

Microscale aspects in the diet of the limpet *Patella vulgata* L.

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The limpet Patella vulgata is a key species of northern Atlantic rocky shore-associated communities, and is commonly considered to be important in regulating populations of canopy-forming Ascophyllum nodosum, through consumption of propagules and young recruits. Although P. vulgata is usually regarded as a non-selective epilithic biofilm grazer, a role in the collapse of established A. nodosum through grazing of adult plants has been repeatedly suggested. Factors controlling the preference of P. vulgata for epilithic biofilm or adult algae are still not clearly established. Here, we test the hypothesis that the diet of P. vulgata is mainly driven by the local availability of food sources. Limpets were sampled along the first 6 metres of an A. nodosum bed – bare rock gradient. Stable isotope ratios of their muscle tissue and digestive glands were measured. The contribution of A. nodosum to the diet of limpets was the highest in the immediate vicinity of macroalgae beds, which confirmed our initial hypothesis. However, the contribution of epilithic biofilm did not match our hypothesis, being the lowest for limpets colonizing bare rock. Instead, these limpets relied on a wide array of sources, including ephemeral green algae, biofilm and drifting A. nodosum fragments. Overall, our results indicate that A. nodosum can be readily grazed by limpets, which challenges the hypothesis that these macroalgae dominate rocky shores due to the absence of strong top-down control exerted by herbivores. Our results also highlight the need to consider the small spatial scale to understand the dynamic of herbivore – algae interactions in natural environments.

Keywords: *Patella vulgata*, *Ascophyllum nodosum*, rocky shore, stable isotopes, spatial variability

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INTRODUCTION

Patellid limpets are the dominant grazers of NE Atlantic rocky shores (Hawkins & Hartnoll, 1983). Their role in preventing the colonization of the shore by canopy-forming fucoids has received a considerable amount of attention by scientists over the last 50 years (e.g. Southward & Southward, 1978; Hawkins & Hartnoll, 1983; Jenkins *et al.*, 1999; Thompson *et al.*, 2004). Experimental studies have shown that removal of limpets invariably leads to proliferation of macroalgae (ephemeral green algae first, then fucoids) (see Coleman *et al.*, 2006), suggesting that limpets' grazing is an important factor controlling macroalgal cover on rocky shores. It is known that limpets consume macroalgal propagules whilst grazing the substrate, thereby preventing the establishment of new algal populations in areas with high limpet densities. Hence, their foraging activity promotes spatial variability in intertidal assemblages, i.e. the co-occurrence of algal canopies and unvegetated areas, with their respective associated biodiversities (Coleman *et al.*, 2006). On NE Atlantic rocky shores, *Patella vulgata* is the main intertidal grazer, and can reach densities over 100 individuals m⁻² (Hawkins & Hartnoll, 1983). *Patella vulgata* is generally regarded as a generalist grazer, that consumes different components of epilithic

biofilm (i.e. benthic microalgae, germinating algal sporelings, bacteria and their associated matrix of organic matter) (Hawkins *et al.*, 1989). *Patella vulgata* usually colonizes bare rock areas adjacent to macroalgae beds formed by the canopy-forming fucoid *Ascophyllum nodosum*, because understory red algal turfs prevent limpets from foraging (Jenkins *et al.*, 1999). *Ascophyllum nodosum* dominates sheltered to semi-exposed rocky shores along the coasts of the northern Atlantic. Even though this algae is consumed by some herbivorous gastropods, such as the periwinkle *Littorina obtusata* (Sarà *et al.*, 2007), it is usually considered of poor nutritive value for herbivores, due to the concentration of herbivore-deterrent secondary metabolites within its tissues (Pavia & Toth, 2000), and direct grazing of *A. nodosum* by limpets is thought to be quite rare. Some events of dramatic herbivory by limpets, leading to local eradication of *A. nodosum*, have nevertheless been reported on western European coasts (Le Roux, 2005), but seem to remain local phenomena (Davies *et al.*, 2007). Trophic supply from *A. nodosum* has been suggested to play a role in sustaining growth rates and lower mortality in limpet populations during winter (Davies *et al.*, 2008). Limpets often aggregate at the vicinity of *A. nodosum* fronts or solitary individuals (Davies *et al.*, 2007), where they have been observed to play a role in increasing the vulnerability of plants to wave-induced breakage (Davies *et al.*, 2007), but are also to be found further away. It is not clear, to our knowledge, how the variability of limpets' direct environment affects their trophic resource, that is, their consumption of *A. nodosum* and/or other food sources.

