 2). Out of the remaining  
 233 phyla, the average number of species per inventory and per phylum ranged from 4.7±3.3 for  
 234 Annelida to 21.1±5.5 for Mollusca. The average number of species per site and per phylum  
 235 ranged from 11.4±6.3 for Annelida to 46.3±21.6 for Cnidaria. The 8 phyla were found in all of the  
 236 sites with similar richness proportions among sites (See Appendix D), with three major phyla  
 237 being Bryozoa, Cnidaria and Porifera.

**Table 2.** Completeness and species richness of each phylum of the database. Completeness is the ratio between observed and estimated species richness (Soberón et al., 2007). For each phylum, the completeness is based on three estimators (Chao2, ICE and Jack1; all values in Appendix A) and is averaged across all sites. Numbers in brackets are standard deviations.

	Annelida	Arthropoda	Bryozoa	Chordata	Cnidaria	Echino- dermata	Mollusca	Porifera
Total richness	32	37	88	61	102	27	88	101
Average completeness	0.83 (0.13)	0.92 (0.06)	0.85 (0.08)	0.85 (0.12)	0.85 (0.05)	0.86 (0.14)	0.84 (0.11)	0.85 (0.06)
Average observed species richness per inventory	4.7 (3.3)	14.3 (2.9)	20.6 (15.7)	14.2 (9.5)	19.5 (10.6)	7.5 (2.9)	21.1 (5.5)	15.7 (10.8)
Average observed species richness per site	11.4 (6.3)	17.2 (8.5)	42.9 (22.7)	29.6 (15.5)	46.3 (21.6)	13.3 (6.1)	31.4 (17.1)	39.6 (21.1)

239 *3.2 Rarity distribution among phyla*

240 Corrected occurrences (see methods) of species ranged from 0.05 to 12, and their distribution  
241 varied between phyla (Figure 1A). As expected, for the majority of phyla, the median was low,  
242 indicating that most species had low occurrences. Four phyla had ubiquitous species (i.e.,  
243 occurrences equal to the maximum: 12): Arthropoda, Bryozoa, Cnidaria, Mollusca (species list  
244 available in Appendix E).



245  
246 **Figure 1.** Box-and-whisker plots of **A.** species occurrences and **B.** rarity weights for each  
247 phylum. Each point stands for a species. Points are transparent; hence, the overlap of  
248 several points results in darker points. Box-and-whiskers represent the non-outlier  
249 range of values with horizontal bars representing from bottom to top: first quartile (bold  
250 horizontal segments in blue), median (bold horizontal segments), third quartile. For  
251 each phylum, rarity weights were calculated with a cut-off point corresponding to the  
252 first quartile of species occurrence.

253  
254 The rarity cut-off point, defined as the first (lowest) quartile of the frequency distribution of  
255 occurrences, varied substantially between phyla, from an occurrence of 0.24 (Mollusca) to an  
256 occurrence of 0.80 (Bryozoa) (Figure 1A). Hence, rare species of Mollusca had occurrences  
257 ranging from 0.05 to 0.24, while rare species of Bryozoa had occurrences ranging from 0.05 to

258 0.80. On the other hand, the global rarity cut-off for all phyla implied a definition of rare species  
 259 for occurrences ranging from 0.05 to 0.44.

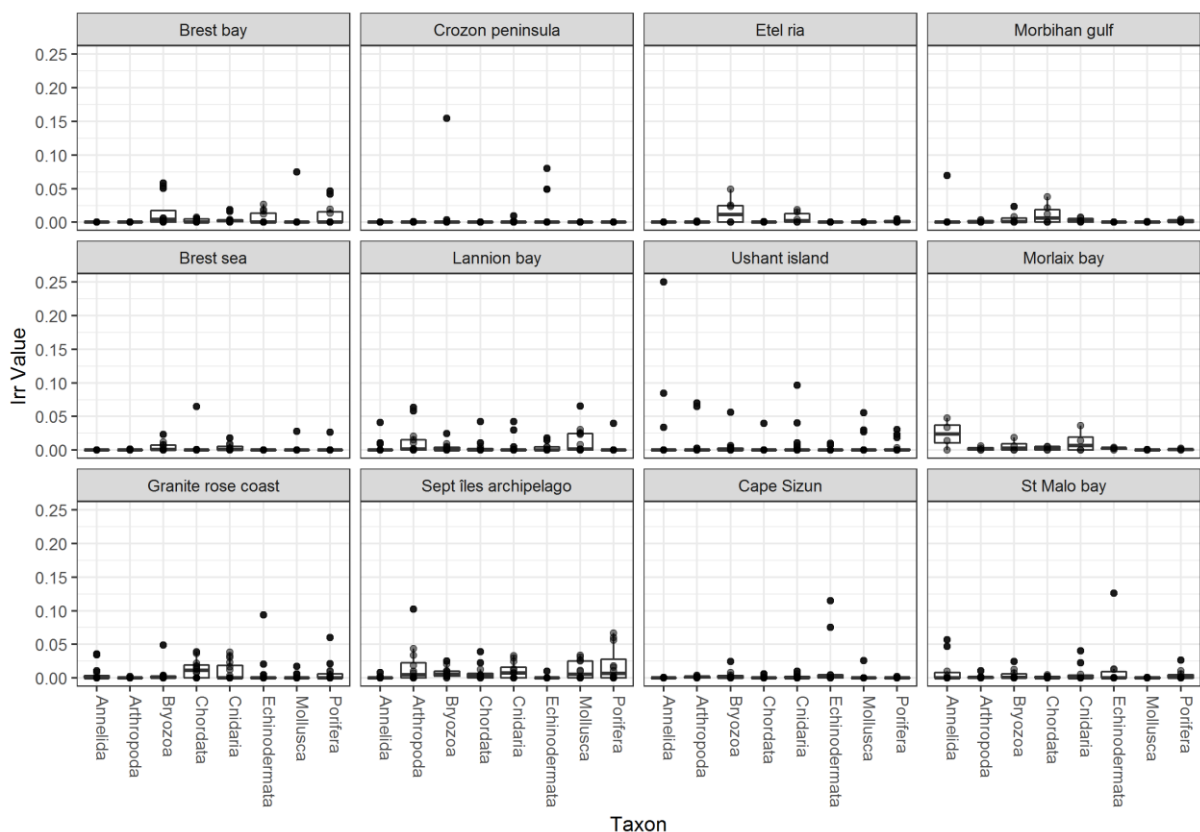
260 Species rarity weights were calculated for each phylum with respect to phylum-specific rarity  
 261 cut-off points. Rare species of each phylum received weights ranging from 0.05 (weight at the  
 262 cut-off) to 1 (weight of the rarest species) (Figure 1B; full list of species with rarity scores in  
 263 Appendix E). Although the range of weights was identical among phyla, several phyla had a  
 264 greater variety of weights because of a higher dispersion of occurrence values among rare  
 265 species (e.g., Bryozoa, Chordata and Cnidaria).

