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

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

Short title: Food web similarity in *Fucus* communities

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ABSTRACT

Intertidal communities dominated by canopy-forming macroalgae typically exhibit some differences in their specific composition that are related to their location along the emersion gradient of rocky shores. Tidal level is also expected to affect resource availability for both primary producers and consumers, potentially leading to divergence in the trophic structure of these communities. Furthermore, in temperate areas, the alternation of seasons has usually a large influence on the primary production and on life-history traits of numerous species, which may induce some changes in the food webs of intertidal communities. Thus, this study aimed to investigate the trophic structure of two intertidal communities located at different tidal levels, over several seasons. Focusing on the dominant species of primary producers and consumers, the food webs of the *Fucus vesiculosus* (Linnaeus, 1753) and *Fucus serratus* (Linnaeus, 1753) communities were studied during four successive seasons, using an isotopic ($\delta^{13}C$ and $\delta^{15}N$) approach. Due to the diversity of primary producers and consumers living in these two communities, food webs were relatively complex and composed of several trophic pathways. These food webs remained rather conserved over the successive seasons, even though some variability in isotopic signature and in diet has been highlighted for several species. Finally, despite their location at different tidal levels, the two *Fucus* spp. communities exhibited nearly the same trophic structure, with common consumer species displaying similar isotopic signature in both of them.

KEYWORDS

Stable isotopes; intertidal zonation; seasons; trophic groups

HIGHLIGHTS

- Food webs of intertidal fucoid communities included several trophic pathways
- Trophic structure of fucoid communities remained highly conserved over the year
- Fucoid communities from different tidal heights exhibited similar food webs

1. INTRODUCTION

Along intertidal rocky shores of temperate areas, sheltered habitats are usually dominated by canopy-forming brown algae (Phaeophyceae) that can cover almost all the substratum. These species are established along a vertical gradient and are typically associated with numerous species of primary producers and consumers in such a way that intertidal rocky shores are composed of a succession of distinct communities from high to low tide levels (Raffaelli & Hawkins 1999). Trophic structure of these intertidal communities has been the focus of intensive research during the past decades, due to the emergence of the stable isotopic approach (e.g. Dauby et al. 1998, Sarà et al. 2007, Riera et al. 2009, Duarte et al. 2015). To our knowledge, only one study was however carried out in the context of vertical zonation (Steinarsdóttir et al. 2009). Tidal zonation is, yet, expected to be a significant driver of community trophic structure. For instance, shore level usually controls resource access for primary producers (e.g. CO_2/HCO_3^- and nutrients, Raven & Hurd 2012), sessile fauna (as some species can only feed when immersed, Raffaelli & Hawkins 1999) and mobile fauna (as the amount of available food might decrease from low to high shore levels, Underwood 1984). Trophic relationships are considered as an important component of community functioning and should be defined more accurately in the context of tidal zonation. The use of stable isotopes seems particularly powerful for this purpose, as they act as chemical tracers of energy flow (Peterson & Fry 1987, Fry 2006). Thus, $\delta^{13}C$ of a consumer usually provides information about its diet sources while its $\delta^{15}N$ value is often related to its trophic position in the food web (Zanden & Rasmussen 2001, Caut et al. 2009).

In temperate areas, abiotic factors such as light and temperature display significant seasonal fluctuations. As a consequence, intertidal communities show seasonal pattern in their metabolism (Golléty et al. 2008, Bordeyne et al. 2015), as well as in their species richness and/or abundance (Rindi & Guiry 2004, Dethier & Williams 2009). These seasonal fluctuations potentially influence species interactions and may therefore lead to modification in their food webs. Furthermore, seasonal changes in isotopic composition of both primary producer and consumer species are regularly evidenced in coastal communities (Nordström et al. 2009, Hyndes et al. 2013), including intertidal habitats (Golléty et al. 2010, Ouisse et al. 2011). These changes, which could be related to numerous biotic and abiotic factors (Jennings et al. 2008, Vanderklift & Bearham 2014, Viana et al. 2015), may also reflect important modifications in the trophic structure of these communities over time (McMeans et al. 2015). In this context, it appears essential to understand how seasonal variations can structure the food webs of benthic communities, and also how these communities respond to existing environmental variations (Hyndes et al. 2013).

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

2. MATERIAL AND METHODS

2.1. Study site

The study site is located in front of the Station Biologique de Roscoff, in the southwestern part of the English Channel (Brittany, France) (48°43.743’N, 3°59.407’W). It consisted of an intertidal boulder reef subjected to semi-diurnal tidal cycle, with maximal amplitude of about 9 m. This semi-sheltered rocky shore is characterized by a vertical succession of communities dominated by canopy-forming Phaeophyceae, where the *Fucus vesiculosus* and *F. serratus* communities are characteristic of the mid-intertidal (3.0 to 4.0 m above chart datum) and low mid-intertidal (2.5 to 3.0 m above chart datum) respectively. These communities are mainly composed of dense *Fucus* spp. canopies, covering up to 100 % of the substratum, which are associated with miscellaneous epibionts (i.e. algae and sessile invertebrates directly attached to the *Fucus*, see Wahl 2009). They are also made up of sub-canopy and encrusting algae, as well as microphytobenthos, and phytoplankton during high tide. Finally, these communities also support a diverse pool of mobile invertebrates (Raffaelli & Hawkins 1999, Migné et al. 2015).

