Community, Trophic Structure and Functioning in two contrasting Laminaria hyperborea forests

Leclerc Jean-Charles [1, 2, *], Riera Pascal [1, 2], Laurans Martial [3], Leroux Cedric [1, 4], Lévêque Laurent [1, 4], Davoult Dominique [1, 2]

[1] Sorbonne Universités, UPMC Univ Paris 6, Station Biologique de Roscoff, Place Georges Teissier, 29680 Roscoff, France
[2] CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, Place Georges Teissier, 29680 Roscoff, France
[3] IFREMER, Laboratoire de Biologie Halieutique, Centre Bretagne, BP 70,29280 Plouzané, France
[4] CNRS, FR 2424, Station Biologique de Roscoff, Place Georges Teissier,29680 Roscoff, France

* Corresponding author : Jean-Charles Leclerc, email address : leclercjc@gmail.com

Abstract :

Worldwide kelp forests have been the focus of several studies concerning ecosystems dysfunction in the past decades. Multifactorial kelp threats have been described and include deforestation due to human impact, cascading effects and climate change. Here, we compared community and trophic structure in two contrasting kelp forests off the coasts of Brittany. One has been harvested five years before sampling and shelters abundant omnivorous predators, almost absent from the other, which has been treated as preserved from kelp harvest. δ15N analyses conducted on the overall communities were linked to the tropho-functional structure of different strata featuring these forests (stipe and holdfast of canopy kelp and rock). Our results yielded site-to-site differences of community and tropho-functional structures across kelp strata, particularly contrasting in terms of biomass on the understorey. Similarly, isotope analyses inferred the top trophic position of Marthasterias glacialis and Echinus esculentus which may be considered as strong interactors in the sub-canopy. We interrogate these patterns and propose a series of probable and testable alternative hypotheses to explain them. For instance, we propose that differences of trophic structure and functioning result from confounded effects of contrasting wave dissipation depending on kelp size-density structure and community cascading involving these omnivorous predators. Given the species diversity and complexity of food web highlighted in these habitats, we call for further comprehensive research about the overall strata and tropho-functional groups for conservation management in kelp forests.

Keywords : Laminaria hyperborea, Community cascade, Stable isotopes, Biomass, Suspension-feeders, Omnivorous predators

1. Introduction

Worldwide kelp forests harbour high biodiversity and host complex biological interactions, expected to promote their stability (see Steneck et al., 2002 and Filbee-Dexter and Scheibling, 2014 for reviews). In North-eastern Atlantic, kelp forests are dominated by

Laminaria hyperborea, a species distributed from Portugal to Northern Norway, at depths ranging from 0 to 30 m (Kain, 1971). In pristine areas, *Laminaria hyperborea* individuals can reach up to 3.5 m in length and can be considered as a habitat of their own composed of three stratified parts: the lamina, the stipe, and the holdfast. Among these strata, associated communities are particularly diverse and differently distributed (Moore, 1973; Schultze et al., 1990; Christie et al., 2003). Community structure and distribution of mobile fauna has often been linked to the structural complexity of kelp individuals (Jones, 1971; Moore, 1973) and epiphytic seaweeds (Norderhaug et al., 2002; Christie et al., 2007). Within epiphytes and holdfasts, environmental factors such as turbidity and wave exposure, interacting with the complexity of seaweed forming-habitat, can also influence mobile fauna distribution (Moore, 1973; Norderhaug et al., 2012; Norderhaug et al., 2014).While these strata have been investigated, understorey communities are still overlooked. The kelp canopy can provide favourable conditions for the development of functionally diverse seaweeds on the surrounding substratum (Norton et al., 1977), expected to shelter complex communities of sessile and mobile fauna.

Among the multiple threats of kelp (see Steneck et al., 2002 for review), sea urchin overgrazing can lead to alternative stable states of the ecosystem dominated by encrusting coralline algae and urchins, commonly named barrens as a consequence of an extensive habitat loss. In northern Europe, some *L. hyperborea* populations have been particularly studied in Norway, and overgrazing events were reported owing to the local abundance of the green sea urchin *Strongylocentrotus droebachiensis*, co-occurring with the edible sea urchin *Echinus esculentus* (Sivertsen, 1997). While *S. droebachiensis* feeds either on adult or young kelp, *E. esculentus* grazing seems mostly restricted to the understorey kelp recruits and other algae, and can exercise some control over *L. hyperborea* forests and associated communities (Jones and Kain, 1967; Sjøtun et al., 2006; Norderhaug and Christie, 2009). On the rocky shores of Brittany, below the southern distribution of *S. droebachiensis*, only a few grazers, including *E. esculentus*, are able to feed directly on kelp. This report has been suggested to favour their local persistence (Leblanc et al., 2011). Interestingly, *E. esculentus* has also been described as an omnivorous (i.e. feeding on several trophic level) and opportunistic predator (Allen, 1899; Forster, 1959; Comely and Ansell, 1988). Variable foraging behaviour such as omnivory can be of critical importance in strengthening food web interactions, including cascading effects (Emmerson and Yearsley, 2004; Bruno and O'Connor, 2005; O'Gorman and Emmerson, 2010). For instance, it has been proposed, on the base of modelled food webs, that a stable community should be favoured since omnivorous interactions are weak (Emmerson

and Yearsley, 2004). In complex coastal mesocosm communities, manipulating the abundance of strong interactors, such as predator echinoderms, has been shown to skew food web properties without any impact on species richness (O'Gorman and Emmerson, 2010).

In Brittany, *L. hyperborea* is harvested for almost two decades, given their quantity of alginic acid, valuable for stabilizing and suspending properties (Chapman and Chapman, 1980). The major part of kelp exploitation is localized within the 'Parc Naturel Marin d'Iroise' which was created in 2007 in order to reconcile the environmental management with the development of human activity, and actually differs from a sanctuary. Within the park, the net kelp trawling ranged officially between 2,000 and 12,300 tons per year during the last decade. With regards to previous studies dealing with kelp dynamics and rate of stipe production with age (Sjøtun et al., 1993; Sjøtun and Fredriksen, 1995), harvesting has been zoned on the basis of a five year-rotation system. Up to now, the lack of knowledge about the recovery of communities and food web associated with kelp forests indicates the need for further long-term researches, taking into account their overall components (Sivertsen, 1997; Christie et al., 1998; Waage-Nielsen et al., 2003; Lorentsen et al., 2010; Smale et al., 2013). An individual *L. hyperborea* may reach up about 20 years old and produce a new hapteron ring around its holdfast during each spring (Kain, 1963; Rinde and Sjøtun, 2005). From one year to another, this peripheral growth increases both the structural complexity and the size of the holdfast forming microhabitat, hence promoting the colonization and the diversity of associated assemblages (Jones, 1971; Christie et al., 1998). Studies of microhabitat complexity should also be improved considering the surrounding substratum, which is mainly overlooked in European kelp forests despite its value for local diversity (Waage-Nielsen et al., 2003). Given the heterogeneous topography and the local cover by functionally diverse and abundant organisms (Norton et al., 1977), the rock represents a complex biotope important in management.

The present study aimed to report biodiversity and trophic structure patterns associated with two *L. hyperborea* forests of contrasting conditions and histories. Though comparable overall kelp densities, one area has been moderately kelp-harvested for almost one decade, whereas the other has been, to our knowledge, preserved from exploitation. In parallel, the former has been consistently observed to shelter large echinoderms (sea-urchins and sea-stars) in important densities, nearly absent from the other. We investigated patterns in diversity and biomass distribution of macroalgae and macrofauna species across kelp forest strata, and understory megafauna densities between sites. These patterns are discussed according to biomass distribution of tropho-functional group and trophic level estimations in order to offer

alternative hypotheses to explain these stratum-dependent patterns and their potential implications in future kelp forest conservation management.

2. Material & Methods

2.1. Study sites

The study sites were located near Roscoff and within the Molène archipelago (Fig. 1) along the north-western coast of Brittany. These sites, separated by 70 km, are part of the same well-mixed (throughout the year) water mass at the English Channel entrance (Birrien et al., 1991). The Roscoff site (48°43.556N, 4°01.415W) is a dense, sheltered boulder field with some coarse interstitial sediment, lying upon a flat rocky reef, situated 1 km from the shore and 2.5 m below chart datum. The kelp forest (≈ 1 km²) is surrounded by mosaic habitats, represented by offshore infralittoral coarse sand/gravel flats, other kelp forests at comparable depth, few *Zostera* spp. beds on the infralittoral fringe, intertidal rocky reefs dominated by Fucales, and intertidal fine sand beaches (Joubin, 1909). Unlike in the Molène area, kelp harvesters started to trawl *L. hyperborea* in 2007, for an official net crop ranging between 300 and 3,300 tons per year up to now. From diver observations and information provided by local fishermen, the Roscoff study site was considered to be preserved from kelp-harvesting, but was frequently exploited for abalones and large decapods. During autumn 2010, *L. hyperborea* densities were measured on the site within 0.25 m² 3-sided quadrats ($n = 60$), for three size classes: 0-10 cm, 10-40 cm, > 40 cm. Densities were estimated at 16.9 ± 11.4 individuals m^{-2} ($\pm$ S.D.), largely dominated by adults from the canopy layer (Stipe > 40 cm, 13.1 ± 6.6 ind. m^{-2}). The Molène site (48°25.089N, 4°54.742W) is located within the 'Parc Naturel Marin d'Iroise'. This site is a boulder field with some coarse interstitial sediment, lying upon a flat rocky reef ('Helle' plateau), situated 3.5 km from the nearest shore (Molène Island) and 9.0 m below chart datum. The 'Helle' plateau (≈ 8 km²) is surrounded by circalittoral heterogeneous sand flats and infralittoral coarse biogenic gravel and heterogeneous sand beds (Raffin, 2003). According to fishermen (Ifremer data), *L. hyperborea* was not harvested at this site for five years before sampling. During March 2011, after winter recruitments, kelp densities were estimated within 1 m² quadrats ($n = 15$) at 18.1 ± 9.1 individuals m^{-2} ($\pm$ S.D.), dominated by medium individuals (Stipe 10-40 cm, 5.1 ± 2.5 ind. m^{-2}) and adults (6.9 ± 3.2 ind. m^{-2}). Although kelp density displayed site-to-site differences in the size-canopy structure, any causal link with kelp trawling cannot be established since initial condition and temporal variability within both sites remains unknown (Osenberg and Schmitt, 1996).

2.2. Community and trophic structure

Sampling was performed by scuba-divers in late March 2011 (early spring). At each sampling site, *L. hyperborea* adults (n = 5) were randomly collected in 1 mm mesh bags (Christie et al., 2003). A substantial part of the within-site variability in the biotic colonisation of kelp can be explained by age and size of kelp (Whittick, 1983; Anderson et al., 2005); therefore only adult kelp from the canopy layer were selected underwater by their total length (1-2 m) before further biometric analyses in the laboratory. Few mobile species inhabit the lamina (Norton et al., 1977; Christie et al., 2003); therefore 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 m² quadrats (n = 5) using an air pump connected to a 1 mm mesh collector.

In the laboratory, each bag was carefully rinsed with seawater over a 500 µm mesh 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) and their ash-free dry mass (AFDM) determined at the species level, except for pooled measurement of the Corallinale/*Peyssonelia* sp. encrusting complex (Kennelly, 1989). In addition to mass measurement of their different parts, adult kelps were processed for age, size and holdfast volume. Individual kelp were aged using the method of Kain (1963), ranging from 3 to 8 years without any difference between sites (Appendix A, t-test, $t = -0.717$, $P = 0.494$). While no difference was detected for stipe length (72-128 cm) and mass (21.5-67.7 gAFDM), the mean diameter (measured from 5 points per stipe) was slightly higher in Molène (2.8 ± 0.5 cm) than in Roscoff (2.3 ± 0.2, $t = -4.30$, $P = 0.003$) but difference in the calculated surface area was not significant ($P = 0.052$). Each holdfast was packed in a thin Ziploc bag and pushed in a transparent water jar, allowing to create a vacuum and to measure its total displacement volume. Holdfast interstitial volume (named 'ecospace' in Jones, 1971) was determined by the difference between total and hapteron displacement volumes, measured in a graduated tube once dissected throughout fauna sorting. Neither these volumes nor holdfast biomass differed significantly between sites ($P > 0.05$, Appendix A).