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Stable isotopes have been used to investigate trophic relationships on rocky shores (Bode *et al.*, 2006; Sarà *et al.*, 2007; Riera *et al.*, 2009; Golléty *et al.*, 2010; Richoux & Ndhlovu, *in press*). Although a trophic link between *Patella vulgata* and *Ascophyllum nodosum* has been suggested in one of these studies (Golléty *et al.*, 2010), most of them did not find any relationships between limpets and macroalgae. In fact, the diet of gastropods is tightly linked to the morphology of their radula (Steneck & Watling, 1982). Limpets in the genus *Patella* are characterized by a docoglossan radula, which is adapted to the consumption of epilithic biofilm, leathery macroalgae (e.g. *Ascophyllum nodosum*) and encrusting macroalgae (Steneck & Watling, 1982). The diet of this gastropod is therefore likely to vary in time and space according to the availability of its potential food sources.

Because rocky shores are naturally highly heterogeneous ecosystems (McGuinness & Underwood, 1986), primary producers (i.e. canopy-forming *Fucales*, understory macroalgae, benthic biofilm) are likely to vary at the small spatial scale. Here, we formulate the hypothesis that the diet of limpets cannot be totally understood without a small-scale perspective, particularly in relation to the spatial distribution of *Ascophyllum nodosum*. Since *Patella vulgata* has been considered to be responsible for the loss of *A. nodosum* canopies in different areas of Europe (Le Roux, 2005; Davies *et al.*, 2007), we expected that limpets found in the immediate vicinity of macroalgal fronts would strongly rely on *A. nodosum* and its associated epiphytic flora for food, while those found far from these fronts would rely mainly on alternative sources, such as benthic biofilm or ephemeral macroalgae.

MATERIALS AND METHODS

Sampling procedure

Field sampling was carried out in July 2010 on a semi-sheltered rocky shore of Porspoder (Western Brittany, France, 04°46.505'W 48°29.230'N). This rocky shore is characterized by the co-occurrence of *Ascophyllum nodosum* beds and bare rock zones, forming unvegetated patches within *A. nodosum* beds, including patches of sponges (*Hymeniacidon perlevis* and *Halichondria panicea*) localized in crevices and underneath the algal canopy. Limpets were abundant everywhere on bare rock areas, but did aggregate at the edges of *A. nodosum* beds (later called fronts). Eight fronts were selected for sampling at mid-shore level. The distance between the different fronts sampled ranged from a few metres to about 10 metres. A tape measure was deployed perpendicular to each front, and all limpets within the first 10 cm from the tape were removed from the substrate, their distance to the algal front noted, and sealed individually in labelled plastic bags. Limpets were sampled up to 6 m from *A. nodosum* fronts, which was the maximal distance found between limpets and algal fronts. Preliminary studies (Grall, unpublished data) indicate that most small individuals keep moving until they find a suitable place to settle. Hence, in order to sample established adults, only individuals larger than 30 mm were kept for analysis. For the eight fronts, 103 individuals were collected.

At each front, samples of *A. nodosum* and other abundant macroalgae (i.e. *Fucus serratus*, *Ulva* spp., *Ceramium* sp., *Vertebrata lanosa*) were also collected. Epilithic biofilm was

sampled by brushing the substrate (0.05 m²) using a thin brush, and then resuspended in filtered (0.7 µm) seawater (Riera *et al.*, 2009; Schaal *et al.*, 2009). The brush was carefully rinsed with fresh water between each sampling to prevent any contamination between two samples. Three samples of water were also collected at incoming tide to characterize the isotopic signature of the suspended particulate organic matter (POM). All samples were stored in a coolbox until being brought back to the laboratory.

Sample processing

Once in the laboratory, limpets were starved overnight in filtered seawater and killed by freezing (−20°C). They were then dissected, and a piece of muscle tissue was cut off from the foot, as well as the entire digestive gland. Muscle and digestive gland samples were freeze-dried, and ground into a fine and homogeneous powder using an automatic grinder.

Sponges were carefully checked for the presence of any carbonate particles, briefly acidified, rinsed with distilled water and freeze-dried, before being ground into powder. Macroalgae were cleaned of any visible epiphytes, and also freeze-dried and ground into powder. Samples of POM and biofilm were filtered once back in the laboratory through pre-combusted (450°C, 4 h) GF/F filters. Biofilm samples were briefly acidified to remove any carbonate contamination. The filters were then freeze-dried and the material retained on the filter scraped using a clean scalpel. All samples were stored frozen (−20°C) until further processing. Powdered samples were then placed in tin capsules before isotope ratio mass spectrometry analysis.

