

Contribution to the Theme Section 'The ecology of temperate reefs in a changing world'

Temporal succession of a macrofaunal community associated with kelp fragment accumulations in an *in situ* experiment

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ABSTRACT: A large part of the production of *Laminaria hyperborea* kelp forests is not directly consumed by grazers, but is exported during storm events or natural annual blade erosion. Drifting kelp fragments are transported and can accumulate temporarily over subtidal benthic habitats. The decay process is particularly slow (>6 mo for complete decay during spring–summer) and *L. hyperborea* fragments are able to maintain their primary production function for several months. If they accumulate in low subtidal habitats, fragments can have a long residence time, thus modifying habitat structure. Based on a 6 mo cage experiment, we investigated macrofaunal colonization and community succession within accumulations of *L. hyperborea* fragments on a low subtidal (–10 m) sandy bottom ecosystem. Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) measurements were carried out to describe the structure and development of the trophic food web and the role of detritus as a food source. Kelp tissues were rapidly and abundantly colonized by macrofauna, and a classical ecological succession occurred, with changes in species dominance and increase in diversity during decay. The food web was based on 2 main sources: particulate organic matter from the water column and decaying kelp tissues. Kelp contributed significantly to the diet of numerous species that are commonly consumed by local predators (fish, shrimp). Following community succession, diets diversified and the food web became more complex during the decay process. Our results indicate that drift kelp accumulations structure their associated communities and food web during the whole decay process.

KEY WORDS: Kelp · Degradation · Macrofauna · Community · Detritus · Food web · Stable Isotopes · *In situ* experiment

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1. INTRODUCTION

Within ecosystems dominated by large primary producers, the majority of production is not directly consumed by herbivory, but instead enters a detrital pathway and slowly decays (Mann 1988, Moore et al. 2004). Detritus can represent more than 80% of initial primary production (Hairston & Hairston 1993,

Krumhansl & Scheibling 2012a) and has long been considered to play a major role in the flow of energy through ecosystems, influencing the dynamics of associated biota (Lindeman 1942, Tenore & Hanson 1980, Polis et al. 1997). In addition to its role in nutrient recycling by associated microorganisms, detritus that settles in a recipient ecosystem can strongly modify habitat structure (Jones et al. 1994) and shape

community dynamics and the trophic food web. More specifically, detritus can enhance macrofaunal biodiversity, increase the complexity of the food web by extending trophic chain length and support a higher number of predators and greater biomass than autotrophic ecosystems (Hairston & Hairston 1993, Moore et al. 2004).

In marine environments, numerous studies have focused on the accumulations of detritus from beach wrack depositions (Dugan et al. 2003, Colombini et al. 2011, Orr et al. 2014), seagrass meadows (Mascart et al. 2015, Boudouresque et al. 2016, Remy et al. 2018) and macrophytic detritus accumulations within submarine canyons (Vetter 1994) or deep Fjord areas (Renaud et al. 2015, Ramirez-Llodra et al. 2016, Vilas et al. 2020). For example, seagrass detritus form beds of litter containing dead material that can accumulate within a seagrass meadow or be exported from the shore to deep ecosystems. When dead leaves reach the coast, they can form large accumulations, modifying beach structure and food web dynamics (Simeone & De Falco 2012, Boudouresque et al. 2016). The underwater litter communities are less diverse in macrofaunal species compared with live *Posidonia* meadow communities, but between 40 and 80 different species are found inhabiting the detritus (Gambi et al. 1992, Gallmetzer et al. 2005, Remy 2016). Another example of the impact of marine detritus on adjacent ecosystems is the accumulation of macroalgae within submarine canyons. Vetter (1995) showed that high biomass of kelp detritus can accumulate within submarine canyons in California. These accumulations support large secondary production of crustacean species, which are in turn consumed by numerous species of commercially exploited fishes (Vetter 1994). However, to date, little is known about the impact of kelp forest detritus on shallow subtidal ecosystems, to where it can be exported and accumulate.

Kelps are large brown macroalgae forming complex forests that are considered to be among the most productive ecosystems in coastal environments (Mann 1973). In the Northeast Atlantic, *Laminaria hyperborea* is the dominant kelp ranging from Portugal to Norway. Only few grazers are able to feed directly on *L. hyperborea* fresh tissue (e.g. *Echinus esculentus*, *Patella pellucida*; Christie et al. 2003, Leclerc et al. 2015) and they consume only 3–8% of the overall production (Norderhaug & Christie 2011). Consequently, about 80% of the production is estimated to be exported as particulate organic matter (POM) via blade shedding and plant dislodgment due to senescence or storm damage (Krumhansl & Scheibling 2012a). This

detritus can drift through adjacent environments and temporarily settle or accumulate over long-term periods if hydrodynamic conditions are favourable (Tzetzlin et al. 1997, de Bettignies et al. 2020). *L. hyperborea* fragment accumulations on shallow subtidal sandy ecosystems (10 m average depth) are characterized by a slow decay process during which fragments can persist several months (de Bettignies et al. 2020) and therefore may strongly affect the recipient ecosystems. These accumulations change the nature of the substratum by adding structural complexity and consequently may influence the dynamics of the associated community.

L. hyperborea forests are known to host a high diversity of macrofauna and -flora, with up to 110 algal and 462 faunal species identified in Brittany, France (Leclerc et al. 2015, 2016). These forests are considered particularly important for some commercially exploited species, such as Atlantic pollock *Pollachius pollachius*, which feeds on motile crustaceans (e.g. *Idotea* spp. isopods and amphipods; Fredriksen 2003). Even if only a small fraction of fresh material is directly consumed, macroalgal detritus can play an important trophic role locally during seasons with low phytoplankton density (Leclerc et al. 2013a). However, macrofauna can influence the kelp decay processes. For example, the grazing activity of mesoherbivores can slow down the decay of kelp fragments by removing the biofilm and thus inhibiting bacterial activity (Bedford & Moore 1984). Furthermore, a recent study on *L. hyperborea* export focusing on deep sandy bottom subsidies showed that an accumulation of kelp fragments was rapidly colonized by a high abundance of macroinvertebrates (Ramirez-Llodra et al. 2016).

