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Trophic structure of two intertidal *Fucus* spp. communities along a vertical gradient: Similarity and seasonal stability evidenced with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

François Bordeyne, Dominique Davoult, Aline Migné, Euriell Bertaud Du Chazaud, Cédric Leroux, Pascal Riera

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1 TITLE: Trophic structure of two intertidal *Fucus* spp. communities along a vertical gradient:
2 similarity and seasonal stability evidenced with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

3

4 Short title: Food web similarity in *Fucus* communities

5

6 Authors names:

7 François Bordeyne^{1,*}, Dominique Davoult¹, Aline Migné¹, Euriell Bertaud du Chazaud¹,
8 Cédric Leroux² and Pascal Riera¹

9

10 Affiliations and addresses:

11 ¹ Sorbonne Universités, UPMC Univ Paris 06, CNRS, UMR 7144 AD2M, Station Biologique
12 de Roscoff, 29680 Roscoff, France

13 ² Sorbonne Universités, UPMC Univ Paris 06, CNRS, FR2424, Station Biologique de
14 Roscoff, 29680 Roscoff, France

15

16 *Corresponding author: François Bordeyne

17 Email address: fbordeyne@sb-roscoff.fr

18 Phone: 0033 298292333

19 Fax number: 0033 298292324

20

21 ABSTRACT

22 Intertidal communities dominated by canopy-forming macroalgae typically exhibit some
23 differences in their specific composition that are related to their location along the emersion
24 gradient of rocky shores. Tidal level is also expected to affect resource availability for both
25 primary producers and consumers, potentially leading to divergence in the trophic structure of

26 these communities. Furthermore, in temperate areas, the alternation of seasons has usually a
27 large influence on the primary production and on life-history traits of numerous species,
28 which may induce some changes in the food webs of intertidal communities. Thus, this study
29 aimed to investigate the trophic structure of two intertidal communities located at different
30 tidal levels, over several seasons. Focusing on the dominant species of primary producers and
31 consumers, the food webs of the *Fucus vesiculosus* (Linnaeus, 1753) and *Fucus serratus*
32 (Linnaeus, 1753) communities were studied during four successive seasons, using an isotopic
33 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) approach. Due to the diversity of primary producers and consumers living in
34 these two communities, food webs were relatively complex and composed of several trophic
35 pathways. These food webs remained rather conserved over the successive seasons, even
36 though some variability in isotopic signature and in diet has been highlighted for several
37 species. Finally, despite their location at different tidal levels, the two *Fucus* spp.
38 communities exhibited nearly the same trophic structure, with common consumer species
39 displaying similar isotopic signature in both of them.

40

41 KEYWORDS

42 Stable isotopes; intertidal zonation; seasons; trophic groups

43

44 HIGHLIGHTS

- 45 • Food webs of intertidal furoid communities included several trophic pathways
- 46 • Trophic structure of furoid communities remained highly conserved over the year
- 47 • Furoid communities from different tidal heights exhibited similar food webs

48

49

50

51 1. INTRODUCTION

52 Along intertidal rocky shores of temperate areas, sheltered habitats are usually dominated by
53 canopy-forming brown algae (Phaeophyceae) that can cover almost all the substratum. These
54 species are established along a vertical gradient and are typically associated with numerous
55 species of primary producers and consumers in such a way that intertidal rocky shores are
56 composed of a succession of distinct communities from high to low tide levels (Raffaelli &
57 Hawkins 1999). Trophic structure of these intertidal communities has been the focus of
58 intensive research during the past decades, due to the emergence of the stable isotopic
59 approach (e.g. Dauby et al. 1998, Sarà et al. 2007, Riera et al. 2009, Duarte et al. 2015). To
60 our knowledge, only one study was however carried out in the context of vertical zonation
61 (Steinarsdóttir et al. 2009). Tidal zonation is, yet, expected to be a significant driver of
62 community trophic structure. For instance, shore level usually controls resource access for
63 primary producers (e.g. $\text{CO}_2/\text{HCO}_3^-$ and nutrients, Raven & Hurd 2012), sessile fauna (as
64 some species can only feed when immersed, Raffaelli & Hawkins 1999) and mobile fauna (as
65 the amount of available food might decrease from low to high shore levels, Underwood
66 1984). Trophic relationships are considered as an important component of community
67 functioning and should be defined more accurately in the context of tidal zonation. The use of
68 stable isotopes seems particularly powerful for this purpose, as they act as chemical tracers of
69 energy flow (Peterson & Fry 1987, Fry 2006). Thus, $\delta^{13}\text{C}$ of a consumer usually provides
70 information about its diet sources while its $\delta^{15}\text{N}$ value is often related to its trophic position in
71 the food web (Zanden & Rasmussen 2001, Caut et al. 2009).

72 In temperate areas, abiotic factors such as light and temperature display significant seasonal
73 fluctuations. As a consequence, intertidal communities show seasonal pattern in their
74 metabolism (Golléty et al. 2008, Bordeyne et al. 2015), as well as in their species richness
75 and/or abundance (Rindi & Guiry 2004, Dethier & Williams 2009). These seasonal

76 fluctuations potentially influence species interactions and may therefore lead to modification
77 in their food webs. Furthermore, seasonal changes in isotopic composition of both primary
78 producer and consumer species are regularly evidenced in coastal communities (Nordström et
79 al. 2009, Hyndes et al. 2013), including intertidal habitats (Golléty et al. 2010, Ouisse et al.
80 2011). These changes, which could be related to numerous biotic and abiotic factors (Jennings
81 et al. 2008, Vanderklift & Bearham 2014, Viana et al. 2015), may also reflect important
82 modifications in the trophic structure of these communities over time (McMeans et al. 2015).
83 In this context, it appears essential to understand how seasonal variations can structure the
84 food webs of benthic communities, and also how these communities respond to existing
85 environmental variations (Hyndes et al. 2013).

86 Using a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ approach, this study focuses on the main taxa inhabiting two
87 communities that are established at adjacent tidal levels. These two communities, widespread
88 in temperate rocky shores, are respectively dominated by the canopy-forming species
89 *Fucus vesiculosus* Linnaeus and *Fucus serratus* Linnaeus. This study aimed to describe the
90 trophic structure of these communities at four periods of the year, assuming that the
91 alternation of seasons is likely to generate significant fluctuations of food webs. Comparisons
92 between communities were also carried out to test the hypothesis that food webs vary
93 according to the tidal level.

94

95 2. MATERIAL AND METHODS

96 2.1. Study site

97 The study site is located in front of the Station Biologique de Roscoff, in the southwestern
98 part of the English Channel (Brittany, France) (48°43.743'N, 3°59.407'W). It consisted of an
99 intertidal boulder reef subjected to semi-diurnal tidal cycle, with maximal amplitude of about
100 9 m. This semi-sheltered rocky shore is characterized by a vertical succession of communities

101 dominated by canopy-forming Phaeophyceae, where the *Fucus vesiculosus* and *F. serratus*
102 communities are characteristic of the mid-intertidal (3.0 to 4.0 m above chart datum) and low
103 mid-intertidal (2.5 to 3.0 m above chart datum) respectively. These communities are mainly
104 composed of dense *Fucus* spp. canopies, covering up to 100 % of the substratum, which are
105 associated with miscellaneous epibionts (i.e. algae and sessile invertebrates directly attached
106 to the *Fucus*, see Wahl 2009). They are also made up of sub-canopy and encrusting algae, as
107 well as microphytobenthos, and phytoplankton during high tide. Finally, these communities
108 also support a diverse pool of mobile invertebrates (Raffaelli & Hawkins 1999, Migné et al.
109 2015).

110

111 2.2. Sampling and preparation for stable isotopes analysis

112 For both *F. vesiculosus* and *F. serratus* communities, the most representative taxa of food
113 sources (i.e. erect and encrusting algae, and epilithon) and consumers were collected by hand
114 during low tide, in four successive seasons (September and December 2013 and March and
115 June 2014, see Supplementary material for the list of sampled taxa). After collection, samples
116 were frozen at -18 °C for later processing. Particular attention was taken to collect consumers
117 from the main trophic groups (filter-feeders, grazers and predators), based on literature
118 knowledge (e.g. Dauby et al. 1998, Riera et al. 2009, Golléty et al. 2010). Stable isotope data
119 for marine suspended particulate organic matter (POM) were obtained from the SOMLIT
120 network, in a place located at approximately 600 m of our study site (Estacade sampling
121 point, Roscoff, France, data available at <http://somlit-db.epoc.u-bordeaux1.fr/bdd.php>).

122 In the laboratory, erect algae were carefully cleaned in filtered seawater (0.45 µm) to remove
123 detrital fragments and attached organisms. The encrusting ones were scrubbed in filtered
124 seawater, which was then filtered onto pre-combusted filters (Whatman GF/F glass microfiber
125 filters). In order to remove inorganic carbon of the encrusting Rhodophyceae

126 *Phymatolithon lenormandii*, HCl 1N was added to seawater prior to filtration. Epilithon was
127 gently removed from small boulders using a smooth brush and collected in filtered seawater,
128 then filtered onto pre-combusted filters. Regarding consumers, organisms belonging to the
129 Cnidaria (except campanulariidae), Mollusca, Arthropoda (except amphipods) and
130 Echinodermata phyla were treated at the individual level, while for colonial taxa (i.e.
131 campanulariidae, Bryozoa and Ascidiacea), *Spirorbis* sp. and amphipods, several organisms
132 were pooled together to get enough material for accurate stable isotope analyses. Gastropods
133 were extracted from their shell to take off foot muscle, whereas for decapods, muscle was
134 taken off from their pereopods. For *Asterina gibbosa*, amphipods, campanulariidae and
135 polyclinidae, half of the samples were acidified to remove inorganic carbon (HCl 1N) while
136 the other part remained untreated. $\delta^{13}\text{C}$ measurements were performed on acidified samples
137 and $\delta^{15}\text{N}$ on untreated ones, as advised by Schlacher & Connolly (2014). Finally, all samples
138 were rinsed with distilled water, before being dried (60°C, 48h) and ground to a fine
139 homogeneous powder using an agate mortar and pestle.

140

141 Carbon and nitrogen stable isotopes ratios were determined using a Flash EA 1112 CHN
142 analyzer (ThermoFinnigan) coupled with a Finnigan Delta Plus mass spectrometer, via a
143 Finnigan Con-Flo III interface. Data are expressed in the standard δ unit:

$$\delta X(\text{‰}) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

144 With X is ^{13}C or ^{15}N and R is $^{13}\text{C}/^{12}\text{C}$ ratio for carbon or $^{15}\text{N}/^{14}\text{N}$ ratio for nitrogen.

