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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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Abstract

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

Key-words

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

1 Introduction

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

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

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

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

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

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

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

2 Material and Methods

2.1 Database compilation

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

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

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

2.2 Database robustness and occurrence estimation

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

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

The number of sampled stations differed between sites, from 4 to 20 sampled stations (Table 1). This difference introduced a bias if the occurrence was calculated from the number of sampled 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 $$Q_{ij} = \frac{q_{ij}}{N_j}$$

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

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

196 Where: w_i is the weight of the i^{th} species of the assemblage; S, species richness; and w_{min} and
197 w_{max}, minimum and maximum possible weights, respectively. The I_{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_{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_{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_{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)

238

3.2 Rarity distribution among phyla

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

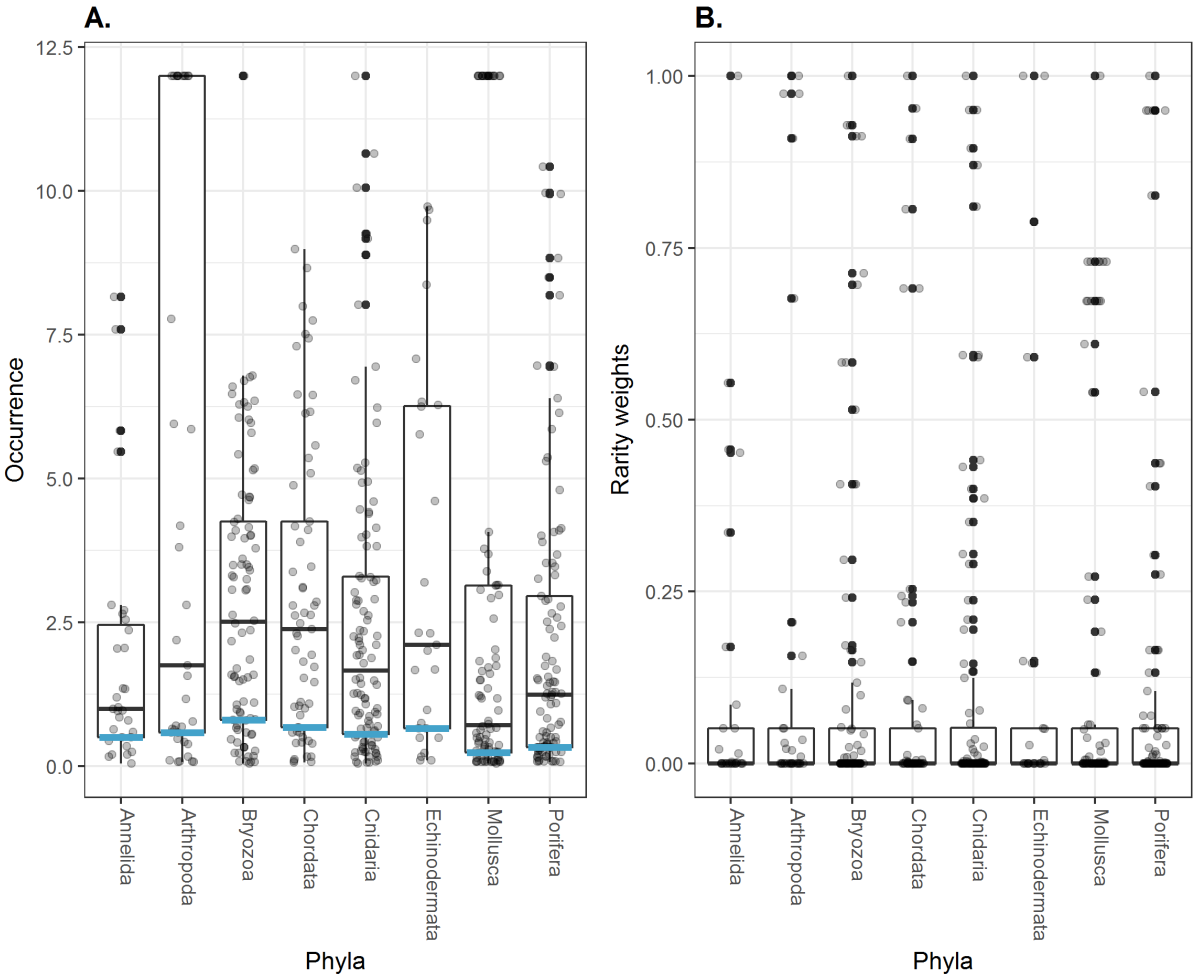


Figure 1. Box-and-whisker plots of **A.** species occurrences and **B.** rarity weights for each phylum. Each point stands for a species. Points are transparent; hence, the overlap of several points results in darker points. Box-and-whiskers represent the non-outlier range of values with horizontal bars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