266

267

### 268 3.3 Rarity scores of species assemblages

269 Indices of relative rarity of inventories ranged from 0 to a maximum of 0.25 for an inventory of  
 270 Annelida at the Ushant Island (Figure 2). A substantial number of inventories had indices of 0 for  
 271 all phyla, but not necessarily for the same sites. Interestingly, all sites had at least one inventory  
 272 with a high value for a phylum. Distributions of rarity indices across sites were clearly different  
 273 between phyla. Some phyla had high rarity values concentrated in only a few sites (Annelida,  
 274 Arthropoda, Echinodermata, Mollusca); other phyla had high rarity values in many sites  
 275 (Bryozoa, Chordata, Cnidaria, Porifera).  
 276



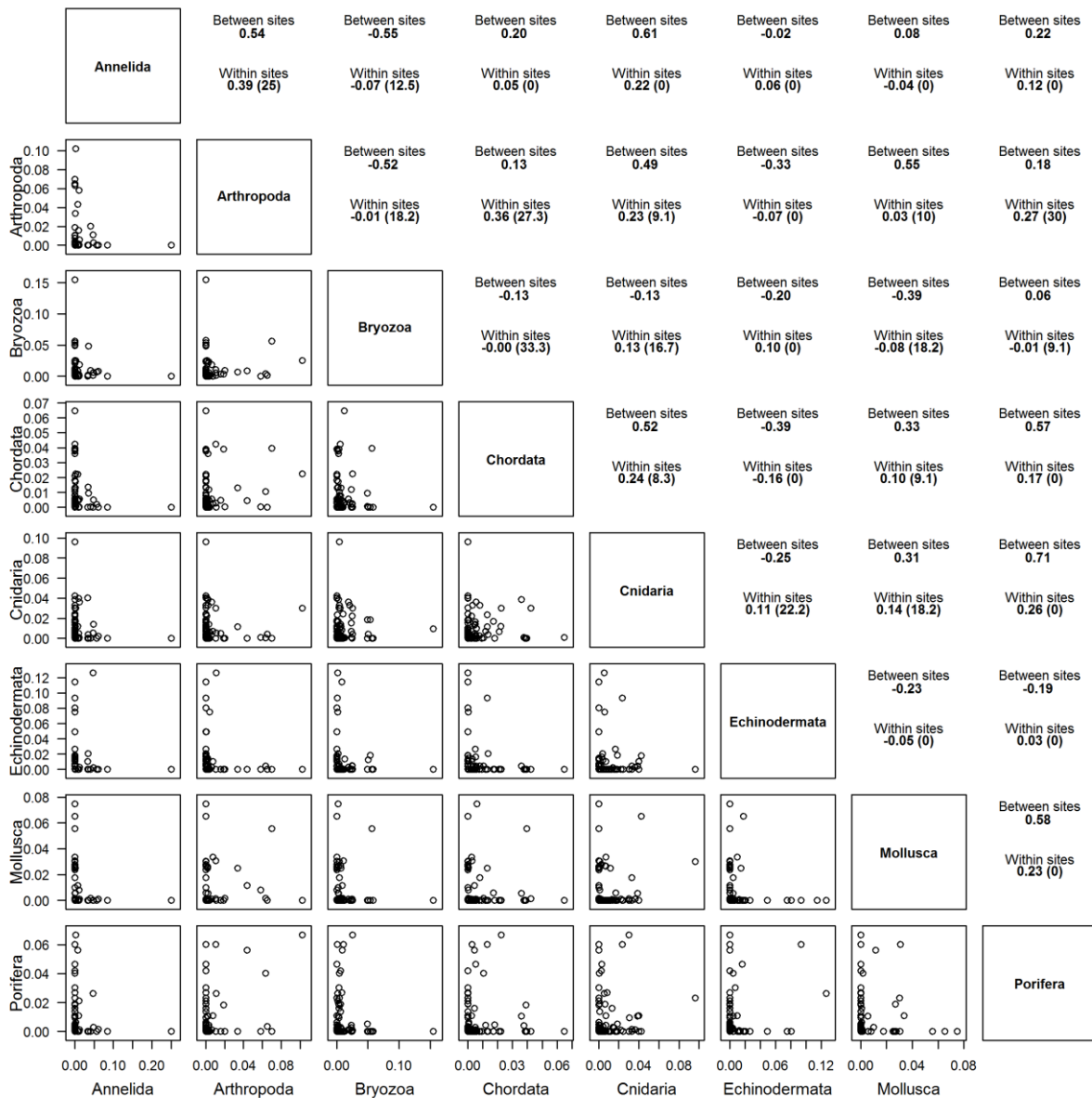
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278 **Figure 2.** Box-and-whisker plots of phylum-specific Indices of Relative Rarity ( $I_{RR}$ ) of the  
 279 133 inventories of our database. Box-and-whiskers represent the non-outlier range of  
 280 values with horizontal bars representing from bottom to top: first quartile, median, third  
 281 quartile.

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### 3.4 Cross-taxon congruence of rarity

Between sites, the correlation among phyla of rarity indices was not significant for all comparisons (Figure 3). Within-site correlations were generally low, with the highest values obtained between Arthropoda and Porifera for which 30% of the station-level correlations were significant. This absence of congruence among phyla was reflected in the graphical comparison of inventory indices (Figure 3). For any given phylum, inventories with no rare species could correspond to the best as well as the worst ranked inventories of most other phyla.