145 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were calculated in relation to the certified reference materials Vienna-Pee Dee
146 Belemnite-limestone (V-PDB) and atmospheric di-nitrogen (N_2). The V-PDB and N_2 at air-
147 scales were achieved using in-house protein standards, calibrated against NBS-19 and IAEA
148 N3 reference materials. The standard deviation of repeated measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

149 values of the laboratory standard was 0.10 ‰ versus V-PDB and 0.05 ‰ versus at-air,
150 respectively.

151

152 *2.3. Taxonomic diversity and density of gastropod grazers*

153 Gastropod grazers (hereafter referred to as “grazers”) constitute the most abundant group of
154 consumers in these communities (approx. 95% of the countable fauna) and likely play a
155 significant role in organic matter fluxes within the food webs. The taxonomic diversity of
156 these grazers was monitored in the same areas and at the same periods than sampling for
157 stable isotopes analyses (i.e. September and December 2013, and March and June 2014).
158 Thus, at each season, grazers were identified at the species level and counted in five replicates
159 of 0.1 m² randomly chosen in each community. To account for spatial variability, intra-
160 community replicates were 3 to 10 m away one from each other.

161

162 *2.4. Data analysis*

163 The trophic structure of each community, its temporal fluctuations, and the potential trophic
164 relationships between diets and consumers, were investigated by drawing dual-isotope plots at
165 each sampling period. The “community-wide” isotopic metrics developed by Cucherousset &
166 Villéger (2015) (i.e. isotopic richness, divergence, dispersion, evenness and uniqueness) were
167 used as a complement to these dual-isotope plots. The isotopic richness is related to the area
168 of the bi-dimensional isotopic space that is filled by all the taxa while the isotopic divergence,
169 dispersion, evenness and uniqueness are related to the distribution of taxa in this space,
170 providing information about trophic diversity and redundancy. These metrics have the benefit
171 to be mathematically independent of the number of replicates used and allow accounting for
172 abundance/biomass of taxa, when available. They were calculated at each sampling period
173 and for each community, using the R functions computed by Cucherousset & Villéger (2015),

174 with R software, version 3.2.2 (R Core Team 2015). Their coefficient of variation across
175 seasons was used to discuss about the seasonal variability in the trophic structure of these two
176 communities.

177 Bayesian stable isotope mixing models (SIAR, Parnell et al. 2010, Parnell & Jackson 2013)
178 were implemented to estimate the relative contribution of food sources to the diet of several
179 consumers, at each season, and for each community. To do so, trophic enrichment factors of
180 0.28 ± 0.23 ‰ for $\delta^{13}\text{C}$ and of 2.5 ± 0.68 ‰ for $\delta^{15}\text{N}$ were assumed (Caut et al. 2009). Thus,
181 these mixing models were run for a set of filter-feeders selected for each community,
182 implementing POM and erect algae as potential food sources. Erect algae were used
183 considering that they may be consumed by filter-feeders through detritus (Leclerc et al. 2013),
184 despite that degradation process might affect their isotopic composition (Lehmann et al.
185 2002). Mixing models were also run for a set of grazers selected for each community,
186 implementing epilithon and erect algae as potential food sources. Grazer selection was
187 realized according to Hawkins et al. (1989), in such a way that diversity of feeding behaviours
188 and of radula types was maximised. In the *F. serratus* community, some erect Rhodophyceae
189 were pooled together according to their characteristics, to limit the number of potential food
190 sources (Phillips et al. 2014).

191
192 For comparisons between communities, we first calculated the overall level of isotopic
193 overlap between the two communities using the isotopic overlap metrics (isotopic similarity
194 and nestedness) developed by Cucherousset & Villéger (2015), from the average isotopic
195 signature of each taxon. We also focused on consumer taxa present in both communities (i.e.
196 shared consumers, see Supplementary Material for their identities). Their average $\delta^{13}\text{C}$ and
197 $\delta^{15}\text{N}$ obtained in the *F. vesiculosus* community were plotted against those obtained in the *F.*
198 *serratus* community. Slopes and intercepts of a Model II regression were then calculated

199 according to the major axis method, using the “lmodel2” R package version 1.7-2 (Legendre
200 2014), for both $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$ and $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$ plots. Student’s t-tests were
201 performed to test if slopes and intercepts of regressions were significantly different from 1
202 and 0, respectively. If not, it would indicate that, on average, the shared consumers’ exhibited
203 similar isotopic signature in the two communities.

204 Focusing on grazers, potential differences between communities were first investigated in
205 terms of taxonomic diversity (i.e. distribution of abundances among taxa) using clustering
206 analysis (group average) and one-way ANOSIM test (for each community, the four seasonal
207 samples were considered as replicates). These analyses were performed on similarity matrix
208 calculated from Bray-Curtis similarity index on square-root transformed abundances, using
209 PRIMER software, version 6.1.12 (Clarke & Gorley 2006). Then, potential difference
210 between communities in term of isotopic diversity of grazers was investigated using the
211 isotopic diversity metrics (isotopic richness, divergence, dispersion, evenness and uniqueness,
212 (Cucherousset & Villéger 2015). These isotopic metrics were calculated at each season and
213 for each community, from grazer isotopic signatures, with and without weighting them by
214 their abundances. Clustering analysis and one-way ANOSIM tests were then performed for
215 each condition on similarity matrices calculated using Bray-Curtis similarity index on the five
216 metrics, following the procedure previously described.

217

218 3. RESULTS

219 3.1. *Trophic structure of Fucus spp. communities and seasonal variability*

220 For each community, primary sources were distributed over a large range of $\delta^{13}\text{C}$ over the
221 sampling seasons. For the *F. vesiculosus* community, *Caulacanthus ustulatus*, POM and
222 epilithon were the most ^{13}C -depleted sources, and displayed $\delta^{13}\text{C}$ ranging from -20.3 to -
223 24.0 ‰, according to sampling seasons. *Ascophyllum nodosum*, *F. vesiculosus*, *Ulva* spp. and

224 *Hildenbrandia rubra* were more ^{13}C -enriched and showed $\delta^{13}\text{C}$ values ranging from -13.0 to -
225 18.4 ‰, according to sampling seasons. These sources were mainly discriminated by their
226 $\delta^{15}\text{N}$, with *A. nodosum* and *F. vesiculosus* being on average more ^{15}N -depleted (5.1 to 7.4 ‰)
227 than *Ulva* spp. and *H. rubra* (6.2 to 8.9 ‰, Figure 1). For the *F. serratus* community,
228 *C. ustulatus*, *Chondracanthus acicularis*, POM and epilithon were the most ^{13}C -depleted
229 sources, and displayed $\delta^{13}\text{C}$ values ranging from -19.5 to -25.0 ‰, according to sampling
230 seasons. The other sources were more ^{13}C -enriched (-14.8 to -19.9 ‰). Among them,
231 *F. serratus* was the most ^{15}N -depleted (3.0 to 5.7 ‰), while *Ulva* spp., *H. rubra*,
232 *Mastocarpus stellatus* and *P. lenormandii* were more closely related ($\delta^{15}\text{N}$ ranging from 6.5
233 to 9.7 ‰, Figure 2). Regarding consumers, filter-feeders were on average the most ^{13}C -
234 depleted, with $\delta^{13}\text{C}$ values ranging from -16.5 to -20.8 ‰ for the *F. vesiculosus* community
235 and from -15.2 to -21.2 ‰ for the *F. serratus* community, according to sampling seasons. In
236 comparison, grazers were more ^{13}C -enriched, with values ranging from -13.9 to -16.4 ‰ for
237 the *F. vesiculosus* community and from -13.1 to -17.0 ‰ for the *F. serratus* community,
238 according to sampling seasons. Predators occupied the top of the food webs, and were the
239 most ^{15}N -enriched consumers. They displayed $\delta^{15}\text{N}$ values ranging from 9.2 to 13.0 ‰ for the
240 *F. vesiculosus* community (filter-feeders and grazers: 7.2 to 10.8 ‰, Figure 1) and from 7.7 to
241 14.0 ‰ for the *F. serratus* community (filter-feeders and grazers: 6.0 to 10.3 ‰, Figure 2),
242 according to sampling seasons.

243 The five isotopic metrics showed low variability across seasons, as their coefficient of
244 variation varied between 3.8 and 14.6% in the *F. vesiculosus* community and between 2.4 and
245 25.4% in the *F. serratus* community (Table 1). Only isotopic richness and uniqueness of the
246 *F. serratus* community exhibited a coefficient of variation higher than 15%. This was mainly
247 due to the high ^{13}C and/or ^{15}N depletions of two basal sources in some seasons (i.e. epilithon

248 was ^{13}C and ^{15}N depleted in both December and March, and *F. serratus* was ^{15}N depleted in
249 March, Figure 2).

250 Relative contributions of potential food sources to the diet of consumers were highly variable
251 between sampling seasons (Table 2). In the *F. vesiculosus* community, the contribution of
252 POM to the diet of filter-feeders was maximal in September and June (17.2 to 49.4% on
253 average) and minimal in December and March (8.8 to 13.1% on average). In contrast, erect
254 macroalgae were the main resources to filter-feeders in December and March (86.9 to 91.2%
255 on average, Table 2). For grazers, no clear seasonal trend in diet was evidenced, even though
256 *Ulva* spp. and *F. vesiculosus* constituted their main trophic resources in March (27.0 to 77.6%
257 on average) and in June (42.9 to 71.2% on average), respectively. In the *F. serratus*
258 community, the contribution of POM to the diet of filter-feeders was maximal in September
259 and June (29.5 to 77.6% on average) and minimal in December and March (6.1 to 16.1% on
260 average) as well. Erect macroalgae were their main resources in December and March (83.9
261 to 93.9% on average, Table 2). No clear seasonal trend in diet of grazers was evident, even
262 though *F. serratus* constituted their main trophic resources in June (69.2 to 86.3% on
263 average).

264

265 3.2. Comparisons between communities

266 No seasonal trend in trophic structure has been observed for these two intertidal communities.
267 As well, when comparisons between communities were performed at each season, any
268 difference were evidenced, neither considering the functional isotopic space of whole
269 communities (i.e. high isotopic similarity and isotopic nestedness), nor considering the
270 isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of consumers species present in both communities.
271 Therefore, comparisons between communities were performed using an average isotopic
272 signature of each taxon, obtained after pooling the stable isotope values of the different

273 sampling periods. Considering these year-round means in isotopic signature, the two
274 communities presented an isotopic similarity of 0.779 and an isotopic nestedness of 0.894
275 (Figure 3). Almost all the taxa (43 of 52) were included in the intersection of the two isotopic
276 spaces. Regarding the consumers shared by the two communities, the model II regressions of
277 dual plots exhibited significant Pearson's coefficient (For $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$, $n = 14$,
278 $R = 0.876$, $p < 0.001$; for $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$, $n = 14$, $R = 0.953$, $p < 0.001$) (Figure 4). The
279 slopes of regressions were equal to 1.2 and 1.0 for $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$ and $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$,
280 respectively, while intercepts were equal to 2.9 and 0.3, respectively. These slopes and
281 intercepts were not significantly different from 1 and 0, respectively (For $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$,
282 $t = 1.42$, $p = 0.091$ for the slope and $t = 1.49$, $p = 0.080$ for the intercept; for $\delta^{15}\text{N}_{\text{Fves}}$ vs
283 $\delta^{15}\text{N}_{\text{Fser}}$, $t = 0.13$, $p = 0.450$ for the slope and $t = 0.40$, $p = 0.349$ for the intercept).

