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Food web structures of subtidal benthic muddy habitats: evidence of microphytobenthos contribution supported by an engineer species

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Running page head: Food web structure of amphipod tube mats

ABSTRACT: Stable C and N isotopic composition of benthic organisms was investigated to understand the effects of a gregarious tubiculous amphipod species (*Haploops nirae*) on benthic food web structures and test whether drastic changes in species composition cause changes in food web structure. The habitat engineered by this species was sampled and compared with the adjacent *Amphiura filiformis* muddy habitat in winter and summer. The isotopic signature of macro- and mega-faunal species associated with both habitats were analysed along with potential food sources at each sampling period. Similar food web structures for each habitat (and each season), with high δ^{15}N ranges, spanning over 3 trophic levels, were reported although omnivory was less frequent in the *Haploops* habitat. The amphipod *Haploops nirae* appears to play a baseline role with the lowest δ^{15}N values and δ^{13}C values indicating that it primarily feeds on phytoplankton. Bayesian mixing models used to estimate the contributions of potential food sources to the diet of the species accounting for most of the biomass in each habitat showed that the epibionts covering tube mats are a key contribution to both habitats food webs. Identified as benthic diatoms, they may minimize inter-specific food competition between dominant suspension-feeders such as *Polititapes virgineus* or *Haploops nirae* within a habitat. This finding highlights the contribution of microphytobenthic producers to subtidal (~ 30 m deep) muddy habitats food webs, mucopolysaccharides composing *Haploops* tubes being suggested to support the growth of a heterotrophic diatom population. As an engineer species, *Haploops* acts as a facilitator for diatoms which ultimately sustain the secondary production of the *Haploops* habitat as well as the immediate surrounding habitats.

KEY WORDS: Stable isotopes · Gregarious amphipod · Source contribution · *Haploops* · Benthic diatoms · *Navicula*

INTRODUCTION

Coastal zones are considered among the most productive marine systems in the world with both high ecological and economic values. They offer a wide variety of ecosystem services for humans but also sustain ecological processes of primary importance for marine wildlife such as nutrient regulation, carbon sequestration and detoxification of polluted waters (Constanza et al. 1997, Gattuso et al. 1998, Barbier et al. 2011). Coastal ecosystems are also known to support particularly species rich and abundant benthic communities, resulting in areas of high benthic secondary production which are of major importance for supporting nursery grounds and feeding areas for most coastal and many oceanic fish species (Kopp et al. 2013). The importance of coastal systems in sustaining marine wildlife has consequently required a much better knowledge of biological and ecological processes in coastal systems. As reviewed in Duffy et al. (2007), the trophic complexity within trophic levels (food chain width and variety of food sources) and across trophic levels (food chain length and omnivory) are essential elements to understand how biodiversity changes affect ecosystem functioning. Yet the understanding of trophic dynamics and pathways in coastal systems remains partly unknown. Indeed, while the primary production in the open-ocean is only dominated by phytoplankton, a large variety of primary producers (*e.g.* macrophytes, salt marshes plants, mangroves, seagrass beds and microphytobenthos) contribute to the organic matter sedimentary pool available for benthic consumers in coastal ecosystems (Evrard et al. 2012). Unlike in shores and estuaries where benthic primary production through microphytopbenthos (MPB) play a key role in benthic food webs (Riera et al. 1996, Dubois et al. 2007, Lefebvre et al. 2009), microphytobenthic primary producers are disregarded in subtidal benthic food webs, despite evidences that δ^{13}C-enriched isotopic compositions of benthic suspension- and deposit-feeders cannot solely be explained by phytoplankton or macroalgae sources (e.g. Grall et al. 2006, Carlier et al 2007). Few studies however have emphasized the potential role of microphytobenthos in the trophic food webs of different coastal habitats such as estuarine systems, mudflats (Middleburg et al. 2000) or shallow sandy permeable sediments (Evrard et al. 2010). Stable carbon and nitrogen isotope ratios have proven to be a powerful tool in evaluating feeding relationships and organic matter flows through marine food webs (Dubois and Grall 2013). As stable isotopes are frequently used to understand feeding behaviour and trophic relationships between species (Peterson & Fry 1987), they can also be used at the community scale to describe the overall structure of a food web such as food web length or trophic niche space (Bearhop et al. 2004, Cornwell et al. 2006, Layman et al. 2007a), for example providing valuable information on the health of the system (Layman et al. 2007b, Zambrano et al. 2010). However stable isotopes (mostly C and N) have been more specifically used to disentangle trophic pathways in coastal systems by ranking the organic matter sources supporting food webs, and to provide estimates of food sources contributions to consumers' diet. When wisely used (but see recommendations in Fry 2013), the development of mixing models has greatly enhanced the power in isotopic tools (Phillips & Gregg 2003, Parnell et al. 2010).

Some benthic coastal systems are considered to have particularly high ecological value (Wright & Jones 2006, Voultsiadou et al. 2007), and these are often habitats which are physically modified by engineer species (as defined in Jones et al. 1994). Mangroves, seagrasses or coral reefs habitats have been shown not only to enhance the local biodiversity of benthic and pelagic species but also to modify the availability of resources for others species (Berkenbusch & Rowden 2007). Ecosystems engineers often are key species in ecosystem functioning. While their effects on the diversity of benthic communities have been widely investigated (see review and references in Reise et al. 2009), only few studies have paid attention to the consequences of ecosystem engineers on the structure of the marine food webs. Yet, ecosystem engineers can induce changes in the intensity of biological interactions (mainly predation-prey interactions) (Irlandi & Peterson 1991) or can alter the food supply to other organisms (Allen & Williams 2003) thus having major consequences on flows of organic pathways in benthic coastal systems.

In South Brittany (France), a benthic community dominated by the gregarious tubicolous Ampeliscid *Haploops nirae* forms dense tube mats in two main coastal ecosystems, namely the Bay of Concarneau and the Bay of Vilaine (Rigolet et al. 2013). As for many gregarious species, *Haploops nirae* is the most abundant species and formsdense populations, with average densities ranging between about 1 000 and 25 000 ind.m^{-2} (Rigolet et al. 2012). Whilst the presence of a *Haploops* community was reported during the first description of shallow benthic communities of South Brittany (Glémarec 1969), recent acoustic surveys showed a significant increase in area of cover (Ehrhold et al. 2006). For example, the mapping of the Bay of Concarneau revealed a 5-fold increase in *Haploops nirae* habitat surface between 1963 (650 ha in Glémarec, 1969) and 2003 (3680 ha in Ehrhold et al., 2006): *Haploops* are then colonizing the adjacent habitat. By investigating the consequences of this expansion on the benthic habitats, Rigolet et al. (2013) showed that *Haploops* significantly modify sediment features (e.g. change in granulometry, increase in C and N organic content) and therefore deeply affect species diversity and benthic composition by creating a unusual and diverse macrofaunal assemblage. Analysis of species composition revealed that *Haploops* community shared very few species with surrounding soft-sediment communities. According to its effects on the physical and chemical properties of the sedimentary habitat, *Haploops nirae* can be defined as an ecosystem engineer (Reise et al. 2009). However, very little is known about its direct effect on food web functioning (e.g. resource availability) and whether changes in species composition can indirectly affect trophic pathways and food web structure. Several studies provided evidence that dense populations of Ampeliscids could play major roles in energy transfer in some marine systems, not only because they can affect benthic-pelagic coupling and have a major grazing impact on phytoplankton production (Grebmeier & Mc Roy 1989, Rigolet et al. 2011) but also because they export a high production towards higher trophic levels (Franz & Tanacredi 1992, Highsmith & Coyle, 1992). In this study, we sampled the diversity of benthic organisms associated with the *Haploops* habitat and the adjacent uncolonised *Amphiura* habitat over two seasons. We used stable C and N isotopes to investigate whether drastic changes in species composition also cause changes in food web structure and to identify the main trophic pathways and main food sources that support the macrofauna assemblages in these systems. More specifically, we aim to address here the following questions: (1) how the expansion of an engineer species, i.e. *Haploops nirae,* influences the food web structure of benthic habitats and (2) how the presence of *Haploops nirae* controls the availability of food source within and among habitats.

MATERIALS AND METHODS

Study area and sampling strategy. This study was conducted in the Bay of Concarneau, situated in the Northern part of the Bay of Biscay (France) (Fig. 2). This area is sheltered by a succession of rocky islets and is characterized by soft-bottom substrata, spanning from muddy to muddy-sands, with a depth ranging from 15 to 35 m (Menesguen 1980, Ehrhold et al. 2006). The western part of the Bay (Mouton Islets and Glénan Islands) is composed of muddy sands and sandy muds with benthic community dominated by the echinoderm *Amphiura filiformis*. The central part of the bay - where currents are strongly reduced - is composed of pure mud supporting a dense population of the tubiculous amphipod *Haploops nirae*.

To investigate the effects of *Haploops* tube mats on benthic trophic structure, we compared the food web structure of the *Haploops* nirae habitat (hereafter *Haploops* habitat) with the adjacent benthic and uncolonized *Amphiura filiformis* habitat (hereafter *Amphiura* habitat). Using a mapping survey of the seabed in the Bay of Concarneau based on geoacoustic approaches and complementary benthic biological grab samples (Ehrhold et al. 2006), we selected 6 stations distributed along two north-south transects reflecting an inshore-offshore gradient (Fig. 2). The six stations were sampled during two contrasting seasons: in winter (February 2010) when food inputs were particularly low and when the benthic fauna has a low metabolic activity, and in summer (August 2010) at the end of a period characterized by high supply of pelagic production in this area.

Samples collection and laboratory processes. To investigate the trophic structure within each habitat (i.e. *Haploops* and *Amphiura* habitats), we collected the largest possible diversity of macrofaunal and megafaunal organisms for isotopic analyses at all stations of each community-transect and for the two seasons. Macrofauna (individual size: 1-10 mm) was sampled using a 0.1 m² Van Veen grab (at least 2 grabs per station) and megafauna (individual size > 10 mm) using a modified beam trawl (width = 2 m, sampled surface = ca. 2300 m²) (Desaunay et al. 2006) with one trawl at each station.

All collected benthic organisms were carefully sorted on board and kept frozen. In the laboratory, organisms were identified to the lowest taxonomic level (i.e. generally at the species level). Species names were checked using the World Register of Marine Species database (updated check 28/10/2013). Isotopic analyses were then performed on muscle tissue samples for megafauna and large macrofauna. The whole body (gut-dissected) was used for smaller species. In rare instances, several individuals were pooled to match the minimum weight required for stable isotope analyses. All samples were rinsed with Milli-Q water and freeze-dried. Three replicates were analyzed. For calcified organisms (crustaceans and echinoderms), a sub-sample was acidified (10% HCl) to remove any inorganic carbonates, then rinsed with distilled water and freeze-dried again for ^{13}C values (a sub-sample was left untreated for ^{15}N value). We used the mean isotopic value of organisms for each habitat by pooling organisms found in 2 or 3 stations of each transect. The mean isotopic value was considered to be a better estimate of the whole habitat and account for any spatial variability.

All potential sources of organic matter available for the benthic fauna were collected for isotopic analyses. Terrestrial inputs of organic matter (TOM) are very limited in this area as it receives freshwater inputs from small rivers only (i.e. mean monthly discharge < 1 m^3 s^{-1}). Because of a reduced light input, subtidal soft-bottom systems are commonly assumed to host very low benthic primary production, especially in muddy turbid waters (Le Loc'h et al. 2008). Consequently, most of the organic matter (OM) available for benthic primary consumers was supposed to originate from the suspended particulate organic matter (POM) (composed mainly of phytoplankton) sedimenting from upper water layers and from the sediment organic matter (SOM). However, close observations of *Haploops* tubes revealed that the surface of tubes was covered with brown epibionts (hereafter EPI) especially during spring blooms, identified as benthic diatoms mats that belong to the genus *Navicula*, (identification Siano R., pers. com.) (Fig. 1). Benthic diatoms attached to *Haploops* tubes were also considered as a potential food source. In addition, macroalgal fragments and detritus originating from adjacent rocky islets (i.e. Glenan and Moutons) were caught in some trawls and were also considered as a potential food source for benthic organisms, even though sampled stations are below the photic limit required by attached macroalgae to grow (ca. 35m deep).

