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To cite this version:

Pierrick Barbier, Tarik Meziane, Martin Forêt, Réjean Tremblay, René Robert, et al.. Nursery function of coastal temperate benthic habitats: New insight from the bivalve recruitment perspective. Journal of Sea Research (JSR), 2017, 121, pp.11 - 23. 10.1016/j.seares.2016.12.007 . hal-01446041

HAL Id: hal-01446041
https://hal.sorbonne-universite.fr/hal-01446041

Submitted on 25 Jan 2017

Title:

Nursery function of coastal temperate benthic habitats: new insight from the bivalve recruitment perspective

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Abstract

Marine habitat function has been typically investigated in terms of biogeochemical regulation but rarely in terms of population renewal, which is mainly controlled by recruitment dynamics. The recruitment phase is crucial for organisms with a bentho-pelagic life cycle, such as bivalves, and it regulates the population renewal success. This study provides new insight on the role of temperate benthic habitats on bivalve recruitment, as a function of nursery areas. Six dominant benthic habitats of the Chausey archipelago (Normandy, France) were studied. In each habitat, bivalve recruit assemblages were described at the end of two reproductive seasons. Furthermore, *Ostrea edulis* juveniles were immerged on each habitat during two months to compare growth performances and feeding status, estimated by fatty acid composition. Recruit assemblages differ from each habitat according to sediment grain-size composition and bathymetrical levels. Subtidal habitats, and especially *Crepidula fornicata* banks and *Glycymeris glycymeris* coarse sands, supported the highest species abundance and richness of recruits. All *O. edulis* juveniles fed on the same trophic resources but digestive glands of juveniles from *C. fornicata* banks were more concentrated in total fatty acids than those from subtidal *G. glycymeris* coarse sands and maerl banks. Our results depict the key role of subtidal and structured habitats, composed of ecosystem engineers, in enhancing bivalve recruitment and extending the bivalve population renewal. This study suggests that the crucial role of these habitats as bivalve nurseries must be integrated in management perspectives.

Keywords

Benthic habitats; bivalve recruitment; nursery function; *Ostrea edulis*; fatty acids

1. Introduction

The marine seafloor is comprised of 70% soft sediment areas, including a large diversity of benthic habitats (Snelgrove 1999), which ensure multiple functions at the base of the ecosystem goods and services (De Groot et al. 2010; Haines-Young et Potschin 2010). A habitat, as strictly defined by Begon et al. (1996), is a place where an organism (microorganisms, plants, animals) lives. However, the most widely used definition is a spatially defined area, where the physical, chemical, or biological environment is distinctly different from those surrounding it (Kostylev et al. 2001). This implies that spatial boundaries coincide with environmental preferences or survival of an organism or a group of organisms that share the same habitat. In Europe, major habitats are defined and surveyed according to the EUNIS (European Union Nature Information System) habitat classification (Davies et al. 2004), providing a comprehensive typology based on hierarchical levels, for which the first concerns "Marine habitats" (EUNIS habitat type hierarchical view http://eunis.eea.europa.eu/habitats-code-browser.jsp). With the exception of the pelagic water column and ice-associated marine habitats, all habitat classifications are benthic. Among these habitat types, several are defined by ecosystem engineer species. These species, as defined by Jones et al. (1994) are "organisms that modulate resource availability for other species through their abiotic or biotic material, leading to the maintenance or creation of new habitats". The engineering effects of structuring species, in addition to their direct impact on resources, positively and negatively affect abundance and species richness at small scales, leading to the emergence of particular habitat functions (Jones et al. 1994; Jones et al. 1997).

According to De Groot et al. (2002) the ecosystem or habitat "function" is "the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly". To propose effective biodiversity conservation policies, Liquete et al. (2013) reviewed ecosystem services associated with marine and coastal environments. Due to the initial influence of comparable terrestrial studies (*i.e.* Bardgett et van der Putten 2014), benthic habitat functions were often investigated solely in terms of energy and matter fluxes. In addition to such physicochemical properties/roles/functions, benthic habitats have ecological functions, such as providing shelter from prey, nursery habitat, and feeding areas, depending on species composition and abundances (Eyre et al. 2011; Snelgrove 1999; Thrush et Dayton 2002). Moreover, these ecological functions can be enhanced when habitats interact (Srivastava 2006). The "reproduction and nursery area" habitat function was almost exclusively assessed for fisheries (Seitz et *al.* 2013). This function, defined as "the provision of the appropriate environmental conditions for reproduction and growing during the early stages of marine species" (Salomidi et al. 2012), is essential for the renewal of dominant populations.

In temperate marine systems, a large majority of marine invertebrates, such as bivalves, have a bentho-pelagic life cycle with a long pelagic phase represented by a large number of planktonotrophic larvae (Thorson 1950). Renewal of bivalve populations is thus mainly due to the recruitment success, i.e. the settlement-metamorphosis, and the subsequent juvenile survival in the benthic compartment. During this critical life stage, the loss ratio between invertebrate larvae and adult stage is generally over 97% (Pedersen et al. 2008). Recruit assemblages observed in a benthic habitat result from pre- and post-settlement processes that condition the presence or absence of organisms. Pre-settlement processes act on the larval pool from fecundation to metamorphosis, and post-settlement processes control post-larval and juvenile stages. Such processes are under the influence of many abiotic factors, including water physicochemical parameters and hydrodynamic disturbances, as well as biotic factors, such as food availability, biological interactions, and species behavior (Hunt et Scheibling 1997; Pechenik 1999; Pineda et al. 2009). It is well known that specific benthic boundary flows can cause sediment resuspension and subsequent drifting of benthic organisms in the water column, which may have important consequences on population dynamics (Olivier et al. 1996; Olivier et Retière 1998). Recent studies have emphasized the crucial role of trophic resources (quality and quantity) in the recruitment success. For example, the bivalve diets at each development stage may affect the genitor gonadic development, the larval survival and growth, and even the trigger of their settlement (González-Araya et al. 2011; González-Araya et al. 2012; Jolivet et al. 2016; Toupoint et al. 2012). Stresses that affect early life cycle stages are sources of latent-effects, inducing within-species variations of juveniles and adults' survival and reproduction (Pechenik 2006). Recently, St-Onge et al. (2015) showed that, at a reproductive season scale, bivalve larvae in a kin aggregated larval pool issued from multi-spawning events do not have the same recruitment survival success and the first produced larvae will mainly regulate the final recruitment composition. It seems thus crucial to understand accurately all factors insuring minimum recruitment to keep bivalve population sustainable.

Bivalves constitute a major component of benthic habitat as they often dominate the biomass of soft-bottom sediments (Peterson 1977) and have key functions (Gosling 2003), including bioturbation and primary consumers, affecting their surrounding environment. The persistence of bivalve populations can provide numerous ecosystem services that include provision, regulating and maintenance services (Katsanevakis et al. 2014; Liquete et al. 2013). Moreover, bivalves are an important economic resource, as shellfish farming areas, like the Mont Saint Michel Bay (MSMB), produce tens of millions of shellfish and generate more than 30 million Euros per year (Cugier et al. 2010). The present study was carried out in Chausey Archipelago (MSMB, Normandy, France), which is characterized by semidiurnal tidal pattern and a maximal tidal range of 14m during spring tides. This archipelago covers a surface of 5100 ha, including emerged islands, subtidal and intertidal seabeds, where almost a third is represented by sandflats (1388 ha; Godet et al. 2009). About nine intertidal and seven subtidal benthic habitats are found across the archipelago supporting 769 marine invertebrate species, with about 100 known bivalve species (Fournier et al. 2014; Godet et al. 2010).

The aim of this study is to provide new insights on the renewal of wild bivalve populations within a temperate coastal megatidal system, and in particular, with regards to the "reproductive and nursery area" habitat function across several benthic habitats (Table 1). We analyzed this function during two main phases of the bivalve recruitment: 1) at the end of a reproductive season by determining the natural bivalve recruit assemblages and 2) during the development of *Ostrea edulis* juveniles, by estimating their growth performances and feeding status.

2. Materials and methods

2.1 Study site

The present study focuses on six main benthic habitats of the archipelago (Table 1) as defined by their surface area and ecological significance. The *Glycymeris glycymeris* coarse sands (Godet 2008; Coarse sands and gravels from coastal circumlittoral with *Mediomastus fragilis, Lumbrineris spp*. and *Veneridae* bivalves, A5.142 EUNIS Classification 2008), the most widespread habitat of the English channel (Larsonneur et al. 1982), were investigated at intertidal (SHI) and subtidal (SHS) levels where they are found on ¼ (350ha) of the Chausey soft-sediment tidal flats (Godet 2008). Intertidal beds of *Lanice conchilega* (*Polychaeta*, *Terebellidae*) (L) (Godet 2008; *L. conchilega* in littoral sand, A2.245 EUNIS Classification 2008), a commonly European found tube-building polychaete and engineer species forming large bioherms when reaching a specific threshold density (Godet et al. 2011). Intertidal *Zostera marina* beds (Z) (Godet 2008; *Z. marina / Z. angustifolia* beds on lower shore or infralittoral clean or muddy sand, A5.5331 EUNIS Classification 2008) are the most represented seagrass over the archipelago acting like a nursery to numerous marine species (Godet et al. 2008a; Boström et al. 2014). This marine plant beds can also be considered as key ecosystem engineer (Jones et al. 1994, but see also Passarelli et al. 2014). Subtidal maerl (Corallinophycidae, Rhodophyta) beds (M) (maerl beds on infralittoral muddy gravel, A5.513 EUNIS Classification 2004) are characterized by a high macrofaunal specific richness, especially of molluscan species (Grall et Glemarec 1997). Subtidal slipper limpet's (*Crepidula fornicata*) banks (C) (*C. fornicata* with ascidians and anemones on infralittoral coarse mixed sediments, A5.431 EUNIS Classification 2004) are constituted by the introduced species from North America, *C. fornicata*, which became invasive on the European coasts at the end of the 19th century (Blanchard 1997). Sampling and experiment sites of this study were carefully chosen according to previous studies conducted in the Chausey archipelago, allowing us to select the most adequate sites for each benthic habitat (Fournier et al. 2014; Godet 2008; Godet et al. 2008a; Godet et al. 2008b; Godet et al. 2009; Godet et al. 2011; Perez et al. 2013; Toupoint et al. 2008).

Habitat	Abb.	Recruitment assessment		*In situ* experiment	
		Min. depth (m)	Max. depth (m)	Min. depth (m)	Max. depth (m)
Crepidula fornicata banks	C	-16.5	-8.8	-6.8	-10.7
Lanice conchilega beds	L	+3	+3.8	0	-0.9
Maerl beds	M	-11	-13.5	-3.2	-5.8
Subtidal coarse sands	SHS	-5.5	-6.6	-1.9	-4.6
Intertidal coarse sands	SHI	+1.9	+3.5		
Zostera marina beds	Z	+0.2	+1	-1	-1.9

Table 1 Main features of the study sites including habitat name, abbreviation, minimum and maximum depth (m) for the recruitment assessment and the *in situ* experiment. Positive and negative depth refers about the zero of the chart datum. Abb: Abbreviation; SHI: Intertidal coarse sands; SHS: Subtidal coarse sands; L: *L. conchilega* beds; Z: *Z. marina* beds; M: Maerl beds; C: *C. fornicata* banks.
1-column fitting table

Sampling sites selection mainly depends on the habitat recovering at the sea bottom. For example, maerl beds are mostly present in the Northern part of the archipelago, while *Lanice conchilega* beds dominated soft bottoms from the West-center area. We consider the effects of a heterogeneous distribution of larval pool along the water column should not be considered due to high hydrodynamic constraints located in this kind of megatidal environment and post-settlement processes (i.e. secondary migration) that structure bivalve recruits assemblages at the end of each reproductive season (Toupoint et al. 2016).