284 In both communities, *Gibbula* spp., *Littorina* spp. and *Patella vulgata* were the most
285 dominant taxa of grazers: *G. umbilicalis* being the most abundant species in the *F. vesiculosus*
286 community (96 to 208 individuals per m^2) and *G. pennanti* was most abundant species in the
287 *F. serratus* community (130 to 508 individuals per m^2 , Table 3). Clustering analysis
288 performed on the taxonomic diversity of grazers discriminated the two communities (Figure
289 5a), which were significantly different according to the ANOSIM test ($R = 0.75$, $p = 0.029$).
290 When performed on isotopic diversity metrics, these analyses did not allow to significantly
291 discriminate the two communities, neither when they were conducted on unweighted data
292 (ANOSIM test, $R = 0.26$, $p = 0.083$, Figure 5b), nor when conducted on data weighted by
293 abundance of grazers (ANOSIM test, $R = 0.12$, $p = 0.229$, Figure 5c).

294

295 4. DISCUSSION

296 4.1. Trophic structure of *Fucus* spp. communities

297 By analysing isotopic composition of the main taxa inhabiting the *Fucus vesiculosus* and
298 *F. serratus* communities, we attempted to depict their global trophic structure. At each season
299 and in each community, groups of consumers were discriminated as filter-feeders, grazers and
300 predators, despite some overlap in their isotopic signatures. As expected, filter-feeders were
301 the most ^{13}C -depleted consumers, while predators were the most ^{15}N -enriched and occupied
302 the top of the food webs. Both sources and consumers were distributed over large $\delta^{13}\text{C}$ and
303 $\delta^{15}\text{N}$ ranges, suggesting that the *Fucus* spp. communities are characterized by a complex
304 trophic structure (Goll ty et al. 2010). This complexity may have been however
305 underestimated during this study, as the ultimate top predators of these communities (i.e.
306 fishes and shore birds, Ellis et al. 2007), as well as one potential food source (epibiotic
307 biofilms) were not sampled. Despite that, the large $\delta^{15}\text{N}$ range of consumers (i.e. $\delta^{15}\text{N}$
308 extended over 4.7 to 7.4 ‰ according to the sampling period) reveals the presence of several
309 trophic levels within the *Fucus* spp. communities. The heterogeneous distribution in $\delta^{15}\text{N}$ of
310 primary consumers prevented, however, to attribute an accurate trophic position to each
311 consumer (Post 2002, Riera et al. 2009). As well, their large $\delta^{13}\text{C}$ range is characteristic of the
312 occurrence of several trophic pathways, as previously reported in rocky shore habitats
313 (Goll ty et al. 2010, Leclerc et al. 2013). This likely results from the high diversity of food
314 sources and feeding behaviors of invertebrates (Riera et al. 2009), which are favored by the
315 multitude of microhabitats that usually characterized rocky shores (Schaal et al. 2010, 2011).
316 Mixing models also highlighted the occurrence of several trophic pathways in fucoid
317 communities. Thus, filter-feeders were supposed to rely mainly on POM and on several
318 species of erect algae through the detrital pathway. As well, the diet of grazers was mainly
319 based on a mix of different species of algae (i.e. *Fucus*, *Ulva* spp., *A. nodosum*, *M. stellatus*).
320 According to these results, filter-feeders and grazers can be considered as generalist species.
321 Therefore, *Fucus* species did not constitute the cornerstone of these food webs, supplying the

322 vast majority of organic carbon for primary consumers (with the exception of June for
323 grazers), as we might reasonably expect from their abundance (i.e. 1.50 to 11.80 kg of fresh
324 weight m⁻² for *Fucus* canopies; 0.02 to 0.28 kg of fresh weight m⁻² for all other erect
325 macroalgae, Bordeyne et al., unpublished data). However, fucoid species are usually
326 considered to have poor nutritional values and can induce anti-grazing defence that may repel
327 primary consumers (Molis et al. 2006). Therefore, primary consumers may show food
328 preference toward more nutritional species (Lubchenco 1978, Littler & Littler 1980, Watson
329 & Norton 1985), despite their lower abundance. Epibiotic biofilms, while not sampled here,
330 may also constitute a complementary trophic resource for some species of grazers, notably
331 those living on fucoid fronds such as *Littorina obtusata* (see Norton et al. 1990 and references
332 therein). Interestingly, according to its isotopic signature and the results of mixing models, the
333 introduced alga *C. ustulatus* has very low contribution to the diet of grazers. This species, first
334 recorded close to our study site almost 30 years ago (Rio & Cabioch 1988), was suggested to
335 be unpalatable for native consumers due to production of secondary metabolites (Smith et al.
336 2014). However, filter-feeders may rely on this species through the detrital pathway. Finally,
337 we should mention that the wide ranges in specific contributions obtained from mixing
338 models reveal some uncertainties, and have to be considered with caution (Phillips et al.
339 2014).

340

341 4.2. Seasonal variability of trophic structure

342 The year-round analysis of the isotopic composition of the main taxa inhabiting the
343 *F. vesiculosus* and *F. serratus* communities revealed an overall preservation of their food
344 webs across seasons. This trend, depicted by comparing the biplots drawn at each season, was
345 supported by the low values of the coefficient of variation across seasons for isotopic
346 diversity metrics, especially in the *F. vesiculosus* community. Such preservation of trophic

347 structure across seasons has already been noticed for a *Fucus*-dominated community (Schaal
348 et al. 2010), even though the studied community was subjected to a strong anthropogenic
349 pressure, which may have influenced isotopic composition of both sources (Viana et al. 2015)
350 and consumers (Warry et al. 2016). Thus, the year-round preservation of food webs we
351 observed in non-impacted furoid communities could have major implications regarding our
352 knowledge of their dynamics. Indeed, temporal modification of species richness and/or
353 abundance is generally considered as a key process in temperate habitats (Dethier & Williams
354 2009) and could potentially lead to a seasonality in resource availability, as observed in the
355 Arctic environments. Such seasonality finally leads to large modifications of food webs in
356 these extreme environments (Forest et al. 2008, Darnis et al. 2012). In the present study,
357 however, most of the common macroalgae are perennial (e.g. *Fucus* spp., *M. stellatus*),
358 providing constant resources for grazers, despite the fall to spring decrease in abundance of
359 ephemeral alga *Ulva* spp. (Migné et al. 2015). Therefore, grazers do not need to switch their
360 diet over the course of the year, explaining their temporal conservation within food webs. In
361 contrast, filter-feeders showed a partial switch in diet over the year, according to the results of
362 mixing models. They were found to rely mainly on phytoplankton-dominated POM during
363 summer and on macroalgae-derived organic matter during winter, which is consistent with
364 seasonal variations in abundance of phytoplankton observed close to our study area (SOMLIT
365 data). Such switch in diet has already been observed in kelp forests of Brittany (Leclerc et al.
366 2013), and strengthens the idea that macroalgae-derived detritus are a significant food source
367 for filter-feeders (Sarà et al. 2007, Crawley et al. 2009, Schaal et al. 2010, Miller & Page
368 2012). They are therefore suggested to be opportunistic species relying on the most abundant
369 food source (Ricciardi & Bourget 1999, Schaal et al. 2010). In spite of this temporal diet
370 variability, the average trophic position of this functional group in the two communities
371 remained unchanged, and filter-feeders stayed ^{13}C -depleted compared to grazers, all over the

372 year. The relative seasonal conservation of predators within the food webs was probably due
373 to the seasonal consistency of their potential diet (i.e. primary consumers) but should also
374 result from a relative degree of omnivory and opportunism (Thompson et al. 2007, Silva et al.
375 2010, Duarte et al. 2015). Finally, the overall preservation of trophic structure across seasons
376 observed despite some seasonal changes in taxonomic diversity of consumers, suggests that
377 some redundancy in the feeding behaviour of these species (Hawkins et al. 1989, Golléty et
378 al. 2010) helps to keep a relative food web stability over time (Christie et al. 2009).

379 The high degree of conservation of their trophic structures exhibited by furoid communities
380 during the sampling year could lead to further new insights about dynamics of these habitats.
381 These results should, however, be complemented by the addition of densities or biomasses for
382 each taxa, as this may thoroughly modify the vision we have of trophic relationships (Rigolet
383 et al. 2015).

384

385 *4.3. Comparisons between communities*

386 By analysing isotopic composition of taxa living in these communities, we had the prospect to
387 do comparisons in the context of vertical zonation of intertidal habitats. Using community-
388 wide metrics, we highlighted an important similarity in the average trophic structure of the
389 two *Fucus* spp. communities. This was supported by the large number of taxa present in the
390 common isotopic space. Despite some differences in the species richness and composition
391 between these two communities (Davoult et al., unpublished data), they shared a roughly
392 similar isotopic functional space, suggesting that the same trophic functions are undertaken by
393 different species in the *F. vesiculosus* and *F. serratus* communities. This is consistent with the
394 fact that intertidal communities are mostly composed of generalists and opportunistic species,
395 that rely mainly on the most abundant food sources (Steinarsdóttir et al. 2009). Such plasticity
396 in diet could favour growth rates of consumers, as demonstrated by Lee et al. (1985),

397 providing them some benefit in intertidal habitats. However, the two *Fucus* spp. communities
398 exhibited significant differences in their photosynthetic activity over the year (Bordeyne et al.
399 2015), potentially leading to important differences in the amount of carbon accumulation at
400 the base of the food webs, and in carbon fluxes toward top predators. Again, further
401 investigations taking into account taxon abundances are needed to understand more faithfully
402 the trophodynamics of these communities.

403 Although the *F. vesiculosus* and *F. serratus* communities exhibit some differences in their
404 specific composition, several taxa of consumers live commonly in the two communities.
405 These taxa were found to exhibit, on average, similar isotopic composition, whether they were
406 found in the *F. vesiculosus* community or in the *F. serratus* one. Steinarsdóttir et al. (2009)
407 observed a similar pattern on a few number of invertebrate species from Icelandic coast.
408 These results are particularly interesting since most of the considered taxa are sessile or slow
409 moving invertebrates. Therefore, this suggests that they used similar diet resources in both
410 locations. The case of the green crab *Carcinus maenas* is slightly different, as for this highly
411 mobile species, migration toward higher intertidal levels for foraging activity has been shown
412 to be usual during high tide (Silva et al. 2010). This species can thus be considered as a
413 coupler that underlie landscape level food webs, as defined by Rooney et al. (2008).