Stable isotope ratios of carbon and nitrogen have been proven to be a powerful tool for investigating food web structure and functioning (Fry 2006, Boecklen et al. 2011). Their analysis can reveal the contribution of various sources to the diet of consumers and determine their relative trophic position (Fry 2006). Many studies have used stable isotopes to investigate the food web structure of kelp forests (e.g. Fredriksen 2003, Schaal et al. 2010, Leclerc et al. 2013b, 2015, Koenigs et al. 2015). However, some issues around their use must be considered, such as variation in space and time of source material (Page et al. 2008, Dethier et al. 2013) or variation of stable isotope composition with tissue type or age of the kelp (Buchholz et al. 2019).

We set up a 6 mo *in situ* experiment to investigate the associated macrofaunal community and succession of species in a kelp fragment accumulation dur-

ing the decay process at a shallow location. Additionally, we studied the trophic food web, its development and the role of kelp detritus as a food resource. We hypothesized that (1) kelp fragments, when accumulated in adjacent ecosystems, are used by numerous macrofaunal species; (2) a complex and abundant community establishes on detritus and classical community succession occurs over time; and (3) kelp fragments are increasingly consumed during the decay processes, constituting a significant food supply in the associated food web.

2. MATERIALS AND METHODS

2.1. Study site

The present study was conducted near Roscoff, in the inner Bay of Morlaix along the north-western coast of Brittany, France. The bay contains numerous rocky reefs supporting high *Laminaria hyperborea* biomass (Gorman et al. 2013) and associated biodiversity (Leclerc et al. 2016). These productive rocky reefs are separated by large areas of sandy sediments that are constantly fuelled by kelp detritus that can seasonally accumulate (F. de Bettignies pers. obs.). The experimental site (Guerhéon: 48° 42' 33.78" N, 3° 57' 12.36" W) was located in a part of the bay protected from the dominant westerly swell. The substratum is characterized by a mixture of coarse sand and shell fragments at 4.5 m depth below chart datum (9 m average depth) and ca. 100 m distant from rocky reefs covered by kelp forests dominated by *L. hyperborea*.

2.2. Experimental design

To study the macrofauna associated with *L. hyperborea* accumulations in a subtidal ecosystem, we set up an *in situ* cage experiment. The study was conducted from 18 April to 5 October 2017 (5.5 mo). In this experiment, we chose to simulate storm damage on kelps that recently shed their old blades. We studied the macrofauna associated with accumulations and the dynamics of the detritus community during decay.

L. hyperborea individuals of 80–90 cm stipe length without any visible signs of decay were randomly collected by SCUBA diving from a rocky reef close (~150 m) to the experimental site. Kelp individuals were kept in seawater and brought back to the harbour pontoon where they were processed within 2 h to avoid excessive stress exposure. Blades were cut

once in length and once in width. This method yielded fragments of various sizes, similar to those found in the field. Fragments from 2 individuals were pooled and weighed with a digital spring scale (Ami-aud; 40 kg \pm 10 g) for a mean (\pm SD) wet weight of 911 \pm 105 g. Batches were gently packed and randomly allocated to homemade numbered plastic litterfall cages (30 \times 25 \times 10 cm, 1 cm mesh) made from hard mesh used in oyster farming (de Bettignies et al. 2020). The quantity of algal material mimicked a 10 cm thick accumulation with a 3-dimensional structure, as previously observed *in natura* during prospection dives. A total of 35 litterfall cages were prepared, kept in seawater and quickly sunk at the experimental site by divers. Cages were attached to 4 anchored chain lines arranged parallel to each other, forming a continuous rectangular accumulation area. At each sampling time (after 2, 4, 6, 11, 15, 20 and 24 wk of deployment), 5 replicates of litterfall cages were randomly selected. Cages were collected with caution using 1 mm mesh bags to retain the macrofauna inhabiting the caged kelp accumulations, brought to the surface and transported in local seawater before any other processing. Cages were then kept in the dark in an open-flow seawater tank with constant air bubbling before laboratory processing within 24 h.

2.3. Sampling and identification

In the laboratory, each cage and mesh bag was opened carefully, and kelp fragments and associated macrofauna were placed in boxes filled with seawater for sorting. First, dominant (in abundance) and characteristic species were collected, starved overnight in seawater filtered at 0.20 μ m to allow gut clearance and frozen at -20°C for later stable isotope processing. During the experiment, 12 species were collected for food web analysis, representing the dominant grazers (*Idotea balthica* and *Steromphala cineraria*), detritus feeders (*Galathea squamifera*, *Gammarus locusta*), omnivore (*Palaemon serratus*), suspension feeder (*Pisidia longicornis*) and predators (*Apletodon dentatus*, *Ciliata mustela*, *Entelurus* sp., *Gobius paganellus*, *Lepadogaster* sp., *Nerophis lombriciformis*). Due to temporal succession, some species were present only at some sampling times. For each cage, 10 disks of 28 mm diameter were randomly cored on kelp fragments, rinsed with freshwater and stored at -20°C before stable isotope processing. Remaining macrofauna and kelp fragments were carefully rinsed with seawater over a 1 mm

sieve. Macrofauna were placed in conservation containers, entirely covered by a 3% formaldehyde-buffered solution before laboratory processing. Fauna samples were rinsed for 12 h with running seawater to remove the formaldehyde buffer before sorting and identification. At each sampling date, 3 cage replicates were randomly selected for complete identification. Specimens were identified under stereo microscope to the lowest taxonomic level (most of the time species level) whenever possible and counted to quantify numerical abundance.

2.4. Preparation of stable isotope samples

Three replicates of seawater (2 l) were collected with manual Niskin bottles 1 m above the experimental system to assess the pelagic source including the living phytoplankton suspended in the water column (i.e. POM). POM sampling was performed prior to any other underwater work to avoid any additional sediment and material resuspension within the water column. Samples were stored in a cold box before laboratory processing within 2 h. In the laboratory, POM samples were filtered on pre-combusted Whatman® GF/F filters (0.7 µm) using a pressure-controlled vacuum pumping ramp. Half of the filters were acidified in an airtight chamber with fuming HCl (37%) for 48 h for ^{13}C measurements. Filters were then dried at 60°C for 48 h.