Additional random collection conducted for isotopic analyses (see below) and scuba-diving observations (≈ 5') provided wider qualitative information on communities and trophic structure in spring 2011. These observations were strengthened by a quantitative survey set up for winter 2013. It should be noted that Molène area was patchily trawled the next day after the spring 2011 sampling and may have influenced, by modifying the dissimilarity between

sites, the results of this additional survey. Megafauna (width > 5 cm) densities were estimated by three scuba-divers in Roscoff (late January) and in Molène (mid-February). Dominant species (large molluscs, crustaceans, echinoderms) were counted on the evident rock substratum and below 10 medium boulders (with a diameter of 50-100 cm) randomly turned over along three parallel 25 × 2 m transects (spaced by 3 m).

2.3. Sampling and preparation for stable isotope analyses

In late March 2011, at Roscoff and Molène sites, three replicates of seawater (5 L) were collected with a Niskin bottle below the surface (− 1 m) to assess the suspended particulate organic matter (POM). Sediment organic matter (SOM) was obtained by scraping the first cm of interstitial sediment into 200 mL containers (3 replicates). Small boulders (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 organic matter pool (called OM pool hereafter). The most abundant macroalgae and consumer species were collected (1 mm mesh bags) from three stipe/lamina samples, three holdfasts and from the surrounding substratum. Zooplankton tows (200 µm) were conducted for 10 minutes at approximately 1 m below the water surface for copepod isotope analyses.

In the laboratory, seawater samples (POM) were filtered on pre-combusted Whatman ® GF/F filters (0.7 µm). Sediment samples were shaken in filtered seawater (0.20 µm) to suspend the SOM. Sampled rock boulders were gently brushed using a smooth brush in filtered seawater (0.20 µm) to suspend ROM. HOM was brushed from within the holdfast base using a similar smooth brush 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. Suspended SOM, ROM, and HOM were sieved separately on a 63 µm mesh and filtered on 0.7 µm GF/F filters. Although stable isotope analyses were focused on $\delta^{15}N$ for trophic level estimations in the present paper, some carbonate removal (identical procedures at both sites) was performed for $\delta^{13}C$ measurements which are presented elsewhere (Leclerc et al., 2013b). Each filter was then briefly acidified (HCL, 1 N), thoroughly 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. *L. hyperborea* samples were separated according to the different thallus parts, namely old lamina (distal part), young lamina (formed during winter), stipe

(close to the meristem) and EPS. EPS were extracted from stipe pieces cut longitudinally, disposed 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. Macro-consumers were starved overnight in 0.20 µm filtered seawater to allow evacuation of their digestive contents. 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 epiphytes and then briefly acidified (HCL, 1 N). Whenever possible, isotope analyses of consumers were conducted on muscle tissue to minimise isotope variability and to reflect integrative assimilation of sources by the consumers (e.g. Pinnegar and Polunin, 1999). Most samples were prepared at the individual level. To obtain sufficient material for accurate stable isotope analyses, a few samples containing several individuals of the same taxa were pooled (Copepoda, Nematoda, *Odontosyllis ctenostoma*, *Rissoa parva*, *Barleeia unifasciata*, *Janira maculosa*, and colonial taxa: Bryozoa and Ascidiacea). Each sample was then briefly acidified (HCL, 1 N), rinsed with distilled water, and dried at 60 °C for 48 h. In order to cope with changes induced by longer acidifications, $\delta^{15}N$ measurements were conducted on untreated samples for calcareous organisms (*Corallina*, *Sycon*, *Crisa, Didemnum, Marthasterias, Asterias and Amphipholis*). Once dried, samples were crushed with a mortar and a pestle then put in tin capsules before mass-spectrometry analyses.

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.

$$\delta^{15}N = [(^{15}N/^{14}N_{sample} / {}^{15}N/^{14}N_{reference}) - 1] \times 10^3$$

These abundances were calculated in relation to the certified reference material atmospheric dinitrogen (at-air). The at-air scale was obtained using in-house protein standards, calibrated against IAEA N3 reference material. The standard deviation of repeated measurements of $\delta^{15}N$ values of a laboratory standard was 0.05 ‰ versus at-air.

2.4. Data analyses

Community structures were analysed for macroalgae and macrofauna separately, according to habitat (stipe/lamina, holdfast and rock) and site (Roscoff, Molène), using

PRIMER 6 (Plymouth Routine in Multivariate Ecological Research) software. Previously, species AFDM were standardised by the total biomass per sample (i.e. biomass percentages). Prior analyses, one outlier sample (rock quadrat from Molène), containing one megafauna individual (*Marthasterias glacialis*, 82 % AFDM of the sample) have been excluded. Similarities among samples were estimated using the Bray-Curtis Similarity Index (Clarke and Warwick, 2001). Samples were ordinated using a non-metric Multidimensional Scaling (nMDS) and differences among sites and habitats (both fixed factors) were analysed using permutational multivariate analyses of variance (PERMANOVA, Anderson et al., 2008), allowing testing whether inter-group similarity is greater than within-group. Species biomass distributions between sites within each habitat were compared using pair-wise tests, depending on significant interactions between the two factors. Within each habitat group, PERMDISP routine revealed that the multivariate dispersion (around the centroid) of biomass distribution of seaweeds and fauna was homogeneous between sites ($P > 0.15$).

For each microhabitat, biomasses of large tropho-functional groups were compared between sites. For that purpose, different biomass standardisations were conducted, according to the microhabitat considered, except for rock samples (0.1 m^{-2}). Biomass of seaweed or consumer groups was standardised either by lamina, stipe or holdfast biomass. In order to characterize habitat features that may influence faunal distribution (Christie et al., 2007; Norderhaug et al., 2014), red, brown and green macroalgae (considered as trophic groups) were separated according to their morphology: crustose, smooth leaf-like (poorly branched), rough leaf-like (coarsely branched), bush-like (densely branched). Consumers were separated according to their major feeding mode: grazer, sessile suspension-feeder (including sessile bivalves), mobile suspension-feeder, deposit-feeder, mobile fauna- and sessile fauna-predators. When the homoscedasticity hypothesis was achieved (Fisher tests), the mean biomass of tropho-functional groups was compared between sites using one-tailed Student *t*-tests. Otherwise, a Wilcoxon-Mann-Whitney *U*-test was applied. Megafauna densities in transects (25 × 2 m, 3 replicates, winter 2013) were considered between Roscoff and Molène using one-tailed Wilcoxon-Mann-Witney *U*-test. For biomass and density site-to-site comparisons, tropho-functional groups of consumers and primary producers were all considered as independent entities owing to the lack of *a priori* knowledge on their interrelationships; therefore multiple site-to-site paired comparisons were chosen. Freeware R statistical environment was used for all these statistical analyses (R Development Core Team, 2012).

Isotopic analyses helped to estimate consumer trophic levels ($TL_{consumer}$) as follows:

$$TL_{consumer} = 2 + (\delta^{15}N_{consumer} - \delta^{15}N_{baseline}) / 2.5$$

where $\delta^{15}N_{baseline}$ corresponds to the mean $\delta^{15}N$ of strict primary consumers (TL = 2.0). Only the species sampled at both sites were used as baseline in order to strengthen TL site-to-site comparisons, regardless of the trophic enrichment factor (TEF) choice. The latter was chosen according to Caut et al. (2009) who reported a mean $\delta^{15}N$-TEF value of 2.5 ‰ for invertebrate whole body. With regard to the large variability of TEF within this group (Caut et al., 2009), the corresponding uncertainty in TL estimation was 0.9 (S.D.). Since $\delta^{15}N$ fractionation depends, among other factors, on the protein content of the mixed food source (Perga and Grey, 2010), considering this variability in estimations is essential when considering strong omnivory occurring in food webs. It should be noted that the TL was estimated from species mean $\delta^{15}N$; hence the intraspecific variability of TL was not taken into account in results.

3. Results

3.1. Community structure

Among the 65 macroalgal taxa identified across sites (Table 1, Appendix B), 9 were found on lamina, 34 on stipe, 43 on holdfast, 53 on the surrounding substratum. These taxa were differently distributed among microhabitats, within each site (Fig. 2A, Table 2A). The canopy (lamina and stipe) epiphytic relative composition did not differ between Roscoff and Molène (pair-wise tests), and was characterised on its own. On lamina, the seaweed species richness (Table 1) and tropho-functional group biomass (Fig. 3A) were similar between sites. Brown algae (on average 20 mgAFDM gAFDM$_{Lamina}^{-1}$) were largely dominated by the filamentous *Ectocarpus* sp. while red algae ($\approx$ 10 mgAFDM gAFDM$_{Lamina}^{-1}$) were dominated by the rough leaf like *Cryptopleura ramosa*. On stipe, biomass of epiphytic seaweeds was dominated (Fig. 3B) by smooth leaf-like (*Palmaria palmata* and *Rhodymenia pseudopalmata*) and rough leaf-like red algae (*Phycodrys rubens*, *Cryptopleura ramosa*). Although the biomasses of these two dominant groups and biomass distribution of the overall species were similar between sites, Roscoff stipes were represented by twofold higher species richness (Table 1) and higher biomass for crustose and bush-like red algae. On holdfast, the species richness did not differ (Table 1), whereas species relative abundances differed significantly between sites (Pair-wise test, Table 2A), as observed at the tropho-functional group level (Fig. 3C). Highly variable on holdfasts, red algae biomass did not differ significantly between sites, except for the crustose corresponding to Corallinale/*Peyssoniella* sp., absent in Molène and abundant in Roscoff). On the surrounding substratum (Table 1), obvious differences were highlighted between sites (Fig. 2A, Table 2A). In Molène, the biomass associated with the

rock substratum was dominated by smooth leaf-like brown algae (Fig. 3D), *i.e. Saccorhiza polyschides* and *Laminaria hyperborea* recruits. In Roscoff, red algae, distributed among diverse functional groups, dominated the biomass. Compared to Molène, greater biomasses were found for smooth leaf-like (e.g. *Dilsea carnosa* and *Callophyllis laciniata*), rough leaf-like (e.g. *Delesseria sanguinea*, *Phyllophora crispa*), and bushy red algae (e.g. *Corallina elongata* and *Heterosiphonia plumosa*).

Among the 279 macrofauna taxa identified on total across sites and habitats (Appendix C), 145 were found on stipe, 191 on and within holdfast and 204 on the rock. Irrespective of the strata analysed, the species richness of sessile fauna (Bivalvia included) was comparable between Roscoff and Molène (Table 1). Mobile fauna richness was comparable on kelp individuals between site, with numerical abundance of 151 to 407 individuals in Molène, and 92 to 360 in Roscoff. On the rocky substratum, mobile fauna species richness was significantly greater in Roscoff (Table 1) and represented by 145-398 ind. 0.1 m^{-2} against 40-97 ind. 0.1 m^{-2} in Molène. Each microhabitat was characterised by its own macrofauna species biomass distribution and differed between sites. (Fig. 2B, Table 2B). These species were largely dominated by sessile suspension-feeders which represented on average 53 to 99 % of the consumer biomass according to microhabitat and site (Fig. 4). On stipe + lamina (Fig. 4A), the biomass of sessile suspension-feeders in Molène (44 mgAFDM gAFDM$_{Stipe}^{-1}$) was double that in Roscoff (16), mainly due to species growing on the stipe itself. In Molène, this group was dominated by the ascidian *Distomus variolosus* (62 %), and the bryozoan *Celleporina calciformis* (12.8) whereas Roscoff stipes were mostly encrusted by the sponge *Ophlitaspongia papilla* and the bryozoan *Phaeostachys spinifera*. Higher grazer biomass was observed in Roscoff (4 mgAFDM gAFDM$_{Stipe}^{-1}$), mostly due to the gastropod *Gibbula cineraria* (67 %). Within holdfast, the macrofauna biomass (Fig. 4B) was higher in Roscoff, particularly for sessile suspension-feeders and deposit-feeders (e.g. *Rissoa parva*, *Eupolymnia nesidensis*). In Roscoff, sessile suspension-feeders were dominated by sponges (*Amphilectus fucorum*, *Myxilla incrustans*, *Ophlitaspongia papilla*, *Halisarca dujardini*) and didemnid ascidian (*Didemnum maculosum*). In Molène, this group was dominated by polyclinid ascidians (*Aplidium glabrum* and *Morchelium argus*) and the bryozoan *Celleporina calciformis*. Between sites, the rocky substratum largely contrasted in biomass distribution of either macrofauna species or trophic group (Table 2B, Fig. 4C). The Roscoff rocky substratum yielded substantial biomass of consumers compared to Molène, except for grazers and mobile fauna-predators (Fig. 4C). The biomass of sessile suspension-feeder was eight-fold higher in Roscoff (0.7 gAFDM 0.1m^{-2}) than in Molène, dominated by sponges as

Phorbas plumosum, *Amphilectus fucorum*, *Dysidea fragilis*, *Myxilla incrustans*, *Halichondria* sp., the ascidians *Polyclinum aurantium* and the bryozoan *Microporella ciliata*. The biomass of mobile suspension-feeders was six-fold higher in Roscoff (0.01 gAFDM 0.1 m^{-2}), and was dominated by the echinoderm *Antedon bifida*, and the sabellid *Branchomma bombyx*. Deposit-feeder biomass was three-fold higher (0.1 mgAFDM 0.1 m^{-2}) in Roscoff, mostly represented by terebellids such as *Pista elongata* or *Eupolymnia nesidensis*, echinoderms as *Amphipholis squamata*, and many gastropods such as *Bittium reticulatum*, *Barleeia unifasciata*, *Rissoa parva*. The biomass of sessile fauna-predators was treble in Roscoff (0.1 mgAFDM 0.1 m^{-2}) than in Molène, and was dominated by the echinoderm *Asterina gibbosa* and several gastropods (e.g. *Trivia arctica*) and annelids (e.g. *Haplosyllis spongicola*).