Freshwater was collected at one site located at the mouth of one small river for TOM. Marine surface water was collected using Niskin bottles for POM analysis at stations along an inshore-offshore transect (Fig. 2) in between the two habitats which shared the same water masses. Water samples were prefiltered on a 100 µm mesh to remove small animals such as zooplankton and then filtered on pre-combusted GFF filters (4h, 550°C). Half of GFF filters were acidified with 10N HCl fumes to remove traces of inorganic carbonates. Sediment organic matter (SOM) was sampled at each of the 6 stations using a Reineck corer to extract undisturbed sediment core: from each core, 2 sub-cores were extracted to analyse both the isotopic composition of the organic matter and the chlorophyll *a* and phaeopigments content. For the 3 *Haploops* stations (H1, H2 and H3, Fig. 2), the surface of several tubes were gently scrapped with a razor blade under a dissecting scope and collected with distilled water. For both SOM and EPI samples, a sub-sample was acidified (10% HCl) to remove inorganic carbonates (^{13}C) and the rest was left untreated (^{15}N). Molar C:N ratio were calculated from the %C and %N values obtained from acidified and untreated sediment samples, respectively. Chlorophyll *a* and phaeopigments content were estimated using the monochromatic technique (Lorenzen 1967) as described in Aminot and Kérouel (2004). Finally, brown, red and green stranded macroalgae were collected from trawls in summer only, as very little macroalgae was noticed during winter.

Isotopic analyses. After freeze-drying, each sample was ground to a homogeneous powder and 1 mg was weighed in tin capsules for isotopic analyses. The isotopic composition of carbon (δ^{13}C) and nitrogen (δ^{15}N) was then measured with a stable isotope ratio mass spectrometer Finnigan MAT Delta Plus, operating in continuous-flow method, coupled to an elemental analyser Carlo Erba NC2500 (Cornell University, Stable Isotope Laboratory, New York). Isotopic ratios for carbon and nitrogen were expressed using the standard δ notation according to the following equation:

$\delta X = ((R_{sample}/R_{reference}) - 1) \times 1000$ (‰)

where X= ^{13}C (carbon) or ^{15}N (nitrogen) and R= ^{13}C/^{12}C for carbon and ^{15}N/^{14}N for nitrogen. The reference for carbon was Vienna Pee Dee Belemnite (VPDB, δ^{13}C=0 ‰) and for nitrogen was atmospheric nitrogen (δ^{15}N=0‰). The analytical precision was 0.2 ‰ for both nitrogen and carbon.

Data analyses. To provide a detailed description of the structure of the food web associated with both habitats, macrofaunal and megafaunal species were classified into five trophic groups: suspension-feeders (SF), surface deposit-feeders (SDF), subsurface deposit-feeders (SSDF), omnivores-carnivores (C-O) and grazers (G). Trophic information on species were gathered from several scientific publications and from the Biological Traits Information Catalogue developed by the Marine Life Information Network (www.marlin.ac.uk/biotic).

The nitrogen isotope ratio is commonly used to estimate the trophic position of aquatic consumers (Cabana & Rasmussen 1996, Vander Zanden et al. 1997, Post 2002) and organisms tend to fractionate nitrogen positively by 3-4 ‰ (Minagawa & Wada 1984, Post 2002). In this context, Vander Zanden & Rasmussen (2001) showed that the δ^{15}N baseline used to determine the trophic level of consumers is of primary importance. They calculated that the error variance in consumer trophic position was three times larger when using primary producers rather than primary consumers as baseline indicator organisms. In this perspective, we considered primary consumers as time (season) integrators of the primary producer isotopic variability and the primary consumer *Haploops nirae* that feeds on phytoplankton (Rigolet et al., 2011) was used as isotopic baseline. As a result, consumer trophic position can be calculated using the following formula:

$$\text{Trophic Level} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{mean } \textit{Haploops}})/3.4 + 2$$

where 3.4 ‰ is the assumed mean ^{15}N trophic-enrichment factor according to Minagawa & Wada (1984). Primary, secondary and tertiary consumers were thus designated as the second, third and fourth trophic levels respectively.

Numerous approaches to solve isotopic mixing models and quantify the relative contributions of primary producers to species diets have been developed (see review in Layman et al. 2012). Conventional linear mixing models such as IsoError and IsoSource (Phillips & Gregg 2003, Phillips 2012) calculate the contribution of food resources to a consumer's diet using a set of mass-balance equations. However, such mixing models cannot incorporate uncertainties and variations in the isotopic compositions of prey and consumers and most importantly, the outputs from these models represent a range of feasible solutions, with no quantification as to which solutions are most likely (Parnell et al. 2010). Quite recently, Bayesian mixing models have been proposed to circumvent many limitations of the linear models. They are also based on a set of linear equations that use Bayesian statistical techniques to identify the relative contributions of different sources but they allow variability in input terms. Furthermore, outputs from the Bayesian models are in the form of true probability distributions and not a list of all feasible solutions (Parnell et al. 2010). In the present study, we ran Bayesian mixing models with the package SIAR (Stable Isotope Analysis in R) of the free software R, version 2.11.1 (R Development Core Team 2010) using default parameters. For a more comprehensive output, the model was performed only on species that account for the greatest part of the benthic biomass (i.e. 80 %), i.e. 6 species on the *Amphiura* habitat and 5 species on the *Haploops* habitat.Biomass data (not presented here) were obtained using grab samples collected in each habitat, from which macrofauna (> 1 mm) was identified and weighed (ash-free dry weight). The relative contribution of each species to the total habitat biomass was then calculated and used to select species (Rigolet et al, in prep). The model was run for summer isotopic compositions only as it has been showed that mixing models results from winter period in temperate regions were irrelevant since turnover in organisms' tissues was close to zero (Leal et al. 2008) and food assimilation ultimately negligible. Two variables ($\delta^{13}C$ and $\delta^{15}N$) were used and three sources (POM, SOM and EPI) were considered for the computation of the model, as *a posteriori* knowledge of isotopic signature and relative importance of macroalgae and TOM sources were likely too low to be integrated in the mixing model and would otherwise increase uncertainties in model outputs (Fry 2013).

Mixing models require an *a priori* estimate of the enrichment in δ^{15}N and δ^{13}C values between preys and predators. Variations in fractionation values contributed to the major part of the error variance in mixing model outputs (Phillips & Gregg 2003, Fry 2013). While it is commonly assumed that the δ^{15}N and the δ^{13}C values of a consumer are typically enriched by 3.4 ‰ and 1 ‰ respectively (Minagawa & Wada 1984), recent reviews indicated that fractionation values are affected by multiple factors, such as food quality, tissues turnover, environmental conditions and even taxonomic group (Vander Zanden & Rasmussen 2001, Vanderklift & Ponsard 2003, McCutchan et al. 2003). Caut et al. (2009) reviewed carbon and nitrogen isotopic discrimination factors from the literature and suggested linear models to estimate discrimination factors according to the signature of food sources. We calculated a trophic enrichment factor (TEF) for each source following the equations provided by Caut et al. (2009) for invertebrates. We used source-specific TEF for the POM (4.04 ± 0.20 ‰ for δ^{15}N and 2.18 ± 0.11‰ for δ^{13}C), for the SOM (3.32 ± 0.12 ‰ for δ^{15}N and 1.68 ± 0.02 ‰ for δ^{13}C) and for the EPI (3.03 ± 0.05 ‰ for δ^{15}N and 0.05 ± 0.07 ‰ for δ^{13}C). For secondary consumers, trophic enrichment factors were multiplied by the number of trophic levels between the basal resources and the consumer, as classically used for community approaches (*e.g.* Phillips 2012, Colombo et al. 2012). Beca use we used a Bayesian approach, we were able to insert variability (standard deviation) in TEF values as well (Parnell et al. 2010).

RESULTS

Food sources

Isotopic ratios of potential organic matter sources for the two transects and the two seasons are listed in Table 1. The $\delta^{13}C$ of potential food sources were well discriminated and varied from -28.58 ‰ (TOM) to -21.14 ‰ (SOM) in winter, and from -34.29 ‰ (*Dasya corymbifera*, a red alga) to -13.19 ‰ (epibionts on *Haploops* tubes) in summer. The potential food sources displayed a $\delta^{13}C$ range of 7.4 ‰ in winter which increased to 21.1‰ in summer mainly due to the ^{13}C-enrichment of benthic diatoms collected on the *Haploops* tubes (epibionts) and the ^{13}C-depletion of benthic red macroalgae (Table 1). Terrestrial inputs (TOM) $\delta^{13}C$ values were depleted in ^{13}C in winter (-28.58 ‰) but were not sampled in summer (dry season) when the riverine flow was at its lowest. As for the phytoplankton (POM), $\delta^{13}C$ values recorded in winter (-24.06 ‰) and summer (-23.73 ‰) did not significantly differ (t-test, $p = 0.626$). The isotopic signature of macroalgae displayed group-specific isotopic ratios ($\delta^{13}C$) with strongly ^{13}C-depleted red algae (*Palmaria palmata*, *Hypoglossum hypoglossoides*, *Dasya corymbifera*) and more ^{13}C-enriched brown (*Laminaria* sp., *Dictyota dichotoma*) and green (*Ulva* sp.) macroalgae. Isotopic ratios of sedimented organic matter (SOM) exhibited the same values between bare sediments stations (sandy mud *Amphiura* habitat) and muddy *Haploops* habitat for both seasons (t-test, $p = 0.508$ in winter and $p = 0.060$ in summer). Therefore, all isotopic values for SOM were averaged into one single average isotopic value for the SOM. The isotopic signature of *Haploops* epibionts varied significantly among seasons (t-test, $p < 0.001$). While it is close to the SOM signature in winter, it was strongly ^{13}C-enriched in summer. The $\delta^{15}N$ values of potential food sources spanned from 3.06 ‰ to 7.67 ‰ in winter and from 4.14 ‰ to 7.21 ‰ in summer.

Chlorophyll *a* and phaeopigments analyses revealed a much higher total content of primary producer pigments in the *Haploops* habitat than in the adjacent *Amphiura* habitat irrespective of the season (Table 2). More specifically, even though phaeopigments are about one order of magnitude higher than Chl. *a*, a significant content of Chl. *a* was found in *Haploops* sediments in winter. The C:N ratio was lower in the *Haploops* habitat suggesting a higher quality of the available organic matter for benthic consumers.

Benthic habitat food web structures

The $\delta^{13}C$ and $\delta^{15}N$ values displayed by the benthic fauna for the two habitats in winter and summer are represented in Fig. 3A and 3B, respectively (mean isotopic compositions of each species are provided as supplement, S1 for winter and S2 for summer). Graphically, three potential food sources (i.e. SOM, POM and EPI) are likely to support the primary consumers in the two communities. A few species showed particular isotopic signatures: in winter the sea slug *Aplysia punctata* (Fig. 3A) displayed very ^{13}C-depleted values (-29.41 ‰ and –30.81 ‰ in both *Amphiura* and *Haploops* habitats) and appeared to rely on ^{13}C-depleted red macroalgae (such as *Palmaria palmata*, *Hypoglossum hypoglossoides* and *Dasya corymbifera*). The polychaete *Nereis* sp. ($\delta^{13}C$ = -24.71 ‰), seemed to partly feed on ^{13}C-depleted red macroalgae too. In summer, the nudibranch *Geitodoris planata* displayed ^{13}C-enriched values (Fig. 3B) in both habitats ($\delta^{13}C$ = -11.83 ‰ and –11.64 ‰ in *Amphiura* and *Haploops* habitat, respectively). The bivalve *Thyasira flexuosa* (not plotted in Figs. 2 and 3) displayed strongly depleted $\delta^{13}C$ (-26.40 ‰) and $\delta^{15}N$ values (-0.3 ‰).

The absolute frequencies of $\delta^{13}C$ and $\delta^{15}N$ compositions displayed by all sampled species in the two habitats in winter and summer are represented in Fig. 4. Apart from a few species with particular isotopic values (namely *Aplysia punctata*, *Nereis* sp., *Thyasira flexuosa* and *Geitodoris planata*), the frequency distributions exhibited a similar range in $\delta^{13}C$ values, with winter compositions spanning from -21.63 ‰ (*Psammechinus miliaris*) to -14.75

‰ (*Aphrodita aculeata*) in *Amphiura* habitat and from –20.48 ‰ (*Schistomeringos rudolphii*) to –14.86 ‰ (*Buccinum undatum*) in the *Haploops* habitat. In summer, δ^{13}C isotopic values displayed the same pattern with values ranging from -20.91 ‰ (*Ampelisca spinipes*) to -13.98 ‰ (*Philine aperta*) in the *Amphiura* habitat and from –20.43 ‰ (*Ampelisca typica*) to –14.26 ‰ (*Luidia ciliaris*) in the *Haploops* habitat. Frequency distributions of δ^{15}N values exhibited close variations in the two habitats as well, ranging from 7.17 ‰ (*Ampharete finmarchica*) to 14.43 ‰ (*Glycera unicornis*) in winter in the *Amphiura* habitat and from 7.02 ‰ (*Haploops nirae*) to 13.28 ‰ (*Maja squinado*) in the *Haploops* habitat. In summer, δ^{15}N values showed almost identical variations with δ^{15}N values ranging from 6.93 ‰ (*Cultellus pellucidus*) to 13.45 ‰ (*Luidia ciliaris*) in the *Amphiura* habitat and from 6.40 ‰ (*Timoclea ovata*) to 15.24 ‰ (*Glycera unicornis*) in the *Haploops* community. The distributions of δ^{15}N values appeared to be bi-modal in winter and summer for the *Haploops* habitat, but less structured for the *Amphiura* habitat. As for the distributions of δ^{13}C values, calculations of the Kurtosis index revealed a decrease between winter and summer for the two habitats (7.4 to 4.1 for the *Amphiura* habitat and 3.4 to 3.3 for the *Haploops* habitat), indicating a sign of flattening in the distribution between the two seasons. This was most noticeable for the *Amphiura* habitat though (Fig. 4).