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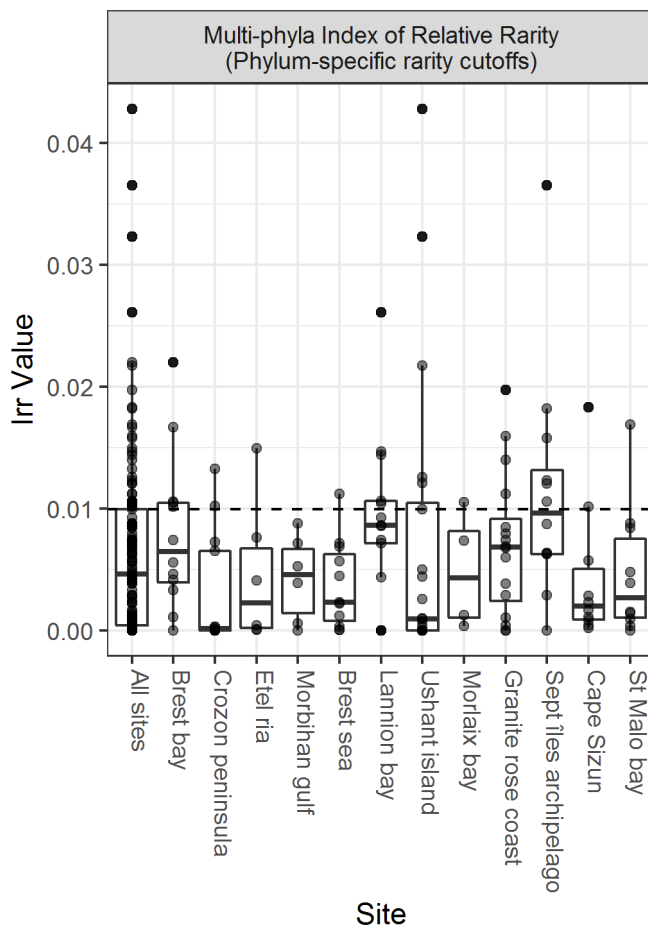
**Figure 3.** Cross-taxon congruence of Indices of Relative Rarity ( $I_{RR}$ ) among the eight studied phyla. The lower half shows the scatter plots of  $I_{RR}$  ranks of inventories among phyla. The upper half shows values of Spearman's rank correlation coefficients between

296 mean  $I_{RR}$  values for each site (“Between sites”, significance: \*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  
 297  $p < 0.05$ ; p-values corrected for false discovery rate), and average values of Spearman’s  
 298 rank correlation coefficients within sites. For average within sites correlations, we  
 299 indicated the percentage of sites where significant correlations were detected ( $p < 0.05$ ).  
 300 The diagonal shows the different phyla and the number of inventories available for each.

301

### 302 3.5 Multi-phyla indices of rarity

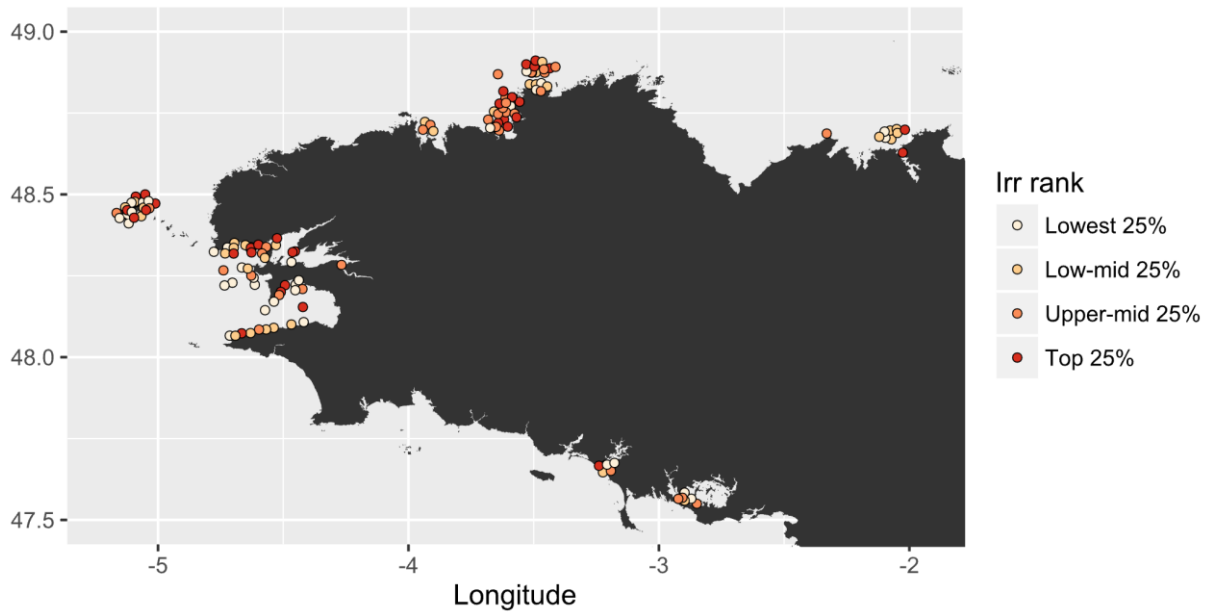
303 Given that no phylum could be identified as a clear indicator of another phylum rarity, we  
 304 included all of them in the multi-phyla index of rarity. The multi-phyla  $I_{RR}$  had values ranging  
 305 from 0 to 0.041 (Figure 4). The most important result was that high values of  $I_{RR}$  were found in  
 306 all sites (Figure 4 and Figure 5). In addition, the top 25% assemblages were distributed in  
 307 almost all of the sites, spread throughout Brittany, with the notable exception of the Morbihan  
 308 Gulf. Nevertheless, higher values were generally found in north (Sept-Îles archipelago, Lannion  
 309 bay, Granite rose coast) and western Brittany (Ushant Island, Brest bay). The rarest assemblages  
 310 were found in both Ushant and Sept Îles islands. Besides, all sites had assemblages with no rare  
 311 species ( $I_{RR}$  equal to 0).



312

313 **Figure 4.** Box-and-whisker plots of multi-phyla Indices of Relative Rarity ( $I_{RR}$ ) based on  
 314 phylum-specific rarity cut-off points for the 133 inventories of our database. Box-and-  
 315 whiskers represent the non-outlier range of values with horizontal bars representing  
 316 from bottom to top: first quartile, median, third quartile. The dashed line represents the

317 third quartile of all  $I_{RR}$  values. Above the dashed lines are the 25% top values of  $I_{RR}$   
318 across all sites.



319

320 **Figure 5.** Spatial distribution of Indices of Relative Rarity ( $I_{RR}$ ) of sampled assemblages  
321 around Brittany.  $I_{RR}$  were coloured according to four equal classes based on quartiles of  
322 all  $I_{RR}$  values: (i) Lowest 25%: sites with  $I_{RR}$  below the first quartile; (ii) Low-mid 25%:  
323 sites with  $I_{RR}$  above the first quartile and below the median; (iii) Upper-mid: sites with  
324  $I_{RR}$  above the median and below the third quartile; (iv) Top 25%: sites with  $I_{RR}$  above  
325 the third quartile.

