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Biogenic reefs affect multiple components of intertidal soft-bottom benthic assemblages: the *Lanice conchilega* case study

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ABSTRACT

Biogenic reefs composed of the tube-building polychaete *Lanice conchilega* are important from a conservation point of view because they noticeably increase the biodiversity in otherwise species poor environments. However, up to now, little or no attention has been paid to the intertidal epi- and hyperbenthic communities associated with the reefs. Therefore, this is the first study which focuses on the effect of *L. conchilega* reefs on the entire bentho-pelagic community at two different locations. Environmental variables were measured and macro-, epi- and hyperbenthic communities were sampled within a *L. conchilega* reef and a control area at two locations in France: the bay of the Mont Saint-Michel (BMSM) and Boulogne-sur-Mer (Boulogne). The effect of the reef presence on the benthic community was studied with a 3-factor (Reef, Location and Period) Permanova. In addition, the relationship between the benthic community and the environmental variables was investigated using Distance-based linear models (DistLM). Most collected organisms were sampled in the reef area (macrobenthos: 91%, epibenthos: 81% and hyperbenthos: 78.5%) indicating that, independent of the location, the *L. conchilega* reefs positively affect all three associated benthic communities. However, the extent of the effect seems to be most pronounced for the macrobenthos and less distinct in case of the hyperbenthos. The macro-, and epibenthos are mainly structured by biotic variables (*L. conchilega* density and macrobenthic food availability respectively), while the hyperbenthos is rather structured by environmental variables. In general, *L. conchilega* reefs do not only affect abundances and diversity but they substantially steer the structure of the intertidal benthic sandy beach ecosystem.

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1. Introduction

Numerous organisms are widely known to modify their environments and influence other species. Recently, there has been a growing interest in biota that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials, so-called ecosystem engineers (Jones et al., 1994). Typically, ecosystem engineers are classified as either *autogenic* (changing the environment via their own physical structures; e.g. corals) or *allogenic* (changing the environment by transforming living or non-living materials from one physical state to another; e.g. woodpeckers, beavers) (Jones et al., 1994). In the marine environment, ecosystem engineers are known to strongly modify coastal sediments in temperate, tropical and semi-tropical locations (Kirtley and Tanner, 1968; Micheletti-Flores and Negreiros-Fransozo, 1999; Bouma et al., 2009a) and possibly create persistent emergent structures referred to as 'biogenic reefs' (Carey, 1987; Rabaut et al., 2009; Callaway et al., 2010; Godet et al., 2011). Seagrass fields (e.g. Bouma et al., 2009b), bivalve accumulations (e.g. Gutiérrez et al., 2003) and polychaete tube assemblages (e.g. Dubois et al., 2002; Chapman et al., 2012) are some of the most striking

biogenic structures composed of ecosystem engineers in coastal environments. A prime example is the aggregations composed of the Sandmason *Lanice conchilega* (Polychaeta, Terebellidae). This species may achieve densities of several thousands of individuals m^{-2} (Van Hoey et al., 2006) and as such generate elevated sediment reefs (Rabaut et al., 2009). *L. conchilega* displays both autogenic (e.g. by providing oxygen supply) and allogenic (by sedimentological and biological alterations) ecosystem engineering properties (Godet et al., 2008; Rabaut et al., 2009) and is therefore bound to receive a higher ecosystem engineer qualification (Braeckman et al., 2014). Hence, this species is considered an ideal model organism for studying the sediment-animal-interactions in a modified habitat (Reise et al., 2009). The habitat modifications of this ecosystem engineer result in an increased habitat complexity and heterogeneity, facilitating the evolution of a more diverse and abundant macrobenthic community (Rabaut et al., 2007; Toupoint et al., 2008).

Biogenic reefs, including *Lanice conchilega* reefs, are listed as Habitat 1170 under Annex I of the EC Habitats Directive EEC/92/43, and are hence important from a conservation point of view (Godet et al., 2008; Rabaut et al., 2009). Nevertheless, research on the structural and functional role of biogenic reefs, and ecosystem engineers in general, mostly focuses on one single ecosystem component at a time (*i.e.* macrobenthos, Rabaut et al. (2007); or fish, Rabaut et al. (2010)) and takes place on the local scale (*i.e.* the Belgian Part of the North Sea for Rabaut et al. (2007, 2010, 2013)). To proceed towards the widespread implementation of conservation measures for biogenic reefs, understanding the general ecological function of the reefs, including their simultaneous effect on multiple ecological components and possible associated food web interactions, is of crucial importance. Additionally, in order to avoid merely local evidence on the importance of the reefs, a generalization of the outcome, and hence conducting research beyond the local scale, should be aimed at. In the case of *L. conchilega*, the impact of a reef is most elaborately studied regarding the associated macrobenthic community (Zühlke, 2001; Rabaut et al., 2007; Van Hoey et al., 2008; De Smet et al., 2013). Furthermore, some top-down effects on meiofauna (Zühlke et al., 1998; Braeckman et al., 2011) and biogeochemical characteristics (Braeckman et al., 2010; Passarelli et al., 2012); and bottom-up effects on juvenile flatfish (Rabaut et al., 2010, 2013) and waders (Petersen and Exo, 1999; De Smet et al., 2013) have been reported. All this suggests that *L. conchilega* reefs play a central role in the link between benthic, pelagic and air-borne parts of the intertidal food web. Nonetheless, rather little or no attention has been paid to the entire intertidal epibenthic (benthic organisms living on the surface of the sediment, such as most crabs, shrimp and starfish, (Baretta-Bekker et al., 1992)) and hyperbenthic community (small animals living in the water layer close to the seabed, (Mees and Jones, 1997)) associated with *L. conchilega* reefs.

This study took into account the entire range of bentho-pelagic components forming part of the intertidal *Lanice conchilega* reef and exceeded the local scale, by incorporating two different locations along the French coast characterized by different environmental settings. The following hypothese were tested:(1) the *L. conchilega* reef does not affect the different components of the benthos community (*i.e.* macro-, epi-, and hyperbenthos); and (2) the reef effect, if any, is not affected by the local environmental characteristics of the reef area.