When pooled into trophic functional groups, organisms’ isotopic signatures revealed that the two habitats have very similar trophic structure. Indeed, the average values of both δ^{13}C and δ^{15}N for each trophic groups did not show significant differences between the two communities (MANOVA, $p>0.05$), irrespective of the season. Trophic groups are characterized by large within-group variations in δ^{13}C values (Table 3). Suspension-feeders (SF) spanned consistently over the same ranges in δ^{13}C values (4.44‰ to 4.85‰), not only between the two seasons but also between the two communities. For the two seasons and the two communities, carnivores-omnivores had the same mean δ^{13}C range (4.47‰ to 4.87‰), except in the *Haploops* habitat in winter where carnivores-omnivores exhibited a larger $\delta^{13}C$ range (i.e. 6.38 ‰). Unlike other trophic groups, surface deposit feeders (SDF) had no clear pattern in $\delta^{13}C$ ranges and varied from 1.82 ‰ up to 4.51 ‰. The *Haploops* community is characterized for both seasons by a narrower $\delta^{13}C$ range in subsurface deposit-feeders (SSDF) (mean 1.25‰) as compared to bare sediment community (mean 3.64‰). Variations in $\delta^{15}N$ among trophic groups showed that subsurface deposit feeders values are consistently above TL = 3 and largely overlapping with carnivores-omnivores. The largest community variation is due to surface deposit-feeders in winter, exhibiting higher $\delta^{15}N$ value in *Haploops* habitat (TL > 3) than in *Amphiura* habitat (TL < 3).

Comparison of isotopic values of species shared by the two communities

A total of 28 (36%) and 17 (18%) species were found in both habitats in winter and summer, respectively. Stable isotopes ratios of common species of the 2 habitats are represented in the same biplots (Fig. 5). Overall, the majority of species falls within the range of the 1:1 ratio, for the two seasons. However, some species exhibited isotopic differences between the two habitats. For example, in winter the $\delta^{15}N$ value of the predators *Eunice vittata* and *Liocarcinus pusillus* and the suspension-feeder *Pecten maximus* were lower in the *Haploops* habitat. Conversely, the predator *Inachus dorsettensis* and the surface deposit-feeder *Terebellides stroemi* exhibited higher $\delta^{15}N$ values in *Haploops* habitat. As for winter $\delta^{13}C$ values, common species tend to be ^{13}C-enriched in the *Haploops* habitat, as evidenced by the two suspension-feeders *Pecten maximus* and *Anapagurus hyndmanni* as well as the deposit-feeder *Oestergrenia digitata* and the predators *Eunice vittata* and *Natatolana neglecta*. The same pattern is observed in summer. Several species showed enriched $\delta^{15}N$ values in the *Haploops* habitat (*Scoletoma fragilis* and *Sabellaria spinulosa*) while others are

^{15}N-depleted (*Sabellidae* sp.). As for summer δ^{13}C values, subsurface deposit-feeders (*Orbinia cuvieri* and *Maldane glebifex*) were ^{13}C-depleted in the *Haploops* habitat while the suspension-feeder *Crepidula fornicata* displayed slightly enriched δ^{13}C values in the *Haploops* habitat.

Contribution of food sources to benthic food webs

Biomass data revealed that 5 and 6 species accounted for more than 80 % of the benthic fauna biomass in summer in the *Haploops* and *Amphiura* habitats, respectively. When plotted along with isotopic compositions, biomass revealed a complete different picture of the food web for each habitat (Fig. 6). In the *Amphiura* habitat, the suspension-feeders *Amphiura filiformis*, *Thyone fusus*, *Dosinia lupinus* and *Chamelea striatula* made up for the bulk of the benthic biomass. The subsurface deposit-feeder *Maldane glebifex* and the surface deposit-feeder *Aspidosiphon muelleri* accounted in a lesser extent for the biomass in this habitat. In the *Haploops* habitat, the amphipod *Haploops nirae* and the bivalve *Polititapes virgineus* each accounted for 35 % of the biomass of the benthic fauna. The other main suspension-feeder *Turritella communis* as well as the surface deposit-feeder *Aspidosiphon muelleri* and the predator *Sthenelais boa* accounted for the remaining benthic biomass in the *Haploops* habitat.

Boxplots showing results of the Bayesian mixing models computed on species that accounted for 80% of the biomass in summer are shown in Fig. 7. Overall, the 2 communities exhibited similar patterns in food sources contributions. Even though large uncertainties hampered accurate quantifications, epiphytes (represented by benthic diatoms *Navicula* sp.) seemed to be the largest contributors, with the smallest uncertainties for most suspension-feeders. The phytoplankton contribution (POM) is however associated with large 95%

confidence intervals but also significantly contributes to suspension-feeders' diets such as *Haploops nirae* in the *Haploops* habitat or *Dosinia lupinus* and *Chamelea striatula* in the *Amphiura* habitat. The predator *Sthenelais boa* seemed to feed primarily on organisms which feed themselves primarily on POM. The contribution of organic matter from the sediment seemed to be less obvious from SIAR outputs, as it is also associated with large uncertainties.

DISCUSSION

In shallow subtidal zones, amphipod populations are common and can generate extensive tube mats that considerably increase local habitat complexity (Bellan-Santini and Dauvin, 1988; Franz and Tanacredi, 1992; Sudo and Azeta, 1996; Göransson, 2002). Engineer species in general and tubiculous species in particular are known to affect species composition of soft-bottom communities (Reise et al. 2009). Rigolet et al. (2013) showed that the presence of *Haploops nirae* in the Bay of Concarneau (South Brittany) affects the local biodiversity and the associated species assemblages. By modifying local sedimentary features, *Haploops* individuals create conditions for an unusual species assemblage to settle and develop, with species only found within *Haploops* community, including species new to science (Myers et al. 2012). To investigate whether drastic changes in species composition also cause changes in food web structure, we sampled the diversity of benthic organisms associated with the *Haploops* habitat and the adjacent uncolonised *Amphiura* habitat over two seasons.

Our results first showed that the overall isotopic food web structure was similar between the two habitats, since the isotopic spaces occupied by the species in the $\delta^{13}C$-$\delta^{15}N$ biplots largely overlap. The distribution of species over a continuum of three trophic levels appears to be a common feature in temperate subtidal macrobenthic ecosystems. Indeed, Le

Loc’h et al. (2008) for the muddy *Nephrops* habitat in the Bay of Biscay, Grall et al. (2006) for the north-eastern Atlantic maerl beds habitat or Carlier et al. (2007) for a variety of soft-sediment habitats of the north-western Mediterranean Bay of Banyuls also reported food web structure of benthic macrofauna with three trophic levels. We also showed here that isotopic values for both primary and secondary consumers spread over a large range of $\delta^{13}C$ values. Such a large range of $\delta^{13}C$ values within primary consumers is also considered a common feature of continental shelf communities (Hobson et al. 2002, Le Loc’h et al. 2008), where a larger number of food sources are available. And yet, the $\delta^{13}C$ ranges for subtidal shallow benthic habitats seem to remain stable between -14‰ and -22‰ for the whole macrofauna community (Grall et al. 2006, Carlier et al. 2007, Le Loc’h et al., 2008). However, we have excluded species exhibiting unusual isotopic signatures from very specific diets, e.g. specialists of very ^{13}C-depleted red macroalgae such as *Aplysia punctata* (Carefoot 1985) or species which host symbiotic sulphur-oxydising bacteria in their gill tissue such as *Thyasira flexuosa* (Dufour & Felbeck 2006). This depletion is likely due to the significant contribution of carbon fixation by symbionts in their food source (Dando & Spiro 1993). It should be noted that between-habitat variations in organisms’ isotopic compositions are not only due to intraspecific trophic plasticity, but are likely to be constrained within food sources’ isotopic compositions at the ecosystem level.

Several studies reported that ampeliscidae can constitute the major prey for some top-predators marine mammals and finfishes (Franz & Tanacredi 1992, Highsmith & Coyle 1992, Cui et al 2012). To our knowledge, few studies have paid special attention to the position of the ampeliscidae in a food web, and even less use stable isotopes to ascertain this. *Haploops nirae* occupied here the lowest $\delta^{13}C$ and $\delta^{15}N$ position in the isotopic biplot. Ampeliscidae always exhibit the lowest $\delta^{15}N$ value in food web structures determined with stable isotopes, as showed from the muddy bottoms of the southern Tyrrhenian Sea (Western Mediterranean) for *Ampelisca* spp. (Fanelli et al. 2009) to the South Orkneys island (Antarctic Peninsula) for *A. richardsoni* (Nyssen et al. 2005). We suggest here that this amphipod family in general, despite laboratory observations reporting strong trophic plasticity and changes in foraging behaviour (e.g. Mills 1967), can be used as isotopic trophic baseline for coastal marine and estuarine systems. This provides a viable alternative to the current practice of using long-live primary consumers like mussels as a trophic baseline (Cabana & Rasmussen 1996).

Despite the strong bioturbating tube-building activity (over 10 000 tubes.m^{-2}, Rigolet et al. 2012) and the active grazing activity (Rigolet et al. 2011), *Haploops* individuals do not appear to affect the higher trophic levels. As suggested by Mills et al. (1993), the feeding activities of dense species greatly affect community features (such as sediment characteristics) but do not necessarily have direct trophic effects on other species. Similarly, Jones et al. (1997) suggested that many engineer species physically affect their environment in numerous ways but that not all of the changes have important (positive or negative) ecological consequences. Studies that compare food webs of engineered habitat with adjacent homogeneous bare sediments using stable isotopes are scarce (but see for example Dubois et al. 2007). Yet, Baeta et al. (2009) investigated whether the occurrence of the eelgrass *Zostera marina* changed the benthic and pelagic food web structures in comparison with uncolonized sediment. They showed no major difference in the structure of the benthic food web, which is consistent with our results in a different system. This result has strong implications in terms of trophic niche partitioning: as composition of species assemblages associated with *Haploops* habitat drastically differs from those in adjacent sediments (Rigolet et al. 2013), it means that each species or each group of species uniquely found in the *Haploops* habitat (ca. 70% of the species) has a trophic-equivalent species or group of species in the adjacent uncolonized sediments. As a result, deep changes in diversity and species composition do not always reflect changes in food web structure, even though the physical environment is remarkably affected by an engineer tubiculous species.

As measured with the δ^{15}N ranges, the length of the benthic food chain in the *Haploops* habitat did not differ from the length in the adjacent *Amphiura* habitat. Both food chains spanned over a continuum of almost three trophic levels, defined according to an isotopic baseline (Post 2002). Food web length in aquatic systems influences ecosystem functioning and food-web stability (Long et al. 2011) but it is also recognized that longer food webs are predicted in more productive systems because more energy can be transferred between trophic levels (Morin & Lawler 1995). Secondary production is not significantly different between *Haploops* habitats and surrounding *Amphiura* habitats (Rigolet et al. 2012), further suggesting a difference in food chain length would be unlikely. However, it is worth noticing differences in the frequencies distributions of δ^{15}N compositions between the *Amphiura* and the *Haploops* habitats. The bi-modal shape of the distribution of the *Haploops* habitat revealed that food chain levels between primary and secondary consumers are well discriminated in *Haploops* habitat, possibly indicating less trophic plasticity and less diet variations at each consumer level, as well as more omnivorous species in the *Amphiura* habitat, with potential consequences on the food-web properties of each habitat. The influence of complexity and omnivory on the food-web dynamics was intensively debated during the last decades with contradictory results: recent empirical and theoretical developments have reported that omnivory in general and omnivorous links between species tend to have a stabilizing effect on the food web dynamics when trophic interactions are weak (Emmerson & Yearsley 2004). With this in mind, we could hypothezised that *Haploops* food web, largely dominated in terms of abundance and biomass by a gregarious small tubiculous species, is less stable than the *Amphiura* food web and would ultimately take more time to return to equilibrium, should large changes in food sources occur.