When possible, isotope processing of macrofauna was conducted on muscle tissue to reflect assimilation of sources by the consumers (e.g. Leclerc et al. 2015). Each sample was prepared at the individual level. Individuals were dried at 60°C for 48 h. Dried samples were crushed with a mortar and a pestle to obtain a homogenous powder and then placed in tin capsules for mass-spectrometry analyses. When muscle dissection was impossible (amphipods, isopods, small anomuran crabs), acidification was performed on powdered samples by fuming (37% HCl) in an airtight chamber for 48 h (Hedges & Stern 1984).

2.5. Food web analyses

Carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were determined for macroalgae and filter using a Flash EA CHN analyser (ThermoFinnigan) coupled with a Finnigan Delta Plus mass spectrometer via a Finnigan Con-Flo III interface (Roscoff Biological Station). Animal samples were analysed at the Oceanology lab (University of Liège) using an isotopic

ratio mass spectrometer (IsoPrime100, Elementar) interfaced in continuous flow with an elemental analyzer (vario MICRO cube™, Elementar). Isotope ratios for carbon and nitrogen were reported conventionally in per mil (‰) using standard delta (δ) notation (DeNiro & Epstein 1978) relative to their respective international standards: Vienna-Pee Dee Belemnite (V-PDB) and atmospheric di-nitrogen (N_2) (Coplen et al. 2006). Pure gases of CO_2 and N_2 were used and calibrated against certified reference materials (IAEA-N2, IAEA-600, IAEA-CH6 and USGS34). The analytical precision was assessed by procedural blanks, internal replicates (i.e. glycine and in-house crustacean and seagrass reference material for ULiège and EMA-2 and Urea from SyLab for Roscoff). The standard deviation of repeated measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the laboratory standard was 0.20‰ versus V-PDB and 0.1‰ versus at-air, respectively.

2.6. Data analysis

2.6.1 Macrofaunal community analyses

Macrofaunal diversity parameters and abundance were measured for each cage. Total abundance (N ; ind. cage $^{-1}$), species richness (S ; sp. cage $^{-1}$), Shannon diversity (H') and Pielou evenness (J') were calculated. A correspondence factor analysis (CFA) was performed on abundance data calculated as the sum of the abundances of the 3 replicate cages. Rare species (one individual of any species sampled only once) were not removed from the analysis because very few changes were observed when comparing CFA results. Species represented on the graph (see Fig. 2) and used for interpretation had a relative contribution (CTR) greater than the null hypothesis of an equal contribution of each species in the analysis (i.e. $\text{CTR} > 100 / n$, where n is the number of species in the matrix). Square cosine (COS^2) values greater than 0.5 (which measure the quality of the representation of variables and objects on the plane projection) were also taken into account.

2.6.2. Isotope analysis

Temporal variation in food sources for primary consumers was assessed using stable isotope mixing models. Two-source Bayesian stable isotope mixing models (Parnell et al. 2010) were used to estimate the CTR of *L. hyperborea* detritus and POM in the diet of primary consumers during the experiment. Trophic

enrichment factors (TEFs) from the literature were used in the models. For gastropod muscle, we applied a TEF of $1.30 \pm 0.30\%$ for $\delta^{13}\text{C}$ and $2.90 \pm 0.32\%$ for $\delta^{15}\text{N}$ (McCutchan et al. 2003) and for other whole body invertebrates, a TEF of $0.28 \pm 0.23\%$ for $\delta^{13}\text{C}$ and $2.5 \pm 0.68\%$ for $\delta^{15}\text{N}$ (Caut et al. 2009). The model was run on 3 species (*Gammarus locusta*, *Stromphala cineraria*, *Pisidia longicornis*) at different sampling dates when these species were present. For each sampling date, the corresponding stable isotope values of the 2 sources were used to run the models. Analyses were performed using the stable isotope analysis in R ('siar') package (Parnell & Jackson 2013).

To study intra-specific variation, we investigated the change in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of 4 species (*S. cineraria*, *G. locusta*, *C. mustela* and *P. serratus*) over the sampling times. Standard ellipses (SEAc) were performed using SIBER (Jackson et al. 2011). SEAc were measured for each time point, and ellipses were plotted to study temporal variation. We visually studied the development of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the 4 species over time, and compared them with that of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *L. hyperborea*.

Statistical analyses were carried out using R v.3.5.2, and graphics were plotted using the 'ggplot2'

package. CFA was performed and drawn using Statbox software v.7.4.3 (Grimmersoft).

3. RESULTS

3.1. Macrofaunal community succession

In total, 170 different species were found associated with the decaying kelp fragments during the 6 mo experiment (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m13391_supp.pdf for the complete list). Over time, with increasing kelp fragment decay, abundance and diversity of associated macrofauna showed clear trends (Fig. 1). The first 2 sampling times (Weeks 2 and 4) were characterized by high abundance (mean $N > 600$ ind. cage⁻¹) of macrofauna and relative low species richness (mean $S < 24$ species cage⁻¹). H' (< 1.6) and J' (< 0.5) were low, indicating that the community was dominated by only a few species with high abundance (mainly *Gammarus locusta* and *Idotea balthica*) during the first stage of decay. Between Weeks 6 and 20, the community was characterized by lower abundance (mean $N < 390$ ind. cage⁻¹) and higher species richness (mean $S = 27\text{--}40$ species cage⁻¹). Further-

