



# Intertidal ecosystem engineer species promote benthic–pelagic coupling and diversify trophic pathways

Auriane G. Jones<sup>1,2,3,6,\*</sup>, Stanislas F. Dubois<sup>1</sup>, Nicolas Desroy<sup>2</sup>, Jérôme Fournier<sup>4,5</sup>

<sup>1</sup>IFREMER, Centre de Bretagne, DYNECO, Laboratoire d'Ecologie Benthique Côtière (LEBCO), 29280 Plouzané, France

<sup>2</sup>IFREMER, Laboratoire Environnement et Ressources Bretagne nord, 35801 Dinard cedex, France

<sup>3</sup>ESE, Ecology and Ecosystems Health, Agrocampus Ouest, INRAE, 35042 Rennes, France

<sup>4</sup>CNRS, UMR 7204 CESCO, 75005 Paris, France

<sup>5</sup>MNHN, Station de Biologie Marine, 29182 Concarneau cedex, France

<sup>6</sup>Present address: MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

**ABSTRACT:** Ecosystem engineering is a ubiquitous process by which the biological activity of a species shapes habitat diversity and often creates local biodiversity hotspots. The honeycomb-worm *Sabellaria alveolata*, an intertidal ecosystem engineer, actively builds reefs across Europe by aggregating sand. Here, we used carbon and nitrogen isotopic compositions measured on basal resources and benthic–demersal consumers (fish, mega- and macroinvertebrates) to empirically investigate how non-trophic interactions (ecosystem engineering) modify food web structure and functioning. Three sediment types corresponding to different substrata and species assemblages were sampled: a control soft sediment (medium to muddy sand, before the establishment of *S. alveolata*), the sediment engineered by *S. alveolata* (hardened 3D structures), and the soft sediment under the influence of *S. alveolata* (associated sediment). Using consumer community isotopic biplots (biomass-weighted), niche metrics (standard ellipse area), and mixing models, we found that *S. alveolata*, through the physical structure it creates, the stimulation of basal resources (microphytobenthos and *Ulva*), and the diversification of suspension-feeding species, promotes benthic–pelagic coupling and a habitat-wide form of 'gardening,' which further leads to trophic pathway diversification and limits trophic competition between the engineer species and associated suspension-feeders. Furthermore, our results help to refine the definition of *S. alveolata* reefs as the sum of the engineered and associated sediments since they are part of a single reef food web coupled by the stimulated basal resources and consumers. Finally, the non-trophic and trophic interactions mediated by *S. alveolata* and the associated macrofauna seem to promote the establishment of a temporally stable and probably highly resilient reef habitat.

**KEY WORDS:** Stable isotopes · Food web · Gardening hypothesis · Non-trophic interactions · Microphytobenthos · Suspension-feeding · Habitat modifier

Resale or republication not permitted without written consent of the publisher

## 1. INTRODUCTION

The study of landscapes, either terrestrial or aquatic, has long included the investigation of habitat diversity and its underlying drivers (McGarigal et al. 2012), classically focusing on environmental factors like geomorphology and physical disturbance (Stallins 2006).

Yet organisms themselves can also be at the origin of habitat diversity through their biological activity, as first conceptualized by Jones et al. (1994). These species are termed 'ecosystem engineers,' a unifying concept characterized by organisms able to directly or indirectly modulate the availability of resources to other species by modifying the physical properties of abiotic

material (e.g. sediment, soil) or biotic material (e.g. trees in the case of beavers, Wright et al. 2002). Ultimately, these organisms can modify, maintain, and create habitats, often leading to changes in species assemblages and the creation of biodiversity hotspots (Jones et al. 1997, Romero et al. 2015). Physical ecosystem engineers, also known as habitat modifiers (van der Zee et al. 2016), often occur in stressful environments like terrestrial deserts and intertidal zones where they create new habitats characterized by less extreme environmental conditions (Jones et al. 1997, Romero et al. 2015). Many such habitat-building ecosystem engineers are present along temperate coasts: autotrophs like cordgrass (e.g. *Spartina* spp.), seagrass (e.g. *Zostera marina*), and macroalgae (e.g. *Laminaria hyperborea*), reef-building heterotrophs like mussels (e.g. *Mytilus edulis*), oysters (e.g. *Crassostrea virginica*), tube-building polychaetes (e.g. *Lanice conchilega*, *Phragmatopoma caudata*), and gastropods (e.g. *Dendropoma petraeum*) (Gutiérrez et al. 2012, Goldberg 2013).

Ecosystem engineering was first based only on relatively complex non-trophic interactions, conceived in opposition to direct interactions such as predator-prey or plant-pollinator interactions (Jones et al. 1994). Indeed, the ecosystem engineer was not considered according to its trophic role or position but as a promoter of new community-wide interactions through a series of structural, abiotic, and biotic changes and associated feedbacks (Jones et al. 2010). Consequently, the ecosystem engineer concept has only recently been integrated in theoretical and empirical food web studies (Sanders et al. 2014, De Smet et al. 2015, van der Zee et al. 2016), despite the ubiquity of ecosystem engineers and the potentially broad-scale conclusions such a coupling could foster. Theoretically, an ecosystem engineer able to modify consumable abiotic resources like nutrients could stimulate primary producer diversity and abundance, which could then modify the properties of the entire food web (Layman et al. 2007, Sanders et al. 2014, van der Zee et al. 2016). For example, higher producer diversity can lead to trophic pathway diversification, consumer niche differentiation, and ultimately to larger community-wide trophic niches and to more stable food webs (Zhao et al. 2019), thereby coupling non-trophic (ecosystem engineering) and trophic interactions.

Coastal reef-building polychaetes and mollusks (i.e. structural ecosystem engineers, Berke 2010) can locally increase the biomass of benthic microalgae through the structures they build, the resulting abiotic changes, and their biological activity (Engel et

al. 2017, Echappé et al. 2018, Jones et al. 2018, Bruschetti 2019), and the resulting reefs can serve as support for various macroalgae (e.g. *Ulva* spp., *Ceramium* sp.) (Vizzini et al. 2012, Dubois & Colombo 2014). Ultimately, many coastal reef-building engineer species (e.g. *M. edulis*, *Magallana gigas*, *D. petraeum*, *Ficopomatus enigmaticus*, *Sabellaria alveolata*) diversify basal trophic resources (higher producer diversity and biomass). Several questions emerge from the producer diversification associated with ecosystem engineering: Is this higher producer diversity associated with larger community-wide trophic niches and primary consumer niche differentiation? How important are these stimulated basal trophic resources in fueling the food web? We investigated these questions using the intertidal ecosystem engineer *S. alveolata* as a case study. Overall, our aim was to understand how structural ecosystem engineers (Berke 2010) like *S. alveolata* affect food web structure and functioning, focusing on littoral organic matter transfers and primary consumers.

The honeycomb-worm *S. alveolata* is a gregarious intertidal polychaete, commonly found along the European coastline from Scotland and Ireland to Morocco (Muir et al. 2016). This sedentary polychaete lives in a tube made of bioclastic sand particles glued together with an organic cement (Le Cam et al. 2011, Buffet et al. 2018). Through the building of these tubes, this species transforms soft sediments into 3-dimensional hard structures (engineered sediments), forming a new habitat (Dubois et al. 2002, Bruschetti 2019). These hard structures, called reefs, are fixed atop rocks and pebbles, and in rarer cases are present exclusively in soft sedimentary areas, covering surfaces from a few square meters to dozens of hectares (Holt et al. 1998, Desroy et al. 2011) and ultimately building the largest intertidal bioconstructions in Europe (Noernberg et al. 2010). *S. alveolata* leads to the establishment of 2 distinct macrobenthic assemblages in the engineered sediments and in the soft sediments under its influence (associated sediments); both assemblages differ from those macrobenthic communities characterizing the soft sediments outside the influence of the reef (control sediments). The engineered sediment community presents the highest species richness and is characterized by an original assemblage of species typically found on rocky shores (e.g. *Perinereis cultrifera*, *Steromphala* spp., *Porcellana platycheles*), in sandy to muddy sediments (e.g. *Glycera alba*, *Mediomastus fragilis*, *Corophium volutator*), and even on land (*Axelsonia littoralis*, *Hydrogamasus* sp.) (Jones et al. 2018).

Through its engineering properties, *S. alveolata* also affects 2 basal trophic resources: microphyto-benthos (MPB) biomass and the presence of green macroalgae (*Ulva* spp.). Indeed, the MPB biomass increases in the presence of this ecosystem engineer, as shown by comparing the associated sediments with the control sediments (Jones et al. 2018). Once resuspended by tidal currents, this stimulated basal trophic resource can become available to the engineered sediment-associated fauna including the engineer species (Dubois et al. 2007, Ubertini et al. 2012). Green macroalgae from the genus *Ulva* also grow on the engineered sediments (Dubois et al. 2006), representing an additional basal trophic resource, directly consumable by grazers and indirectly consumable by suspension- and deposit-feeders once detached and fragmented (Dubois & Colombo 2014, Hondula & Pace 2014). Consequently, 2 additional questions arise: (1) Are the stimulated basal trophic resources, MPB and *Ulva* spp., consumed by the ecosystem engineer, as evidenced in the ‘gardening’ hypothesis (Hylleberg 1975)? This hypothesis was first developed for the lugworm *Abarenicola pacifica*, which stimulates microbes naturally present around its burrow, via its digestion and the production of feces, and then consumes these stimulated microbes. (2) The second question extends this gardening hypothesis to other primary consumers associated with the engineer species and paves the way to a potential habitat-wide form of gardening, as previously shown for the tubicolous amphipod *Haploops nirae* (Rigolet et al. 2014).

To answer the aforementioned questions, we extensively sampled the consumers (macro- and mega-fauna) and potential basal resources present in the previously defined engineered, associated, and control sediments, and measured their carbon and nitrogen isotopic compositions (Majdi et al. 2018). We first focused on the consumer community and compared the food web structure (biomass distribution and isotopic niche) of the 3 sediment type communities. We then estimated the relative importance of local benthic basal resources (i.e. MPB and *Ulva* spp.) in fueling each food web, by focusing on the primary consumer trophic level and in line with the gardening hypothesis. We hypothesized that the engineered and associated sediment communities would: ( $H_1$ ) show wider isotopic niches than the control sediment community, and ( $H_2$ ) rely more on local benthic basal resources (i.e. MPB and *Ulva* spp.) than the control sediment community (i.e. only MPB) because of the additional resources stimulated by *S. alveolata* through reef engineering. We also estimated the as-

simulated diet of the engineer species along with 4 associated and abundant suspension-feeding species, to further investigate the gardening hypothesis and the potential inter-specific trophic niche differentiation (Dubois et al. 2007, Dubois & Colombo 2014) in the very densely populated engineered sediment (Jones et al. 2018). Finally, to get a sense of the temporal variability in the food web structure and functioning of each sediment type, we sampled the consumers in late February and mid-September, 2 highly contrasted times of the year in terms of phytoplankton productivity (low vs. high), abundance of basal trophic resources (low vs. high), and benthic community dynamics (pre- and post-recruitment) (Marín Leal et al. 2008, Cugier et al. 2010, Ubertini et al. 2012).

## 2. MATERIALS AND METHODS

### 2.1. Study sites

This study was conducted in the Mont-Saint-Michel Bay, a semi-diurnal macrotidal bay (14 m maximal tidal range) with an extensive intertidal zone (250 km<sup>2</sup>), located in the western part of the English Channel (France) (Bonnot-Courtois et al. 2002). The central area of the bay, where our 2 study sites are located, is at the junction of 2 tidal current regimes, a western gyre rotating clockwise and an eastern current alternating north–south (Salomon & Breton 1991, Bonnot-Courtois et al. 2002). Our first study site was the Sainte-Anne reef (i.e. reef site, 48° 38' 70" N, 1° 40' 10" W), the largest bioconstruction in Europe (Holt et al. 1998, Noernberg et al. 2010). This 2.5 km long by 1 km wide site spreads parallel to the coast and is composed of previously defined engineered sediments (ES) and associated sediments (AS), with the ES representing ca. 32 ha in 2014 (A. Jones unpubl. data).

We defined a second study site as the control site, hereafter denoted as the control sediments (CS). This 24 ha soft sediment zone was outside of the influence of the reef (1.5 km northeast of the reef), on the same bathymetric level as the reef (i.e. between the –2 and –4 m isobaths, Noernberg et al. 2010), and characterized by medium to muddy sands (Bonnot-Courtois et al. 2009) and by a species-poor community typified by the bivalve *Limecola balthica* (formerly *Macoma balthica*) (Dubois et al. 2002). This site did not present any hard structures such as rocks or boulders. We considered the CS as representing the local soft sediments before the establishment of the Sainte-Anne reef and before the combined physical and bio-

logical effects of the reef and its associated organisms on the local tropho-dynamics. Indeed, these 2 effects cannot be separated, since a reef structure with no live *Sabellaria alveolata* worms and their building activity degrades and disappears after a few years (Gruet 1972, Wilson 1976).