326

327

## 328 **4 Discussion**

329 This study provides a method for a quantitative assessment of the importance for conservation  
330 of subtidal rocky habitats, based on the rarity of sessile and low-mobility species. Although the  
331 reference database has limitations and needs to be completed with more observations, with this  
332 method we evaluated for the first time, the rarity patterns of invertebrate phyla of the subtidal  
333 rocky benthos around Brittany. Our study highlighted three main findings. Firstly, rarity  
334 appeared to be unevenly distributed among the studied phyla, which emphasised the need to fit  
335 rarity metrics according to each phylum. Secondly, the distribution of rarity in subtidal  
336 assemblages of species was not clearly congruent among phyla, which prevented any attempt to  
337 identify indicator phyla. Thirdly, according to multi-phyla indices of rarity, assemblages of high  
338 rarity were not concentrated within a few sites: they were distributed across all of our studied  
339 sites, and were spread throughout our study region. These three findings have important  
340 implications both for future research investigating the rarity of different invertebrate phyla, as  
341 well as for the conservation and monitoring of subtidal rocky assemblages.

### 342 *4.1 A flexible approach to weigh species rarity*

343 In this study, we investigated the rarity of species and assemblages of species of eight different  
344 phyla. We chose to analyse rarity on the basis of the most widespread definition of rarity in  
345 conservation literature, i.e. rare species are the 25% species with the lowest occurrence (Flather  
346 and Sieg, 2007; Gaston, 1994). Such a cut-off criterion was chosen because it ensures that all  
347 phyla have equal contribution to the ranking of assemblages (Appendix C), thus preserving  
348 phylogenetic diversity in the targeted rare species. This cut-off criterion was proven to be  
349 appropriate for other marine invertebrate taxa, particularly because it standardises the  
350 definition and enables comparisons across assemblages and phyla (Benkendorff and  
351 Przeslawski, 2008). With this criterion, we showed that cut-off values differed between phyla:  
352 several phyla had very low cut-offs (e.g., Mollusca), whereas other phyla had relatively high cut-  
353 offs (e.g., Bryozoa, Chordata, Cnidaria and Echinodermata). Because of the differences in rarity  
354 cut-offs between phyla, a flexible weight function was required to fit the weight assignment with  
355 respect to the rarity of each phylum. The function we applied here explicitly integrated the rarity  
356 cut-off point, thereby ensuring that assemblages of different phyla with different rarity cut-offs  
357 could be compared (Leroy et al., 2013, 2012). While we advocate here the use of a phylum-  
358 specific definition of rarity, one can argue that the conservation of the rarest species, regardless  
359 of their phylogenetic origin, is primordial. In such a case, the use of a single criterion for all phyla  
360 may be preferred, which can be done with the application of a single rarity cut-off for all phyla.

### 361 *4.2 Discrepancy in cross-taxon congruence prevents the identification of surrogate phyla*

362 We did not observe any striking congruence in the rarity of assemblages among the studied  
363 phyla of the subtidal rocky areas of Brittany. In other words, the spatial distribution of rarity in  
364 Brittany differed between the 8 phyla of marine subtidal organisms we studied. The major  
365 consequence of this finding is that no single phylum or group of phyla can be chosen as a  
366 surrogate to monitor subtidal rocky areas. Furthermore, given the diversity of rarity patterns  
367 among phyla, the choice of any restricted set of phyla to monitor subtidal rocky areas for  
368 conservation would neglect the rare species of omitted phyla. Consequently, our approach did  
369 not permit us to reveal any easy taxonomic shortcut to monitor subtidal rocky areas for  
370 conservation around Brittany, which is worrying given the costs of sampling multiple phyla in  
371 such biota.



372 Interestingly, the identification of surrogate phyla by cross-taxon congruence (not limited to  
373 rarity) in marine species assemblages yielded contrasting results in the literature. On the one  
374 hand, the same incongruence was reported for marine biota similar to the ones we studied  
375 (Hirst, 2008), as well as related marine biota such as intertidal zones in the United Kingdom  
376 (Reddin et al., 2015) or structurally less similar biota such as coral reefs (Jimenez et al., 2012)  
377 and tropical seabeds (Sutcliffe et al., 2012). On the other hand, studies on a similar set of phyla  
378 found that molluscs constituted an appropriate surrogate phylum for rapid assessments of  
379 biodiversity (Smith, 2005); and neither annelids, arthropods nor molluscs were appropriate  
380 surrogate phyla for estuarine conservation (Shokri et al., 2008). Thus, the ability to identify  
381 surrogate phyla and the identity of these surrogate phyla appear region-dependant. In  
382 accordance with Sutcliffe et al. (2012), we therefore recommend that the effectiveness of  
383 surrogate phyla requires testing when defining surrogates in a new region. However, even if we  
384 recognise that studying rare species requires time-consuming sampling protocols and is thus  
385 problematic because of limited funds available for monitoring, we disagree with Sutcliffe *et al.*  
386 (2012) regarding their proposal to exclude rare species for monitoring biodiversity, because  
387 rarity is one of the only measures directly characterising species extinction risk for lesser-  
388 known taxa (Flather and Sieg, 2007; Leroy, 2012).

#### 389 *4.3 Spatial distribution of rarity*

390 On the basis of the multi-phyla index of relative rarity, we showed that assemblages of high  
391 rarity were distributed across all the sites around Brittany. Indeed, each site exhibited at least  
392 one assemblage of high rarity. Nevertheless, assemblages with rare species occurred more  
393 frequently in northern Brittany (Granite rose coast, Sept-Îles archipelago, Lannion bay) and also  
394 western Brittany (Brest bay, Ushant island). These sites concentrating potentially vulnerable  
395 species can therefore be targeted for further investigation for their conservation. Interestingly,  
396 this spatial pattern is similar to the spatial pattern of genetic diversity in two brown macroalgae:  
397 Robuchon et al. (2014) have shown, using a similar spatial distribution of samples, that the  
398 highest genetic diversity was found in both northern and western Brittany, compared to north-  
399 eastern and southern Brittany. This peculiar pattern may be explained by the seemingly more  
400 stable temperatures in north-western Brittany than elsewhere (Gallon et al., 2014). North-  
401 western Brittany is also characterised by a widespread and continuous rocky bottom, separated  
402 from the more fragmented rocky bottom of the other regions of Brittany by large sandy beaches  
403 (Cabioch, 1968; Méléder et al., 2010; Raffin, 2003; Retière, 1979). Indeed, habitat fragmentation  
404 increases extinction probability (Roberts and Hawkins, 1999). Stable environmental conditions  
405 and widespread habitat may therefore offer suitable conditions for species with narrow  
406 ecological requirements, an intrinsic cause of species rarity (Flather and Sieg, 2007), and this  
407 may explain the observation of higher concentrations of rarity in north-western Brittany. In  
408 addition, this area is the location of the transition zone between two biogeographical provinces  
409 (the Lusitanian province in the south and the Boreal province in the north; Cox and Moore 2000,  
410 Spalding et al. 2007). Consequently, north-western Brittany is an area where the range limits of  
411 both Lusitanian and Boreal species overlap. This overlap may explain the concentration of rarity  
412 in this transition zone, since species which are rare in Brittany may be at the edge of their  
413 geographical ranges (e.g., Leroy et al. 2013). Therefore, north-western Brittany is likely to  
414 concentrate rare species, not only because this area exhibits environmental characteristics  
415 favourable for specialist species, but also because it constitutes a transition zone between two  
416 biogeographical regions, thus increasing the likelihood of having species at the edge of their  
417 range.