2.2 Assemblages of bivalve recruits at the end of the reproductive season

In order to compare bivalve recruitment assemblages on dominant benthic habitats of the archipelago, two sampling campaigns (September the 10th 2013 and October the 3rd 2014) were conducted at the end of the reproductive season of most wild bivalves species of European coasts (reviewed by Gosling 2003). Distributed from the center towards the West of the archipelago (Fig. 1a), three sites per habitat were sampled using a Smith-McIntyre

Grab (one replicate of 0.2 m^{-2} per site; Smith and McIntyre 1954). Collected material was sorted through a 5 and 2 mm circular mesh sieves to keep only bivalve recruits of the sampled year. Even if few studies have examined bivalve post-larvae growth, they mostly presented a large variability in growth according to species and locations (Andresen et al. 2013; Bownes et McQuaid 2009; Chicharo et Chicharo 2001; Jenewein et Gosselin 2013; Martel et al. 2014; Toupoint et al. 2016; Van der Geest et al. 2011). Only veliger larvae of 300 µm, mean size at metamorphosis and a mean post-larval growth rate of 30 µm d^{-1} were considered. The latter growth rate induced a final post-larval/juvenile size in September/October falling into the 2-5 mm range for a large part of bivalve species. We are aware that the mesh size used to retain the recruits certainly does not allow the collection of all the species recruiting based on their variable growth rates and reproductive cycles. However, the 2-5 mm size range adopted in our sampling protocol optimized a reasonable sorting effort with the collection of most of the bivalve species found in the studied habitats as shown by concomitant work (Toupoint et al. 2016).

After fixation (4% buffered formalin) of sieved material, bivalve recruits were sorted, counted and identified to the lowest taxonomic level, and finally preserved in 70% ethanol. For each benthic habitat, a simplified classification of sediments derived from nomenclature of Folk (1954) was elaborated, by using five sedimentary textural groups: sandy gravel, gravelly sand, sand, muddy sand and sandy mud. Sedimentary data (percentages of grain-size classes) originate from previous field works on close sites of the Chausey Archipelago (Fournier et al. 2014; Godet 2008; unpublished data).

2.3 Growth performances and feeding status of Ostrea edulis juveniles

2.3.1 Biological material and experimental design

Ostrea edulis recruits were produced at the experimental station of Ifremer Argenton (Brittany, France). Briefly, 100 of 4 y-old flat oysters free from *Bonamia ostreae* and *Marteilia refringens* were conditioned at 19°C and ambient 34 ppt salinity in a 600L tank in flow through and continuously fed 6% of microalgal dry weight (DW) (*Rhodomonas salina* + *Chaetoceros neogracile)* per g of oyster DW). The release of larvae (760,000) recorded on mid-October 2013, were used for the present grow out trials. Expelled larvae were distributed at 40 larvae ml^{-1}, reared at 25°C and ambient 34 ppt salinity, in six 5L transparent tank with a diet of 1500 μm^3 μl^{-1} of *Tisochysis lutea* (T) and *Chaetoceros neogracile* (Cg). Post-larvae were transferred in upwellers (7g total weight ≈ 1850 individuals per unit) on mid-November 2013, reared at 25°C on filtered 1 µm seawater at a flow rate increasing progressively from 5 to 30 l^{-1} and fed a standard TCg diet (González-Araya et al. 2012; Rico-Villa et al. 2006) before their transfer 1.5 months later at a density of ≈ 10 000 spat per bag on the sea bottom at St Anne in the bay of Brest.

In late April 2014, 7500 six month-old juveniles were acclimatized during a 4-weeks period in a plastic bag (5 mm square mesh size) fixed on a mooring located in the Chausey Sound Channel, below the water surface (~ 2m). Then on May 27th 2014, oysters mean length was of 13.4 ± 0.37 mm (mean ± SE) and 15 batches of 500 randomly selected individuals were redistributed in bags (5 mm square mesh size). One bag was deployed per experimental site of each of the chosen habitats (three bags per habitats; Fig. 1b), at low tidal level for the intertidal sites, during 2 months. For this experiment, only the subtidal level of *Glycymeris glycymeris* coarse sands habitat was investigated because of the natural distribution of *Ostrea edulis* in the subtidal zone (Rufino et al. 2010). Sampling sites were mainly distributed at the northwestern part of the archipelago since all 5 habitats studied were concentrated in that area, enabling easy accessibility for the technical support available. On July 25th 2014, those 15 batches were recovered and the bivalves immediately frozen at -80°C until further laboratory analysis.

2.3.2 Biometry and fatty acid analyses of recruits

Shell morphology (length, width, thickness in mm) was recorded, as well as shell (g) and soft tissues (mg) dry weight, on 10 reared juvenile oysters after acclimation (i.e. before deployment; control) and 24 juveniles collected from each experimental batch after experimentation (24 oysters x 3 sites x 5 habitats). Shell length, width and thickness, defined as the longest dimension along the hinge-margin, antero-posterior and the two valves axis, respectively, were measured with a digital caliper (0.01 mm accuracy). Tissues and shells for dry weight measurements were freeze-dried for 24h and weighed on a precision balance.

Digestive glands of 4 juveniles per experimental batch were dissected (4 digestive glands x 3 sites x 5 habitats), humid mass measured and fatty acids (FAs) extraction done according to a modified method of Bligh and Dyer (1959) as described in Meziane et al. (2006). Saponification and methylation of extracts were realized in order to collect total FAs and to permit their quantification by gas chromatography (Leroy et al 2013). Isotopic ratio analyses were performed with the whole tissue (excluding the digestive gland) of each individual. Each sample was soaked during 24h in Milli-Q water, lyophilized and finally 0.7 mg of dry weight tissue was encapsulated in a tin capsule. Carbon and Nitrogen were reported in ‰ using the standard delta notation ($\delta^{13}C$ and $\delta^{15}N$).

2.4 Statistical analyses

The matrix of bivalve species abundances (individuals m^{-2}) and FA relative abundances (%) from all samples, were used to create two triangular matrix based on Bray-Curtis similarity index which were used to generate n-MDS plots (Legendre et Legendre 1998). Assumptions of homoscedasticity were verified with PERMDISP tests. A 2-way PERMANOVA was then performed to test potential effects of benthic habitats, years and their interaction on bivalve recruits. Differences in the relative abundance of FAs between habitats were tested using a 1-way PERMANOVA. Similarity percentages (SIMPER) analyses were performed on bivalve species abundance and FAs relative abundance to determine similarity index within habitats and to identify which FA contributed the most to differences between groups (Clarke et Gorley 2006). Those analyses were performed with PRIMER-E v6 software (Anderson et al. 2008).

The species covariance between benthic habitats was analyzed using a factorial correspondence analysis (FCA). To estimate the proportion of variance in bivalve species assemblages by sedimentary textures of benthic habitats, a redundancy analysis (RDA) was performed (Legendre et Legendre 1998). The statistical significance of the relationship between bivalve species and sedimentary variables was evaluated using a permutation test (9999 permutations). Differences in mean total abundances, specific richness, rare species abundances, as well as mean concentrations, sums and ratios of FAs (selected from multivariate analysis), biometric data and isotopic ratios in each habitat were tested using a 1-way ANOVA followed by a Tukey's HSD post-hoc test. Box-Cox transformations of FA concentrations values were performed prior the analyses in order to achieve normality (Shapiro-Wilk test). In case of non-normality or heteroscedasticity (Bartlett test) of data (raw and transformed), both tested on residues arising from 1-way ANOVA, a Kruskal-Wallis test was performed and *a posteriori* comparisons made using a Mann-Whitney test. Latest tests were achieved on R software.

The condition index (CI) of each *Ostrea edulis* juvenile was determined as a ratio between dried meat weight and the sum of cooked meat weight and shell weight according to Davenport and Chen (1987). The daily growth rate (GR; mm j^{-1}) was calculated as a ratio between shell length and number of experiment days. Both CI and GR were calculated using biometric parameters measured on *O. edulis* juvenile after 2 months of immersion.

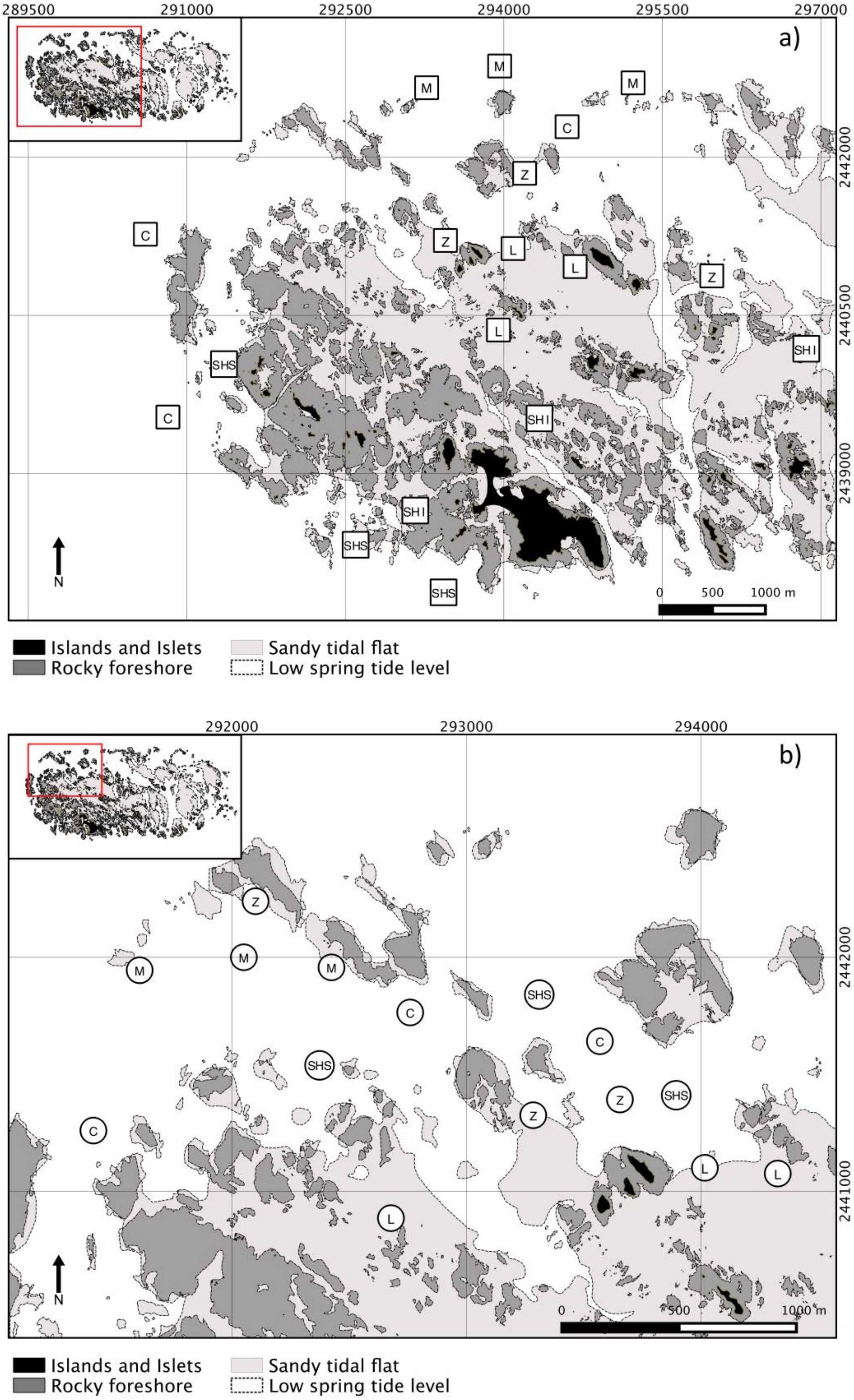


Fig. 1. Map of the Chausey Archipelago showing locations of sampling points for **a)** the recruitment assessment (square) and **b)** the *in situ* experiment (circle). Letters refers to benthic habitats: SHI: Intertidal coarse sands; SHS: Subtidal coarse sands; L: *L. conchilega* beds; Z: *Z. marina* beds; M: Maerl beds; C: *C. fornicata* banks
2-column fitting image