2.2. Sampling and preparation for stable isotopes analysis

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

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

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

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

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

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

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

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

2.3. Taxonomic diversity and density of gastropod grazers

Gastropod grazers (hereafter referred to as “grazers”) constitute the most abundant group of consumers in these communities (approx. 95% of the countable fauna) and likely play a significant role in organic matter fluxes within the food webs. The taxonomic diversity of these grazers was monitored in the same areas and at the same periods than sampling for stable isotopes analyses (i.e. September and December 2013, and March and June 2014). Thus, at each season, grazers were identified at the species level and counted in five replicates of 0.1 m^2 randomly chosen in each community. To account for spatial variability, intra-community replicates were 3 to 10 m away one from each other.

2.4. Data analysis

The trophic structure of each community, its temporal fluctuations, and the potential trophic relationships between diets and consumers, were investigated by drawing dual-isotope plots at each sampling period. The “community-wide” isotopic metrics developed by Cucherousset & Villéger (2015) (i.e. isotopic richness, divergence, dispersion, evenness and uniqueness) were used as a complement to these dual-isotope plots. The isotopic richness is related to the area of the bi-dimensional isotopic space that is filled by all the taxa while the isotopic divergence, dispersion, eveness and uniqueness are related to the distribution of taxa in this space, providing information about trophic diversity and redundancy. These metrics have the benefit to be mathematically independent of the number of replicates used and allow accounting for abundance/biomass of taxa, when available. They were calculated at each sampling period and for each community, using the R functions computed by Cucherousset & Villéger (2015), with R software, version 3.2.2 (R Core Team 2015). Their coefficient of variation across seasons was used to discuss about the seasonal variability in the trophic structure of these two communities.

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

For comparisons between communities, we first calculated the overall level of isotopic overlap between the two communities using the isotopic overlap metrics (isotopic similarity and nestedness) developed by Cucherousset & Villéger (2015), from the average isotopic signature of each taxon. We also focused on consumer taxa present in both communities (i.e. shared consumers, see Supplementary Material for their identities). Their average $\delta^{13}C$ and $\delta^{15}N$ obtained in the *F. vesiculosus* community were plotted against those obtained in the *F. serratus* community. Slopes and intercepts of a Model II regression were then calculated according to the major axis method, using the “lmodel2” R package version 1.7-2 (Legendre 2014), for both $\delta^{13}C_{Fves}$ vs $\delta^{13}C_{Fser}$ and $\delta^{15}N_{Fves}$ vs $\delta^{15}N_{Fser}$ plots. Student’s t-tests were performed to test if slopes and intercepts of regressions were significantly different from 1 and 0, respectively. If not, it would indicate that, on average, the shared consumers’ exhibited similar isotopic signature in the two communities.

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

3. RESULTS

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

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

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

The five isotopic metrics showed low variability across seasons, as their coefficient of variation varied between 3.8 and 14.6% in the *F. vesiculosus* community and between 2.4 and 25.4% in the *F. serratus* community (Table 1). Only isotopic richness and uniqueness of the *F. serratus* community exhibited a coefficient of variation higher than 15%. This was mainly due to the high ^{13}C and/or ^{15}N depletions of two basal sources in some seasons (i.e. epilithon was ^{13}C and ^{15}N depleted in both December and March, and *F. serratus* was ^{15}N depleted in March, Figure 2).

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

3.2. Comparisons between communities

No seasonal trend in trophic structure has been observed for these two intertidal communities. As well, when comparisons between communities were performed at each season, any difference were evidenced, neither considering the functional isotopic space of whole communities (i.e. high isotopic similarity and isotopic nestedness), nor considering the isotopic composition (δ^{13}C and δ^{15}N) of consumers species present in both communities. Therefore, comparisons between communities were performed using an average isotopic signature of each taxon, obtained after pooling the stable isotope values of the different sampling periods. Considering these year-round means in isotopic signature, the two communities presented an isotopic similarity of 0.779 and an isotopic nestedness of 0.894 (Figure 3). Almost all the taxa (43 of 52) were included in the intersection of the two isotopic spaces. Regarding the consumers shared by the two communities, the model II regressions of dual plots exhibited significant Pearson's coefficient (For $\delta^{13}C_{Fves}$ vs $\delta^{13}C_{Fser}$, n = 14, R = 0.876, $p < 0.001$; for $\delta^{15}N_{Fves}$ vs $\delta^{15}N_{Fser}$, n = 14, R = 0.953, $p < 0.001$) (Figure 4). The slopes of regressions were equal to 1.2 and 1.0 for $\delta^{13}C_{Fves}$ vs $\delta^{13}C_{Fser}$ and $\delta^{15}N_{Fves}$ vs $\delta^{15}N_{Fser}$, respectively, while intercepts were equal to 2.9 and 0.3, respectively. These slopes and intercepts were not significantly different from 1 and 0, respectively (For $\delta^{13}C_{Fves}$ vs $\delta^{13}C_{Fser}$, t = 1.42, $p = 0.091$ for the slope and t = 1.49, $p = 0.080$ for the intercept; for $\delta^{15}N_{Fves}$ vs $\delta^{15}N_{Fser}$, t = 0.13, $p = 0.450$ for the slope and t = 0.40, $p = 0.349$ for the intercept).