Isotopic analyses were performed by Mylnefield Research Services Ltd. (Dundee, Scotland) using a SerCon 20/20 Geo Isotope Ratio Mass Spectrometer with ANCA-GSL Combustion/Reduction interface. The data are expressed in ‰ in the standard δ unit:

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

with $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen. These abundances were calculated in relation to the certified reference materials Vienna Pee Dee Belemnite-limestone (carbon) and atmospheric dinitrogen (nitrogen).

Data analysis

Limpets were classified in six classes of distance to front for data analysis (0–20 cm, 20–50 cm, 50–100 cm, 100–200 cm, 200–300 cm, >300 cm) (Table 1). Analysis of

Table 1. δ¹³C and δ¹⁵N of limpets (*Patella vulgata*) foot and digestive glands measured at various distances from the closest *Ascophyllum nodosum* front.

d(cm)	N	Foot		Digestive gland	
		δ ¹³ C	δ ¹⁵ N	δ ¹³ C	δ ¹⁵ N
0–20	27	−15.2 ± 0.96	7.6 ± 0.61	−18.6 ± 1.21	7.5 ± 0.71
20–50	16	−15.5 ± 0.87	7.8 ± 0.58	−17.3 ± 0.90	7.5 ± 0.45
50–100	11	−15.5 ± 0.48	7.8 ± 0.38	−17.5 ± 0.66	7.3 ± 0.34
100–200	28	−15.8 ± 0.66	8.7 ± 0.62	−17.6 ± 0.76	7.8 ± 0.83
200–300	9	−15.7 ± 0.55	8.5 ± 0.84	−17.6 ± 0.58	7.6 ± 0.65
>300	9	−15.7 ± 1.09	9.1 ± 0.72	−17.8 ± 1.23	8.0 ± 0.71

variance was used to compare the stable isotope ratios of limpets among those different classes, after checking for normality (Shapiro–Wilk's tests) and homogeneity of variances (Levene's tests). *Post-hoc* Tukey's tests were then performed to identify differences. Differences were considered as significant at $P < 0.05$.

The contribution of each potential food source to the diet of *Patella vulgata* was estimated using the Bayesian stable isotope mixing model SIAR (Parnell *et al.*, 2010; available at <http://cran.r-project.org/web/packages/siar/index.html>). This model estimates the contribution of different potential food sources to the diet of a consumer, taking into account the variability of their respective stable isotope signature, as well as the variability of trophic enrichment. Different potential food sources were considered: Fucales (regarded as the average isotopic ratios of *Ascophyllum nodosum* and *Fucus serratus*), the Chlorophyta *Ulva* spp. (two species were present, foliose and filamentous) and the Rhodophyta *Vertebrata lanosa*, epiphyte of *A. nodosum*. Because limpets have sometimes been reported to ingest encrusting invertebrates (Camus *et al.*, 2008), the two main sponges (*Halichondria panicea* and *Hymeniacidon perlevis*), as well as benthic biofilm, were also considered as potential food sources for SIAR modelling. Because limpets are exclusive grazers, POM was not considered as a potential food source. The isotopic fractionation occurring between a consumer and its source is known to be variable according to the taxa or the environment considered (Vander Zanden & Rasmussen, 2001). Consequently, we considered for this study a $\delta^{15}\text{N}$ fractionation of $1.2 \pm 0.8\text{‰}$, according to Vanderklift & Ponsard (2003). For $\delta^{13}\text{C}$, the fractionation considered was $0.5 \pm 0.13\text{‰}$, according to McCutchan *et al.* (2003).

RESULTS

Primary producers and potential food sources

Primary producers displayed similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ over the different *Ascophyllum nodosum* fronts considered. Consequently, the data (both primary producers and limpets) from all the fronts were pooled together for subsequent analyses.

The $\delta^{13}\text{C}$ of potential food items ranged from -23.6‰ (suspended particulate organic matter, POM) to -14.4‰ (*Ulva* sp.) (Figure 1). Among co-occurring potential food sources, *A. nodosum* was the second most ^{13}C -enriched (-16.7‰), but its $\delta^{13}\text{C}$ was close to those displayed by the Phaeophyta *Fucus serratus* and the Rhodophyta *Ceramium* sp. (-17.6 and -17.2‰ , respectively). The $\delta^{13}\text{C}$ of biofilm was much lower than most macroalgae (-21.5‰). $\delta^{15}\text{N}$ values ranged from 5.8‰ (Biofilm) to 10.8‰ (*Ulva* sp.). Most primary producers' $\delta^{15}\text{N}$ comprised between 5.8 and 8.5‰ . The two sponges (*Halichondria panicea* and *Hymeniacidon perlevis*) and the Chlorophyta *Ulva* sp. displayed higher $\delta^{15}\text{N}$ than other potential food sources.