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

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

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

3.3 Rarity scores of species assemblages

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

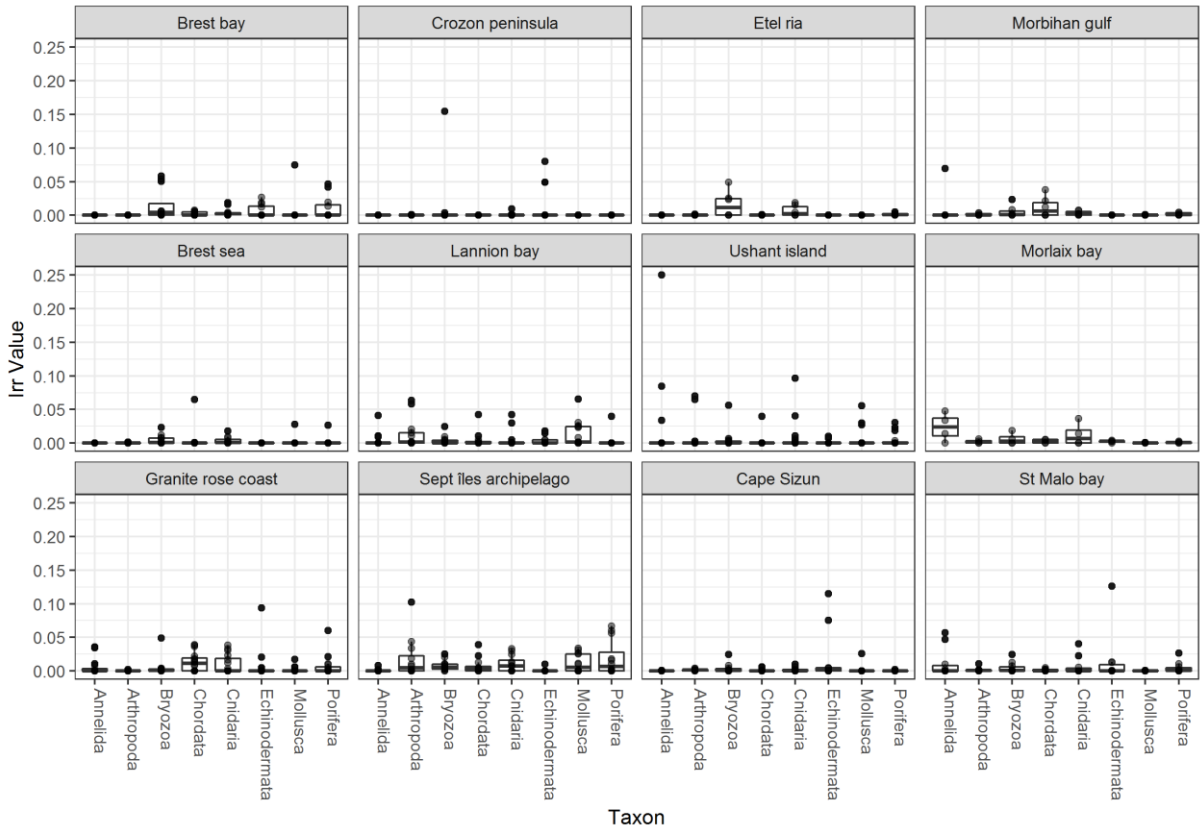


Figure 2. Box-and-whisker plots of phylum-specific Indices of Relative Rarity (I_{RR}) of the 133 inventories of our database. Box-and-whiskers represent the non-outlier range of values with horizontal bars representing from bottom to top: first quartile, median, third quartile.

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.