3. Results

3.1 Assemblages of bivalve recruits at the end of the reproductive season

From a pool of 16 bivalve species collected in the studied habitats, only five of them were dominant (≥ 5% of total cumulative abundances, all species pooled; by decreasing abundance): *Nucula* sp.*, Parvicardium scabrum, Goodalia triangularis, Lucinoma borealis and Timoclea ovata,* whereas the remaining species were rare (< 5% of total cumulative abundances, all species pooled; by decreasing abundance): *Glycymeris glycymeris, Abra alba, Abra tenuis, Spisula ovalis, Loripes lucinalis, Paphia rhomboides, Venus verrucosa, Ensis ensis, Gari depressa, Modiolus modiolus* and *Epilepton clarkiae*. When pooling data of the two sampling seasons, it appears that some species were restricted to a particular habitat such as *L. lucinalis*, *E. clarkiae*, *M. modiolus* and *V. verrucosa* in *Zostera marina* beds, *Crepidula fornicata* banks, maerl beds and subtidal coarse sands, respectively. In contrast, no exclusive species were found in *Lanice* and the intertidal coarse sands habitats (Table A1).

The assemblage structure of bivalve recruits significantly differs between habitats (PERMANOVA, p = 0.001), with no significant differences between years and without interactions between both factors (p > 0.05, Table 2). Pairwise comparisons tests reveal only significant differences between intertidal and subtidal assemblages (p < 0.05). Moreover, the recruit assemblages differed significantly between *Zostera marina* beds and both intertidal coarse sands and *Lanice* habitats (p = 0.041 and p = 0.032, respectively), which were similar (p > 0.05). Therefore, if there is no effect of the sampling year and the interaction between year and habitat on bivalve assemblage, further analyzes were performed by grouping samples from the two years as replicates (6 per habitat).

Sources of variation	**df**	**SS**	***F***	**p**
Ha	5	56426.0	5.1398	**0.001**
Da	1	2455.2	1.1182	0.326
Ha x Da	5	13059.0	1.1895	0.240
Residuals	22	48304.0		

Table 2 Results of permutational multivariate analyze of variance (PERMANOVA) testing the effect of Habitat (Ha), Date (Da) and their interaction (Ha x Da) on the assemblage of bivalve recruits based on the Bray-Curtis dissimilarity matrix. Significant values (p < 0.05) in bold. df: Degree of freedom; SS: Sum of square; *F*: Fisher's statistic; p: p-value**.**
1-column fitting table

The n-MDS results showed a clear distinction between sub- and intertidal habitats (Fig. 2). The intra-group similarity index was higher in *Zostera marina, Crepidula fornicata* and maerl beds (50.6%, 44.1% and 42.9%, respectively) in comparison to sub- and intertidal coarse sands and *Lanice* beds (26.5%, 20.2% and 14.7%, respectively) (Fig. 2).

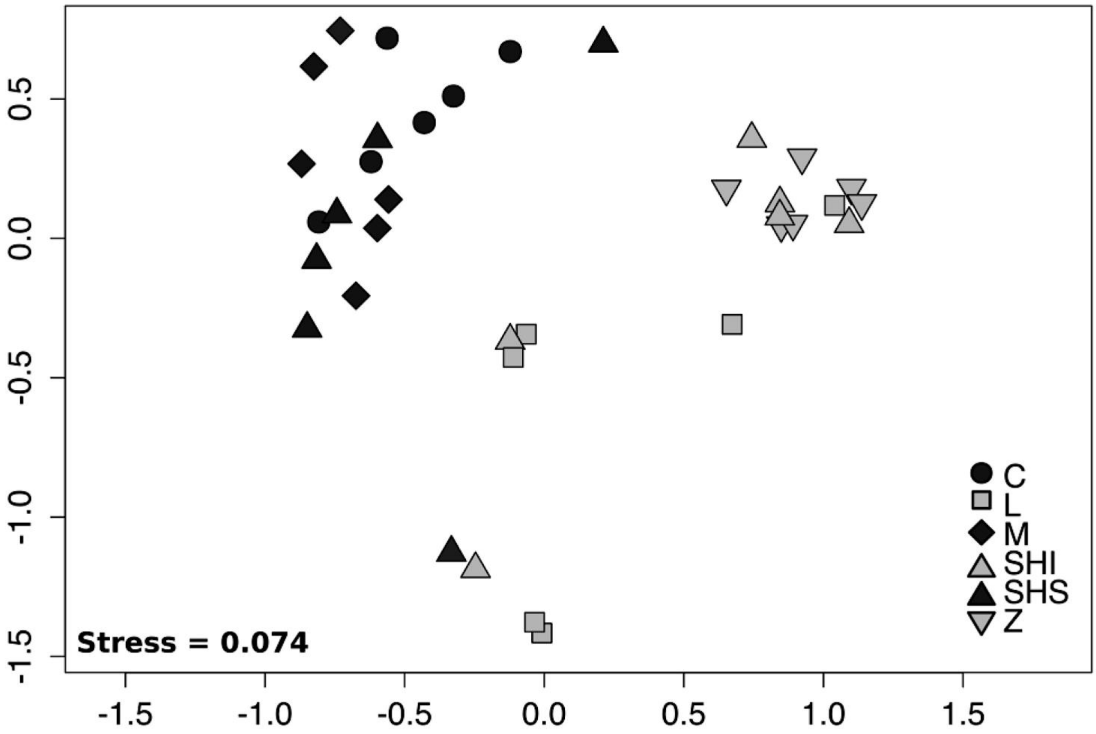


Fig. 2. n-MDS ordination plot of Bray-Curtis similarities based on assemblages of bivalve recruits for each sampling sites with superimposed symbols for benthic habitats (n=6): Intertidal coarse sands (SHI), Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C). Grey and black symbols represent intertidal and subtidal benthic habitats, respectively
1-column fitting image

Covariance results showed that the first three axes explained 56.6% of total variance. Axis 1 (24.4% of the total inertia) distinguishes principally inter- and subtidal habitats with the abundance of *Lucinoma borealis, Loripes lucinalis* and *Abra tenuis* contributing to 49.0%, 16.6% and 15.2% of the axis 1 total inertia, respectively (Fig. A1). Axis 2 (20.2% of the total inertia) discriminates sites mostly dominated by *Goodalia triangularis, Nucula* sp. and *Glycymeris glycymeris*, which explained 51.6%, 29.3% and 8.5% of the axis 2 total inertia, respectively (Fig. A1).

RDA results showed that the first two axes explain 72% of the variance of constrained data (Fig. 3). Axis 1 is correlated with gravelly sand (17.8%), muddy sands (15.8%), sand (28.8%)

and sandy gravel (23.8%), whereas axis 2 is correlated with sandy mud (61.4%) (Fig. 3). Only sandy gravel, gravelly sand and muddy sand had significant influence ($p < 0.05$) with 60% of the total explained inertia.

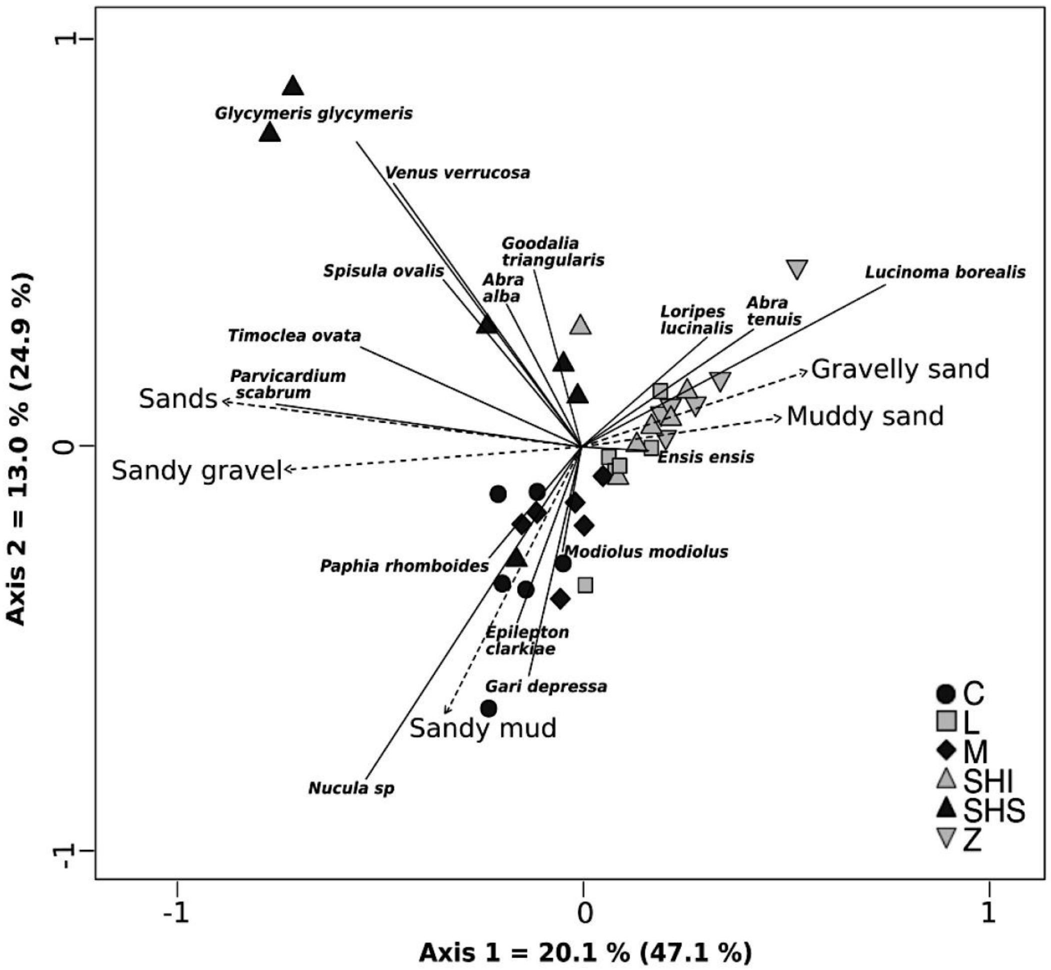
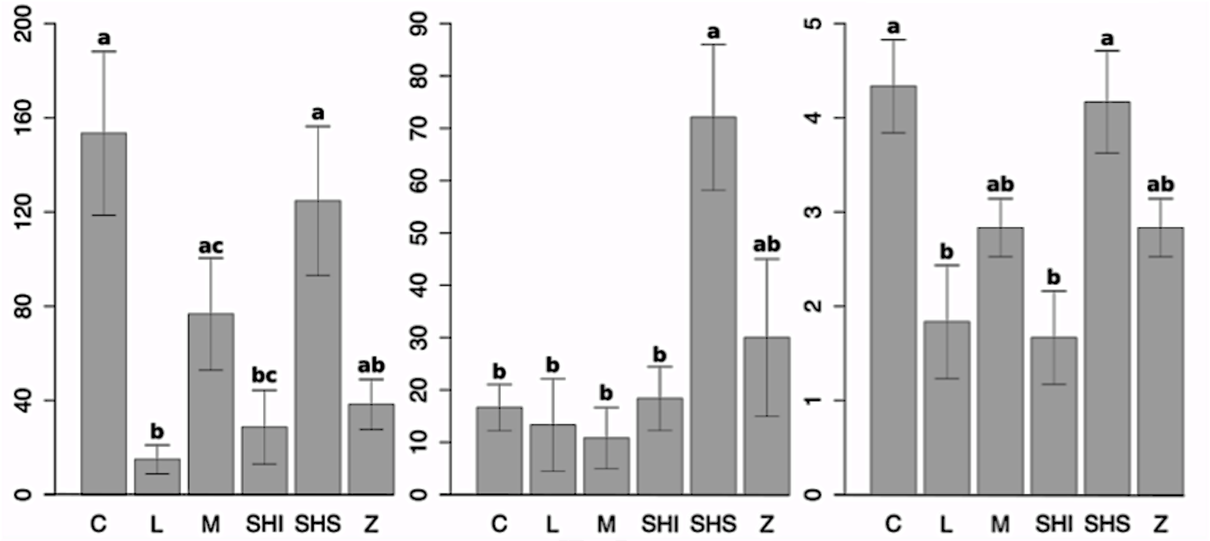