Megafauna species were differently distributed between sites (Fig. 5). In Roscoff, the rocky substratum and sub-boulders were dominated by grazing gastropods and predatory decapods, whereas in Molène, these habitats were dominated by echinoderms (mostly predators). The abalone *Haliotis tuberculata* was found in ten-fold greater density in Roscoff compared to Molène. Among crustaceans, the edible and swimming crabs *Cancer pagurus* and *Necora puber* were significantly more abundant in Roscoff, where large echinoderms were almost absent except for *Henricia sanguinolenta*. Important sea cucumber densities (*Cucumaria frondosa* and *Holothuria forskali*) were observed in Molène, significantly higher compared to Roscoff for *Holothuria forskali*. Predatory echinoderms displayed important densities in Molène, especially for *Echinus esculentus* (6.7 ± 3.2 ind. 50 m^{-2}) and *Marthasterias glacialis* (18.3 ± 8.4).

3.2. δ^{15}N of the main sources and consumers

Sources showed important δ^{15}N variations in both sites (Fig. 6). Brown algae δ^{15}N values ranged from 2.1 to 6.1 ‰ in Roscoff and from 1.2 to 8.1 ‰ in Molène, for *Laminaria hyperborea* young lamina and EPS respectively (Table 3). Red algae δ^{15}N ranged from 3.4 (*Phycodrys rubens*) to 5.8 ‰ (*Rhodymenia pseudopalmata*) in Roscoff and from 4.2 (*Callophyllis laciniata*) to 6.4 ‰ (*Delesseria sanguinea*) in Molène. The OM pool (POM, SOM, HOM, ROM) δ^{15}N ranged from 4.6 (POM) to 8.9 ‰ (HOM) in Roscoff and from 5.3 (HOM) to 6.7 ‰ (ROM) in Molène.

As for primary sources, primary consumers displayed large intra-group variability in δ^{15}N (Fig. 6, Table 3). This variability in the baseline (strict primary consumers) induced uncertainty in the trophic level estimation of consumers. Considering fifteen species, the δ^{15}N-baseline was 6.9 ± 1.3 (SD) in Roscoff and 6.7 ± 1.2 in Molène. For grazer group, the

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δ^{15}N values ranged from 6.4 (*Gammaropsis maculata*) to 9.7 ‰ (*Gibbula cineraria*) in Roscoff and from 6.5 (*Patella pellucida*) to 9.0 ‰ (*Gibbula cineraria*) in Molène. Among suspension-feeders, the δ^{15}N ranged from 4.7 (*Musculus subpictus*) to 8.2 ‰ (*Ophlitaspongia papilla*) in Roscoff and from 4.7 (*Alcyonidium gelatinosum*) to 7.6 ‰ (*Ophlitaspongia papilla*) in Molène. Among mobile suspension-feeder species, δ^{15}N ranged from 5.9 (*Jassa falcata*) to 8.2 ‰ (*Branchiomma bombyx*) in Roscoff and from 6.4 (*Branchiomma bombyx*) to 7.6 ‰ (*Jassa falcata*) in Molène. The δ^{15}N of deposit-feeders (including omnivores) ranged from 6.8 (*Rissoa parva*) to 8.8 ‰ (*Maera inaequipes,* TL = 2.8) in Roscoff and from 4.7 (*Apseudes talpa*) to 9.1 ‰ (*Leucothoe spinicarpa,* TL = 3.0). Sessile fauna-predator δ^{15}N ranged from 8.8 (*Ocinebrina aciculata*, TL = 2.8) to 11.8 ‰ (*Calliostoma zizyphinum*, TL = 4.0) in Roscoff and from 8.3 (*Odontosyllis ctenostoma*, TL = 2.6) to 11.7 ‰ (*Echinus esculentus*, TL = 4.0) in Molène. Mobile fauna-predator δ^{15}N ranged from 11.1 (*Gnathia dentata*, TL = 3.7) to 14.4 ‰ (*Homarus gammarus*, TL = 5.0) in Roscoff and from 10.9 (*Harmothoe impar*, TL = 2.6) to 11.9 ‰ (*Eualus occultus*, TL = 4.1) in Molène.

4. Discussion

4.1. Patterns of community, trophic structure and functioning

Overall, observed patterns in diversity and species distribution were dependent on the taxonomic/functional group (e.g. seaweed, macrofauna, megafauna), as well as on the stratum considered (lamina, stipe, holdfast of canopy plants and rock). Molène and Roscoff *Laminaria hyperborea* canopy plants (lamina, stipe) hosted similar macroalgal biomass distribution, represented by 37 species in total. In both sites, algal epiphytes were dominated by filamentous *Ectocarpus* sp. on lamina, smooth leaf-like *Palmaria palmata* on uppermost part of stipe, rough leaf-like *Phycodrys rubens* on the middle part, and smooth leaf-like *Rhodymenia pseudopalmata*, on the lower level of stipe and on holdfast. Across European kelp forests, *Palmaria palmata* occurs in shallow waters, its lower distribution being limited by light (Norton, 1968; Norton et al., 1977; Whittick, 1983; Castric-Fey, 1996), therefore its abundance as an epiphyte on the same part of stipe in both sites suggests that the irradiance reaching the canopy layer is somewhat comparable in spite of difference in depth (Whittick, 1983). Compared to their well-studied Norwegian counterparts, Brittany *Laminaria hyperborea* stipes were almost devoid of boreal bushy algae species such as *Rhodomela confervoides* and *Ptilota gunneri* (Christie et al., 2007). In lieu of [check if text missing] (see discussion in Whittick, 1983), in Brittany, the split leaf-like *Cryptopleura ramosa* was found either on the mid-level of stipe, on lamina or on holdfast. Despite similar macroalgae taxa and

morphologic group biomass distribution between sites, the macrofauna associated with the canopy significantly differed (see also Appendix C) but was mostly due to differences in sessile taxa growing on stipe itself. The absence of *Phaeostachys spinifera* on Molène stipes can be attributed to its southern limit of distribution in Roscoff, and may explain the development of competitive species such as *Distomus variolosus* and *Celleporina calcifo*rmis. The lower abundance of mobile fauna among abundant macroalgal epiphytes in Molène is more difficult to explain since most species are currently reported in European kelp forests (Jones, 1973; Norton et al., 1977; Schultze et al., 1990; Christie et al., 2003; 2014) and may result from patterns observed on the overall forest. While an important dissimilarity in species composition was found among strata, a substantial connectivity exists horizontally among kelp plants and vertically among strata for several mobile taxa (Norderhaug et al., 2002; Waage-Nielsen et al., 2003). The abundance of mobile fauna in kelp epiphytes may therefore interfere with habitat complexity on the understorey and kelp size-density structure (density of adults hosting abundant epiphytes), factors interacting with wave force dissipation (Eckman et al., 1989; Norderhaug et al., 2014). In Norway, Norderhaug et al. (2014) showed higher richness and abundance of mobile fauna associated to kelp epiphytes in intermediate wave-exposed sites. Although contrasting with our findings, this study was performed among sites displaying equivalent kelp densities in the canopy layer, therefore limiting any generalisation to heterogeneous kelp forests.

At the holdfast level, taxonomic and trophic structures differed between sites. Biomass of deposit- and suspension-feeders was higher in Roscoff, and could result from higher particulate organic matter retention (Jones, 1971; Edwards, 1980) in this more sheltered site. Disregarding local hydrodynamics, such retention can be due to contrasting canopy structures (size-density, Eckman et al., 1989) and structural complexity near the bottom. Despite similar interstitial volumes between sites, holdfast from Roscoff hosted important biomass of structurally diverse red algae. For instance, important encrusting by the Corallinale/*Peyssonelia* sp. complex forms a hard substratum and enhances habitat size for sessile fauna as sponges (e.g. *Amphilectus fucorum, Myxilla incrustans*) and ascidians (e.g. *Didemnum maculosum*), and for other red algae species (dominated by smooth and split leaf-like species). The seaweed structural complexity (Gee and Warwick, 1994), in addition to the active selective suspension-feeding of ascidians and sponges (Levinton, 1972; Bell, 2008) may favour holdfast organic matter retention (Moore, 1972; Dixon and Moore, 1997), hence amplifying site-to-site differences. Biomass of mobile fauna such as the dominant deposit feeders, *Rissoa parva* and *Eupolymnia nesidensis*, considered as 'Turbidity indifferent

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species' by Moore (1973) can benefit from habitat size/complexity and resource availability. Site-to-site differences in holdfast organic matter retention can also be suggested from isotope composition of HOM, more ^{15}N-enriched in Roscoff than the other sources of the OM pool, suggesting a higher bacterial activity (Thornton and McManus, 1994).

On the rocky substratum, taxonomic and functional composition contrasted between the two sites. The biomass of functionally diverse epilithic red algae was higher in Roscoff compared to Molène. Among the dominant red algae inhabiting Roscoff understorey, the bushy *Corallina elongata* and the smooth leaf-like *Dilsea carnosa* are generally restricted to shallow waters (Norton, 1968; Norton et al., 1977) and was not expected to be abundant in Molène. Conversely, the deep species (Norton, 1968) *Phyllophora crispa* and *Calliblepharis ciliata* represented 37 % of red algae biomass in Roscoff but were nearly absent in Molène. While epiphytic algal composition may be similar on canopy kelp in areas of contrasting histories (Christie et al., 1998), patterns in epilithic structure remain overlooked. Particularly abundant in Roscoff samples, the perennial species *Phyllophora crispa* has a rigid and rough leaf-like habit, favourable to host diverse red algae, sessile (sponges, bryozoans, ascidians) and mobile fauna, as already reported (Kostylev et al., 2010). *Phyllophora crispa* and associated epiphytes form a habitat quite comparable to adult kelp holdfasts in terms of complexity and OM retention (unpubl. obs.). Between sites, the rock habitat was thus profoundly different between sites in term of algal composition and resulting feature. Nearby the bare bottom in Molène, the large variability of brown algae biomass observed on holdfast and rock (Fig. 3C, D) suggests patchy and opportunistic winter settlement of the annual kelp *s.l. Saccorhiza polyschides* (Norton, 1978; Engelen et al., 2011) and *Laminaria hyperborea* recruits (Sjøtun et al., 2006).