2. Material & methods

2.1. Study area

The two sampling locations were selected based on the presence of a well-established intertidal *Lanice conchilega* reef and are located along the French side of the English Channel: (1) the bay of the Mont Saint-Michel (BMSM), a large-scale intertidal sand flat located in the Normand-Breton Gulf (48°39.70′ N-01°37.41′ W; Lower Normandy, France), and (2) Boulogne-sur-Mer (further referred to as Boulogne), a small-scale beach along the northern part of the English Channel (50°44.01′N-01°35.15′E; Northern France). The main *L. conchilega* reef of the BMSM is situated in the central part of the bay and in the lower section of the tidal flats, covering 25 000 ha. The large tidal flats result from the extreme megatidal regime (tidal range up to 15.5 m during spring tides) which dominates the BMSM (Larsonneur et al., 1994). Boulogne is characterized by a tidal range up to 7 m and in comparison to the BMSM, the beach of Boulogne is less pristine and sheltered by two harbour walls (Rabaut et al., 2008). The *L. conchilega* reef is situated in the lower intertidal and the majority is only exposed during extreme mean low water spring tide conditions.

2.2. Sampling design, sampling and laboratory treatment

Sampling took place in 2012, during spring (from 7th until 13th of March in the BMSM and from 22nd until 25th of March in Boulogne) and autumn (from 17th until 21st of September in BMSM and from 15th until 18th of October in Boulogne). To cover an adequate amount of reef heterogeneity, an *Lanice conchilega* reef area of 100 × 100 m was defined at each location. In addition, a second 100 × 100 m sampling area (control), in the absence of any bioengineering species was defined. The bathymetric level between the reefs and their respective control areas was similar and the sampling areas were at least 300 m apart. At all sampling areas, several components of the soft-bottom assemblage were sampled simultaneously: water, sediment, macro-, epi-, and hyperbenthos.

Three water samples were taken during ebbing tide for the determination of suspended particulate matter (SPM, mg L^{-1}) and chlorophyll *a* (Chl *a*, μg L^{-1}) concentrations. For both SPM and Chl *a*, an appropriate subsample was filtered onto precombusted (450 °C for 2 h) and pre-weighed Whatman GF/F filters (47 mm) and subsequently stored at −80 °C until analysis. Filters for Chl *a* were lyophilized and pigments were extracted in 90% acetone. Chl *a* concentrations of the supernatant were determined using HPLC (Gilson) analysis (Wright and Jeffrey, 1997).

Within each sampling area, ten sediment samples were randomly taken during low tide with a core (Ø 3.6 cm) for sediment factors (median grain size and mud content) and the total amount of organic matter (TOM). Sediment grain size was analysed by means of a Malvern Mastersizer 2000; TOM was determined per sample by weighing the difference between the dry weight (48 h by 60 °C) and the weight after 2 h by 500 °C. The Chl *a* concentration (μg g^{-1} dry sediment) of the upper sediment layer was determined using HPLC (Gilson) analysis (as described above) and used as a proxy for the microphytobenthos (MPB) biomass (Jeffrey et al., 1997). *L. conchilega* densities were estimated by counting the tube tops with fringes on photographs of ten randomly placed metal frames (0.25 m^2) (Ropert and Dauvin, 2000; Van Hoey et al., 2006). Finally, per sampling area, ten macrobenthos samples were collected with an inox corer (Ø 12 cm, 40 cm deep), sieved through a 1-mm circular mesh size and fixed with a neutralized 8% formalin solution. In the laboratory, samples were rinsed and preserved using a neutralized 4% formalin solution with 0.01% Rose Bengal until processing. All macrobenthos was sorted, counted and identified to the lowest possible taxonomic level.

The lower water column (up to 40 cm) covering the sampling areas was sampled to study the epi- and hyperbenthic communities of the *Lanice conchilega* reef. Epibenthos was sampled with a 2 m beam trawl during daytime ebbing tide. The net was 3 m long, had a mesh size of 9 × 9 mm and was equipped with a tickler-chain in the

ground rope. Similarly, hyperbenthos was collected with a hyperbenthic sledge during daytime ebbing tide. The sledge consisted of a metal frame (100×40 cm) and was equipped with two identical nets: a lower and an upper net. Both nets were 3 m long and (at the mouth) 20 cm high with a mesh size of 1×1 mm. The epi- and hyperbenthic devices were towed in the surf zone across the defined sampling area and parallel to the coastline for 100 m. In Boulogne, they were pulled by two persons, while in the BMSM a zodiac was used at a speed of one knot, due to the extreme tides and the extent of the bay. At least three epibenthos and three hyperbenthos replicates (trawls) were taken at each sampling area. Catches were fixed in a neutralized 8% formalin solution. In the laboratory, samples were stained with 0.01% Rose Bengal, rinsed, sorted and identified to the lowest possible taxonomic level. Because of the large content of three hyperbenthos Boulogne autumn samples, subsamples (20% of the total sample weight) were taken.

2.3. Data analysis

2.3.1. Environmental variables

Since the assumptions of parametric statistical approaches were not fulfilled for none of the environmental variables (water SPM and Chl a concentrations; sediment grain size, mud content and TOM; MPB biomass), the effect of the presence of a *Lanice conchilega* reef on the selected environmental variables was explored with a permutational ANOVA (Permanova) in which Reef (reef versus control), Location (BMSM versus Boulogne) and Period (spring versus autumn) were fixed factors. The analysis was based on an Euclidean distance resemblance matrix and performed on untransformed data, except for TOM which was fourth-root transformed in order to meet homogeneity of dispersions (Anderson et al., 2008). In case a significant effect was found, pair-wise tests among all pairs of levels of the given factor(s) were carried out. Although Permanova makes no explicit assumptions regarding the distributions of the original variables, a test for the homogeneity of multivariate dispersions was ran, using the PERMDISP routine. Factors were considered significant at $p < 0.05$ in all analyses. For mud content, MPB biomass, water SPM and Chl a concentrations the PERMDISP test was significant for some factors (even after transformation), indicating differences in dispersion. Therefore, prudence is advised when interpreting the results and the relative sizes of the within and between-group resemblances deserve further attention (Anderson et al., 2008).

