Temporal variation in organic matter supply in kelp forests: linking structure to trophic functioning

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ABSTRACT: Owing to their productivity, kelps may be the main primary carbon source for consumers in coastal areas. Their contribution has often been compared to that of phytoplankton, but the potential involvement of the red algae associated with kelp forests has been overlooked. All these 3 primary sources have distinct life cycles and may contribute to the particulate organic matter pool differently according to season. In the present study, we characterised the trophic structure of a pristine *Laminaria hyperborea* forest off the coast of Brittany (France) in terms of the organic carbon biomass of the main primary producers and consumer trophic groups on 4 sampling dates over a 1 yr period. Senescence of many red algae species occurred during their resting period (i.e. before November), whereas the kelp regrowth period (i.e. before March) was accompanied by the fragmentation of old lamina. During these periods, when phytoplankton biomass is comparable, stable isotope analyses (δ^{13}C and δ^{15}N) were conducted in an attempt to link structure to trophic functioning. By combining analyses of temporal variability in primary source and consumer isotopic ratios and using mixing models, we inferred changes in the trophic significance of macroalgae in the associated food web. Decaying kelp laminae were a major contributor to the particulate organic matter pool, and the fragmentation of old lamina promoted their contribution to the diet of deposit- and suspension-feeders in March. Growth of red algae enhanced direct grazer consumption in March, while their senescence contributed significantly to primary consumer diets in November via indirect consumption.

KEY WORDS: *Laminaria hyperborea* · Trophic structure · Stable isotopes · Biomass · Temporal patterns · Subtidal

INTRODUCTION

Kelp forests are one of the most emblematic ecosystems in the marine environment. Their dense canopies harbour high biodiversity and host complex biological interactions (Newell et al. 1982, Steneck et al. 2002, Christie et al. 2003, Graham 2004). Kelp forests are often compared to their terrestrial counterparts in terms of stratification and productivity (Steneck et al. 2002). Kelp forests produce 400 to 1900 gC m^{-2} yr^{-1} (Mann 1972); values that are comparable to terrestrial rates, with net primary production of 238 gC m^{-2} yr^{-1} on average in boreal forests and 1098 gC m^{-2} yr^{-1} in tropical evergreen forests (Melillo et al. 1993). In these marine and terrestrial forest ecosystems, only a few grazers feed directly on the main primary producer (Fittkau & Klinge 1973, Newell et al. 1982). Both systems are also characterised by seasonal senescence. Senescence of macroalgae and terrestrial plants supplies large

amounts of organic matter to consumers through microbial processes (Linley et al. 1981, Lucas et al. 1981, Hairston & Hairston 1993). However, the organic matter pool of kelp and terrestrial forests differs in energetic content and degradability. Drifting macroalgae are quickly degraded by microheterotrophs and largely exported to adjacent ecosystems (Linley et al. 1981, Lucas et al. 1981, Koop et al. 1982, Bustamante & Branch 1996, Wernberg et al. 2006, Vanderklift & Wernberg 2008, Krumhansl & Scheibling 2012); they therefore have a rapid turnover and a reduced standing crop (Bedford & Moore 1984, Harrold & Reed 1985, Bustamante & Branch 1996). In contrast, terrestrial litter has a high cellulose content, resulting in slow turnover and a large standing crop (Fittkau & Klinge 1973, Hairston & Hairston 1993). Unlike that of terrestrial environments, the composition of the particulate organic matter (POM) pool in coastal environments is still a subject of debate, because many sources belonging to phytoplankton and the phytobenthos may be involved (Nadon & Himmelman 2006, Miller & Page 2012). According to Mann (1972), seaweed productivity is expected to balance that of phytoplankton in a coastal strip extending several kilometres from the shore.

For the estimation of the contribution of kelp-derived carbon to associated and adjacent food webs, stable isotope analyses have proved useful (Dunton & Schell 1987, Duggins et al. 1989, Bustamante & Branch 1996, Fredriksen 2003, Schaal et al. 2010). The contribution of kelp has mostly been studied on suspension-feeders — the usual dominant trophic group (i.e. 30 to 70% of the consumer biomass in coastal environments, e.g. Miller & Page 2012). In a recent review (Miller & Page 2012) of worldwide phytoplankton and kelp $\delta^{13}C$ measurements (e.g. Dunton & Schell 1987, Duggins et al. 1989, Fredriksen 2003), it has been suggested that the contribution of kelp suspension-feeder diet is overestimated in most studies due to the proxy estimations of $\delta^{13}C$ values (e.g. offshore POM, diatom cultures), rather than using phytoplankton itself.

Seasonal variability in the contribution of kelp to the understory food web has often been overlooked. Organic matter release may vary according to the life cycles of the kelp species and those of its associated macroalgae (Kain 1963, Whittick 1983, Maggs & Hommersand 1993, Sjøtun et al. 1996, Wernberg & Goldberg 2008). Habitat architecture determined by the macroalgae themselves may also change throughout the year. Seasonality is therefore expected to affect trophic structure and consumer behaviour. One way to characterise ecosystem trophic

structure and functioning is to study biomass measurements in conjunction with stable isotope analyses. In addition to realistic isotopic mixing models (Parnell et al. 2010, Fry 2013), temporal covariation in stable isotope values between sources and consumers may be analysed as spatial covariation to infer their trophic link (e.g. Vanderklift & Wernberg 2010).

In Europe, kelp forests are dominated by *Laminaria hyperborea*, a species encountered from 0 to 34 m depth (Kain 1971). Densities of at least 10 canopy-height individuals and a number of smaller individuals per square meter have been estimated in Norway with a production of 600 to 1000 gC m^{-2} yr^{-1} (Abdullah & Fredriksen 2004). Kelp individuals can reach up to 3.5 m in length and can be considered as a habitat of their own composed of 3 stratified parts: the lamina, the stipe, and the holdfast (Kain 1963). Macroalgal epiphytes develop along the entire thallus, and make up a high amount of biomass (Whittick 1983) with different structural features. The associated complex communities are differently distributed among these microhabitats (Schultze et al. 1990, Christie et al. 2003, Christie et al. 2007), with high diversity observed within the holdfasts (Moore 1973). Communities associated with the surrounding substratum are often overlooked and would be interesting to study (Norton et al. 1977). In Norway, some trophic pathways found in *L. hyperborea* forests and have been described, demonstrating the trophic role of kelp particles as a major ultimate carbon source (Fredriksen 2003, Norderhaug et al. 2003). Although the associated epiphytes have not been explicitly described as an important trophic resource, their role as a habitat for mobile macrofauna, which are prey for large predators, has been highlighted (Norderhaug et al. 2005).

The present study aimed to characterise the organic matter supply in the food web associated with a *Laminaria hyperborea* forest. The biomasses of the dominant primary sources were analysed throughout 1 yr to identify growing and senescing processes, which are expected to influence their direct and indirect consumption. We explored whether macroalgae life cycles and the turnover of the POM pool cause changes in the stable isotope compositions of these primary sources. Once characterised, these changes were linked to temporal variability in consumer signatures at the trophic group and species level. These analyses were combined with mixing models performed on primary consumer species sampled at both periods to describe and identify any temporal changes in the main trophic pathways found in this kelp forest.

MATERIALS AND METHODS

Study site

The study site was located near Roscoff (48° 43. 556′ N, 4° 01.415′ W). It is a dense, sheltered boulder field with some coarse interstitial sediment, situated 2.5 m below chart datum. During autumn 2010, *Laminaria hyperborea* densities were measured within 0.25 m^2 3-sided quadrats (60 replicates), for 3 stipe-length classes: 0−10 cm, 10−40 cm, >40 cm. Densities were estimated at 16.9 ± 11.4 ind. m^{-2} (±SD), largely dominated by adults (stipe >40 cm, 13.1 ± 6.6 ind. m^{-2}).

Trophic structure of the community

Sampling was performed by SCUBA divers in mid-November 2010, late March 2011, late June 2011 and mid-September 2011. At each sampling occasion, 5 *Laminaria hyperborea* adults were collected in 1 mm mesh bags (Christie et al. 2003). Few mobile species inhabit the lamina (Norton et al. 1977, Christie et al. 2003); therefore, the stipe and its adjoining lamina were collected in the same bag, and the holdfast was collected separately. The surrounding substratum was sampled in 0.1 m^2 quadrats using an air pump connected to a 1 mm mesh collector (5 replicates).

In the laboratory, each bag was carefully rinsed with seawater over a 500 μm sieve. Bag contents were fixed in their entirety with a buffered formaldehyde solution (3%). Fauna and flora were sorted according to origin (stipe/lamina, holdfast or rock substratum), and their ash-free dry mass (AFDM) determined at the species level (Crisp 1984). AFDM was then converted into organic carbon mass according to the taxon considered (algal families and fauna sub-phyla) using the extensive data base compiled by Brey et al. (2010).

In order to analyse trophic structures, standing stocks (measured on 5 adult kelps and within 5 quadrats of 0.1m^2 at each sampling date) were standardised to square meter. According to kelp densities of the study site, a 'theoretical' square meter was composed of 13 average *Laminaria hyperborea* adults (representing 0.2 m^2 cover) and 8 average quadrats (for the remaining surface, 0.8 m^2). The particulate organic carbon (POC) concentration data were provided by the 'Service d'Observation en Milieu Littoral' (SOMLIT), INSU-CNRS, Roscoff Biological Station (SBR). These concentrations (μg l^{-1}) were converted to g m^{-2} given the homogenous mid-tide water column above the study site (7.5 m).