4.2. Hypotheses about processes involved in observed patterns

While the present sampling framework does not allow a complete interpretation of the observed patterns, a series of probable and testable hypotheses can be formulated as thoughts for future research. Differences in habitat structure on the bottom (holdfast and surrounding substratum) between Molène and Roscoff may result from confounding physical and biotic effects. Kennelly (1989) found that subcanopy scouring by the small kelp *Ecklonia radiata* (C.Agardh) J.Agardh decreases as the stipe length increases. While *Laminaria hyperborea* adults have an erect and rigid stipe which reduces contacts between the blades and the bottom, young short-stiped forms are more flexible and could have a wider sweeping area and a more intensive scouring, as reported for kelp of comparable habit, e.g. *L. pallida* Greville

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(Velimirov and Griffiths, 1979) and *Pterygophora californica* (Reed and Foster, 1984). Consequently, kelp abrasion of understorey turfs (Irving and Connell, 2006) and sessile fauna (Connell, 2003) may be greater within a kelp forest dominated by young plants. Whether such effect occurs during the kelp growth, especially during the recovery of kelp-harvested areas, may be of interest for future research. As explained above, the epiphytic composition suggested that incident light was comparable on upper stratum. However, contrasting kelp size-density structure and turbidity may affect the light reaching the bottom. While adults dominated the Roscoff kelp forest (November 2010), kelp size classes were more evenly distributed in Molène (March 2011). While the negative shading effect of high kelp density on understorey algae is a well-known phenomenon (e.g. Norton et al., 1977; Reed and Foster, 1984; Wernberg et al., 2005), the effect of evenness in multi-layered kelp forests on these parameters remains, to our knowledge, unexplored. Since kelp are known to interfere with turbulence (e.g. Eckman et al., 1989), it would be worth exploring whether this turbulence vary with evenness in size and flexibility and, in turn with light resource partitioning (Middelboe et al., 2006). Nonetheless, the lower abundance of both sciaphilic and photophilic red algae, combined importance of *S. polyschides* in Molène on the rock indicates that additional factors are involved in these patterns. The lower red algae and sessile fauna cover on Molène subcanopy may also partially result from a cascading effect, which includes indirect and direct interactions involving large echinoderms. Although megafauna densities were measured two years after macrofauna sampling, these estimations reflected the survey observations and isotopic random collections, highlighting the rarity of large echinoderms at Roscoff and their commonness at Molène site. Often reported as a kelp grazer (Jones and Kain, 1967; Fredriksen, 2003), the edible sea urchin *Echinus esculentus* has also been described as a browsing opportunistic predator (Allen, 1899; Forster, 1959; Comely and Ansell, 1988). Within the Molène benthic community, *E. esculentus* exhibited one of the highest $\delta^{15}N$ (measured on Aristotle lantern), corresponding to a mean trophic level of 4.0 ($\pm$ 0.9 considering the variability in TEF for invertebrate whole body, Caut et al., 2009). This estimation is consistent with our observations of digestive contents conducted on individuals that have been sampled for stable isotope analyses. Guts contained some seaweed fragments but were dominated by sessile fauna (bivalves, cirripeds, sponges, bryozoans, and ascidians) and associated poorly mobile organisms (e.g. nematodes, TL = 3.9), of higher fitness interest compared to macroalgal based diet (e.g. Hughes et al., 2005; Vanderklift et al., 2006). Given the sea urchin densities in Molène, this omnivorous species may be partly responsible of the lower biomass of sessile fauna and seaweed. When *E. esculentus* has been described as an

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important kelp recruit grazer, its density exceeded 3-4 ind. m^{-2} (in summer, Jones and Kain, 1967; Sjøtun et al., 2006), substantially higher compared to Molène (0.1-0.2 ind. m^{-2} in winter). Hence, any density-dependant feeding behaviour of *E. esculentus* according to food availability should be of interest for future research. In the present study, a greater effect can be expected from the spiny sea-star *Marthasterias glacialis* (TL = 3.8) which shows greater density (0.3-0.6 ind. m^{-2} in winter). This voracious species feeds opportunistically either on macroalgae, sessile or mobile macrofauna, and can be considered as a key predator in communities of coastal rocky shores (Frid, 1992; Verling et al., 2003; Bonaviri et al., 2009; Tuya and Duarte, 2012). Furthermore, *M. glacialis* is one of the main predators of the abalone *Haliotis tuberculata* (Forster, 1962), poorly represented in Molène. While the spiny sea-star can influence the ormer distribution, other controls should be tested. *Haliotis* spp. require diverse seaweeds in their diet, including fresh red algae of the understorey (Guest et al., 2008; Leclerc et al., 2013a).

In European kelp forests, the dominant starfish predators are the edible and the swimming crabs: *Cancer pagurus* and *Necora puber* (Ramsay et al., 2000). In Roscoff, these species and the lobster *Hommarus gammarus* were the highest benthic predators according to their estimated trophic levels (4.2-5.0). Both *Cancer* spp. and *Necora* spp., more abundant in Roscoff, can forage significantly on large echinoderms and play a key role in their regulation (Freire and Gonzalez-Gurriaran, 1995; Ramsay et al., 2000; Steneck et al., 2004; Fagerli et al., 2014). However, given the absence of *E. esculentus* and *M. glacialis* in Roscoff, any contribution to the decapod diets cannot be inferred. Since these predators are not echinoderm specialists, it seems improbable that their densities are sufficient to control, even collapse, large echinoderm populations at Roscoff site (Miller, 1985; Sivertsen, 2006), but information about echinoderm recruitments and predation-rate on young stages (Fagerli et al., 2014) is lacking in the area. Multi-scale spatio-temporal variability of large echinoderms population can be altered, at different life history stages, by several crossed factors including the nature of the substratum (Laur et al., 1986; Hamel and Mercier, 1996; Balch and Scheibling, 2000), the depth (Reid, 1935; Jones and Kain, 1967; Comely and Ansell, 1988; Verling et al., 2003), the food availability (Laur et al., 1986; Tuya and Duarte, 2012), the predation pressure (Steneck et al., 2004; Estes et al., 2011), the temperature and epizootics (Scheibling and Stephenson, 1984). In the English Channel, the stochastic repartition of large echinoderm taxa has intrigued several authors for decades (Allen, 1899; de Beauchamp, 1914; Holme, 1966; Ellis and Rogers, 2000). For example, *Marthasterias glacialis* from shallow waters seems to

decrease in abundance from the West to the East, but to our knowledge, this issue remains unexplored.

4.3. Ecological and management implications

Omnivorous species can be of critical importance for stability and emergent ecosystem properties which strongly depend on the interaction strength (Emmerson and Yearsley, 2004; Bascompte et al., 2005). In the present study, adult *E. esculentus* and *M. glacialis* sampled in Molène were estimated to operate from the fourth trophic level, feeding upon a range of three trophic levels. While the diversity of interaction strengths linking these opportunist species to the associated community remains unclear, our results highlighted direct interactions that were concentrated upon the overall sessile suspension-feeder group. Owing to their large body-size and their energetic requirement (O'Gorman and Emmerson, 2010), these species may thus be considered as collectively strong interactors (sensu Berlow, 1999). Their collective effect may be of critical importance for the associated trophic structure and functioning, through community cascading effects, by reducing the morphological diversity toward the bottom, seemingly affecting habitat structure and organic matter retention. In addition to affecting habitat complexity, sessile suspension-feeders composition and abundance can have dramatic influence on ecosystem properties (Gili and Coma, 1998). In kelp forests, many suspension- and deposit-feeders (e.g. *Ophiothrix fragilis* and *Maera inaequipes* for ubiquitous examples) are able to select kelp-derived particles (including propagules) among the organic matter pool (e.g. Beviss-Challinor and Field, 1982), and one can wonder whether this function affect kelp recruitments and survival (Dayton, 1985). While experimental manipulations involving direct grazer provide substantial insights on cascading effects, manipulating particle-consumers faces to the difficulty of quantifying particulate basal resource in marine reproduction (O'Gorman and Emmerson, 2010) and limit understanding of their interactions with other species. In the present study, we found more abundant kelp recruits and reduced biomass of suspension-feeder and red algae simultaneously. If omnivorous predators are involved in the observed patterns, these results provides new insights about the sustainability of kelp primary production in Brittany, often attributed to the local rarity of direct kelp consumers (Arzel, 1998; Leblanc et al., 2011). However, *Echinus esculentus* and *Marthasterias glacialis* behave opportunistically, so comprehensive analyses of seasonal and density-dependant variations of their diet are required to state on this indirect interaction. Apart from contrasting structure and functioning nearby the bottom, our results highlighted that kelp canopy individuals are major refuges for the development of diverse and

abundant sessile organisms, in spite of contrasting size structure and kelp forest histories. Alternatively, these results are strong arguments in favour of further comprehensive analyses of the overall kelp forest strata, including the water column (e.g. Lorentsen et al., 2010) for conservative management and understanding of resilience in structure and functioning in kelp forests.

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Fig. 1 Location of the two study sites in the Molène archipelago and Roscoff, Brittany (France). Intertidal areas are in clear grey.

Fig. 2 Non-metric Multidimensional Scaling conducted from the Bray Curtis similarities among relative ash free dry mass (standardized by sample total) of macroalgae (A) and macrofauna (B) species in Roscoff (full symbols) and in Molène (empty symbols).

Fig. 3 Macroalgae biomass (AFDM ± SD) according to microhabitats (A: lamina, B: stipe, C: holdfast, D: rock) and sites (Roscoff: full bars, Molène: empty bars) in early spring 2011. Significance of mean difference is indicated: *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$), NS ($P > 0.05$), as determined Student or Mann-Whitney tests, according to the homoscedasticity of the data. GA: green algae, BA: brown algae, RA: red algae, Cr: crustose, SmL : smooth leaf-like, RoL: Rough leaf-like, Bu: bush-like.

Fig. 4 Trophic group biomass (AFDM ± SD) according to microhabitats (A: stipe + lamina, B: holdfast, C: rock) and sites (Roscoff: full bars, Molène: empty bars) in early spring 2011. Significance of mean difference is indicated: *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$), NS ($P > 0.05$), as determined Student or Mann-Whitney tests, according to the homoscedasticity of the data. G: grazers, SSF: sessile suspension-feeders, MSF: mobile suspension-feeders, DF: deposit-feeders, sf-P: sessile fauna-predators, mf-P: mobile fauna-predators.

Fig. 5 Megafauna densities (± SD) per transects (50 m²) measured on the rocky substratum and above 10 boulders in winter 2013 at Roscoff (full bars) and at Molène (empty bars) sites. Significance of mean difference is indicated: *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$), NS ($P > 0.05$), as determined Student or Mann-Whitney tests, according to the homoscedasticity of the data. Trophic groups (G: grazers, MSF: mobile suspension-feeders, DF: deposit-feeders, sf-P: sessile fauna-predators, mf-P: mobile fauna-predators) and Phyla (Moll: Mollusca, Crus: Crustacea, Echi: Echinodermata) are indicated above. *Hal*: *Haliotis tuberculata*, *Hen*: *Henrica sanguinolenta*, *Cuc*: *Cucumaria frondosa*, *Hol*: *Holothuria forskali*, *Mar*: *Marthasterias glacialis*, *Ech*: *Echinus esculentus*, *Ast*: *Asterias rubens*, *Lui*: *Luidia ciliaris*, *Can*: *Cancer pagurus*, *Maj*: *Maja squinado*, *Nec*: *Necora puber*, *Lop*: *Lophozozymus incisus*, *Gal*: *Galathea* spp.

Fig. 6 Individual $\delta^{15}N$ (‰) values of the main sources of organic matter and consumers according to their dominant trophic group (brown algae (BA), red algae (RA), deposited POM (DPOM), suspended POM (SPOM), grazers (G), sessile suspension-feeders (SSF), mobile suspension-feeders (MSF), deposit-feeders (DF), sessile fauna-predators (sf-P), mobile fauna-predator (mf-P) within Roscoff (full dots) and Molène (empty dots) *Laminaria hyperborea* forests in early spring 2011.

Table 1 Species richness (Mean ± S.D. [total]) of macroalgae, mobile fauna and sessile fauna, according to habitat and site. Mean richness were considered between seasons by two-tailed Student *t*-test depending on homoscedasticity of the data. Otherwise a Mann-Whitney *U*-test (marked $^{M.W.}$) was applied. Significant *P*-values are in bold.

Table 2 Results of PERMANOVA and pair-wise tests conducted from the Bray Curtis similarities of macroalgal (A, 65 species) and macrofauna (B, 279 species) species ash free dry mass (standardized by sample total). Site (Roscoff, Molène), Habitat (Lamina, Stipe, Holdfast, Rock), and their interaction were tested. Significant *P* (perm) are in bold.

Table 3 $\delta^{15}N$ (‰, ± SD) of the main primary sources and consumers of the *Laminaria hyperborea* forests in Roscoff and in Molène, according to their microhabitat (Hab) : stipe (S), holdfast (H), rock (R). Trophic groups (TG) are indicated for consumers: grazers (G), sessile suspension-feeders (SSF), mobile suspension-feeders (MSF), deposit-feeders (DF), sessile fauna-predators (sf-P), mobile fauna-predator (mf-P). Consumer trophic levels (TL ± 0.9 SD_{TEF}) were estimated according to the mean species $\delta^{15}N$, or set at the lowest threshold 2.0.

Electronic Supplementary Materials

Appendix A Morphometric parameters measured on kelp canopy individuals collected in Roscoff and in Molène. Parameters are compared between sites by Student *t*-tests according to the achievement of homoscedasticity hypothesis.