Fig. 3. Redundancy analysis (RDA) biplots of bivalve recruit abundances (plain line), in six benthic habitats, constrained to sedimentary textures variables (dotted line). Letters refers to benthic habitats (n=6): Intertidal coarse sands (SHI), Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C). Grey and black symbols represent intertidal and subtidal benthic habitats, respectively. Percentage inertia: species data and between brackets: species environment relation
2-column fitting image

Bivalves total abundance was low, ranging from 15 ± 6 ind.m^{-2} in the *Lanice* beds to 153 ± 35 ind.m^{-2} in the slipper-limpet habitat. The recruitment was significantly higher in areas colonized by *Crepidula fornicata* and in subtidal coarse sands than in the *Lanice* habitat and of the intertidal coarse sands ($p < 0.05$) (Fig. 4a). In general, the recruitment was inferior in intertidal *vs* subtidal habitats ($p < 0.002$). Abundances of individuals of rare species were significantly higher in subtidal coarse sands ($p < 0.01$) than in the other benthic habitats, with the exception of *Zostera marina* (Fig. 4b). Species richness (SR) differed strongly between three groups of habitats. Firstly, SR related to *C. fornicata* banks and subtidal coarse sands was about twice than that of *Lanice* habitat and intertidal coarse sands ($p < 0.05$; Fig. 4c). SR of maerl and *Z. marina* beds was intermediate and did not differ significantly that of other habitats (Fig. 4c).



a) Total abundance (ind.m^{-2})

b) Rare species abundance (ind.m^{-2})

c) Species richness (number of species)

Fig. 4. Boxplots of **a)** bivalve recruits total abundance (mean ± SE), **b)** abundance of rare species (mean ± SE) and **c)** species richness (mean ± SE) as a function of benthic habitats studied (n=6). Letters refers to benthic habitats: Intertidal coarse sands (SHI), Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C). Bold letters indicate significant differences ($p \leq 0.05$) between benthic habitats
2-column fitting image

3.2 Growth performances and feeding status of Ostrea edulis juveniles

Mean length (27.64 ± 0.5 mm) and thickness (4.97 ± 0.1 mm) of oyster recruits did not differ between habitat treatment ($p > 0.05$ for both). Also, dry shell (1.12 ± 0.2 g) and soft tissues (25.75 ± 1.4 mg) weights were similar between treatments ($p > 0.05$; Table 3). In contrast, significant differences between treatments were observed *(*$p < 0.05$) for shell width, ranging from 21.26 ± 0.9 mm in subtidal coarse sands to 26.21 ± 1.3 mm in *Zostera marina* habitat (Table 3). During the experimental period, the mean daily shell growth rate was equal to 0.24 ± 0.01 mm day^{-1} and was the same for all habitats. By contrast, the condition index was significantly higher in subtidal coarse sands (2.98 ± 0.5) than in *Z. marina* beds (1.94 ± 0.1) (Table 3).

	C	L	M	SHS	Z
L (mm)	26.93 ± 1.08	28.97 ± 1.04	27.32 ± 1.04	26.10 ± 1.11	28.89 ± 1.27
W (mm)	25.01 ± 1.11 **ab**	25.68 ± 0.99 **a**	24.86 ± 0.96 **ab**	21.26 ± 0.95 **b**	26.21 ± 1.30 **a**
T (mm)	4.93 ± 0.28	5.22 ± 0.34	4.70 ± 0.29	4.71 ± 0.36	5.26 ± 0.24
M_{shell} *(g)*	1.11 ± 0.32	1.37 ± 0.39	1.09 ± 0.31	0.89 ± 0.26	1.17 ± 0.34
$M_{tissues}$ *(mg)*	22.8 ± 0.00	31.4 ± 0.00	24.9 ± 0.00	23.6 ± 0.00	26.0 ± 0.00
CI	2.27 ± 0.06 **ab**	2.24 ± 0.09 **ab**	2.38 ± 0.15 **ab**	2.98 ± 0.53 **a**	1.94 ± 0.11 **b**
GR (mm/d)	0.22 ± 0.02	0.25 ± 0.02	0.24 ± 0.02	0.22 ± 0.02	0.25 ± 0.02

Table 3 Means ± SE of biometric measures for *Ostrea edulis* juveniles from each benthic habitats (n=72): Length (L), Width (W), Thickness (T), shell (M_{shell}) and soft tissues ($M_{tissues}$) dry weight, Condition Index (CI) and daily Growth Rate (GR). Letters on column labels refers to benthic habitats: Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C). Bold letters indicate significant differences (p ≤ *0.05*)
2-column fitting table

About 48 individual FAs were identified in the digestive gland of *Ostrea edulis* juveniles (Table A2). Polyunsaturated FA (PUFA) dominated (44.4 to 50.1%) the oysters digestive gland, with high proportions of saturated FAs (SFA; 30.0 to 33.1%), monounsaturated FAs (MUFA; 17.6 to 21.7%) and a low contribution of branched FAs (BFA; 1.01 to 1.09%). PERMANOVA analysis and n-MDS results show a clear segregation between FA profiles of reared oysters (control) and those of the other treatments ($p < 0.001$) (Fig. 5), which were all similar to each other ($p > 0.05$). Indeed, PERMANOVA analysis performed on the relative contribution of all FAs does not show significant differences between benthic habitats ($p > 0.05$). The PUFA 20:5ω3, 22:6ω3, 22:2ω6, 20:4ω6 and 18:4ω3, the SFA 16:0, 18:0 and 14:0 and the MUFA 20:1ω7, 18:1ω7, 16:1ω7 and 18:1ω9 were the most abundant FAs (Table 4). Subsequent SIMPER analysis revealed that 25 FAs contributed to 90% of the dissimilarities within and between FAs profiles of the groups (Table 4).

Total FAs concentration in the digestive gland ranged from 19.5 ± 0.1 to 32.5 ± 0.1 mg.g^{-1} dry weight in maerl and slipper-limpet beds, respectively (Table 4). Also, total FA concentration differed significantly between juveniles settled in both maerl beds and subtidal coarse sands from *Crepidula fornicata* areas ($p < 0.05$). In *Lanice* and *Zostera* habitats concentration were of intermediate range (Table 4). The PERMANOVA analysis performed on the concentrations of 25 FAs (Table 4) reveal significant differences only between the bivalves settled on the slipper limpet beds and all of the other habitats ($p < 0.014$). The concentration of FAs differed significantly between habitats, with higher values associated to *C. fornicata* and lower values in maerl beds, except for the 14:0, 16:1ω7, 18:1ω7, 16C and 18C PUFA that were equal between habitats (Table 4). In *L. conchilega*, *Z. marina* beds and subtidal coarse sands, FAs concentrations were in intermediate levels from *C. fornicata* banks and maerl beds (Table 4). Total SFA, MUFA, PUFA were significantly higher in *C. fornicata* than in maerl beds, and total BFA was also higher in area colonized by the slipper-limpet than in the other habitats (Table 4).