Sampling and preparation for stable isotope analyses

Stable isotope analyses were performed on additional samples collected in mid-November 2010 and in late March 2011. At each sampling occasion, 3 replicates of seawater (5 l) were collected with a Niskin bottle below the surface (1 m depth) to assess the suspended particulate organic matter (site POM). Sediment organic matter (SOM) was obtained by scraping the first cm of interstitial sediment into 200 ml containers (3 replicates). Large rocks (3 replicates with a volume of approximately 1 l) were collected to sample epilithic biofilms (rock organic matter, ROM). Additional kelp holdfasts (3 replicates) were also brought back to the laboratory to extract the associated organic matter (holdfast organic matter, HOM). SOM, ROM and HOM were considered as the components of the deposited POM pool (called deposited POM hereafter). Surface offshore (5 km offshore, Astan Station, 48° 46.666′ N, 3° 56.250′ W) and nearshore POM data (Estacade Station, 48° 43.933′ N, 3° 58.966′ W) were provided by 'SOMLIT'. These data were derived from measurements taken 3 times a month, approximately 30, 15 and 0 d before the sampling dates. Site, nearshore, and offshore POM were considered as the components of the suspended POM pool (suspended POM). Suspended and deposited POM pools were finally considered as the total particulate organic matter pool (called the OM pool hereafter). The most abundant macroalgae and consumer species were collected (1 mm mesh bags) from 3 stipe/lamina samples, 3 holdfasts, and from the surrounding substratum. Additional samplings were performed for zooplankton and large predator isotope analyses. At each sampling occasion, baited traps were left overnight at the study site and zooplankton tows (200 μm) were conducted for 10 min at approximately 1 m below the water surface.

In the laboratory, seawater samples (POM) were filtered on pre-combusted Whatman® GF/F filters (0.7 μm). Sediment samples were stirred in filtered seawater (0.20 μm) to suspend the SOM. Sampled large blocks were gently brushed using a smooth brush in filtered seawater (0.20 μm) to suspend ROM (Golléty et al. 2010). HOM was also brushed from within the holdfast base in filtered seawater (0.20 μm). Brushing was brief to minimise the release of extracellular polymeric substances (EPS) by the holdfast which could bias the isotope signature of the HOM. Suspensions of SOM, ROM and HOM were sieved separately on 63 μm and filtered on 0.7 μm

GF/F. Each filter was then briefly acidified (1 N HCl) to remove any carbonate, rinsed with distilled water and dried at 60°C for 48 h.

Macroalgae were sorted by species, washed, and stored in plastic bags at −30°C until preparation and analysis. *Laminaria hyperborea* samples were separated according to the different thallus parts, namely old lamina (distal part), young lamina (formed during winter), stipe (close to the meristematic zone), and EPS. EPS were extracted from stipe pieces cut longitudinally, which were placed above large glass containers and maintained for 1 h at ambient temperature. EPS samples were directly dried at 60°C (48 h) before grinding. Zooplankton samples were placed in a test tube from which light was excluded except for the top tenth of the tube. A cold light source was placed at the top, and copepods attracted by the light were sorted from the living material using a pipette and kept in 0.20 µm filtered seawater for 3 h to allow gut clearance (Feuchtmayr & Grey 2003). Macroconsumers were starved overnight in 0.20 µm filtered seawater to allow evacuation of their digestive contents. The samples were then stored in glass containers at −30°C until preparation and analysis.

Macroalgae pieces were scraped with a scalpel, rinsed with freshwater to remove any epiphytes and then briefly acidified (1 N HCl). Whenever possible, consumer isotopic analyses were conducted on muscle tissue to minimise isotope variability and to reflect integrative assimilation of sources by consumers (De Niro & Epstein 1978, 1981, Pinnegar & Polunin 1999). Most samples were prepared at the individual level. To obtain enough material for accurate stable isotope analyses, a few samples were pooled (Copepoda, Nematoda, *Odontosyllis ctenostoma*, *Rissoa parva*, *Barleeia unifasciata*, *Chauvetia brunnea*, *Janira maculosa*, and colonial taxa; Bryozoa and Ascidiacea). Each sample was then briefly acidified (1 N HCl), rinsed with distilled water and dried at 60°C for 48 h. Special treatments were performed for calcareous organisms (e.g. *Corallina*, *Amphipholis*) to avoid changes induced by longer acidifications (Mateo et al. 2008). $\delta^{13}C$ measurements were conducted on acidified samples, whereas $\delta^{15}N$ measures were conducted on untreated ones. Once dried, samples were crushed with a mortar and a pestle then put in tin capsules before mass-spectrometry analyses.

Carbon and nitrogen isotope ratios were determined using a Flash EA CN analyser coupled with a Finnigan Delta Plus mass spectrometer, via a Finnigan Con-Flo III interface. Data are expressed in the standard δ unit:

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

where X is the element in question, $R = {}^{13}C/{}^{12}C$ for carbon and ${}^{15}N/{}^{14}N$ for nitrogen. These abundances were calculated in relation to the certified reference materials Vienna Pee Dee Belemnite-limestone (V-PDB) and atmospheric dinitrogen (at-air). The V-PDB and at-air scales were obtained 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 laboratory standards was 0.10‰ versus V-PDB and 0.05‰ versus at-air, respectively.

Data analyses

The biomass of the dominant primary producers were compared among sampling dates using 1-way ANOVA to infer growth and loss throughout the year (Kain 1963, Lüning 1979, Whittick 1983, Breda & Foster 1985). When necessary, biomass data were log-transformed to achieve normality and homoscedasticity prior to analyses. ANOVAs were followed by Student-Newman-Keuls (SNK) post-hoc tests for comparisons of the mean biomass when appropriate. Temporal biomass variations of *Laminaria hyperborea* were considered separately for the whole individual and for the lamina alone. Red algae biomass was assessed among sampling dates according to their substratum (rock or kelp). Complementary analyses were conducted on the pooled biomasses of both annual and pseudo-perennial red algae species (Delesseriaceae, Kallymeniaceae, Cystocloniaceae, and Dumontiaceae); hereafter called senescent red algae.

Between November and March, isotope variations were analysed at different levels. Winter changes were interpreted from isotope differences between November and March at the species level. Changes in $\delta^{13}C$ and in $\delta^{15}N$ of consumers sampled at both time points were analysed using 1-tailed statistical tests. When the homoscedasticity condition was fulfilled (Fisher tests), species $\delta^{13}C$ and $\delta^{15}N$ means were compared using Student's *t*-test. Otherwise, a Wilcoxon-Mann-Whitney *U*-test was applied. The isotope temporal variability was also analysed at the trophic group level. These analyses were conducted on the entire data set which reflected the isotope distribution of the whole community according to sampling date. Mean $\delta^{13}C$ and $\delta^{15}N$ values for trophic groups were compared using Student's *t*-test or the Wilcoxon-Mann-Whitney *U*-test, depending on the homoscedasticity of the data.

In order to strengthen these analyses, Bayesian isotope mixing models (SIAR; Parnell et al. 2010) were used to infer the feasible contribution of the main primary sources to the diet of species sampled at both sampling dates. Average invertebrate (whole body) trophic enrichment factors (±SD) were considered for $\delta^{13}C$ and $\delta^{15}N$ values according to Caut et al. (2009). Different potential sources were tested according to trophic groups and sampling dates. Mixing models for particle-feeder (suspension- and deposit-feeder) species were run for 3 primary sources in November: kelp, senescent red algae, and suspended POM. In March, a period during which senescent red algae grow and are not expected to release organic matter (see Results), only kelp and suspended POM were studied. Kelp data were derived from measurements of old *Laminaria hyperborea* lamina (distal parts) while senescent red algae were represented by old tissues of Delesseriaceae species and *Callophyllis laciniata*. Although some species-specific isotope changes are expected to occur during degradation (e.g. Hill & McQuaid 2009), macroalgal detritus was assumed to have the same isotope composition and variability as old tissues (as shown for kelp $\delta^{13}C$; Stephenson et al. 1986). Site POM data were compiled with offshore and nearshore Roscoff POM 'SOMLIT' measurements to reflect the potential spatio-temporal variability of suspended POM (e.g. Cresson et al. 2012, Miller & Page 2012) in Roscoff coastal waters. Mixing models for grazer species were run, for both sampling dates, for 3 primary sources: kelp, senescent red algae and perennial red algae. Kelp data were derived from measurements of the overall *L. hyperborea* parts (except EPS successfully measured in March only), while perennial red algae were represented by *Palmaria palmata*, *Rhody-menia pseudopalmata* and *Corallina elongata*. Feasible contributions were discussed according to biomass data and isotope temporal covariations of sources and consumers to infer the dominant trophic pathways occurring in the kelp forest and their potential temporal changes.

The freeware R statistical environment was used for all statistical (R Development Core Team 2012) and SIAR analyses (Parnell & Jackson 2011).

RESULTS

Trophic structure of the community

At the study site, biomass decreased with increasing trophic level at all sampling dates (Table 1).

Primary producers were dominated by *Laminaria hyperborea* kelp (from 95% C in November to 88% C in early June), which reached up to 1216.0 gC m^{-2} in June. *L. hyperborea* individuals with comparable stipe length (1-way ANOVA; $F_{3,16} = 3.23$, p = 0.05), displayed greater biomass in June and September compared to November and March ($F_{3,16} = 4.38$, p < 0.05, SNK: N = M < J = S). Lamina biomass (standardized by stipe biomass) decreased marginally from November to March (SNK: p = 0.056), period during which the old lamina decays and a new lamina grows actively ($F_{3,16} = 9.48$, p < 0.001, SNK: N = M < J < S), as confirmed by the temporal change in % ash ($F_{3,16} = 13.07$, p < 0.001, SNK: N > M = J < S). Red algae were the second largest primary producers in terms of biomass, ranging from 4.8% C in November to 10% C in March. Biomass of senescent red algae species (Delesseriaceae, Kallymeniaceae, Cystocloniaceae, and Dumontiaceae) was on average 6.2, 26.7, 42.7 and

Table 1. Standing crop (gC m^{-2}) ranges (mean value) of primary sources and consumers in the *Laminaria hyperborea* forest based on densities per m^2 (13 adults + 0.80 m^2 of rocky substratum). For each sampling date, carbon mass was obtained from the conversion of ash-free dry mass (AFDM) data using the global data bank virtual handbook (Brey et al. 2010)