Appendix B Macroalgal species found at Roscoff and Molène sites during the survey (samples and observations). Relative occurrence is indicated: x: 1-10 % in samples, xx: 20-40 %, xxx 40-100% according to diversity sampling; °: species found in 1transect, °°: in 2 transects, °°°: in 3 transects during the megafauna survey.

Appendix C Animal species found at Roscoff and Molène sites during the survey (samples and observations). Relative occurrence is indicated: x: 1-10 % in samples, xx: 20-40 %, xxx 40-100% for diversity samples; °: species found in 1transect, °°: in 2 transects, °°°: in 3 transects during the megafauna survey.

	ROSCOFF				MOLENE				Two-tailed comparison (*P*-value)
Richness									
MACROALGAE (Total = 65)									
Lamina	4.6	±	1.5	[9]	3	±	0.8	[6]	0.104
Stipe	17.0	±	3.6	[31]	8.8	±	2.2	[14]	**0.004**
Holdfast	14.4	±	3.4	[33]	11.6	±	3.6	[26]	0.253
Rock	25.8	±	2.5	[42]	20.8	±	7.7	[37]	0.050
SESSILE FAUNA (Total = 99)									
Stipe	25.8	±	4.4	[41]	22.2	±	5.4	[39]	0.281
Holdfast	22.2	±	5.4	[54]	31.2	±	8.6	[52]	0.841[M.W.]
Rock	28.8	±	5.4	[57]	26	±	5	[55]	0.389
MOBILE FAUNA (Total = 180)									
Stipe	26.8	±	3.9	[55]	28.6	±	9.4	[65]	0.701
Holdfast	31.8	±	12.2	[77]	42	±	11.8	[93]	0.215
Rock	40.0	±	7.8	[94]	25.5	±	4.4	[72]	**0.007**
Density									
MOBILE FAUNA (Total = 4531)									
Kelp individual	184.2	±	109.3		244.6	±	102.9		0.394
Stipe	81.2	±	32.5		82.4	±	32.2		0.955
Holdfast	103.0	±	80.8		162.2	±	77.1		0.050
Rock	243.2	±	58.6		76.0	±	27.3		**<0.001**

A. Macroalgae Structure

Source	d.f.	Pseudo-F	P (perm)
Site	1	2.0577	**0.028**
Habitat	3	10.68	**<0.001**
Site × Habitat	3	1.835	**0.004**
Residual	32		
Total	39		

Pairwise tests between Sites
  within levels of Factor "Habitat"

Levels	t	P (perm)
Lamina	0.4479	0.751
Stipe	1.3542	0.199
Holdfast	1.2778	**0.049**
Rock	1.6934	**0.016**

B. Macrofauna Structure

Source	d.f.	Pseudo-F	P (perm)
Site	1	9.1935	**<0.001**
Habitat	2	10.219	**<0.001**
Site × Habitat	2	3.673	**<0.001**
Residual	23		
Total	28		

Pairwise tests between Sites
  within levels of Factor "Habitat"

Levels	t	P (perm)
Stipe	2.6752	**0.008**
Holdfast	2.1784	**0.007**
Rock	2.1859	**0.01**

	TG	Hab.	Roscoff δ¹⁵N ± SD	TL	n	Molène δ¹⁵N ± SD	TL	n
Sources								
Rhodophyceae								
Callophyllis laciniata		R	5.4 ± 0.4		3	4.2 ± 0.1		3
Corallina elongata		R	3.8 ± 0.6		3			
Delesseria sanguinea		R	5.3 ± 0.3		3	6.4 ± 0.3		3
Dilsea carnosa		R	5.3 ± 0.3		3			
Heterosiphonia plumosa		R				6.1 ± 0.3		
Palmaria palmata		S	3.9 ± 0.8		5	4.6 ± 0.2		5
Phycodrys rubens		S	3.4 ± 0.4		5	4.4 ± 0.3		5
Plocamium cartilagineum		R	5.2 ± 0.9		3			
Rhodymenia pseudopalmata		S	5.8 ± 0.4		3	5.7 ± 0.5		3
Phaeophyceae								
Cystoseira sp.		R	3 ± 1.5		3			
Ectocarpus sp.		S	3.1 ± 0.1		3	3.6 ± 0.4		3
Laminaria hyperborea Juvenile		R	2.2		1	3.2 ± 0.1		3
Laminaria hyeperborea Stipe		S	4.7 ± 0.4		3	5.4 ± 0.3		5
Laminaria hyperborea EPS		S	6.1 ± 0.5		3	8.1 ± 0.1		3
Laminaria hyperborea Old Lamina		S	4.9 ± 0.7		3	3.6 ± 0.4		6
Laminaria hyperborea Young Lamina		S	2.1 ± 0.6		5	1.2 ± 0.1		5
Saccorhiza polyschides		R	2.7 ± 0.7		3	2.8 ± 0.2		3
Ulvophyceae								
Ulva rigida		S	4.3 ± 0.1		3			
OM pool								
HOM		H	8.9 ± 0.1		3	5.3 ± 0.1		3
POM		W	4.6 ± 0.6		3	5.5 ± 0.3		3
ROM		R	7.8 ± 0.2		3	6.7 ± 0.6		3
SOM		R	6.5 ± 0.1		3	6.1 ± 0.1		3
Consumers								
Porifera								
Amphilectus fucorum	SSF	H	5.5 ± 0.3	2	3	6.7 ± 0.2	2	3
Halichondria panicea	SSF	R				6.7 ± 0.2	2	3
Ophlitaspongia papilla	SSF	S	8.2 ± 0.2	2.5	3	7.5 ± 0.2	2.3	5
Phorbas plumosum	SSF	S	7.6 ± 0.3	2.3	3			
Sycon ciliatum	SSF	S				5.4 ± 0.2	2	3
Nematoda								
Nematoda spp.	sf-P	S	11.2	3.7	1	11.4	3.9	1
Nemertea								
Lineus longissimus	P	H	13.2	4.5	1			
Annelida								
Branchiomma bombyx	MSF	H	8.2 ± 0.6	2.5	3	6.4 ± 0.4	2	3
Eupolymnia nesidensis	DF	S + H	8.7 ± 1.3	2.7	10			
Nicolea venustula	DF	H	8.3 ± 0.1	2.6	5	8.4 ± 0.2	2.7	3
Nicolea zostericola	DF	R	7.3 ± 0.4	2.2	3			
Pista elongata	DF	R	7.2	2.1	1			
Harmothoe impar	mf-P	H	12.8	4.4	1	10.9 ± 0.3	3.7	5
Leonnates glauca	sf-P	H				9.7 ± 0.2	3.2	3
Odontosyllis ctenostoma	sf-P	H				8.3 ± 0.3	2.6	5
Platynereis dumerilii	G	S + H	9 ± 0.6	2.8	10			
Syllis columbretensis	sf-P	S	9.9	3.2	1			

Species										
Syllis variegata	sf-P	H	11 ± 0.1	3.6	3		9.6		3.2	1
Trypanosyllis zebra	sf-P	S	11.5 ± 0.2	3.8	2					
Crustacea										
Copepoda spp.	MSF	W	7.5	2.2	1	7.1 ± 0.2			2.2	3
Gnathia dentata	mf-P	S	11.1	3.7	1					
Janira maculosa	DF	H					7.9		2.5	1
Apseudes talpa	DF	H	7.6	2.3	1		3.7		2	1
Elasmopus rapax	G	H	8.8	2.8	1	8.7 ± 0.4			2.8	3
Gammaropsis maculata	G	H	6.4 ± 0.3	2	3					
Hommarus gammarus	P	R	14.4	5	1					
Jassa falcata	MSF	S	5.9 ± 0.3	2	5	7.6 ± 0.3			2.4	5
Leucothoe spinicarpa	DF	R				9.1 ± 0.1			3	3
Maera inaequipes	DF	H	8.8 ± 0.5	2.8	3					
Eualus occultus	mf-P	R					11.9		4.1	1
Cancer pagurus	mf-P	R	13.7 ± 0.1	4.7	5		11.4		3.9	1
Galathea squamifera	DF	R				6.8 ± 0.3			2	3
Necora puber	mf-P	R	12.3 ± 0.1	4.2	3					
Pisidia longicornis	MSF	H	7.2 ± 0.9	2.1	3	7.3 ± 0.5			2.2	3
Porcellana platycheles	MSF	H	7.4	2.2	1					
Mollusca										
Acanthochitona crinita	sf-P	H				10.8 ± 0.2			3.6	3
Barleeia unifasciata	DF	R	8.6	2.7	1					
Bittium reticulatum	DF	H	8.7	2.7	1					
Calliostoma zizyphinum	sf-P	R	11.8 ± 0	4	3		11		3.7	1
Gibbula cineraria	G	S	9.7 ± 0.1	3.1	3		9		2.9	1
Haliotis tuberculata	G	R	7.8 ± 0.4	2.4	5		6.5		2	1
Ocenebra erinacea	sf-P	R	9.9	3.2	1					
Ocinebrina aciculata	sf-P	R	8.8	2.8	1	10 ± 0.1			3.3	2
Patella pellucida	G	S	6.9 ± 0.3	2	5	6.5 ± 0.3			2	5
Rissoa parva	DF	H + R	6.8	2	1	5.7 ± 0.9			2	3
Tricolia pullus	G	R	7.8 ± 0.3	2.4	3					
Trivia arctica	sf-P	R	11.7 ± 0.2	3.9	3	9.9 ± 0.1			3.3	3
Anomia ephippium	SSF	S	6.4 ± 0.7	2	3	6.5 ± 0.3			2	5
Hiatella arctica	SSF	H	6.4 ± 0.2	2	3	6.6 ± 0.4			2	3
Musculus subpictus	SSF	S + R	4.7	2	1	6.1 ± 0.7			2	4
Bryozoa										
Alcyonidium gelatinosum	SSF	S	5.5 ± 0.2	2	3	4.7 ± 0			2	3
Crisia eburnea	SSF	S				4.4 ± 0.2			2	3
Electra pilosa	SSF	S	5.5 ± 0.7	2	3	5.4 ± 0.2			2	3
Echinodermata										
Amphipholis squamata	DF	S	7.7 ± 0.4	2.3	3	9 ± 0.1			2.9	3
Asterias rubens	sf-P	R				9.5 ± 0.3			3.1	3
Asterina gibbosa	sf-P	S + R	10.5 ± 0.2	3.4	3	9.4 ± 0.1			3.1	5
Echinus esculentus	sf-P	R				11.7 ± 0.2			4	3
Marthasterias glacialis	sf-P	R				11.1 ± 0.1			3.8	3
Psammechinus milliaris	sf-P	R					9.5		3.1	1
Chordata										
Botryllus schlosseri	SSF	S	6 ± 0.8	2	3	5.2 ± 0.3			2	3
Didemnum maculosum	SSF	H	6.1 ± 0.2	2	3	6.4 ± 0.5			2	3
Distomus variolosus	SSF	S				7 ± 0.3			2.1	5
Polyclinum aurantium	SSF	R	7.1 ± 0.1	2.1	3	7.2 ± 0.4			2.2	3