2.3.2. Macro-, epi-, and hyperbenthic community descriptors

Faunistic terms are used here as working definitions based on the efficiency of the sampling gear, following Beyst et al. (2001a; 2001b), resulting in a semi-artificial classification. For the macrobenthos, *Lanice conchilega* itself was excluded; as well as strictly hyper-, or epibenthic organisms (Appendix A). The remaining abundance data was standardised per m². For the hyperbenthos, strictly macrobenthic, larger epibenthic and sessile organisms were removed from the dataset (Appendix B), while for the epibenthos, strictly macrobenthos and animals which were more efficiently caught with the hyperbenthic sledge (small sized crustaceans such as isopods and mysids; early postlarval fish and jellyfish) were excluded (Appendix C). Different developmental stages of decapods (zoea, megalopa and juveniles) were treated as different 'taxa', since they have a different ecology (Beyst et al., 2001a). Epi-, and hyperbenthic abundances were standardized per 1000 m². Univariate Permanova analyses were based on Euclidean distance resemblance matrices and performed on untransformed data; except for macrobenthic species abundance and epibenthic species richness which were fourth-root transformed in order to meet

homogeneity of dispersions (Anderson et al., 2008). Prior to Permanova, analysis of similarity (one-way ANOSIM) based on Bray−Curtis resemblance matrices of untransformed data was used to test for (dis-)similarities in the hyperbenthic community between the lower and upper net. The same 3-factor Permanova design as for the environmental variables was used on the macro-, hyper-, and epibenthic community descriptors (species abundance N, species richness S, Shannon−Wiener diversity index H' and Pielou's evenness index J'). In case a significant effect was found, pair-wise tests were carried out. Since our main interest is the effect of a *L. conchilega* reef on the associated communities, only significant results including the factor Reef are shown. All PERMDISP tests were significant for one of more factors, except for macrobenthic species abundance and H'; epibenthic species richness, J' and H'; and hyperbenthic species richness, species abundance and J'. Multivariate 3-factor Permanova analyses (see univariate analysis) were based on Bray−Curtis resemblance matrices of fourth-root transformed macro-, epi-, and hyperbenthos community abundance data. According to a PERMDISP test, the Reef x Period and the Reef $\times$ Location interactions for the macrobenthic community and the factor Reef for the epibenthic community showed significant differences in dispersion. In addition, data were visualized by a Principal Coordinates Analysis (PCO) (Anderson et al., 2008). Based on Spearman correlations, only species of the macro-, epi-, and hyperbenthic community that correlated >50% with one of the first 2 PCO axes were plotted. Distance-based linear models (DistLM) was carried out to investigate the relationship between the benthic community and the environmental variables (Anderson et al., 2008). For the macrobenthic DistLM, all environmental variables (grain size, mud content, TOM, MPB, Chl a and SPM) and one biotic predictor variable (*L. conchilega* density) were used. In comparison to the macrobenthic community, 3 additional biotic predictor variables (macrobenthic N, S and H') were used for the epi-, and hyperbenthic DistLMs. Macro-, epi-, and hyperbenthic abundance data was fourth-root transformed and a Bray−Curtis resemblance matrix was used. If necessary, environmental and biotic predictor variables were square-root or log transformed to avoid skewness. Variables were tested for multi-collinearity and redundant variables were removed from the analysis in case the correlation $|r| \geq 0.95$ (Anderson et al., 2008). A significance level of $p < 0.05$ was used in all tests. All statistical analyses were performed within PRIMERv6 with the PERMANOVA+ add-on software (Clarke and Gorely, 2006; Anderson et al., 2008).

3. Results

3.1. Environmental variables

Fine (125−250 μm) and medium (250−500 μm) sand were the major sediment fractions in all samples. Median grain size in the BMSM ranged from 196 to 324 μm, while in Boulogne from 185 to 261 μm (Table 1). A significant Reef x Location x Period effect for average median grain size was revealed (3-factor Permanova: pseudo-F = 5.27, $p = 0.026$; Appendix D). However, differences due to Reef were only significant in the BMSM (pair-wise tests: reef < control in spring: $p = 0.0001$; and reef < control in autumn $p = 0.0002$). The average mud content (fractions < 63 μm; Table 1) was significantly affected by the Reef $\times$ Location interaction (3-factor Permanova: Pseudo-F = 11.80, $p = 0.0001$; Appendix D). Pairwise tests showed a significant difference between the reef and control area of the BMSM (reef > control: $p = 0.0001$). Mean TOM content (Table 1) was shown to be significantly different due to the factors Reef (Permanova: Pseudo-F = 17.41, $p = 0.0001$; reef > control; Appendix D), Location (Permanova: Pseudo-F = 55.94, $p = 0.0001$; BMSM > Boulogne; Appendix D) and Period

Table 1
Median grain size ($n = 10$), mud content ($n = 10$), total organic matter ($n = 10$), microphytobenthos (MPB) biomass ($n = 10$), SPM ($n = 3$) and Chl a ($n = 3$) (mean ± SE) for different combinations of Reef (reef vs. control), Location (BMSM vs. Boulogne) and Period (spring vs. autumn).

	BMSM				Boulogne			
	Spring		Autumn		Spring		Autumn	
	Reef	Control	Reef	Control	Reef	Control	Reef	Control
Median grain size (μm)	228 ± 5	285 ± 6	234 ± 8	315 ± 5	221 ± 6	231 ± 5	227 ± 5	226 ± 3
Mud content (%)	6.66 ± 2.74	0 ± 0	5.3 ± 1.24	0 ± 0	0.86 ± 0.59	0 ± 0	0.44 ± 0.44	0 ± 0
Total organic matter (%)	1.67 ± 0.17	1.13 ± 0.04	1.5 ± 0.14	1 ± 0.08	1.4 ± 0.55	0.53 ± 0.04	0.59 ± 0.08	0.52 ± 0.03
MPB (μg g^{-1} sediment)	1.68 ± 0.25	0.74 ± 0.06	1.55 ± 0.21	1.77 ± 0.82	5.84 ± 1.51	1.31 ± 0.26	0.89 ± 0.12	0.46 ± 0.03
SPM (mg L^{-1} water)	770.46 ± 66.69	953 ± 60.8	98 ± 2.04	256 ± 7	257.45 ± 36.25	172.98 ± 5.6	184.5 ± 4.09	182.83 ± 1.48
Chl a (μg L^{-1} water)	49.13 ± 2.76	45.45 ± 11.16	3.56 ± 0.24	6.53 ± 0.68	43.15 ± 2.52	21.6 ± 0.7	3.73 ± 0.06	3.3 ± 0.37

(Permanova: Pseudo-F = 6.44, $p = 0.0081$; spring > autumn; Appendix D).