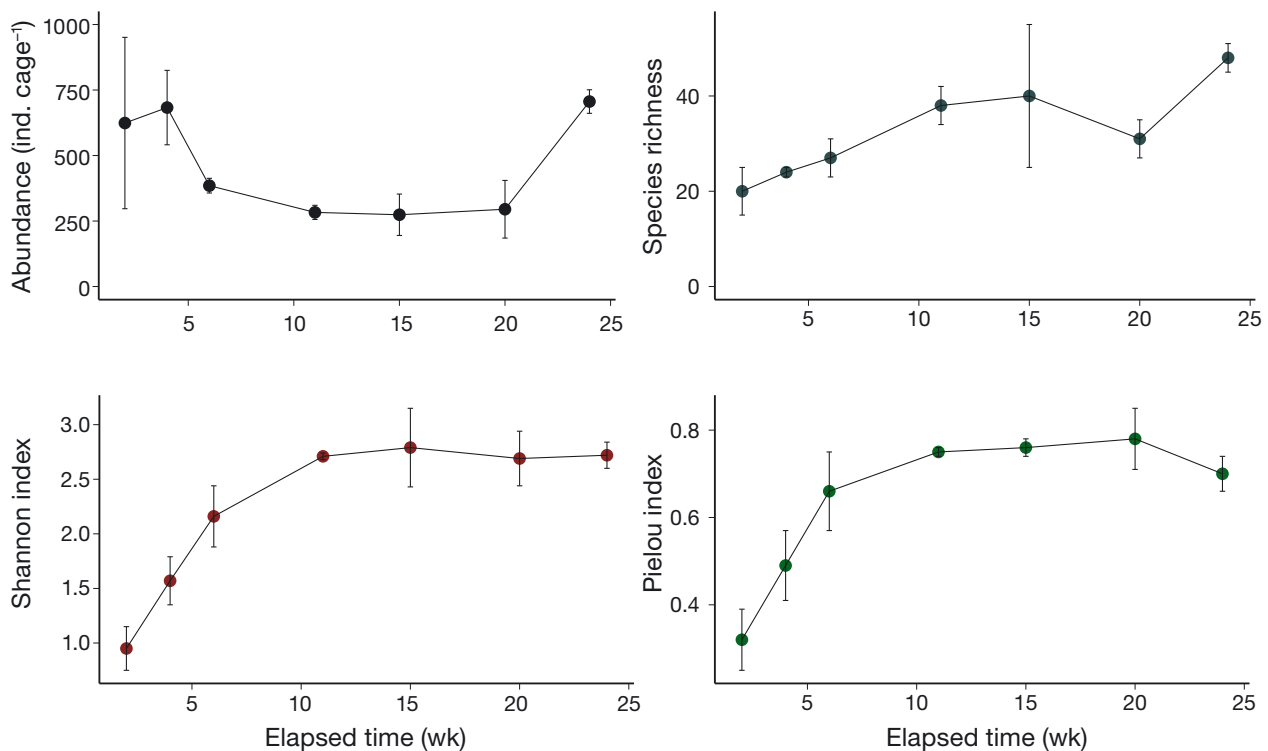


Fig. 1. Mean (\pm SD) change in macrofaunal community parameters in kelp *Laminaria hyperborea* fragment accumulations over time and with decay (from 2–24 wk) ($n = 3$ cages)

more, diversity was higher ($H' > 2.16$), as was evenness ($J' > 0.66$), reflecting a more regular relative abundance of each species. At the end of the experiment, the community was characterized by high abundance (mean $N > 700$ ind. cage⁻¹) and maximum species richness (mean $S = 48$ species). H' (2.72) and J' (0.70) values remained high, although some taxa dominated the community in terms of abundance (e.g. *Pisidia longicornis*, *Rissoa* spp., *Anomia ephippium*).

The CFA showed that 74% of the total inertia was explained by the first 2 axes (Fig. 2). The temporal variation of the community was interpreted on axes 1

and 2 of the CFA. The first axis explained 54% of the total inertia and clearly contrasted the community of the 2 first sampling times (Weeks 2 and 4; $\sum\text{CTR} = 49.5\%$) to the intermediate (Weeks 11 and 15; $\sum\text{CTR} = 13.0\%$) and final (Weeks 20 and 24; $\sum\text{CTR} = 36.6\%$) sampling times. The community at Weeks 2 and 4 was dominated in abundance by the amphipod *G. locusta* and the isopods *I. balthica* and *Idotea neglecta*. In contrast, Weeks 20 and 24 were characterized by numerous species: the decapods *Galathea squamifera* and *P. longicornis*, the amphipod *Aora gracilis*, the gastropod *Steromphala cineraria* and the microgastro-