In coastal shallow systems, the biomass and the secondary production of benthic consumers originate from a diversity of sources (Peterson, 1999). For example, in the Bay of Concarneau, many sources are potentially available for the benthic fauna, such as particulate organic matter (POM) and sedimented organic matter (SOM), terrestrial inputs of organic matter (TOM) as well as macroalgae detritus from surroundings hard bottoms. It is commonly assumed that the subsurface POM (used as a proxy for phytoplankton) directly or indirectly (after sedimentation and resuspension) is the major contribution to the benthic primary consumers in subtidal environments (Grall et al. 2006, Le Loc'h et al. 2008). However, a growing body of literature recently focused on subtidal benthic primary production in subtidal sedimentary habitats (see review in Cahoon 1999). For example, Grippo et al. (2011) investigated the microphytobenthos as potential support of benthic food web in Louisiana shoals (Gulf of Mexico) and revealed that subtidal sandy dunes (peaking between 5 and 10 m depth) are supporting a secondary benthic production during spring and summer times. In temperate shallow subtidal sedimentary systems of the Wadden Sea (ca. 2 m depth), ^{13}C-labelling *in situ* experiences revealed the pivotal role of autochtonous MPB production *vs.* allochtonous phytoplankton in benthic consumers diets (Evrard et al. 2012) and within the bulk MPB, benthic consumers preferentially select benthic diatoms and benthic cyanobacteria (Evrard et al. 2010). An extensive survey of the subtidal MPB production was carried out in the Bay of Brest (Brittany, France) between 5 and 13 meters deep (Ni Longphuirt et al. 2007). These authors highlighted that the MPB production represented up to 20% of total primary production, with the highest MPB biomass in bare muddy sediments. Our results from sediment analyses showed that even during the winter season, and despite a higher turbidity due to wave activity, *Haploops* sediment contains Chl. *a*. This probably indicates benthic primary production in *Haploops* sediments, supported by a low C:N ratio close to what was expected for marine microalgae (i.e. C:N = 6.6 ; Redfield et al. 1963). Visual observations showed that *Haploops* tube can be a physical support for epiphytes in general and benthic diatoms mats in particular (*Navicula* sp.) (Fig. 1). The $\delta^{13}C$ value from the tube epibionts falls perfectly within the expected value of microphytobenthos in summer (ca. –13‰) (Riera & Richard 1996, Leal et al. 2008, Grippo et al. 2011). However in winter (higher turbidity and lower luminosity), tube scrapings revealed a $\delta^{13}C$ value similar to the sedimented organic matter, suggesting an absence of growing mats of primary producers on *Haploops* tubes. Yet a low Chl. *a* concentration indicates a residual growing population of microalgae. *Haploops* tubes are made of mud, with pseudofeces and mucus secreted by individuals (Rigolet et al. 2011) and potentially offer a high quality habitat of polysaccharides for benthic diatom to grow. Benthic diatoms (including *Navicula* species) can compensate for low nutrients or luminosity with adaptations such as mixotrophy (Cloern & Dufford 2005, Ross & Sharples 2007). For example, Barillé & Cognie (2000) showed that growth of benthic diatoms was stimulated by oyster pseudofaeces, enriching sediment in mucopolysaccharides which diatom can exploit. Carbohydrates derived from *Haploops* tubes can likely be used by diatoms to grow under limited light condition.

SIAR Bayesian mixing models incorporate isotope and fractionation uncertainty in the development of posterior probability distributions of sources contributions. As a result, model outputs include a margin of error that can be high when too many food sources are incorporated or when consumer's isotopic composition do not perfectly fall within the isotopic space defined by selected food sources (Fry 2013). Since SOM and POM are not well isotopically discriminated in this study, results of the mixing model are associated with high uncertainty for those two food sources. Epibionts (benthic diatoms) exhibited very significantly enriched $\delta^{13}C$ value (-13.19 ± 0.34 ‰) and their contribution to the diet to the species with the most enriched $\delta^{13}C$ values is undoubted. The species with the highest $\delta^{13}C$

value (-11.64 ± 0.2 ‰) is indeed the micrograzer *Geitodoris planata*, likely feeding solely on the epibionts of *Haploops* tubes. Also, many species can benefit from this food source, especially deposit-feeders which abundances are indeed greater in the *Haploops* habitat (Rigolet et al., 2013), or suspension-feeding species if benthic diatoms are resuspended. Interestingly, while investigating isotopic signatures of benthic invertebrates in a coastal-estuarine gradient, Koop et al. (2013) noticed an unexpected enrichment in organisms' $\delta^{13}C$ isotopic composition only in several offshore stations (Bay of Biscay, France). These stations were actually colonized by *Haploops* sp. and our findings suggest a contribution of MPB to the macrofauna diet.

Our understanding of food web structure can be very different depending on whether one considers all the species or only the species that account for most of the biomass. Those species play a key functional role in trophic webs (Villéger et al., 2008). From the species contributing the most to the total biomass in each community, Bayesian mixing models revealed that epibionts can contribute to 50% to the diet of suspension-feeders such as *Polititapes virgineus* or *Amphiura filiformis*, while other suspension-feeders rely mainly on particulate organic matter (*Haploops nirae*), suggesting differences in food selectivity among filter-feeding organisms but also a limited competition within the suspension-feeders among the *Haploops* habitat. The bivalve *P. virgineus* is only found in *Haploops* habitat and represents one of the largest biomass. Mackenzie et al. (2006) similarly reported high biomass of bivalves *Mercenaria mercenaria* in *Ampelisca* mats of the southeastern Raritan Bay (New Jersey). We suggest that the *Haploops* habitat offers a broader diversity and quantity in food sources, and that the *Haploops* tubes act as a substrate for MPB species. These results are supported by several mesocosm experiments designed to disentangle impacts of species assemblages and environmental characteristics on MPB biomass and production. For example, Dyson et al. (2007) showed that the sedimentary patchiness in organic matter enrichment affects macrofaunal (diversity and abundance) distribution which in turn affects MPB production. With similar experiments, Hicks et al. (2011) showed that changes in grazing invertebrate assemblages are likely to influence MPB biomass. These investigations highlighted that in complex systems, such as natural habitats engineered by a tubiculous species, changes in species composition could fundamentally influence the resource provision and its utilisation, and ultimately the equilibrium between autotrophic and heterotrophic production.

Benthic organisms from adjacent habitats largely benefit from benthic primary production in *Haploops* sediments, as the overall isotopic space is similar between the two habitats (see convex hull of species isotopic composition in Figs. 2 and 3) and the isotopic $\delta^{13}C$ signature of the SOM in adjacent sediments did not show enriched $\delta^{13}C$ values. Despite very low benthic primary production in the adjacent *Amphiura* habitat, resuspended microbenthic algae are the major component of the diet of the most dominant species in the bare sediment, the amphiurid *Amphiura filiformi*, and significantly support the secondary production of the bare sediment. *Haploops* habitats – and potentially all large tube mats in muddy coastal systems – appear to be food exporters to adjacent communities. This study reveals that benthic habitat engineered by species potentially have strong trophic connections with surrounding other habitats and can – because of their biological activity – export primary production. This supports the definition of engineer species not only as species modifying diversity and species assemblages but as species with the capacity to directly or indirectly control resources for others species (Allen & Williams 2003).

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FIGURES CAPTIONS

Fig. 1. Top picture: close up of several *Haploops* tubes, protruding a few centimetres above the sediments (May 2010). Bottom picture: close up of a distal end of an *Haploops* tube under a dissecting scope showing numerous *Navicula* sp. diatoms (appearing as dark brown sticks) (May 2012)

Fig. 2. Spatial distribution of the subtidal benthic habitat of the Bay of Concarneau and the six stations sampled seasonally along two transects (*i.e.* within the *Haploops* habitat: CO16, CO9 and CO14 and within the adjacent *Amphiura* habitat: CO4, CO24 and CO28). Sampling stations for the benthic fauna are labelled with triangles and sampling stations for water column phytoplankton (POM) and terrestrial inputs (TOM) are labelled with squares. Contours of benthic habitats are retrieved from previous acoustic and benthic survey mappings (Ehrhold et al., 2006)

Fig. 3. Isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of the sampled species and potential dietary organic matter sources during winter (A) and summer (B) in the sandy mud *Amphiura* habitat (white triangles) and in the muddy *Haploops* habitat (black dots). Mean isotope composition (n = 3) of all species are plotted. Sources are represented with squares: D. COR = *Dasya corymbifera*, P. PAL = *Palmaria palmata*, H. HYP = *Hypoglossum hypoglossoides*, D. DIC = *Dictyota dichotoma*, LAM sp = *Laminaria* sp., ULV sp = *Ulva* sp., TOM = Terrestrial Organic Matter inputs, SOM_H = Sedimented Organic Matter from the *Haploops* habitat, SOM_A = Sedimented Organic Matter from the *Amphiura* habitat, EPI = Epiphytes scrapped from *Haploops* tubes. For benthic consumers isotopic compositions, mean $\delta^{13}C$ and $\delta^{15}N$ values are represented without error bars for clarity. *Thyasira flexuosa* ($\delta^{15}N$ =-0.30 ± 0.46;

$\delta^{13}C = -26.40 \pm 0.29$) was not represented on this graphic. A. PUN = Aplysia punctata, NER sp = Nereis sp, H. NIR = *Haploops nirae,* G. PLA = *Geitodoris planata*

Fig. 4. Frequency distributions of ^{13}C and ^{15}N isotopic compositions of all organisms sampled in the two habitats (*Amphiura* with black bars and *Haploops* with grey bars) for the two seasons (winter on the left panels and summer on the right panels). A size-class of 0.5‰ was used for both elements

Fig. 5. Comparison of ^{15}N (left panels) and ^{13}C (right panels) isotope ratios of species co-occurring both in the *Amphiura* and the *Haploops* habitats in winter (top panels) and summer (bottom panels). The bold dotted line indicates a 1:1 correlation (95% interval confidence in light dotted line): a species standing on the 1:1 line indicates no significant differences in isotopic composition between the two habitats. Species labels are coded according to their trophic group. A.MUE = *Aspidosiphon muelleri*, A.ACU = *Aphrodita aculeata*, H.ANT = *Harmothoe antilopes*, H.GRA = *Hilbigneris gracilis*, E.VIT = *Eunice vitata*, N.UNI = *Nematonereis unicornis*, SAB1 = Sabellidae sp. undetermined, M.SAN = *Macroclymene santanderansis,* M.GLE = *Maldane glebifex,* T.STR = *Terebellides stroemii*, O.CUV = *Orbinia cuvierii,* S.SPI = *Sabellaria spinulosa,* E.PUL = *Euspira pulchella,* T.COM = *Turritella communis,* N.NIT = *Nucula nitidosa*, C.FOR = *Crepidula fornicata*, B.UND = *Buccinum undatum,* D.LUP = *Dosinia lupines,* A.OPE = *Aequipecten opercularis,* P.MAX = *Pecten maximus,* A.SPI = *Ampelisca spinipes*, P.SER = *Palaemon serratus*, A.HYN = *Anapagurus hyndmanni,* P.PRI = *Pagurus prideaux,* N.NEG = *Natatolana neglecta,* I.DOR = *Inachus dorsettensis,* L.PUS = *Liocarcinus pusillus,* P.LON = *Pisidia longicornis,* O.ALB = *Ophiura albida,* A.RUB = *Asterias rubens,* M.GLA = *Martasterias glacialis,* L.CIL = *Luidia ciliaris*, O.DIG = *Oestergrenia digitata*

Fig. 6. Dual isotopic $\delta^{13}C$ *vs.* $\delta^{15}N$ biplot of species collected in the two habitats in summer. Bubble values represent relative contribution of each species to the total biomass of each habitat. Species representing 80% of the total biomass are labelled

Fig. 7. Estimated contributions of the 3 main food sources, particulate organic matter (POM), sedimented organic matter (SOM) and tube epiphytes (EPI) for the *Amphiura* (left panels) and the *Haploops* habitats in summer, using SIAR mixing model. Boxplots indicate 50%, 75% and 95% confidence intervals for the species that account for 80% of the biomass in each habitat: M.GLE = *Maldane glebifex*, A.FIL = *Amphiura filiformis*, A.MUE = *Aspidosiphon muelleri*, T.FUS = *Thyone fusus*, D.LUP = *Dosinia lupinus*, C.STR = *Chamelea striatula*, H.NIR = *Haploops nirae*, P.VIR = *Polititapes virgineus*, T.COM = *Turritella communis*, S.BOA = *Sthenelais boa*