Limpets' isotopic ratios and diet

The isotopic ratios of muscle tissue were consistently ^{13}C -enriched ($2.2 \pm 0.6\text{‰}$) compared with digestive glands (Figure 2). Overall, the $\delta^{13}\text{C}$ of muscle comprised between -18.7 and -13.1‰ , while the $\delta^{13}\text{C}$ of digestive glands ranged from -20.8 to -15.2‰ . While no significant

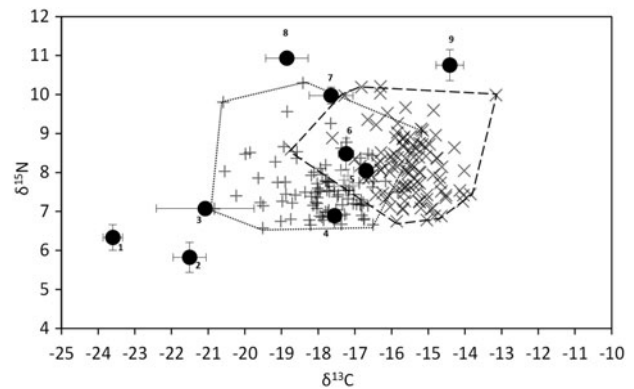


Fig. 1. $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ of the most abundant primary producers and sponges (black dots), and of the limpet *Patella vulgata*. (+, fine dashes) = muscle, (x, long dashes) = digestive gland. 1, Suspended particulate organic matter; 2, benthic biofilm; 3, *Vertebrata lanosa*; 4, *Fucus serratus*; 5, *Ascophyllum nodosum*; 6, *Ceramium* sp.; 7, *Hymeniacidon perlevis*; 8, *Halichondria panicea*; 9, *Ulva* sp.

difference was found among the different categories for the $\delta^{13}\text{C}$ of muscle (one-way ANOVA, $F_{5,97} = 1.76$, $P = 0.13$), some significant differences occurred for the digestive glands (one-way ANOVA, $F_{5,97} = 5.35$, $P < 0.001$), mostly due to the differences between samples next to the front (0–20 cm) and those further away (>20 cm) (*post-hoc* Tukey's pairwise comparisons, $P < 0.05$). The opposite pattern was observed for $\delta^{15}\text{N}$, with no difference being observed among distances for digestive gland tissues (one-way ANOVA, $F_{5,97} = 1.85$, $P = 0.11$), while some significant differences were observed for muscle (one-way ANOVA, $F_{5,97} = 14.97$, $P < 0.001$), revealing a pattern of ^{15}N -enrichment in the most distant groups from the front (*post-hoc* Tukey's pairwise comparisons, $P < 0.05$).

The results of SIAR modelling of *Patella vulgata*'s diet showed that, regardless of the tissues analysed or the distance from an *Ascophyllum nodosum* front, Fucales (i.e. *A. nodosum* and *F. serratus*) and the biofilm formed the major part of the diet (Figure 3). SIAR modelling, either based on muscle or digestive gland tissues, indicated a higher contribution of both Fucales and biofilm at the vicinity of *A. nodosum* fronts, while the diet of limpets collected more than 200 cm from the fronts appeared more diversified, including small but significant amounts of the Chlorophyta *Ulva* sp. and *Enteromorpha* sp. (maximal estimated contribution around 35% of the diet) (Figure 4).

DISCUSSION

This study is, to our knowledge, the first one to investigate the diet of *Patella vulgata* with a microscale spatial perspective. Recent studies have highlighted the need to consider small spatial scales in order to fully understand the diets of benthic invertebrates, and the possible factors influencing their diets (Guest & Connolly, 2004; Kon *et al.*, 2007; Schaal *et al.*, 2011). These studies have emphasized the limits of trophic pattern generalization without a thorough consideration of local-scale structural features of the environment that are likely to affect food source availability. Here, we showed that the diet of *P. vulgata* varies at the centimetre scale, with respect to its distance to macroalgal beds.