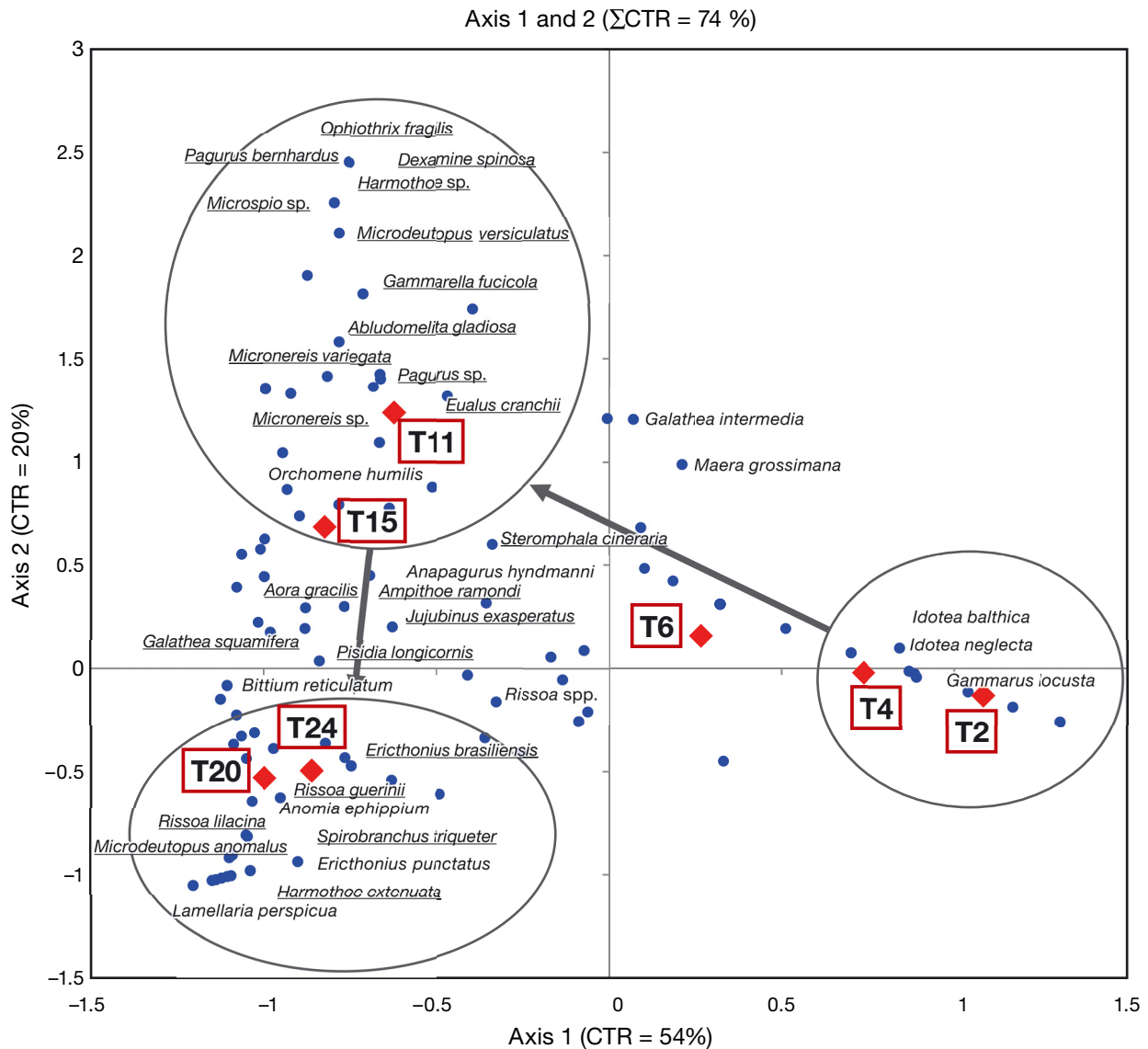


Fig. 2. Correspondence factor analysis of macrofauna community colonizing kelp *Laminaria hyperborea* fragment accumulations over time and with decay (from 2–24 wk). Projection of time and species structuring on the plane of factorial axes 1 and 2. A total of 170 species were included in the analysis. Species with a relative contribution (CTR) greater than the null hypothesis of equal contribution are named; species with a squared cosine > 0.5 are underlined. The community at each sampling time is represented by a red square. Community succession is indicated with grey arrows that connect the 3 distinct community stages (circled in black)

pods *Rissoa* spp., and some sessile species, such as the bivalve *A. ephippium* and the annelid *Spirobranchus triqueter* that was found on decayed fronds.

The second axis explained 20% of the total inertia and contrasted the community of intermediate sampling times (Weeks 11 and 15; Σ CTR = 67.2%) to that of the final sampling times (Weeks 20 and 24; Σ CTR = 30.4%). The community at Weeks 11 and 15 was characterized by numerous species: amphipods (e.g. *Gammarella fucicola*, *Abludomelita gladiosa*, *Dexamine spinosa*), polychaetes (e.g. *Micronereis variegata*, *Microspio* sp.), and crustacean decapods (e.g. *Pagurus* sp., *Eualus cranchii*) and a high abundance of the gastropod *S. cineraria*.

3.2. Description of the food web and changes in basal food source

The $\delta^{13}\text{C}$ values of macrofauna species were located between the $\delta^{13}\text{C}$ of the 2 major food sources: POM and decaying *Laminaria hyperborea* (Fig. 3). These 2 sources had distinct $\delta^{13}\text{C}$ values with no overlap of data. *L. hyperborea*, more ^{13}C -enriched,

had mean values of -17.1 ± 1.4 and $5.7 \pm 0.6\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, and POM had values of -22.7 ± 1.1 and $5.9 \pm 1.8\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The associated food web was globally characterized by 2 levels of consumers: primary consumers, represented by suspension feeders, grazers and detritus feeders, and secondary consumers (or predators), represented by several species of fish and large individuals of *P. serratus* at the last sampling times.

Source contributions for primary consumer diets estimated using Bayesian mixing models are shown in Fig. 4. *G. locusta* and *S. cineraria* diets depended mainly on the *L. hyperborea* source. The CTR of *L. hyperborea* was nearly constant during the experiment for these 2 species. The contribution of *L. hyperborea* varied from 0.70–0.75 for *G. locusta* between Weeks 2 and 6 (Fig. 4A) and from 0.60–0.75 for *S. cineraria* for the whole experiment (Fig. 4B). In contrast, *P. longicornis* fed preferentially on POM. The contribution of the POM in its diet varied from 0.75–0.90 between Weeks 6 and 15 (Fig. 4C).

Intra-specific variation during the decay process showed different patterns depending on the species. *S. cineraria* showed a very stable isotopic composi-