	November	March	June	September
Primary sources				
Laminaria hyperborea	366.1–901.9 (700.9)	367.9–651.9 (525.3)	630.6–1215.9 (934.7)	592.2–1201.5 (930.2)
Phaeophyceae – brown algae (others)	0.1–4.2 (1.3)	0.0–20.0 (9.2)	0.4–87.3 (18.6)	0.1–2.0 (1.0)
Rhodophyta – red algae	5.9–62.2 (35.2)	23.0–109.6 (53.7)	73.7–155.0 (106.6)	29.7–126.4 (74.9)
Chlorophyta – green algae	0.0–0.2 (0.2)	0.0–0.2 (0.1)	0.0–0.9 (0.3)	0.0–0.1 (0.1)
Particulate organic carbon (POC)	0.9–1.8 (1.4)	0.7–1.2 (0.9)	1.3–1.5 (1.4)	1.2–1.8 (1.4)
Consumers				
Predators	2.5–11.3 (7.1)	0.4–4.1 (1.5)	1.3–3.2 (2.2)	0.6–3.7 (1.8)
Deposit-feeders	0.8–1.6 (1.1)	0.5–1.9 (1.2)	0.8–2.2 (1.5)	1.0–1.8 (1.3)
Suspension-feeders	3.8–29.8 (18.4)	3.5–13.0 (7.9)	8.5–24.0 (15.2)	6.8–17.7 (10.5)
Grazers	0.4–4.2 (1.8)	0.1–2.6 (1.0)	1.1–5.3 (2.3)	0.6–3.7 (2.3)

35.5 gC m^{-2} in November, March, June and September, respectively. The lowest richness in red algae species was encountered in November (35 species) compared to the other sampling dates (54 to 57 species). Among red algae, biomass was dominated by epiphytic species represented mostly by *Palmaria palmata* (6.3 to 46.5%), *Rhodymenia pseudopalmata* (11.4 to 23.2%) and many Delesseriaceae species (14.4 to 26.7%). Total biomass of epiphytic red algae was significantly lower in November and March than in June and September ($F_{3,16}$ = 3.61, p < 0.05, SNK: N = M < J = S). The same pattern was observed for epiphytic senescent red algal species ($F_{3,16}$ = 5.66, p < 0.01, SNK: N = M < J = S). The dominant epilithic algal species were *Callophyllis laciniata* (1.5 to 8.2%), *Phyllophora crispa* (2.8 to 6.3%), and *Corallina elongata* (1.2 to 3.0%). Epilithic red algae increased in biomass from November to June and was stable between June and September ($F_{3,16}$ = 7.37, p < 0.01, SNK: N < M < J = S). In this group, the lowest biomass of senescent red algae was observed in November

and increased 14 fold until June-September ($F_{3,16}$ = 16.97, p < 0.001, SNK: N < M < J = S).

Compared to macroalgae, POM only accounted for 0.1 to 0.2% C of the standing stock at each sampling dates.

Suspension-feeders dominated consumer biomass (64.6 to 71.7%) and were represented by 93 to 104 taxa according to sampling dates. Deposit-feeders (48 to 58 taxa) and grazers (19 to 25 taxa) represented only 3.9 to 10.0% and 6.3 to 14.5% of consumer biomass, respectively. Predators (46 to 76 taxa) accounted for 10.2 to 25% of the biomass. Consumer biomass was highest in November (28.5 gC m^{-2}) and lowest in March samples (11.2 gC m^{-2}).

Temporal changes in source isotope compositions

Primary sources were mostly discriminated by their $\delta^{13}C$ values (Table 2) with depleted values for red algae (−38.0 to −15.5‰) compared to brown algae

Table 2. $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) ranges, and C:N ratios (±SD) of the main primary sources in the *Laminaria hyperborea* forest, according to their habitat (Hab): water column (W), rock substratum (R), holdfast (H), stipe (S) and lamina (L)

Organic matter source	Hab		November				March		
		n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ± SD	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ± SD
SOM	R	3	−21.0 to −20.3	5.4 to 5.9		3	−19.8 to −19.3	6.5 to 6.6	
ROM	R	3	−20.3 to −18.9	6.5 to 8.0		3	−19.5 to −18.9	7.6 to 7.8	
HOM	H	3	−18.9 to −18.8	7.8 to 8.2		3	−18.3 to −18.0	8.8 to 8.9	
POM (surface)	W	3	−22.2 to −21.4	7.1 to 7.2		3	−21.8 to −21.0	4.0 to 5.2	
POM (bottom)	W	3	−21.2 to −21.0	7.4 to 8.5					
POM (nearshore)	W	3	−22.0 to −20.8	5.9 to 6.7	7.5 ± 0.6	3	−22.9 to −22.1	6.5 to 7.0	6.5 ± 0.3
POM (offshore)	W	3	−22.4 to −21.4	7.0 to 9.0	4.7 ± 0.3	3	−24.0 to −22.9	5.5 to 7.4	6.6 ± 0.1
Brown algae									
Cystoseira sp.	R	5	−24.9 to −22.3	5.2 to 7.7	17.1 ± 0.9	3	−20.6 to −18.9	2.0 to 4.8	16.9 ± 0.8
Ectocarpus sp.	L					3	−14.0 to −13.5	2.9 to 3.2	
L. hyperborea Young lamina	R					5	−16.5 to −14.0	1.4 to 2.7	10.9 ± 0.6
L. hyperborea Old lamina	R	5	−17.0 to −16.2	4.8 to 5.8	18.2 ± 2.4	3	−16.3 to −15.6	4.4 to 5.7	13.9 ± 0.8
L. hyperborea Stipe	R	5	−18.2 to −16.1	4.5 to 5.6	24.0 ± 0.1	3	−18.2 to −17.1	4.4 to 5.1	20.9 ± 1.4
L. hyperborea EPS	R					3	−17.0 to −15.6	5.5 to 6.5	10.9 ± 2.6
L. hyperborea Juvenile	R					1	−18.6	2.2	12.1
Saccorhiza polyschides	R					3	−19.8 to −18.7	2.2 to 3.6	8.8 ± 0.2
Red algae									
Apoglossum ruscifolium	S	3	−32.1 to −31.8	6.0 to 6.7	7.4 ± 0.7				
Callophyllis laciniata	R	5	−34.6 to −33.7	6.2 to 6.5	7.3 ± 0.4	3	−35.7 to −35.1	5.0 to 5.6	6.4 ± 0.0
Corallina elongata	R	3	−21.5 to −20.7	6.0 to 6.2	9.6 ± 0.1	3	−23.3 to −23.0	3.2 to 4.2	10.6 ± 0.0
Cryptopleura ramosa	S	3	−34.5 to −33.7	6.1 to 6.6	7.4 ± 0.5				
Delesseria sanguinea	R					3	−35.1 to −35.0	5.1 to 5.6	6.9 ± 0.2
Dilsea carnosa	R					3	−23.7 to −22.4	4.9 to 5.6	10 ± 0.5
Palmaria palmata	S	5	−21.0 to −20.0	6.1 to 6.7	9.1 ± 0.6	5	−20.0 to −15.5	2.9 to 5.2	8.3 ± 0.3
Phycodrys rubens	S	5	−37.1 to −35.9	6.3 to 6.9	7.8 ± 0.6	5	−37.0 to −36.2	2.9 to 3.9	6.4 ± 0.2
Plocamium cartilagineum	R	3	−32.5 to −32.3	7.5 to 7.9	11.1 ± 0.7	3	−35.8 to −35.0	4.2 to 6.0	10.8 ± 0.6
Polysiphonia sp.	S	3	−30.3 to −30.1	5.3 to 5.7	8.4 ± 0.6				
Rhodymenia pseudopalmata	S	3	−34.7 to −34.6	7.5 to 7.6	7.3 ± 0.1	3	−38.0 to −37.1	5.6 to 6.3	7.8 ± 0.2
Green algae									
Cladophora sp.	L	3	−17.4 to −17.1	6.1 to 6.5	10.9 ± 1.2				
Ulva rigida	L	3	−18.7 to −18.2	3.2 to 4.7	9.9 ± 0.7	3	−17.9 to −16.9	4.3 to 4.4	9.1 ± 0.0

(−24.9 to −13.5‰), whereas the OM pool showed intermediate $\delta^{13}C$ values (Fig. 1). Within this OM pool, the deposited POM (−21.0 to −18.0‰) was distinguished from the suspended POM (−24.0 to −20.8‰). $\delta^{13}C$ values also distinguished between 2 distinct groups of red algae. The first group, composed of *Dilsea carnosa*, *Palmaria palmata* and *Corallina elongata*, displayed enriched $\delta^{13}C$ values (−23.7 to −15.5‰) compared to the other red algae. The second group (−38.0 to −30.1‰) was composed

of subtidal species such as several Delesseriaceae species, *Callophyllis laciniata*, *Plocamium cartilagineum*, *Rhodymenia pseudopalmata*, and *Polysiphonia* sp.