FAs concentration (mg.g-1)	**C**	**L**	**M**	**SHS**	**Z**
Saturated					
14:0	0.88 ± 0.1	0.73 ± 0.0	0.66 ± 0.1	0.89 ± 0.1	0.65 ± 0.0
15:0	0.26 ± 0.0 ^{a}	0.15 ± 0.0 ^{b}	0.14 ± 0.0 ^{b}	0.16 ± 0.0 ^{b}	0.17 ± 0.0 ^{b}
16:0	5.40 ± 0.5 ^{a}	3.91 ± 0.2 ^{ab}	3.39 ± 0.4 ^{b}	3.96 ± 0.3 ^{ab}	3.90 ± 0.2 ^{ab}
17:0	0.38 ± 0.0 ^{a}	0.26 ± 0.0 ^{b}	0.22 ± 0.0 ^{b}	0.25 ± 0.0 ^{b}	0.27 ± 0.0 ^{b}
18:0	3.25 ± 0.3 ^{a}	1.75 ± 0.1 ^{b}	1.77 ± 0.1 ^{b}	1.99 ± 0.1 ^{b}	2.13 ± 0.1 ^{b}
Σ Mean SFA	10.3 ± 0.6 ^{a}	6.89 ± 0.4 ^{ab}	6.28 ± 0.3 ^{b}	7.36 ± 0.4 ^{ab}	7.22 ± 0.4 ^{ab}
Monounsaturated					
16:1ω7	0.91 ± 0.1	0.81 ± 0.1	0.68 ± 0.1	0.87 ± 0.1	0.70 ± 0.0
18:1ω7	1.00 ± 0.1	0.76 ± 0.0	0.71 ± 0.1	0.80 ± 0.1	0.78 ± 0.0
18:1ω9	0.84 ± 0.0 ^{a}	0.61 ± 0.0 ^{ab}	0.49 ± 0.0 ^{b}	0.56 ± 0.0 ^{b}	0.63 ± 0.0 ^{ab}
20:1ω7	1.82 ± 0.1 ^{a}	1.36 ± 0.1 ^{ab}	1.05 ± 0.1 ^{b}	1.15 ± 0.0 ^{b}	1.39 ± 0.0 ^{ab}
20:1ω9	0.16 ± 0.0 ^{a}	0.10 ± 0.0 ^{b}	0.09 ± 0.0 ^{b}	0.10 ± 0.0 ^{b}	0.10 ± 0.0 ^{b}
20:1ω11	0.70 ± 0.0 ^{a}	0.49 ± 0.0 ^{ab}	0.38 ± 0.0 ^{b}	0.41 ± 0.0 ^{b}	0.50 ± 0.0 ^{ab}
Σ Mean MUFA	5.74 ± 0.1 ^{a}	4.31 ± 0.1 ^{ab}	3.58 ± 0.1 ^{b}	4.07 ± 0.1 ^{ab}	4.29 ± 0.1 ^{ab}
Polyunsaturated					
16:2ω4	0.06 ± 0.0	0.05 ± 0.0	0.04 ± 0.0	0.06 ± 0.0	0.03 ± 0.0
16:3ω4	0.01 ± 0.0	0.01 ± 0.0	0.01 ± 0.0	0.02 ± 0.0	0.01 ± 0.0
16:4ω1	0.03 ± 0.0	0.03 ± 0.0	0.02 ± 0.0	0.03 ± 0.0	0.01 ± 0.0
18:2ω3	0.05 ± 0.0	0.05 ± 0.0	0.04 ± 0.0	0.05 ± 0.0	0.04 ± 0.0
18:2ω6	0.40 ± 0.0	0.34 ± 0.0	0.27 ± 0.0	0.33 ± 0.0	0.33 ± 0.0
18:3ω3	0.45 ± 0.0	0.38 ± 0.0	0.3 ± 0.0	0.38 ± 0.0	0.34 ± 0.0
18:4ω3	0.60 ± 0.1	0.48 ± 0.0	0.41 ± 0.0	0.52 ± 0.0	0.41 ± 0.0
20:4ω6	1.58 ± 0.1 ^{a}	1.11 ± 0.0 ^{ab}	0.86 ± 0.0 ^{b}	0.94 ± 0.0 ^{b}	1.14 ± 0.0 ^{ab}
20:5ω3	5.07 ± 0.7 ^{a}	3.69 ± 0.2 ^{ab}	3.15 ± 0.4 ^{b}	3.64 ± 0.4 ^{ab}	3.65 ± 0.3 ^{ab}
22:2ω6	2.16 ± 0.2 ^{a}	1.49 ± 0.1 ^{ab}	1.15 ± 0.1 ^{b}	1.22 ± 0.1 ^{b}	1.63 ± 0.1 ^{ab}
22:2ω9	0.30 ± 0.0 ^{a}	0.17 ± 0.0 ^{b}	0.16 ± 0.0 ^{b}	0.18 ± 0.0 ^{b}	0.19 ± 0.0 ^{ab}
22:4ω6	0.33 ± 0.0 ^{a}	0.17 ± 0.0 ^{ab}	0.12 ± 0.0 ^{b}	0.14 ± 0.0 ^{ab}	0.21 ± 0.0 ^{ab}
22:5ω3	0.42 ± 0.0 ^{a}	0.29 ± 0.0 ^{ab}	0.22 ± 0.0 ^{b}	0.25 ± 0.0 ^{b}	0.29 ± 0.0 ^{ab}
22:6ω3	3.80 ± 0.4 ^{a}	2.59 ± 0.1 ^{ab}	2.14 ± 0.2 ^{b}	2.41 ± 0.2 ^{b}	2.58 ± 0.1 ^{b}
Σ Mean PUFA	16.1 ± 0.2 ^{a}	11.4 ± 0.2 ^{ab}	9.44 ± 0.1 ^{b}	10.8 ± 0.1 ^{ab}	11.4 ± 0.2 ^{ab}
Σ Mean EFA	10.4 ± 1.0 ^{a}	7.39 ± 0.7 ^{ab}	6.17 ± 0.6 ^{b}	7.00 ± 0.7 ^{ab}	7.38 ± 0.7 ^{ab}
Σ Mean BFA	0.34 ± 0.0 ^{a}	0.24 ± 0.0 ^{b}	0.20 ± 0.0 ^{b}	0.22 ± 0.0 ^{b}	0.25 ± 0.0 ^{b}
ω3	10.8 ± 0.6 ^{a}	7.83 ± 0.4 ^{ab}	6.54 ± 0.4 ^{b}	7.57 ± 0.4 ^{ab}	7.65 ± 0.4 ^{ab}
ω6	4.79 ± 0.2 ^{a}	3.34 ± 0.1 ^{ab}	2.60 ± 0.1 ^{b}	2.88 ± 0.1 ^{b}	3.53 ± 0.2 ^{ab}
ω3/ω6	2.26 ± 0.1	2.34 ± 0.1	2.51 ± 0.1	2.63 ± 0.1	2.17 ± 0.1
16:1ω7/16:0	0.17 ± 0.0	0.21 ± 0.0	0.20 ± 0.0	0.22 ± 0.0	0.18 ± 0.0
DHA/EPA	0.78 ± 0.0	0.72 ± 0.0	0.71 ± 0.0	0.68 ± 0.0	0.73 ± 0.0
Total FAs	32.5 ± 0.1 ^{a}	22.9 ± 0.1 ^{ab}	19.5 ± 0.1 ^{b}	22.4 ± 0.1 ^{b}	23.2 ± 0.1 ^{ab}

Table 4 Concentration (mg g^{-1} ± SE) of fatty acids in digestive gland of *Ostrea edulis* juveniles after 2 months growth in five benthic habitats (n=12). Letters on column labels refers to benthic habitats: Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C). Bold letters indicate significant differences ($p \leq 0.05$) for one FA between benthic habitats

2-column fitting table

Values of $\delta^{15}N$ and $\delta^{13}C$ in *O. edulis* tissues, ranged from 8.60 ± 0.09 ‰ to 8.90 ± 0.12 ‰ and -22.24 ± 0.15 ‰ to -21.64 ± 0.18 ‰, respectively (Fig. A2). No significant differences were found in $\delta^{15}N$ and $\delta^{13}C$ values according to the habitats ($p = 0.53$ and 0.56, respectively) with mean signature of $\delta^{15}N$ and $\delta^{13}C$ of 8.76 ± 0.05 ‰ and -21.84 ± 0.09 ‰, respectively. No significant differences in nitrogen and carbon contents (%) of oyster tissues were observed between habitats ($p = 0.52$ and 0.62, respectively) with mean values of 13.27 ± 0.65% and 46.98 ± 2.14%, respectively.

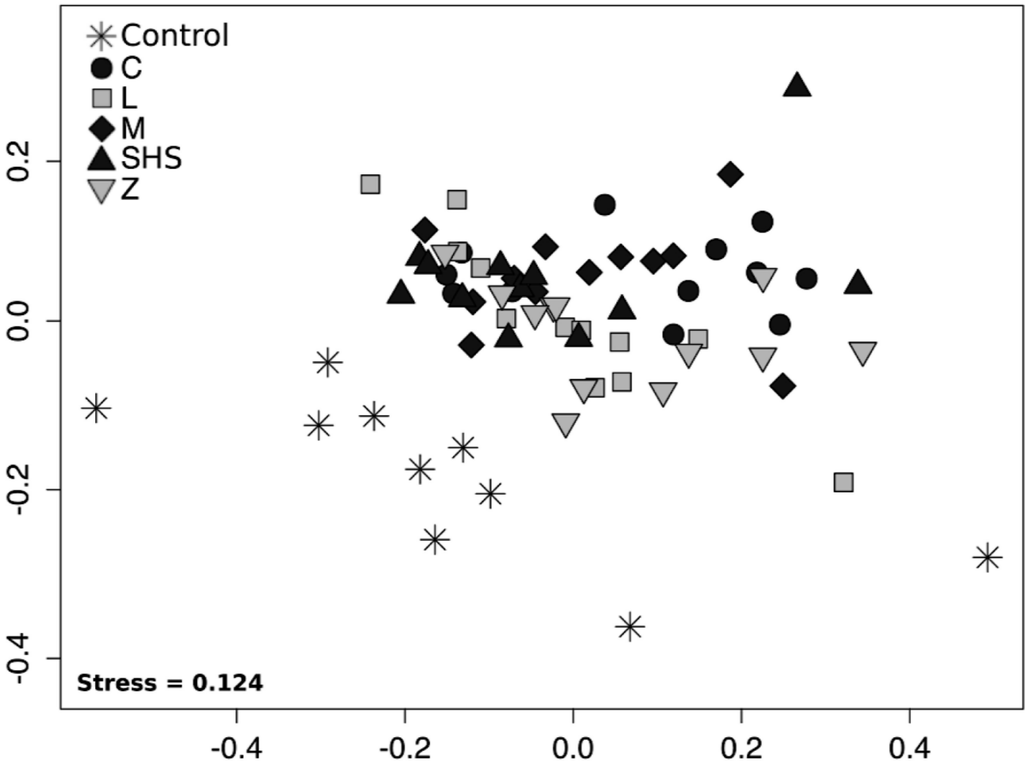


Fig. 5. n-MDS ordination plot of Bray-Curtis similarities based on FA composition of *Ostrea edulis* digestive gland after two months growth in five benthic habitats (n=12): Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *Crepidula fornicata* banks (C); and Control refers reared oysters after acclimation (n=10). Grey and black symbols represent intertidal and subtidal benthic habitats, respectively
1-column fitting image

4. Discussion

4.1 Assemblages of bivalve recruits at the end of the reproductive season

Bivalve recruit assemblages in 6 benthic habitats were investigated at the end of two succeeding reproductive seasons. During the period of this study, temporal variability in bivalve assemblages was not observed. This indicates that benthic habitats have a strong control on the bivalve recruitment in the absence of local perturbations such as localized pollution or storms, which strongly impact the structure of benthic communities at short (Negrello Filho et Lana 2013) or long-time scales (e.g. climate changes) (Novoa et al. 2016; Underwood 1999).

The abundance and diversity of bivalve recruits clearly differs between inter- and subtidal habitats. In general, intertidal habitats have fewer recruits and are less diverse than subtidal habitats. The strongest example of this can be seen between the two bathymetric levels of the coarse sands habitats, where there are nearly three times as many recruits, four times as many rare species and a doubled species richness value in the subtidal in comparison with the intertidal counterpart. Such results are in agreement with previous studies that have compared macrofaunal assemblages at intertidal and subtidal levels within a given site (Borja et al. 2009; Dörjes et al. 1986; McLusky et al. 1993; Ysebaert et al. 2003). Several environmental factors explain these differences in macrofaunal assemblages and may have an influence on post-larvae of bivalves. The main factor differing between bathymetric levels is the immersion time, which directly impacts the duration of the bivalve settlement period and aerial exposure (Ysebaert et al. 2003). In a diurnal and megatidal system such as the Chausey archipelago, immersion time drastically affects sediment properties (*e.g.* temperature, salinity and oxygen concentration) and animal behaviors (*e.g.* feeding time, burrowing). Moreover, hydrodynamic pressures, such as wave action or storm perturbations, make the intertidal zone a more stressful environment than the subtidal zone, forcing the species to live within their optimal range of distribution (Bouma et al. 2001; Dörjes et al. 1986; Karleskint et al. 2010).

Bivalve recruit assemblages from the Chausey benthic habitats can be portrayed by the sediment grain-size composition, which explains at least 60% of the species composition. This result is consistent with previous studies on the relationship between environmental factors and macrofauna community structure, which find average grain-size and particle size distribution to be the most important structuring factor for benthic invertebrates (Bloom et al. 1972; Sanders 1958). For example, juveniles of *Glycymeris glycymeris, Paphia rhomboides, Timoclea ovata* and *Venus verrucosa* recruit on *G. glycymeris* coarse sands assemblage, the natural habitat of the adults of such species (Godet et al. 2009; Trigui 2009). *V. verrucosa* was only recorded in subtidal area whereas adults were present in intertidal area (Godet 2008). This difference could be a result of secondary migration processes that did not occur at that sampling time, or to a non-adequate sampling effort in intertidal areas. Due to the lower recruit abundance in the intertidal area, more sediment cores may be required to have an accurate estimation of their abundance.