418 However, the more general pattern showing that rare species occur everywhere around Brittany  
419 is more difficult to explain. Among the few studies investigating the causes of spatial patterns of  
420 rarity in the marine benthos, Ellingsen et al. (2007) showed that on soft substrates, habitat  
421 characteristics might play an important role. Indeed, they highlighted the fact that the number of  
422 rare species was strongly correlated to the number of habitats and environmental variability,  
423 suggesting that the number of rare species increased with both within-and between-site  
424 heterogeneity, and that these relationships may arise from habitat-specific species with  
425 restricted ranges. The coastline of Brittany exhibits a huge mosaic of benthic habitats (Bajjouk et  
426 al., 2011; Guillaumont et al., 2008) and displays an important medium-scale (> 100km)  
427 environmental heterogeneity (Ayata et al., 2010; Gallon et al., 2014).

428 Another interesting hypothesis suggests that local water flow direction and velocity drives  
429 diversity by mediating the delivery (larval recruitment) of rare species (Palardy and Witman,  
430 2011). The high complexity of flows around Brittany, generating multiple distinct hydrographic  
431 areas (Mènesguen and Gohin, 2006; Pingree et al., 1982; Salomon and Breton, 1991), may also  
432 explain the observed spatial distribution of rarity. To summarise, our study area is characterised  
433 by a complex diversity of habitats and environmental conditions, which might explain why rare  
434 assemblages seem to occur everywhere in Brittany. However, this hypothesis requires further  
435 testing by correlating rarity patterns with environmental patterns, and also the investigation of  
436 a higher number of locations following a nested sampling design.

#### 437 *4.4 Caveats and future directions*

438 Estimating rarity is highly dependent on uneven sampling intensities among sites, and cross-  
439 taxon analyses are highly dependent on uneven sampling between phyla. As a consequence, we  
440 decided to make several corrections to improve the quality of the database before conducting  
441 cross-taxon analyses of rarity. For example, we defined a quality threshold for our sampling.  
442 While the choice of the threshold value was arbitrary, it has the advantage of ensuring that  
443 sampling intensity was similar among phyla and among sites, by the removal of phyla and sites  
444 with the poorest sampling intensities. Another correction we applied was the use of a corrected  
445 index of occurrence to account for sampling discrepancies among sites. This index has the  
446 advantage of addressing the issue of occurrence overestimation in sites with many stations vs.  
447 sites with few stations. However, because of its mathematical formulation, rare species from  
448 sites with few stations will have higher occurrences, and thus lower weights than rare species  
449 from sites with many stations (e.g. a species found in one of four inventories has an occurrence  
450 of 0.25, while a species found in one of 20 inventories has an occurrence of 0.04). As a  
451 consequence, less sampled sites may be penalised by this correction, which may partly explain  
452 the lower overall indices of Morlaix Bay (N = 4), Morbihan Gulf (N = 6) and Etel Ria (N = 6). We  
453 believe that this correction is conservative, and the results may be improved in the future by  
454 targeting new sampling stations in these sites in order to achieve comparable sampling  
455 intensities with other sites. Overall, the pros derived from these corrections are that we estimate  
456 that our main findings regarding the discrepancy in cross-taxon rarity and the spatial  
457 distribution of rare assemblages are reliable. These results are the first step to refine the  
458 identification of important assemblages or habitats for conservation. Once this step is  
459 performed, further investigations can be undertaken on a subset of selected assemblages or  
460 habitats, which greatly reduce the costs of sampling in these habitats, inflated by the absence of  
461 surrogate phyla. To this aim, we recommend investigating species abundances that can be  
462 included in the Index of Relative Rarity (Leroy, 2015; Leroy et al., 2014), in order to target  
463 assemblages containing species regionally rare, but locally abundant.

464 We focused only on animal taxa, and thus omitted the primary producers which are macroalgae  
465 (Heterokontophyta, Chlorophyta and Rhodophyta) despite the fact that they represent a  
466 significant proportion of the total biodiversity and biomass of subtidal rocky communities.  
467 However, our omission of macroalgae is at least partly offset by the indicator that has been  
468 specifically developed for the assessment of macroalgae under the European Water Framework  
469 Directive (Le Gal and Derrien-Courtel, 2015). Nevertheless, we recommend further sampling of  
470 macroalgae to include them in future studies investigating biodiversity surrogates and/or rarity  
471 patterns in subtidal assemblages of rocky shores in Brittany.

472 Biodiversity patterns of marine benthos are known to be scale-dependant for species richness  
473 and assemblage structure (e.g. Smale et al. 2011), as well as for rarity (Ellingsen et al., 2007).  
474 This scale-dependency also holds for the effectiveness of biodiversity surrogates (e.g. Smale  
475 2010, Sutcliffe et al. 2012). In our analysis, we detected this scale-dependency: rarity of Cnidaria  
476 was correlated to rarity of Porifera between sites but not within sites. Given that evidence  
477 regarding scale-dependency in biodiversity patterns of marine benthos and the probable role of  
478 environmental variability in explaining spatial distribution of rarity, we recommend that scale-  
479 dependency should be tested specifically in future studies investigating biodiversity surrogates  
480 and/or rarity patterns in subtidal assemblages of rocky shores in Brittany. In addition, the  
481 database used to estimate species rarity in this paper is limited to Brittany, and thus does not  
482 permit us to distinguish between species which are intrinsically rare or are rare because they  
483 are at the edge of their geographical range. Therefore, future work to improve the explanation of  
484 the observed patterns should also investigate multi-scale patterns from a larger spatial  
485 perspective (Leroy et al., 2013).

486 Furthermore, we were not able to investigate temporal patterns because of the limited sampling  
487 costs. Yet, changes have been shown to occur in subtidal algal communities over the temporal  
488 span of our database samplings (Gallon et al., 2014). Among changes, it can be expected that  
489 some rare species may have become more common (such as warm-water species at their  
490 northern range limits), and common species may have become rare (such as cold-water species  
491 close to their southern range limits). Nevertheless, since (i) these changes have been rather  
492 slowly occurring, (ii) western and north-western Brittany have been identified as the most  
493 stable zones for other phyla (red seaweeds) (Gallon et al., 2014) and (iii) our metric is averaged  
494 at the community level, we assume that these changes would not have major impacts on our  
495 findings. We nonetheless recognize that, given the accelerating environmental changes, the  
496 temporal aspect is a major challenge for such understudied and costly-to-sample habitats, and  
497 this challenge should be rapidly tackled in future studies.