In both communities, *Gibbula* spp., *Littorina* spp. and *Patella vulgata* were the most dominant taxa of grazers: *G. umbilicalis* being the most abundant species in the *F. vesiculosus* community (96 to 208 individuals per m²) and *G. pennanti* was most abundant species in the *F. serratus* community (130 to 508 individuals per m², Table 3). Clustering analysis performed on the taxonomic diversity of grazers discriminated the two communities (Figure 5a), which were significantly different according to the ANOSIM test (R = 0.75, $p = 0.029$). When performed on isotopic diversity metrics, these analyses did not allow to significantly discriminate the two communities, neither when they were conducted on unweighted data (ANOSIM test, R = 0.26, $p = 0.083$, Figure 5b), nor when conducted on data weighted by abundance of grazers (ANOSIM test, R = 0.12, $p = 0.229$, Figure 5c).

4. DISCUSSION

4.1. Trophic structure of Fucus spp. communities

By analysing isotopic composition of the main taxa inhabiting the *Fucus vesiculosus* and *F. serratus* communities, we attempted to depict their global trophic structure. At each season and in each community, groups of consumers were discriminated as filter-feeders, grazers and predators, despite some overlap in their isotopic signatures. As expected, filter-feeders were the most ^{13}C-depleted consumers, while predators were the most ^{15}N-enriched and occupied the top of the food webs. Both sources and consumers were distributed over large δ^{13}C and δ^{15}N ranges, suggesting that the *Fucus* spp. communities are characterized by a complex trophic structure (Golléty et al. 2010). This complexity may have been however underestimated during this study, as the ultimate top predators of these communities (i.e. fishes and shore birds, Ellis et al. 2007), as well as one potential food source (epibiotic biofilms) were not sampled. Despite that, the large δ^{15}N range of consumers (i.e. δ^{15}N extended over 4.7 to 7.4 ‰ according to the sampling period) reveals the presence of several trophic levels within the *Fucus* spp. communities. The heterogeneous distribution in δ^{15}N of primary consumers prevented, however, to attribute an accurate trophic position to each consumer (Post 2002, Riera et al. 2009). As well, their large δ^{13}C range is characteristic of the occurrence of several trophic pathways, as previously reported in rocky shore habitats (Golléty et al. 2010, Leclerc et al. 2013). This likely results from the high diversity of food sources and feeding behaviors of invertebrates (Riera et al. 2009), which are favored by the multitude of microhabitats that usually characterized rocky shores (Schaal et al. 2010, 2011). Mixing models also highlighted the occurrence of several trophic pathways in fucoid communities. Thus, filter-feeders were supposed to rely mainly on POM and on several species of erect algae through the detrital pathway. As well, the diet of grazers was mainly based on a mix of different species of algae (i.e. *Fucus*, *Ulva* spp., *A. nodosum*, *M. stellatus*). According to these results, filter-feeders and grazers can be considered as generalist species. Therefore, *Fucus* species did not constitute the cornerstone of these food webs, supplying the vast majority of organic carbon for primary consumers (with the exception of June for grazers), as we might reasonably expect from their abundance (i.e. 1.50 to 11.80 kg of fresh weight m^{-2} for *Fucus* canopies; 0.02 to 0.28 kg of fresh weight m^{-2} for all other erect macroalgae, Bordeyne et al., unpublished data). However, fucoid species are usually considered to have poor nutritional values and can induce anti-grazing defence that may repel primary consumers (Molis et al. 2006). Therefore, primary consumers may show food preference toward more nutritional species (Lubchenco 1978, Littler & Littler 1980, Watson & Norton 1985), despite their lower abundance. Epibiotic biofilms, while not sampled here, may also constitute a complementary trophic resource for some species of grazers, notably those living on fucoid fronds such as *Littorina obtusata* (see Norton et al. 1990 and references therein). Interestingly, according to its isotopic signature and the results of mixing models, the introduced alga *C. ustulatus* has very low contribution to the diet of grazers. This species, first recorded close to our study site almost 30 years ago (Rio & Cabioch 1988), was suggested to be unpalatable for native consumers due to production of secondary metabolites (Smith et al. 2014). However, filter-feeders may rely on this species through the detrital pathway. Finally, we should mention that the wide ranges in specific contributions obtained from mixing models reveal some uncertainties, and have to be considered with caution (Phillips et al. 2014).