Mean microphytobenthos (MPB) biomass of the upper sediment layer (Table 1) was significantly affected by the interactions of Reef x Location (3-factor Permanova: Pseudo-F = 5.67, $p = 0.0163$; Appendix D), and Reef x Period (3-factor Permanova: Pseudo-F = 8.74, $p = 0.0025$; Appendix D). A pair-wise test for the Reef × Location interaction showed a significantly higher MPB biomass for the reef vs. control area of Boulogne ($p = 0.0014$) but not for the BMSM, while a pair-wise test for the Reef × Period interaction showed a significantly higher MPB biomass for the reef vs. control area in spring ($p = 0.0007$), but not in autumn. A 3-factor Permanova revealed a significant difference in mean SPM (Table 1) for Reef x Location (Pseudo-F = 16.86, $p = 0.0012$; Appendix D), resulting from a significant difference between the reef and control area both in the BMSM (pair-wise test: reef > control: $p = 0.0163$) and Boulogne (pair-wise test: reef < control: $p = 0.03$). Finally, regardless of the location, the mean Chl a concentration of the water was observed to be substantially higher in spring samples compared to autumn samples (Table 1). The mean Chl a concentration was significantly affected by the Reef × Period interaction (3-factor Permanova: Pseudo-F = 4.88, $p = 0.0375$; Appendix D), as a result of a significant difference in autumn (pair-wise test: reef < control: $p = 0.0096$), and was significantly higher in the BMSM (3-factor Permanova; Location: Pseudo-F = 6.85, $p = 0.01$).

3.2. Effect of reef and location on the macrobenthic community

In total, 100 910 macrobenthic organisms belonging to 57 different taxa were sampled in the BMSM, of which 83 637 organisms (belonging to 44 taxa) in the reef area and 17 273 organisms (belonging to 34 taxa) in the control area. In Boulogne, 299 185 macrobenthic organisms were sampled (of which 294 548 in the reef area and 4727 in the control area), belonging to 58 taxa (53 taxa in the reef area and 16 taxa in the control area). Mean *Lanice conchilega* density (±SE) in the BMSM reef was 1724 ± 292 ind m^{-2} and 5044 ± 589 ind m^{-2} in the Boulogne reef. Excluding *L. conchilega*, 96% of the remaining macrobenthos was classified in three major taxa: polychaetes (61%), amphipods (23.4%) and bivalves (15.6%). The macrobenthic community in the BMSM was dominated by the bivalves *Cerastoderma edule* (39.5%) and *Macoma balthica* (13.3%), and the polychaete *Malmgreniella arenicolae* (6.8%). In Boulogne, the amphipod genus *Urothoe* (26%) and the polychaetes *Eumida sanguinea* (19.1%), *Pygospio elegans* (16.3%), *Heteromastus filiformis* (13.5%) and *Capitella* sp. (11.6%) were dominant. Permanova revealed that all community descriptors (Table 2) were

Table 2
Overview of *L. conchilega* densities and of the calculated community descriptors (mean ± SE) for the macrobenthic, epibenthic and hyperbenthic communities of the *L. conchilega* reef and control area of the bay of the Mont Saint-Michel (BMSM) and Boulogne-sur-Mer.

	BMSM				Boulogne			
	Spring		Autumn		Spring		Autumn	
Macrobenthos	Reef ($n = 10$)	Control ($n = 10$)	Reef ($n = 10$)	Controlf ($n = 10$)	Reef ($n = 10$)	Control ($n = 10$)	Reef ($n = 10$)	Control ($n = 10$)
L. conchilega density	1090 ± 269	0 ± 0	2358 ± 444	0 ± 0	6720 ± 868	0 ± 0	3368 ± 296	0 ± 0
Species abundance N	4964 ± 478	800 ± 239	3400 ± 529	927 ± 225	13 446 ± 1708	209 ± 45	16009 ± 3192	255 ± 45
Species richness S	11.0 ± 1.1	4.9 ± 0.8	10.1 ± 1.0	6.2 ± 1.1	16.0 ± 0.9	2.0 ± 0.4	14.9 ± 1.0	2.0 ± 0.3
Shannon diversity index H′	1.555 ± 0.123	1.341 ± 0.149	1.775 ± 0.129	1.546 ± 0.155	1.829 ± 0.120	0.509 ± 0.267	1.714 ± 0.103	0.569 ± 0.165
Pielou's eveness index J′	0.655 ± 0.032	0.925 ± 0.023	0.778 ± 0.031	0.930 ± 0.022	0.665 ± 0.047	0.976 ± 0.016	0.638 ± 0.029	0.966 ± 0.017
Epibenthos	Reef ($n = 3$)	Control ($n = 4$)	Reef ($n = 3$)	Control ($n = 3$)	Reef ($n = 3$)	Control ($n = 3$)	Reef ($n = 4$)	Control ($n = 4$)
Species abundance N	487 ± 111	155 ± 44	755 ± 421	406 ± 190	1452 ± 674	205 ± 128	9912 ± 2983	353 ± 83
Species richness S	9.3 ± 0.7	5.8 ± 0.9	8.3 ± 1.5	10.7 ± 3.4	5.7 ± 0.7	3.0 ± 0.6	9.0 ± 0.0	9.0 ± 1.2
Shannon diversity index H′	1.176 ± 0.108	1.284 ± 0.112	1.186 ± 0.097	1.316 ± 0.245	0.855 ± 0.225	0.500 ± 0.159	0.547 ± 0.219	1.463 ± 0.107
Pielou's eveness index J′	0.532 ± 0.068	0.757 ± 0.069	0.568 ± 0.006	0.594 ± 0.012	0.509 ± 0.153	0.450 ± 0.063	0.249 ± 0.100	0.674 ± 0.027
Hyperbenthos	Reef ($n = 3$)	Control ($n = 3$)	Reef ($n = 3$)	Control ($n = 3$)	Reef ($n = 3$)	Control ($n = 4$)	Reef ($n = 3$)	Control ($n = 3$)
Species abundance N	3350 ± 1360	5363 ± 1832	27853 ± 14977	8107 ± 153	23323 ± 9219	2965 ± 1015	7357 ± 5087	450 ± 217
Species richness S	20.3 ± 3.5	21.0 ± 3.0	38.3 ± 2.9	38.7 ± 3.5	1.0 ± 4.0	14.7 ± 1.4	19.0 ± 4.5	11.7 ± 5.6
Shannon diversity index H′	1.864 ± 0.175	1.662 ± 0.119	1.306 ± 0.438	2.361 ± 0.159	1.015 ± 0.167	1.482 ± 0.305	1.477 ± 0.323	1.413 ± 0.713
Pielou's eveness index J′	0.638 ± 0.101	0.549 ± 0.031	0.358 ± 0.116	0.646 ± 0.028	0.365 ± 0.042	0.555 ± 0.116	0.526 ± 0.142	0.752 ± 0.008