## 2.2. Sample collection and preparation for consumer stable isotope analyses

### 2.2.1. Over-dispersed macrofauna and infauna sampling

For the macrofauna, we randomly sampled 10 stations in the 2 sediment types from the reef site (AS and ES) and in the sediment type from the control site (CS). Each station was separated by at least 75 m. We sampled these 30 stations on foot during low spring tides, once in late February and once in mid-September 2015, hereafter referred to as winter and summer for a generalization purpose, to investigate the food web structure and functioning of the communities associated with each sediment type (CS, AS, and ES) at 2 contrasted times of the year. Winter is characterized by a low abundance of basal trophic resources, whereas in late summer, benthic and pelagic basal resources are more abundant and benthic invertebrates have recruited (Marín Leal et al. 2008, Cugier et al. 2010, Ubertini et al. 2012).

Over-dispersed macrofauna, mostly mollusk species, were sampled using a 1 m<sup>2</sup> quadrat with 3 replicates per station. For the AS and CS quadrat sampling, the first 5 cm of soft sediment were sieved through a 5 mm square mesh, while for the ES quadrat sampling, we hand-collected all visible macrofauna located on the reef and inside the reef interstices within the area of the 1 m<sup>2</sup> quadrat. Infauna and smaller macrofauna organisms were sampled using an 18.5 cm side corer (surface area = 269 cm<sup>2</sup>) to a depth of 15 cm with 1 replicate per station. To sample the CS and AS, we used a mainstream hand corer for soft sediments and sieved the soft sediment cores on site through a 1 mm square mesh. The resulting sediments were sorted in the laboratory. To sample the hardened ES (i.e. reef material), we used a specially designed metal hand corer with teeth. The ES cores were taken to the lab where they were broken apart under water, and the organisms retained on a 1 mm square mesh were collected. Finally, all collected organisms were identified to the lowest taxonomic level (generally the species level) and stored at –20°C for stable isotope analyses.

### 2.2.2. Vagile macro- and megafauna sampling

Vagile benthic and demersal macro- and megafauna organisms were sampled at the site scale (not at the sediment type scale) using traditional set nets from Mont-Saint-Michel Bay, which are like fyke nets but without wings (Secula 2011). In the control and reef sites, 6 nets were positioned at low tide, once in early March 2015 and once in mid-September 2015, with their opening landward and left for 2 consecutive tidal cycles (24 h). In the lab, all the sampled organisms were sorted, identified to the lowest taxonomic level (generally the species level), and finally stored at –20°C for stable isotope analyses.

### 2.2.3. Sample preparation

For fish, mollusks, and shrimps, we dissected muscle tissue. For smaller species (e.g. polychaetes), we used the whole body, and removed the guts when possible. For very small species (e.g. Collembola), we pooled several individuals to meet the minimum required weight for stable isotope analyses. For calcified organisms (crustaceans other than shrimp and echinoderms), a subsample was acidified (10% HCl) to remove any inorganic carbonates and then used to determine the carbon isotopic composition, while a subsample was left untreated for the nitrogen isotopic composition. All samples were then rinsed with Milli-Q water and freeze-dried. Each animal sample was ground to a homogeneous powder and 1 mg was encapsulated. When possible, at least 3 replicates per species and per station were analyzed. We used ultra-clean light tin capsules for all samples (consumers and organic matter sources).

## 2.3. Sample collection and preparation for organic matter source stable isotope analyses

We sampled the different basal trophic resources every month over a period of 1 yr (January 2015 to January 2016) to consider the temporal variability of their respective isotopic composition. At the control site (CS), the organic matter available to primary consumers was mainly composed of marine suspended particulate organic matter (POM; mainly phytoplankton) and of MPB. At the reef site (AS and ES), green macroalgae (*Ulva* spp., ULV) growing on the ES was considered as a third potential basal resource. We verified *a posteriori* that the sediment organic matter (SOM) was a mixture of the 2 or 3

aforementioned basal resources. At the 2 study sites, the riverine terrestrial inputs of organic matter are extremely limited and therefore were not considered as a potential basal resource (Riera 2007).

### 2.3.1. Marine suspended POM

For POM, marine subsurface water (1 m below the surface) was collected just before high tide using a Niskin bottle and at 1 sampling point seaward of the reef site. We considered POM as being distributed homogeneously between our 2 study sites based on the tidal regimes (see Section 2.1) and the strong tidal currents ( $0.4\text{--}1.5\text{ m s}^{-1}$ ) characterizing the zone of the Mont-Saint-Michel Bay where both sites are located (Salomon & Breton 1991, Bonnot-Courtois et al. 2002). Consequently, we considered POM to have similar isotopic compositions in the reef and control sites (Ayata et al. 2009). In the lab, water samples were prefiltered on a  $200\text{ }\mu\text{m}$  square mesh to remove macrodetritus and zooplankton (Marín Leal et al. 2008), then filtered on 3 precombusted GF/F filters (4 h,  $450^\circ\text{C}$ ) and finally rinsed with Milli-Q water (3 replicates  $\text{mo}^{-1}$ ). The filters were freeze-dried, and half of each filter was acidified for 48 h with 32 M HCl fumes to remove any traces of inorganic carbonates (Lorrain et al. 2003), before being oven dried at  $30^\circ\text{C}$ . Every half filter was then scraped with a clean scalpel and ground to a homogeneous powder, and 10 mg of the powder were encapsulated for stable isotope analyses. The non-acidified samples were used to determine the nitrogen isotopic compositions while the acidified ones were used for the carbon isotopic compositions.

### 2.3.2. MPB, SOM, and *Ulva* spp.

MPB, SOM, and ULV were sampled during low spring tides. For MPB and SOM, the first centimeter of the AS was sampled, using a 1 cm deep plastic petri dish ( $57\text{ cm}^2$ ), at 2 points inside the reef site (6 replicates  $\text{mo}^{-1}$ ). For ULV, green macroalgae (*Ulva* spp.) were collected from the ES within a 10 m radius of the same 2 previously mentioned points in the reef (2 replicates  $\text{mo}^{-1}$ ). All samples were kept at  $-20^\circ\text{C}$  for stable isotope analyses. To extract the MPB from the sediment, we followed the protocol of Marín Leal et al. (2008), which is a modified version of Blanchard et al. (1988) (Text S1 in the Supplement at [www.int-res.com/articles/suppl/m660p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m660p119_supp.pdf)). The extracted MPB was freeze-dried and ground to a homo-

geneous powder, and 1 mg of powder was encapsulated. For the SOM analyses, a sediment subsample was acidified (10% HCl) to remove inorganic carbonates and rinsed with Milli-Q water, while the rest was left untreated. All of the material was then freeze-dried, and 40 mg of sediment were encapsulated. The non-acidified samples were used to determine the nitrogen isotopic compositions while the acidified ones were used for the carbon isotopic compositions. For the ULV analyses, epibionts were scraped off the green algae fragments using a clean scalpel. The clean algae fragments were then rinsed with Milli-Q water, freeze-dried, and finally ground to a homogeneous powder, 3 mg of which were encapsulated.

## 2.4. Stable isotope analyses and data preparation

Carbon and nitrogen isotopic compositions were measured with a Thermo Delta V isotope mass spectrometer coupled via a ConFlo IV to a Carlo Erba NC2500 elemental analyzer (Cornell University Stable Isotope Laboratory). Isotope ratios of carbon and nitrogen were reported using the standard  $\delta$  notation as units of parts per thousand (‰) relative to the international reference standards:

$$\delta X = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 1000 \quad (1)$$

where  $X = {}^{13}\text{C}$  or  ${}^{15}\text{N}$ , and  $R = {}^{13}\text{C}/{}^{12}\text{C}$  for carbon and  ${}^{15}\text{N}/{}^{14}\text{N}$  for nitrogen. Vienna Pee Dee belemnite limestone and atmospheric nitrogen were used as reference standards for carbon and nitrogen, respectively. The analytical precision was 0.09‰ for both isotopes.

The biomass (wet weight) per  $\text{m}^2$  of the species sampled across the cores and quadrats was estimated using the catch per unit effort (CPUE) method, i.e. the ratio between the total catch biomass and the total amount of effort to harvest the catch biomass (Jones et al. 2018). If a species was collected by only one sampling method, its biomass per  $\text{m}^2$  was estimated using the corresponding sampling surface ( $1\text{ m}^2$  for the quadrats and  $269\text{ cm}^2$  for the cores). For the 17 species in winter and 15 species in summer sampled by both methods, their biomass per  $\text{m}^2$  was calculated using the cumulated biomass divided by the sum of the surface sampled by each equipment type ( $1.0269\text{ m}^2$ ) (Jones et al. 2018). In order to jointly consider the species sampled by the cores and/or quadrats and by the set nets, we estimated the instantaneous mean sediment surface sampled by the nets ( $S$ , in  $\text{m}^2$ ) using the annual mean bottom current speeds for the area ( $v = 0.188\text{ m s}^{-1}$  in 2015) extracted from the 500 m resolution MARS3D-AGRIF model (Caillaud et al.

2016), the mean width of the set nets ( $w = 1.45$  m), and the mean fishing time of each net ( $t = 7$  h). Using the following formula,  $S = v \times w \times t \times 3600$ , we estimated  $S$  as 6869 m<sup>2</sup> and used it to calculate the biomass per m<sup>2</sup> of the sampled species. Based on the biomass per m<sup>2</sup> estimated with the cores, the quadrats, and the set nets, we calculated the mean relative contribution of each species to the total biomass of the CS, AS, and ES communities in winter and summer.

The monthly basal resource sampling was used to calculate the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (and associated standard deviations) of the POM, SOM, MPB, and ULV, which is displayed on the isotopic biplots (see Fig. 1) and used in the Bayesian mixing models. All January to March and October to January (2016) MPB samples (plus two April replicates and one August replicate) could not be considered because the quantity of MPB extracted was too low to allow a clean signal. All March, May, and July to September POM samples (plus two January 2016 replicates) were not considered because of abnormally high  $\delta^{13}\text{C}$  values ( $> -15\text{‰}$ ). None of the November and December 2015 ULV samples were considered because of abnormally low  $\delta^{15}\text{N}$  values ( $< 4\text{‰}$ ). Finally, one May, two August, and one January 2016 SOM sample were not considered either because of abnormally high  $\delta^{13}\text{C}$  values ( $> -12.5\text{‰}$ ) or low  $\delta^{15}\text{N}$  ( $< 4\text{‰}$ ).

Finally, the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the megafauna species sampled using the set nets deployed in the reef site were displayed on both the AS and ES isotopic biplots (see Fig. 1), and we applied a correction factor to all *Crepidula fornicata* isotopic compositions, as recent observations revealed calcium carbonate nodules in the muscular foot of *C. fornicata* (Androuin et al. 2019).

## 2.5. Data analyses

First, to estimate the overall width of each community food web (CS, AS, and ES), we calculated several community-wide metrics based on the mean consumer  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, using the 'siar' (Parnell & Jackson 2013) and 'SIBER' (Jackson et al. 2011) packages developed in R (R Core Team 2018). The total area of the convex hull (TA), which encompasses all the consumer isotopic compositions (Layman et al. 2007), was first calculated to account for the overall trophic niche space occupied by each consumer community. The major drawback of the TA is its high sensitivity to extreme isotopic compositions (Brind'Amour & Dubois 2013). In order to limit this bias, we also calculated the standard ellipse area (SEA), which

only encompasses 40% of the data, and a Bayesian estimate of this metric (SEA<sub>B</sub>) to account for the uncertainty in the isotopic compositions (Jackson et al. 2011). To compare the size of 2 SEAs (between sediment types or between sampling times), we considered their respective Bayesian posterior distributions and calculated the probability that one SEA is smaller than another. Finally, we calculated the percent overlap between 2 isotopic niches (SEA) in relation to the surface of the smallest ellipse (%).

Pelagic organic matter, MPB, and ULV differ in their respective  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Riera 2007, Dubois & Colombo 2014), and this isotopic dissimilarity is passed on to the primary consumers relying on each basal resource. Species reported in the literature (Fauchald & Jumars 1979, Navarro-Barranco et al. 2013, Guerra-García et al. 2014, Jumars et al. 2015) or in online biological trait databases (BIOTIC, WoRMS) as being strictly suspension-feeders and/or deposit-feeders and/or grazers were considered here as primary consumers. To evaluate the importance of the different basal resources in fueling each food web, we plotted the frequency distribution of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of all primary consumers sampled in the 3 sediment types.