4.2. Seasonal variability of trophic structure

The year-round analysis of the isotopic composition of the main taxa inhabiting the *F. vesiculosus* and *F. serratus* communities revealed an overall preservation of their food webs across seasons. This trend, depicted by comparing the biplots drawn at each season, was supported by the low values of the coefficient of variation across seasons for isotopic diversity metrics, especially in the *F. vesiculosus* community. Such preservation of trophic structure across seasons has already been noticed for a *Fucus*-dominated community (Schaal et al. 2010), even though the studied community was subjected to a strong anthropogenic pressure, which may have influenced isotopic composition of both sources (Viana et al. 2015) and consumers (Warry et al. 2016). Thus, the year-round preservation of food webs we observed in non-impacted fucoid communities could have major implications regarding our knowledge of their dynamics. Indeed, temporal modification of species richness and/or abundance is generally considered as a key process in temperate habitats (Dethier & Williams 2009) and could potentially lead to a seasonality in resource availability, as observed in the Arctic environments. Such seasonality finally leads to large modifications of food webs in these extreme environments (Forest et al. 2008, Darnis et al. 2012). In the present study, however, most of the common macroalgae are perennial (e.g. *Fucus* spp., *M. stellatus*), providing constant resources for grazers, despite the fall to spring decrease in abundance of ephemeral alga *Ulva* spp. (Migné et al. 2015). Therefore, grazers do not need to switch their diet over the course of the year, explaining their temporal conservation within food webs. In contrast, filter-feeders showed a partial switch in diet over the year, according to the results of mixing models. They were found to rely mainly on phytoplankton-dominated POM during summer and on macroalgae-derived organic matter during winter, which is consistent with seasonal variations in abundance of phytoplankton observed close to our study area (SOMLIT data). Such switch in diet has already been observed in kelp forests of Brittany (Leclerc et al. 2013), and strengthens the idea that macroalgae-derived detritus are a significant food source for filter-feeders (Sarà et al. 2007, Crawley et al. 2009, Schaal et al. 2010, Miller & Page 2012). They are therefore suggested to be opportunistic species relying on the most abundant food source (Ricciardi & Bourget 1999, Schaal et al. 2010). In spite of this temporal diet variability, the average trophic position of this functional group in the two communities remained unchanged, and filter-feeders stayed ^{13}C-depleted compared to grazers, all over the year. The relative seasonal conservation of predators within the food webs was probably due to the seasonal consistency of their potential diet (i.e. primary consumers) but should also result from a relative degree of omnivory and opportunism (Thompson et al. 2007, Silva et al. 2010, Duarte et al. 2015). Finally, the overall preservation of trophic structure across seasons observed despite some seasonal changes in taxonomic diversity of consumers, suggests that some redundancy in the feeding behaviour of these species (Hawkins et al. 1989, Golléty et al. 2010) helps to keep a relative food web stability over time (Christie et al. 2009).

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

4.3. Comparisons between communities

By analysing isotopic composition of taxa living in these communities, we had the prospect to do comparisons in the context of vertical zonation of intertidal habitats. Using community-wide metrics, we highlighted an important similarity in the average trophic structure of the two *Fucus* spp. communities. This was supported by the large number of taxa present in the common isotopic space. Despite some differences in the species richness and composition between these two communities (Davoult et al., unpublished data), they shared a roughly similar isotopic functional space, suggesting that the same trophic functions are undertaken by different species in the *F. vesiculosus* and *F. serratus* communities. This is consistent with the fact that intertidal communities are mostly composed of generalists and opportunistic species, that rely mainly on the most abundant food sources (Steinarsdóttir et al. 2009). Such plasticity in diet could favour growth rates of consumers, as demonstrated by Lee et al. (1985), providing them some benefit in intertidal habitats. However, the two *Fucus* spp. communities exhibited significant differences in their photosynthetic activity over the year (Bordeyne et al. 2015), potentially leading to important differences in the amount of carbon accumulation at the base of the food webs, and in carbon fluxes toward top predators. Again, further investigations taking into account taxon abundances are needed to understand more faithfully the trophodynamics of these communities.

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

Diversity monitoring highlighted significant differences in the composition of grazers between the two communities, in accordance with the tidal control of species distribution and abundances (Raffaelli & Hawkins 1999). However, when considering isotopic composition, no significant difference between communities was evidenced, whether the abundance of grazers is accounted for or not. These results suggest that the two groups of grazers exhibited similar trophic functions within the two communities, despite some differences in species identities and abundances. Besides, within each community, the diversity of radula types and feeding mechanisms described for these grazers indicated that some functional complementarity occurs (for instance, *P. vulgata* is considered as a scraper of hard substrata, while *Gibbula* spp. seem rather to brush algae, Hawkins et al. 1989), and is likely to promote species coexistence in relatively high abundances.