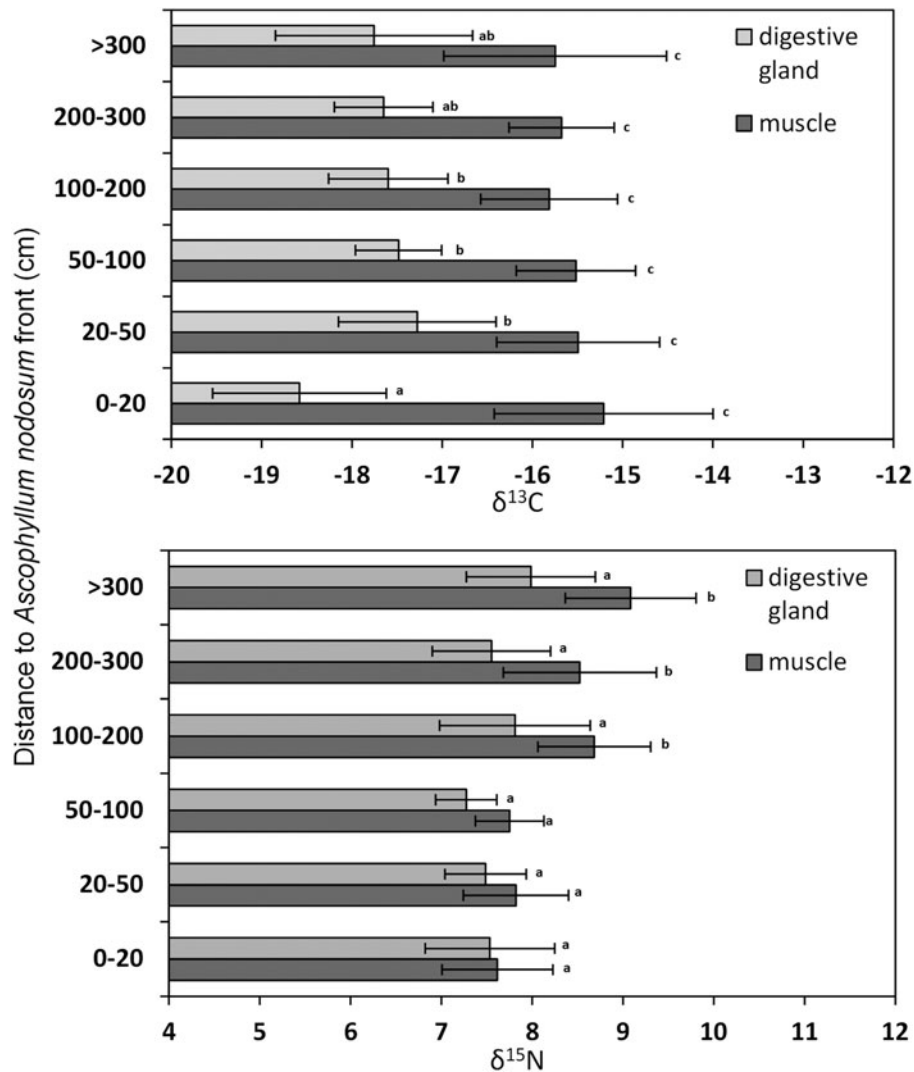


Fig. 2. Differences of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ observed between muscle and digestive gland in *Patella vulgata* along the *Ascophyllum nodosum* front–bare rock gradient. Letters indicate the results of pairwise comparisons realized among each tissue/isotope category.

In this study, we analysed both muscle and digestive glands of limpets, each reflecting the food assimilated over different time spans (Tieszen *et al.*, 1983). Although turnover times have mostly been investigated in the different tissues of fish, and few studies have addressed this issue in molluscs, isotopic ratios from the digestive glands are expected to correspond to the diet assimilated recently (i.e. from days to weeks; Raikow & Hamilton, 2001), while muscle is known to integrate the food assimilated over a longer period (from weeks to months; McIntyre & Flecker, 2006). This difference is of particular importance, because *Ascophyllum nodosum* can experience strong seasonal variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Goll  ty *et al.*, 2010). Consequently, the stable isotope ratios measured for muscle tissue are likely to be representative of the assimilation of food sources consumed over a longer time period and whose $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differ from food assimilated leading up to and during the course of the sampling period. In the case of a single time study, such as the present one, the analysis of fast-turnover tissues, such as digestive glands, may therefore be more relevant and representative of the potential food sources analysed during the sampling.

In spite of the higher relevance of considering the digestive glands of limpets to infer the composition of their diet in single time studies, the storage of lipids in this tissue is likely to affect the conclusions of stable isotope analyses. Molluscs typically store lipids in their digestive gland and their gonads (Wenne & Polak, 1989). Among biochemical compounds in animals, lipids are known to be ^{13}C -depleted compared with proteins (De Niro & Epstein, 1977), which sometimes requires the application of correction factors to the stable isotope ratios of these tissues (e.g. Bodin *et al.*, 2007). We did not measure the lipid content in limpet tissues during the present study. We are, however, confident that any potential variability in the lipid content of digestive glands would only marginally affect our conclusions. For instance, lipid content in lake fish varying from 3% (northern pike) to 26% (lake trout) only resulted in a 2‰ $\delta^{13}\text{C}$ difference (Post *et al.*, 2007), which is much lower than the isotopic variability observed in this study. Moreover, using correction factors accounting for the effects of lipids on stable isotope ratios would yield higher $\delta^{13}\text{C}$ for digestive glands, potentially higher than the most ^{13}C -enriched potential food source. Finally, it is likely that lipids contained in digestive glands affect the $\delta^{13}\text{C}$ in the same way along the *A. nodosum*