Finally, to quantify the relative contributions of pelagic (POM) and benthic basal resources (MPB in the CS community, MPB and ULV in the AS and ES communities) to a species' assimilated diet in winter and summer, Bayesian mixing models based on Markov chain Monte Carlo (MCMC) were implemented using the 'simmr' package in R (Parnell 2016). This method works by repeatedly guessing the values of the dietary proportions and finding the values closest to the actual data. The best estimates of dietary proportions, given the data and the model, compose the posterior distribution (Parnell et al. 2013). The mixing models were set with no *a priori* basal resource contribution (uninformative prior), using 2 tracers ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and considering 2 (POM and MPB in the CS model) or 3 (POM, MPB, and ULV in the AS and ES models) basal resources. We used the mean basal resource  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and their associated standard deviations presented in Section 2.4. To run the mixing models, *a priori* estimates of the variation in the isotopic compositions between the basal resources and consumers is required, which are termed the trophic discrimination factors (TDFs). We considered a TDF between the basal resource and primary consumer of 1 and 3.4‰ for carbon and nitrogen, respectively (McCutchan et al. 2003), with a standard deviation of 1 for both tracers. This high standard deviation was chosen to take

into account the known variability in the TDFs linked to multiple factors such as food quality, tissue turnover, environmental conditions, and taxonomic group (Vander Zanden & Rasmussen 2001, McCutchan et al. 2003, Vanderklift & Ponsard 2003). Overall, we hypothesized that consumers were feeding ad libitum and had normal growth, hence having standard turnover rates for small invertebrates and standard TDFs (Lefebvre & Dubois 2016).

Bayesian stable isotope mixing models (100 000 iterations, 3 chains) were implemented for each species known to feed at least partly on MPB, POM, or ULV and for which we had at least 3  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  replicate values. We also implemented these models at the primary consumer scale by pooling the isotope compositions of all the primary consumers sampled in each community and at each sampling time. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of some species were not located inside the space encompassing the 2 or 3 basal resources once corrected for the TDF (e.g. *Lekanesphaera rugicauda* in the summer AS, see Fig. 1) or the number of replicates was sometimes limited (e.g. *Ruditapes philippinarum*,  $n = 3$  in the winter ES, see Table S2 in the Supplement), leading to large uncertainties in the estimated dietary proportions. Using

the Bayesian mixing model outputs, we also built ternary plots representing the relative contributions of POM, MPB, and ULV to the assimilated diets of the 5 most abundant suspension-feeders of the ES. In these plots, each set of points represents the realized trophic niche of a species in winter or summer. The lack of replicates of the consumer community during each season (winter and summer) prevented us from being able to rigorously evaluate seasonal variations. Consequently, we only used our bi-annual sampling to get a sense of the similarities and differences in the food web structure and functioning of each sediment type between 2 contrasted productivity and recruitment regimes. We used R version 3.5.1.

### 3. RESULTS

#### 3.1. General structure of the consumer communities

To start, we present the general community structure of each sediment type at both sampling times by considering their respective species diversity (by taxonomic class) and the dominant (biomass) species (Table 1). The CS and AS communities were

Table 1. Species richness measured in the control (CS), associated (AS), and engineered (ES) sediments in winter (W) and summer (S) resolved into taxonomic classes with the number left of the slash indicating the total consumer richness and the number right of the slash indicating the primary consumer richness. Species accounting for >1% of the total community biomass are also indicated, with the asterisk designating secondary consumers. See Table S1 for the complete data

CS	W	S	AS	W	S	ES	W	S
<b>Polychaeta</b>	15/6	15/6	<b>Polychaeta</b>	11/7	14/7	<b>Polychaeta</b>	12/4	12/3
<i>Lanice conchilega</i>	7.2%	12.3%	<i>Cirriformia tentaculata</i>	15.1%	7.1%	<i>Sabellaria alveolata</i>	57.8%	22.7%
			<i>Goniadella bobrezkii*</i>	1.5%	0.5%			
			<i>Mediomastus fragilis</i>	0.9%	1.3%			
<b>Malacostraca</b>	13/3	9/3	<b>Malacostraca</b>	9/2	9/2	<b>Malacostraca</b>	11/3	12/3
<i>Carcinus maenas*</i>	1.2%	0.5%	<i>Carcinus maenas*</i>	2.1%	0.6%	<i>Carcinus maenas*</i>	0.04%	1.4%
						<i>Porcellana platycheles</i>	4.5%	19.4%
<b>Bivalvia</b>	9/9	10/10	<b>Bivalvia</b>	9/9	10/10	<b>Bivalvia</b>	7/7	6/6
<i>Cerastoderma edule</i>	79.9%	4.3%	<i>Magallana gigas</i>	–	1.9%	<i>Magallana gigas</i>	31.9%	49.2%
<i>Limecola balthica</i>	4.4%	80.9%	<i>Ruditapes philippinarum</i>	2.6%	9.9%	<i>Mytilus cf. galloprovincialis</i>	0.2%	1.1%
			<i>Venerupis corrugata</i>	1.0%	0.4%			
<b>Gastropoda</b>	2/1	1/0	<b>Gastropoda</b>	5/2	3/1	<b>Gastropoda</b>	8/5	8/5
<i>Tritia reticulata*</i>	1.1%	0.1%	<i>Crepidula fornicata</i>	59.0%	61.9%	<i>Crepidula fornicata</i>	1.9%	0.7%
<b>Anthozoa</b>	1/0	0/0	<b>Anthozoa</b>	1/0	1/0	<b>Anthozoa</b>	3/0	2/0
			<i>Cereus pedunculatus*</i>	4.9%	0.4%			
<b>Actinopterygii</b>	7/0	7/0	<b>Actinopterygii</b>	12/0	5/0	<b>Actinopterygii</b>	13/0	6/0
<b>Ophiuroidea</b>	1/0	2/1	<b>Ophiuroidea</b>	0/0	0/0	<b>Ophiuroidea</b>	0/0	0/0
<b>Pycnogonida</b>	1/0	0/0	<b>Pycnogonida</b>	0/0	0/0	<b>Pycnogonida</b>	2/0	1/0
<b>Sipunculidea</b>	0/0	0/0	<b>Sipunculidea</b>	3/3	2/2	<b>Sipunculidea</b>	3/3	3/3
			<i>Golfingia vulgaris</i>	6.0%	2.6%			
<b>Ascidacea</b>	0/0	0/0	<b>Ascidacea</b>	0/0	1/1	<b>Ascidacea</b>	2/2	3/3
<b>Other</b>	0/0	0/0	<b>Other</b>	0/0	0/0	<b>Other</b>	3/1	4/2
<b>Total</b>	<b>49/19</b>	<b>44/26</b>	<b>Total</b>	<b>50/20</b>	<b>45/23</b>	<b>Total</b>	<b>64/25</b>	<b>57/25</b>

characterized by a lower consumer richness than the ES. Polychaetes, followed by malacostracan crustaceans and bivalves, were the most diversified taxonomic classes in the 2 soft-sediment communities, whereas in the ES, gastropods were as diversified as the aforementioned taxonomic classes. Diversity patterns were different when considering only the strict primary consumers. In the CS and AS, first bivalves and then polychaetes were the most diversified taxonomic classes, whereas in the ES, bivalves and gastropods were equally diversified (Table 1).

Two bivalves and 1 polychaete species dominated the CS consumer community, reflecting the primary consumer diversity structure. The cockle *Cerastoderma edule* and the Baltic tellin *Limecola balthica*, both suspension-feeders, alternately dominated the biomass in winter and summer, with the polychaete *Lanice conchilega* also accounting for 7–15% of the biomass (Table 1). Conversely, in the AS, the gastropod *Crepidula fornicata*, reported to be mostly a suspension-feeder, accounted for 59–62% of the total consumer biomass, followed by the deposit-feeding polychaete *Cirriformia tentaculata* (Table 1). Similarly to the consumer diversity structure, the ES consumer biomass was dominated by a polychaete, the suspension-feeding engineer species *Sabellaria alveolata*; a bivalve, the Japanese oyster *Magallana gigas*; and a malacostracan crustacean, the porcelainid crab *Porcellana platycheles* (Table 1).

Overall, the patterns identified in each sediment type were quite similar in winter and summer, with a change in the species dominating the CS and ES community biomass. In the CS, *C. edule* dominated in winter and *L. balthica* in summer and in the ES, *S. alveolata* dominated in winter and *M. gigas* dominated in summer (Table 1).

### 3.2. Food web structure and consumer community isotopic niches

The food web structure of each consumer community was assessed by focusing on the isotopic biplots (Fig. 1) and by comparing their respective isotopic niche widths in summer and winter (Fig. 2, Table 2). The basal resources and macrofauna displayed an organization in the isotopic biplots characteristic of benthic intertidal communities with values constrained between  $-24$  and  $-13\%$  on the  $\delta^{13}\text{C}$  axis and between 4 and 15‰ on the  $\delta^{15}\text{N}$  axis. The benthic basal resources (MPB and ULV) had higher  $\delta^{13}\text{C}$  values than the pelagic resource (POM), and green

macroalgae (ULV) had higher  $\delta^{15}\text{N}$  values than MPB and POM. As hypothesized, SOM appeared graphically as a mixture of POM and MPB in the CS with the addition of ULV in the AS and ES (Fig. 1). The mean  $\pm$  SD  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of the basal resources were respectively  $-22.92 \pm 1.31$  and  $5.43 \pm 0.91\%$  for POM,  $-17.75 \pm 1.57$  and  $5.54 \pm 0.55\%$  for MPB,  $-15.93 \pm 0.75$  and  $8.93 \pm 0.85\%$  for ULV, and  $-20.75 \pm 0.31$  and  $6.94 \pm 0.27\%$  for SOM.

These 2 or 3 basal resources supported the main primary consumers in the different sediment types except for Collembola (ES in summer), which displayed extreme isotopic compositions relative to the majority of species (Fig. 1 and Table S1) indicating that they probably rely on non-sampled basal resources with very high  $\delta^{13}\text{C}$  values (e.g. cyanobacteria). The TA of the consumer convex hull was driven by species showing extreme isotopic compositions, such as *Lekanesphaera rugicauda* in the summer AS isotopic biplot (Fig. 1), while the consumer SEAs were, as expected, less influenced by these extreme values (Fig. 2).

The ES consumer community had a broader isotopic niche (TA and SEA) than the CS consumer community (Table 2a), as indicated by the Bayesian probabilities above 0.70 in winter and summer (Table 2b). The ES community also presented a more stable isotopic niche in terms of width and position than the CS and AS communities, as indicated by the similar niche widths, a Bayesian probability close to 0.5, and high SEA overlap between winter and summer (Fig. 2, Table 2a). Finally, the isotopic niches of the 2 reef communities (ES and AS) overlapped more with each other than either of them with the CS consumer community (Table 2b).

Between the winter and summer samplings, the CS isotopic niche shifted towards higher  $\delta^{13}\text{C}$  values compared to the AS and ES isotopic niches (Fig. 2) while the AS isotopic niche increased in width (Table 2a), presenting a width similar to the ES isotopic niche in summer (Table 2b), as indicated by the summer ES–AS Bayesian probability close to 0.5. Finally, all consumer community isotopic niches were broader in summer than in winter (Bayesian probabilities  $>0.76$ , Table 2a).