Between the November and March sampling dates, in the OM pool, the deposited POM and suspended POM pools showed contrasting variations in isotope signatures (Fig. 2). The suspended POM pool $\delta^{13}C$ decreased by 0.8‰ (Student's *t*-test, *t* = −1.99, p < 0.05) owing mostly to change in nearshore and offshore

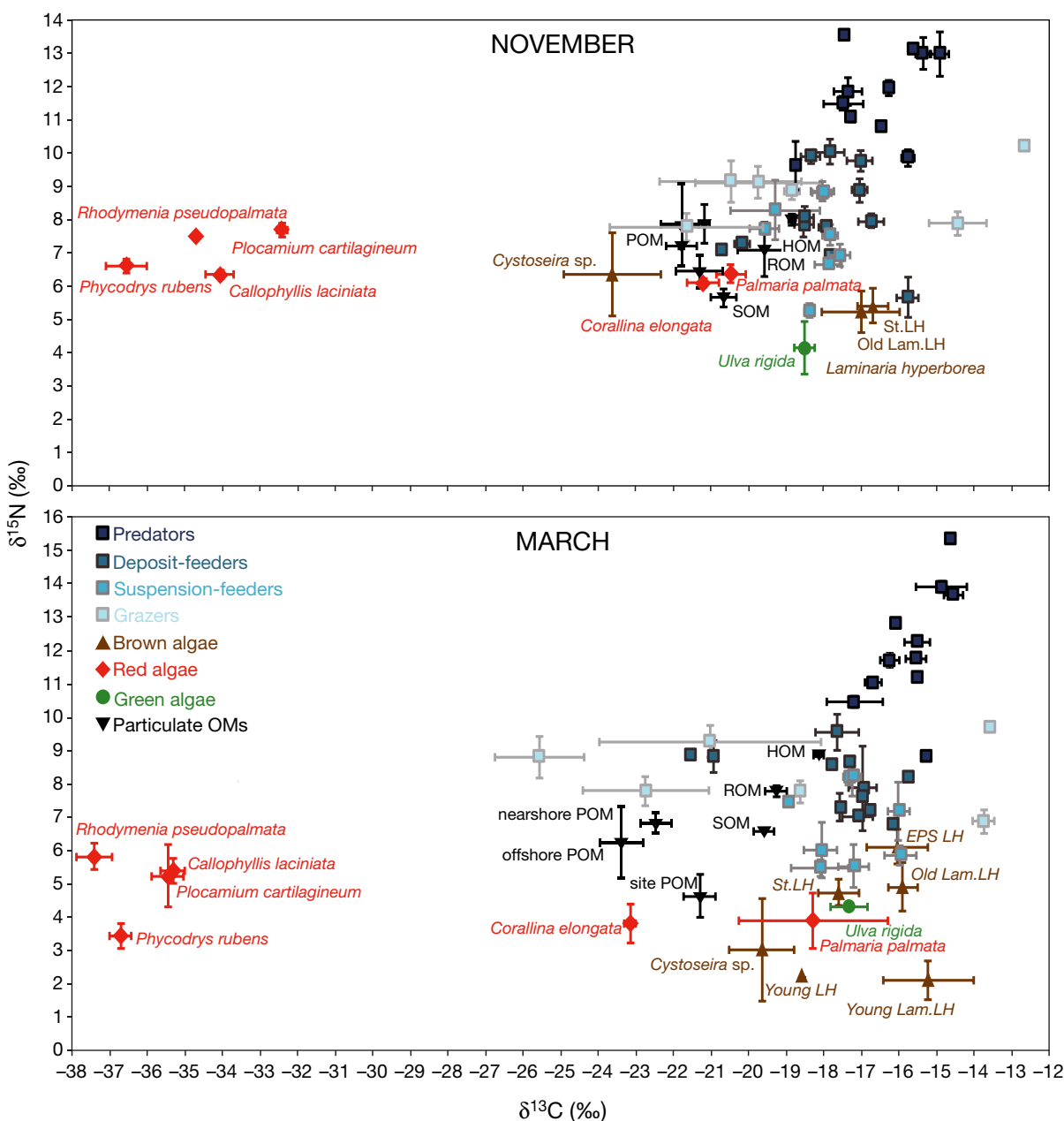Fig. 1. Mean $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values (±SD) of the main sources of organic matter (macroalgae and total particulate organic matter, OM, pool) and consumers (grazers, deposit-feeders, suspension-feeders and predators) within the *Laminaria hyperborea* forest in November 2010 and March 2011. Only species sampled on both dates are shown
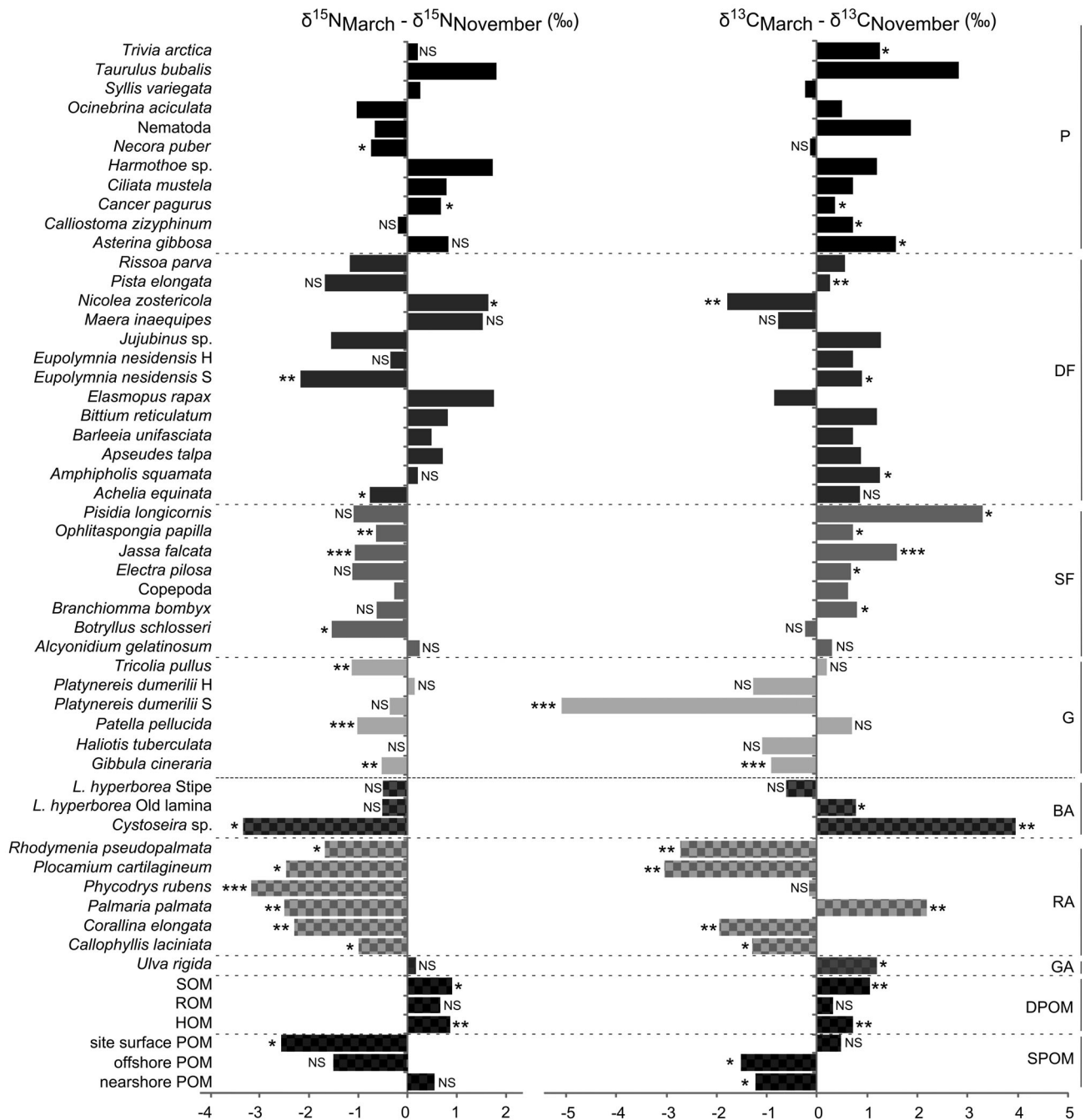
Fig. 2. Winter changes (March to November) in the mean δ^{13}C (‰) and δ^{15}N (‰) values of primary sources and consumers sampled on both dates. Trophic groups: predators (P), deposit-feeders (DF), suspension-feeders (SF), grazers (G), brown algae (BA), red algae (RA), green algae (GA) and particulate organic matter pool (DPOM, SPOM). Significance of mean difference is indicated: ***p < 0.001, **p < 0.01, *p < 0.05, NS = p > 0.05, as determined from Student or Mann-Whitney tests, according to the homoscedasticity of the data

POM. For suspended POM, δ^{15}N decreased by 1.2‰ (t = 2.52, p < 0.05), which can be attributed to site depletion (3‰). Conversely, deposited POM δ^{15}N and δ^{13}C means did not significantly differ between the 2 sampling dates (Mann-Withney test, U = 36, p = 0.12)

but SOM and HOM showed significant enrichment in both δ^{15}N and δ^{13}C (1‰). For brown algae, δ^{13}C values did not increase significantly (U = 76, p = 0.12). However, at the species level (Fig. 2), *Cystoseira* sp. and old blades of *Laminaria hyperborea* became

more ^{13}C-enriched. A depletion in ^{15}N was observed between November and March ($t = -4.47$, $p < 0.001$), which can be attributed to *Cystoseira* sp. (Fig. 2). Red algae were more ^{15}N-depleted in March compared to November ($U = 32$, $p < 0.001$). This trend was also observed at the species level (Fig. 2). The overall red algal $\delta^{13}C$ values did not vary between sampling dates ($t = 0.14$, $p = 0.89$) due to large species-specific variation. Significant depletions in [13]C (1 to 3‰) were, however, observed for *Corallina elongata*, *Callophyllis laciniata*, *Plocamium cartilagineum* and *Phycodrys rubens*. In contrast, *Palmaria palmata* became ^{13}C-enriched during winter.

Temporal changes in consumer isotopic compositions

Most consumer $\delta^{13}C$ values were close to the OM pool and kelp values in November and in March (Fig. 1). Grazer species were particularly distinctive with regards to their $\delta^{13}C$ values (-31.2 to $-13.4‰$; Table 3), whereas suspension-feeders (-19.9 to $-14.9‰$) and deposit-feeders displayed intermediate ranges (-21.5 to $10.7‰$).