#### 498 *4.5 Concluding remarks*

499 Our initial aim was to identify surrogate phyla to indicate rarity of other phyla, to be used for the  
500 monitoring of subtidal assemblages of rocky shores in Brittany. Unfortunately, such surrogates  
501 could not be identified because of the observed discrepancy in rarity patterns among phyla. This  
502 finding has an important implication for the conservation of subtidal rocky habitats as it means  
503 that there is no shortcut to monitor their rarity: working on a subset of phyla implies a biased  
504 evaluation of biodiversity. Nevertheless, the method proposed here allowed us to successfully  
505 evaluate the rarity of sessile and low-mobility species as one facet of the conservation needs of  
506 subtidal rocky habitats. This method is thus a working indicator for the implementation of  
507 European directives as the MSFD, WFD and Habitat Directive.

508

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## 515 **Supplementary Material**

516 **Appendix A.** Completeness analyses based on three richness estimators: Chao2, ICE and Jack1.

517 **Appendix B.** Sensitivity analysis of the cut-off choice.

518 **Appendix C.** Comparison of a multi-phyla index of rarity based on a phylum-specific choice of  
519 rarity cut-offs versus a global choice of rarity cut-off.

520 **Appendix D.** Relative proportions of species of each phylum in each of the sampled sites.

521 **Appendix E.** List of the sampled species with their associated corrected occurrence values,  
522 rarity status and rarity weights.

523 **Appendix F.** Indices of Relative Rarity and associated rankings of the 133 inventories of our  
524 database.

## 525 **References**

- 526 Ayata, S.D., Lazure, P., Thiébaud, E., 2010. How does the connectivity between populations  
527 mediate range limits of marine invertebrates? A case study of larval dispersal between the  
528 Bay of Biscay and the English Channel (North-East Atlantic). *Prog. Oceanogr.* 87, 18–36.  
529 doi:10.1016/j.pocean.2010.09.022
- 530 Bajjouk, T., Derrien-Courtel, S., Gentil, F., Hily, C., Grall, J., 2011. Typologie d'habitats marins  
531 benthiques: Analyse de l'existant et propositions pour la cartographie. Habitats côtiers de la  
532 région Bretagne-Note de synthèse n° 2, Habitats du circalittoral. Projets REBENT-Bretagne  
533 et Natura 2000-Bretagne. RST/IFREMER/DYNEC.
- 534 Benkendorff, K., Przeslawski, R., 2008. Multiple measures are necessary to assess rarity in  
535 macro-molluscs: a case study from southeastern Australia. *Biodivers. Conserv.* 17, 2455–  
536 2478. doi:10.1007/s10531-008-9392-6
- 537 Cabioch, L., 1968. Contribution à la connaissance des peuplements benthiques de la Manche  
538 occidentale. *Cah. Biol. Mar.* 9, 493–720.
- 539 Chapman, M.G., 1999. Are there adequate data to assess how well theories of rarity apply to  
540 marine invertebrates? *Biodivers. Conserv.* 8, 1295–1318.
- 541 Costello, M.J., Emblow, C., White, R., 2001. European register of marine species. A check-list of  
542 the marine species in Europe and a bibliography of guides to their identification. SPN /  
543 IEGB / MNHN, Paris.
- 544 Cox, C.B., Moore, P.D., 2000. *Biogeography: an ecological approach*. Blackwell Scientific  
545 Publications, London.
- 546 Ellingsen, K.E., Hewitt, J.E., Thrush, S.F., 2007. Rare species, habitat diversity and functional

- 547 redundancy in marine benthos. *J. Sea Res.* 58, 291–301. doi:10.1016/j.seares.2007.10.001
- 548 Flather, C.H., Sieg, C.H., 2007. Species rarity: definition, causes and classification, in: Raphael,  
549 M.G., Molina, R. (Eds.), *Conservation of Rare or Little-Known Species*. Island Press,  
550 Washington, District of Columbia, pp. 40–66.
- 551 Gallon, R.K., Robuchon, M., Leroy, B., Le Gall, L., Valero, M., Feunteun, E., 2014. Twenty years of  
552 observed and predicted changes in subtidal red seaweed assemblages along a  
553 biogeographical transition zone: inferring potential causes from environmental data. *J.*  
554 *Biogeogr.* 41, 2293–2306. doi:10.1111/jbi.12380
- 555 Gallon, R.K., Ysnel, F., Feunteun, E., 2013. Optimization of an “in situ” subtidal rocky-shore  
556 sampling strategy for monitoring purposes. *Mar. Pollut. Bull.* 74, 253–263.
- 557 Gaston, K.J., 1994. *Rarity*. Chapman & Hall, London, United Kingdom.
- 558 Gaston, K.J., Blackburn, T.M., 2000. *Pattern and Process in Macroecology*. Blackwell Science,  
559 Oxford.
- 560 Girard-Descatoire, A., Castric-Fey, A., L’Hardy-Halos, M., 2000. Inventaire de la faune et de la  
561 flore sur les fonds rocheux de la Baie de Lannion. Complément d’inventaire. Rapport Diren  
562 et Conseil Général des Cotes d’Armor.
- 563 Girard-Descatoire, A., Castric-Fey, A., L’Hardy-Halos, M., 1999. Inventaire de la faune et de la  
564 flore sur les fonds rocheux de la Baie de Lannion. Rapport Diren, Région et Conseil Général  
565 des Côtes d’Armor.
- 566 Girard-Descatoire, A., Castric-Fey, A., L’Hardy-Halos, M., 1998. Inventaire de la faune et de la  
567 flore sur les fonds rocheux de l’archipel des Sept-Iles. Rapport Diren, Convention ZNIEFF  
568 94.
- 569 Girard-Descatoire, A., Castric-Fey, A., L’Hardy-Halos, M., 1997. Inventaire de la faune et de la  
570 flore sur les fonds rocheux de Saint-Malo et de Dinard. Rapport Diren, Convention ZNIEFF  
571 94.
- 572 Girard-Descatoire, A., Castric-Fey, A., L’Hardy-Halos, M., 1996a. Inventaire de la faune et de la  
573 flore sur les fonds rocheux de l’archipel de Glenan. Rapport DIREN Rennes. Convention  
574 ZNIEFF 94.
- 575 Girard-Descatoire, A., Castric-Fey, A., L’Hardy-Halos, M., 1995. Inventaire de la faune et de la  
576 flore sur les fonds rocheux autour de l’île d’Ouessant. Rapport Convention ZNIEFF 94,  
577 Direction régionale de l’Environnement, Rennes.
- 578 Girard-Descatoire, A., L’Hardy-Halos, M., Castric-Fey, A., 1996b. Inventaire de la faune et de la  
579 flore sur les fonds rocheux sublittoraux en Proche Iroise et Rade de Brest. Rapport  
580 Convention ZNIEFF 94, Direction régionale de l’Environnement, Rennes.
- 581 Girard-Descatoire, A., L’Hardy-Halos, M., Castric-Fey, A., 1996c. Inventaire de la faune et de la  
582 flore sur les fonds rocheux du Golfe du Morbihan et de la Ria d’Etel. Rapport DIREN,  
583 Convention ZNIEFF 94.
- 584 Girard-Descatoire, A., L’Hardy-Halos, M., Castric-Fey, A., 1993. Inventaire des fonds rocheux de  
585 grand intérêt biologique en milieu marin dans la zone subtidale (Côte de Granite Rose).  
586 Rapport Convention NJ/CONSMVM, Direction Départementale de l’Équipement des Côtes  
587 d’Armor.
- 588 Grantham, H.S., Pressey, R.L., Wells, J. a, Beattie, A.J., 2010. Effectiveness of biodiversity  
589 surrogates for conservation planning: different measures of effectiveness generate a  
590 kaleidoscope of variation. *PLoS One* 5, e11430. doi:10.1371/journal.pone.0011430
- 591 Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson,