Between habitats, differences in grain-size composition can be explained by structure, often created by engineer species/ecosystem engineers. *Crepidula fornicata*, *Zostera marina*, maerl, and *Lanice conchilega* spatially structure environments through their rugosity elements (shells, leaves, rigid formation and sandy tube) and are considered as engineer species (Passarelli et al. 2013). Vertical structures provided by these species drastically affect near-bottom hydrodynamics by decreasing shear stress (Katsanevakis et al. 2014; Passarelli et al. 2014). Bottom current strength directly influences both organic and inorganic particle sedimentation, such that low current enriches near-bottom waters in fine sediment while high current enriches near-bottom waters in larger particles (Sanders 1958). Silted slipper limpet's banks of Chausey are typically old colonies, characterized by dense populations, promoting sediment trapping (Blanchard 1997; Herhold et al. 1998) and explaining the high abundances of species that are typically recruited on muddy sediments, like deposit-feeders (De Montaudouin et Sauriau 1999), such as *Abra alba*, *Abra tenuis* and *Nucula sp*., (Creutzberg 1986; Hughes 1973). Moreover, Bouma et al. (2001) showed that environments characterized by high hydrosedimentary dynamics directly control the spatial distribution of bivalve recruits by promoting their passive resuspension.

The presence of engineer species, both living and non-living, effects the structure of macrofaunic assemblages by increasing both the total abundance and species richness (De Montaudouin et Sauriau 1999; Godet et al. 2008; Grall et al. 2006; Jackson et al. 2004; van der Heide et al. 2012; Wilson et al. 2004). Biogenic structures provide physical complexity that create suitable habitats for numerous taxa (De Montaudouin et Sauriau 1999) and diversify carbon sources (Grall et al. 2006; Wilson et al. 2004). This enhances biodiversity by improving species richness and abundance relative to the surrounding environment (Blanchard 1997; De Montaudouin et Sauriau 1999). With respect to bivalve recruits, *Crepidula fornicata* banks provide the highest species richness and abundance, highlighting a novel and positive influence of this habitat on bivalve recruitment dynamics. Thus, structured habitats, directly and indirectly, influence the abundance and diversity of bivalve recruit assemblages by promoting fine particle sedimentation and post-larval establishment success.

In *Lanice conchilega* beds, both adults and recruits of the typical bivalve species are present (Godet 2008), but ecosystem engineers were not found to have a positive influence on the bivalve recruitment in this habitat. When the density of sandy tubes exceeds a threshold value, they induce a "skimming flow" at the benthic boundary layer; this effect diverts the main water flow above structures and decreases flow velocity and turbulence levels through these structures (Nowell et Jumars 1984). Experiments conducted with artificial *Lanice* like tubes show the effect of a "skimming flow" in *L. conchilega* beds when densities exceed 2000 tubes.m^{-2} (Friedrichs et al. 2000). This flow facilitates fine particle deposition, increases sediment stability, and increases organic matter content by stimulating the microphytobenthic compartment (Friedrichs et al. 2000; Passarelli et al. 2013). Surprisingly, the *Lanice* habitat was characterized by the smallest total species abundance and among the lowest in terms of species richness of bivalve recruits. Such results suggest the density of *L. conchilega* is below the threshold density required for such beneficial effects on the associated fauna. Moreover, the population dynamics of this ecosystem engineer are strongly influenced by shellfish farming. In Chausey, manila clam cultivation decreases *Lanice* density, from 460 ind.m^{-2} in non-impacted areas to less than 70 ind.m^{-2} one year after seeding (Toupoint et al. 2008). Thus, the shellfish industry may prohibit the positive engineering effect of "skimming flow" by reducing *Lanice* densities (Friedrichs et al. 2000; Passarelli et al. 2013).

In *Zostera marina* beds, whose sediment usually contains a high concentration of toxic sulfides (van der Heide et al. 2012), *Lucinoma borealis* and *Loripes lucinalis* recruits are present in high abundances. In fact, *Lucinidae* may dominate the infauna of these anoxic substrata due to their mixotrophic diet. *Lucinidae* can shift their feeding behavior from heterotrophic deposit feeding on POM to chemotrophic nutrition via their sulfide-oxidizing endosymbionts, which provide carbon metabolites from sulfate (van der Geest et al. 2014; van der Heide et al. 2012). Considering that recruits of these bivalve species are well adapted to anoxic conditions, sulfides may act as chemical cues at young bivalve stages (Hadfield et Paul 2001), by promoting the preferential selection of this habitat. For its part, maerl habitat displays similar photosynthetic and respiratory metabolisms as the *Z. marina* habitat (Martin et al. 2005). *Nucula* sp. dominated bivalve recruit assemblages of maerl beds, thus confirming previous studies of Bosence (1979) and Jackson et al. (2004) on bivalve species associated to maerl assemblages (Carlier et al. 2007; Creutzberg 1986).

Results highlight the prevailing homogeneity in such structured habitats. In fact, more than 43% similarity in recruit assemblages was found in ecosystem engineer habitats in comparison with flat bottom habitats, which showed a maximum similarity of 27%. Habitat-modifying species are known to increase heterogeneity of the environment, by transforming the flat and two-dimensional landscape to complex, three-dimensional structures (Bruno and Bertness 2001). However, at the habitat scale, highly complex structures generated by ecosystem engineers provide an environmental stability. This stability is obtained by the reduction of multiple stresses, like the flow velocity or hydro-sedimentary disturbances (Bruno et Bertness 2001), and permits the stable establishment of similar communities within specific habitats. For example, Barnes and Hendy (2015) compared three macrofaunal assemblages of intertidal seagrass meadows from northeast Atlantic, southwest Indian and southwest Pacific oceans and found taxa and functional group compositions to be closely similar.

Our results show that subtidal *Glycymeris glycymeris* coarse sands and *Crepidula fornicata* banks are two distinct habitats, according to their spatial configurations (*i.e.* in two- and three-dimensions), sedimentary compositions, and recruits assemblages. However, both of these habitats provide a suitable environment for early stage bivalve recruitment in a highly hydrodynamic coastal temperate area. Globally, bivalve recruitment is intensified and diversified in structured habitats, while recruit assemblages are specific to particular habitats, according to hydro-sedimentary characteristics. These unique assemblages likely result from habitat selection processes (Hadfield et Paul 2001), such as delay of metamorphosis or secondary migrations (bysso-pelagic drifting; Toupoint 2012), as well as differential mortalities of bivalve perimetamorphic stages. More studies are needed to quantify the importance of each process in the composition of bivalve assemblages.

4.2 Growth performances and feeding status of Ostrea edulis juveniles

The flat oyster, *Ostrea edulis*, is a native European oyster and largely widespread along French coasts. This fast-growing bivalve (Laing et Millican 1986; Utting 1988) is able to colonize a large number of habitats in shallow coastal waters (Launey et al. 2002; McKenzie et al. 1997), and was therefore selected as a model species to assess the role of benthic habitats on bivalve feeding related to recruitment success.

No clear evidence was found on differential growth performances between oysters implanted in the benthic habitats during this study, and no difference in shell growth and tissue weight was observed after two months of immersion. However, significant differences were observed in the CI, which represents a differential energy allocation between the shell and tissue growth. This observation suggests local variability in the feeding conditions encountered by oysters between habitats. The temperature and the quality and quantity of trophic resources are the main factors conditioning the *Ostrea edulis* growths (Berntsson et al 1997; Laing et Millican 1986; Nerot et al. 2012; Richardson et al. 1980; Utting 1988). While a lack of growth differences could originate from use of plastic bags, this set up is similar to the one used by professional shellfish farmers, who have not detected growth limitation; moreover, any potential impact should effect both sites in a similar manner. Consequently, the benthic habitats of Chausey seem to provide similar trophic environments. Fatty acid profiles of *O. edulis* sampled at the end of the experiment did not differ between the 5 tested habitats. At the archipelago scale, FA biomarkers (Dalsgaard et al. 2003; Kelly et Scheibling 2012; Meziane et al. 1997) show a predominant microalgal diet, as shown by the abundance of specific markers of diatoms (16:1ω7 and 20:5ω3) and dinoflagellates (18:4ω3 and 22:6ω3; Dalsgaard et al. 2003; Kelly et Scheibling 2012). This result corroborates those of Perez et al. (2012) who found that the diet of *Venus verrucosa,* a filter-feeder like *O. edulis* (Bremner et al. 2003), does not differ at the archipelago scale. Moreover, isotopic data reveal that oysters from different habitats are of equal trophic level. No significant differences were found in carbon isotope signatures between juveniles, which supports the hypothesis that their diet is comprised on the same carbon sources. However, while all oysters feed on similar food sources, the CI values show that food availability varies across habitats. Significant differences in FA concentrations in the digestive glands of oysters recovered from the different habitats were also in accordance with this observation. At the end of the experiment, oysters from *Crepidula fornicata* banks are fatter, and of the majority of FAs classes, compared to maerl beds and *Glycymeris glycymeris* coarse sands habitat. The discrepancy in FA quantity can be explained by different intensities of hydro-sedimentary stresses occurring between habitats, especially when habitats contain complex structures (Gonzales-Ortiz et al. 2014). Among stresses, the benthic boundary layer flows can determine bivalve food access. Nevertheless, this effect is short-term in scale, as fatty acid concentration differences in the digestive glands at the end of the experiment were not related to growth differences. Likewise, Fréchette et al. (1989) explain that the diffusion of phytoplankton is an important mechanism controlling energy flow for benthic suspension feeders. Bivalve filtration can be inhibited when currents are too weak or too strong, limiting the rates of food assimilation (Kamermans 1994; Newell et al. 2001; Wildish et al. 1992; Wildish et Kristmanson 1985; Wildish et Saulnier 1992). Additionally, sediment instability may force bivalves to bury several times into the sediment, which would constitute a major energetic loss (St-Onge et al. 2007; Urban 1994).

FAs have both important structural and functional roles in cells. PUFAs play a key role in building cell membranes and assist cells in responding to external stimuli, and the oxidation of FAs provides an important source of energy (Dalsgaard et al. 2003; Lee et Patton 1989; Sargent et al, 1993; Sargent et Whittle 1981). Nevertheless, in contrast with previous studies, we do not find that high densities of *Crepidula fornicata* negatively affect the survival and fitness of bivalve adults, such as *Crassostrea gigas* and *Mytilus edulis* (see review in Thieltges et al. 2006).

Our study clearly suggests that benthic habitats associated with ecosystem engineering species have a more important role in the bivalve juvenile survival than flat habitats. Additional studies are needed to compare these results with other bivalve models and to test additional factors influencing early-stage recruit survival, such as the vulnerability of recruits to pathogens or inter-specific relationships within a highly fragmented habitat.

5. Conclusion

For the first time in megatidal temperate coastal waters, the nursery function of benthic habitats was studied in terms of bivalve population renewal, by investigating two steps of their recruitment cycle. *Crepidula fornicata* banks appear to be a favorable habitat for bivalve recruitment, with regards to the early-recruitment intensity (recruit abundance and diversity) and the feeding quality (fatty acids contents of digestive gland) of juveniles. Amongst other habitats, each of them provides some advantages for benthic recruitment, namely sustaining more diversified and abundant assemblages or greater juveniles physiological quality. Overall, the “reproductive and nursery area” habitat function is higher in the subtidal zone than in the intertidal zone. Habitats comprised of ecosystem engineers, who govern hydrodynamic properties, play a structural role in bivalve recruit assemblages and juvenile survival. However, more studies are needed to compare this function between different habitats and with other species models. Thus, to preserve the goods and services provided by bivalve populations, management perspectives must consider bivalve recruitment as an essential component of the “reproductive and nursery areas” function of benthic habitats. Moreover, the influence of anthropogenic pressure and climate change in coastal zones is increasing, with cascading effects on the goods and services of related ecosystems (Barbier et al. 2008). Additional studies are needed to determine the combined effects of these two stressors at different spatial scales. For example, Hughes et al. (2015) demonstrate how climate change (*i.e.* precipitation) increases anthropogenic nutrient loading within nursery habitats of estuaries, which ultimately decreased offshore flatfish production. Finally, results from our study should be integrated into ecosystem-based management models to predict variations of ecological functions and their associated economic values, in order to facilitate community-based conservation decisions (Barbier et al. 2008; Hughes et al. 2015; Sinclair et Byrom 2006).