Neither the $\delta^{13}C$ nor the $\delta^{15}N$ values of grazers varied significantly between sampling dates (Student t-tests, $p > 0.33$). However, at the species level (Fig. 2), significant depletions in ^{13}C were observed for *Platynereis dumerilii* living on stipes and for *Gibbula cineraria*. These 2 species and *Tricolia pullus* also displayed ^{15}N depletion. Suspension-feeders displayed lower $\delta^{15}N$ values in March than in November ($t = -2.26$, $p < 0.05$) and their $\delta^{13}C$ values significantly increased during winter ($U = 572$, $p < 0.001$). These patterns were also highlighted at the species level (Fig. 2). [15]N depletion was significant for *Botryllus schlosseri*, *Jassa falcata*, and *Ophlitaspongia papilla* and ^{13}C enrichment was significant for these species and also for *Pisidia longicornis* and *Branchiomma bombyx*. For the overall deposit-feeder group, the $\delta^{15}N$ values did not change during winter ($U = 889$, $p = 0.83$) due to contrasting species-specific variations. For instance, among terebellids, *Eupolymnia nesidensis* living on the stipe was more ^{15}N-depleted in March than in November, whereas *Nicolea zostericola* was more enriched. Deposit-feeder $\delta^{13}C$ values significantly increased ($t = 1.98$, $p < 0.05$) during winter. This trend was significant for the terebellids *E. nesidensis* (stipe) and *Pista elongata,* and contrasted with *Nicolea zostericola* $\delta^{13}C$ values, which decreased. Predators became ^{13}C-enriched ($t = 4.90$, $p < 0.001$) and ^{15}N-enriched ($U = 661$, $p < 0.05$) during winter. Similar [13]C

enrichments were found for *Calliostoma zizyphinum*, *Trivia arctica*, *Cancer pagurus* and *Asterina gibbosa*. Only *C. pagurus* became significantly ^{15}N-enriched between November and March and a significant ^{15}N depletion was observed for *Necora puber*.

Temporal changes in the species' diets

Although the range of feasible contributions to the diet of suspension-feeder species was wide for each potential source (particularly for species with n < 5, Table 4) and reflected a substantial uncertainty, these sources can be ranked, and temporal change in their utilisation can be inferred with regard to 1st percentile, 99th percentile and mean, simultaneously. According to mixing models and among the 3 primary sources considered (i.e. suspended POM, red algae and kelp), the feasible contribution estimated for *Laminaria hyperborea* (Table 4) suggested that kelp was the main trophic resource for the overall suspension-feeders on both sampling dates (11.1 to 99.4%). Between November and March, the feasible contribution of kelp consistently increased (with regards to 1st percentile, 99th percentile and mean) for all suspension-feeders, except *Alcyonidium gelatinosum*. This increasing contribution of kelp between sampling dates was minimal for *Electra pilosa* (by 3.5 to 9.6%) and maximal for *Pisidia longicornis* (9.8 to 20.3%). Organic matter derived from senescent red algae appeared to represent a significant part of suspension-feeder diets in November (0.0 to 49.6%). Suspended POM was the second main food source for the overall suspension-feeder species (0.7 to 81.2%). Between November and March, suspended POM decreased in the contribution to *Jassa falcata* diet (by 0.1 to 8.6%), whereas its contribution slightly increased in the diet of the other suspension-feeder species (by 1.3 to 10%), except *Pisidia longicornis*.

The feasible contribution of kelp, among the other potential sources, suggested that *Laminaria hyperborea* was the main trophic resource for most deposit-feeder species (Table 4). Red algae contributed significantly to the diet of deposit-feeders in November, and suspended POM was their second main food sources on both sampling dates. Between November and March, the contribution of kelp increased consistently in the diet of *Eupolymnia nesidensis* living either on stipe or within holdfast (by 2.9 to 16.5%) and in the diet of *Amphipholis squamata* (by 1.1 to 8.2%). For the other species, the contribution of kelp did not change between sampling dates, whereas the contribution of suspended POM increased by 0.9 to 24.8%.

Table 3. δ^{13}C (‰), δ^{15}N (‰) ranges of the main consumers in the *Laminaria hyperborea* forest, according to their habitat (Hab): water column (W), rock (R), holdfast (H), and stipe (S); and to their trophic group (TG): predators (P), deposit-feeders (DF), suspension-feeders (SF) and grazers (G)

Consumer taxon	TG	November				March			
		Hab	n	δ^{13}C (‰)	δ^{15}N (‰)	Hab	n	δ^{13}C (‰)	δ^{15}N (‰)
Porifera									
Amphilectus fucorum	SF					H	3	−18.5 to −18.4	5.1 to 5.7
Haliclona simulans	SF	H	3	−18.0 to −17.8	7.1 to 7.3				
Halichondria panicea	SF	R	3	−18.2 to −17.9	9.3 to 9.9				
Ophlitaspongia papilla	SF	S	5	−18.3 to −17.8	8.6 to 9.0	S	3	−17.4 to −17.3	7.9 to 8.4
Phorbas plumosus	SF					S	3	−17.9 to −17.6	7.2 to 7.9
Bryozoa									
Alcyonidium gelatinosum	SF	S	3	−18.5 to −18.2	5.0 to 5.5	S	3	−18.8 to −17.3	5.2 to 5.7
Crisia denticulata	SF	S	3	−18.2 to −18.0	5.7 to 5.9				
Electra pilosa	SF	S	3	−18.1 to −17.4	6.6 to 6.7	S	2	−17.5 to −16.9	5.1 to 6.0
Nematoda									
Nematoda species	P	H	3	−17.7 to −17.0	11.4 to 12.3	H	1	−15.5	11.2
		S	1	−18.2	10.5				
Nemertea									
Lineus longissimus	P					H	1	−17.4 to −17.4	13.2 to 13.2
Annelida									
Amphiglena mediterranea	SF	S	3	−18.3 to −18.0	6.4 to 7.0				
Branchiomma bombyx	SF	H	3	−18.2 to −17.7	8.5 to 9.1	H	3	−17.3 to −16.9	7.6 to 8.8
Eupolymnia nesidensis	DF	S	5	−18.3 to −17.3	9.7 to 10.7	S	5	−17.4 to −16.4	6.5 to 9.3
		H	5	−18.6 to −18.0	9.7 to 10.1	H	5	−18.5 to −16.9	8.9 to 10.2
Nicolea zostericola	DF		3	−15.9 to −15.4	5.2 to 6.4	R	3	−17.6 to −17.4	6.8 to 7.7
Nicolea venustula	DF						3	−16.9 to −16.3	8.9 to 9.0
Pista elongata	DF		3	−17.2 to −16.8	8.5 to 9.1	R	1	−16.8	7.2
						S	3	−17.7 to −17.1	7.7 to 9.8
Platynereis dumerilii	G	S	5	−23.3 to −18.4	8.9 to 9.7	S	5	−26.9 to −23.8	8.3 to 9.5
		H	5	−22.5 to −18.0	8.6 to 9.4	H	5	−24.1 to −17.1	8.7 to 10.0
Odontosyllis ctenostoma	P	H	3	−16.9 to −16.6	11.5 to 12.2				
Syllis variegata	P	S	1	−16.5	10.8	S	3	−16.9 to −16.5	10.9 to 11.2
Syllis columbretensis	P					S	1	−16.2	9.9
Trypanosyllis zebra	P					S	2	−17.8 to −15.9	11.3 to 11.6
Harmothoe sp.	P	H	3	−17.3 to −17.2	10.9 to 11.2	H	1	−16.1 to −16.1	12.8 to 12.8
Mollusca									
Acanthochiton crinita	P	H	3	−16.9 to −16.3	11.9 to 12.1				
Barleeia unifasciata	DF	R	3	−18.7 to −18.2	7.7 to 8.4	R	1	−17.8	8.6
Bittium reticulatum	DF	H	3	−18.7 to −18.2	7.6 to 8.2	H	1	−17.3	8.7
Calliostoma zizyphinum	P	R	3	−16.3 to −16.2	11.8 to 12.1	R	2	−15.7 to −15.3	11.7 to 11.8
Chauvetia brunnea	DF	H	3	−17.2 to −16.8	9.3 to 9.7				
Gibbula cineraria	G		3	−12.7 to −12.6	10.1 to 10.3	S	3	−13.6 to −13.5	9.6 to 9.8
Haliotis tuberculata	G	R	8	−26.3 to −19.8	6.9 to 8.5	R	5	−25.6 to −21.3	7.4 to 8.5
Jujubinus sp.	DF	H	3	−17.3 to −16.6	9.4 to 10.0	H	1	−15.7 to −15.7	8.2 to 8.2
Lacuna parva	G	R	6	−31.2 to −19.3	6.5 to 9.0				
Rissoa parva	DF	H	5	−16.9 to −16.2	7.5 to 8.0				
		R	5	−17.1 to −16.3	7.7 to 8.2	R	1	−16.1	6.8
Tricolia pullus	G	R	3	−19.0 to −18.6	8.7 to 9.2	R	3	−18.6 to −18.5	7.5 to 8.3
		S	1	−16.7	11.9				
Trivia arctica	P	R	3	−18.1 to −17.0	11.3 to 11.6	R	3	−16.5 to −17.0	11.5 to 11.9
Ocinebrina aciculata	P	H	3	−15.9 to −15.6	9.6 to 10.1	R	1	−15.3	8.8
Ocenebra erinaceus	P					R	1	−17.3	9.9
Patella pellucida	G	S	5	−15.3 to −13.5	7.7 to 8.3	S	5	−14.2 to −13.4	6.5 to 7.2
Anomia ephippium	SF					S	3	−17.5 to −16.6	6.0 to 7.3
Hiatella arctica	SF					H	2	−18.5 to −18.3	6.3 to 6.5
Musculus subpictus	SF	H	5	−18.7 to −18.2	6.3 to 7.4	R	1	−18.8	4.7
Arthropoda									
Copepoda species	SF	SW	3	−19.8 to −19.1	7.6 to 7.8	SW	1	−18.9	7.5
Dynamene magnitorata	G	R	3	−13.6 to −13.1	3.9 to 6.2				

Table 3 (continued)