414 Diversity monitoring highlighted significant differences in the composition of grazers
415 between the two communities, in accordance with the tidal control of species distribution and
416 abundances (Raffaelli & Hawkins 1999). However, when considering isotopic composition,
417 no significant difference between communities was evidenced, whether the abundance of
418 grazers is accounted for or not. These results suggest that the two groups of grazers exhibited
419 similar trophic functions within the two communities, despite some differences in species
420 identities and abundances. Besides, within each community, the diversity of radula types and
421 feeding mechanisms described for these grazers indicated that some functional

422 complementarity occurs (for instance, *P. vulgata* is considered as a scraper of hard substrata,
423 while *Gibbula* spp. seem rather to brush algae, Hawkins et al. 1989), and is likely to promote
424 species coexistence in relatively high abundances.

425 By focusing on grazers, the present study confirms that considering species abundance or
426 biomass in association with stable isotope approach is a fresh opportunity to bring some new
427 insights about community functioning (Cucherousset & Villéger 2015, Rigolet et al. 2015). In
428 this study, this approach allowed us to exclude significant difference in the trophic structure
429 of grazers between the two communities, as discussed before. Without this, any evident
430 conclusion would have been drawn, as the doubt could still subsist with a p-value of 0.08
431 (obtained for unweighted isotopic data of grazers), especially when specific composition and
432 abundance varied between the two communities.

433

434 4.4. *Conclusion*

435 This study highlighted that the two widespread *Fucus vesiculosus* and *F. serratus*
436 communities exhibited trophic structures that remained highly conserved over a year, despite
437 some seasonal fluctuations in physiological processes and in species composition and
438 abundance. Thus, such food web approaches should be carried on, not only at the seasonal
439 scale but also at various temporal scales (McMeans et al. 2015), to better understand the
440 dynamics of food webs, especially according to the specific features of their environment.
441 Furthermore, the two *Fucus* spp. communities exhibited similar trophic structure while they
442 are located at different shore levels and exhibit some differences in their specific composition.
443 In this context of vertical zonation, it would be interesting to go further, and for instance have
444 a look to the specific composition and food webs of several communities dominated by
445 canopy-forming macroalgae that are established on the whole intertidal gradient.

446

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453

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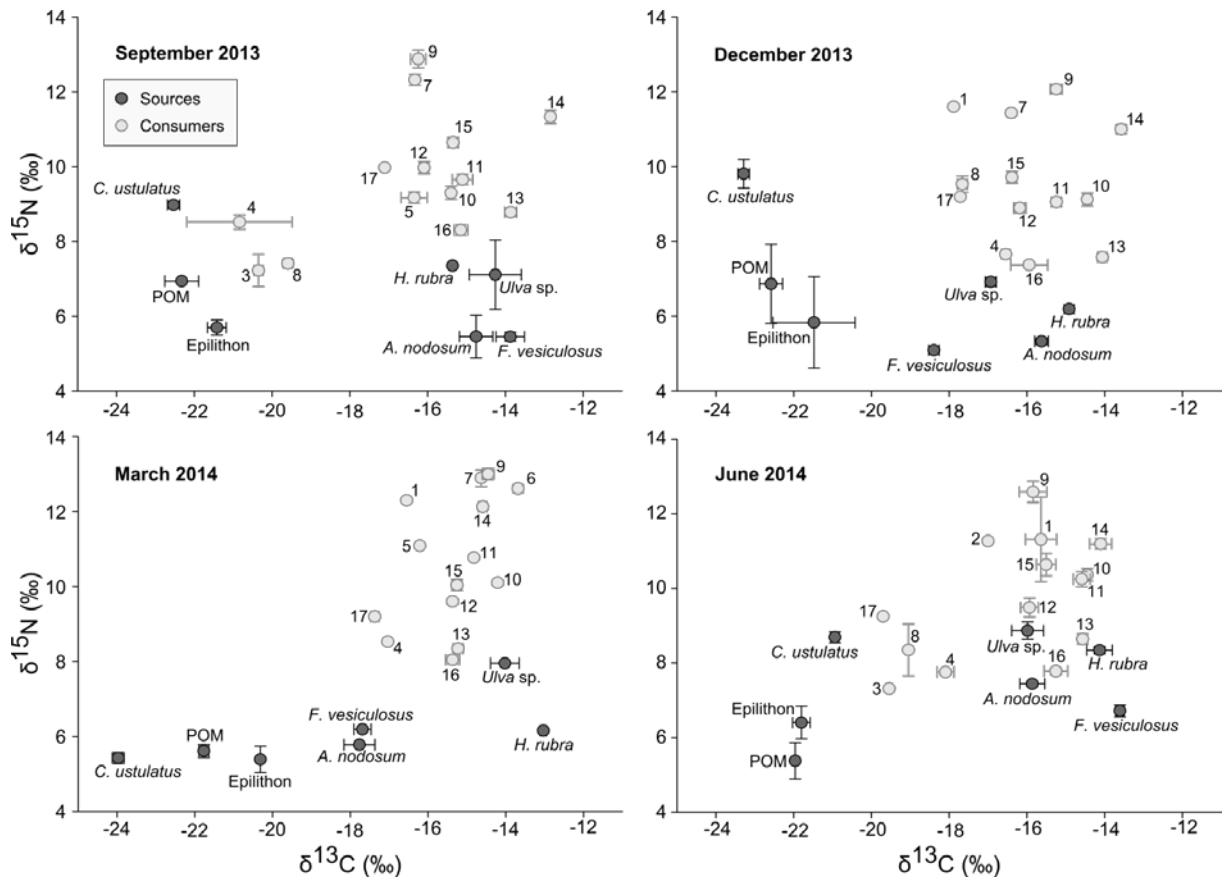
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602

603 **Figure 1:** Mean \pm SE of $\delta^{15}\text{N}$ (‰) vs $\delta^{13}\text{C}$ (‰) for primary producers and consumers of the

604 *Fucus vesiculosus* community, sampled in September and December 2013 and March and

605 June 2014. Sources are represented by dark-grey rounds and their names are indicated nearby,

606 while consumers are represented by light-grey rounds. Consumers : 1 *Actinia equina*; 2

607 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7

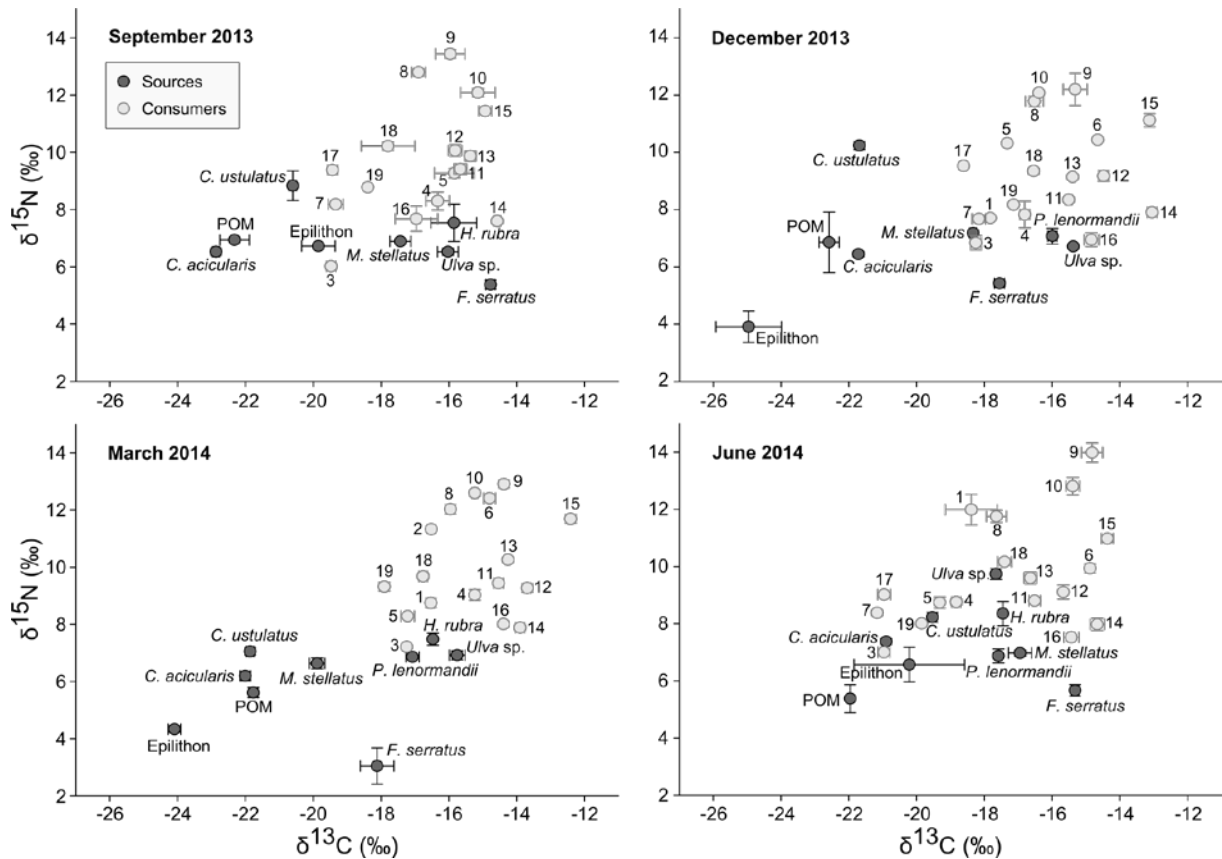
608 *Calliostoma zizyphinum*; 8 Campanulariidae; 9 *Carcinus maenas*; 10 *Gibbula pennanti*; 11

609 *Gibbula umbilicalis*; 12 *Littorina littorea*; 13 *Littorina obtusata*; 14 *Nucella lapillus*; 15

610 *Phorcus lineatus*; 16 *Patella vulgata*; 17 *Spirorbis* sp. Values are given in Supplementary

611 Material 1.

612



613

614 **Figure 2:** Mean \pm SE of $\delta^{15}\text{N}$ (‰) vs $\delta^{13}\text{C}$ (‰) for primary producers and consumers of the
 615 *Fucus serratus* community, sampled in September and December 2013 and March and June