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

4.4. *Conclusion*

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

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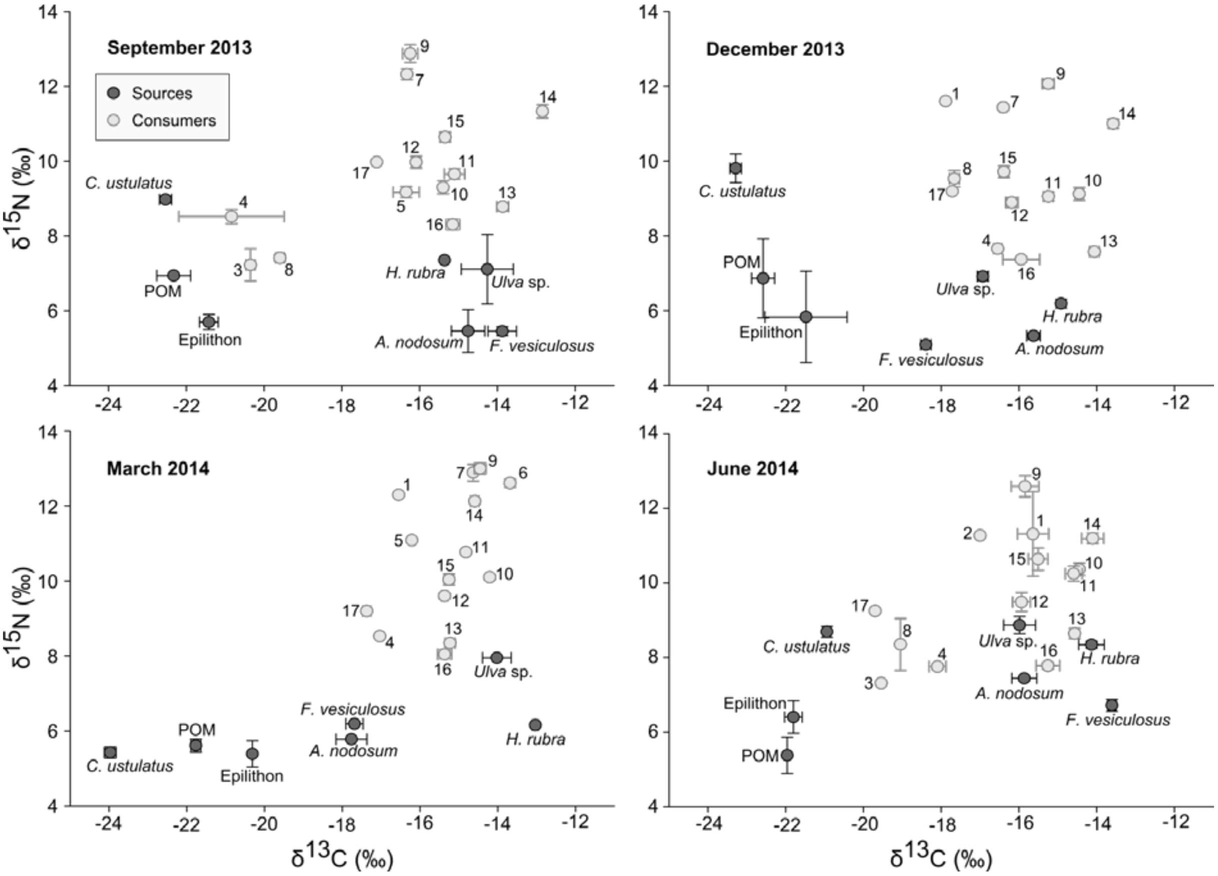

Figure 1: Mean ± SE of δ^{15}N (‰) vs δ^{13}C (‰) for primary producers and consumers of the *Fucus vesiculosus* community, sampled in September and December 2013 and March and June 2014. Sources are represented by dark-grey rounds and their names are indicated nearby, while consumers are represented by light-grey rounds. Consumers : 1 *Actinia equina*; 2 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7 *Calliostoma zizyphinum*; 8 Campanulariidae; 9 *Carcinus maenas*; 10 *Gibbula pennanti*; 11 *Gibbula umbilicalis*; 12 *Littorina littorea*; 13 *Littorina obtusata*; 14 *Nucella lapillus*; 15 *Phorcus lineatus*; 16 *Patella vulgata*; 17 *Spirorbis* sp. Values are given in Supplementary Material 1.