Fig. 1.
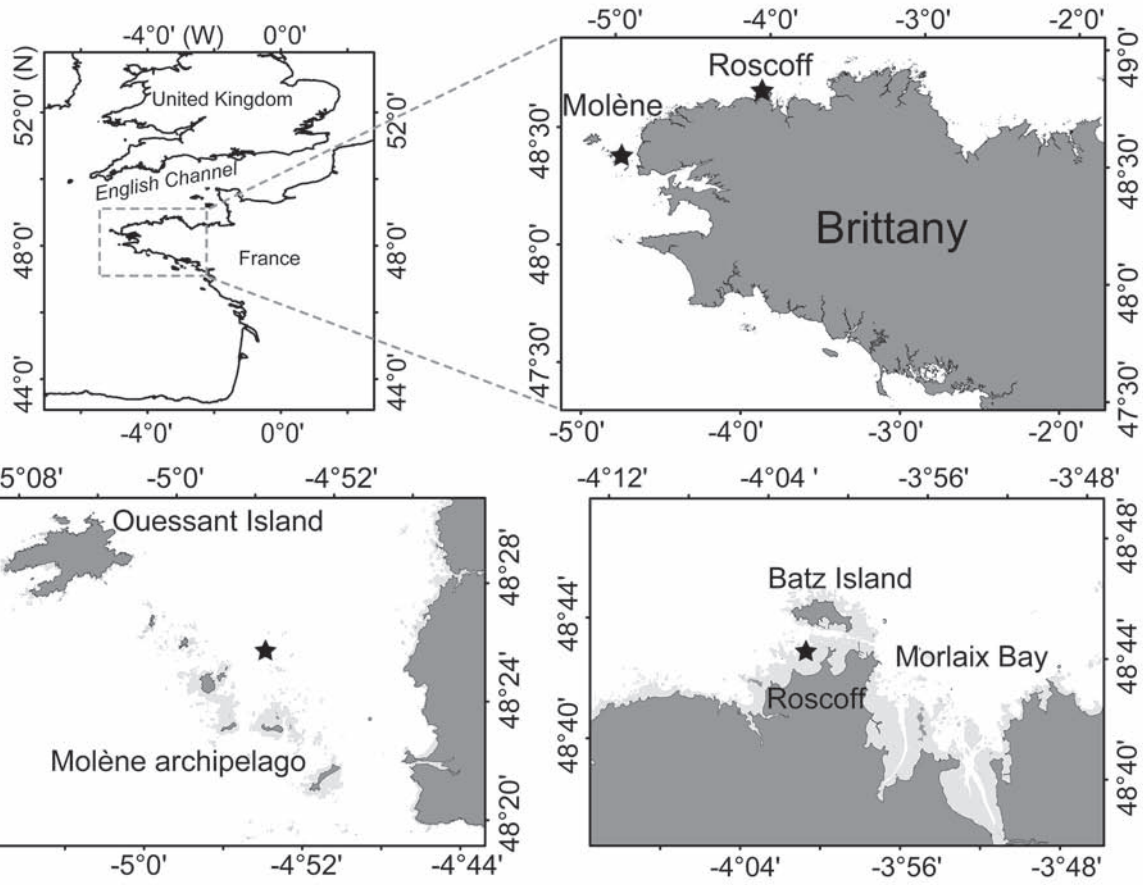
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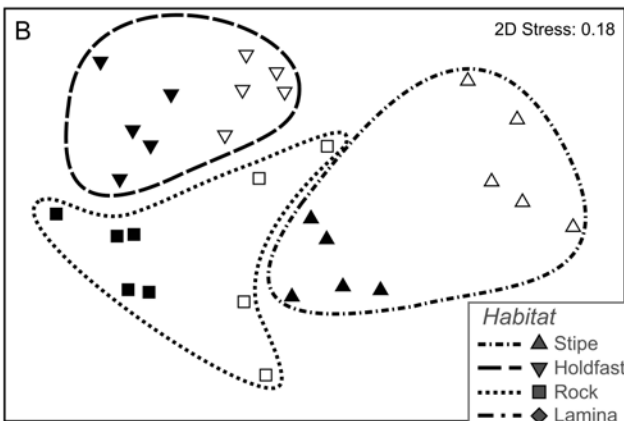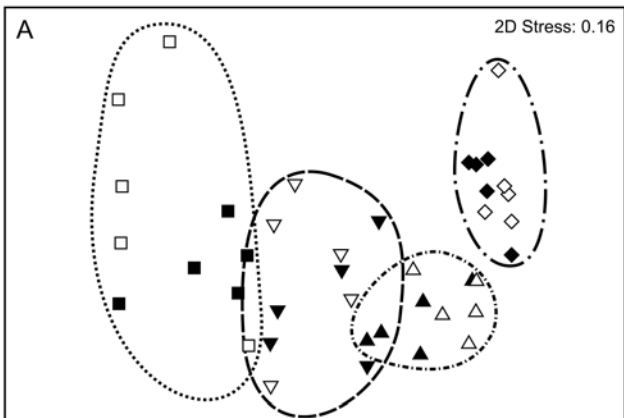
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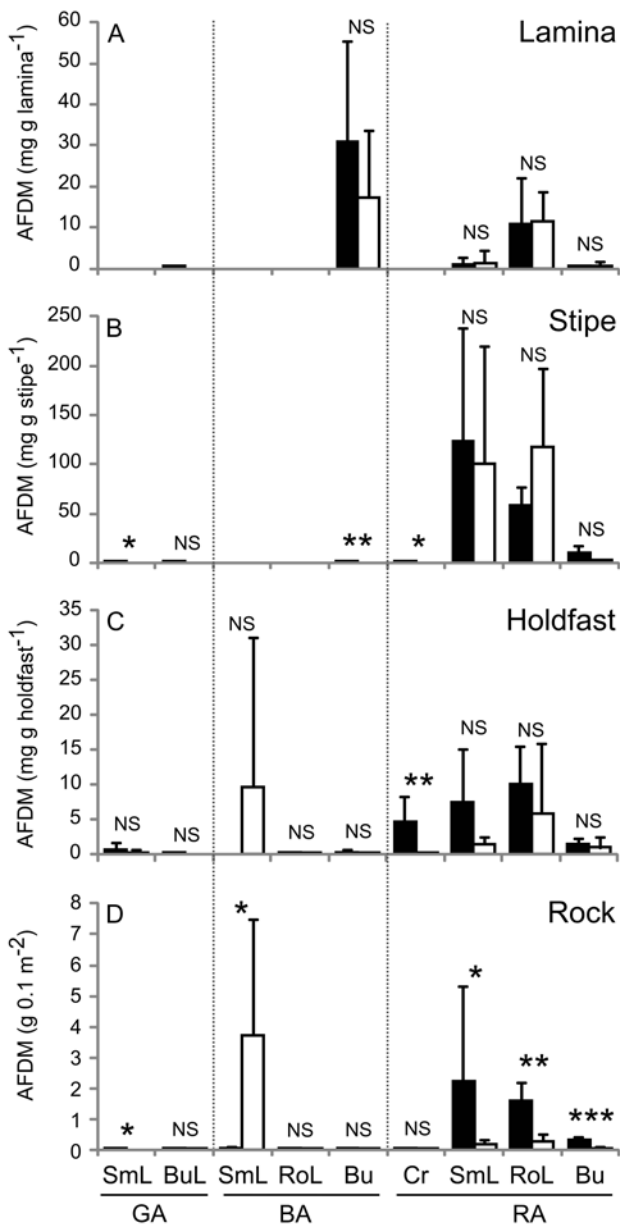
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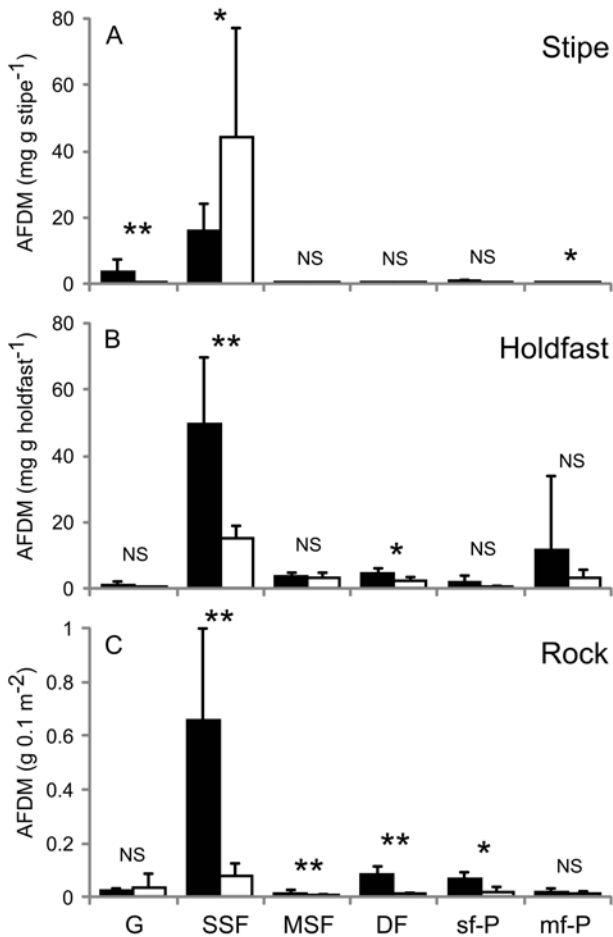
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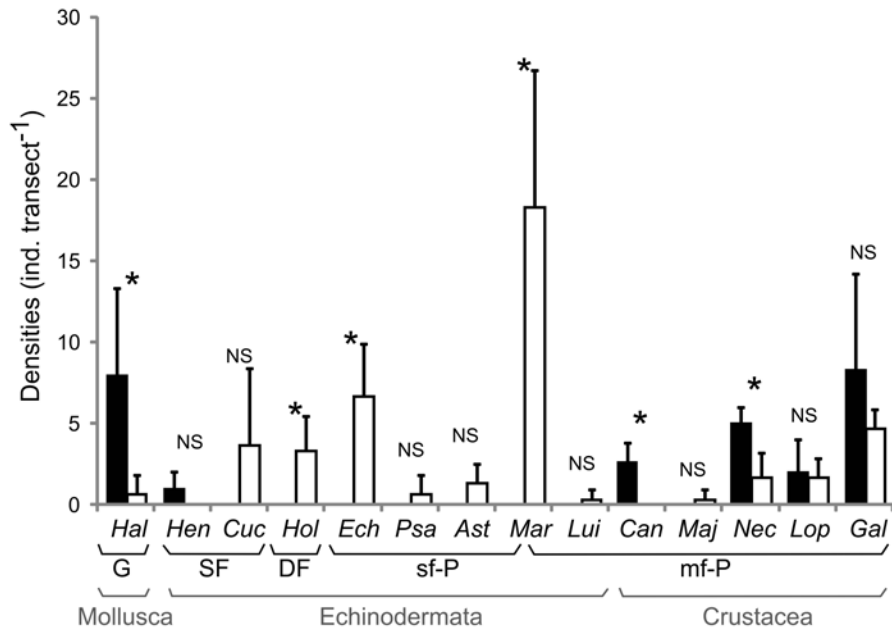
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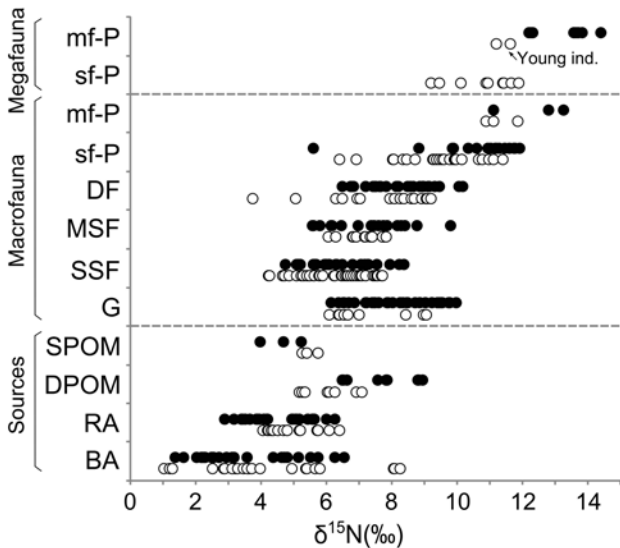
	ROSCOFF			MOLENE			Two-tailed comparison (P-value)
KELP plants							
Age (y)	5.7	±	1.5	5.3	±	1.1	0.494
Biomass (gAFDM)	89.8	±	20.9	106.7	±	25.6	0.285
LAMINA							
Biomass (gAFDM)	43.3	±	14.5	3	±	0.8	0.815
STIPE							
Length (cm)	89.0	±	9.3	92.9	±	21.8	0.725
Biomass (gAFDM)	32.0	±	9.5	41.5	±	15.8	0.283
Mean diameter (mm)	22.8	±	2.4	28.2	±	1.5	**0.003**
Total volume (mL)	203.5	±	35.0	264.1	±	74.1	0.137
Surface area (cm²)	368.7	±	98.5	590.74	±	193.83	0.052
HOLDFAST							
Biomass (gAFDM)	14.5	±	4.8	19.6	±	4.1	0.108
Total volume (mL)	511.2	±	338.2	597.0	±	202.3	0.639
Interstitial volume (mL)	356.2	±	267.7	390.0	±	159.8	0.815