- 592 V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J.,  
593 Gittleman, J.L., Owens, I.P.F., 2006. Global distribution and conservation of rare and  
594 threatened vertebrates. *Nature* 444, 93–6. doi:10.1038/nature05237
- 595 Guillaumont, B., Bajjouk, T., Rollet, C., Hily, C., Gentil, F., 2008. Typologie d'habitats marins  
596 benthiques : analyse de l'existant et propositions pour la cartographie (Habitats côtiers de  
597 la région Bretagne)-Note de synthèse, Projets REBENT-Bretagne et Natura-Bretagne,  
598 RST/IFREMER/DYNECO/AG/08-06/REBENT.
- 599 Hirst, A.J., 2008. Surrogate measures for assessing cryptic faunal biodiversity on macroalgal-  
600 dominated subtidal reefs. *Biol. Conserv.* 141, 211–220. doi:10.1016/j.biocon.2007.09.025
- 601 Hortal, J., Borges, P.A. V., Gaspar, C., 2006. Evaluating the performance of species richness  
602 estimators: Sensitivity to sample grain size. *J. Anim. Ecol.* 75, 274–287. doi:10.1111/j.1365-  
603 2656.2006.01048.x
- 604 Jimenez, H., Bigot, L., Bourmaud, C., Chabanet, P., Gravier-Bonnet, N., Hamel, M.A., Payri, C.,  
605 Mattio, L., Menou, J.L., Naeem, S., Rilwan, Y., Sattar, S., Scott, L., Shiham, A., Vigliola, L.,  
606 Andréfouët, S., 2012. Multi-taxa coral reef community structure in relation to habitats in the  
607 Baa Atoll Man and Biosphere UNESCO Reserve (Maldives), and implications for its  
608 conservation. *J. Sea Res.* 72, 77–86. doi:10.1016/j.seares.2012.04.011
- 609 L'Hardy-Halos, M., Castric-Fey, A., 2001. Inventaire de la faune et de la flore sur les fonds  
610 rocheux de l'île de Groix. Rapport Contrat Nature 2000-2003 Tranche 1, Conseil Régional  
611 de Bretagne - Direction Régionale de l'Environnement, Rennes.
- 612 L'Hardy-Halos, M., Castric-Fey, A., 2000a. Inventaire de la faune et de la flore sur les fonds  
613 rocheux de la presqu'île de Crozon et autour du Cap Sizun. Programme Morgane 2, Fonds  
614 Feoga, Diren, Ministère de l'Agriculture et de la Pêche.
- 615 L'Hardy-Halos, M., Castric-Fey, A., 2000b. Inventaire de la faune et de la flore sur les fonds de  
616 l'estuaire du Trieux. Rapport Contrat Nature 2000-2003 Tranche 1, Conseil Régional de  
617 Bretagne - Direction régionale de l'Environnement, Rennes.
- 618 L'Hardy-Halos, M., Castric-Fey, A., Derrien-Courtel, S., 2001. Inventaire de la faune et de la flore  
619 sur les fonds rocheux de l'estuaire du Jaudy. Programme Contrat Nature Tranche 2.  
620 Rapport Conseil Régional de Bretagne / Fonds Européens / Conseil Régional des Côtes  
621 d'Armor. Rennes.
- 622 Larsen, F.W., Blatt, J., Rahbek, C., 2007. Improving the performance of indicator groups for the  
623 identification of important areas for species conservation. *Conserv. Biol.* 21, 731–40.  
624 doi:10.1111/j.1523-1739.2007.00658.x
- 625 Lawler, J.J., White, D., Sifneos, J.C., Master, L.L., 2003. Rare Species and the Use of Indicator  
626 Groups for Conservation Planning. *Conserv. Biol.* 17, 875–882. doi:10.1046/j.1523-  
627 1739.2003.01638.x
- 628 Le Gal, A., Derrien-Courtel, S., 2015. Quality Index of Subtidal Macroalgae (QISubMac): A suitable  
629 tool for ecological quality status assessment under the scope of the European Water  
630 Framework Directive. *Mar. Pollut. Bull.* 101, 334–348.  
631 doi:10.1016/j.marpolbul.2015.10.053
- 632 Leroy, B., 2015. Rarity: Calculation of Rarity Indices for Species and Assemblages of Species.
- 633 Leroy, B., 2012. Using biodiversity databases for the conservation of invertebrate taxa:  
634 Assemblage-level indices of rarity and species distribution models. *Muséum National*  
635 *d'Histoire Naturelle*.
- 636 Leroy, B., Canard, A., Ysnel, F., 2013. Integrating multiple scales in rarity assessments of  
637 invertebrate taxa. *Divers. Distrib.* 19, 794–803. doi:10.1111/ddi.12040