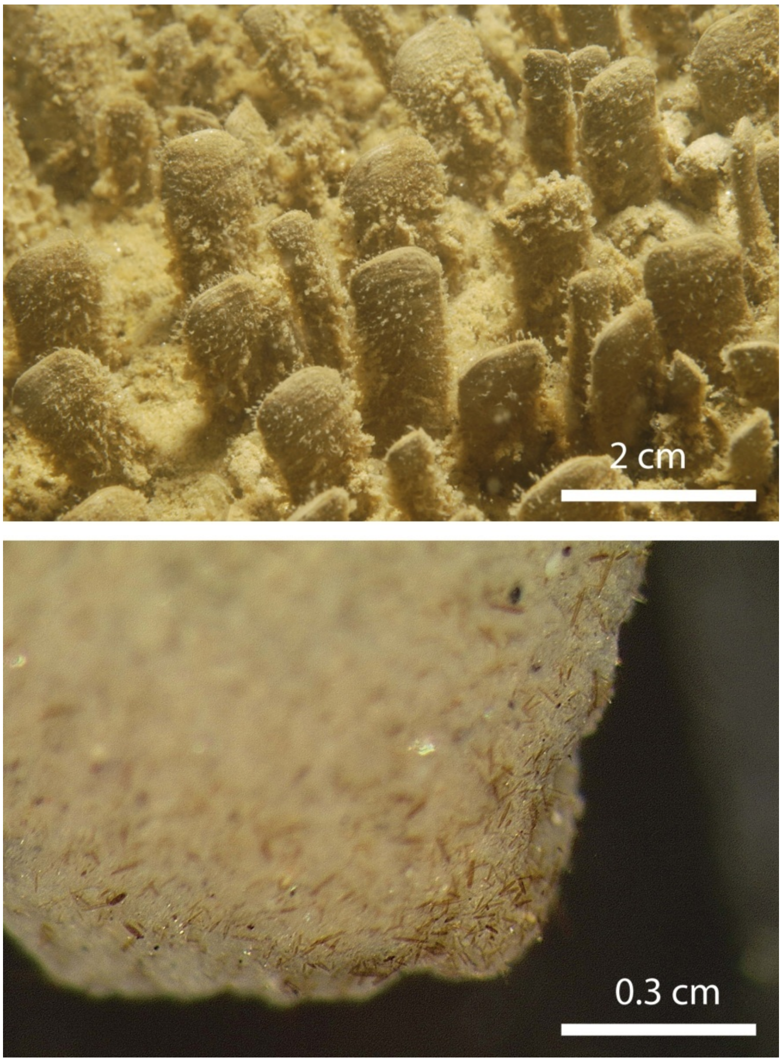


Fig. 1

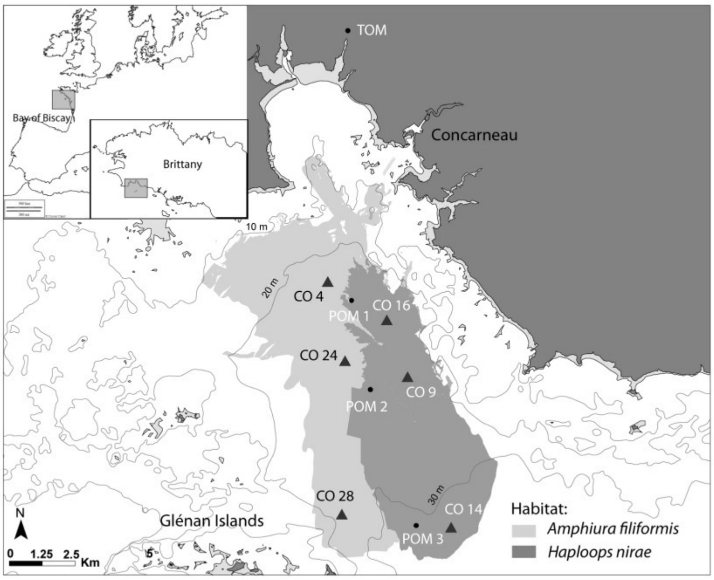
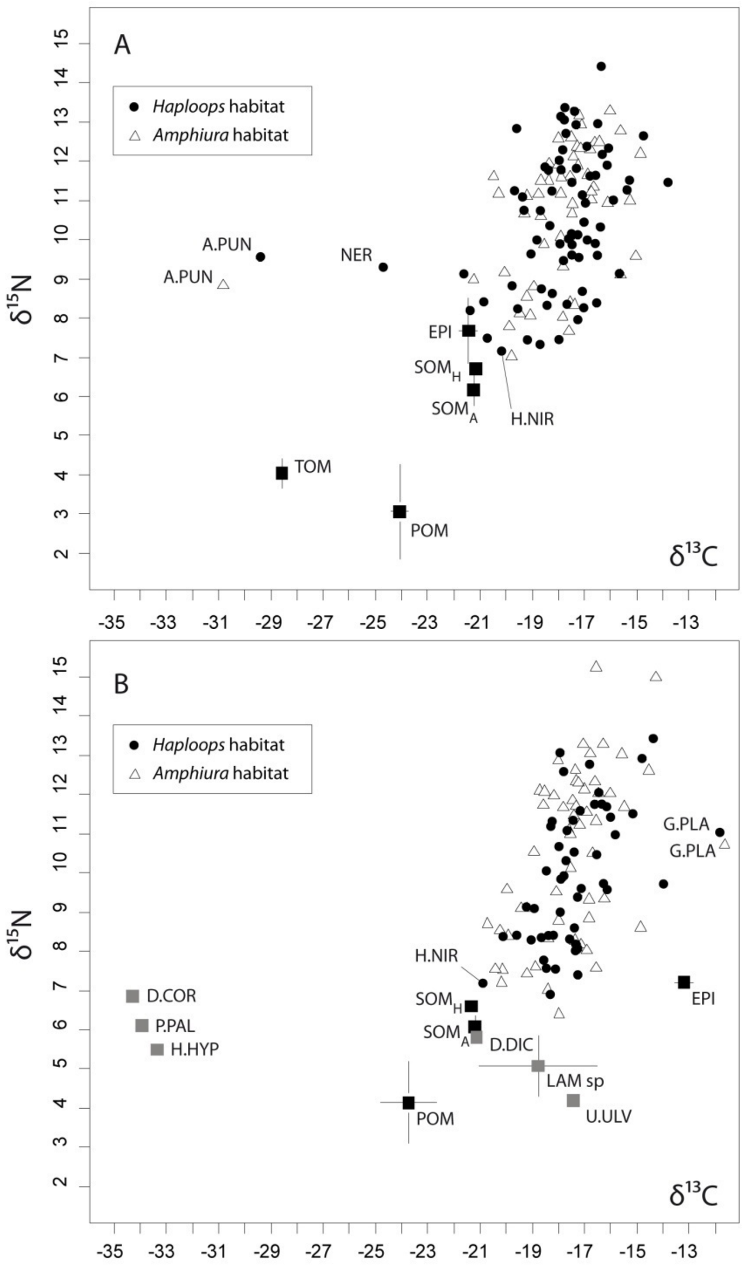

TOM
Concarneau
Bay of Biscay
Brittany
10 m
20 m
30 m
CO 4
POM 1
CO 16
CO 24
CO 9
POM 2
CO 28
CO 14
POM 3
Glénan Islands
N
0 1.25 2.5 Km
Habitat:
Amphiura filiformis
Haploops nirae

Fig. 2


A
Haploops habitat
Amphiura habitat
A.PUN
A.PUN
NER
EPI
SOM_H
SOM_A
H.NIR
TOM
POM
δ15N
δ13C
B
Haploops habitat
Amphiura habitat
G.PLA
G.PLA
H.NIR
SOM_H
SOM_A
D.DIC
LAM sp
U.ULV
POM
EPI
D.COR
P.PAL
H.HYP
δ15N
δ13C
15
14
13
12
11
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9
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4
3
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-35
-33
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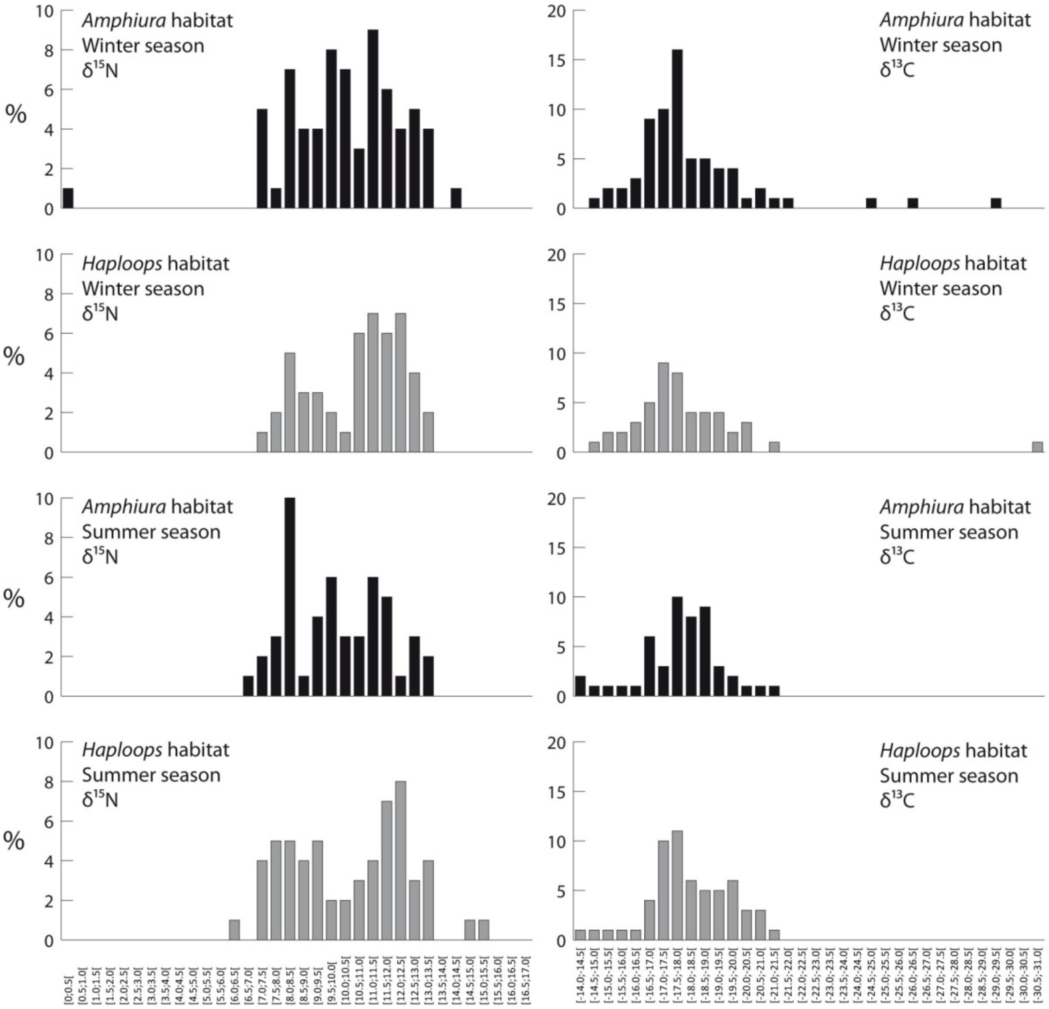
-21
-19
-17
-15
-13

Fig. 3


Amphiura habitat
Winter season
δ15N
%
10
8
6
4
2
0
Amphiura habitat
Winter season
δ13C
20
15
10
5
0
Haploops habitat
Winter season
δ15N
%
10
8
6
4
2
0
Haploops habitat
Winter season
δ13C
20
15
10
5
0
Amphiura habitat
Summer season
δ15N
%
10
8
6
4
2
0
Amphiura habitat
Summer season
δ13C
20
15
10
5
0
Haploops habitat
Summer season
δ15N
%
10
8
6
4
2
0
Haploops habitat
Summer season
δ13C
20
15
10
5
0
[0;0.5[
[0.5;1.0[
[1.0;1.5[
[1.5;2.0[
[2.0;2.5[
[2.5;3.0[
[3.0;3.5[
[3.5;4.0[
[4.0;4.5[
[4.5;5.0[
[5.0;5.5[
[5.5;6.0[
[6.0;6.5[
[6.5;7.0[
[7.0;7.5[
[7.5;8.0[
[8.0;8.5[
[8.5;9.0[
[9.0;9.5[
[9.5;10.0[
[10.0;10.5[
[10.5;11.0[
[11.0;11.5[
[11.5;12.0[
[12.0;12.5[
[12.5;13.0[
[13.0;13.5[
[13.5;14.0[
[14.0;14.5[
[14.5;15.0[
[15.0;15.5[
[15.5;16.0[
[16.0;16.5[
[16.5;17.0[
[-14.0;-14.5[
[-14.5;-15.0[
[-15.0;-15.5[
[-15.5;-16.0[
[-16.0;-16.5[
[-16.5;-17.0[
[-17.0;-17.5[
[-17.5;-18.0[
[-18.0;-18.5[
[-18.5;-19.0[
[-19.0;-19.5[
[-19.5;-20.0[
[-20.0;-20.5[
[-20.5;-21.0[
[-21.0;-21.5[
[-21.5;-22.0[
[-22.0;-22.5[
[-22.5;-23.0[
[-23.0;-23.5[
[-23.5;-24.0[
[-24.0;-24.5[
[-24.5;-25.0[
[-25.0;-25.5[
[-25.5;-26.0[
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[-28.0;-28.5[
[-28.5;-29.0[
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[-29.5;-30.0[
[-30.0;-30.5[
[-30.5;-31.0[