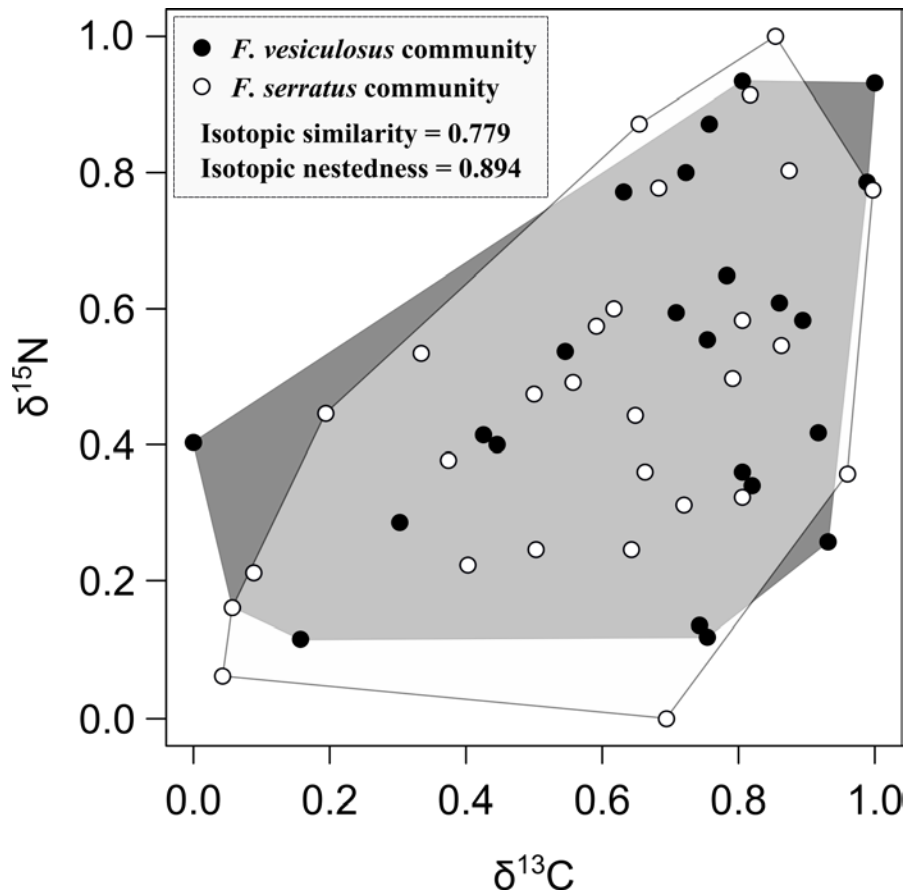
616 2014. Sources are represented by dark-grey rounds and their names are indicated nearby,
 617 while consumers are represented by light-grey rounds. Consumers : 1 *Actinia equina*; 2

618 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7
 619 *Botryllus schlosseri*; 8 *Calliostoma zizyphinum*; 9 *Cancer pagurus*; 10 *Carcinus maenas*; 11

620 *Gibbula cineraria*; 12 *Gibbula pennanti*; 13 *Gibbula umbilicalis*; 14 *Littorina obtusata*; 15
 621 *Nucella lapillus*; 16 *Patella vulgata*; 17 Polyclinidae; 18 *Porcellana platycheles*;

622 19 *Spirorbis* sp. Values are given in Supplementary Material 2.

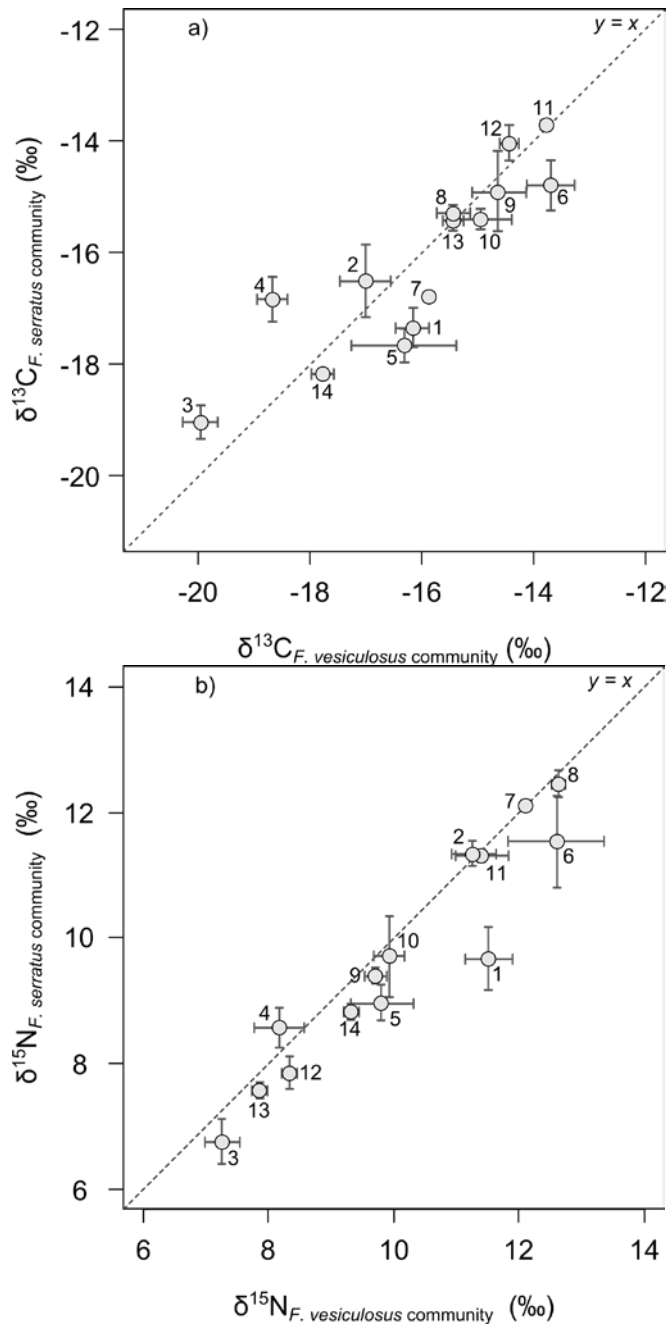
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624

625 **Figure 3:** Annual mean of scaled $\delta^{15}\text{N}$ vs scaled $\delta^{13}\text{C}$ for primary producers and consumers of
 626 the *F. vesiculosus* (black rounds) and *F. serratus* (white rounds) communities. Isotopic spaces
 627 are represented in dark-grey for the *F. vesiculosus* community and in white for the *F. serratus*
 628 community. The light-grey space represents the intersection of these two isotopic spaces.

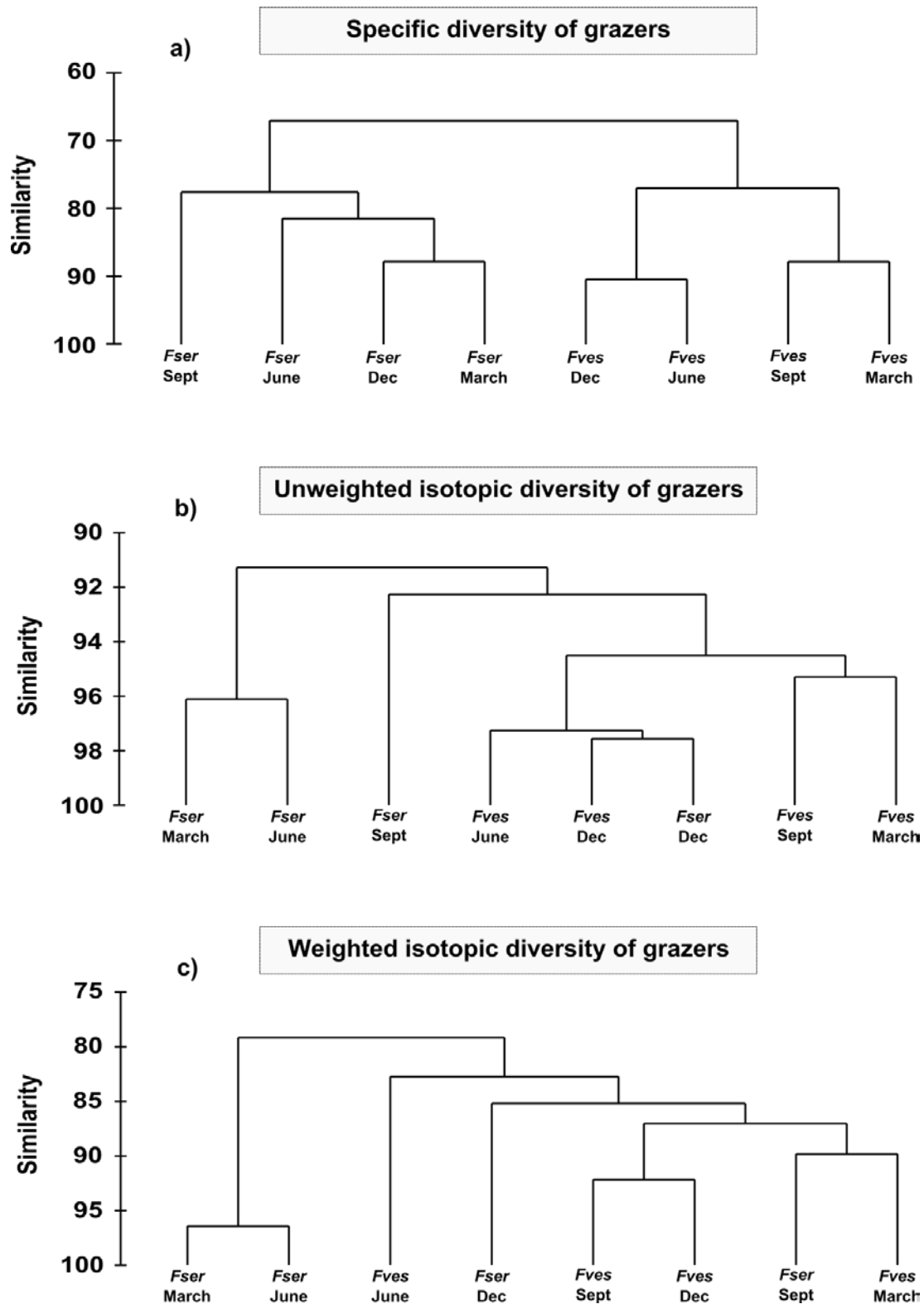
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631

632 **Figure 4:** Annual mean of a) $\delta^{13}\text{C} \pm \text{SE}$ (‰) of shared taxa obtained in the *F. vesiculosus*
 633 community vs those obtained in the *F. serratus* community, and of b) $\delta^{15}\text{N} \pm \text{SE}$ (‰) of
 634 shared taxa obtained in the *F. vesiculosus* community vs those obtained in the *F. serratus*
 635 community. Dashed lines represent the function $f(x) = y$. Shared taxa: 1 *Actinia equina*; 2
 636 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7
 637 *Calliostoma zizyphinum*; 8 *Carcinus maenas*; 9 *Gibbula pennanti*; 10 *Gibbula umbilicalis*; 11
 638 *Nucella lapillus*; 12 *Littorina obtusata*; 13 *Patella vulgata*; 14 *Spirorbis* sp.