6. Glossary

BFA: Branched Fatty Acids are mostly saturated fatty acids with one or more methyl branches on the carbon chain and they are found in two distinct families: the iso-series and anteiso-series

EUNIS: European Union Nature Information System

FA: Fatty Acids are lipidic components

MUFA: MonoUnsaturated Fatty Acids have one double bond in the fatty acid chain

PUFA : PolyUnsaturated Fatty Acids have more than one double bond in the fatty acid chain

SFA: Saturated Fatty Acids have no double bond in the fatty acid chain

7. Appendix

	C	L	M	SHI	SHS	Z
Abra alba	2.50 ± 1.71	2.50 ± 2.50	0 ± 0.00	0 ± 0.00	5.83 ± 4.9	3.33 ± 1.67
Abra tenuis	1.67 ± 1.05	0.83 ± 0.83	0 ± 0.00	5.74 ± 2.12	0.83 ± 0.83	4.17 ± 2.01
Ensis ensis	0 ± 0.00	1.67 ± 1.67	0 ± 0.00	1.15 ± 1.15	0 ± 0.00	0 ± 0.00
Epilepton clarkiae	0.83 ± 0.83	0 ± 0.00	0 ± 0.00	0 ± 0.00	0 ± 0.00	0 ± 0.00
Gari depressa	1.67 ± 1.05	0.83 ± 0.83	0 ± 0.00	0 ± 0.00	0 ± 0.00	0 ± 0.00
Glycymeris glycymeris	0 ± 0.00	0 ± 0.00	2.92 ± 1.36	2.30 ± 2.30	16.39 ± 7.22	0 ± 0.00
Goodalia triangularis	1.67 ± 1.67	4.17 ± 2.01	0 ± 0.00	13.78 ± 13.78	15.19 ± 11.49	0 ± 0.00
Loripes lucinalis	0 ± 0.00	0 ± 0.00	0 ± 0.00	0 ± 0.00	0 ± 0.00	7.5 ± 5.59
Lucinoma borealis	0.83 ± 0.83	4.17 ± 2.39	0 ± 0.00	4.59 ± 3.41	0 ± 0.00	21.67 ± 5.27
Modiolus modiolus	0 ± 0.00	0 ± 0.00	0.83 ± 0.83	0 ± 0.00	0 ± 0.00	0 ± 0.00
Nucula sp	115.83 ± 37.91	0 ± 0.00	62.92 ± 20.78	0 ± 0.00	35.47 ± 16.55	1.67 ± 1.05
Paphia rhomboides	0.83 ± 0.83	0.83 ± 0.83	1.67 ± 1.05	0 ± 0.00	0.83 ± 0.83	0 ± 0.00
Parvicardium scabrum	19.17 ± 4.55	0 ± 0.00	6.25 ± 3.97	1.15 ± 1.15	24.89 ± 10.31	0 ± 0.00
Spisula ovalis	0.83 ± 0.83	0 ± 0.00	0 ± 0.00	0 ± 0.00	8.33 ± 8.33	0 ± 0.00
Timoclea ovata	7.50 ± 3.82	0 ± 0.00	2.08 ± 1.36	0 ± 0.00	13.08 ± 8.27	0 ± 0.00
Venus verrucosa	0 ± 0.00	0 ± 0.00	0 ± 0.00	0 ± 0.00	3.8 ± 2.43	0 ± 0.00

Table A1 Means ± SE of bivalve recruits abundances (ind.m^{-2}) from each benthic habitats (n=6), compiled from the two sampling years. Letters on column labels refers to benthic habitats: Intertidal coarse sands (SHI), Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C)
2-column fitting table

FAs relative contribution (%)	Control	C	L	M	SHS	Z
Saturated						
12:0	0.04 ± 1.3	0.10 ± 0.0	0.01 ± 0.0	0.09 ± 0.0	0.06 ± 0.0	0.06 ± 0.0
13:0	0.02 ± 0.0	0.02 ± 0.0	0.02 ± 0.0	0.03 ± 0.0	0.04 ± 0.0	0.01 ± 0.0
14:0	3.77 ± 0.0	2.70 ± 0.3	3.13 ± 0.3	3.12 ± 0.2	3.87 ± 0.3	2.76 ± 0.2
15:0	0.71 ± 0.0	0.84 ± 0.0	0.67 ± 0.0	0.76 ± 0.0	0.75 ± 0.0	0.78 ± 0.0
16:0	18.3 ± 0.2	16.7 ± 0.2	17.0 ± 0.3	17.3 ± 0.3	17.9 ± 0.7	16.7 ± 0.2
17:0	1.29 ± 0.0	1.20 ± 0.0	1.16 ± 0.0	1.17 ± 0.0	1.16 ± 0.0	1.17 ± 0.0
18:0	8.36 ± 0.0	10.1 ± 0.7	7.73 ± 0.4	9.42 ± 0.4	9.04 ± 0.7	9.37 ± 0.7
19:0	0.19 ± 1.1	0.20 ± 0.0	0.14 ± 0.0	0.18 ± 0.0	0.17 ± 0.0	0.18 ± 0.0
20:0	0.05 ± 0.1	0.11 ± 0.0	0.08 ± 0.0	0.11 ± 0.0	0.12 ± 0.0	0.09 ± 0.0
Σ Mean SFA	32.8 ± 2.0	32.0 ± 1.9	30.0 ± 1.9	32.2 ± 1.9	33.1 ± 2.0	31.2 ± 1.9
Branched						
15:0iso	0.13 ± 1.2	0.15 ± 0.0	0.14 ± 0.0	0.15 ± 0.0	0.16 ± 0.0	0.16 ± 0.0
15:0anteiso	0.02 ± 0.0	0.04 ± 0.0	0.03 ± 0.0	0.04 ± 0.0	0.04 ± 0.0	0.04 ± 0.0
16:0iso	0.24 ± 5.6	0.20 ± 0.0	0.17 ± 0.0	0.19 ± 0.0	0.17 ± 0.0	0.19 ± 0.0
17:0iso	0.44 ± 0.0	0.44 ± 0.0	0.45 ± 0.0	0.43 ± 0.0	0.41 ± 0.0	0.45 ± 0.0
17:0anteiso	0.12 ± 0.0	0.16 ± 0.0	0.19 ± 0.0	0.16 ± 0.0	0.16 ± 0.0	0.17 ± 0.0
18:0iso	0.04 ± 0.0	0.08 ± 0.0	0.06 ± 0.0	0.09 ± 0.0	0.06 ± 0.0	0.05 ± 0.0
Σ Mean BFA	1.01 ± 0.0	1.09 ± 0.0	1.06 ± 0.0	1.08 ± 0.0	1.03 ± 0.0	1.09 ± 0.0
Monounsaturated						
14:1	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
16:1ω5	0.12 ± 0.3	0.15 ± 0.0	0.17 ± 0.0	0.20 ± 0.0	0.19 ± 0.0	0.16 ± 0.0
16:1ω7	4.18 ± 2.8	2.79 ± 0.3	3.46 ± 0.3	3.23 ± 0.2	3.75 ± 0.3	2.97 ± 0.2
16:1ω9	0.20 ± 0.0	0.26 ± 0.0	0.17 ± 0.0	0.13 ± 0.0	0.19 ± 0.0	0.13 ± 0.0
17:1ω7	0.51 ± 0.1	0.32 ± 0.0	0.19 ± 0.0	0.25 ± 0.0	0.22 ± 0.0	0.18 ± 0.0
18:1ω5	0.14 ± 0.3	0.15 ± 0.0	0.13 ± 0.0	0.16 ± 0.0	0.15 ± 0.0	0.14 ± 0.0
18:1ω7	4.98 ± 0.0	3.05 ± 0.1	3.29 ± 0.1	3.47 ± 0.1	3.48 ± 0.2	3.35 ± 0.1
18:1ω9	3.12 ± 0.0	2.60 ± 0.1	2.67 ± 0.1	2.58 ± 0.1	2.50 ± 0.0	2.73 ± 0.1
20:1ω7	6.62 ± 1.6	5.63 ± 0.2	5.96 ± 0.2	5.55 ± 0.1	5.18 ± 0.1	6.07 ± 0.2
20:1ω9	0.43 ± 0.1	0.50 ± 0.0	0.46 ± 0.0	0.50 ± 0.0	0.47 ± 0.0	0.46 ± 0.0
20:1ω11	1.34 ± 0.7	2.16 ± 0.1	2.17 ± 0.1	2.04 ± 0.0	1.87 ± 0.1	2.21 ± 0.1
Σ Mean MUFA	21.7 ± 0.7	17.6 ± 0.5	18.7 ± 0.5	18.1 ± 0.5	18.0 ± 0.5	18.4 ± 0.5
Polyunsaturated						
16:2ω4	0.63 ± 0.0	0.18 ± 0.0	0.21 ± 0.0	0.20 ± 0.0	0.27 ± 0.0	0.14 ± 0.0
16:2ω6	0.07 ± 0.0	0.06 ± 0.0	0.05 ± 0.0	0.04 ± 0.0	0.07 ± 0.0	0.03 ± 0.0
16:3ω4	0.45 ± 0.1	0.05 ± 0.0	0.07 ± 0.0	0.06 ± 0.0	0.08 ± 0.0	0.04 ± 0.0
16:4ω1	0.58 ± 0.0	0.10 ± 0.0	0.12 ± 0.0	0.12 ± 0.0	0.16 ± 0.0	0.07 ± 0.0
18:2ω3	0.81 ± 0.0	0.16 ± 0.0	0.23 ± 0.0	0.20 ± 0.0	0.21 ± 0.0	0.18 ± 0.0
18:2ω6	1.27 ± 1.1	1.24 ± 0.0	1.48 ± 0.0	1.36 ± 0.0	1.46 ± 0.0	1.39 ± 0.0
18:3ω3	1.33 ± 0.0	1.37 ± 0.1	1.68 ± 0.1	1.48 ± 0.0	1.66 ± 0.1	1.44 ± 0.1
18:3ω6	0.19 ± 0.0	0.16 ± 0.0	0.19 ± 0.0	0.18 ± 0.0	0.20 ± 0.0	0.16 ± 0.0
18:4ω3	4.79 ± 0.0	1.80 ± 0.2	2.06 ± 0.1	1.96 ± 0.1	2.22 ± 0.1	1.71 ± 0.1
20:2ω7	0.05 ± 5.0	0.06 ± 0.0	0.03 ± 0.0	0.09 ± 0.0	0.11 ± 0.1	0.00 ± 0.0
20:2ω9	0.11 ± 0.5	0.11 ± 0.0	0.09 ± 0.0	0.10 ± 0.0	0.08 ± 0.0	0.09 ± 0.0
20:3ω6	0.14 ± 5.7	0.20 ± 0.0	0.21 ± 0.0	0.18 ± 0.0	0.21 ± 0.0	0.18 ± 0.0
20:4ω3	0.52 ± 0.0	0.32 ± 0.0	0.43 ± 0.0	0.36 ± 0.0	0.42 ± 0.0	0.36 ± 0.0
20:4ω6	1.60 ± 0.0	4.88 ± 0.1	4.86 ± 0.2	4.57 ± 0.2	4.23 ± 0.2	4.97 ± 0.1
20:5ω3	13.7 ± 0.0	15.3 ± 0.7	16.1 ± 0.6	15.9 ± 0.4	15.9 ± 0.7	15.6 ± 0.9
21:5ω3	1.03 ± 0.0	0.95 ± 0.0	0.97 ± 0.0	0.95 ± 0.0	0.93 ± 0.0	0.98 ± 0.0
22:2ω6	6.61 ± 0.0	6.70 ± 0.4	6.54 ± 0.5	6.21 ± 0.4	5.52 ± 0.4	7.11 ± 0.4
22:2ω9	0.64 ± 0.0	0.92 ± 0.0	0.77 ± 0.0	0.92 ± 0.0	0.81 ± 0.0	0.83 ± 0.0
22:4ω6	3.12 ± 0.4	1.02 ± 0.1	0.80 ± 0.1	0.65 ± 0.0	0.67 ± 0.0	0.92 ± 0.1
22:5ω3	0.76 ± 0.5	1.31 ± 0.0	1.29 ± 0.0	1.19 ± 0.0	1.10 ± 0.0	1.29 ± 0.0
22:5ω6	0.42 ± 0.0	0.51 ± 0.0	0.52 ± 0.0	0.45 ± 0.0	0.51 ± 0.0	0.51 ± 0.0
22:6ω3	5.49 ± 0.7	11.6 ± 0.2	11.3 ± 0.2	11.1 ± 0.3	10.7 ± 0.5	11.1 ± 0.4
Σ Mean PUFA	44.4 ± 0.6	49.1 ± 0.8	50.1 ± 0.8	48.4 ± 0.8	47.7 ± 0.8	49.2 ± 0.8
Σ Mean EFA	20.8 ± 3.5	31.8 ± 3.0	32.3 ± 3.2	31.6 ± 3.2	30.9 ± 3.3	31.7 ± 3.0
ω3	28.5 ± 1.6	32.9 ± 2.0	34.1 ± 2.1	33.2 ± 2.1	33.2 ± 2.0	32.7 ± 2.0
ω6	13.4 ± 0.7	14.8 ± 0.8	14.6 ± 0.8	13.6 ± 0.8	12.9 ± 0.7	15.3 ± 0.9
ω3/ω6	2.46 ± 0.4	2.30 ± 0.2	2.43 ± 0.2	2.49 ± 0.1	2.64 ± 0.2	2.21 ± 0.2
16:1ω7/16:0	0.23 ± 0.0	0.17 ± 0.0	0.20 ± 0.0	0.19 ± 0.0	0.21 ± 0.0	0.18 ± 0.0
DHA/EPA	0.41 ± 0.0	0.78 ± 0.0	0.72 ± 0.0	0.71 ± 0.0	0.68 ± 0.0	0.73 ± 0.0