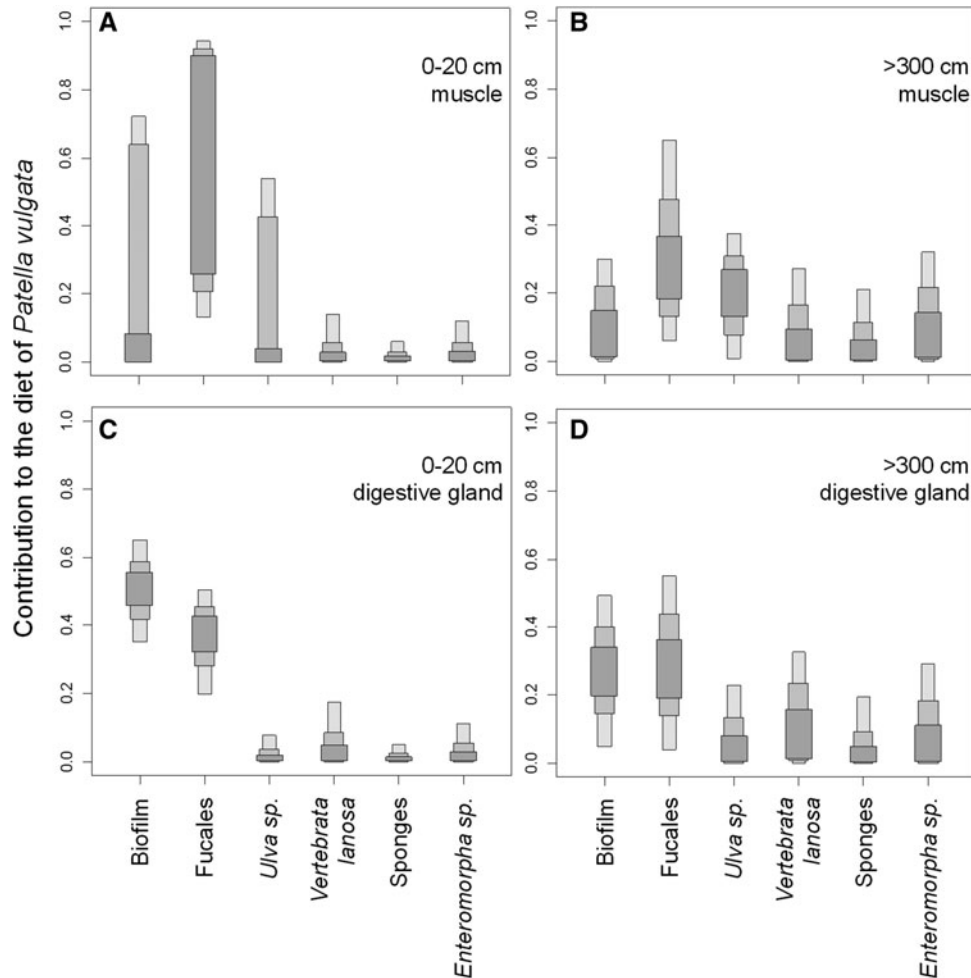


Fig. 3. Contribution of the different potential food sources to the diet of *Patella vulgata* at the immediate vicinity of *Ascophyllum nodosum* fronts and more than 300 cm away, estimated through the use of SIAR based on the stable isotope ratios of muscle and digestive gland tissues. Boxplots indicate the 5, 25, 75, 95 percentiles, and the credibility intervals of contributions' distribution.

front–bare substrate gradient. Hence, the variability in the diet of limpets along this gradient is also unlikely to be affected by this potential bias.