	Roscoff	Molène
Rhodophyceae		
Acrosorium ciliolatum (Harvey) Kylin, 1924	xxx	xxx
Aglaothamnion bipinnatum (P.L.Crouan & H.M.Crouan) Feldmann & G.Feldmann, 1948	x	xx
Aglaothamnion gallicum (Nägeli) Halos ex Ardré, 1970		xx
Aglaothamnion priceanum Maggs, Guiry & Rueness, 1991	xx	xx
Aglaothamnion sp. Feldmann-Mazoyer, 1941		x
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer, 1941		xx
Antithamnionella sp. Lyle, 1922	xx	
Apoglossum ruscifolium (Turner) J.Agardh, 1898	xxx	xxx
Asparagopsis armata Harvey, 1855 (*Falkenbergia rufolanosa* Stage (Harvey) F.Schmitz, 1897)	xxx	
Bonnemaisonia asparagoides (Woodward) C.Agardh, 1822	xx	
Brongniartella byssoides (Goodenough & Woodward) F.Schmitz, 1893		x
Calliblepharis ciliata (Hudson) Kützing, 1843	xxx	x
Callithamnion tetragonum (Withering) S.F.Gray, 1821	xx	xx
Callophyllis laciniata (Hudson) Kützing, 1843	xxx	xxx
Ceramium pallidum (Nägeli ex Kützing) Maggs & Hommersand, 1993	xx	
Chondria dasyphylla (Woodward) C.Agardh, 1817	xx	x
Corallina elongata J.Ellis & Solander, 1786	xx	
Corallinale sp. */ Peyssoniella* sp. Complex	xxx	xx
Cryptopleura ramosa (Hudson) L.Newton, 1931	xxx	xxx
Dasya sp. C.Agardh, 1824		x
Delesseria sanguinea (Hudson) J.V.Lamouroux, 1813	xx	xxx
Dilsea carnosa (Schmidel) Kuntze, 1898	xx	
Gracilaria sp. Greville, 1830		x
Halurus flosculosus (J.Ellis) Maggs & Hommersand, 1993	xx	xx
Haraldiophyllum bonnemaisonii (Kylin) A.D.Zinova, 1981	xxx	xx
Heterosiphonia plumosa (J.Ellis) Batters, 1902	xxx	xxx
Hypoglossum hypoglossoides (Stackhouse) F.S.Collins & Hervey, 1917	xx	
Kallymenia reniformis (Turner) J.Agardh, 1842	xx	xxx
Lomentaria articulata (Hudson) Lyngbye, 1819	xxx	xx
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon, 1828	xx	
Membranoptera alata (Hudson) Stackhouse, 1809	xx	xxx
Palmaria palmata (Linnaeus) Weber & Mohr, 1805	xxx	xxx
Phycodrys rubens (Linnaeus) Batters, 1902	xxx	xxx
Phyllophora crispa (Hudson) P.S.Dixon, 1964	xx	xx
Plocamium cartilagineum (Linnaeus) P.S.Dixon, 1967	xxx	xxx
Plumaria plumosa (Hudson) Kuntze, 1891	xx	xxx
Polyneura bonnemaisonii (C.Agardh) Maggs & Hommersand, 1993	xxx	xxx
Polysiphonia brodiaei (Dillwyn) Sprengel, 1827	x	
Polysiphonia elongata (Hudson) Sprengel, 1827	xx	
Polysiphonia sp. Greville, 1823		xx
Pterosiphonia parasitica (Hudson) Falkenberg, 1901	xx	xx
Pterothamnion crispum (Ducluzeau) Nägeli, 1862	xx	
Ptilothamnion pluma (Dillwyn) Thuret, 1863	xx	xxx
Ptilothamnion sphaericum (P.L.Crouan & H.M.Crouan ex J.Agardh) Maggs & Hommersand, 1993		xx
Pyllophoraceae sp.		x
Rhodochorton purpureum (Lightfoot) Rosenvinge, 1900		x
Rhodophyllis divaricata (Stackhouse) Papenfuss, 1950	xxx	xxx
Rhodymenia pseudopalmata (J.V.Lamouroux) P.C.Silva, 1952	xxx	xxx
Sphaerococcus coronopifolius Stackhouse, 1797	xx	xx
Sphondylothamnion multifidum (Hudson) Nägeli, 1862		xx
Phaeophyceae		
Chaetopteris plumosa (Lyngbye) Kützing, 1843	xx	xx
Cutleria multifida (Turner) Greville, 1830		xxx
Cystoseira sp. C.Agardh, 1820	o	x
Dictyota dichotoma (Hudson) J.V.Lamouroux, 1809	xx	
Ectocarpus fasciculatus Harvey, 1841	xx	
Ectocarpus sp. Lyngbye, 1819 / *Hincksia hincksiae* (Harvey) P.C.Silva, 1987	xxx	xx
Halopteris filicina (Grateloup) Kützing, 1843	xxx	xxx
Laminaria digitata (Hudson) J.V.Lamouroux, 1813	x	o
Laminaria hyperborea (Gunnerus) Foslie, 1884	xxx	xxx

Saccorhiza polyschides (Lightfoot) Batters, 1902	o	xx
Ulvophyceae		
Cladophora sp.1 Kützing, 1843	xx	x
Cladophora sp.2 Kützing, 1844	x	
Ulva sp. (*compressa*) Linnaeus, 1753	xx	
Ulva rigida C.Agardh, 1823	xx	x
Umbraulva sp. E.H.Bae & I.K.Lee, 2001	xx	

	Roscoff	Molène
Porifera		
Amphilectus fucorum (Esper, 1794)	xxx	xx
Axinella (Schmidt, 1862) sp.	x	
Clathrina (Gray, 1867) sp.	xx	xxx
Dysidea fragilis (Montagu, 1818)	xxx	
Grantia compressa (Fabricius, 1780)		xx
Guancha lacunosa (Johnston, 1842)	xx	
Halichondria (Fleming, 1828) sp.	xxx	xxx
Halichondria (Halichondria) panicea (Pallas, 1766)	xx	
Haliclona (Grant, 1836) spp.	xxx	xxx
Halisarca dujardinii (Johnston, 1842)	xxx	xxx
Hymeniacidon perlevis (Montagu, 1818)		xx
Leucandra gossei (Bowerbank, 1862)		xx
Leuconia johnstonii (Carter, 1871)	xx	
Leuconia nivea (Grant, 1826)	x	
Myxilla (Myxilla) incrustans (Johnston, 1842)	xxx	
Myxilla (Myxilla) rosacea (Lieberkühn, 1859)	xxx	xx
Ophlitaspongia papilla (Bowerbank, 1866)	xx	x
Phorbas plumosus (Montagu, 1818)	xx	
Porifera sp.	xxx	xx
Suberitidae sp.	xx	x
Sycon ciliatum (Fabricius, 1780)	xxx	xxx
Tethya aurantium (Pallas, 1766)	x	
Tethya citrina (Sarà & Melone, 1965)	x	
Cnidaria		
Amphisbetia operculata (Linnaeus, 1758)	x	xx
Anemonia viridis (Forskål, 1775)	o	o
Diphasia attenuata (Hincks, 1866)		x
Dynamena pumila (Linnaeus, 1758)	xx	xx
Dyphasia (Agassiz, 1862) sp.		x
Kirchenpaueria pinnata (Linnaeus, 1758)		xx
Lucernariopsis cruxmelitensis (Corbin, 1978)		o
Orthopyxis integra (MacGillivray, 1842)		xx
Sertularella polyzonias (Linnaeus, 1758)	xx	xx
Urticina felina (Linnaeus, 1761*)*	o	o
Entoprocta		
Pedicellina nutans (Dalyell, 1848)	xx	xx
Nemertea		
Cyanophthalma cordiceps (Friedrich, 1933)	xx	xxx
Lineus (Sowerby, 1806) sp. (*ruber/sanguineus*)	xx	xx
Micrura (Ehrenberg, 1871) sp.	xx	xx
Nemertea sp.		xxx
Oerstedia dorsalis (Abildgaard, 1806)	xx	xx
Tubulanus linearis (McIntosh, 1874)	xx	
Mollusca		
Polyplacophora		

Acanthochitona crinita (Pennant, 1777)	xxx	xxx
Callochiton septemvalvis (Montagu, 1803)		x

Gastropoda

Alvania cancellata (da Costa, 1778)	x	
Barleeia unifasciata (Montagu, 1803)	xxx	xx
Bittium reticulatum (da Costa, 1778)	xxx	
Calliostoma zizyphinum (Linnaeus, 1758)	x	xx
Cerithiopsis barleei (Jeffreys, 1867)	x	
Cerithiopsis tubercularis (Montagu, 1803)	xx	x
Chauvetia brunnea (Donovan, 1804)	xxx	xx
Crisilla semistriata (Montagu, 1808)	xxx	xx
Gibbula cineraria (Linnaeus, 1758)	xxx	x
Gibbula umbilicalis (da Costa, 1778)	x	
Haliotis tuberculata (Linnaeus, 1758)	ooo	o
Jujubinus (Monterosato, 1884) sp.	xxx	
Lacuna pallidula (da Costa, 1778)	x	x
Lacuna parva (da Costa, 1778)		x
Lamellaria latens (Müller O.F., 1776)	xx	x
Manzonia crassa (Kanmacher, 1798)	xx	x
Marshallora adversa (Montagu, 1803)		x
Nassarius incrassatus (Strøm, 1768)	xx	x
Ocenebra erinaceus (Linnaeus, 1758)	x	
Ocinebrina aciculata (Lamarck, 1822)	xx	
Odostomia unidentata (Montagu, 1803)	xx	
Onoba aculeus (Gould, 1841)		x
Onoba semicostata (Montagu, 1803)	xx	xx
Patella pellucida (Linnaeus, 1758)	xxx	xxx
Pleurobranchus membranaceus (Montagu, 1815)	x	x
Pusillina inconspicua (Alder, 1844)	x	
Raphitoma linearis (Montagu, 1803)	x	
Raphitoma purpurea (Montagu, 1803)	x	
Retusa truncatula (Bruguière, 1792)	x	
Rissoa lilacina (Récluz, 1843)	x	x
Rissoa membranacea (J. Adams, 1800)	x	
Rissoa parva (da Costa, 1778)	xxx	xxx
Tectura virginea (O.F. Müller, 1776)	xx	xx
Tricolia pullus (Linnaeus, 1758)	xxx	xxx
Trivia arctica (Pulteney, 1799)	xx	x

Bivalvia

Aequipecten opercularis (Linnaeus, 1758)		x
Anomia ephippium (Linnaeus, 1758)	xxx	xxx
Rhomboidella prideauxi (Leach, 1815)	x	
Mimachlamys varia (Linnaeus, 1758)		x
Hiatella arctica (Linnaeus, 1767)		xx
Kellia suborbicularis (Montagu, 1803)	xx	xx
Modiolula phaseolina (Philippi, 1844)		xx
Musculus discors (Linnaeus, 1767)	xx	xxx
Musculus subpictus (Cantraine, 1835)	xx	xx

Sipuncula

Nephasoma (Nephasoma) minutum (Keferstein, 1862a)	xx	xx

Bryozoa

Aetea anguina (Linnaeus, 1758)	xx	xxx
Alcyonidium gelatinosum (Linnaeus, 1761)	xxx	xx
Alcyonidium hirsutum (Fleming, 1828)	xx	xx
Amathia lendigera (Linnaeus, 1758)	xx	x
Bicellariella ciliata (Linnaeus, 1758)	xx	xx
Caberea boryi (Audouin, 1826)	xx	x
Callopora lineata (Linnaeus, 1767)	xxx	xxx
Cellepora pumicosa (Pallas, 1766)	xx	xxx
Celleporella hyalina (Linnaeus, 1767)	xxx	xxx
Celleporina caliciformis (Lamouroux, 1816)	xxx	xxx
Crisia aculeata (Hassall, 1841)	xx	
Crisia denticulata (Lamarck, 1816)	xxx	xxx
Crisia eburnea (Linnaeus, 1758)	xx	xxx
Crisidia cornuta (Linnaeus, 1758)	xx	xxx
Electra pilosa (Linnaeus, 1767)	xxx	xxx
Escharella (Gray, 1848) spp.	xxx	x
Escharoides coccinea (Abildgaard, 1806)	xxx	xxx
Filicrisia geniculata (Milne Edwards, 1838)	xx	xx
Flustrellidra hispida (O. Fabricius, 1780)	xx	
Haplopoma impressum (Audouin, 1826)	xxx	xxx
Lichenopora verrucaria (O. Fabricius, 1780)	xx	
Membranipora membranacea (Linnaeus, 1767)	x	x
Membraniporella nitida (Johnston, 1838)		xx
Microporella ciliata (Pallas, 1766)	xxx	xxx
Oshurkovia littoralis (Hastings, 1944)		x
Phaeostachys spinifera (Johnston, 1847)	xxx	x
Plagioecia sarniensis (Norman, 1864)	x	
Plesiothoa gigerium (Ryland & Gordon, 1977)	xxx	xx
Ramphonotus minax (Busk, 1860)	x	
Schizomavella auriculata (Hassall, 1842)		xx
Schizomavella hastata (Hincks, 1862)		xxx
Schizomavella linearis (Hassall, 1841)	xx	xx
Scruparia chelata (Linnaeus, 1758)	xx	xxx
Scrupocellaria reptans (Linnaeus, 1758)	xx	xxx
Scrupocellaria scabra (van Beneden, 1848)		x
Scrupocellaria scruposa (Linnaeus, 1758)	xx	x
Tubulipora plumosa (Thompson in Harmer, 1898)	xxx	xxx
Turbicellepora magnicostata (Barroso, 1919)	x	
Vesicularia spinosa (Linnaeus, 1758)	xx	x