Fig. 4

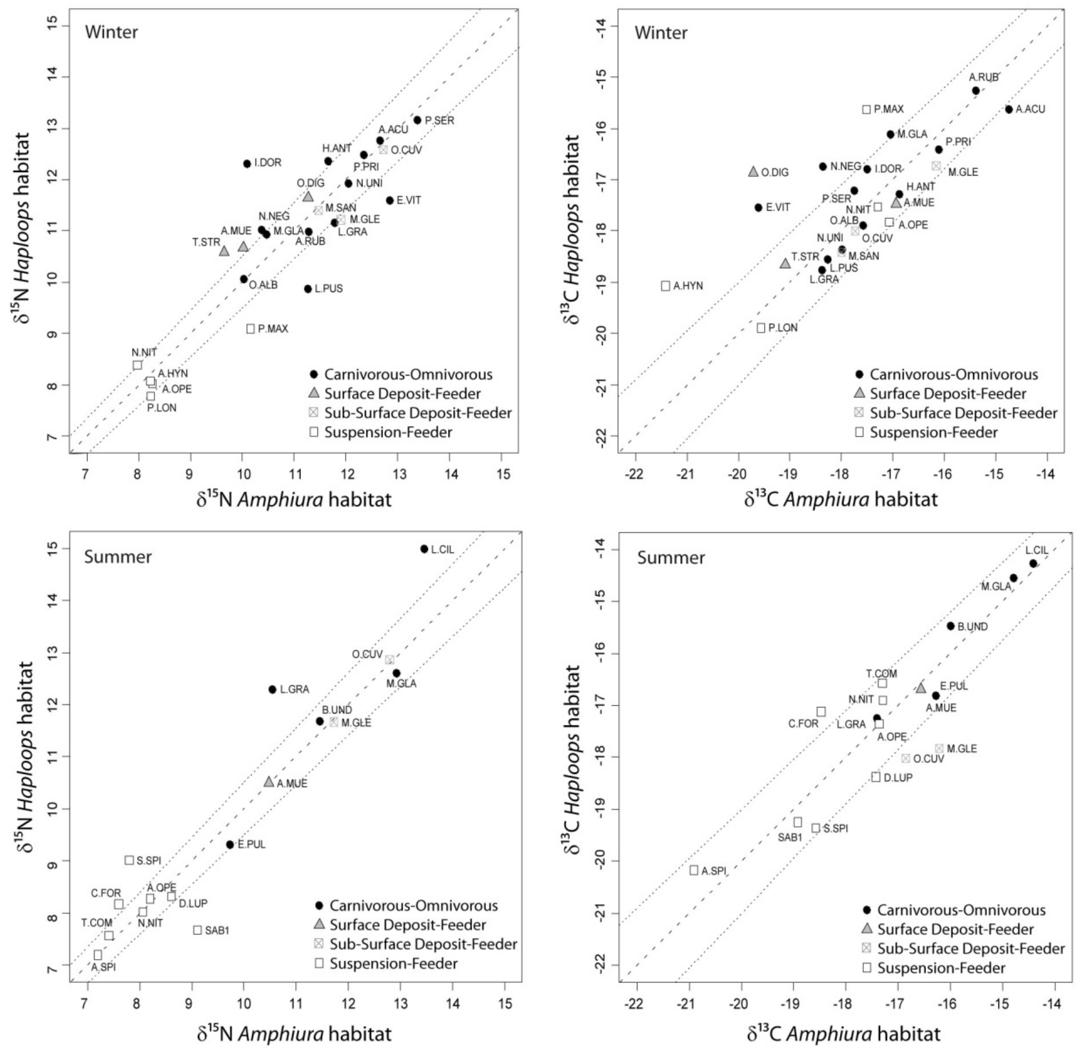
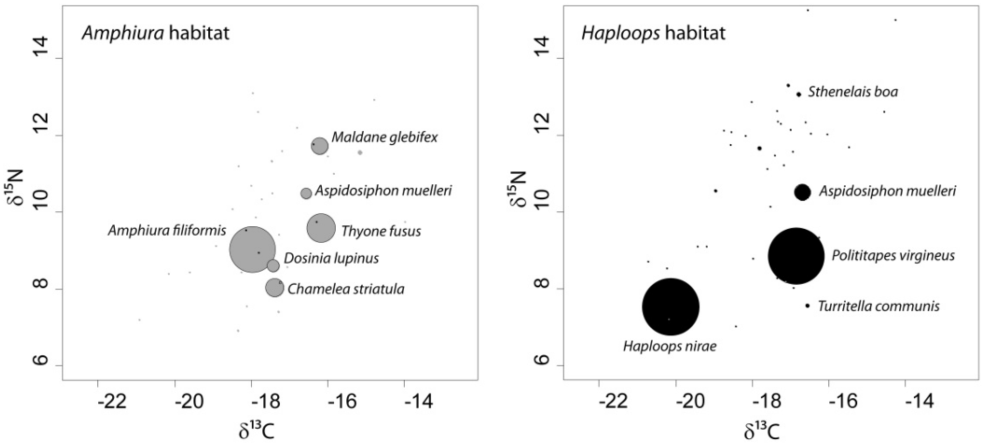

Winter
δ15N Haploops habitat
δ15N Amphiura habitat
7
8
9
10
11
12
13
14
15
P.SER
A.ACU
H.ANT
O.CUV
I.DOR
P.PRI
O.DIG
N.UNI
E.VIT
M.SAN
N.NEG
M.GLE
A.MUE
M.GLA
L.GRA
T.STR
A.RUB
O.ALB
L.PUS
P.MAX
N.NIT
A.HYN
A.OPE
P.LON
● Carnivorous-Omnivorous
▲ Surface Deposit-Feeder
☒ Sub-Surface Deposit-Feeder
☐ Suspension-Feeder
Winter
δ13C Haploops habitat
δ13C Amphiura habitat
-14
-15
-16
-17
-18
-19
-20
-21
-22
A.RUB
P.MAX
A.ACU
M.GLA
P.PRI
O.DIG
N.NEG
I.DOR
M.GLE
H.ANT
P.SER
A.MUE
E.VIT
N.NIT
O.ALB
A.OPE
O.CUV
N.UNI
T.STR
M.SAN
L.PUS
L.GRA
A.HYN
P.LON
● Carnivorous-Omnivorous
▲ Surface Deposit-Feeder
☒ Sub-Surface Deposit-Feeder
☐ Suspension-Feeder
Summer
δ15N Haploops habitat
δ15N Amphiura habitat
L.CIL
O.CUV
M.GLA
L.GRA
B.UND
M.GLE
A.MUE
E.PUL
S.SPI
C.FOR
A.OPE
D.LUP
T.COM
N.NIT
SAB1
A.SPI
● Carnivorous-Omnivorous
▲ Surface Deposit-Feeder
☒ Sub-Surface Deposit-Feeder
☐ Suspension-Feeder
Summer
δ13C Haploops habitat
δ13C Amphiura habitat
L.CIL
M.GLA
B.UND
T.COM
E.PUL
N.NIT
A.MUE
C.FOR
L.GRA
A.OPE
M.GLE
O.CUV
D.LUP
SAB1
S.SPI
A.SPI
● Carnivorous-Omnivorous
▲ Surface Deposit-Feeder
☒ Sub-Surface Deposit-Feeder
☐ Suspension-Feeder

Fig. 5



Amphiura habitat
Maldane glebifex
Aspidosiphon muelleri
Amphiura filiformis
Thyone fusus
Dosinia lupinus
Chamelea striatula
Haploops habitat
Sthenelais boa
Aspidosiphon muelleri
Polititapes virgineus
Turritella communis
Haploops nirae
14
12
10
8
6
-22
-20
-18
-16
-14
$\delta^{15}N$
$\delta^{13}C$

Fig. 6

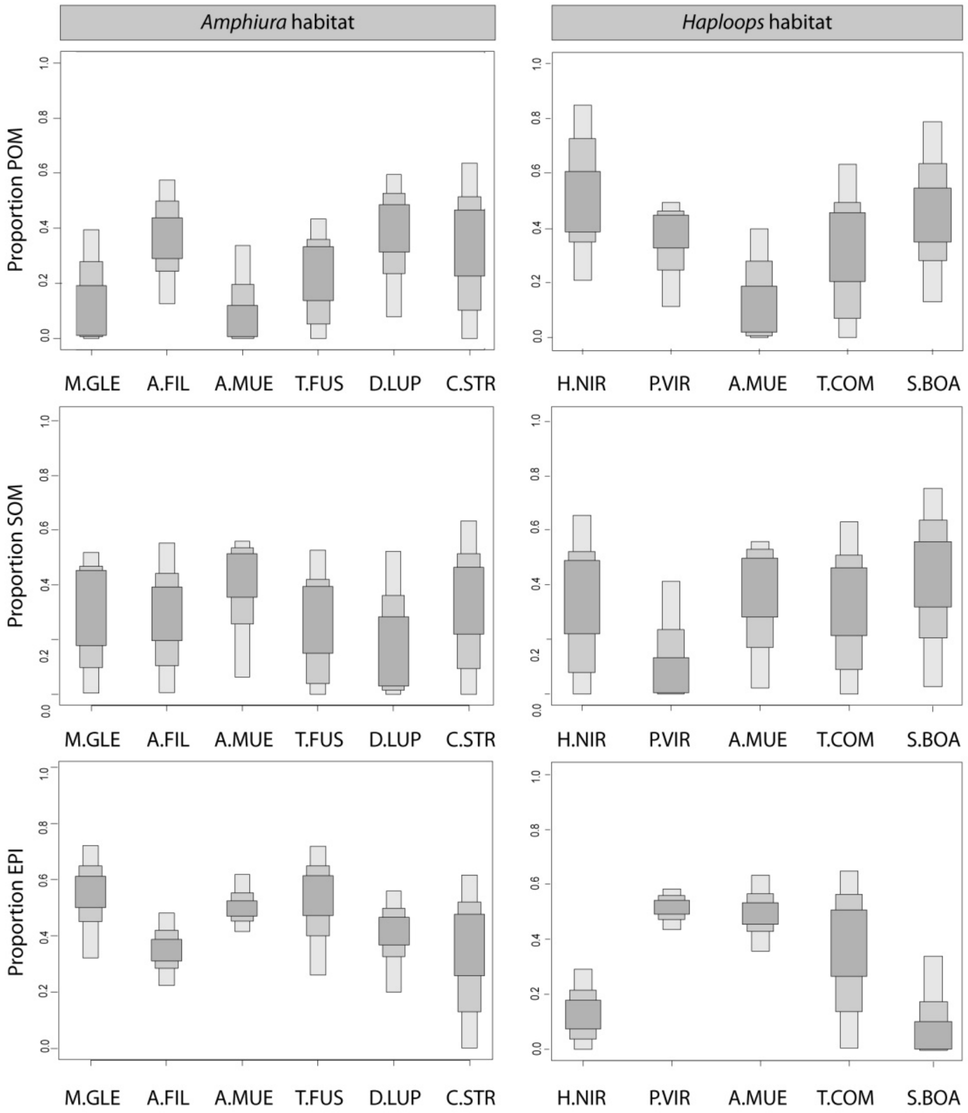

Amphiura habitat
Haploops habitat
Proportion POM
Proportion SOM
Proportion EPI
0.0
0.2
0.4
0.6
0.8
1.0
M.GLE
A.FIL
A.MUE
T.FUS
D.LUP
C.STR
H.NIR
P.VIR
A.MUE
T.COM
S.BOA

Fig. 7

Table 1. Stable nitrogen and stable carbon isotope values (mean and standard deviation) of the potential organic matter (OM) sources in the Bay of Concarneau, during winter and summer times. NA indicates that the sources were not sampled, either because the occurrence was very limited (in the case of macroalgae in winter), or because the water level was too low (in the case of riverine outputs in summer).