639

640 **Figure 5:** Dendrograms from clustering analyses conducted on the grazers' data; a) on square-
 641 root transformed abundances, b) on isotopic diversity metrics calculated from unweighted
 642 isotopic data, and c) on isotopic diversity metrics calculated from isotopic data weighted by
 643 grazers' abundances.

644 **Table 1:** Isotopic diversity metrics calculated at each season and for each community, and
 645 their associated coefficient of variation (CV, in %).

| | Date | Sept | Dec | March | June | CV |
|--|---------------------|-------------|------------|--------------|-------------|-----------|
| <i>F. vesiculosus</i> community | Isotopic richness | 0.590 | 0.565 | 0.528 | 0.413 | 13.3 |
| | Isotopic divergence | 0.765 | 0.729 | 0.695 | 0.743 | 3.8 |
| | Isotopic dispersion | 0.607 | 0.535 | 0.429 | 0.461 | 13.1 |
| | Isotopic evenness | 0.785 | 0.791 | 0.774 | 0.844 | 4.0 |
| | Isotopic uniqueness | 0.455 | 0.349 | 0.394 | 0.500 | 14.6 |
| | Date | Sept | Dec | March | June | CV |
| <i>F. serratus</i> community | Isotopic richness | 0.269 | 0.415 | 0.389 | 0.308 | 25.4 |
| | Isotopic divergence | 0.709 | 0.701 | 0.681 | 0.722 | 2.4 |
| | Isotopic dispersion | 0.503 | 0.334 | 0.400 | 0.447 | 14.3 |
| | Isotopic evenness | 0.828 | 0.737 | 0.743 | 0.801 | 5.4 |
| | Isotopic uniqueness | 0.538 | 0.274 | 0.249 | 0.425 | 25.2 |

646

647

648 **Table 2:** Ranges (1st - 99th percentiles) and mean of potential contributions (%) of primary
649 sources to the diet of several species of filter-feeders and grazers, according to SIAR mixing
650 models. Analyses were carried out for each community and during all sampling seasons.

F. vesiculosus community

| | Date | <i>A. nodosum</i> | <i>F. vesiculosus</i> | <i>C. ustulatus</i> | Epilithon | <i>Ulva</i> spp. |
|----------------------------|-----------|--------------------|-----------------------|---------------------|--------------------|--------------------|
| Filter-feeders | | | | | | |
| <i>Campanulariidae</i> | September | 0.2 - 32.2 (12.3) | 0.2 - 28.3 (10.9) | 2.3 - 62.5 (31.5) | 5.7 - 67.5 (36.2) | 0.2 - 28.3 (9.2) |
| | December | 1.9 - 55.9 (28.2) | 0.3 - 45.1 (15.6) | 0.6 - 33.6 (14.7) | 0.2 - 29.9 (8.8) | 2.6 - 69.4 (32.8) |
| | June | 0.3 - 36.5 (13.4) | 0.3 - 27.8 (10.9) | 0.8 - 56.2 (24.9) | 11.7 - 63.8 (39.4) | 0.2 - 34.4 (11.5) |
| <i>Spirorbis</i> sp. | September | 0.6 - 45.4 (19.0) | 0.7 - 43.1 (19.1) | 1.2 - 40.5 (21.5) | 0.5 - 39.8 (17.2) | 1.6 - 47.3 (23.3) |
| | December | 3.4 - 57.2 (29.9) | 0.5 - 46.3 (18.6) | 0.4 - 25.7 (11.4) | 0.2 - 28.9 (9.7) | 2.4 - 61.5 (30.5) |
| | March | 0.7 - 47.1 (20.6) | 0.9 - 52.5 (23.1) | 0.3 - 28.2 (10.7) | 0.3 - 34.1 (13.1) | 14.1 - 50.8 (32.5) |
| | June | 0.2 - 46.5 (14.4) | 1.4 - 39.0 (23.3) | 0.1 - 20.5 (5.6) | 36.3 - 59.7 (49.4) | 0.1 - 29.6 (7.3) |
| Grazers | | | | | | |
| <i>Gibbula umbilicalis</i> | September | 0.5 - 50.3 (19.8) | 1.0 - 51.8 (24.3) | 0.7 - 32.4 (12.2) | 0.1 - 20.6 (5.9) | 10.1 - 64.2 (37.7) |
| | December | 3.2 - 64.5 (30.5) | 0.3 - 41.0 (15.5) | 0.4 - 28.8 (12.7) | 0.1 - 30.0 (8.1) | 3.1 - 67.7 (33.1) |
| | March | 0.1 - 23.5 (6.6) | 0.1 - 26.4 (8.1) | 0.1 - 10.6 (3.3) | 0.1 - 15.3 (4.4) | 63.0 - 89.3 (77.6) |
| | June | 0.4 - 52.7 (18.5) | 14.3 - 71.3 (44.4) | 0.1 - 22.5 (4.9) | 0.1 - 15.6 (3.3) | 2.3 - 53.5 (28.9) |
| <i>Littorina obtusata</i> | September | 0.5 - 47.3 (17.8) | 17.9 - 77.3 (48.7) | 0.1 - 7.8 (2.0) | 0.1 - 7.4 (1.9) | 8.7 - 51.1 (29.6) |
| | December | 20.1 - 94.4 (67.6) | 0.4 - 64.9 (21.1) | 0.1 - 5.8 (1.4) | 0.1 - 21.4 (4.5) | 0.1 - 20.4 (5.4) |
| | March | 0.5 - 57.2 (20.4) | 0.3 - 45.6 (15.9) | 0.1 - 26.6 (4.2) | 0.1 - 38.0 (9.0) | 2.0 - 76.4 (50.5) |
| | June | 0.2 - 41.7 (12.8) | 49.1 - 84.2 (71.2) | 0.1 - 12.7 (3.5) | 0.3 - 15.1 (7.3) | 0.1 - 24.3 (5.2) |
| <i>Patella vulgata</i> | September | 2.1 - 58.6 (28.4) | 8.5 - 68.5 (38.1) | 0.1 - 15.5 (5.8) | 0.5 - 22.8 (10.6) | 0.7 - 41.4 (17.1) |
| | December | 9.2 - 86.7 (52.3) | 0.8 - 70.0 (27.8) | 0.1 - 11.8 (2.4) | 0.1 - 32.5 (7.9) | 0.1 - 41.9 (9.6) |
| | March | 0.6 - 59.2 (23.3) | 0.5 - 50.8 (19.7) | 0.1 - 43.3 (12.0) | 0.2 - 51.0 (18.0) | 0.3 - 73.5 (27.0) |
| | June | 0.6 - 60.1 (25.0) | 13.8 - 72.2 (42.9) | 0.1 - 24.1 (6.8) | 0.2 - 26.6 (8.6) | 0.3 - 49.2 (16.7) |

F. serratus community

| | Date | <i>F. serratus</i> | <i>C. ustulatus</i> & <i>C. acicularis</i> | <i>M. stellatus</i> | Epilithon | <i>Ulva</i> spp. |
|---------------------------|-----------|--------------------|--|---------------------|--------------------|--------------------|
| Filter-feeders | | | | | | |
| <i>Alcyonidium</i> sp. | September | 0.2 - 27.3 (9.5) | 0.8 - 56.2 (23.9) | 0.4 - 42.5 (16.1) | 15.2 - 60.2 (39.2) | 0.2 - 32.2 (11.2) |
| | December | 1.5 - 66.7 (28.1) | 0.2 - 35.2 (13.1) | 0.5 - 49.2 (19.5) | 0.6 - 35.4 (16.1) | 1.2 - 45.0 (23.3) |
| | March | 8.5 - 61.5 (41.2) | 0.1 - 17.3 (5.0) | 0.1 - 27.3 (8.2) | 0.1 - 21.5 (6.1) | 17.4 - 61.2 (39.5) |
| | June | 0.1 - 18.2 (4.2) | 0.1 - 39.1 (9.7) | 0.1 - 20.1 (4.7) | 36.5 - 91.9 (77.6) | 0.1 - 16.8 (3.8) |
| <i>Spirorbis</i> sp. | September | 0.9 - 40.8 (19.7) | 0.4 - 39.4 (15.4) | 0.4 - 47.4 (18.2) | 10.8 - 46.7 (29.5) | 0.4 - 44.1 (17.2) |
| | December | 2.4 - 75.5 (37.4) | 0.1 - 21.7 (6.2) | 0.2 - 43.8 (14.1) | 0.1 - 21.5 (6.7) | 8.6 - 62.9 (35.7) |
| | March | 0.2 - 36.7 (9.3) | 0.3 - 37.2 (13.1) | 0.6 - 51.6 (22.3) | 0.2 - 32.8 (10.5) | 19.3 - 61.8 (44.9) |
| | June | 0.3 - 27.6 (11.0) | 0.3 - 49.1 (16.1) | 0.2 - 36.3 (12.0) | 29.9 - 73.3 (54.1) | 0.1 - 25.3 (6.9) |
| Grazers | | | | | | |
| <i>Gibbula pennanti</i> | September | 1.1 - 62.5 (29.4) | 0.2 - 45.1 (12.7) | 0.4 - 48.4 (18.9) | 0.1 - 30.8 (7.7) | 1.5 - 76.1 (31.4) |
| | December | 0.5 - 45.4 (18.9) | 0.2 - 33.1 (10.7) | 0.5 - 53.6 (22.4) | 0.1 - 23.5 (5.6) | 4.8 - 88.2 (42.5) |
| | March | 0.1 - 20.0 (4.9) | 2.7 - 50.9 (17.4) | 0.5 - 57.8 (23.1) | 0.1 - 20.7 (5.0) | 10.6 - 87.4 (49.6) |
| | June | 45.2 - 83.1 (69.2) | 0.1 - 11.5 (3.1) | 0.3 - 42.2 (13.6) | 0.1 - 10.7 (2.6) | 0.4 - 26.3 (11.5) |
| <i>Littorina obtusata</i> | September | 76.6 - 97.1 (89.9) | 0.1 - 4.3 (1.1) | 0.1 - 9.7 (2.5) | 0.1 - 6.0 (1.5) | 0.1 - 18.1 (5.0) |
| | December | 7.3 - 74.8 (37.8) | 0.1 - 14.3 (3.6) | 0.2 - 31.5 (10.1) | 3.0 - 44.8 (26.4) | 1.2 - 46.1 (22.1) |
| | March | 9.3 - 41.5 (26.2) | 0.2 - 34.0 (12.3) | 0.5 - 39.9 (16.8) | 0.3 - 38.8 (15.7) | 5.8 - 57.9 (30.0) |
| | June | 60.8 - 96.9 (86.3) | 0.1 - 10.5 (2.3) | 0.1 - 28.4 (6.0) | 0.1 - 13.0 (2.9) | 0.1 - 10.6 (2.5) |
| <i>Patella vulgata</i> | September | 2.3 - 55.9 (27.1) | 0.2 - 35.4 (12.1) | 0.4 - 48.2 (19.5) | 0.6 - 45.6 (20.0) | 0.7 - 50.5 (21.3) |
| | December | 1.1 - 64.8 (27.6) | 0.1 - 34.7 (9.1) | 0.3 - 45.3 (15.6) | 0.3 - 64.2 (20.4) | 0.7 - 79.2 (27.4) |
| | March | 3.9 - 40.1 (22.4) | 0.4 - 38.9 (15.6) | 0.6 - 43.4 (18.9) | 0.3 - 41.2 (16.1) | 2.9 - 57.3 (27.0) |
| | June | 35.9 - 93.3 (76.7) | 0.1 - 17.0 (3.8) | 0.2 - 42.8 (10.3) | 0.1 - 22.2 (5.0) | 0.1 - 20.5 (4.2) |