significantly affected by the Reef × Location interaction (Appendix E). Pair-wise comparisons revealed a significantly higher macrobenthic abundance (Fig. 1) and species richness, and a significantly lower J' in reef areas compared to control areas, both in the BMSM and Boulogne (for all pair-wise tests: $p = 0.0001$). Although significant differences between the reef and control area were detected for H' in Boulogne (pair-wise test: reef > control: $p = 0.0001$), none could be detected for the BMSM (pair-wise test: $p = 0.1249$). Seasonal variances of all calculated indices were negligible in comparison to variances as a result of Reef and/or Location, except for *L. conchilega* density.

Multivariate analyses revealed a significant interaction effect of Reef x Location (3-factor Permanova: Pseudo-F = 14.49, $p = 0.0001$) and Reef x Period (3-factor Permanova: Pseudo-F = 3.40, $p = 0.0041$) on the macrobenthic community. Differences between the *Lanice conchilega* reef and control areas were highly significant for the two locations and the two periods (all four pair-wise tests: $p = 0.0001$). The PCO analysis (Fig. 2) showed a clear separation of reef samples vs. control samples. Moreover, the reef areas of the BMSM and Boulogne were clearly distinguishable from one another, while this was not the case for the control areas. PCO axis 1 explained 30.2% of the total variation inherent in the resemblance matrix and separated reef samples and control samples. Besides, reef areas were characterized by a larger array of taxa compared to areas in the absence of *L. conchilega*. PCO axis 2 explained 17.9% of the total variation and distinguished the locations, albeit not clearly for the control areas. The DistLM analysis showed that the variables *L. conchilega* density (15.1%), mud content (9.0%) and grain size (4.4%) together explain 28.45% of the variation in the macrobenthic community structure (Appendix F).

3.3. Effect of reef and location on the epibenthic community

In the BMSM, 5565 organisms belonging to 29 different taxa were sampled. The majority was sampled in the reef area (3725 organisms; 21 taxa) in comparison to the control area (1840 organisms; 24 taxa). The Boulogne sampling yielded 46 030 organisms (23 taxa), of which 44 005 organisms (17 taxa) were caught in the reef area and 2025 organisms (16 taxa) in the control area. 94.6% of the epibenthos was confined to three taxonomic groups: *Crangon crangon* (89.8%), *Pomatoschistus* spp. (9%) and flatfish species (1.2%). The epibenthic community in the BMSM reef and
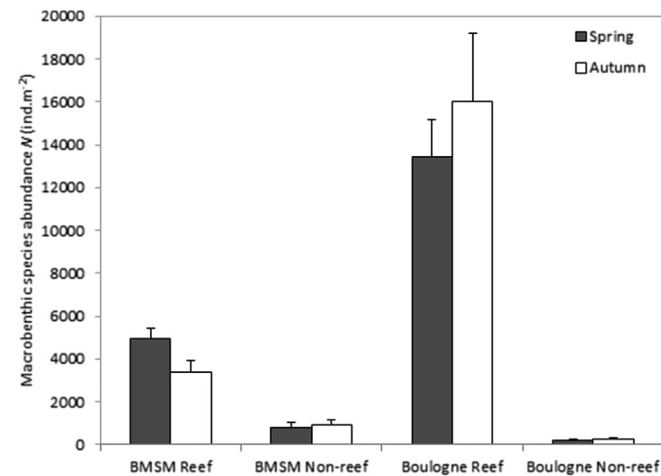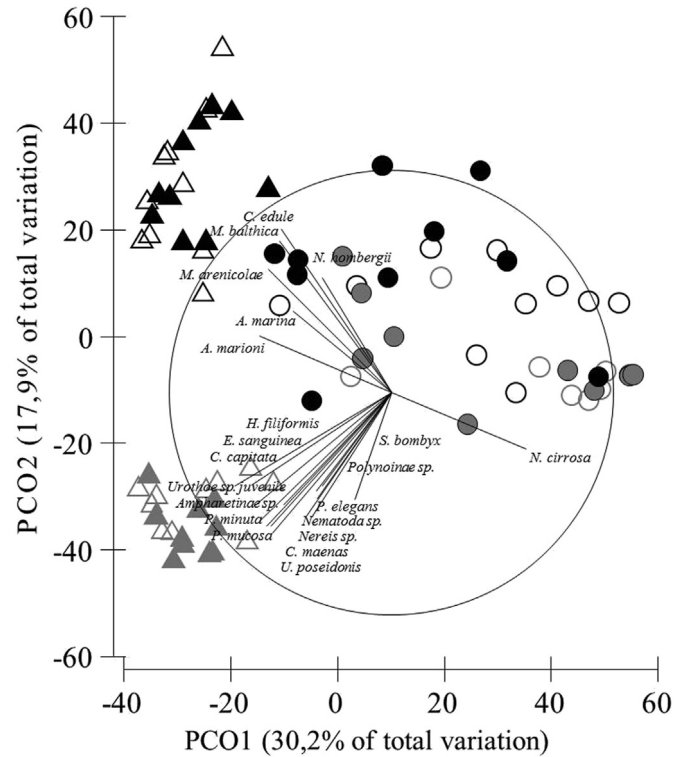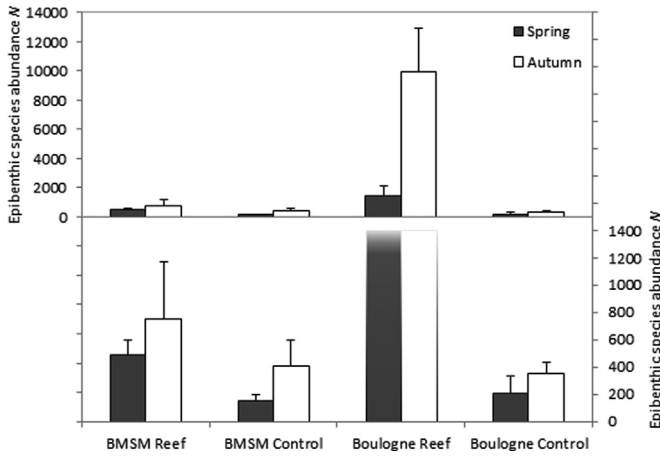