Table A2 Relative contribution (%) of fatty acids in digestive gland of *Ostrea edulis* juveniles after 2 months growth in five benthic habitats (n=12). Letters on column labels refers to benthic habitats: Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C); and Control refers to reared oysters after acclimation (n=10)

2-column fitting table

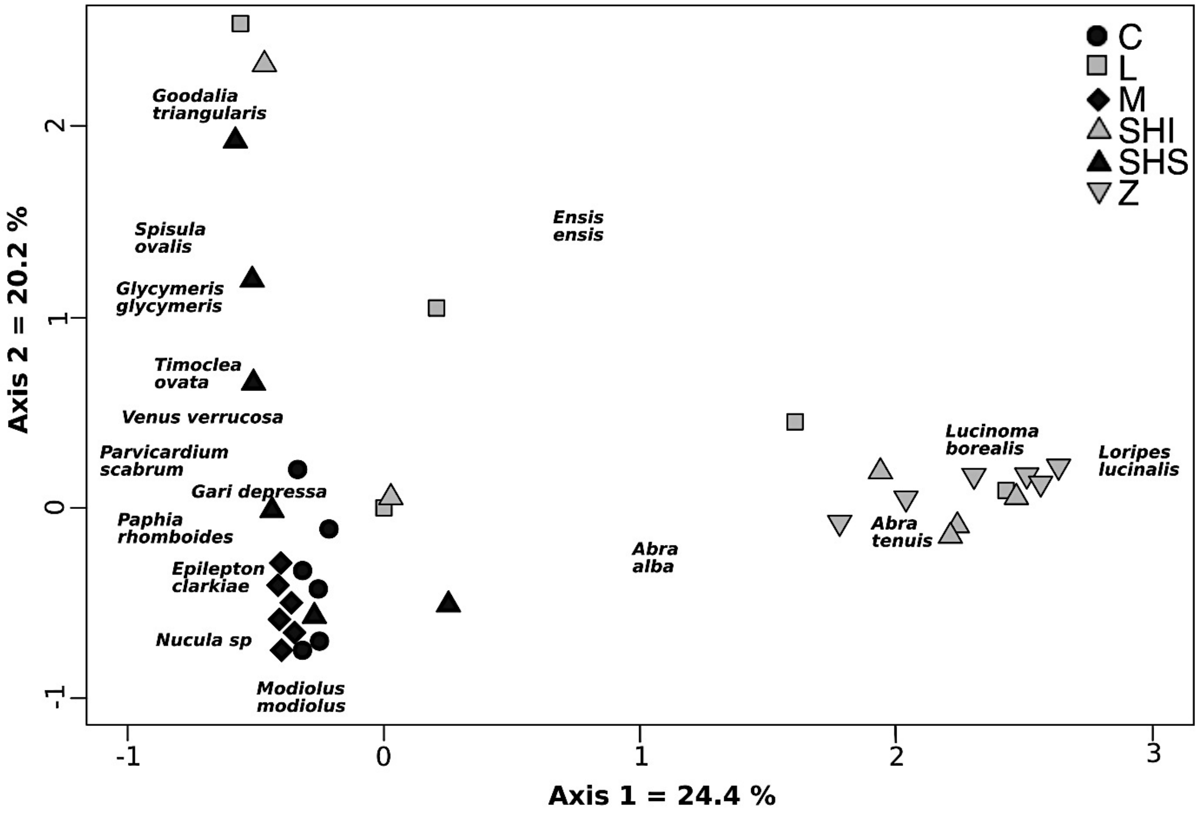


Fig. A1. Biplot of the first two factorial axes form factorial correspondence analysis (FCA) resulting of bivalve recruits sorting (n=6). Letters refer to benthic habitats: Intertidal coarse sands (SHI), Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C). Grey and black symbols represent intertidal and subtidal benthic habitats, respectively
2-column fitting image

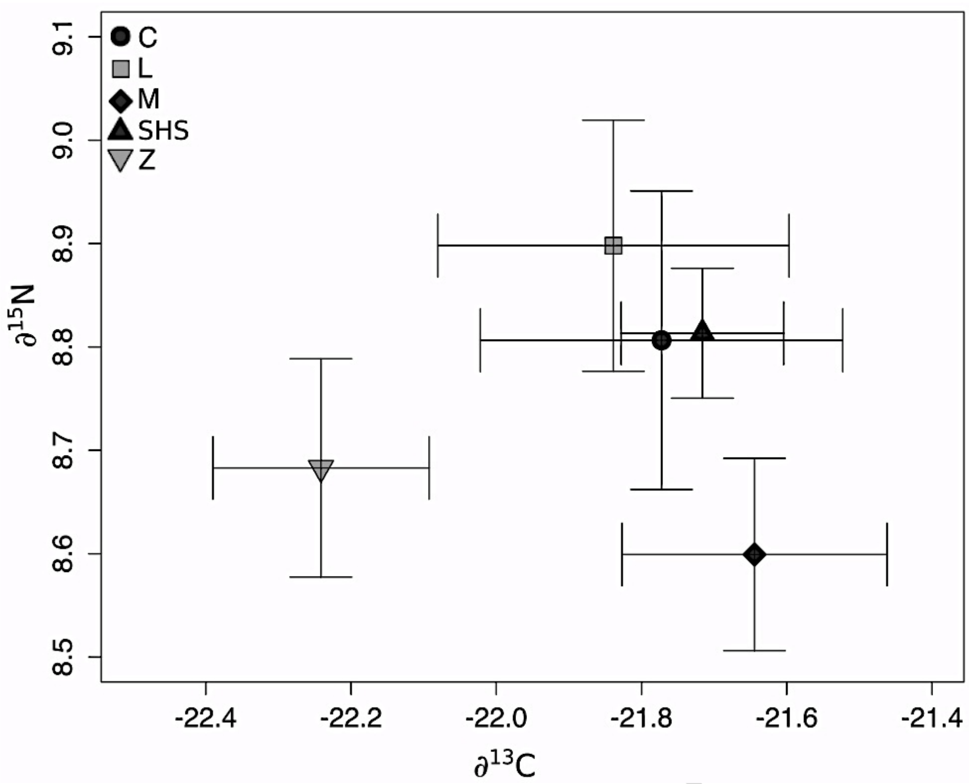


Fig. A2. Carbon and nitrogen isotopic signatures (mean ± SE) from *Ostrea edulis* tissues after two months growth in five benthic habitats (n=12). Letters refers to benthic habitats: Subtidal coarse sands (SHS), *L. conchilega* beds (L), *Z. marina* beds (Z), Maerl beds (M), *C. fornicata* banks (C)
1-column fitting image

8. Acknoledgements

Part of the HEIMa (Habitats, species and marine interactions) action program, this research was sustained by the Conservatoire de l’Espace Littoral (CEL) and the Syndicat Mixte des Espaces Littoraux de la Manche (SyMEL), and funded by the Agence de l’Eau Seine Normandie (AESN), the Fondation Total and the Direction régionale de l'environnement, de l'aménagement et du logement (DREAL) de Basse-Normandie. Integrated within the DRIVER workpackage (Determinism of bivalves recruitment under environmental and anthropic constraints), the present study was supported by the Ressources Aquatiques du Québec (RAQ) network. We thank the Centre de Recherche et d'Enseignement sur les Systèmes Côtiers (CRESCO, MNHN, Dinard, France), the experimental station of Argenton (IFREMER, France with special regards to Christian Mingant for oyster rearing), the Comité Régional des Pêches Maritimes et des Elevages Marins de Basse-Normandie, and the professional fisherman Patrick Delacour, for all the technical and logistic supports. We address special thanks to Nicolas Toupoint, the littoral guards Pierre Scolan and Arnaud Guigny and project managers (SyMEL, France) for their help with sampling. This work was performed in the framework of the International Laboratory BeBEST funded by the Institut des Sciences de la Mer de Rimouski (UQAR, Quebec) and the Institut Environnement Ecologie (CNRS, France).

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Highlights

- The “nursery” function of 6 benthic habitats was investigated for wild bivalve populations.
- *C. fornicata* banks and *G. glycymeris* coarse sands habitats exhibit the most abundant and diversified assemblages of bivalve recruits.
- The digestive glands of experimental flat oyster spat have higher fatty acid contents when settled on *C. fornicata* banks.
- Engineers species associated habitats constitute better nursery areas for bivalve species than unstructured ones.