Annelida
Ctenodrilidae

Ctenodrilidae sp. (Kennell, 1882)	x	x

Eunicidae

Eunicidae (Berthold, 1827) indet.		x
Lumbrineris funchalensis (Kinberg, 1865)	xx	x

Species	Col 1	Col 2
Lysidice ninetta (Audouin & Milne-Edwards, 1833)	xx	

Nereidae

Species	Col 1	Col 2
Leonnates glauca (Claparède, 1870)	xx	xxx
Nereis pelagica (Linnaeus, 1758)		xxx
Platynereis dumerilii (Audouin & Milne Edwards, 1834)	xxx	xxx

Syllidae

Species	Col 1	Col 2
Amblyosyllis formosa (Claparède, 1863)	x	xx
Autolytinae (Langherans, 1879) indet.		x
Eurysyllis tuberculata (Ehlers, 1864)	xx	xx
Eusyllis assimilis (Marenzeller, 1875)		xx
Eusyllis blomstrandi (Malmgren, 1867)		xxx
Exogone (Exogone) naidina (Örsted, 1845)	xx	xx
Exogone (Örsted, 1845) sp.		xx
Haplosyllis spongicola (Grube, 1855)	xxx	x
Myrianida prolifera (O.F. Müller, 1788)		xx
Odontosyllis ctenostoma (Claparède, 1868)	xxx	xxx
Pionosyllis lamelligera (Saint Joseph, 1887)	x	x
Sphaerosyllis hystrix (Claparède, 1863)		x
Syllis (Lamarck, 1818) sp.		xx
Syllis armillaris (O.F. Müller, 1776)	xx	xxx
Syllis columbretensis (Campoy, 1982)	xxx	xxx
Syllis gracilis (Grube, 1840)	x	xxx
Syllis hyalina (Grube, 1863)		x
Syllis variegata (Grube, 1860)	xxx	xxx
Trypanosyllis (Trypanosyllis) coeliaca (Claparède, 1868)	x	x
Trypanosyllis zebra (Grube, 1840)	xx	xx

Phyllodocidae

Species	Col 1	Col 2
Eumida sanguinea (Örsted, 1843)		xx
Nereiphylla rubiginosa (Saint-Joseph, 1888)		xx
Phyllodoce (Lamarck, 1818) sp.		x

Polynoidae

Species	Col 1	Col 2
Harmothoe extenuata (Grube, 1840)	xx	xxx
Harmothoe impar (Johnston, 1839)	xx	xx
Harmothoe spinifera (Ehlers, 1864)		xx
Lepidonotus clava (Montagu, 1808)		xx
Pholoe inornata (Johnston, 1839)	xx	xx
Subadyte pellucida (Ehlers, 1864)	xx	x

Orbiniidae

Species	Col 1	Col 2
Proscoloplos cygnochaetus (Day, 1954)	xx	

Maldanidae

Species	Col 1	Col 2
Nichomache (Malmgren, 1865) spp.	x	

Arenicolidae

Species	Col 1	Col 2
Arenicolides ecaudata (Johnston, 1835)		x

Spionidae

Species	Col 1	Col 2
Aonides oxycephala (Sars, 1862)	xx	xx
Dipolydora (Verrill, 1881) sp.	xx	xx
Pseudopolydora (Czerniavsky, 1881) sp.		x
Scolelepis tridentata (Southern, 1914)	xx	xx

Sabellidae

Amphiglena mediterranea (Leydig, 1851)	xxx	xxx
Branchiomma bombyx (Dalyell, 1853)	xxx	xxx
Branchiomma lucullanum (Delle Chiaje, 1828)	x	
Fabricia sabella (Ehrenberg, 1836)	xx	xx
Jasmineira elegans (Saint-Joseph, 1894)	xx	xxx
Oridia armandi (Claparède, 1864)		x
Parasabella langerhansi (Knight-Jones, 1983)	xx	xx
Pseudopotamilla reniformis (Bruguière, 1789)	x	
Sabella discifera (Grube, 1874)	x	x

Sabellariidae

Sabellaria spinulosa (Leuckart, 1849)	xx	

Serpudidae

Protula tubularia (Montagu, 1803)	x	
Salmacina (Claparède, 1870) sp.	xx	x
Spirorbis corrugatus (Montagu, 1803)	x	
Spirorbis (Daudin, 1800) sp.	xxx	xxx
Spirobranchus triqueter (Linnaeus, 1758)		xx

Terebellidae

Amphitrite johnstoni (Malmgren, 1865)	x	
Eupolymnia nebulosa (Montagu, 1818)	x	
Eupolymnia nesidensis (Delle Chiaje, 1828)	xxx	xx
Nicolea venustula (Montagu, 1818)	xxx	xxx
Nicolea zostericola (Örsted, 1844)	xxx	xx
Pista elongata (Moore, 1909)	xxx	xx
Polycirrus medusa (Grube, 1850)	xx	xxx
Trichobranchus glacialis (Malmgren, 1866)	xx	

Chaetognatha

Spadella (Langerhans, 1880) sp.		x

Platyhelminthes

Cycloporus papillosus (Sars in Jensen, 1878) Lang, 1884	x	xx
Stylochoplana maculata (Quatrefage, 1845)		x

Nematoda

Nematoda spp.	xxx	xxx

Pycnogonida

Achelia echinata (Hodge, 1864)	xxx	xxx
Achelia hispida (Hodge, 1864)	xx	xx
Ammothella longipes (Hodge, 1864)	x	x
Anoplodactylus angulatus (Dohrn, 1881)	x	
Callipallene brevirostris (Johnston, 1837)		x
Endeis spinosa (Montagu, 1808)		x
Nymphon gracile (Leach, 1814)		x
Nymphon brevirostre (Hodge, 1863)	xx	

Crustacea

Cirripedia

Verruca stroemia (O.F. Müller, 1776)	xxx	xxx

Isopoda

Astacilla danmoniensis (Stebbing, 1874)	xx	

Calathura norvegica (Sars, 1872)	x	
Dynamene bidentata (Adams, 1800)	x	
Dynamene magnitorata (Holdich, 1968)	x	
Gnathia dentata (G. O. Sars, 1872)	x	
Gnathia maxillaris (Montagu, 1804)		x
Janira maculosa (Leach, 1814)	xx	xxx
Stenosoma lancifer (Miers, 1881)	x	xx
Isopoda sp.		x
Leptostraca		
Nebalia bipes (Fabricius, 1780)	x	
Mysida		
Praunus inermis (Rathke, 1843)	x	
Tanaidacea		
Apseudes talpa (Montagu, 1808)	x	x
Apseudopsis latreillii (Milne-Edwards, 1828)	x	
Amphipoda		
Aora spinicornis (Afonso, 1976*)*	xx	xx
Ampithoe gammaroides (Bate, 1856)	xx	xx
Ampithoe ramondi (Audouin, 1826)	xx	xx
Ampithoe rubricata (Montagu, 1818)		x
Apherusa bispinosa (Bate, 1857)	xxx	x
Apherusa cirrus (Bate, 1862)	xx	
Apherusa jurinei (Milne-Edwards, 1830)		xx
Caprella acanthifera (Leach, 1814)	xx	
Caprella fretensis (Stebbing, 1878)	xx	
Crassicorophium bonellii (Milne Edwards, 1830)		xx
Dexamine spinosa (Montagu, 1813)	xx	
Dexamine thea (Boeck, 1861)	xx	
Elasmopus (Costa, 1853)	xx	xx
Gammaropsis maculata (Johnston, 1828)	xx	xx
Iphimedia obesa (Rathke, 1843)		x
Jassa falcata (Montagu, 1808)	xx	xxx
Lembos websteri (Bate, 1857)		x
Leucothoe spinicarpa (Abildgaard, 1789)	xxx	xx
Lysianassa ceratina (Walker, 1889)	xx	xx
Maera grossimana (Montagu, 1808)		x
Maera inaequipes (Costa, 1857)	xx	xx
Melita hergensis (Reid, 1939)		x
Microprotopus (Norman, 1867 sp.		x
Nannonyx spinimanus (Walker, 1895)	x	xx
Orchomene humilis (Costa, 1853)	x	xx
Phtisica marina (Slabber, 1769)	x	
Sunamphitoe pelagica (Milne-Edwards, 1830)		x
Triphosella (Bonnier, 1893) sp.		xx
Tritaeta gibbosa (Bate, 1862)		xx
Decapoda		
Anapagurus hyndmanni (Bell, 1846)	xxx	x
Cancer pagurus (Linnaeus, 1758)	oo	o

Eualus occultus (Lebour, 1936)		x
Eualus pusiolus (Krøyer, 1841)	x	
Eurynome spinosa (Hailstone, 1835)	x	x
Galathea squamifera (Leach, 1814)	oo	oo
Galathea strigosa (Linnaeus, 1761)	o	
Homarus gammarus (Linnaeus, 1758)	o	
Lophozozymus incisus (H. Milne Edwards, 1834)	o	o
Maja squinado (Herbst, 1788)		o
Necora puber (Linnaeus, 1767)	oo	o
Pagurus bernhardus (Linnaeus, 1758)	x	
Philocheras fasciatus (Risso, 1816)	x	
Pilumnus hirtellus (Linnaeus, 1761)	xx	xx
Pisidia longicornis (Linnaeus, 1767)	xxx	xxx
Porcellana platycheles (Pennant, 1777)	o	
Xantho pilipes (A. Milne-Edwards, 1867)	o	

Echinodermata

Amphipholis squamata (Delle Chiaje, 1828)	xxx	xxx
Antedon bifida (Pennant, 1777)	xxx	
Aslia lefevrii (Barrois, 1882)	x	xx
Asterias rubens (Linnaeus, 1758)	o	o
Asterina gibbosa (Pennant, 1777)	xxx	xx
Cucumaria frondosa (Gunnerus, 1767)	o	oo
Echinus esculentus (Linnaeus, 1758)		oo
Henricia sanguinolenta (O.F. Müller, 1776)	o	
Holothuria (Panningothuria) forskali (Delle Chiaje, 1823)		oo
Luidia ciliaris (Philippi, 1837)		o
Marthasterias glacialis (Linnaeus, 1758)		ooo
Ocnus lacteus (Forbes & Goodsir, 1839)	xxx	xx
Ophiothrix fragilis (Abildgaard, in O.F. Müller, 1789)	xx	xxx
Pawsonia saxicola (Brady & Robertson, 1871)	x	xx
Psammechinus miliaris (P.L.S. Müller, 1771)	o	oo

Chordata

Aplidium pallidum (Verrill, 1871)	xx	xx
Aplidium punctum (Giard, 1873)	xx	xx
Aplidium glabrum (Verrill, 1871)	x	xxx
Aplidium (Savigny, 1816) spp.	xxx	xx
Ascidia mentula (Müller, 1776)	xx	xxx
Botryllus schlosseri (Pallas, 1766)	xxx	xxx
Clavelinidae [*Archidistoma aggregatum* (Garstang, 1891)]		xx
Dendrodoa grossularia (Van Beneden, 1846)	xxx	xxx
Didemnum maculosum (Milne-Edwards, 1841)	xxx	
Distomus variolosus (Gaertner, 1774)	xxx	xxx
Lissoclinum perforatum (Giard, 1872)	xx	xx
Molgula crinita (Sluiter, 1904)	xxx	xxx
Morchellium argus (Milne-Edwards, 1841)	x	xxx
Polycarpa (Heller, 1877) sp.	xxx	xxx
Polyclinum aurantium (Milne-Edwards, 1841)	xxx	xx

Pyura (Molina, 1782) sp.	x	x
Styela (Fleming, 1822) sp.		x
Trididemnum (Della Valle, 1881) sp.	xx	xx