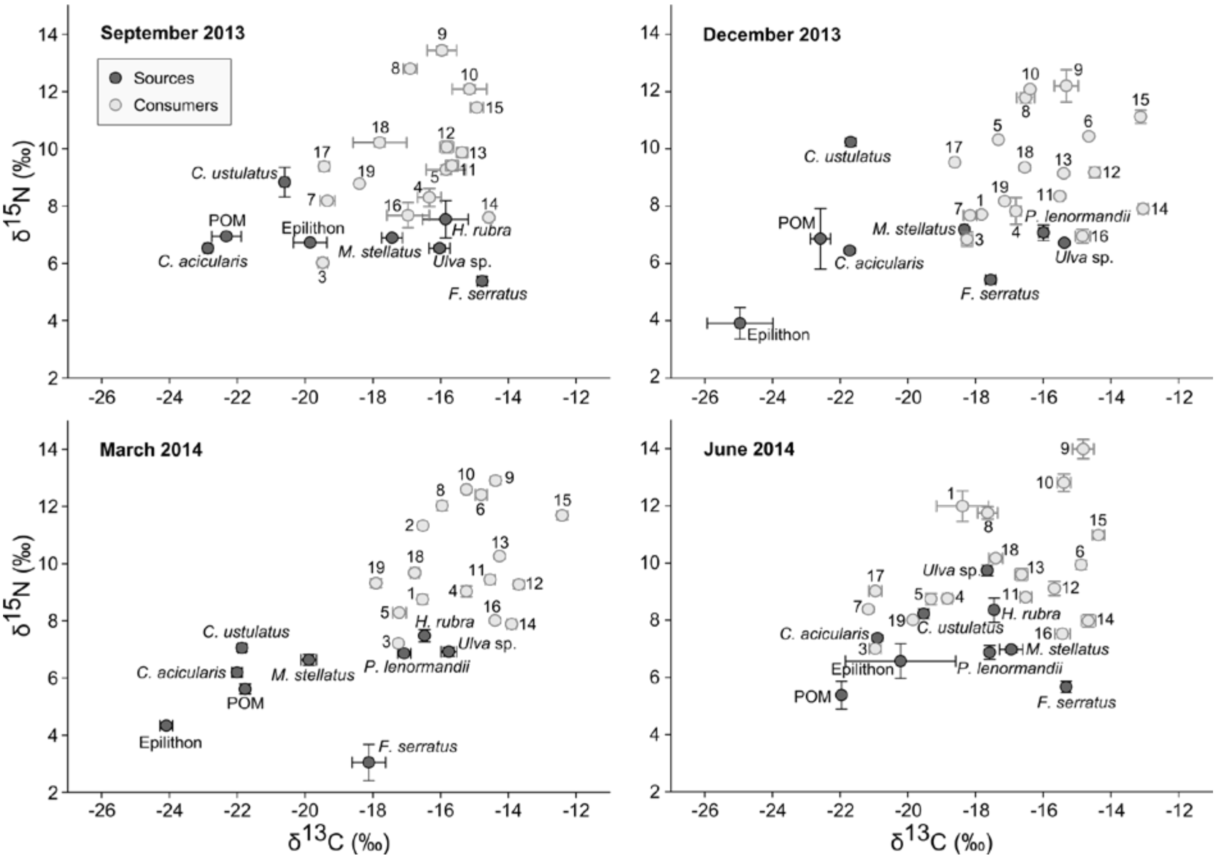

Figure 2: Mean ± SE of δ^{15}N (‰) vs δ^{13}C (‰) for primary producers and consumers of the *Fucus serratus* community, sampled in September and December 2013 and March and June 2014. Sources are represented by dark-grey rounds and their names are indicated nearby, while consumers are represented by light-grey rounds. Consumers : 1 *Actinia equina*; 2 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7 *Botryllus schlosseri*; 8 *Calliostoma zizyphinum*; 9 *Cancer pagurus*; 10 *Carcinus maenas*; 11 *Gibbula cineraria*; 12 *Gibbula pennanti*; 13 *Gibbula umbilicalis*; 14 *Littorina obtusata*; 15 *Nucella lapillus*; 16 *Patella vulgata*; 17 Polyclinidae; 18 *Porcellana platycheles*; 19 *Spirorbis* sp. Values are given in Supplementary Material 2.