- 638 Leroy, B., Le Viol, I., Pétilion, J., 2014. Complementarity of rarity, specialisation and functional  
639 diversity metrics to assess community responses to environmental changes, using an  
640 example of spider communities in salt marshes. *Ecol. Indic.* 46, 351–357.  
641 doi:10.1016/j.ecolind.2014.06.037
- 642 Leroy, B., Pétilion, J., Gallon, R., Canard, A., Ysnel, F., 2012. Improving occurrence-based rarity  
643 metrics in conservation studies by including multiple rarity cut-off points. *Insect Conserv.*  
644 *Divers.* 5, 159–168. doi:10.1111/j.1752-4598.2011.00148.x
- 645 Méléder, V., Populus, J., Guillaumont, B., Perrot, T., Mouquet, P., 2010. Predictive modelling of  
646 seabed habitats: Case study of subtidal kelp forests on the coast of Brittany, France. *Mar.*  
647 *Biol.* 157, 1525–1541. doi:10.1007/s00227-010-1426-4
- 648 Mellin, C., Delean, S., Caley, J., Edgar, G., Meekan, M., Pitcher, R., Przeslawski, R., Williams, A.,  
649 Bradshaw, C., 2011. Effectiveness of biological surrogates for predicting patterns of marine  
650 biodiversity: a global meta-analysis. *PLoS One* 6, e20141.  
651 doi:10.1371/journal.pone.0020141
- 652 Ménesguen, A., Gohin, F., 2006. Observation and modelling of natural retention structures in the  
653 English Channel. *J. Mar. Syst.* 63, 244–256. doi:10.1016/j.jmarsys.2006.05.004
- 654 Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M.,  
655 Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J., Thuiller, W., 2013. Rare  
656 species support vulnerable functions in high-diversity ecosystems. *PLoS Biol.* 11,  
657 e1001569. doi:10.1371/journal.pbio.1001569
- 658 Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-  
659 S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston,  
660 K.J., Owens, I.P.F., 2005. Global hotspots of species richness are not congruent with  
661 endemism or threat. *Nature* 436, 1016–9. doi:10.1038/nature03850
- 662 Palardy, J.E., Witman, J.D., 2011. Water flow drives biodiversity by mediating rarity in marine  
663 benthic communities. *Ecol. Lett.* 14, 63–68. doi:10.1111/j.1461-0248.2010.01555.x
- 664 Pearman, P.B., Penskar, M.R., Schools, E.H., Enander, H.D., 2006. Identifying potential indicators  
665 of conservation value using natural heritage occurrence data. *Ecol. Appl.* 16, 186–201.
- 666 Pingree, R.D., Mardell, G.T., Holligan, P.M., Griffiths, D.K., Smithers, J., 1982. Celtic Sea and  
667 Armorican current structure and the vertical distributions of temperature and chlorophyll.  
668 *Cont. Shelf Res.* 1, 99–116. doi:10.1016/0278-4343(82)90033-4
- 669 R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for  
670 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 671 Raffin, C., 2003. Bases biologiques et écologiques de la conservation du milieu marin en mer  
672 d'Iroise. Université de Bretagne Occidentale, Brest.
- 673 Reddin, C.J., Bothwell, J.H., Lennon, J.J., 2015. Between-taxon matching of common and rare  
674 species richness patterns. *Glob. Ecol. Biogeogr.* 24, 1476–1486. doi:10.1111/geb.12372
- 675 Retière, C., 1979. Contribution à la connaissance des peuplements benthiques du golfe  
676 normanno-breton. Université de Caen, France.
- 677 Revelle, W., 2016. psych: Procedures for Personality and Psychological Research, Northwestern  
678 University, Evanston, Illinois, USA.
- 679 Roberts, C.M., Hawkins, J.P., 1999. Extinction risk in the sea. *Trends Ecol. Evol.* 14, 241–246.  
680 doi:10.1016/S0169-5347(98)01584-5
- 681 Robuchon, M., Le Gall, L., Mauger, S., Valero, M., 2014. Contrasting genetic diversity patterns in  
682 two sister kelp species co-distributed along the coast of Brittany, France. *Mol. Ecol.* 23,

- 683 2669–2685. doi:10.1111/mec.12774
- 684 Salomon, J.-C., Breton, M., 1991. Courants résiduels de marée dans la Manche. *Oceanol. Acta SP*,  
685 47–53.
- 686 Sanderson, W.G., 1996. Rarity of marine benthic species in Great Britain: development and  
687 application of assessment criteria. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 6, 245–256.
- 688 Shokri, M.R., Gladstone, W., Kepert, A., 2008. Annelids, arthropods or molluscs are suitable as  
689 surrogate taxa for selecting conservation reserves in estuaries. *Biodivers. Conserv.* 18,  
690 1117–1130. doi:10.1007/s10531-008-9474-5
- 691 Smale, D., 2010. Monitoring marine macroalgae: The influence of spatial scale on the usefulness  
692 of biodiversity surrogates. *Divers. Distrib.* 16, 985–995. doi:10.1111/j.1472-  
693 4642.2010.00709.x
- 694 Smale, D. a, Kendrick, G. a, Wernberg, T., 2011. Subtidal macroalgal richness, diversity and  
695 turnover, at multiple spatial scales, along the southwestern Australian coastline. *Estuar.  
696 Coast. Shelf Sci.* 91, 224–231. doi:10.1016/j.ecss.2010.10.022
- 697 Smith, S.D.A., 2005. Rapid assessment of invertebrate biodiversity on rocky shores: where  
698 there's a whelk there's a way. *Biodivers. Conserv.* 14, 3565–3576. doi:10.1007/s10531-  
699 004-0828-3
- 700 Soberón, J., Jiménez, R., Golubov, J., Koleff, P., 2007. Assessing completeness of biodiversity  
701 databases at different spatial scales. *Ecography.* 30, 152–160. doi:10.1111/j.0906-  
702 7590.2007.04627.x
- 703 Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z. a., Finlayson, M., Halpern, B.S.,  
704 Jorge, M. a., Lombana, A., Lourie, S. a., Martin, K.D., Mcmanus, E., Molnar, J., Recchia, C. a.,  
705 Robertson, J., 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and  
706 Shelf Areas. *Bioscience* 57, 573. doi:10.1641/B570707
- 707 Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond Species Richness:  
708 Community Similarity as a Measure of Cross-Taxon Congruence for Coarse-Filter  
709 Conservation. *Conserv. Biol.* 18, 167–173. doi:10.1111/j.1523-1739.2004.00337.x
- 710 Sutcliffe, P.R., Pitcher, C.R., Caley, M.J., Possingham, H.P., 2012. Biological surrogacy in tropical  
711 seabed assemblages fails. *Ecol. Appl.* 22, 1762–1771. doi:10.1890/11-0990.1
- 712 Van Rein, H.B., Brown, C.J., Quinn, R., Breen, J., 2009. A review of sublittoral monitoring methods  
713 in temperate waters: a focus on scale. *Underw. Technol. Int. J. Soc. Underw.* 28, 15.  
714 doi:http://dx.doi.org/10.3723/ut.28.099
- 715 Vavrek, M., 2011. fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontol.  
716 Electron.* 14.
- 717 Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- 718 WoRMS Editorial Board, 2016. World Register of Marine Species. Available from  
719 <http://www.marinespecies.org> at VLIZ. Accessed 2016-12-11. doi:10.14284/170