Although the SIAR diet modelling based on the two different tissues leads to contrasting conclusions, there is some consistency in the contribution of both *Ascophyllum nodosum* and biofilm to the diet of *Patella vulgata* along the *A. nodosum* front–bare substrate gradient. According to our initial hypothesis, the contribution of *A. nodosum* was higher at the front vicinity (less than 50 cm) than far away from it (more than 200 cm). However, even the diet of limpets sampled more than 3 m away from the front was still significantly based on this alga. Limpets predominantly graze during high tide and at night, making a complete loop centred around their home scar, where they come back before emersion (Evans & Williams, 1991; Noël *et al.*, 2009). Although a consistent lag between *P. vulgata*'s resting area and foraging area has already been reported around rock-pools (Noël *et al.*, 2009), this could hardly explain the reliance of limpets on *A. nodosum* more than 3 m away from their resting area (L.M.-L.J. Noël, personal communication). Even though limpets have sometimes been observed foraging more than 2 m away from their resting area (J. Grall, personal observation), such a consistent directional

foraging would involve energetic expenses that would seriously reduce the advantage of feeding on a potentially higher nutritive value source. The trapping of drifting macroalgae fragments is known to be an important feature of limpets' feeding behaviour (Bustamante & Branch, 1996). The significant contribution of *A. nodosum* to the diet of limpets colonizing bare substrate far from the fronts studied here might thus indicate that *P. vulgata* is able to trap detached fragments of this algae and to readily feed on them, as previously suggested by Lorenzen (2007). This behaviour can play a significant role in sustaining important populations of limpets in unvegetated areas (Bustamante & Branch, 1996).

Surprisingly the contribution of the biofilm to the diet of *Patella vulgata* did not match our initial expectations, since it was highest at the immediate vicinity of *A. nodosum* fronts, and only contributed about 20% of the diet for the furthest individuals (based on digestive gland stable isotope ratios). The high contribution of biofilm at the vicinity of *A. nodosum* challenges the conclusions of Davies *et al.* (2007), who found that this alga, when present, was the prime food source of *P. vulgata*. A possible alternative explanation for this unexpected high contribution of biofilm is the secretion by *A. nodosum* of high amounts of extracellular polymeric

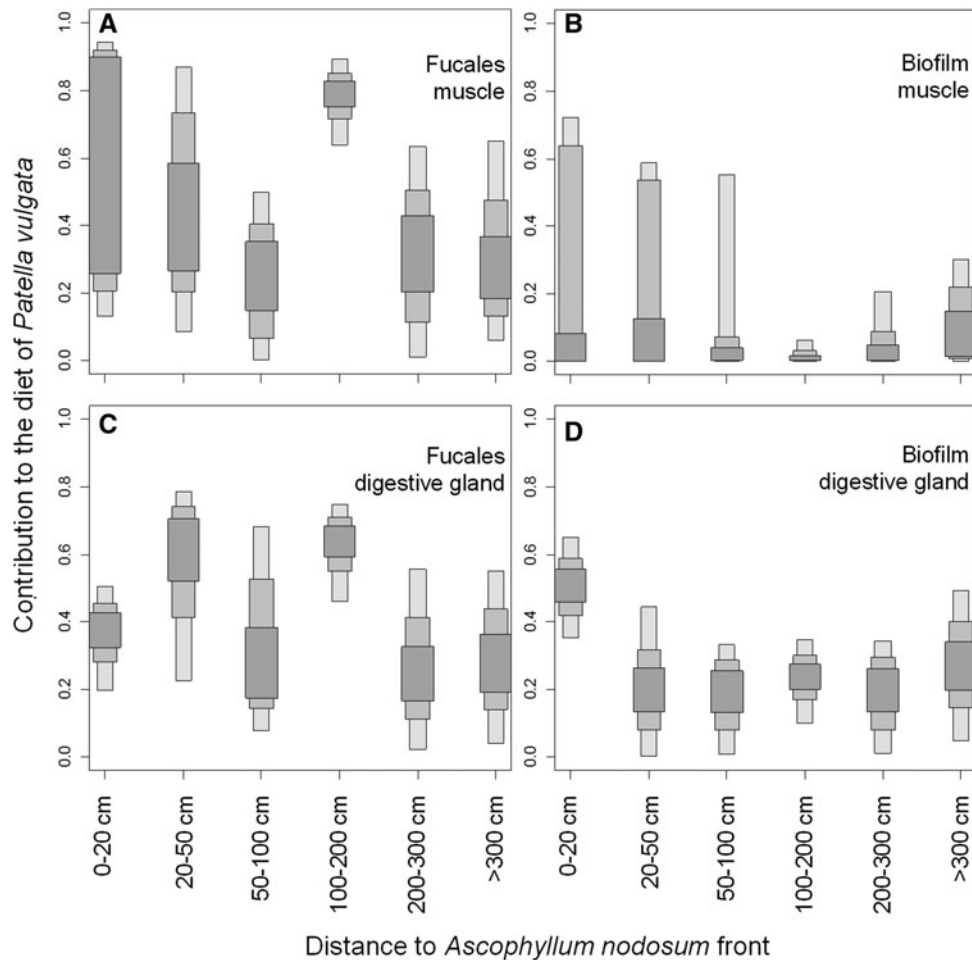


Fig. 4. Variations in the contribution of *Ascophyllum nodosum* and epilithic biofilm to the diet of *Patella vulgata* along the *Ascophyllum nodosum* front–bare rock gradient estimated through the use of SIAR based on the stable isotope ratios of muscle and digestive gland tissues. Boxplots indicate the 5, 25, 75, 95 percentiles, and the credibility intervals of contributions' distribution.