### 3.3. Isotopic compositions of the primary consumers and relative importance of benthic and pelagic basal resources

Here we consider only the primary consumer trophic level and investigate the relative importance



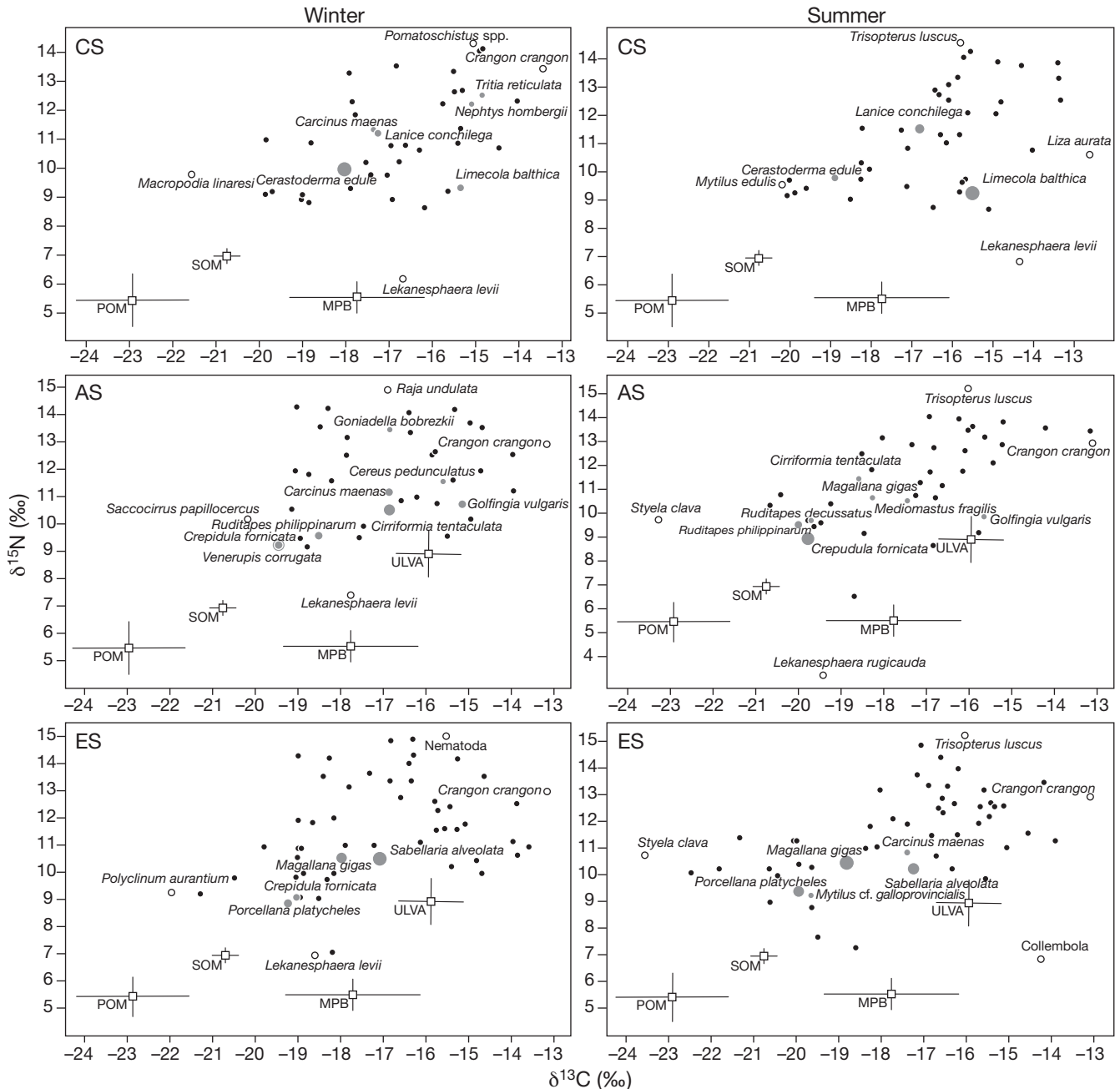


Fig. 1. Carbon and nitrogen isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , ‰) of the consumer species (round symbols) and basal resources (white squares) sampled in the control (CS), associated (AS), and engineered (ES) sediments. The mean and standard deviations of the basal resources (particulate organic matter [POM], sediment organic matter [SOM], microphytobenthos [MPB], *Ulva* spp. [ULVA]) are calculated as annual averages. For consumers, mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are represented without error bars for clarity. The gray symbols are proportional to the relative contribution of each species to the total biomass in each sediment type (for contributions >1%, species names are labeled) and the other symbols indicate a relative contribution <1%. The species displaying extreme  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are also labeled (white symbols). In the winter AS biplot, the symbols for *Venerupis corrugata* and *Ruditapes philippinarum* are stacked, as their respective  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are almost identical

of benthic and pelagic basal resources in fueling all primary consumers present in each sediment type and specific primary consumer species, using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  histograms (Fig. 3) and Bayesian mixing models (Fig. 4, Table 3; Table S2). The CS primary

consumers presented the highest mean  $\delta^{13}\text{C}$  values across the 3 sediment types (Fig. 3), indicating a higher contribution of  $^{13}\text{C}$ -enriched basal resources, like MPB (Fig. 1), to their overall diet. Indeed, the global mixing model (Table 3) indicated that the CS

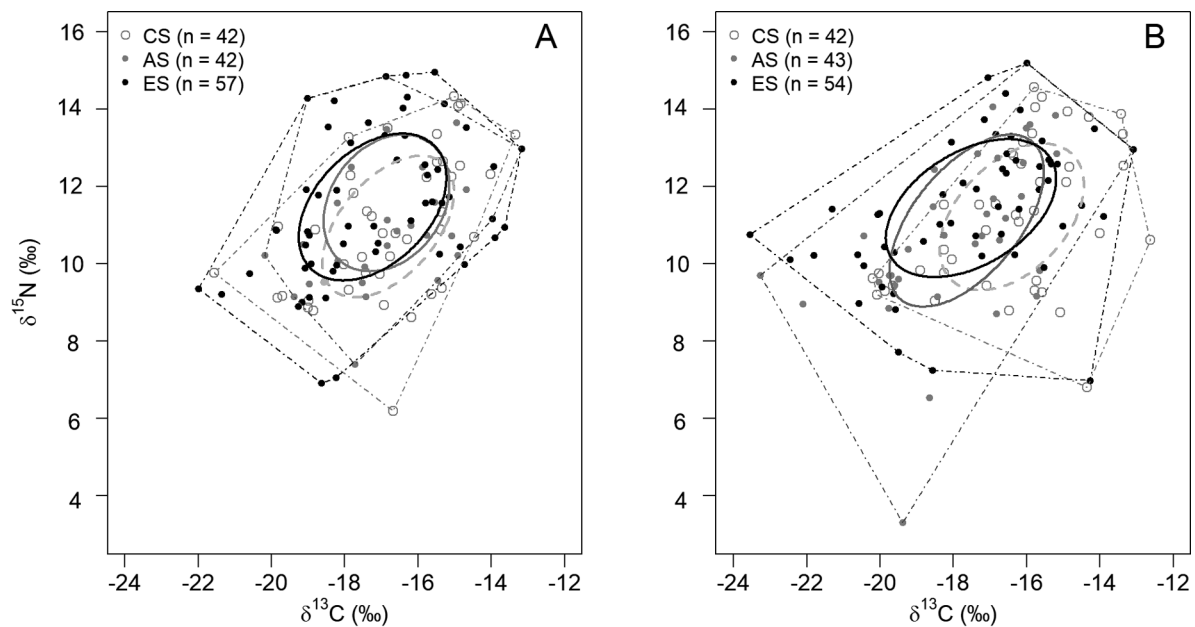


Fig. 2. Mean carbon and nitrogen isotopic compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , ‰) of the consumers sampled in the control (CS), associated (AS), and engineered (ES) sediments in (A) winter and (B) summer. The dashed light gray ellipse encloses the standard ellipse area (SEA) of the CS consumer community. The solid dark gray and black ellipses respectively enclose the SEAs of the AS and ES consumer communities. The thinner dot-dashed lines represent the total isotopic niche width of each of the consumer communities, using the same color code as for the SEA

Table 2. (a) Community-wide metrics (number of sampled consumer species, total area of the convex hull [TA], and standard ellipse area [SEA]) calculated for the consumer communities in the 3 sediment types (control [CS], associated [AS], and engineered [ES]) in winter and summer, using the mean consumer isotopic compositions. The probability comparing the Bayesian SEA of each consumer community between the winter and summer sampling and the corresponding SEA overlaps are also indicated. (b) Two-by-two probability comparing the Bayesian SEA of each consumer community in winter and summer and the corresponding SEA overlaps. For example, the values 0.83 and 0.71 for the Bayesian probabilities SEA (CS) < SEA (ES) in winter and summer mean that there is an 83 and 71% chance that the CS isotopic niche is smaller than the ES isotopic niche in winter and summer, respectively

(a) Consumer comparison	Winter			Summer			Probability SEA (winter) < SEA (summer)	SEA overlap (%)
	n	TA (‰ <sup>2</sup> )	SEA (‰ <sup>2</sup> )	n	TA (‰ <sup>2</sup> )	SEA (‰ <sup>2</sup> )		
CS	42	33.99	8.94	42	34.80	10.51	0.76	92.43
AS	42	31.36	9.20	43	54.93	12.09	0.89	85.75
ES	57	42.39	11.02	54	53.19	11.77	0.65	93.36
(b) Community comparison A vs. B	Winter			Summer			Probability SEA (A) < SEA (B)	SEA overlap (%)
	Bayesian probability SEA (A) < SEA (B)	SEA overlap (%)		Bayesian probability SEA (A) < SEA (B)	SEA overlap (%)			
CS vs. AS	0.54	77.03		0.75	61.50			
CS vs. ES	0.83	78.40		0.71	63.33			
AS vs. ES	0.79	95.00		0.44	86.17			

primary consumers relied strongly on benthic basal resources (MPB contribution: ca. 88–90%), whereas the ES and AS relied less on these resources (MPB+ULV contribution: ca. 48–76%) and more on POM (contribution: ca. 23–52%). More specifically, the dominant CS primary consumers relied on MPB

in both winter and summer for more than 70% of their diet, except for *Lekanesphaera levii* and *C. edule*, which relied on a mixture of MPB and POM in winter and summer, respectively (Fig. 4; Table S2). Benthic basal resources also contributed more to the ES primary consumers than they did to the AS

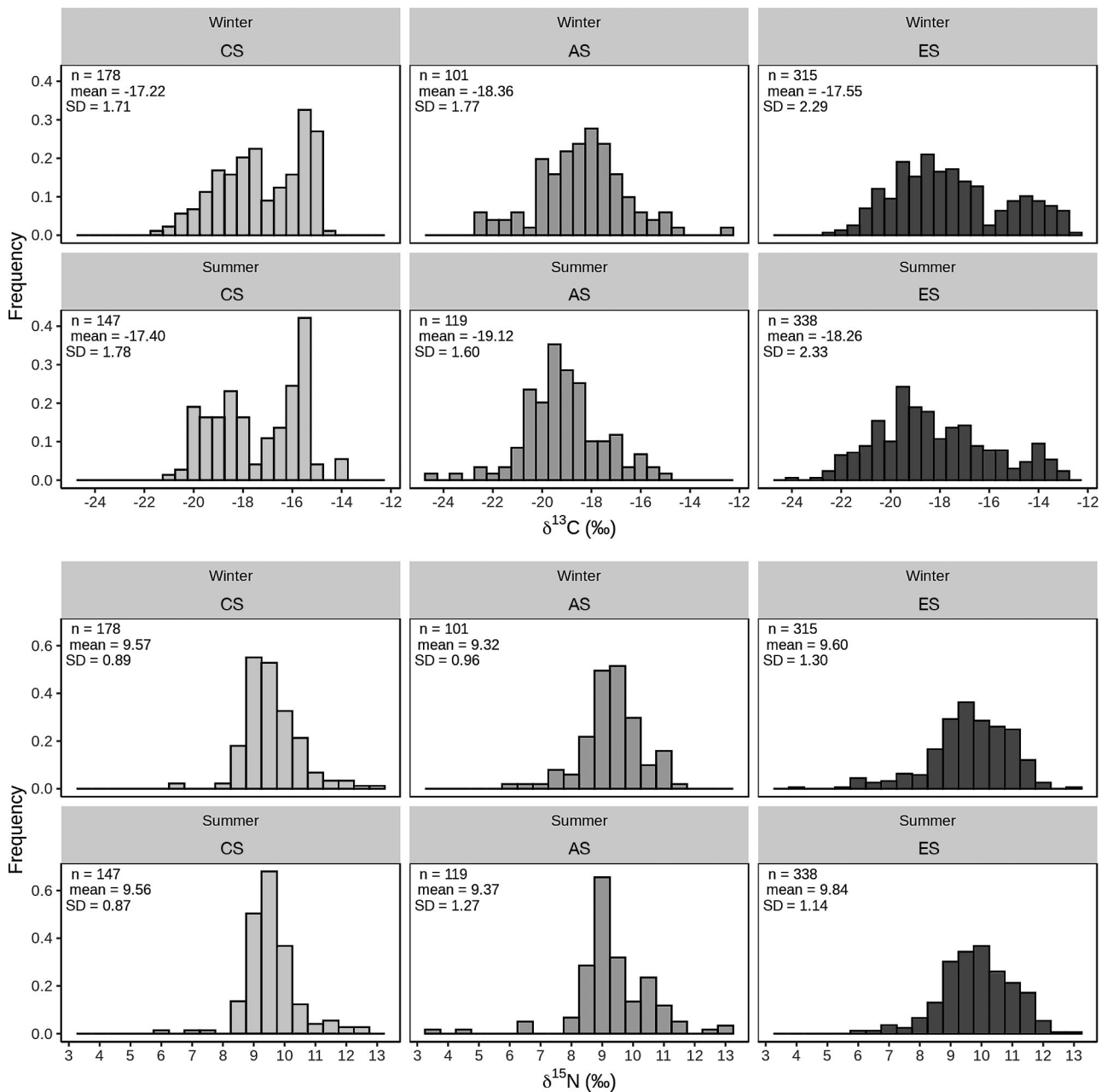


Fig. 3. Frequency distributions of carbon (top) and nitrogen (bottom) isotopic compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , ‰) of all primary consumers sampled in the control (CS), associated (AS), and engineered (ES) sediments in winter and summer with the associated sample sizes (n), mean values, and standard deviations (SD). A size class of 0.5‰ was used for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$

primary consumers (Table 3), a difference visible through the higher mean  $\delta^{13}\text{C}$  of the ES primary consumers compared to the AS ones (Fig. 3) and mainly related to the stronger contribution of ULV to the diet of the ES primary consumers (Table 3).