653 **Table 3:** Abundance of grazers recorded at each period of observation in the two
 654 communities.

| | Date | Sept | Dec | March | June |
|--|----------------------------|-------------|------------|--------------|-------------|
| <i>F. vesiculosus</i> community | <i>Gibbula cineraria</i> | 0 | 2 | 0 | 2 |
| | <i>Gibbula pennanti</i> | 58 | 170 | 32 | 226 |
| | <i>Gibbula umbilicalis</i> | 208 | 106 | 174 | 96 |
| | <i>Littorina littorea</i> | 6 | 12 | 16 | 2 |
| | <i>Littorina obtusata</i> | 172 | 76 | 118 | 86 |
| | <i>Littorina saxatilis</i> | 4 | 0 | 0 | 0 |
| | <i>Patella vulgata</i> | 32 | 62 | 20 | 22 |

| | Date | Sept | Dec | March | June |
|---|-----------------------------|-------------|------------|--------------|-------------|
| <i>F. serratus</i> community | <i>Gibbula cineraria</i> | 20 | 26 | 54 | 26 |
| | <i>Gibbula pennanti</i> | 130 | 430 | 508 | 240 |
| | <i>Gibbula umbilicalis</i> | 36 | 38 | 24 | 46 |
| | <i>Lamellaria perspicua</i> | 0 | 4 | 0 | 0 |
| | <i>Littorina obtusata</i> | 94 | 80 | 70 | 18 |
| | <i>Patella vulgata</i> | 2 | 12 | 36 | 32 |
| | <i>Tricolia pullus</i> | 0 | 0 | 2 | 0 |

655

Supplementary material 1: Mean \pm SE (‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sources and consumers of the *F. vesiculosus* community, with the number of replicates (n) analysed for each sampling period (September and December 2013 and March and June 2014). Groups: ER = Erect alga; EN = Encrusting alga; G = Grazer; FF = Filter-feeder; P = Predator.

| | Group | September | | | December | | | March | | | June | | |
|-------------------------------|-------|---------------------------|---------------------------|----|---------------------------|---------------------------|----|---------------------------|---------------------------|----|---------------------------|---------------------------|----|
| | | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n |
| Sources | | | | | | | | | | | | | |
| <i>Ascophyllum nodosum</i> | ER | -14.8 \pm 0.4 | 5.5 \pm 0.6 | 3 | -15.6 \pm 0.2 | 5.3 \pm 0.1 | 3 | -17.8 \pm 0.4 | 5.8 \pm 0.1 | 3 | -15.9 \pm 0.3 | 7.4 \pm 0.1 | 3 |
| <i>Caulacanthus ustulatus</i> | ER | -22.5 \pm 0.2 | 9.0 \pm 0.1 | 3 | -23.3 \pm 0.1 | 9.8 \pm 0.4 | 3 | -24.0 \pm 0.2 | 5.4 \pm 0.1 | 3 | -20.9 \pm 0.1 | 8.7 \pm 0.1 | 3 |
| <i>Fucus vesiculosus</i> | ER | -13.9 \pm 0.4 | 5.5 \pm 0.1 | 3 | -18.4 \pm 0.1 | 5.1 \pm 0.1 | 3 | -17.7 \pm 0.2 | 6.2 \pm 0.1 | 3 | -13.6 \pm 0.1 | 6.7 \pm 0.2 | 3 |
| <i>Hildenbrandia rubra</i> | EN | -15.4 | 7.4 | 1 | -14.9 \pm 0.1 | 6.2 \pm 0.2 | 3 | -13.0 \pm 0.1 | 6.2 \pm 0.1 | 2 | -14.1 \pm 0.3 | 8.3 \pm 0.1 | 3 |
| <i>Ulva</i> sp. | ER | -14.3 \pm 0.7 | 7.1 \pm 0.9 | 3 | -16.9 \pm 0.1 | 6.9 \pm 0.1 | 3 | -14.0 \pm 0.4 | 7.9 \pm 0.1 | 3 | -16.0 \pm 0.4 | 8.9 \pm 0.2 | 3 |
| Epilithon | | -21.4 \pm 0.2 | 5.7 \pm 0.2 | 2 | -21.5 \pm 1.1 | 5.8 \pm 1.2 | 2 | -20.3 \pm 0.1 | 5.4 \pm 0.4 | 2 | -21.8 \pm 0.2 | 6.4 \pm 0.4 | 2 |
| POM | | -22.3 \pm 0.4 | 6.9 (1) | 2 | -22.6 \pm 0.3 | 6.9 \pm 1.1 | 3 | -21.8 \pm 0.1 | 5.6 \pm 0.2 | 3 | -22.0 (1) | 5.4 \pm 0.5 | 2 |
| Cnidaria | | | | | | | | | | | | | |
| <i>Actinia equina</i> | P | | | | -17.9 | 11.6 | 1 | -16.5 | 12.3 | 1 | -15.6 \pm 0.4 | 11.3 \pm 1.1 | 4 |
| <i>Actinia fragacea</i> | P | | | | | | | | | | -17.0 | 11.3 | 1 |
| <i>Anemonia viridis</i> | P | -16.3 \pm 0.3 | 9.2 \pm 0.1 | 2 | | | | -16.2 | 11.1 | 1 | | | |
| Campanulariidae | FF | -19.6 \pm 0.1 | 7.4 \pm 0.1 | 4 | -17.7 \pm 0.1 | 9.5 \pm 0.2 | 3 | | | | -19.0 \pm 0.1 | 8.4 \pm 0.7 | 3 |
| Annelida | | | | | | | | | | | | | |
| <i>Spirorbis</i> sp. | FF | -17.1 | 10.0 | 1 | -17.7 | 9.2 | 1 | -17.4 \pm 0.1 | 9.2 \pm 0.1 | 3 | -19.7 | 9.3 | 1 |
| Mollusca | | | | | | | | | | | | | |
| <i>Calliostoma zizyphinum</i> | P | -16.3 \pm 0.1 | 12.3 \pm 0.1 | 2 | -16.4 \pm 0.1 | 11.4 \pm 0.1 | 3 | -14.6 \pm 0.1 | 12.9 \pm 0.2 | 2 | | | |
| <i>Gibbula pennanti</i> | G | -15.4 \pm 0.1 | 9.3 \pm 0.2 | 6 | -14.4 \pm 0.1 | 9.1 \pm 0.2 | 6 | -14.2 \pm 0.1 | 10.1 \pm 0.1 | 6 | -14.5 \pm 0.1 | 10.4 \pm 0.2 | 6 |
| <i>Gibbula umbilicalis</i> | G | -15.1 \pm 0.3 | 9.7 \pm 0.1 | 6 | -15.2 \pm 0.1 | 9.1 \pm 0.1 | 6 | -14.8 \pm 0.1 | 10.8 \pm 0.1 | 6 | -14.6 \pm 0.2 | 10.2 \pm 0.2 | 6 |
| <i>Littorina littorea</i> | G | -16.1 \pm 0.1 | 10.0 \pm 0.2 | 6 | -16.2 \pm 0.2 | 8.9 \pm 0.1 | 6 | -15.4 \pm 0.1 | 9.6 \pm 0.1 | 6 | -15.9 \pm 0.2 | 9.5 \pm 0.2 | 6 |
| <i>Littorina obtusata</i> | G | -13.9 \pm 0.2 | 8.8 \pm 0.1 | 10 | -14.1 \pm 0.1 | 7.6 \pm 0.1 | 10 | -15.2 \pm 0.1 | 8.3 \pm 0.1 | 10 | -14.6 \pm 0.1 | 8.6 \pm 0.1 | 10 |
| <i>Nucella lapillus</i> | P | -12.8 \pm 0.1 | 11.3 \pm 0.2 | 6 | -13.6 \pm 0.1 | 11.0 \pm 0.1 | 6 | -14.6 \pm 0.1 | 12.1 \pm 0.1 | 6 | -14.1 \pm 0.3 | 11.2 \pm 0.1 | 6 |
| <i>Patella vulgata</i> | G | -15.1 \pm 0.2 | 8.3 \pm 0.1 | 6 | -15.9 \pm 0.5 | 7.4 \pm 0.1 | 6 | -15.4 \pm 0.2 | 8.0 \pm 0.1 | 5 | -15.3 \pm 0.3 | 7.8 \pm 0.1 | 6 |
| <i>Phorcus lineatus</i> | G | -15.3 \pm 0.1 | 10.6 \pm 0.1 | 6 | -16.4 \pm 0.1 | 9.7 \pm 0.2 | 6 | -15.3 \pm 0.1 | 10.0 \pm 0.2 | 6 | -15.5 \pm 0.2 | 10.6 \pm 0.3 | 6 |
| Ectoprocta | | | | | | | | | | | | | |
| <i>Alcyonidium</i> sp. | FF | -20.3 \pm 0.1 | 7.2 \pm 0.4 | 6 | | | | | | | -19.5 \pm 0.1 | 7.3 \pm 0.1 | 6 |
| Arthropoda | | | | | | | | | | | | | |
| Amphipods | FF | -20.8 \pm 1.4 | 8.5 \pm 0.2 | 6 | -16.5 \pm 0.1 | 7.7 \pm 0.1 | 3 | -17.0 \pm 0.1 | 8.5 \pm 0.1 | 3 | -18.1 \pm 0.2 | 7.8 \pm 0.1 | 3 |
| <i>Carcinus maenas</i> | P | -16.2 \pm 0.2 | 12.9 \pm 0.2 | 5 | -15.2 \pm 0.2 | 12.1 \pm 0.1 | 5 | -14.5 \pm 0.2 | 13.0 \pm 0.1 | 5 | -15.8 \pm 0.4 | 12.6 \pm 0.3 | 4 |
| Echinodermata | | | | | | | | | | | | | |
| <i>Asterina gibbosa</i> | P | | | | | | | -13.7 \pm 0.1 | 12.6 \pm 0.1 | 2 | | | |