Fig. 2. PCO analysis of macrobenthos communities in reef and control areas in the BMSM and Boulogne during spring and autumn 2012 based on Bray−Curtis similarities of fourth-root transformed abundance data. Vectors represent species correlating >50% (based on Spearman correlation coefficients) with one of the first two PCO axes (▲ Reef/BMSM/Spring; △ Reef/BMSM/Autumn; ◮ Reef/Boulogne/Spring; △ Reef/Boulogne/Autumn; ● Control/BMSM/Spring; ○ Control/BMSM/Autumn; ◐ Control/Boulogne/Spring; ○ Control/Boulogne/Autumn).

control area was mainly dominated by the brown shrimp *Crangon crangon* (54.6% & 57.6% resp.) and by the gobies *Pomatoschistus lozanoi* (14.6% & 13.6% resp.) and *Pomatoschistus microps* (18.8% & 3% resp.). *Crangon crangon* was dominant in the epibenthic community of the Boulogne reef (90.5%) and control area (43.7%). In the latter area its dominance was complemented by the common shore-crab *Carcinus maenas* (23.5%) and *Pomatoschistus minutus* (21%). Species richness (Table 2) differed significantly between various combinations of Reef x Period (3-factor Permanova: Pseudo-F = 5.93, $p = 0.0243$), which is the result of a significantly higher species richness in the reef vs. control area during spring (pair-wise test: $p = 0.0049$). Mean epibenthic abundance (Fig. 3), J' and H' (Table 2) were significantly affected by the Reef x Location × Period interaction (Appendix E). In case of the mean epibenthic abundance, the significant effect was due to significant differences between the reef and control areas in the BMSM during spring (pair-wise test: reef > control: $p = 0.032$) and in Boulogne during autumn (pair-wise test: reef > control: $p = 0.0283$). For both J' and H', the significant differences between the reef and control areas resulted from differences in Boulogne during autumn (pair-wise test J': reef < control: $p = 0.0273$; pairwise test H': reef < control: $p = 0.0284$).

Multivariate analyses suggested that the epibenthic community differed among the Reef × Period interaction (3-factor Permanova: Pseudo-F = 2.36, $p = 0.016$). Pair-wise tests showed that the epibenthic communities of the *Lanice conchilega* reef area and the control area differed both in spring ($p = 0.0139$) and autumn ($p = 0.0016$). Simultaneously, Permanova revealed highly significant community differences between the locations (*Location*:

Fig. 1. Mean macrobenthic species abundance (*excluding L. conchilega*) N (±SE) per m^2 for different combinations of Reef (reef vs. control), Location (BMSM vs. Boulogne) and Period (spring vs. autumn).

Fig. 3. Mean epibenthic species abundance N ($\pm$SE) per 1000 m^2 for different combinations of Reef (reef vs. control), Location (BMSM vs. Boulogne) and Period (spring vs. autumn). An overall abundance view is given in the upper panel, while the lower panel shows a more detailed view on the abundances of BMSM − Reef, BMSM − Control and Boulogne − Control.

Pseudo-F = 17.56, p = 0.0001). According to the PCO analysis, PCO axis 1 mainly showed a distinction between locations (explaining 34.6% of the total variation), while PCO axis 2 separated spring samples and autumn samples (explaining 20.6% of the total variation) (Fig. 4). The DistLM analysis showed that the variables SPM (17%), macrobenthic H' (11.8%), macrobenthic N (21%) and Chl a (9.8%) together explain 59.6% of the variation in the epibenthic community structure (Appendix F).

### 3.4. Effect of reef and location on the hyperbenthic community

In the BMSM, 134 020 organisms belonging to 100 different taxa were sampled. The majority was sampled in the reef area (93 610 organisms; 74 taxa) in comparison to the control area (40 410 organisms; 72 taxa). In Boulogne, 105 250 organisms