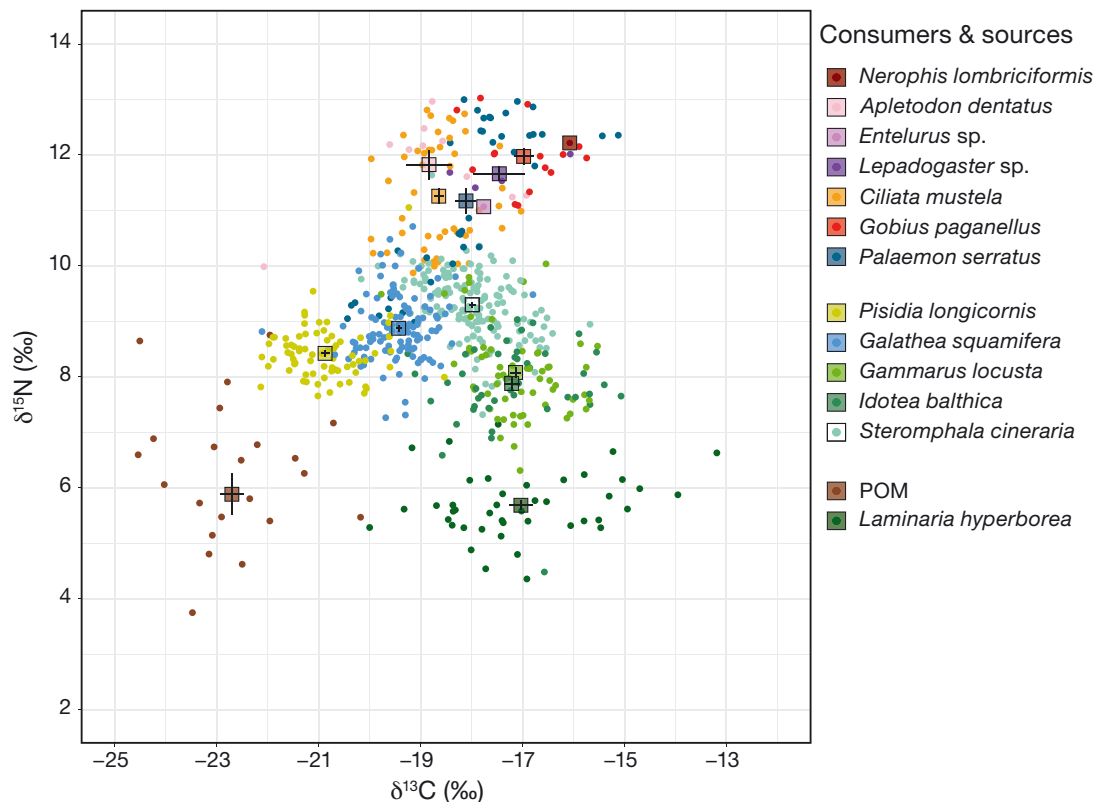


Fig. 3. Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions of the 2 main food sources (decaying kelp *Laminaria hyperborea* and particulate organic matter, POM) and the most abundant or characteristic consumers within the kelp fragment accumulations for all sampling times

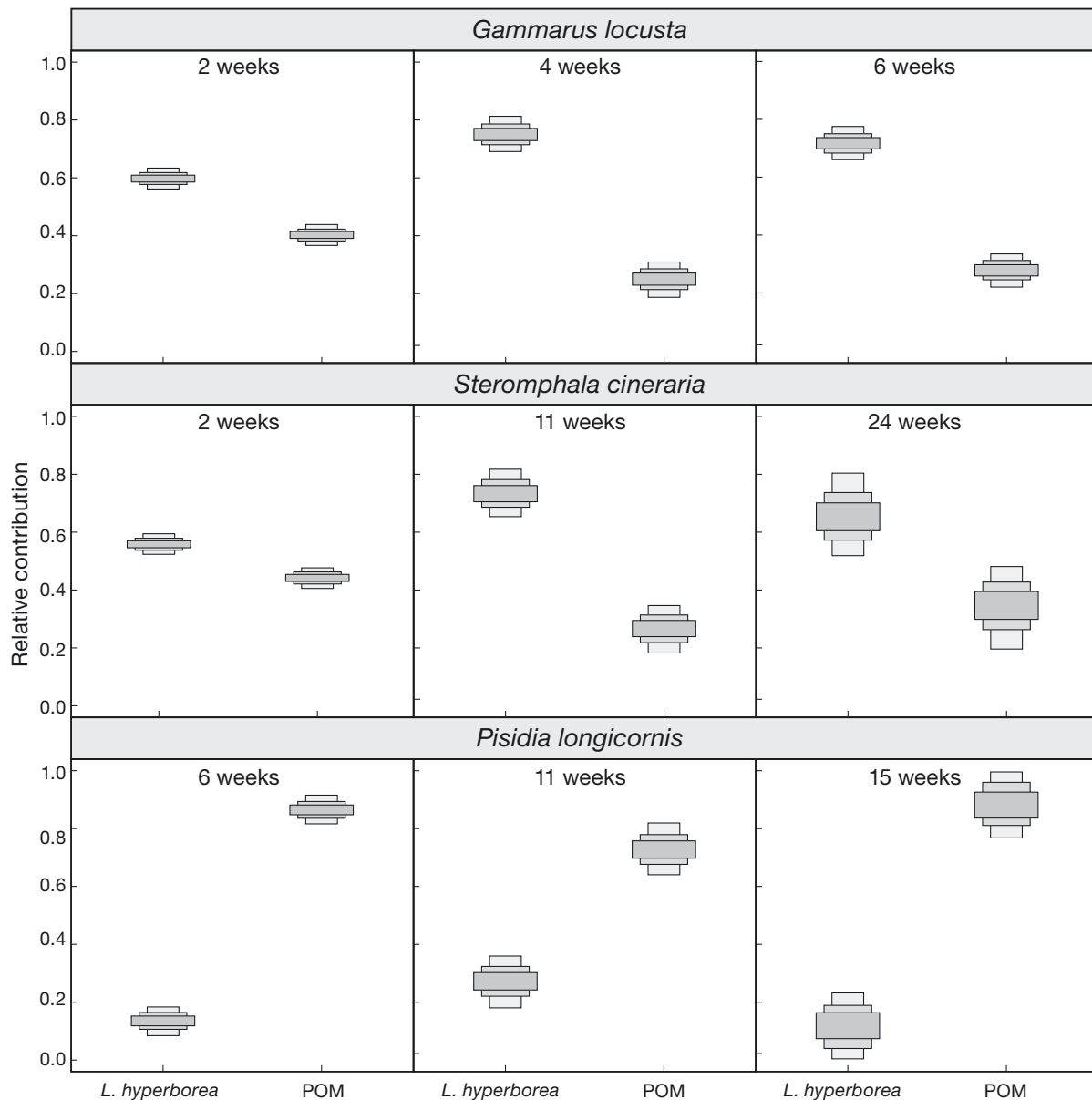


Fig. 4. Relative contribution of the 2 main food sources (decaying *Laminaria hyperborea* and particulate organic matter, POM) to the diet of 3 macrofaunal species at different sampling times, obtained using the stable isotope mixing model package in R. Density plots indicate the 50, 75 and 95% credible intervals

tion with a slight depletion in ^{13}C that mimicked the *L. hyperborea* depletion in ^{13}C over time. *G. locusta* showed an increase in $\delta^{13}\text{C}$ values, but no change in $\delta^{15}\text{N}$ values. Its isotopic composition tended to converge towards *L. hyperborea* $\delta^{13}\text{C}$ values. Inversely, *Ciliata mustela* showed no change in $\delta^{13}\text{C}$, but an increase in $\delta^{15}\text{N}$ over time. *P. serratus* showed a strong change in isotope composition for both carbon and nitrogen: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ increased from Weeks 4–15 (Fig. 5).