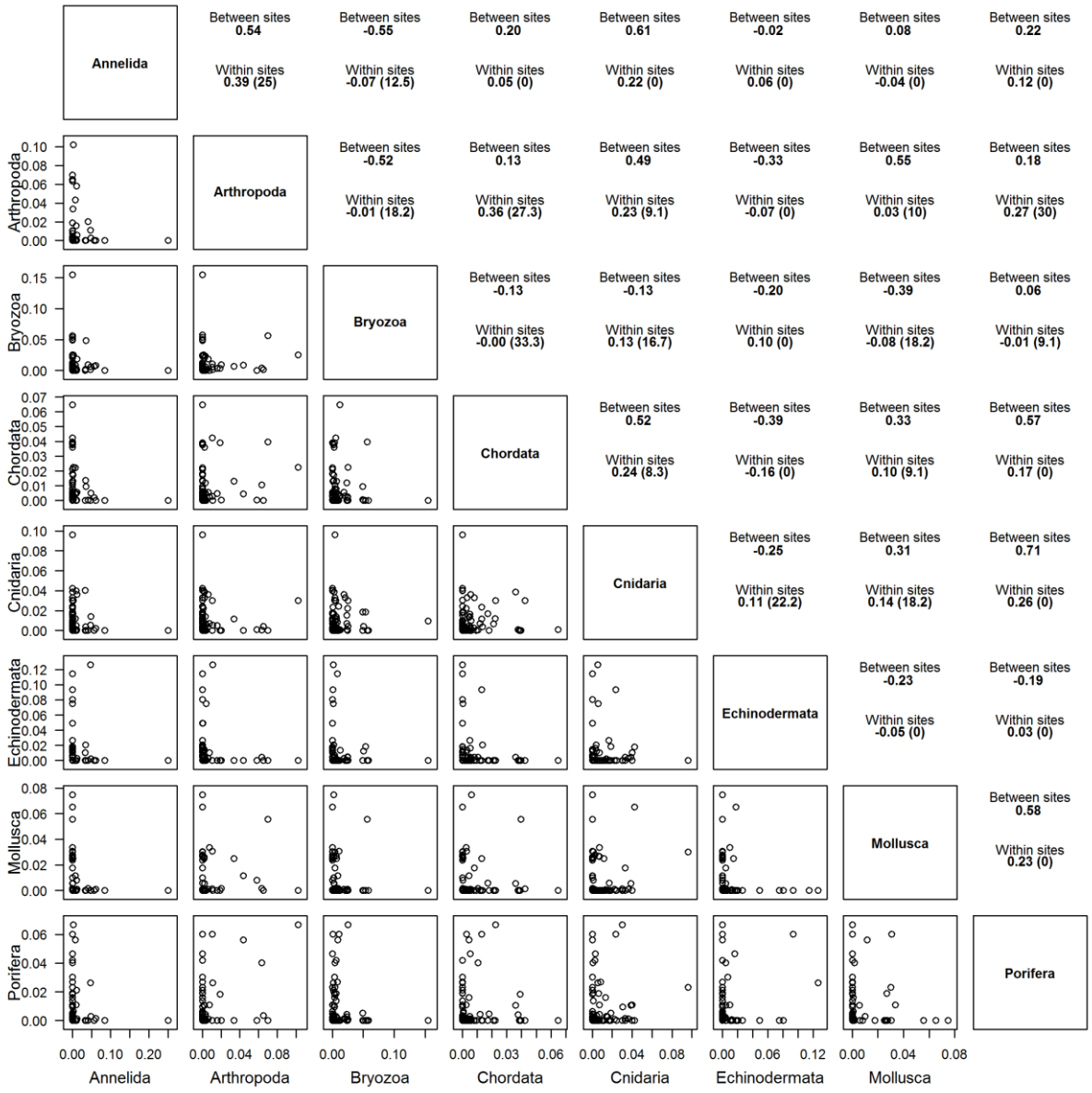


Figure 3. Cross-taxon congruence of Indices of Relative Rarity (I_{RR}) among the eight studied phyla. The lower half shows the scatter plots of I_{RR} ranks of inventories among phyla. The upper half shows values of Spearman's rank correlation coefficients between