belonging to 72 taxa were caught, of which 92 040 organisms (56 taxa) in the reef area and 13 210 (41 taxa) in the control area. 98.2% of the hyperbenthos could be classified in 5 taxonomic groups: mysidae (61.3%), shrimp (15.5%), amphipoda (13.9%), juvenile fish (6.9%) and juvenile crab (2.4%). The hyperbenthic community of the BMSM was mainly dominated by mysid shrimp: *Mesopodopsis slabberi* (72.3%) in the reef area; and *Schistomysis kervillei* (20.2%), *M. slabberi* (18.1%), *Schistomysis spiritus* (13%) and Mysidae sp. (12.7%) in the control area. In the Boulogne reef area, the hyperbenthic community was dominated by *Mesopodopsis slabberi* (27.5%), *Crangon crangon* juveniles (24.2%) and the amphipod *Nototropis swammerdamei* (17.9%); while dominated by sandeel *Ammodytes tobianus* juveniles (48.7%), *Crangon crangon* juveniles (16.1%) and Pleuronectiformes sp. juveniles (10.2%) in the control area. The hyperbenthic community was not significantly different between the lower and upper nets (one-way ANOSIM: p = 0.543; R = 0.008). Consequently, further statistical analyses were done excluding the factor Net. A 3-factor Permanova revealed that hyperbenthic abundance (Fig. 5) and J' (Table 2) are significantly affected by Reef (N: Pseudo-F = 6.48, reef > control: p = 0.0107; J': Pseudo-F = 4.93, reef < control: p = 0.0421; Appendix E), while species richness (Table 2) was affected by Location (Pseudo-F = 30.11, BMSM > Boulogne: p = 0.0001; Appendix E) and Period (Pseudo-F = 11.52, spring < autumn: p = 0.0048; Appendix E). H' (Table 2) did not differ significantly for any of the factorial interactions.

Multivariate analyses revealed that the Reef x Location × Period interaction affects the hyperbenthic community (3-factor Permanova: Pseudo-F = 2.14, p = 0.0339). However, only in Boulogne during spring the hyperbenthic community seemed to be significantly different between the *Lanice conchilega* reef and the control area (pair-wise test: p = 0.0139). According to the PCO analysis, PCO axis 1 explained 27.3% of the total variation; distinguishing samples from the BMSM and Boulogne (Fig. 6). Moreover, the hyperbenthic community of the BMSM was characterized by a diverse species composition compared to Boulogne. PCO axis 2 explained 20% of the total variation and separated spring and autumn samples, which was more pronounced for Boulogne. The DistLM analysis showed that the variables TOM (16.1%), Chl a (15.5%), SPM (18.6%) and grain size (8.2%) together explain 58.5% of the variation in the hyperbenthic community structure (Appendix F).
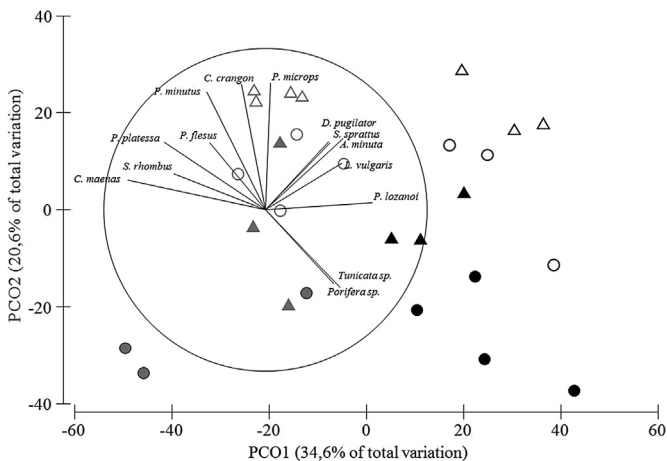
Fig. 4. PCO analysis of epibenthos communities in reef and control areas in the BMSM and Boulogne during spring and autumn 2012 based on Bray−Curtis similarities of fourth-root transformed abundance data. Vectors represent species correlating >50% (based on Spearman correlation coefficients) with one of the first two PCO axes (▲ Reef/BMSM/Spring; △ Reef/BMSM/Autumn; ▲ Reef/Boulogne/Spring; △ Reef/Boulogne/Autumn; ● Control/BMSM/Spring; ○ Control/BMSM/Autumn; ◉ Control/Boulogne/Spring; ○ Control/Boulogne/Autumn).
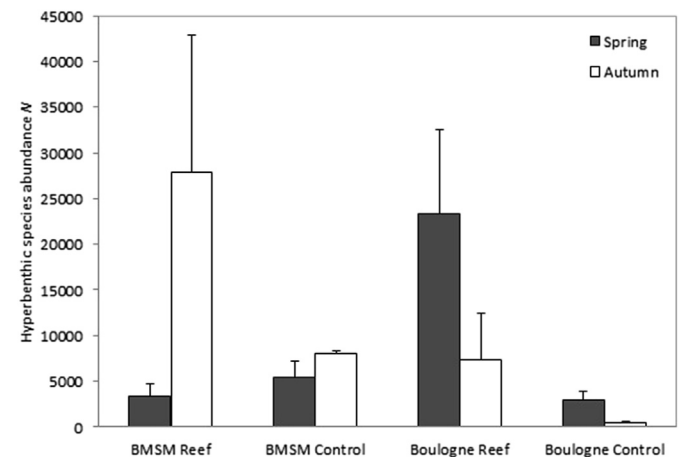
Fig. 5. Mean hyperbenthic species abundance N ($\pm$SE) per 1000 m^2 for different combinations of Reef (reef vs. control), Location (BMSM vs. Boulogne) and Period (spring vs. autumn).
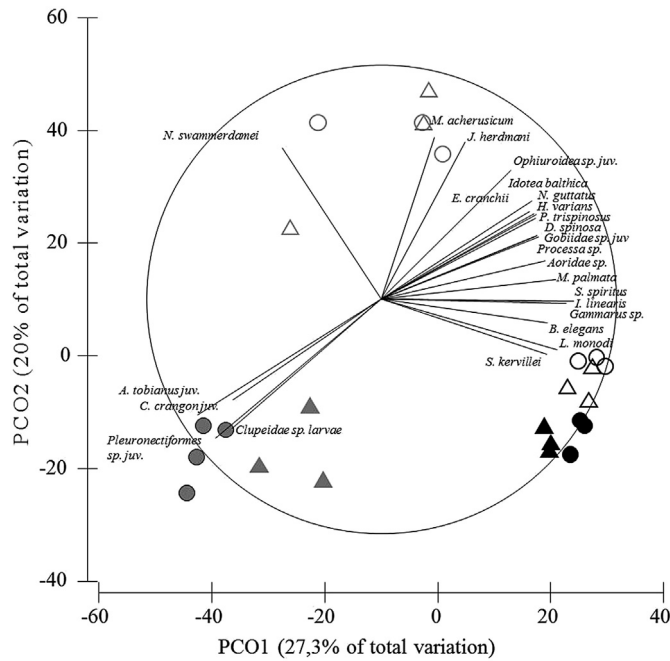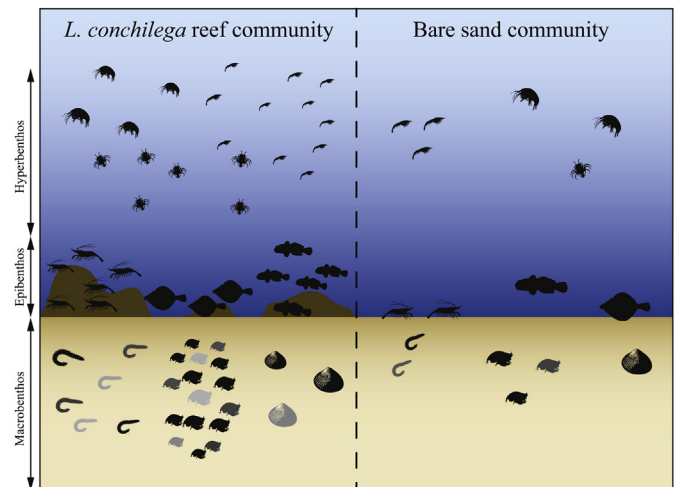
Fig. 6. PCO analysis of hyperbenthos communities in reef and control areas in the BMSM and Boulogne during spring and autumn 2012 based on Bray—Curtis similarities of fourth-root transformed abundance data. Vectors represent species correlating >50% (based on Spearman correlation coefficients) with one of the first two PCO axes (▲ Reef/BMSM/Spring; △ Reef/BMSM/Autumn; ▲ Reef/Boulogne/Spring; △ Reef/Boulogne/Autumn; ● Control/BMSM/Spring; ○ Control/BMSM/Autumn; ◉ Control/Boulogne/Spring; ○ Control/Boulogne/Autumn).