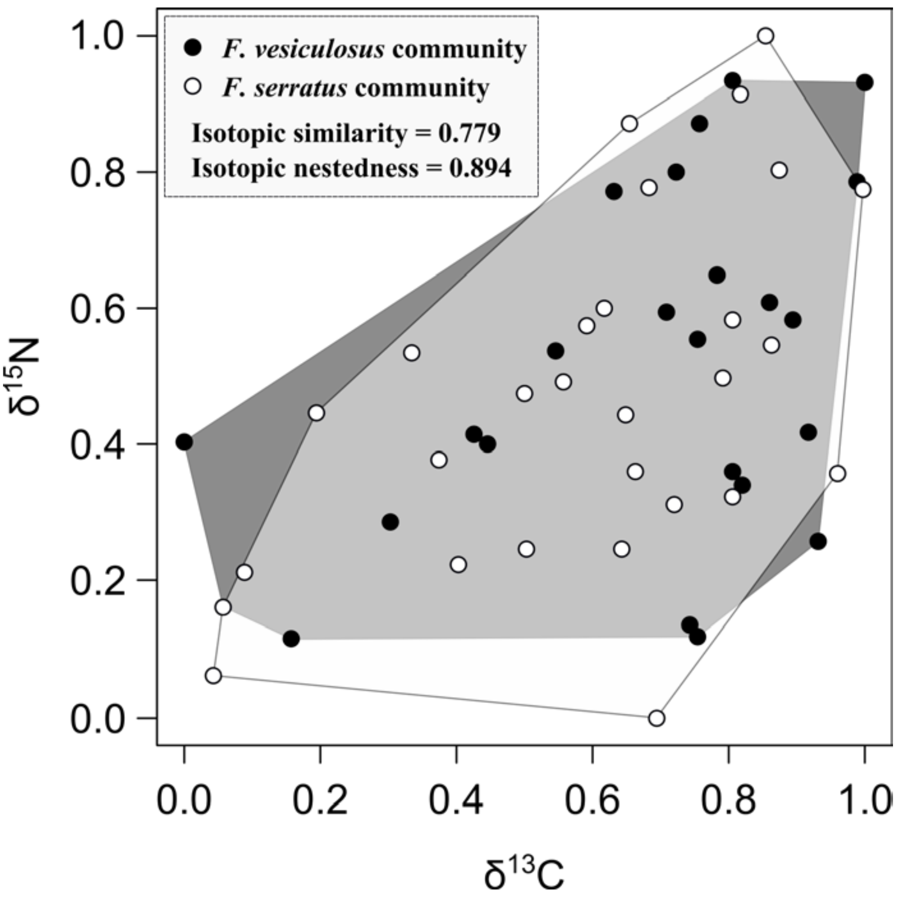

Figure 3: Annual mean of scaled $\delta^{15}N$ vs scaled $\delta^{13}C$ for primary producers and consumers of the *F. vesiculosus* (black rounds) and *F. serratus* (white rounds) communities. Isotopic spaces are represented in dark-grey for the *F. vesiculosus* community and in white for the *F. serratus*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

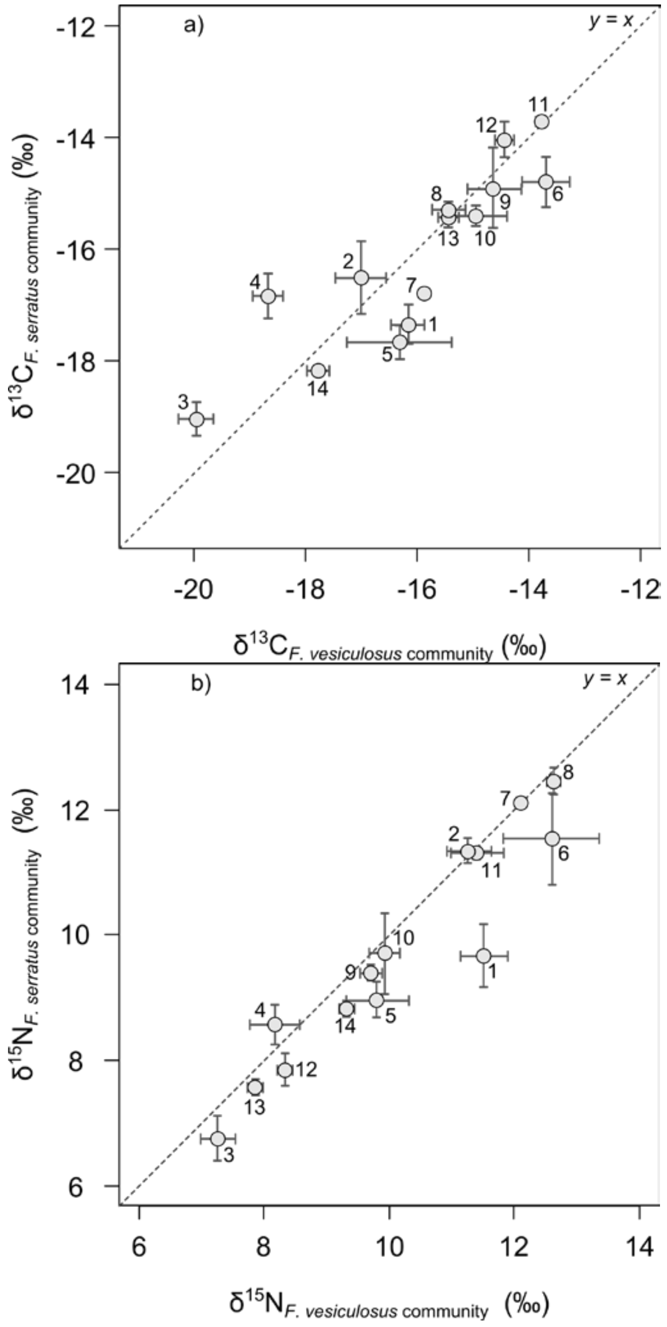

Figure 4: Annual mean of a) $\delta^{13}C$ ± SE (‰) of shared taxa obtained in the *F. vesiculosus* community vs those obtained in the *F. serratus* community, and of b) $\delta^{15}N$ ± SE (‰) of shared taxa obtained in the *F. vesiculosus* community vs those obtained in the *F. serratus* community.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