Consumer taxon	TG	November				March			
		Hab	n	δ^{13}C (‰)	δ^{15}N (‰)	Hab	n	δ^{13}C (‰)	δ^{15}N (‰)
Gnathia dentata	P					S	1	−12.5	11.1
Janira maculosa	DF	H	3	−17.8 to −17.4	9.7 to 10.1				
Apseudes talpa	DF	H	3	−17.8 to −17.7	6.8 to 7.1	H	1	−16.9	7.6
Aora spinicornis	DF	S	3	−21.7 to −21.5	5.5 to 6.3				
Apherusa bispinosa	DF					S	1	−17.4	5.3
Elasmopus rapax	DF	R	3	−22.1 to −19.7	4.3 to 6.5				
		H	1	−20.7	7.1	H	1	−21.5	8.8
Gammaropsis maculata	G					S	1	−23.6	6.2
						H	1	−21.4	6.7
Jassa falcata	SF	S	5	−18.0 to −17.2	6.6 to 7.3	S	5	−16.4 to −15.5	5.6 to 6.2
Leucothoe spinicarpa	DF	S	3	−17.9 to −17.2	8.2 to 8.5				
Lysianassa ceratina	P	R	3	−19.1 to −19.1	10.1 to 10.3				
Maera inaequipes	DF	H	3	−20.4 to −20.0	7.2 to 7.5	H	2	−21.0 to −20.8	8.5 to 9.2
Cancer pagurus	P	R	5	−15.2 to −14.6	12.2 to 13.6	R	5	−14.9 to −14.3	13.6 to 13.8
Eualus occultus	P	H	3	−17.6 to −17.3	11.3 to 12.8				
Homarus gammarus	P					R	1	−16.2	14.4
Necora puber	P	R	3	−15.6 to −15.2	12.5 to 13.5	R	3	−15.8 to −15.1	12.2 to 12.3
Pilumnus hirtellus	P	H	3	−18.0 to −17.5	9.9 to 10.4				
Pisidia longicornis	SF	H	3	−2.4 to −18.4	7.5 to 9.3	H	3	−16.3 to −15.6	6.5 to 8.2
Porcellana platycheles	SF					H	1	−14.9 to −14.9	7.4 to 7.4
Achelia echinata	DF	S	3	−18.1 to −17.8	7.8 to 7.8	S	2	−17.4 to −16.8	6.9 to 7.1
Echinodermata									
Amphipholis squamata	DF	S	3	−16.0 to −15.7	7.4 to 7.6	S	3	−15.2 to −14.1	7.5 to 8.1
Antedon bifida	SF	R	3	−18.2 to −17.7	7.8 to 8.5				
Asterina gibbosa	P	S	3	−18.8 to −18.7	8.9 to 10.3	S	3	−17.7 to −16.7	10.3 to 10.6
	P	R	5	−18.5 to −18.2	9.8 to 10.1				
Chordata									
Botryllus schlosseri	SF	S	3	−18.1 to −17.6	7.3 to 7.9	S	3	−18.4 to −17.6	5.2 to 6.8
Didemnum maculosum	SF	H	3	−19.9 to −18.7	4.4 to 6.7				
Polyclinum aurantium	SF					R	2	−19.2 to −18.5	7.0 to 7.2
Ciliata mustela	P	R	1	−15.6	13.1	R	3	−15.3 to −14.1	13.8 to 14.1
Conger conger	P					R	1	−14.4	16.4
Parablennius gattorugine	P					R	1	−16.3	14.5
Taurulus bubalis	P	R	1	−17.4	13.6	R	1	−14.6	15.4

According to the mixing models, which reflected both direct and indirect consumptions, kelp was the main trophic resource for grazer species (Table 5) during the sampling dates. Between November and March, kelp contribution to the diet of *Platynereis dumerilii* and *Haliotis tuberculata* decreased, while contribution of senescent red algae increased. This trend was particularly evident for individuals of *P. dumerilii* living on the stipe, whose consumption of senescent red algae increased by 13.0 to 24.2%.

DISCUSSION

Organic matter sources of the kelp forest

The dominant primary producer *Laminaria hyperborea* was ^{13}C-enriched compared to other primary sources. Isotope analyses on kelp have suggested that they become enriched in heavy isotopes with age. Fredriksen (2003) described a similar pattern in Norway for both δ^{13}C and δ^{15}N. In the present study, only one juvenile kelp individual (both ^{13}C- and ^{15}N-depleted compared to adults) was measured in spring. In addition, we observed ^{15}N enrichment between young and old blades while δ^{13}C values remained similar. There are reports that the latter is highly variable among individuals, and even within a single blade (Stephenson et al. 1984, Dunton & Schell 1987). For a given macroalgal species, the isotope signature can be affected by many factors such as depth, light partitioning, and nutrient availability (Foley & Koch 2010, Hepburn et al. 2011). Although active tidal hydrodynamics most likely prevent nutrient limitation in the Roscoff area (Wafar et al. 1983), light levels may have influenced the isotopic signal because high variation in light is expected particularly in kelp forest strata (Norton et al. 1977).

Table 4. Range (expressed as 1st to 99th percentiles) of feasible contributions (mean, %) of the dominant organic matter sources according to SIAR mixing models: kelp, senescent red algae (Sen-RA) and suspended POM (SPOM) to the diet of particle-feeder species (deposit- and suspension-feeders) sampled in both November and March

Date		Kelps	Sen-RA	S-POM
Deposit-feeders				
Eupolymnia nesidensis H	November	26.3–86.2 (56.6)	0.1–18.1 (4.7)	4.1–69.7 (38.7)
n = 5	March	32.9–89.1 (60.3)		10.9–67.1 (39.7)
Eupolymnia nesidensis S	November	25.7–89.8 (60.1)	0.1–19.4 (4.3)	2.8–68.4 (35.5)
n = 5	March	42.2–95.4 (69.2)		4.5–57.8 (30.7)
Nicolea zostericola	November	5.8–97.1 (60.6)	0.1–59.8 (13.9)	0.4–74.5 (25.5)
n = 3	March	23.9–94.9 (61.1)		5.1–76.1 (38.9)
Amphipholis squamata	November	7.5–96.0 (56.9)	0.1–58.4 (14.8)	0.7–73.8 (28.3)
n = 3	March	16.2–97.1 (65.1)		0.6–83.7 (28.4)
Maera inaequipes	November	14.4–81.7 (50.7)	0.6–41.3 (13.4)	1.6–77.4 (35.9)
n = 2 or 3 (see Table 3)	March	1.8–92.6 (39.3)		7.3–98.1 (60.7)
Achelia echinata	November	13.8–90.9 (58.3)	0.1–47.6 (10.0)	1.3–69.6 (31.6)
n = 2 or 3 (see Table 3)	March	9.3–97.7 (60.4)		2.2–90.7 (39.6)
Suspension-feeders				
Jassa falcata	November	42.6–94.6 (73.1)	0.1–17.1 (4.7)	0.7–54.2 (22.2)
n = 5	March	54.3–99.4 (82.6)		0.6–45.6 (17.3)
Pisidia longicornis	November	12.0–89.3 (51.5)	2.9–47.1 (12.0)	1.7–76.3 (36.5)
n = 3	March	23.2–99.0 (71.8)		1.0–76.8 (28.2)
Ophlitaspongia papilla	November	11.1–89.3 (54.8)	0.1–49.4 (10.6)	1.7–72.4 (34.6)
n = 3	March	23.3–95.2 (61.7)		4.8–76.7 (38.3)
Branchiomma bombyx	November	10.6–89.6 (54.8)	0.1–49.6 (10.6)	2.0–72.5 (34.6)
n = 3	March	24.0–95.3 (62.4)		4.6–76.0 (37.6)
Alcyonidium gelatinosum	November	15.2–92.2 (60.0)	0.1–44.4 (9.0)	0.9–73.1 (31.0)
n = 3	March	18.8–95.4 (58.9)		4.6–81.2 (41.1)
Electra pilosa	November	15.9–93.5 (63.3)	0.1–46.3 (8.3)	0.8–68.4 (28.0)
n = 3	March	25.5–97.8 (66.8)		2.2–74.5 (33.2)

Table 5. Range (expressed as 1st to 99th percentiles) of feasible contributions (mean, %) of the dominant organic matter sources according to SIAR mixing models: kelp, senescent red algae (Sen-RA) and perennial red algae (Per-RA) to the diet of grazer species sampled in both November and March

Grazers	Date	Kelp	Sen-RA	Per-RA
Platynereis dumerilii S	November	19.7–80.8 (53.3)	0.6–41.1 (15.2)	1.5–65.9 (31.5)
n = 5	March	9.1–57.5 (39.7)	13.6–54.9 (39.4)	0.5–60.6 (20.9)
Platynereis dumerilii H	November	21.4–84.8 (57.5)	0.4–38.8 (12.5)	1.2–64.5 (29.9)
n = 5	March	8.8–94.7 (43.7)	0.5–45.6 (17.3)	1.0–75.7 (31.2)
Haliotis tuberculata	November	33.3–74.2 (56.6)	2.4–34.4 (18.9)	1.3–53.9 (25.4)
n = 5 or 8 (see Table 3)	March	13.4–70.2 (47.0)	3.1–45.4 (25.8)	1.0–64.3 (27.1)
Gibbula cineraria	November	1.5–88.3 (37.2)	0.5–71.2 (27.1)	1.2–81.3 (35.7)
n = 3	March	1.7–94.7 (43.7)	0.3–69.6 (22.4)	0.8–84.0 (33.3)
Tricolia pullus	November	7.1–89.4 (53.2)	0.4–56.2 (16.6)	0.9–71.9 (30.2)
n = 3	March	4.8–89.6 (52.4)	0.4–57.5 (17.3)	0.9–74.5 (30.3)
Patella pellucida	November	0.0–100.0		
n = 5	March	0.0–100.0		

Senescent red algae associated with the kelp forest appeared to decay in November until new growth commenced before March and continued to June-September. Although our sampling regime does not provide conclusive evidence, these patterns may represent seasonal variation as reported for *Laminaria hyperborea* epiphytes in Scotland (Whittick 1983). Epiphytic senescent red algae persist as vegetative stages in November (especially Delesseriaceae species such as *Phycodrys rubens*), and this persistence may explain why their increase from November to March was not significant (SNK; p = 0.06). Recruitment and regeneration in this group are, however, expected to occur during winter (Whittick 1983, Breda & Foster 1985). The biomass of senescent epiphytic red algae reached values 4 fold higher in June

and September than in November. The biomass of many epilithic species also greatly increased from November to June, particularly *Delesseria sanguinea*, *Callophyllis laciniata*, *Calliblepharis ciliata* and *Dilsea carnosa*. Over the year, pseudo-perennial and annual red algae associated with the kelp forest are thus expected to grow and multiply from winter to summer until senescence in autumn (Breda & Foster 1985). Furthermore, the ^{13}C and ^{15}N depletions observed in red algae in March compared to November suggest that heavy isotopes are stored during the growth of new algal tissue found between the newly formed and old fronds (Raven et al. 2002).