Supplementary material 2: Mean \pm SE (‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sources and consumers of the *F. serratus* community, with the number of replicates (n)

analysed for each sampling period (September and December 2013 and March and June 2014). Groups: ER = Erect alga; EN = Encrusting alga; G = Grazer;

FF = Filter-feeder; P = Predator.

| | Group | September | | | December | | | March | | | June | | |
|----------------------------------|-------|---------------------------|---------------------------|----|---------------------------|---------------------------|----|---------------------------|---------------------------|----|---------------------------|---------------------------|----|
| | | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n |
| Sources | | | | | | | | | | | | | |
| <i>Caulacanthus ustulatus</i> | ER | -20.6 \pm 0.1 | 8.8 \pm 0.5 | 3 | -21.7 \pm 0.1 | 10.2 \pm 0.1 | 3 | -21.9 \pm 0.1 | 7.1 \pm 0.1 | 3 | -19.5 \pm 0.1 | 8.2 \pm 0.2 | 3 |
| <i>Chondracanthus acicularis</i> | ER | -22.9 \pm 0.1 | 6.5 \pm 0.1 | 3 | -21.7 \pm 0.1 | 6.4 \pm 0.1 | 3 | -22.1 \pm 0.2 | 6.2 \pm 0.2 | 3 | -20.9 \pm 0.1 | 7.4 \pm 0.1 | 3 |
| <i>Fucus serratus</i> | ER | -14.8 \pm 0.1 | 5.4 \pm 0.2 | 3 | -17.6 \pm 0.1 | 5.4 \pm 0.1 | 3 | -18.1 \pm 0.5 | 3.0 \pm 0.6 | 3 | -15.3 \pm 0.1 | 5.7 \pm 0.2 | 3 |
| <i>Hildenbrandia rubra</i> | EN | -15.9 \pm 0.7 | 7.5 \pm 0.7 | 2 | | | | -16.5 \pm 0.1 | 7.5 \pm 0.2 | 2 | -17.5 \pm 0.1 | 8.4 \pm 0.4 | 3 |
| <i>Mastocarpus stellatus</i> | ER | -17.4 \pm 0.3 | 6.9 \pm 0.1 | 3 | -18.3 \pm 0.1 | 7.2 \pm 0.1 | 3 | -19.9 \pm 0.2 | 6.6 \pm 0.2 | 3 | -16.9 \pm 0.3 | 7.0 \pm 0.1 | 3 |
| <i>Phymatolithon lenormandii</i> | EN | | | | -16.0 \pm 0.1 | 7.1 \pm 0.3 | 3 | -17.1 \pm 0.2 | 6.9 \pm 0.1 | 3 | -17.6 \pm 0.1 | 6.9 \pm 0.2 | 3 |
| <i>Ulva</i> sp. | ER | -16.0 \pm 0.3 | 6.5 \pm 0.1 | 3 | -15.4 \pm 0.1 | 6.7 \pm 0.1 | 3 | -15.8 \pm 0.2 | 6.9 \pm 0.2 | 3 | -17.7 \pm 0.1 | 9.7 \pm 0.2 | 3 |
| Epilithon | | -19.9 \pm 0.5 | 6.7 \pm 0.1 | 2 | -25.0 \pm 1.0 | 3.9 \pm 0.6 | 2 | -24.1 \pm 0.2 | 4.3 \pm 0.1 | 2 | -20.2 \pm 1.6 | 6.6 \pm 0.6 | 2 |
| POM | | -22.3 \pm 0.4 | 6.9 (1) | 2 | -22.6 \pm 0.3 | 6.9 \pm 1.1 | 3 | -21.8 \pm 0.1 | 5.6 \pm 0.2 | 3 | -22.0 (1) | 5.4 \pm 0.5 | 2 |
| Cnidaria | | | | | | | | | | | | | |
| <i>Actinia equina</i> | P | | | | -17.8 | 7.7 | 1 | -16.5 \pm 0.1 | 8.7 \pm 0.2 | 3 | -18.4 \pm 0.8 | 12.0 \pm 0.5 | 2 |
| <i>Actinia fragacea</i> | P | | | | | | | -16.5 \pm 0.1 | 11.3 \pm 0.1 | 2 | | | |
| <i>Anemonia viridis</i> | P | -15.8 \pm 0.6 | 9.3 \pm 0.2 | 2 | -17.3 | 10.3 | 1 | -17.2 \pm 0.2 | 8.3 \pm 0.1 | 2 | -19.3 \pm 0.1 | 8.7 \pm 0.2 | 3 |
| Annelida | | | | | | | | | | | | | |
| <i>Spirorbis</i> sp. | FF | -18.4 | 8.8 | 1 | -17.1 | 8.2 | 1 | -17.9 \pm 0.1 | 9.3 \pm 0.2 | 3 | -19.9 | 8.0 | 1 |
| Mollusca | | | | | | | | | | | | | |
| <i>Calliostoma ziphyinum</i> | P | -16.9 \pm 0.2 | 12.8 \pm 0.1 | 6 | -16.5 \pm 0.3 | 11.8 \pm 0.2 | 5 | -16.0 \pm 0.1 | 12.0 \pm 0.2 | 5 | -17.6 \pm 0.3 | 11.6 \pm 0.2 | 6 |
| <i>Gibbula cineraria</i> | G | -15.7 \pm 0.2 | 9.4 \pm 0.2 | 6 | -15.5 \pm 0.1 | 8.3 \pm 0.1 | 6 | -14.5 \pm 0.1 | 9.4 \pm 0.1 | 6 | -16.5 \pm 0.2 | 8.8 \pm 0.1 | 6 |
| <i>Gibbula pennanti</i> | G | -15.8 \pm 0.2 | 10.1 \pm 0.2 | 6 | -14.5 \pm 0.1 | 9.2 \pm 0.2 | 6 | -13.7 \pm 0.1 | 9.3 \pm 0.1 | 6 | -15.7 \pm 0.1 | 9.1 \pm 0.3 | 6 |
| <i>Gibbula umbilicalis</i> | G | -15.4 \pm 0.2 | 9.9 \pm 0.2 | 6 | -15.4 \pm 0.1 | 9.1 \pm 0.1 | 6 | -14.3 \pm 0.1 | 10.3 \pm 0.1 | 6 | -16.6 \pm 0.2 | 9.6 \pm 0.2 | 6 |
| <i>Littorina obtusata</i> | G | -14.6 \pm 0.1 | 7.6 \pm 0.1 | 10 | -13.1 \pm 0.1 | 7.9 \pm 0.1 | 10 | -13.9 \pm 0.1 | 7.9 \pm 0.1 | 10 | -14.7 \pm 0.2 | 8.0 \pm 0.2 | 10 |
| <i>Nucella lapillus</i> | P | -14.9 \pm 0.2 | 11.4 \pm 0.1 | 6 | -13.1 \pm 0.1 | 11.1 \pm 0.2 | 6 | -12.4 \pm 0.1 | 11.7 \pm 0.1 | 6 | -14.4 \pm 0.2 | 11.0 \pm 0.1 | 6 |
| <i>Patella vulgata</i> | G | -17.0 \pm 0.6 | 7.7 \pm 0.4 | 6 | -14.8 \pm 0.2 | 7.0 \pm 0.2 | 5 | -14.4 \pm 0.1 | 8.0 \pm 0.1 | 6 | -15.4 \pm 0.2 | 7.5 \pm 0.1 | 6 |
| Ectoprocta | | | | | | | | | | | | | |
| <i>Alcyonidium</i> sp. | FF | -19.5 \pm 0.1 | 6.0 \pm 0.1 | 6 | -18.3 \pm 0.2 | 6.8 \pm 0.2 | 6 | -17.2 \pm 0.1 | 7.2 \pm 0.1 | 5 | -21.0 \pm 0.2 | 7.0 \pm 0.1 | 6 |
| Arthropoda | | | | | | | | | | | | | |
| Amphipods | FF | -16.3 \pm 0.3 | 8.3 \pm 0.3 | 2 | -16.8 \pm 0.1 | 7.8 \pm 0.5 | 2 | -15.2 \pm 0.1 | 9.0 \pm 0.2 | 3 | -18.8 \pm 0.1 | 8.8 \pm 0.1 | 3 |
| <i>Cancer pagurus</i> | P | -16.0 \pm 0.4 | 13.4 \pm 0.1 | 3 | -15.3 \pm 0.4 | 12.2 \pm 0.6 | 2 | -14.4 \pm 0.1 | 12.9 \pm 0.1 | 5 | -14.8 \pm 0.3 | 14.0 \pm 0.3 | 3 |
| <i>Carcinus maenas</i> | P | -15.1 \pm 0.5 | 12.1 \pm 0.1 | 6 | -16.4 | 12.1 | 1 | -15.2 \pm 0.1 | 12.6 \pm 0.1 | 6 | -15.4 \pm 0.2 | 12.8 \pm 0.3 | 5 |
| <i>Porcellana platycheles</i> | FF | -17.8 \pm 0.8 | 10.2 \pm 0.1 | 5 | -16.5 \pm 0.1 | 9.3 \pm 0.1 | 5 | -16.6 \pm 0.1 | 9.7 \pm 0.1 | 5 | -17.4 \pm 0.2 | 10.2 \pm 0.1 | 5 |
| Chordata | | | | | | | | | | | | | |
| <i>Botryllus schlosseri</i> | FF | -19.3 \pm 0.2 | 8.2 \pm 0.1 | 3 | -18.2 \pm 0.2 | 7.7 \pm 0.1 | 5 | | | | -21.2 \pm 0.1 | 8.4 \pm 0.1 | 3 |
| Polyclinidae | FF | -19.4 \pm 0.1 | 9.4 \pm 0.1 | 6 | -18.6 \pm 0.1 | 9.5 \pm 0.1 | 5 | | | | -21.0 \pm 0.2 | 9.0 \pm 0.1 | 5 |
| Echinodermata | | | | | | | | | | | | | |
| <i>Asterina gibbosa</i> | P | | | | -14.7 | 10.4 | 1 | -14.8 \pm 0.2 | 12.4 \pm 0.1 | 5 | -14.9 \pm 0.1 | 9.9 \pm 0.2 | 2 |