Histograms of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of species sampled in the ES were overall flatter than the CS and AS histograms, a visual characteristic confirmed by the higher variability (standard deviation) in their

carbon and nitrogen isotopic compositions than the CS and AS primary consumers (except the AS in summer) (Fig. 3). The  $\delta^{13}\text{C}$  ES histograms also displayed a secondary mode corresponding to higher  $\delta^{13}\text{C}$  values of ca.  $-15$  and  $-14$ ‰ in winter and summer, respectively (Fig. 3), indicating a high contribution of  $^{13}\text{C}$ -enriched basal resources such as MPB and/or ULV (Fig. 1) to the diet of certain primary consumers. Furthermore, the  $\delta^{15}\text{N}$  histograms of the ES were slightly

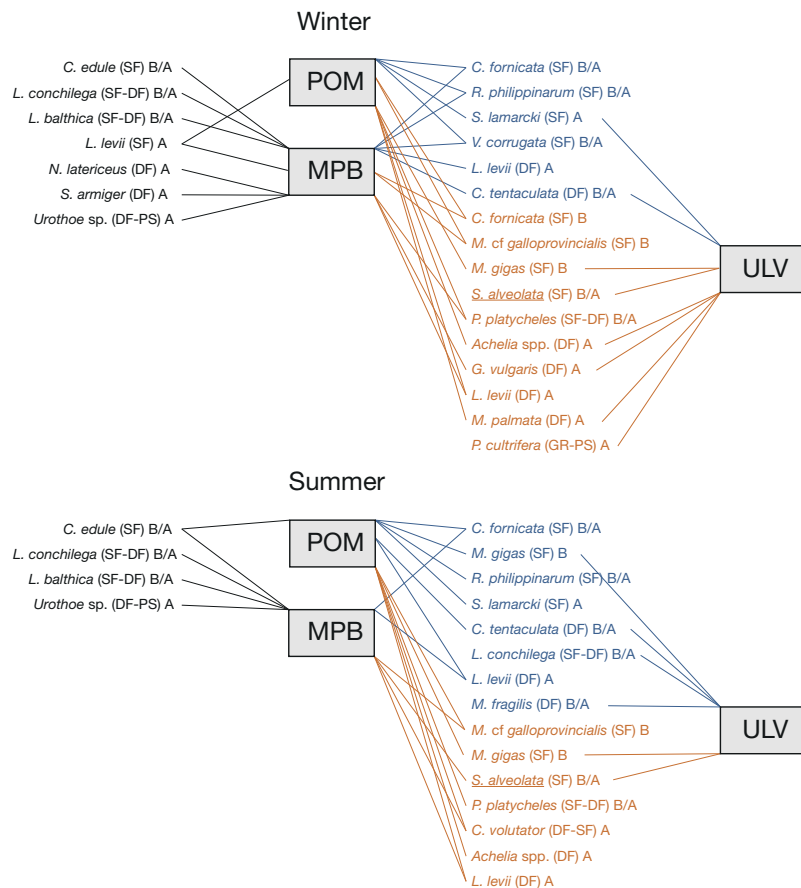


Fig. 4. Basal resources (particulate organic matter [POM], microphytobenthos [MPB], *Ulva* spp. [ULV]) contributing more than 30% to the assimilated diet of the primary consumers that account for >1% of the total biomass ('B') and/or >1% of the total abundance ('A') in the control sediments (black), associated sediments (blue), and engineered sediments (orange) in winter (top) and summer (bottom), as calculated by the Bayesian mixing models. The feeding mode of each species is specified as suspension-feeder (SF), deposit-feeder (DF), predator/scavenger (PS), and/or grazer (GR), and the engineer species *Sabelaria alveolata* is underlined; full species names are given in Table S1.

Figure adapted from Jankowska et al. (2018)

shifted towards higher values (Fig. 3), indicating a higher contribution of  $^{15}\text{N}$ -enriched basal resources, such as ULV (Fig. 1), to the diet of certain primary consumers. Indeed, the grazing gastropods *Steromphala umbilicalis* (formerly known as *Gibbula umbilicalis*) and *Littorina littorea*, both present in the ES, relied exclusively on benthic basal resources (MPB and ULV, Table S2).

Across sediment types, the primary consumers displayed a lower average  $\delta^{13}\text{C}$  in summer than in winter, with a stronger shift visible for the AS and ES primary consumers than for the CS primary consumers (Fig. 3), indicating an overall higher contribution of  $^{13}\text{C}$ -depleted basal resources, such as POM (mostly phytoplankton, Fig. 1), to their diets in summer than in winter. Indeed, the global mixing model indicated a strong increase in the importance of POM for the AS and ES primary consumers between winter (ca. 23–39%) and summer (ca. 40–52%) and only a very small shift for the CS primary consumers (Table 3).

More specifically, most of the dominant AS and ES primary consumers mainly relied (>70% contribution) on mixtures in winter: POM and MPB (AS: *C. fornicata*, *Ruditapes philippinarum*, and *Venerupis corrugata*, ES: *C. fornicata*, *Mytilus* cf. *galloprovincialis*, *P. platycheles*, and *L.*

Table 3. Mean  $\pm$  SD [2.5–97.5% confidence intervals] of the relative contribution (%) of the 2 or 3 basal resources (e.g. marine suspended particulate organic matter [POM]) to the assimilated diet of all primary consumers sampled in each sediment type in winter and summer, estimated using Bayesian mixing models. The overall mean dietary contribution of benthic organic matter sources is equal to the microphytobenthos (MPB) dietary contribution in the control sediments (CS) and to the sum of the mean MPB and *Ulva* spp. contributions in the associated (AS) and engineered (ES) sediments

	Winter			Summer		
	CS	AS	ES	CS	AS	ES
n	185	87	352	141	107	348
POM	10.0 $\pm$ 2.3 [5.6–14.6]	39.2 $\pm$ 3.5 [32.3–46.0]	23.5 $\pm$ 2.5 [18.7–28.3]	12.1 $\pm$ 2.7 [6.9–17.5]	52.4 $\pm$ 3.1 [46.2–58.5]	40.2 $\pm$ 2.5 [35.2–45.0]
MPB	90.0 $\pm$ 2.3 [85.4–94.4]	53.2 $\pm$ 4.9 [43.4–62.6]	50.9 $\pm$ 3.8 [43.5–58.4]	87.9 $\pm$ 2.7 [82.5–93.1]	33.0 $\pm$ 5.4 [22.4–43.5]	30.2 $\pm$ 3.6 [23.2–37.2]
<i>Ulva</i> spp.		7.6 $\pm$ 2.5 [2.8–12.8]	25.5 $\pm$ 2.2 [21.3–29.8]		14.6 $\pm$ 3.3 [8.1–21.2]	29.6 $\pm$ 1.9 [26.0–33.4]
Benthic basal resources	90.0	60.8	76.4	87.9	47.6	59.8

*levii*) or POM and ULV (AS: *Spirobranchus lamarckii*, ES: *M. gigas*, *Achelia* spp., and *Melita palmata*). Conversely, in summer, 4 primary consumers from the reef site (AS: *R. philippinarum* and *S. lamarckii*, ES: *P. platycheles* and *Achelia* spp.) relied on POM for over 70% of their diet and most of the other primary consumers relied on mixtures which contained POM, namely POM and MPB (AS: *C. fornicata* and *L. levii*, ES: *M. cf. galloprovincialis*, *Corophium volutator*, and *L. levii*) or POM and ULV (AS: *C. tentaculata* and *M. gigas*, ES: *M. gigas*). Finally, respectively 5 and 3 of the dominant primary consumers of the reef site mainly relied on benthic basal resources in winter and summer, a list always containing the engineer species; winter: *C. tentaculata* (AS) and *Golfingia vulgaris* (ES) on MPB and ULV, *L. levii* (AS) on MPB, *Perinereis cultrifera* (ES) and *S. alveolata* (ES) on ULV; and summer: *L. conchilega* (AS) and *Mediomastus fragilis* (AS) on ULV, *S. alveolata* (ES) on MPB and ULV (Fig. 4; Table S2).

### 3.4. Trophic niches of dominant suspension-feeders in the engineered sediments

Finally, we focus on the dominant suspension-feeders co-occurring in the engineered sediments and compare their respective realized trophic niches estimated with the Bayesian mixing models (Fig. 5). The engineer species *S. alveolata* showed a stable

realized trophic niche (Fig. 5) with only a slight increase in the MPB mean dietary contribution between winter (28%) and summer (35%), compensated by a slight decrease in the ULV mean dietary contribution (Table S2). The realized trophic niches of *S. alveolata* and *M. gigas*, the 2 dominant species of the ES (Fig. 1; Table S1), only slightly overlapped in winter and were very different from the realized trophic niches of the other co-occurring suspension-feeders in winter and summer (Fig. 5). *M. gigas* relied more on POM and less on MPB than *S. alveolata*, especially in summer and they both relied on ca. 40–50% ULV (Fig. 5). *C. fornicata*, *M. cf. galloprovincialis*, and *P. platycheles* displayed very similar realized trophic niches in winter and summer, relying on a mixture of POM and MPB with a contribution of ULV below 20% (Fig. 5; Table S2). Overall, all the dominant primary consumers except *S. alveolata* consumed more POM in summer than in winter (Fig. 5).

## 4. DISCUSSION

Jones et al. (1994, p. 374) defined ecosystem engineers as ‘organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic material.’ Examples of such modulated resources included water, sediments, and nutrients. In this

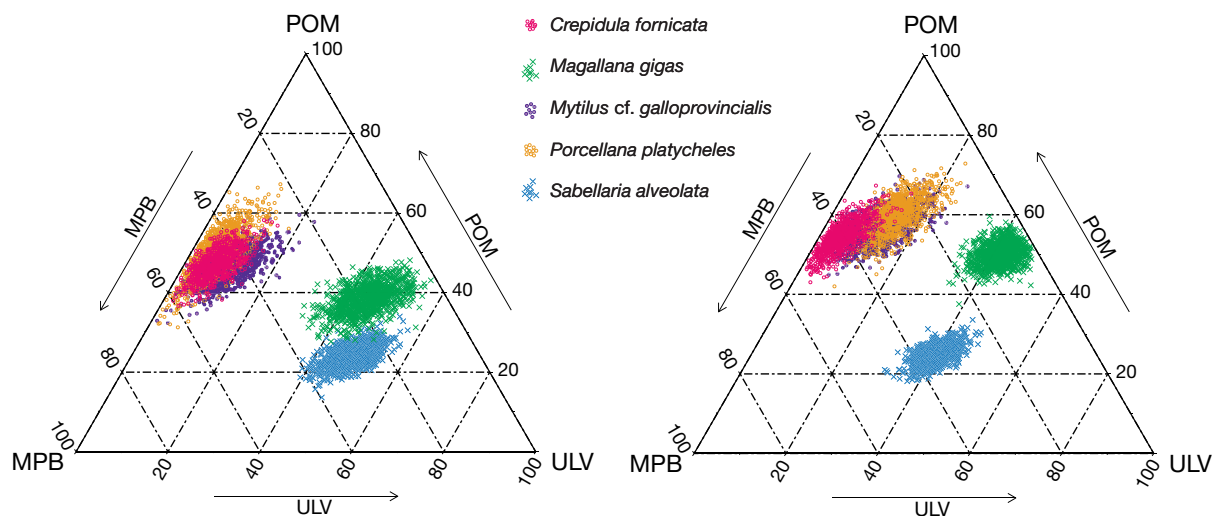


Fig. 5. Ternary plots of the relative contributions of particulate organic matter (POM), microphytobenthos (MPB), and *Ulva* spp. (ULV) to the assimilated diet of the engineer species *Sabellaria alveolata* and 4 abundant suspension-feeders co-occurring in the engineered sediments (*Magallana gigas*, *Mytilus cf. galloprovincialis*, *Crepidula fornicata*, and *Porcellana platycheles*) in winter (left) and summer (right). Each point represents the posterior dietary proportions calculated by the Bayesian mixing models using the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measured for each organism. As an illustration, the assimilated summer diet of *S. alveolata* is composed of ca. 40% ULV, 35% MPB, and 25% POM

paper, we go further than ecosystem engineering by looking into the fate of the modulated resources that are trophic in our case and discuss our results with regard to the gardening hypothesis. This hypothesis, developed for the lugworm *Abarenicola pacifica*, links the stimulation of a food source by a species (the lugworm stimulates microbes surrounding its burrow via its digestion and the production of feces) and the consumption of the stimulated or gardened resource by the same species (Hylleberg 1975). More recently, a similar mechanism has been highlighted in the case of oysters (Cognie & Barillé 1999) and the tubiculous amphipod *Haploops nirae* (Rigolet et al. 2014). We argue here that engineer species can also promote a habitat-wide form of gardening where an engineered habitat, in the present case a sabellariid reef composed of the engineered and associated sediments, stimulates 2 basal trophic resources, which are then consumed by the engineer species and the associated organisms. We also stress the role played by this habitat-wide gardening in coupling 2 distinct communities, in our case the engineered and associated sediment communities (Jones et al. 2018), into a single reef food web and the different consequences this habitat-wide gardening has on the trophic structure and functioning of the engineered and associated sediment communities.