Contribution of kelp to its associated food web may vary seasonally due to the erosion rate (Krumhansl & Scheibling 2011), exudation (Abdullah & Fredriksen 2004), and fragmentation processes. During winter, *Laminaria hyperborea* regrows a new blade, which extends from the meristematic zone near the stipe until the old blade is shed (Kain 1963, Lüning 1979). This decaying blade may quickly become palatable to consumers via bacterial processes. Bacterial communities display higher cell densities (by a factor of 10^5 to 10^6) on non-growing compared to newly formed blades (Bengtsson et al. 2010). Aerobic bacterial degradation is expected to induce an increase in *L. hyperborea* nitrogen content and a decrease in phlorotannins (Moen et al. 1997, Norderhaug et al. 2003, 2006). Similar bacterial blooms occurring during kelp (*Ecklonia maxima* and *Laminaria pallida*) fragmentation lead to a succession of flagellates and ciliates (Linley et al. 1981, Stuart et al. 1981) which may also supply the benthic food web. In the present study, *L. hyperborea* lamina biomass (12.4 to 48.9 gC) was estimated at 161.5 to 636.2 gC m^{-2} in November, indicating that 1300.0 to 4900.0 mgC m^{-2} d^{-1} is expected to be shed into the surrounding waters during kelp fragmentation in the winter. During the same period in the Roscoff area, phytoplankton productivity ranges from 1.0 to 25.0 mgC m^{-3} d^{-1} (Wafar et al. 1983). Considering the whole water column of the study site (7.5 m on average), the phytoplankton may thus have produced 7.5 to 187.5 mgC m^{-2} d^{-1}. Therefore, during winter, contribution of kelp primary carbon sources for consumers is likely to exceed that of phytoplankton at the study site and in adjacent areas.

Suspended POC may serve as a proxy for the whole OM pool in the well-mixed waters of the studied area, and represented only 0.2% of primary carbon. In the present study, we discriminated suspended POM from deposited POM pools by their contrasting isotope variation between the 2 studied sampling dates. Among the deposited POM pool,

HOM was the component the most enriched in both ^{13}C and ^{15}N, indicating to what extent holdfasts trap sediment organic matter and act as shelters for bacterial communities (Moore 1972, Schaal et al. 2012). In addition, owing to the complex communities associated with holdfasts, HOM is likely composed of primary sources, decaying fauna and faecal pellets (Moore 1972, Beviss-Challinor & Field 1982, Dixon & Moore 1997), that all have different ^{13}C and ^{15}N enrichment. In contrast, SOM was the most ^{13}C- and ^{15}N-depleted component of the deposited POM pool. The coarse sediment found among the boulders appeared to be relatively oxygenated and contained mostly sparse, small debris derived from macroalgae (J.-C. Leclerc pers. obs.). Among the deposited POM, both HOM and SOM became more ^{13}C-enriched ($\approx 1.0‰$) over winter, suggesting the dominance of kelp-derived organic matter — probably in greater quantities that derived from the associated red algae.

The suspended POM pool and kelp isotope signatures varied independently from one sampling date to the other. ^{13}C-enriched values observed in site POM may result from a greater contribution of kelp detritus in nearshore waters (Fredriksen 2003, Schaal et al. 2010) compared to the offshore waters (differences of 1.1‰ in November and 2.1‰ in March). However, the phytoplankton proportion of site POM may have higher $\delta^{13}C$ values than offshore POM independently of the presence of kelp beds (Miller & Page 2012, Miller et al. 2013). Between sampling dates and sites, chlorophyll *a* (chl *a*) concentrations were similar (≈ 0.6 µg l^{-1}; SOMLIT data) and corresponded to the usual non-diatom-bloom period in the Roscoff area (Sournia & Birrien 1995, Wafar et al. 2004) compared to 1.0 to 3.0 µg l^{-1} in diatom blooms, which occur from May to September (Sournia & Birrien 1995, Romari & Vaulot 2004). This does not exclude any change in phytoplankton composition (dominated by nano- and pico-plankton), affecting the POM isotope values (Sachs et al. 1999, Miller & Page 2012, Miller et al. 2013), among sites or sampling dates (Not et al. 2004, Romari & Vaulot 2004, Wafar et al. 2004).

Trophic structure and functioning of the kelp forest

Suspension-feeders became ^{13}C-enriched between November and March as demonstrated for some components of the deposited POM pool (SOM and HOM). Once re-suspended by currents and biotic process, this POM pool may be an important food

source for suspension-feeders (Dixon & Moore 1997, Schaal et al. 2012). As explained above, observations and temporal variation in isotopic signals suggest that organic matter derived from macroalgae and macrofauna contribute greatly in the deposited POM. This potential source has not been considered in the isotope mixing model conducted to estimate suspension-feeder diets. This choice aims to prevent redundancy in outputs and allow better resolved 2- or 3-primary source models (see Fry 2013 for review). In contrast, suspended POM and kelp isotope signals varied independently between sampling dates, during winter kelp fragmentation. Suspended POM isotope values may, therefore, reflect the variable phytoplankton communities (Miller et al. 2013, Leclerc et al. 2013) in the study area. According to the mixing models, suspended POM ranked second as the primary source in the diets of suspension-feeders during the sampling dates (1 to 81%) and its contribution to the diet may change differently between November and March according to the species analysed. These contrasting variations may reflect species-specific selectivity facing a change in the OM pool composition (including phytoplankton communities; Wafar et al. 1983, Not et al. 2004) between November and March, periods during which [chl *a*] was similar (SOMLIT). Kelp-derived organic matter exceeded the suspended POM in the feasible diet of associated suspension-feeder species (42 to 99% in *Jassa falcata* diet) during these periods and consistently increased between November and March for each species analysed (except *Alcyonidium gelatinosum*). This pattern was also suggested by the concomitant ^{13}C enrichment of kelp, deposited POM and suspension-feeder values. Kelp erosion occurs throughout the year and is responsible for continuous and highly variable release of particulate and dissolved organic matter (Krumhansl & Scheibling 2012). This phenomenon can compensate for phytoplankton sources during poorly productive periods and be enhanced by kelp fragmentation at the end of winter. Moreover, kelp exudation of DOM (mostly carbohydrates and phenols) is higher during the most productive period (spring to summer in Norway; Abdullah & Fredriksen 2004). The contribution of DOM via micro-heterotrophs to the suspension-feeder diet cannot be excluded and may vary seasonally (Lucas et al. 1981, Newell et al. 1982, Abdullah & Fredriksen 2004). In the present study, δ^{13}C values of *Laminaria hyperborea* EPS (−17.0 to −15.6‰, in the same range as adult thallus parts) suggest that this component may contribute partially to the food web. Moreover, EPS C:N was lower (10.9 ± 2.6) than of the

stipe (20.9 ± 1.4) or old lamina (13.9 ± 0.8) and showed higher δ^{15}N values (5.5 to 6.5‰). These results indicated bacterial activity that may increase kelp palatability (see Lucas et al. 1981). For example, kelp tissue incubated in sterile seawater for 10 d showed a significant decrease in the C:N ratio (from 10.5 to 5.4 for *Ecklonia maxima* and from 5.9 to 2.3 for *Laminaria pallida*). Finally, red algae biomass was lower in November due to the senescence of many species, as highlighted by the trophic structure (Table 1). During autumn, although some part of these algae may be directly consumed by grazers (e.g. *Lacuna parva*) (Ockelmann & Nielsen 1981, this study: Table 3), high amount of material is expected to be shed in the water column (Newell et al. 1982). A comparison of November (2010) and September (2011) senescent red algae standing stocks shows that a biomass loss of 3.5 to 89.0 gC m^{-2} can be expected during the early autumn (September to November), corresponding to 58.3 to 1448.3 mgC m^{-2} d^{-1}. This amount is comparable to phytoplankton productivity, ranging from 75.0 to 300.0 mgC m^{-2} d^{-1} during this period (Wafar et al. 1983). During autumn, organic matter derived from senescent red algae may represent a significant part of the suspension-feeder diets as suggested by the feasible contributions of this pool estimated for the November sampling date (0 to 50% depending on species). According to our observations and biomass analyses, organic matter derived from red algae is expected to be negligible in the OM pool during the winter regrowth and up until summer. Most of the red algae-derived material shed before November is probably partially exported, degraded and consumed before March and should not be considered as a potential source in March.

Both biomass and stable isotope analyses suggest that kelp-derived organic matter dominates the diet of suspension-feeders inhabiting this sheltered study site. Hydrodynamics are known to influence to what extent kelp contribute to the food web through organic matter exportation, retention (e.g. Schaal et al. 2009) and potential kelp dislodgment during winter storms. Although the latter was not observed during our survey, the present estimations cannot be extrapolated from one site to another in the Roscoff area. Temporal patterns described in this study also suggest that these estimations should be interpreted with regard to the sampling date. Particular caution is also needed due to the use of isotope values from macroalgal old tissue (in spite of detritus) in the mixing models (Hill & McQuaid 2009). Furthermore, suspension-feeder species could be identified by their

$\delta^{13}C$ and $\delta^{15}N$ values, which encompass high ranges (5.0 and 5.5‰, respectively) as observed in several studies (e.g. Nyssen et al. 2002). In addition to natural fractionation variability (Vanderklift & Ponsard 2003, Caut et al. 2009), these species may be able to differentiate among and select a mix of food sources within the whole OM pool (Levinton 1972, Nadon & Himmelman 2006, Schaal et al. 2010). For instance, sponges (^{15}N-enriched compared to other suspension-feeders) can retain small particles (<10 μm), such as bacteria, more efficiently (see Bell 2008 for review). Bayesian mixing models, by integrating the isotope variability of sources and the uncertainty in trophic enrichment factors, help to estimate the primary source utilisation by suspension-feeders but cannot determine such selectivity. This issue may partially explain the overlapping ranges among feasible contributions of potential sources to the diet of the different species analysed.

