

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

447 ACKNOWLEDGMENTS

448 The authors thank the SOMLIT network for providing isotopic data of particulate organic
449 matter of our study area. Two anonymous reviewers and the associate editor are thanked for
450 constructive comments. This work benefited from the support of the Brittany Regional
451 Council and of the French Government through the National Research Agency with regard to
452 the investment expenditure programme IDEALG ANR-10-BTBR.

453