#### **4.1. Reef habitat stimulates benthic trophic resources and increases access to phytoplankton**

Large *Sabellaria alveolata* reefs, like the Sainte-Anne reef, stimulate 2 basal trophic resources, green macroalgae from the genus *Ulva* (higher producer diversity), which relies on the physical structure of the engineered sediments to attach and grow (Dubois et al. 2006, Dubois & Colombo 2014), and MPB biomass (higher producer biomass), which mainly develops on the associated sediments (Jones et al. 2018), through various physical and biological mechanisms mediated by the engineer species and the resulting biogenic structures. First, the engineered sediments are home to a diverse and abundant community of suspension-feeders (e.g. *S. alveolata*, *Magallana gigas*, Table 1) (Jones et al. 2018) that produce, through their filtration activity (Dubois et al. 2003, Cugier et al. 2010), large amounts of feces and pseudofeces (Haven & Morales-Alamo 1966, Dubois et al. 2005). These biodeposits end up trapped between the *S. alveolata* tubes or sediment on the associated sediments (A. Jones unpubl. data) where they become a source of nutrients for benthic microalgae, once remineralized

through the microbial loop (Hubas et al. 2007, van Broekhoven et al. 2015). Secondly, the physical structure of the engineered sediments acts as a wave-breaker, sheltering the associated sediments from the strong tidal currents and further promoting the development of dense MPB mats on these soft sediments (Jones 2017).

Structurally complex habitats like oyster reefs and polychaete tube mats often lead to the establishment of a skimming flow over them (Friedrichs et al. 2000, Passarelli et al. 2014). This flow promotes the local settlement of pelagic larvae (Commito et al. 2005, Donadi et al. 2014) and concentrates POM just behind the biogenic structures (Colden et al. 2016). Consequently, this hydrodynamic phenomenon, combined with the elevated position of ES above the surrounding soft sediments, probably results in a higher availability of phytoplankton for the primary consumers living in the ES and AS (González-Ortiz et al. 2014). Overall, through the physical structure of the ES and the abundant associated suspension-feeders, *S. alveolata* stimulates 2 basal trophic resources, MPB and green macroalgae, and increases the availability of phytoplankton to primary consumers.

#### **4.2. Habitat-wide gardening takes place inside the reef**

The global mixing model indicated that MPB and green macroalgae combined supported 76 and 60% of the ES food web in winter and summer, respectively, revealing the importance of the 2 gardened resources in the trophic functioning of this community (Table 3). A few primary consumers (i.e. *S. alveolata*, *Littorina littorea*, *Steromphala umbilicalis*, *Golfingia vulgaris*) from different trophic guilds strongly drove this trend while the rest of the primary consumers relied less (i.e. no more than 60%) on green macroalgae and MPB, globally supporting the gardening hypothesis to a greater or lesser extent depending on the species (Fig. 4; Table S2). *L. littorea* and *S. umbilicalis*, 2 common grazing gastropods present at low densities across the engineered sediments, and the more abundant deposit-feeding sipunculid *G. vulgaris* (Dubois et al. 2002, Jones et al. 2018), relied (>90%) on MPB and/or green macroalgae, with shifts between the 2 contrasted sampling periods (winter and summer). Furthermore, the suspension-feeding engineer species *S. alveolata* displayed a very similar realized trophic niche in winter and summer, based 75% on the gardened trophic resources, green macroalgae (40–48%) and MPB

(28–35%), indicating a positive and stable trophic feedback between the engineer species and the engineered habitat.

Globally, the gardened resources fueled the AS food web less, with a 61 and 48% contribution in winter and summer, respectively (Table 3). Nonetheless, these resources contributed >70% to the winter diet of a few suspension-feeders like the cockle *Cerastoderma edule* and the solid surf clam *Spisula solida* and of the deposit-feeding polychaete *Cirri-formia tentaculata* (Table S2). The promotion of a trophic resource by one species, here *S. alveolata* via the habitat it creates, and its consumption by associated species, expands the ecosystem engineering definition, which historically only focused on the modulation of the availability of resources to other species (Jones et al. 1994). This process has been observed in the case of *H. nira*e tube mats, where the diatoms growing on the tubes contribute up to 50% of the diet of the dominant species associated with this engineered habitat, such as the bivalve *Politi-tapes virgineus* (Rigolet et al. 2014). Overall, our results support the hypothesis of habitat-wide gardening at the scale of the ES and AS, albeit with high inter-specific variability in the reliance of each primary consumer on the gardened resources.

Finally, the similar realized trophic niche of the engineer species in winter and summer seems to indicate that *S. alveolata* creates optimal and very stable trophic conditions for itself (Fig. 5). Conversely, the other primary consumers present in the ES and AS changed diets between winter and summer, maybe indicating that the engineered habitat does not provide them with such optimal conditions (Figs. 4 & 5; Table S2). These primary consumers likely shift their diet according to the spatio-temporal abundance and availability of basal resources, for example by consuming more phytoplankton and/or green macroalgae in summer when these resources are more abundant (Dubois et al. 2006, Marín Leal et al. 2008, Cugier et al. 2010).

#### **4.3. Phytoplankton, a key trophic resource for the reef primary consumers, locally couples the pelagic and benthic compartments**

Our second hypothesis stated that the increased MPB biomass in the associated sediments and the presence of green macroalgae growing on the engineered sediments would lead to a higher trophic contribution of these locally stimulated benthic resources to the engineered and associated sediment

communities than to the control sediment community. The global mixing model revealed the opposite trend, with an average 21–34% lower contribution of these benthic basal resources to the diet of the ES and AS primary consumers (MPB + ULV) than to the diet of the CS primary consumers (MPB) (Table 3). MPB fueled around 90% of the winter and summer basal carbon flows taking place inside the CS, confirming the importance of benthic primary producers in sustaining temperate intertidal soft-sediment food webs, as previously demonstrated in similar systems like the Wadden Sea (Middelburg et al. 2000, Christianen et al. 2017).

The engineered habitat (ES and AS) also concentrates phytoplankton (Section 4.1), which is then consumed by the ES and AS primary consumers, as indicated by the diverse suspension- and deposit-feeders present in both sediment types and the mixing model results (Figs. 1 & 4, Tables 1 & 3; Table S2). The 2 sediment types composing the engineered habitat are home to a high diversity of suspension-feeders (e.g. *S. alveolata*, *M. gigas*, *Venerupis corrugata*, *Crepidula fornicata*, *Ruditapes philippinarum*) that can directly consume phytoplankton, and to surface deposit-feeders that can consume phytoplankton once deposited on the engineered (e.g. *Corophium volutator*, *Lekanesphaera levii*) or on the associated sediments (*Mediomastus fragilis*, *Cirri-formia tentaculata*). Furthermore, phytoplankton represented over 30% of the assimilated diet of at least half of the dominant ES and AS primary consumers, fueled 23–40% of the basal carbon flows taking place in the ES, and even more in the associated sediments (39–52%), with a higher contribution in summer than in winter across both sediment types. Consequently, phytoplankton appears as a key trophic resource for the 2 reef communities, especially in summer when it is more abundant (Marín Leal et al. 2008, Cugier et al. 2010). Our results also indicate that through its physical properties that promote phytoplankton sedimentation and its rich and diverse macrofauna which consumes it, the habitat engineered by *S. alveolata* and composed of the ES and AS, acts as a local hotspot for benthic–pelagic coupling (Griffiths et al. 2017), similarly to bivalve reefs (Dame et al. 2000).

#### **4.4. Trophic connections link the ES and AS communities into a single reef food web**

Communities from the ES and AS have thus far been studied independently because of their different structural nature and distinct species assem-

blages (Jones et al. 2018), but many mechanisms link these 2 communities into a single reef food web, starting with trophic connections associated with the habitat-wide gardening. Trophic connections between adjacent habitats can be established through the movements of nutrients (e.g. carbon, nitrogen, and phosphorus), detritus (e.g. biodeposits and phytodetritus), prey (e.g. primary producers), and consumers (Polis et al. 1997). For example, in the case of *H. nira* beds and the adjacent *Amphiura filiformis* muddy habitat, a trophic connection exists through the exportation of benthic microalgae growing on *Haploopsis* tubes (Rigolet et al. 2014).

In our case, the ES and AS are probably primarily connected throughout the year by movements of basal resources (see Section 4.1), biodeposits (see Section 4.1), and consumers (Fig. 4, Table 1; Table S2). Indeed, deposit-feeders exclusively present in the associated sediments (e.g. *C. tentaculata*) assimilate green macroalgae, indicating that macroalgae fragments move from the ES to the AS. A diversity of primary consumers exclusively present in the ES (*C. volutator*, *Porcellana platycheles*) and the engineer species itself assimilate MPB, meaning there is movement of MPB from the AS to the ES via resuspension (Ubertini et al. 2012), as found for cultivated oysters and associated suspension-feeders (Dubois et al. 2007). Furthermore, a number of vagile primary (e.g. *L. levii*) and secondary consumers (e.g. *Tritia reticulata*, *Carcinus maenas*, *Crangon crangon*, *Pomatoschistus* sp.) inhabiting both sediment types presented very similar isotopic compositions, suggesting they move and forage between the ES and AS (Table S1). These trophic connections were established indirectly using naturally present carbon and nitrogen stable isotopes, but *in situ* isotope labeling of the MPB present in the associated sediments and of the green macroalgae present on the engineered sediments would provide an interesting complementary line of evidence (Middelburg et al. 2000, Majdi et al. 2018).

Overall, the engineered and associated sediment communities, despite their different sedimentary nature and species composition, appear connected through energy flows mostly linked to the basal node modulation induced by *S. alveolata*. Accordingly, the habitat engineered by *S. alveolata* is composed of 2 sediment type communities but, most likely, is organized into a single reef food web, lending more weight to the hypothesis that the *S. alveolata* reefs present on soft substrates are a unique ecological entity composed of the biogenic structures and the adjacent soft sediments (Jones et al. 2018).

#### 4.5. Global effects of habitat-wide gardening on the reef food web structure and functioning

The ecosystem engineer *S. alveolata* builds a habitat composed of 2 sediment types, the ES and AS, different in their physical nature, abiotic characteristics, and species assemblages, which actually seem to be coupled into a single reef habitat and food web by movements of locally stimulated basal trophic resources (MPB and green macroalgae), biodeposits resulting from the high filtration activity of the ES suspension-feeders and mobile consumers. Furthermore, the gardening hypothesis seems validated at the reef habitat scale (ES and AS), as indicated by the stimulation of 2 basal trophic resources, MPB and green macroalgae, which partly fuel the reef food web via their consumption by diverse primary consumers and especially the suspension-feeding engineer species and grazers. This habitat-wide gardening also has consequences on the food web organization and functioning of the ES and AS communities, notably with a widening of their community isotopic niches and a limitation of the inter-specific trophic competition between the engineer species and abundant co-occurring suspension-feeders.

First, the presence of *S. alveolata* increased the ES consumer community isotopic niche width in winter and summer (Fig. 2, Table 2), agreeing with our first hypothesis and a theoretical framework that links ecosystem engineering and food webs via node and link modulation (Sanders et al. 2014). Indeed, basal node modulation (i.e. stimulation of MPB and green macroalgae) diversifies available trophic niches, which can lead to the establishment of a more diverse consumer community, the development of new energy pathways, and an overall increase in the width of the consumer community isotopic niche (Layman et al. 2007). Trophic (i.e. gardened basal resources) and spatial niche diversification (i.e. habitat provisioning) promoted by *S. alveolata* probably led to the observed increase in the engineered sediment species richness (Jones et al. 2018, Table 1), a result partly linked to the establishment of gardened resource trophic specialists, and finally led to the overall wider isotopic niche. Overall, habitat modifiers like cordgrass and seagrass increase species richness across trophic levels and increase link density through their non-trophic facilitative role rather than through their trophic role (van der Zee et al. 2016), as seems to be the case for *S. alveolata*.