4. DISCUSSION

The ecological role of kelp forests is well documented, but the role of exported kelp detritus has certainly been underestimated in terms of resource availability and habitat structure. Studying the communities and food webs associated with kelp fragment accumulations helps us understand the role of kelp after exportation and accumulation in shallow subtidal conditions. During our experiment, *Lami-*

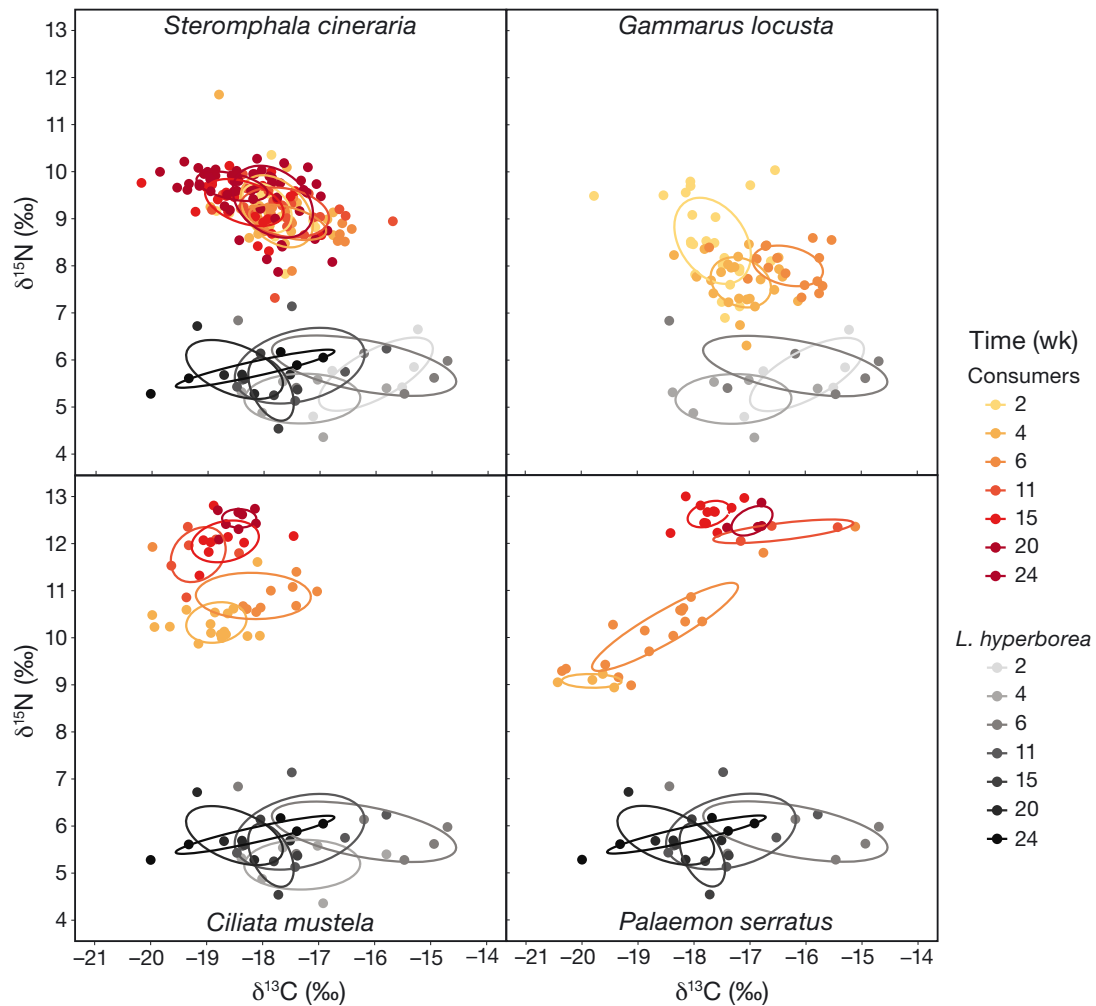


Fig. 5. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of 4 species of consumers (orange scale) and *Laminaria hyperborea* (grey scale) during the sampling time (from 2–24 wk). Ellipses: standard ellipses analysis (SEAc), performed using stable isotope Bayesian ellipses in R (Jackson et al. 2011)

naria hyperborea fragments were rapidly colonized by an abundant and diverse macrofaunal community. A total of 170 species was found inhabiting the accumulation during the 24 wk experiment. Macrofaunal species included grazers, detritus feeders, omnivores, suspension feeders and predators.

4.1. Macrofauna community succession

Our experimental accumulation acted as magnet for the surrounding fauna as described by Duggins et al. (2016) and were very rapidly colonized. The patterns of colonization and succession were typical of dynamics observed in systems when new spaces or new resources become available (Frontier et al. 2008). The first stage was characterized by a community with low

diversity, composed of 'pioneer' or 'opportunistic' species that rapidly colonized the fragments in high abundances (Frontier et al. 2008). *Gammarus locusta* and *Idotea balthica* can be considered pioneer species in our community succession. The arrival of amphipod populations at the first stage of a succession has also been observed in an experimental accumulation of *L. hyperborea* in a deep area of the Oslofjord in Norway (Ramirez-Llodra et al. 2016) as well as on *Saccharina latissima* detritus deposits on a shallow sandy bottom site off Nova Scotia, Canada (Krumhansl & Scheibling 2012b). This is also the case with seagrass detritus; litter accumulations may be considered as a pulsed system, where the arrival of new material boosts the presence of pioneer species (Remy et al. 2017).

