

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

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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

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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. CO₂/HCO₃⁻ 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