Interestingly, empirical studies on habitats engineered by the amphipod *H. nira* (Rigolet et al. 2014), the polychaete *Lanice conchilega* (De Smet et



al. 2015), and the marine plant *Zostera marina* (Jankowska et al. 2018) did not detect strong effects of these species on the food web structure of soft-bottom communities, despite drastic changes in environmental conditions, consumer richness, and species assemblages. These contrasting findings could result from the level of structural and spatio-temporal stability of each habitat (Jones et al. 1994, 1997). Indeed, the structures engineered by *S. alveolata* (engineered sediments) are solid and very resistant (Le Cam et al. 2011), much closer structurally to coral reefs than to habitats built by *H. nirae*, *L. conchilega*, or *Z. marina* (Goldberg 2013). The Sainte-Anne reef has also been recorded at the same site and with similar dimensions for decades (Caline et al. 1992, Dubois et al. 2002), whereas seagrass meadows undergo substantial seasonal changes with often clear declines in shoot density and aboveground biomass during winter (Jankowska et al. 2018). Similarly, intertidal *L. conchilega* beds are characterized by an inter-annual variability in their surface and in the engineer density (Callaway et al. 2010).

We also observed a similar width of the ES isotopic niche between our 2 contrasted sampling times, as we observed for the engineer species, and a similar biomass distribution, indicating that *S. alveolata* not only creates stable trophic conditions for itself, but also for the entire consumer community associated with the ES (Figs. 1 & 2, Table 1). Complex food webs can emerge from the establishment of engineer species via habitat provisioning, limited physical stress, and mediated energy and nutrient flow (van der Zee et al. 2016). In our case, the emergence of a complex and relatively stable ES food web was probably driven by the spatio-temporal stability of the engineer density and of the resulting physical structure (e.g. surface, height), known to directly and indirectly affect the stability of assembling food webs (Neutel et al. 2007).

Furthermore, the AS community presented the highest isotopic niche width difference between winter and summer and the strongest temporal variability in the dominant trophic groups, pointing to a less stable trophic structure of this community compared with the ES and CS communities (Figs. 1 & 2, Tables 1 & 2). The turbulent hydrodynamic environment created by the engineered sediments (Colden et al. 2016) and the recurrent disturbance by local fishermen of the associated sediments (Watson et al. 2017) result in a high spatio-temporal variability in the abiotic (e.g. principal grain size mode, mud content) and biotic (species assemblage) characteristics of these sediments (Desroy et al. 2011, Jones et al.

2018). Nonetheless, in summer, the AS and ES isotopic niches had similar widths, a result partly agreeing with our first hypothesis. This stronger trophic connection between the 2 reef communities observed in summer is probably linked to the higher abundance of gardened basal resources in summer (Dubois et al. 2006, Marín Leal et al. 2008) and to the recruitment-promoting role of the ES (Jones et al. 2018) that led to the establishment in the AS of a community more characterized by suspension- and deposit-feeders, 2 trophic groups that benefit from the gardened basal resources, in summer than in winter. The isotopic niche overlap between the ES and AS communities was also higher than between each community and the CS community in winter and summer (Fig. 2, Table 2). Consequently, the 2 reef communities are more similar overall in their trophic structure than the *L. balthica* community characterizing the CS (Bonnot-Courtois et al. 2009), and in summer, the 'trophic effect' of *S. alveolata* (isotopic niche widening) seems to extend beyond the physical border of the ES and towards the AS.

Sabellariid reefs also provide hard substrata for many epibionts, including the Japanese oyster *M. gigas* which sometimes dominates the biogenic structures (Dubois et al. 2006, Jones et al. 2018; Table 1) and a diversity of other suspension-feeders like mussels (*Mytilus* cf. *galloprovincialis*), slipper limpets (*C. fornicata*), and porcellanid crabs (*P. platycheles*), which sometimes reach densities over 2500 ind. m<sup>-2</sup> and account for over 10% of the community biomass (Jones et al. 2018). As suspension-feeders, these co-occurring species may share similar diets. Using stable isotopes, we did not detect an overlap between the realized trophic niche of *S. alveolata* and the co-occurring suspension-feeders, expect a small one with *M. gigas* in winter (Fig. 5) when the main food sources of *M. gigas* (i.e. phytoplankton and green macroalgae) are more limiting (Dubois et al. 2006, Marín Leal et al. 2008). Overall, there appears to be no trophic competition between the engineer and the most abundant suspension-feeders, probably as a result of inter-specific trophic partitioning directly linked to the strong reliance of the engineer species (ca. 75%) on the gardened resources (i.e. MPB and green macroalgae). Similarly, the development of benthic diatoms on the tubes of the ecosystem engineer *H. nirae* limits inter-specific food competition between the engineer and the dominant primary consumers (Rigolet et al. 2014), a mechanism also highlighted in other *S. alveolata* reefs (Dubois & Colombo 2014) and inside oyster farms (Dubois et al. 2007).

Most co-occurring suspension-feeders use different feeding mechanisms to capture, transport, and sort particles from the water column, resulting in different selection capacities and retention efficiencies (Dubois et al. 2005), hence favoring inter-specific trophic partitioning. The stimulation of basal trophic resources by an engineer species which then consumes them, i.e. gardening, also limits inter-specific trophic competition for the engineer species (Dubois et al. 2007, Dubois & Colombo 2014, Rigolet et al. 2014), as demonstrated here for *S. alveolata*. Overall, *S. alveolata* appears to engineer a habitat where its chances of survival are maximized mainly through basal trophic resource gardening. Nonetheless, *S. alveolata* and *M. gigas* are at high risk of competing for space (Dubois et al. 2006) and for food in winter, especially if MPB and phytoplankton become less abundant. Consequently, the non-native Japanese oysters could jeopardize the survival of *S. alveolata* reefs in the long run, a potentially negative role that should be further investigated to help protect these habitats, as encouraged by the European Union's Habitats Directive 92/43/EEC (habitat type 1170 'Reef').

#### 4.6. Conclusion

The honeycomb-worm *S. alveolata* can build extensive and long-lived reefs composed of engineered structures and adjacent soft sediments in intertidal zones. Our analysis of the food web structure and functioning of the consumer communities associated with these 2 sediment types (AS and ES) and their comparison with a control soft sediment provides an integrated view on the coupling of non-trophic (ecosystem engineering) and trophic (basal resource consumption) interactions by a structural ecosystem engineer (Berke 2010). First, a habitat-wide gardening takes place within *S. alveolata* reefs, characterized by the stimulation of basal trophic resources, via abiotic (physical structure of the engineered sediments) and biotic (suspension-feeding) mechanisms, which are then consumed by diverse primary consumers including the engineer species. These reefs also promote phytoplankton sedimentation, a key trophic resource for a diversity of suspension- and deposit-feeders especially in summer, hence locally increasing benthic–pelagic coupling. Secondly, basal trophic resource stimulation and the associated feeding activity and movements of the consumers, couple the ES and AS communities into a single reef food web. These stimulated basal resources also diversify the trophic pathways inside the

reef, promote trophic resource partitioning, and limit trophic competition between the engineer species and associated suspension-feeders. In the end, *S. alveolata* engineers a temporally stable and probably highly resilient coastal habitat, which strongly controls energy flows in coastal environments.

We believe the results we found at the scale of the Sainte-Anne reef can be generalized to any engineered habitat in which trophic basal resources are stimulated, a mechanism probably more intense in extensive and cohesive engineered habitats (i.e. surface area >1000 m<sup>2</sup>) that persist over time (i.e. several years) like coral, polychaete, and bivalve reefs (Engel et al. 2017). Indeed, structural engineers like tube-building invertebrates and bivalves are expected to 'operate through similar processes and have similar types of effects' (Berke 2010, p. 150–151). Expanding our study over multiple years and performing similar studies on extensive mussel and oyster reefs would help to better evaluate the temporal stability of the *S. alveolata* reef food web, to investigate how general our findings are and to eventually determine more precisely engineered habitat characteristics associated to temporally stable and resilient food webs. Finally, as suggested by Bulleri et al. (2018), protecting habitats with these characteristics could help buffer the effects of climate change on coastal ecosystems.

*Acknowledgements.* This project was funded by an EC2CO DRIL (CNRS AO2016-993962) grant. A.G.J. was supported by the 'Laboratoire d'Excellence' LabexMER (ANR-10-LABX-19) and co-funded by a grant from the French government under the program 'Investissements d'Avenir' and by a Région Bretagne/Ifremer PhD grant. This work is partially based on the doctoral thesis of A.G.J. Our funding source had no involvement in this study. We thank everyone who helped us in the field (Ludovic Goyot, Ségolène Jambut, François Gaudin, Patrick Le Mao, Anthony Sturbois, Daniel Gerla, Julien Chevé, Claire Rollet, Renée Taraud, Priscilla Decottignies, Pierre Gernez, Laurent Barillé, and Bernard 'Pompon' Delaunay) and in the lab (Angelica Navarro, Sarah Gouge, and Maiwenn Lescop). Special thanks to Kimberley Sparks from the Cornell Stable Isotope lab and Oanez Lebeau from the IUEM Stable Isotope lab for the swift stable isotope analysis. A final thanks to Helen McCombie Boudry from the translation office of the University of Western Brittany.

#### LITERATURE CITED

- ✦ Androuin T, Dubois SF, Decottignies P, Pelleter E, Carlier A (2019) The dark side of soft tissues: unexpected inorganic carbonate in the invasive slipper limpet *Crepidula fornicata* and its implications for stable isotope interpretations. *Rapid Commun Mass Spectrom* 33: 107–115
- ✦ Ayata SD, Ellien C, Dumas F, Dubois S, Thiebaut E (2009) Modelling larval dispersal and settlement of the reef-