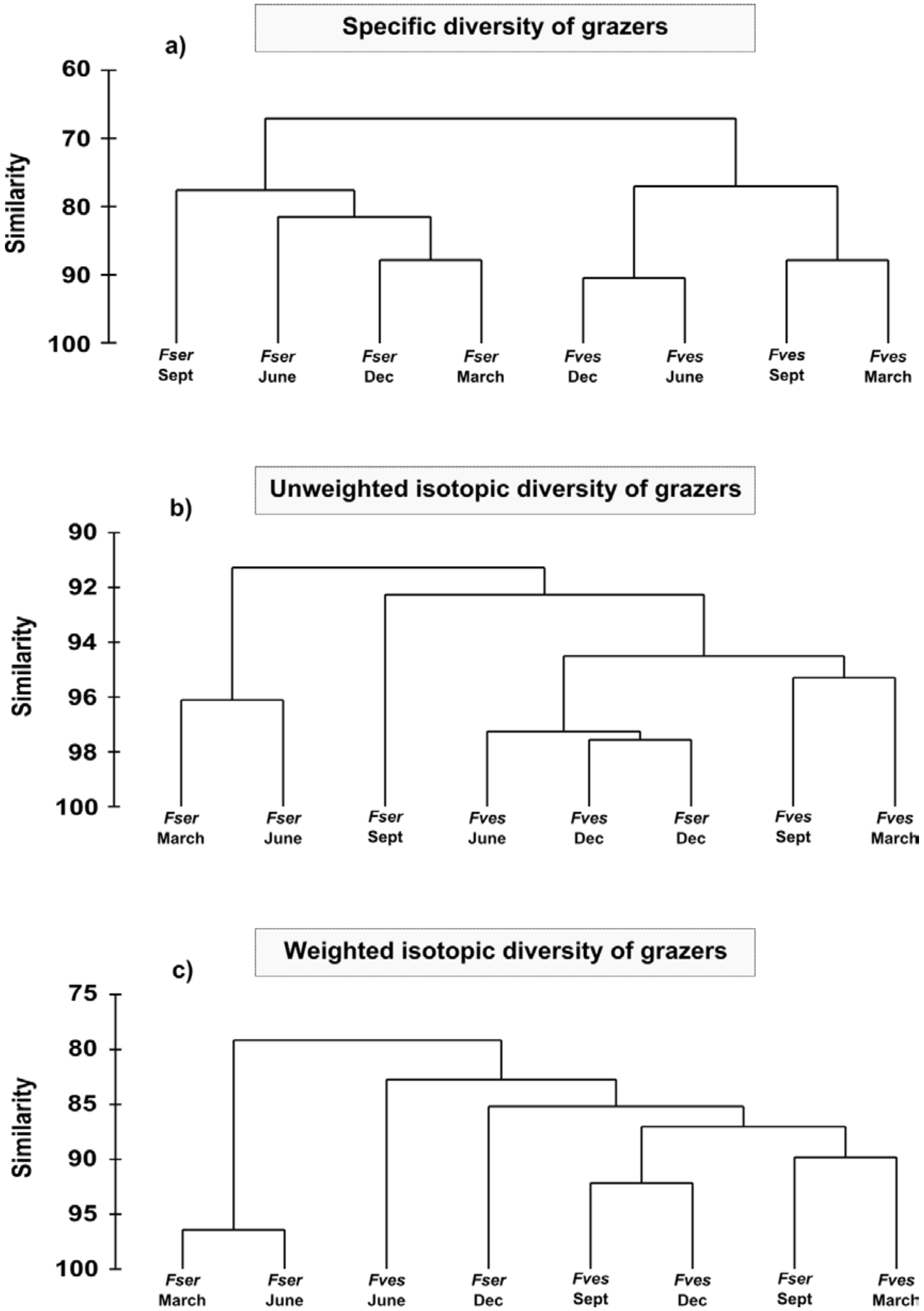

Figure 5: Dendrograms from clustering analyses conducted on the grazers' data; a) on square-root transformed abundances, b) on isotopic diversity metrics calculated from unweighted isotopic data, and c) on isotopic diversity metrics calculated from isotopic data weighted by grazers' abundances.

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

	Date	**Sept**	**Dec**	**March**	**June**	**CV**
***F. vesiculosus* 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 eveness	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**
***F. serratus* 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 eveness	0.828	0.737	0.743	0.801	5.4
	Isotopic uniqueness	0.538	0.274	0.249	0.425	25.2

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

***F. vesiculosus* community**

	Date	*A. nodosum*	*F. vesiculosus*	*C. ustulatus*	Epilithon	*Ulva* spp.
Filter-feeders						
Campanulariidae	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)
Spirorbis 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						
Gibbula umbilicalis	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)
Littorina obtusata	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)
Patella vulgata	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	*F. serratus*	*C. ustulatus* & *C. acicularis*	*M. stellatus*	Epilithon	*Ulva* spp.
Filter-feeders						
Alcyonidium 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	01 - 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)
Spirorbis 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						
Gibbula pennanti	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)
Littorina obtusata	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)
Patella vulgata	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)

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

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

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

Supplementary material 1: Mean ± SE (‰) of $\delta^{13}C$ and $\delta^{15}N$ 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.

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

Supplementary material 2: Mean ± SE (‰) of $\delta^{13}C$ and $\delta^{15}N$ 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.

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