	Winter			Summer		
Potential Sources for Primary Consumers	δ^{15}N (SD)	δ^{13}C (SD)	n	δ^{15}N (SD)	δ^{13}C (SD)	n
Terrestrial Organic Matter	4.05 (0.20)	-28.58 (0.20)	3	NA	NA	-
Phytoplankton (sub-surface seawater)	3.06 (1.20)	-24.06 (0.34)	3	4.14 (1.04)	-23.73 (1.08)	3
Sedimented OM (*Haploops* habitat)	6.70 (0.03)	-21.14 (0.04)	3	6.60 (0.14)	-21.35 (0.04)	3
Sedimented OM (*Amphiura* habitat)	6.17 (0.40)	-21.23 (0.21)	3	6.08 (0.30)	-21.18 (0.10)	3
Epiphytes on *Haploops* tubes	7.67 (0.82)	-21.43 (0.36)	3	7.21 (0.15)	-13.19 (0.34)	3
Laminaria sp. (brown macroalgae)	NA	NA	-	5.07 (0.78)	-18.77 (2.26)	3
Dictyota dichotoma (brown macroalgae)	NA	NA	-	5.80 (0)	-21.13 (0)	3
Palmaria palmata (red macroalgae)	NA	NA	-	6.09 (0)	-33.94 (0)	3
Hypoglossum hypoglossoides (red macroalgae)	NA	NA	-	5.49 (0)	-33.35 (0)	3
Dasya corymbifera (red macroalgae)	NA	NA	-	6.85 (0)	-34.29 (0)	3
Ulva sp. (green macroalgae)	NA	NA	-	4.18 (0)	-17.42 (0)	3

Table 2. Chlorophyll *a* (µg.g^{-1}), phaeopigments (µg.g^{-1}) and sedimented organic matter C:N ratios in sediments of the two habitats (*Amphiura* and *Haploops*) for the two seasons (winter and summer). Mean values (±SD) are calculated for the 3 stations in each habitat.

	Winter		Summer	
	Amphiura	*Haploops*	*Amphiura*	*Haploops*
Chlorophyll *a* (µg.g^{-1})	0.22 (± 0.15)	1.06 (± 0.44)	1.67 (± 0.24)	2.04 (± 0.11)
Phaeopigments (µg.g^{-1})	8.74 (± 2.85)	26.25 (± 4.48)	7.99 (± 3.70)	18.03 (± 2.14)
C:N ratio	7.12 (± 0.58)	5.90 (± 0.17)	7.36 (± 0.71)	5.76 (± 0.17)

Table 3. Ranges in $\delta^{13}C$ values (min – max, ‰) for each trophic functional groups found in the two habitats (*Amphiura* and *Haploops*) for the two seasons (winter and summer). Because of specific and unique diet (see Fig. 3), *Thyasira flexuosa*, *Aplysia punctata* and *Nereis* sp. were excluded from the calculations. n = number of species.

	Winter		Summer	
Habitat	*Amphiura*	*Haploops*	*Amphiura*	*Haploops*
Carnivorous-omnivorous	4.87 ; n = 35	6.38 ; n = 27	4.51 ; n = 15	4.93 ; n = 23
	(-19.62 ; -14.75)	(-21.24 ; -14.86)	(-18.49 ; -13.98)	(-19.19 ; -14.26)
Sub-surface deposit-feeders	4.11 ; n = 9	1.68 ; n = 5	3.17 ; n = 8	0.87 ; n = 6
	(-19.39 ; -15.28)	(-18.42 ; -16.74)	(-18.33 ; -15.16)	(-18.18 ; -17.31)
Surface deposit-feeders	4.51 ; n = 7	3.64 ; n = 5	1.82 ; n = 5	3.28 ; n = 9
	(-20.18 ; -15.67)	(-18.67 ; -15.03)	(-18.38 ; -16.56)	(-19.97 ; -16.69)
Suspension-feeders	4.85 () n = 19	4.44 ; n = 12	4.74 ; n = 19	4.45 ; n = 20
	(-21.42 ; -16.57)	(-20.07 ; -15.63)	(-20.91 ; -16.17)	(-20.71 ; -16.26)

Supplement S1. Mean (± SD) isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) of all species sampled in winter for both *Amphiura* and *Haploops* habitats. TG = Trophic Group, n = number of samples, TP = Trophic Position calculated after Post 2002 using *Haploops nirae* as a trophic baseline. Information on trophic groups gathered from the Biological Traits Information Catalogue developed by the Marine Life Information Network, as C-O = Carnivorous and/or Omnivorous, SF = Suspension-Feeders, SDF = Surface Deposit-Feeders, SSDF = Sub-Surface Deposit-Feeders, G = Grazers or micro-Grazers. Species names were checked using world register of marine species database on November 28th 2013

			Amphiura habitat				*Haploops* habitat		
	TG	n	TP	$\delta^{15}N$	$\delta^{13}C$	n	TP	$\delta^{15}N$	$\delta^{13}C$
Cnidarians									
Cerianthus lloydii	C-O					1	3.5	12.13	-17.43
Alcyonium digitatum	C-O	1	2.85	9.92	-16.62				
Sipunculids									
Aspidosiphon muelleri	SDF	3	2.88	10.02 ± 0.04	-16.93 ± 0.13	2	3.07	10.67 ± 0.13	-17.48 ± 0.28
Nemerteans									
Nemertina sp.A	C-O					2	3.2	11.12 ± 0.01	-19.19 ± 0.55
Nemertina sp.B	C-O					3	3.07	10.67 ± 0.39	-19.28 ± 0.59
Polychaetes									
Aphrodita aculeata	C-O	3	3.66	12.66 ± 0.19	-14.75 ± 0.27	1	3.69	12.77	-15.62
Alentia gelatinosa	C-O					1	3.64	12.61	-17.51
Harmothoe antilopes	C-O	3	3.36	11.66 ± 0.90	-16.88 ± 0.83	1	3.57	12.37	-17.28
Malmgreniella andreapolis	C-O					1	3.73	12.92	-17.12
Malmgreniella sp.A	C-O	3	3.75	12.97 ± 0.37	-16.52 ± 0.04				
Malmgreniella sp.B	C-O	1	3.4	11.78	-17.9				
Glycera alba	C-O	1	3.85	13.3	-17.42				
Glycera unicornis	C-O	1	4.18	14.43	-16.38				
Goniada maculata	C-O	3	3.8	13.14 ± 0.91	-17.92 ± 0.20				
Phyllodoce lineata	C-O					1	3.56	12.32	-17.14
Labioleanira yhleni	C-O	3	3.58	12.41 ± 0.20	-16.94 ± 0.46				
Sthenelais boa	C-O					1	3.44	11.92	-18.01
Sthenelais sp.	C-O	2	3.42	11.84 ± 0.21	-17.34 ± 0.58				
Pholoe inornata	C-O	2	3.36	11.64 ± 0.10	-16.62 ± 0.62				
Nephtys hombergii	C-O	3	3.52	12.18 ± 0.44					
Nereidae sp.A	C-O					1	2.58	8.98	-21.24

Nereis sp.A	C-O	2	2.67	9.31 ± 0.50	-24.71 ± 1.31				
Nereis sp.B	C-O	1	3.56	12.31	-17.86	2	3.22	11.17 ± 1.88	-20.27 ± 3.37
Hilbigneris gracilis	C-O	2	3.4	11.78 ± 0.65	-18.39 ± 0.27	3	3.22	11.16 ± 0.87	-18.75 ± 0.85
Lumbrineridae sp. A	C-O	1	3.22	11.16	-17.08				
Schistomeringos rudolphii	C-O					1	3.35	11.61	-20.48
Eunice vittata	C-O	1	3.71	12.84	-19.62	2	3.35	11.60 ± 1.00	-17.54 ± 0.13
Nematonereis unicornis	C-O	1	3.48	12.05	-17.98	3	3.45	11.94 ± 0.72	-18.36 ± 0.52
Arabella iricolor	C-O	2	3.79	13.10 ± 0.05	-17.81 ± 0.21				
Hyalinoecia bilineata	C-O	3	3.09	10.74 ± 0.15	-18.69 ± 0.41				
Sternaspis scutata	SDF	1	2.62	9.14	-15.67				
Notomastus latericeus	SSDF	3	3.32	11.50 ± 0.19	-17.52 ± 0.07				
Dasybranchus caducus	SSDF					2	2.67	9.30 ± 0.26	-17.81 ± 0.30
Euclymene oerstedi	SSDF	2	2.88	10.01 ± 0.34	-18.87 ± 0.03				
Euclymene robusta	SSDF	1	3.74	12.95	-17.33				
Praxillura longissima	SSDF	1	3.2	11.12	-19.39				
Macroclymene santandarensis	SSDF	4	3.31	11.48 ± 0.82	-17.99 ± 1.07	2	3.29	11.40 ± 0.07	-18.42 ± 0.14
Maldane glebifex	SSDF	3	3.44	11.90 ± 0.44	-16.15 ± 1.38	6	3.23	11.22 ± 0.14	-16.74 ± 0.42
Metasychis gotoi	SSDF					1	3.22	11.17	-17.89
Piromis eruca	SDF					3	2.75	9.57 ± 0.21	-15.03 ± 0.46
Pherusa plumosa	SDF	1	2.85	9.91	-17.96				
Ampharete finmarchica	SDF	1	2.04	7.17	-20.18				
Terebellides stroemii	SDF	3	2.77	9.65 ± 0.32	-19.09 ± 0.86	3	3.05	10.59 ± 0.38	-18.65 ± 0.06
Pista cristata	SDF					2	3.32	11.50 ± 0.32	-18.67 ± 0.89
Pectinaria (Amphictene) auricoma	SSDF	3	2.72	9.48±0.50	-17.82±0.57				
Sabellidae sp.	SF	1	2.41	8.41	-20.87				
Euchone rubrocincta	SF					1	2.63	9.15	-20.07
Orbinia cuvierii	SSDF	1	3.68	12.73	-17.73	2	3.64	12.58 ± 0.25	-18.00 ± 0.13
Owenia fusiformis	SDF	3	2.76	9.61 ± 0.46	-17.50 ± 0.17				
Gatropods									
Scaphander lignarius	SSDF	1	3.32	11.52	-15.28				
Crepidula fornicata	SF					3	2.19	7.66 ± 0.21	-17.59 ± 1.01
Nassarius reticulatus	C-O	4	3.18	11.04 ± 2.64	-15.91 ± 0.67				
Buccinum undatum	C-O					3	3.52	12.20 ± 0.28	-14.86 ± 0.14
Gibbula cineraria	G	3	2.75	9.56 ± 0.10	-17.25 ± 1.52				
Philine aperta	C-O	3	2.76	9.61 ± 0.07	-16.53 ± 0.31				
Aplysia punctata	G	3	2.75	9.57 ± 0.16	-29.41 ± 1.62	1	2.53	8.83	-30.81
Bivalves									
Nucula nitidosa	SF	3	2.28	7.97 ± 0.22	-17.29 ± 0.43	2	2.4	8.39 ± 0.02	-17.54 ± 0.08
Thyasira flexuosa	SF	3	-0.15	-0.30 ± 0.46	-26.40 ± 0.29				
Kurtiella bidentata	SF	1	2.4	8.37	-17.69				
Polititapes virgineus	SF					9	2.39	8.34 ± 0.77	-17.38 ± 0.97
Chamelea striatula	SF	2	2.38	8.32 ± 0.05	-18.46 ± 0.83				
Dosinia lupinus	SF	3	2.49	8.69 ± 0.12	-17.09 ± 0.22				
Spisula subtruncata	SF	1	2.1	7.35	-18.69				
Gari fervensis	SF	2	2.09	7.33 ± 0.07	-18.71 ± 0.40				
Solecurtus scopula	SF					1	3.14	10.91	-17.45
Abra alba	SF	3	2.51	8.74 ± 0.25	-18.65 ± 0.22				
Phaxas pellucidus	SF	3	2.13	7.46 ± 0.04	-19.21 ± 0.47				
Aequipecten opercularis	SF	3	2.37	8.27 ± 0.26	-17.06 ± 0.17	2	2.29	8.02 ± 0.20	-17.83 ± 0.86
Pecten maximus	SF	1	2.92	10.16	-17.51	7	2.61	9.09 ± 0.24	-15.63 ± 0.43
Palliolum tigerinum	SF					1	2.32	8.12	-19.47