Most deposit-feeder species became ^{13}C-enriched between November and March. This result confirms that deposit-feeders rely on deposited organic matter mainly derived from macroalgae; the origin of this pool may vary through time, depending on the relative contributions of kelp versus red algae. According to the mixing models, kelp may represent the dominant part in the diet of deposit-feeder species during the sampling dates and senescent red algae contributed significantly in November. The suspended POM ranked second as the primary source in the deposit-feeder diets, indicating an important reliance on phytoplankton, which can result from flexible suspension-feeding activity and deposit-feeding on settled particles (Beviss-Challinor & Field 1982, Dixon & Moore 1997). Among deposit-feeders, species-specific variation in $\delta^{15}N$ appeared during winter (Fig. 2), likely resulting from different feeding strategies adopted within this complex trophic group (Levinton 1972). For instance, both terebellid annelids *Eupolymnia nesidensis* and *Nicolea zostericola* displayed marked intra and inter-seasonal differences in $\delta^{13}C$ and $\delta^{15}N$ values. According to the mixing models, *E. nesidensis* living either on stipe or holdfast increased their consumption of kelp while *N. zostericola* promoted their reliance on the suspended POM between November and March. These variations reflect the plasticity in feeding strategies of this annelid family, but caution is needed on associated estimations. Terebellid diets include diatoms, small invertebrates and DOM (Fauchald & Jumars 1979), and their selectivity within the OM pool can vary seasonally (Grémare 1988). Among deposit-feeder species, omnivory (including coprophagous behaviour) can be substan-

tial (Beviss-Challinor & Field 1982, Dixon & Moore 1997), and challenges inferences made using mixing models which cannot reflect the actual diversity of potential sources.

Grazing may vary over time due to growth and senescence processes highlighted by biomass analyses and according to grazer densities. According to the mixing models, kelp may represent the dominant part of the diet of grazer species during the sampling dates, but the distinction between direct and indirect consumptions is uncertain. Grazers can feed upon the deposited POM, on drift seaweeds, or be restricted to macroalgae external cells and to the biofilms that grow on macroalgae, including bacteria feeding on derived DOM. The latter behaviour is expected, for instance, for *Gibbula cineraria* (Steneck & Watling 1982) whose feasible diet was poorly resolved (Table 5). Unlike this species, the blue-rayed limpet *Patella pellucida* is a known direct kelp grazer living on kelp blades (Dauby et al. 1998, Fredriksen 2003, Schaal et al. 2010, Leblanc et al. 2011, Leclerc et al. 2013). The observation of over 560 individuals on 1 kelp lamina in November, and observed enriched $\delta^{13}C$ values confirmed these reports; therefore, kelp was considered as its exclusive potential source (Table 4). Among grazers, the annelid *Platynereis dumerilli* living either on the kelp stipe or within the holdfast showed similar isotope ratios in November. In November, a similar diet can thus be expected among individuals wherever they settle within the thin-walled tube; this diet most likely consists of a mix of diverse macroalgae and organic material selected from the OM pool (Rasmussen 1973, Fauchald & Jumars 1979, Bedford & Moore 1984) dominated by kelp debris, as the mixing models tend to confirm. In March, *P. dumerilli* individuals living on the stipe became significantly ^{13}C-depleted compared to November and compared to individuals inhabiting the holdfast. This depletion reflects an increasing grazing activity on newly formed epiphytic red algae, represented by the senescent class in the mixing models. This trend was less evident for individuals collected within holdfast and indicates intra-specific variability in microhabitat utilisation. The cryptic ormer *Haliotis tuberculata* (4 to 14 ind. 50 m^{-2} on the undersurface of boulders in late January 2013; Leclerc et al. unpubl. data), whose biomass has been underestimated by our sampling of the upper surface of boulders, showed a similar increase in grazing activity on senescent red algae in March. Depleted $\delta^{13}C$ values observed for many grazers in March (which could unfortunately not all be measured in November) suggested higher graz-

ing pressure during red algae growth (Cronin & Hay 1996). Given that senescent red algae should not contribute to the OM pool in March, ranges of feasible contribution of senescent red algae to the diet of these grazer species may reflect their actual direct consumption of newly formed red algae.

Predators may belong to at least 2 trophic levels according to their $\delta^{15}N$ range (4.7‰ in autumn), considering the average trophic enrichment factors for fish muscles and invertebrate whole body tissue (3.2 and 2.5‰, respectively, Sweeting et al. 2007, Caut et al. 2009). High $\delta^{15}N$ ranges and temporal variation observed in primary consumers and producers prevent realistic estimation of the trophic positions because several trophic scales probably overlap within the food web (Riera 1998). Likewise, predator $\delta^{13}C$ values were slightly enriched compared to the dominant primary consumers, suggesting that most of these species feed within the kelp forest they inhabit. This appears the case even for highly mobile fish (Norderhaug et al. 2005) such as *Taurulus bubalis* and *Ciliata mustela*. The significant increase in $\delta^{13}C$ in both the predator group and at the specific level during winter supports this hypothesis. For instance, *Calliostoma zizyphinum*, *Trivia arctica* and Nematoda, all thought to feed on encrusting suspension-feeders, were clearly more ^{13}C-enriched in March than in November. This trend was also significant for the edible crab *Cancer pagurus,* which forages on mobile fauna.

Our observations and trophic structure analyses of kelp forest in Brittany suggest that red algae contribute a high amount of the OM pool before November. Winter regrowth, particularly pronounced in epilithic red algae (Fig. 3), appears to induce changes in isotope composition and increased palatability. This change promoted their direct consumption in March, due to the trophic plasticity of some grazers. Conversely, direct grazing on kelp was higher in November when the blue-rayed limpet *Patella pellucida* was observed in high densities on old lamina before it was shed. During winter, the shedding of the old lamina appears to increase the kelp contribution to the OM pool, whereas red algae no longer contribute. The dominance of kelp in the suspension-feeder diets was enhanced in March compared to November, despite similar phytoplankton biomass. The same variability in reliance on kelp-derived organic matter within the deposited POM also applies to several highly selective deposit-feeder species. During winter, suspension-and deposit-feeders (that dominate primary consumer biomass) and predators became ^{13}C-enriched, providing clear evidence that predators

feed in the kelp forest that they inhabit. Finally, the present study demonstrated that macroalgal biomass, turn-over and life cycle should be considered when addressing the potential trophic pathways involved in kelp forests and adjacent areas.
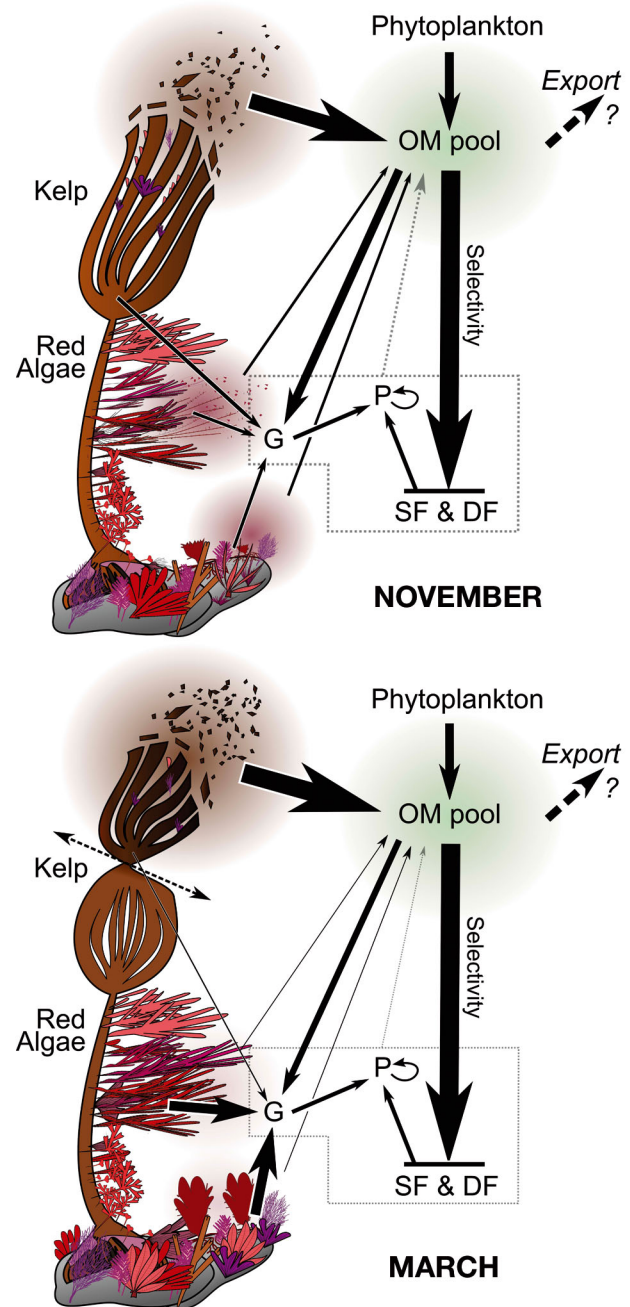

Fig. 3. Simplified main trophic transfers according to sampling date (November and March). Arrowhead widths represent hypothetical interaction intensities. A question mark indicates the export process for which the intensity is unknown. Dotted grey arrows represent consumer excretion: predators (P), deposit-feeders (DF), suspension-feeders (SF) and grazers (G)

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