- building polychaete *Sabellaria alveolata*: role of hydroclimatic processes on the sustainability of biogenic reefs. *Cont Shelf Res* 29:1605–1623
- ✦ Berke SK (2010) Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integr Comp Biol* 50:147–157
- Blanchard G, Chretiennot-Dinet MJ, Dinet A, Robert JM (1988) Méthode simplifiée pour l'extraction du microphytobenthos des sédiments marins par le gel de silice Ludox. *C R Acad Sci Sér III Sci Vie* 307:569–576
- Bonnot-Courtois C, Caline B, L'Homer A, Le Vot M (2002) The Bay of Mont-Saint-Michel and the Rance Estuary. Recent development and evolution of depositional environments. CNRS, EPHE, Pau
- Bonnot-Courtois C, Maze JP, Le Vot M, Augris C, Ehrhold A, Simplet L, Blanchard M (2009) Carte morpho-sédimentaire de la baie du Mont Saint-Michel (Ille-et-Vilaine et Manche) échelle 1/25000. Ifremer, Éditions Quae, Versailles
- ✦ Brind'Amour A, Dubois SF (2013) Isotopic diversity indices: how sensitive to food web structure? *PLOS ONE* 8: e84198
- ✦ Bruschetti M (2019) Role of reef-building, ecosystem engineering polychaetes in shallow water ecosystems. *Diversity* 11:168
- ✦ Buffet JP, Corre E, Duvernois-Berthet E, Fournier J, Lopez PJ (2018) Adhesive gland transcriptomics uncovers a diversity of genes involved in glue formation in marine tube-building polychaetes. *Acta Biomater* 72:316–328
- ✦ Bulleri F, Eriksson BK, Queirós A, Airolidi L and others (2018) Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. *PLOS Biol* 16:e2006852
- ✦ Caillaud M, Petton S, Dumas F, Rochette S, Mickael V (2016) Rejeu hydrodynamique à 500 m de résolution avec le modèle MARS3D-AGRIF-8 zooms. <https://sextant.ifremer.fr/record/c1371cc1-f116-4c4f-aaff-bc2ef71a1729/> (accessed 8 January 2017)
- Caline B, Gruet Y, Legendre C, Le Rhun J, L'Homer A, Mathieu R, Zbinden R (1992) The sabellariid reefs in the bay of Mont Saint-Michel, France: ecology, geomorphology, sedimentology, and geologic implications. Florida Oceanographic Society, Stuart, FL
- ✦ Callaway R, Desroy N, Dubois SF, Fournier J and others (2010) Ephemeral bio-engineers or reef-building polychaetes: How stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? *Integr Comp Biol* 50: 237–250
- ✦ Christianen MJA, Middelburg JJ, Holthuijsen SJ, Jouta J and others (2017) Benthic primary producers are key to sustain the Wadden Sea food web: stable carbon isotope analysis at landscape scale. *Ecology* 98:1498–1512
- ✦ Cognie B, Barillé L (1999) Does bivalve mucus favour the growth of their main food source, microalgae? *Oceanol Acta* 22:441–450
- ✦ Colden AM, Fall KA, Cartwright GM, Friedrichs CT (2016) Sediment suspension and deposition across restored oyster reefs of varying orientation to flow: implications for restoration. *Estuaries Coasts* 39:1435–1448
- ✦ Commito JA, Celano EA, Celico HJ, Como S, Johnson CP (2005) Mussels matter: postlarval dispersal dynamics altered by a spatially complex ecosystem engineer. *J Exp Mar Biol Ecol* 316:133–147
- ✦ Cugier P, Struski C, Blanchard M, Mazurié J and others (2010) Assessing the role of benthic filter feeders on phytoplankton production in a shellfish farming site: Mont Saint Michel Bay, France. *J Mar Syst* 82:21–34
- Dame RF, Koepfler E, Gregory L (2000) Benthic–pelagic coupling in marsh–estuarine ecosystems. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Springer Netherlands, Dordrecht, p 369–390
- ✦ De Smet B, Fournier J, Troch MD, Vincx M, Vanaverbeke J (2015) Integrating ecosystem engineering and food web ecology: testing the effect of biogenic reefs on the food web of a soft-bottom intertidal area. *PLOS ONE* 10: e0140857
- ✦ Desroy N, Dubois SF, Fournier J, Ricquiers L and others (2011) The conservation status of *Sabellaria alveolata* (L.) (Polychaeta: Sabellariidae) reefs in the Bay of Mont-Saint-Michel. *Aquat Conserv* 21:462–471
- ✦ Donadi S, van der Zee EM, van der Heide T, Weerman EJ and others (2014) The bivalve loop: intra-specific facilitation in burrowing cockles through habitat modification. *J Exp Mar Biol Ecol* 461:44–52
- ✦ Dubois SF, Colombo F (2014) How picky can you be? Temporal variations in trophic niches of co-occurring suspension-feeding species. *Food Webs* 1:1–9
- ✦ Dubois S, Retière C, Olivier F (2002) Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs: effects of human disturbances. *J Mar Biol Assoc UK* 82:817–826
- ✦ Dubois S, Barillé L, Retière C (2003) Efficiency of particle retention and clearance rate in the polychaete *Sabellaria alveolata* L. *C R Biol* 326:413–421
- ✦ Dubois S, Barillé L, Cognie B, Beninger PG (2005) Particle capture and processing mechanisms in *Sabellaria alveolata* (Polychaeta: Sabellariidae). *Mar Ecol Prog Ser* 301: 159–171
- ✦ Dubois S, Commito JA, Olivier F, Retière C (2006) Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. *Estuar Coast Shelf Sci* 68:635–646
- ✦ Dubois S, Orvain F, Marin-Léal JC, Ropert M, Lefebvre S (2007) Small-scale spatial variability of food partitioning between cultivated oysters and associated suspension-feeding species, as revealed by stable isotopes. *Mar Ecol Prog Ser* 336:151–160
- ✦ Echappé C, Gernez P, Méléder V, Jesus B and others (2018) Satellite remote sensing reveals a positive impact of living oyster reefs on microalgal biofilm development. *Biogeosciences* 15:905–918
- ✦ Engel FG, Alegria J, Andriana R, Donadi S and others (2017) Mussel beds are biological power stations on intertidal flats. *Estuar Coast Shelf Sci* 191:21–27
- Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- ✦ Friedrichs M, Graf G, Springer B (2000) Skimming flow induced over a simulated polychaete tube lawn at low population densities. *Mar Ecol Prog Ser* 192:219–228
- Goldberg WM (2013) *The biology of reefs and reef organisms*. The University of Chicago Press, Chicago, IL
- ✦ González-Ortiz V, Egea LG, Jiménez-Ramos R, Moreno-Marín F, Pérez-Lloréns JL, Bouma TJ, Brun FG (2014) Interactions between seagrass complexity, hydrodynamic flow and biomixing alter food availability for associated filter-feeding organisms. *PLOS ONE* 9:e104949
- ✦ Griffiths JR, Kadin M, Nascimento FJA, Tamelander T and others (2017) The importance of benthic–pelagic cou-

- pling for marine ecosystem functioning in a changing world. *Glob Change Biol* 23:2179–2196
- Gruet Y (1972) Aspects morphologiques et dynamiques de constructions de l'annelide polychete *Sabellaria alveolata* (Linne). *Rev Trav Inst Peches Marit* 36:131–161
- ✦ Guerra-García JM, Tierno de Figueroa JM, Navarro-Barranco C, Ros M, Sánchez-Moyano JE, Moreira J (2014) Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. *J Sea Res* 85:508–517
- Gutiérrez JL, Jones CG, Byers JE, Arkema KK and others (2012) Physical ecosystem engineers and the functioning of estuaries and coasts. In: Wolanski E, McClusky DS (eds) *Treatise on Estuarine and Coastal Science*, Vol 7. Academic Press, Waltham, MA, p 53–81
- ✦ Haven DS, Morales-Alamo R (1966) Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnol Oceanogr* 11:487–498
- Holt TJ, Rees EI, Hawkins SJ, Seed R (1998) Biogenic reefs Vol IX. An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science, UK Marine SACs Project, Port Erin
- ✦ Hondula KL, Pace ML (2014) Macroalgal support of cultured hard clams in a low nitrogen coastal lagoon. *Mar Ecol Prog Ser* 498:187–201
- ✦ Hubas C, Lamy D, Artigas LF, Davoult D (2007) Seasonal variability of intertidal bacterial metabolism and growth efficiency in an exposed sandy beach during low tide. *Mar Biol* 151:41–52
- ✦ Hylleberg J (1975) Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. *Ophelia* 14:113–137
- ✦ Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602
- ✦ Jankowska E, De Troch M, Michel LN, Lepoint G, Włodarska-Kowalczyk M (2018) Modification of benthic food web structure by recovering seagrass meadows, as revealed by trophic markers and mixing models. *Ecol Indic* 90:28–37
- Jones A (2017) Effect of an engineer species on the diversity and functioning of benthic communities: the *Sabellaria alveolata* reef habitat. PhD thesis, Université de Bretagne occidentale, Brest
- ✦ Jones AG, Dubois SF, Desroy N, Fournier J (2018) Interplay between abiotic factors and species assemblages mediated by the ecosystem engineer *Sabellaria alveolata* (Annelida: Polychaeta). *Estuar Coast Shelf Sci* 200:1–18
- ✦ Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- ✦ Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957
- ✦ Jones CG, Gutiérrez JL, Byers JE, Crooks JA, Lambrinos JG, Talley TS (2010) A framework for understanding physical ecosystem engineering by organisms. *Oikos* 119:1862–1869
- ✦ Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. *Annu Rev Mar Sci* 7:497–520
- ✦ Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- ✦ Le Cam JB, Fournier J, Etienne S, Couden J (2011) The strength of biogenic sand reefs: visco-elastic behaviour of cement secreted by the tube building polychaete *Sabellaria alveolata*, Linnaeus, 1767. *Estuar Coast Shelf Sci* 91:333–339
- Lefebvre S, Dubois SF (2016) The stony road to understand isotopic enrichment and turnover rates: insight into the metabolic part. *Vie Milieu* 66:305–314
- ✦ Lorrain A, Savoye N, Chauvaud L, Paulet YM, Naulet N (2003) Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. *Anal Chim Acta* 491:125–133
- ✦ Majdi N, Hette-Tronquart N, Auclair E, Bec A and others (2018) There's no harm in having too much: a comprehensive toolbox of methods in trophic ecology. *Food Webs* 17:e00100
- ✦ Marín Leal JC, Dubois S, Orvain F, Galois R and others (2008) Stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) and modelling as tools to estimate the trophic ecology of cultivated oysters in two contrasting environments. *Mar Biol* 153:673–688
- ✦ McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390
- ✦ McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, MA. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- ✦ Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR (2000) The fate of intertidal microphytobenthos carbon: an in situ  $^{13}\text{C}$ -labeling study. *Limnol Oceanogr* 45:1224–1234
- ✦ Muir AP, Nunes FLD, Dubois SF, Pernet F (2016) Lipid remodelling in the reef-building honeycomb worm, *Sabellaria alveolata*, reflects acclimation and local adaptation to temperature. *Sci Rep* 6:35669
- ✦ Navarro-Barranco C, Tierno-de-Figueroa JM, Guerra-García JM, Sánchez-Tocino L, García-Gómez JC (2013) Feeding habits of amphipods (Crustacea: Malacostraca) from shallow soft bottom communities: comparison between marine caves and open habitats. *J Sea Res* 78:1–7
- ✦ Neutel AM, Heesterbeek JAP, van de Koppel J, Hoenderboom G and others (2007) Reconciling complexity with stability in naturally assembling food webs. *Nature* 449:599–602
- ✦ Noernberg MA, Fournier J, Dubois S, Populus J (2010) Using airborne laser altimetry to estimate *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs volume in tidal flat environments. *Estuar Coast Shelf Sci* 90:93–102
- ✦ Parnell AC (2016) Simmr: a stable isotope mixing model. v. 0.4.1. <https://cran.r-project.org/src/contrib/Archive/simmr/>
- ✦ Parnell AC, Jackson JBC (2013) Siar: Stable Isotope Analysis in R. v. 4.2. <https://cran.r-project.org/web/packages/siar/index.html>
- ✦ Parnell AC, Phillips DL, Bearhop S, Semmens BX and others (2013) Bayesian stable isotope mixing models. *Environmetrics* 24:387–399
- ✦ Passarelli C, Olivier F, Paterson DM, Meziane T, Hubas C (2014) Organisms as cooperative ecosystem engineers in intertidal flats. *J Sea Res* 92:92–101
- ✦ Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316

- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Riera P (2007) Trophic subsidies of *Crassostrea gigas*, *Mytilus edulis* and *Crepidula fornicata* in the Bay of Mont Saint Michel (France): a  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  investigation. *Estuar Coast Shelf Sci* 72:33–41
- ✦ Rigolet C, Thiébaud E, Dubois SF (2014) Food web structures of subtidal benthic muddy habitats: evidence of microphytobenthos contribution supported by an engineer species. *Mar Ecol Prog Ser* 500:25–41
- ✦ Romero GQ, Gonçalves-Souza T, Vieira C, Koricheva J (2015) Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biol Rev Camb Philos Soc* 90:877–890
- Salomon JC, Breton M (1991) Courants résiduels de marée dans la Manche. *Oceanol Acta* 11:47–53
- ✦ Sanders D, Jones CG, Thébaud E, Bouma TJ, van der Heide T, van Belzen J, Barot S (2014) Integrating ecosystem engineering and food webs. *Oikos* 123:513–524
- Secula C (2011) Acteurs et gestion du littoral. Une anthropologie de la baie du Mont-Saint-Michel. PhD thesis, Museum national d'histoire naturelle, Paris
- ✦ Stallins JA (2006) Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. *Geomorphology* 77:207–216
- ✦ Ubertini M, Lefebvre S, Gangnery A, Grangeré K, Gendre RL, Orvain F (2012) Spatial variability of benthic–pelagic coupling in an estuary ecosystem: consequences for microphytobenthos resuspension phenomenon. *PLOS ONE* 7:e44155
- ✦ van Broekhoven W, Jansen H, Verdegem M, Struyf E, Troost K, Lindeboom H, Smaal A (2015) Nutrient regeneration from feces and pseudofeces of mussel *Mytilus edulis* spat. *Mar Ecol Prog Ser* 534:107–120
- ✦ van der Zee EM, Angelini C, Govers LL, Christianen MJA and others (2016) How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proc R Soc B* 283:20152326
- ✦ Vander Zanden MJ, Rasmussen JB (2001) Variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  trophic fractionation: implications for aquatic food web studies. *Limnol Oceanogr* 46:2061–2066
- ✦ Vanderklift MA, Ponsard S (2003) Sources of variation in consumer–diet  $\delta^{15}\text{N}$  enrichment: a meta-analysis. *Oecologia* 136:169–182
- ✦ Vizzini S, Colombo F, Costa V, Mazzola A (2012) Contribution of planktonic and benthic food sources to the diet of the reef-forming vermetid gastropod *Dendropoma petraeum* in the western Mediterranean. *Estuar Coast Shelf Sci* 96:262–267
- ✦ Watson GJ, Murray JM, Schaefer M, Bonner A, Gillingham M (2017) Assessing the impacts of bait collection on inter-tidal sediment and the associated macrofaunal and bird communities: the importance of appropriate spatial scales. *Mar Environ Res* 130:122–133
- ✦ Wilson DP (1976) *Sabellaria alveolata* (L.) at Duckpool, North Cornwall, 1975. *J Mar Biol Assoc UK* 56: 305–310
- ✦ Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101
- ✦ Zhao Q, Van den Brink PJ, Carpentier C, Wang YXG and others (2019) Horizontal and vertical diversity jointly shape food web stability against small and large perturbations. *Ecol Lett* 22:1152–1162

Editorial responsibility: Simonetta Fraschetti,  
Naples, Italy  
Reviewed by: 2 anonymous referees

Submitted: March 30, 2020  
Accepted: November 27, 2020  
Proofs received from author(s): February 12, 2021