substances (EPS) (Khailov & Burlakova, 1969), which can stimulate the growth of the microbial epilithic biofilm, through providing dissolved organic matter that is assimilated by bacteria (Golléty *et al.*, 2008), making this source locally more abundant and more nutritive. The ^{15}N -enrichment observed in limpets' muscle along the front–bare rock gradient might also be explained to some extent by a slight omnivory in limpets colonizing bare rock. Apart from the sponges *Halichondria panicea* and *Hymeniacion perlevis*, no potential animal dietary items (especially barnacle settlers and recruits) were sampled. This was contrary to some studies where limpets have been reported to derive a small portion of their diet from animal items (Hawkins *et al.*, 1989; Hill & Hawkins, 1991; Camus *et al.*, 2008). However, we did not observe any significant barnacle recruitment during sampling or in the weeks before on the sampling site, which limits the possibility that other animal sources contribute to the diet of *P. vulgata*. Moreover, one could reasonably argue that other sessile animals would be isotopically more or less similar to sponges, because they all are suspension-feeders. Results from SIAR modelling clearly show that these items do not contribute to the diet of limpets. Consequently, the diet of limpets at the vicinity of *A. nodosum* fronts is almost only composed of this alga and biofilm, while limpets colonizing bare substrate are characterized by a more diversified

diet, including a lower contribution of *A. nodosum* and biofilm, and a significant contribution of green algae (*Ulva* sp., *Enteromorpha* sp.).

Overall, our results highlight the microscale variability in the diet of the limpet *Patella vulgata*. Although a recent study pointed out the microscale variability occurring in the diet of suspension-feeding invertebrates colonizing rocky shores (Schaal *et al.*, 2011), this is, to our knowledge, the first time that this variability is observed in a field study for rocky shore-associated grazers. The differences in the diet of limpets along the *Ascophyllum nodosum* front–bare substrate gradient illustrate the need to consider small-scale features of ecosystems, that are particularly likely to affect community structure and functioning in heterogeneous habitats, such as rocky shores (Le Hir & Hily, 2005). This study shows that limpets are able to assimilate a wide array of food sources, thanks to their feeding apparatus (Steneck & Watling, 1982), and their ability to cope with the presence of herbivore-deterrent secondary metabolites in their diet. These characteristics make limpets generalist and opportunistic consumers. Together with their ability to exclude their space competitors from the substrate through removal and/or consumption, these constitute key factors likely to explain their dominance on eastern Atlantic rocky shores.

CONCLUSIONS

North Atlantic sheltered rocky shores are typically dominated by canopies of *Ascophyllum nodosum*. This species is considered as a foundation species (sensu Bruno & Bertness, 2001), enhancing both local algal and animal diversity (Jenkins *et al.*, 1999). Rocky shore-associated communities are thought to be characterized by a predominance of detritus-based food chains (Bustamante & Branch, 1996; Riera *et al.*, 2009; Schaal *et al.*, 2009). The main reasons for this functional predominance are the low regulative effect of littorinid grazers (Jenkins *et al.*, 2008), which have long been thought to be the main grazers of *A. nodosum*, and the high content of herbivore-deterrent secondary metabolites found in this alga's tissues (Pavia & Toth, 2000). However, this study, along with recent works on the relationships between *A. nodosum* and *Patella vulgata* (Le Roux, 2005; Davies *et al.*, 2007, 2008; Lorenzen, 2007), seriously challenges this paradigm, not only pointing out a strong trophic link between *P. vulgata* and *A. nodosum*, but also suggesting an important top-down regulation of *A. nodosum* by limpet grazing. The dominance of *A. nodosum* on northern Atlantic rocky shores has long been a mystery for ecologists, considering its extremely low growth rate and recruitment intensity (Vadas *et al.*, 1990). The main reason commonly advanced was related to the relative absence of efficient grazers, which allowed the persistence of *A. nodosum* stands for long periods. Considering the consistent evidence of *A. nodosum* overgrazing by limpets, this explanation cannot stand any longer. Further effort should therefore be devoted in future to the understanding of ecological factors allowing the maintenance of extensive stands of *A. nodosum* in the northern Atlantic.

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