Crustaceans									
Natatolana neglecta	C-O	1	2.98	10.37	-18.36	1	3.18	11.02	-16.73
Ampelisca spinipes	SF	1	2.14	7.5	-20.74				
Haploops nirae	SF					3	2	7.02 ± 0.29	-19.79 ± 0.24
Palaemon serratus	C-O	3	3.87	13.38 ± 0.71	-17.76 ± 0.99	3	3.8	13.16 ± 0.32	-17.21 ± 0.18
Anapagurus hyndmanni	SF	2	2.35	8.22 ± 0.51	-21.42 ± 0.34	1	2.31	8.07	-19.07
Pagurus bernhardus	C-O					3	3.43	11.90 ± 0.19	-17.25 ± 0.51
Pagurus cuanensis	SF					2	2.52	8.80 ± 0.01	-18.93 ± 0.72
Pagurus prideaux	C-O	3	3.57	12.35 ± 0.40	-16.11 ± 0.28	3	3.61	12.49 ± 0.14	-16.42 ± 0.64
Inachus dorsettensis	C-O	3	2.9	10.09 ± 1.08	-17.50 ± 0.73	3	3.55	12.31 ± 0.73	-16.79 ± 0.24
Macropodia rostrata	C-O	1	3.1	10.76	-19.34				
Maja squinado	C-O					1	3.84	13.28	-16.04
Liocarcinus pusillus	C-O	3	3.25	11.26 ± 0.62	-18.27 ± 1.07	1	2.84	9.88	-18.55
Liocarcinus depurator	C-O					3	3.6	12.48 ± 0.66	-16.62 ± 0.14
Pisidia longicornis	SF	1	2.36	8.23	-19.56	1	2.22	7.78	-19.89
Xantho pilipes	C-O					2	3.27	11.33 ± 0.05	-16.66 ± 0.01
Upogebia deltaura	SF	1	2.54	8.85	-19.78				
Echinoderms									
Astropecten irregularis	C-O	3	3.16	10.96 ± 0.30	-16.94 ± 0.62				
Asterias rubens	C-O	3	3.25	11.28 ± 0.16	-15.39 ± 0.95	3	3.17	11.00 ± 0.10	-15.25 ± 0.02
Marthasterias glacialis	C-O	1	3.01	10.46	-17.05	2	3.15	10.94 ± 0.37	-16.11 ± 0.11
Ophiura ophiura	C-O	2	3.31	11.24 ± 1.36	-16.49 ± 1.56				
Ophiura albida	C-O	1	2.88	10.03	-17.58	3	2.9	10.07 ± 0.55	-17.89 ± 0.15
Amphiura filiformis	SF	3	2.87	10.00 ± 0.17	-17.40 ± 0.40				
Ophiothrix fragilis	SF	3	2.47	8.63 ± 0.49	-18.28 ± 0.29				
Psammechinus miliaris	G	3	2.62	9.13 ± 0.89	-21.63 ± 0.87				
Thyone fusus	SF	3	2.4	8.40 ± 0.88	-16.57 ± 0.26				
Oestergrenia digitata	SDF	1	3.25	11.27	-19.71	1	3.36	11.65	-16.86

Supplement S2. Mean (± SD) isotopic compositions (δ^{13}C and δ^{15}N) of all species sampled in summer for both *Amphiura* and *Haploops* habitats. TG = Trophic Group, n = number of samples, TP = Trophic Position calculated after Post 2002 using *Haploops nirae* as a trophic baseline. Information on trophic groups gathered from the Biological Traits Information Catalogue developed by the Marine Life Information Network, as C-O = Carnivorous and/or Omnivorous, SF = Suspension-Feeders, SDF = Surface Deposit-Feeders, SSDF = Sub-Surface Deposit-Feeders, G = Grazers or micro-Grazers. Species names were checked using world register of marine species database on November 28th 2013

		Amphiura habitat				*Haploops* habitat			
	TG	n	TP	$\delta^{15}N$	$\delta^{13}C$	n	TP	$\delta^{15}N$	$\delta^{13}C$
Cnidarians									
Adamsia carciniopados	C-O					2	3.27	11.84 ± 0.41	-17.45 ± 0.42
Epizoanthus incrustatus	C-O	1	2.61	9.6	-17.14				
Sipunculids									
Aspidosiphon muelleri	SDF	3	2.87	10.48 ± 0.50	-16.56 ± 0.20	3	2.87	10.50 ± 0.73	-16.69 ± 0.41
Golfingia vulgaris	SDF					2	3.08	11.22 ± 0.59	-17.18 ± 0.44
Nemerteans									
Nemertina sp.A	C-O					2	3.02	11.00 ± 0.34	-17.54 ± 0.18
Polychaetes									
Aphrodita aculeata	C-O					1		13.03	-15.56
Glycera alba	C-O	3	3.49	12.60 ± 0.45	-17.82 ± 0.40				
Glycera unicornis	C-O					1	4.27	15.24	-16.54
Glycinde nordmanni	C-O	1	3.64	13.1	-17.95				
Labioleanira yhleni	C-O	1	3.12	11.34	-17.46				
Sthenelais boa	C-O					3	3.62	13.05 ± 0.43	-16.77 ± 0.16
Sthenelais limicola	C-O	1	2.82	10.33	-17.72				
Nephtys assimilis	C-O	1	3.33	12.06	-16.46				
Nephtys hombergii	C-O	3	3.25	11.78 ± 0.43	-16.60 ± 0.26				
Hilbigneris gracilis	C-O	1	3.19	11.59	-17.2				
Scoletoma fragilis	C-O	3	2.89	10.54 ± 0.36	-17.41 ± 0.05	1	3.4	12.3	-17.24
Schistomeringos rudolphii	C-O					1	3.35	12.11	-18.73
Eunice vittata	C-O					3	3.05	11.11 ± 0.10	-17.61 ± 0.06
Nematonereis unicornis	C-O					3	3.5	12.62 ± 0.35	-17.35 ± 0.55
Arabella iricolor	C-O					3	3.69	13.29 ± 0.64	-17.05 ± 0.22
Sternaspis scutata	SDF					1	2.46	9.09	-19.43
Notomastus latericeus	SSDF	2	3.24	11.76 ± 0.31	-16.37 ± 0.13				
Dasybranchus caducus	SSDF					1	2.58	9.51	-18.08
Euclymene oerstedi	SSDF	1	2.93	10.69	-18				
Euclymene lombricoides	SSDF					1	3.15	11.46	-17.4
Praxillura longissima	SSDF	1	3.08	11.19	-18.33				
Macroclymene santandarensis	SSDF					3	3.31	11.97 ± 0.18	-18.18 ± 0.18
Maldane glebifex	SSDF	3	3.23	11.72 ± 0.19	-16.21 ± 0.64	3	3.22	11.67 ± 0.71	-17.82 ± 0.12
Metasychis gotoi	SSDF					1	3.23	11.7	-17.31
Piromis eruca	SDF					2	2.76	10.13 ± 0.56	-17.53 ± 0.14
Pherusa plumosa	SDF					1	2.37	8.79	-17.98
Lysippe labiata	SDF					1	2.6	9.57	-19.97
Terebellides stroemii	SDF					3	2.88	10.54 ± 0.19	-18.95 ± 0.27
Lanice conchilega	SF	1	2.24	8.36	-18.67				
Pista cristata	SDF					2	3.24	11.74 ± 0.06	-18.56 ± 0.20
Amaeana trilobata	SDF	1	3.12	11.33	-18.28				
Lagis koreni	SSDF	2	2.71	9.94 ± 0.21	-17.81 ± 0.83				
Sabellidae sp.	SF	1	2.46	9.11	-18.92	1	2.04	7.67	-19.25
Euchone rubrocincta	SF	1	2.47	9.14	-19.25				
Demonax brachychona	SF	1	2.25	8.4	-20.14				
Sabellaria spinulosa	SF	1	2.08	7.8	-18.58	2	2.44	9.02	-19.36
Hydroides elegans	SF	1	2.23	8.31	-19.07				
Orbinia cuvierii	SSDF	1	3.55	12.8	-16.85	3	3.57	12.86 ± 0.81	-18.01 ± 0.29
Owenia fusiformis	SDF	3	2.27	8.44 ± 1.04	-18.38 ± 0.59				

Aricidea (Aricidea) pseudoarticulata	SDF					1	3.34	12.08	-18.55
Scalibregma inflatum	SDF	2	2.26	8.43 ± 0.60	-18.24 ± 0.24				
Gastropods									
Scaphander lignarius	SSDF	1	3.02	10.99	-15.83				
Crepidula fornicata	SF	3	2.02	7.60 ± 0.08	-18.48 ± 0.07	3	2.19	8.17 ± 0.14	-17.12 ± 0.48
Euspira pulchella	C-O	2	2.65	9.74 ± 0.29	-16.28 ± 0.07	1	2.53	9.32	-16.81
Buccinum undatum	C-O	1	3.15	11.45	-16	2	3.22	11.68 ± 1.02	-15.47 ± 0.96
Turritella communis	SF	2	1.96	7.41 ± 0.70	-17.30 ± 0.47	1	2.01	7.57	-16.57
Gibbula sp.	G	3	2.55	9.40 ± 0.98	-17.27 ± 0.68				
Trivia monacha	C-O	1	2.75	10.08	-18.49				
Philine aperta	C-O	1	2.65	9.74	-13.98				
Geitodoris planata	G	2	3.04	11.06 ± 0.33	-11.83 ± 0.90	1	2.93	10.71	-11.64
Bivalves									
Nucula nitidosa	SF	4	2.16	8.06 ± 0.35	-17.29 ± 0.12	2	2.14	8.02 ± 0.04	-16.91 ± 0.05
Corbula gibba	SF					1	1.97	7.43	-19.19
Polititapes virgineus	SF					6	2.38	8.84 ± 0.26	-16.83 ± 0.33
Timoclea ovata	SF					1	1.67	6.4	-17.98
Chamelea striatula	SF	1	2.15	8.03	-17.38				
Dosinia lupinus	SF	3	2.32	8.60 ± 0.46	-17.43 ± 0.62	1	2.23	8.32	-18.38
Abra alba	SF	3	2.23	8.33 ± 0.62	-17.61 ± 0.20				
Phaxas pellucidus	SF	2	1.82	6.93 ± 0.54	-18.35 ± 0.01				
Lyonsia norwegica	SF					1	2.02	7.6	-18.87
Aequipecten opercularis	SF	9	2.2	8.20 ± 0.36	-17.36 ± 0.46	9	2.22	8.27 ± 0.58	-17.36 ± 0.30
Pecten maximus	SF					7	2.53	9.33 ± 0.37	-16.26 ± 0.30
Anomia ephippium	SF					1	1.85	7.02	-18.42
Antalis novemcostata	SDF	1	3.04	11.08	-17.69				
Crustaceans									
Ampelisca brevicornis	SF	1	2	7.54	-18.11				
Ampelisca spinifer	SF	1	2.27	8.44	-19.61				
Ampelisca spinipes	SF	2	1.9	7.19 ± 0.64	-20.91 ± 0.66	3	1.9	7.20 ± 1.33	-20.17 ± 0.45
Ampelisca typica	SF					1	2.01	7.55	-20.43
Haploops nirae	SF					3	2	7.53 ± 0.15	-19.74 ± 0.67
Pandalina brevirostris	C-O					3	3.41	12.34 ± 0.59	-17.33 ± 0.19
Pontophilus spinosus	C-O					2	3.69	13.29 ± 0.20	-16.28 ± 0.57
Paguroidea spp.	SF					1	2.29	8.53	-20.22
Pagurus prideaux	C-O					3	3.32	12.02 ± 0.25	-16.03 ± 0.11
Galathea intermedia	SF					1	2.34	8.7	-20.71
Inachus dorsettensis	C-O					3	3.32	12.03 ± 0.45	-16.47 ± 0.12
Macropodia rostrata	C-O					1	2.46	9.09	-19.19
Atelecyclus rotundatus	C-O					1	3.12	11.33	-16.55
Liocarcinus navigator	C-O					1	3.41	12.33	-16.59
Liocarcinus pusillus	C-O					3	3.35	12.13 ± 0.09	-17.00 ± 0.20
Xantho pilipes	C-O					3	3.18	11.56 ± 0.19	-16.93 ± 0.26
Echinoderms									
Luidia ciliaris	C-O	1	3.74	13.45	-14.41	1	4.19	14.99	-14.26
Marthasterias glacialis	C-O	2	3.59	12.92 ± 0.65	-14.79 ± 0.31	3	3.49	12.61 ± 0.35	-14.54 ± 0.03
Amphiura filiformis	SF	3	2.44	9.01 ± 0.54	-17.95 ± 0.33				
Psammechinus miliaris	G	1	2.68	9.86	-17.88				
Thyone fusus	SF	3	2.6	9.58 ± 0.75	-16.17 ± 0.86				
Leptopentacta elongata	SSDF	2	3.18	11.54 ± 0.26	-15.16 ± 0.29				
Sponges									

Sycon ciliatum	SF	1	1.97	7.43	-19.21
Suberites suberia	SF	1	2.25	8.39	-19.91