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

3.5 Multi-phyla indices of rarity

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

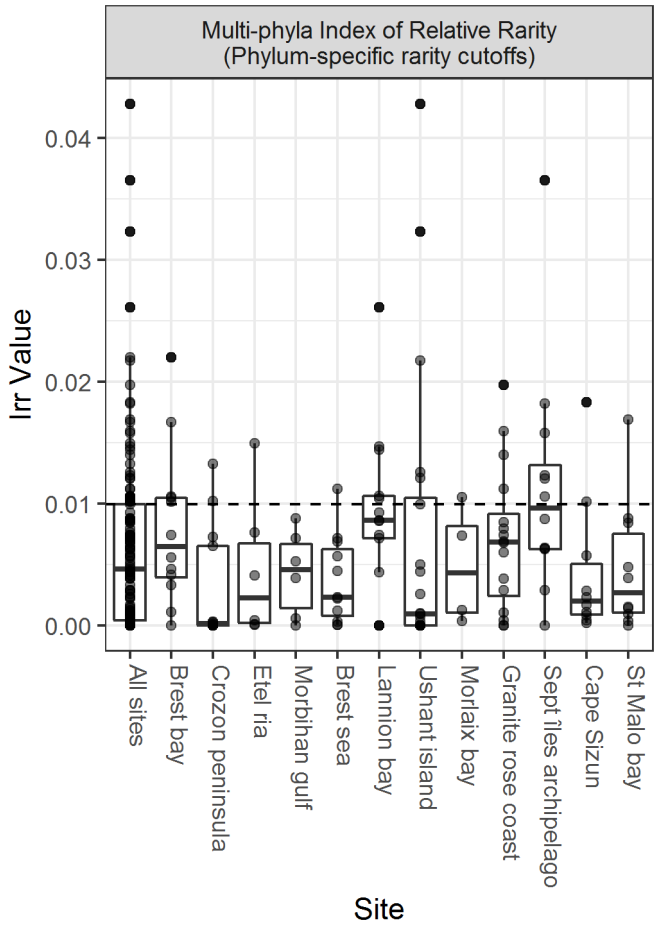


Figure 4. Box-and-whisker plots of multi-phyla Indices of Relative Rarity (I_{RR}) based on phylum-specific rarity cut-off points for the 133 inventories of our database. Box-and-whiskers represent the non-outlier range of values with horizontal bars representing from bottom to top: first quartile, median,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

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

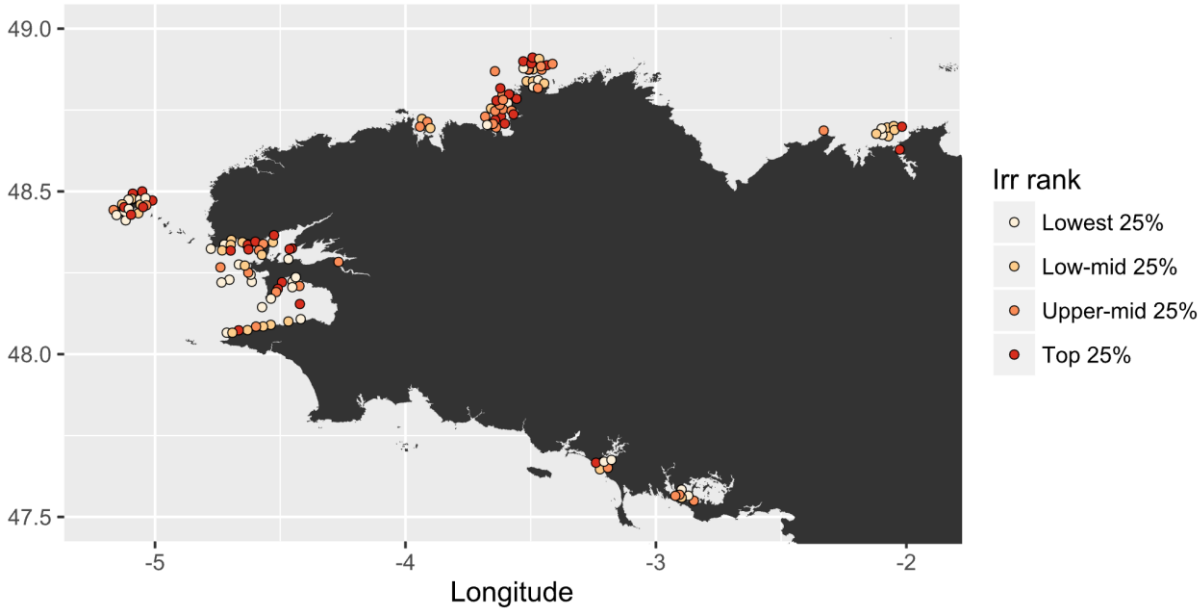


Figure 5. Spatial distribution of Indices of Relative Rarity (I_{RR}) of sampled assemblages around Brittany. I_{RR} were coloured according to four equal classes based on quartiles of all I_{RR} values: (i) Lowest 25%: sites with I_{RR} below the first quartile; (ii) Low-mid 25%: sites with I_{RR} above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

4 Discussion

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

4.1 A flexible approach to weigh species rarity

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

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

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

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

4.3 Spatial distribution of rarity

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

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

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

4.4 Caveats and future directions

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

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

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

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

4.5 Concluding remarks

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

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Supplementary Material

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

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

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

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

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

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

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