The second stage was associated with community 'maturation'. The community became more diverse

and the food web, more complex. The community was influenced by new species interactions with more trophic guilds. The abundance of suspension feeders increased (e.g. *Pisidia longicornis*) and predators appeared and increased in abundance (e.g. *Ciliata mustela*). Species were more specialized on resources and space.

The third stage was distinctive because the kelp fragment accumulation, which constituted the main food source and habitat, began to decay. The biomass of kelp fragments was lower (25% of initial biomass at Week 20) and as a consequence, habitat complexity reduced. Furthermore, the fragments showed signs of degradation with a weakening of tissue structure and an increase of biofilm microbial activity (de Bettignies et al. 2020). The community changed with the recruitment of sessile fauna on the fragment surfaces (e.g. *Anomia ephippium*, *Spirobranchus triqueter*) accompanied by a shift in dominance, favouring small gastropods that fed on kelp biofilm. Changes in communities due to modification of the properties of the resources has been observed in various systems, such as deposit of detritus of *S. latisima* and *Codium fragile* in a shallow subtidal area (Krumhansl & Scheibling 2012b) or wood falls in a mangrove swamp (Laurent et al. 2013).

4.2. Structure and development of the food web and contribution of *L. hyperborea* as a food source

In total, 12 species were selected for food web analyses, representing the most abundant and characteristic species of the different guilds (grazers, detritus feeders, omnivores, suspension feeders and predators) according to the literature. Species were located in the isotope space between the 2 sources, POM and *L. hyperborea*. POM represented the pelagic food source from the water column, composed of suspended organic matter and phytoplankton. The *L. hyperborea* fragments represented the benthic source, composed of kelp tissues, the microbiome forming the biofilm and the micro-epiphytes present on the blade fragment surfaces. It was not possible to discriminate among these different sources attached to the fragment surface during the *in situ* experiments. Furthermore, the superficial microphytobenthos of the underlying sediment was hard to sample by SCUBA diving. We assumed that the kelp fragments and their associated epiflora were the major benthic sources for the macrofauna inhabiting the accumulation.

The considered food web showed 2 trophic levels: primary consumers and predators composed of sev-

eral fish species and adult *Palaemon serratus*. In this experiment, we excluded the presence of large predators by our experimental setup, because the mesh size (1 cm) of the cages limited access to species belonging to the third trophic level. The fragments of *L. hyperborea* showed a decrease in $\delta^{13}\text{C}$ values over the degradation process. The same pattern of decreasing $\delta^{13}\text{C}$ values has been described for more distal and decaying tissues compared to the basal part of blades for *L. hyperborea* (Fredriksen 2003) and for *L. digitata* (Buchholz et al. 2019). Among the primary consumers investigated, some species seemed to preferentially feed on *L. hyperborea* during its decay (*Steromphala cineraria*, *I. balthica*, *G. locusta*). In contrast, *P. longicornis* fed preferentially on POM, in accordance with its suspension-feeding behaviour (Nicol 1932). Interestingly *P. serratus* individuals appeared to change their feeding preference from POM at Week 6 to *L. hyperborea* from Week 11, and their $\delta^{15}\text{N}$ values simultaneously increased, possibly indicating a change in trophic level from primary to secondary consumer. These changes can be related to the maturation of individuals from juvenile to adult stages, because individuals sampled at Week 6 were small compared with those at Weeks 11–24. According to Forster (1959), *P. serratus* can graze on diatoms and macrophytes, scavenge detritus and prey on small crustaceans. As predators, the size and type of prey is often related to their body size (Guerao & Ribera 1996). The changes in isotope composition during the experiment indicated differences in feeding habits depending on individual maturation.

4.3. Comparison with other systems

Kelp accumulations showed clear structural similarities with *Posidonia oceanica* leaf litter. *P. oceanica* litter and kelp detritus can form large accumulations with a complex 3-dimensional structure, and both kinds of detritus decay at a similar rate (Harrison 1989, Hemminga & Nieuwenhuize 1991, de Bettignies et al. 2020). Furthermore, communities from these 2 macrophytodetritum accumulations strongly resemble each other. Arthropods dominate the communities, with a prevalence of amphipods followed by isopods. The 2 genera *Gammarus* and *Idotea* are particularly abundant. Annelids, especially *Platyneireis dumerilii*, are well represented in both habitats. Gastropods are also well represented, but the species differ. Comparing total diversity, the *L. hyperborea* detritus community appears more diverse, with a total of 170 species compared with the *P. oceanica*

detritus community harbouring a total of 115 species (Remy 2016).

In contrast, kelp detritus accumulation and kelp forest communities are very different. Although many species are found in both ecosystems (e.g. *S. cineraria*, *Rissoa parva*, *Galathea squamifera*, *P. dumerilii*), kelp forests are 4 times more diverse than kelp detritus, and their communities are dominated in biomass by sessile suspension feeders (Leclerc et al. 2013b, 2015). These differences are explained by the high number of niches within kelp forests and the high complexity provided by associated epiphyte macroalgae (Leclerc et al. 2016). Furthermore, kelp forests are perennial habitats in which sessile communities can mature, whereas kelp detritus is limited in time (de Bettignies et al. 2020).

5. CONCLUSIONS

Our study showed that accumulated kelp detritus in the shallow subtidal was rapidly colonized by an abundant and diverse community of macrofauna. During kelp decay, clear community succession occurred with a maturation of community and food web structure, although the habitat that it constituted was destined to disappear. Detritus derived from *L. hyperborea* became the trophic base of a complex food web that included numerous species belonging to various feeding guilds. Other kelp species and different locations of detritus accumulations still have to be investigated to more precisely understand the role of kelp detritus in shaping the macrofaunal community and trophic food web in the receiving ecosystems. The dependency of certain coastal ecosystems on kelp detritus needs to be incorporated more in ecosystem modelling. In coastal environments, the coupling between kelp detritus and the receiving ecosystem can be particularly important within soft-sediment ecosystems, where primary production is generally low and the annual budget is sometimes heterotrophic (e.g. intertidal soft sediment; Migné et al. 2009).

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