Fig. 7. Schematic overview of the effect of the *L. conchilega* reef (left) and a bare sand habitat (right) on the macro-, epi-, and hyperbenthic communities of an intertidal sandy beach food-web. Differential dependency of the benthic communities to the sea floor account for differences in the extent of the structuring effect of the *L. conchilega* reef in terms of abundances (number of symbols) and species diversity (different shades of grey). *Macrobenthos: polychaetes (e.g. Eumida sanguinea), amphipods (e.g. Urothoe poseidonis) and bivalves (e.g. Cerastoderma edule); Epibenthos: Crangon crangon, Pomatoschistus sp., flatfish sp. (Pleuronectes platessa); Hyperbenthos: mysida (Mesopodopsis slabberi), amphipoda (Nototropis swammerdamei) and decapod megalopa larvae.*

4. Discussion

4.1. Lanice conchilega reef effect on the macro-, epi-, and hyperbenthic community

This study shows that the presence of *Lanice conchilega* reefs affect the associated macro-, epi-, and hyperbenthic communities. For all three investigated communities, the majority of the collected organisms was sampled in the reef (macrobenthos: 91%; epibenthos: 81%; hyperbenthos: 78.5%), showing a more abundant benthic reef community compared to bare sands. Based on the proportion of animals in the reef versus control areas, the extent of the structuring effect seems to be most pronounced for the macrobenthos and least strong for the hyperbenthos. We suggest that this is due to the differential dependency of the three communities to the sea floor. The link between the benthic community and the sediment, where the effects of *L. conchilega* are most pronounced, is much more intimate for the macro- and epibenthos than for the hyperbenthos (Fig. 7). Moreover, the reefs predominantly affect the macrobenthic part of the benthos, which corroborates previous observations (Zühlke et al., 1998; Rabaut et al., 2007; Van Hoey et al., 2008; De Smet et al., 2013). The increased macrobenthic abundance, species richness and diversity is attributed to an increased habitat heterogeneity and shelter/refuge provision accomplished by the high tubeworm density. Similarly, epibenthic animals, which are considered to be free-living and highly mobile species in soft bottom assemblages, seem to select for *L. conchilega* reefs. Their mobile character enables them to actively move to and feed upon the macrobenthos within the biogenic habitat. As shown by the epibenthic DistLM analysis, the increased macrobenthic diversity (H′) and abundance (N) in the reef are in favour of the epibenthic community, as demonstrated before for e.g. (flat) fish

(Rabaut et al., 2013). The macrobenthic reef community in this study is characterized by a large array of taxa, of which bivalves (*Cerastoderma edule* and *Macoma balthica*), polychaetes (*Eumida sanguinea*) and amphipods (*Urothoe poseidonis*) are most abundant (Fig. 7). The positive effect of macrobenthos on higher trophic levels is in accordance with preliminary results of trophic relationships within *L. conchilega* reefs based on stable isotope and stomach content analysis (De Smet et al., unpublished). Similarly, polychaetes, amphipods and other small benthic animals are counted as a non-negligible part of the diet of macrocrustaceans such as the omnivorous brown shrimp, *Crangon crangon* (Boddeke et al., 1986; Oh et al., 2001). Abundances of this epibenthos species in the reef areas largely exceeded those from bare sand patches. In general, *C. crangon* is one of the most abundant epibenthic species in the European intertidal zones (Hostens, 2000; Beyst et al., 2001b) and supports a large commercial fishery in northern European waters (Temming and Damm, 2002). Hence, by fuelling stocks of commercial fish species, *C. crangon* might be one of the most important inhabitants of the *L. conchilega* reef. Besides shrimp, *Pomatoschistus* spp. and flatfish species were notably represented in the reefs (Fig. 7). Several (commercial) benthic fish species were already shown to be attracted to biogenic habitats because they provide preferred prey species and/or act as refuges against predation (Kaiser et al., 1999; Rabaut et al., 2010; Chapman et al., 2012). Hyperbenthic communities were affected by the presence of the *L. conchilega* reefs. However, neither *L. conchilega* density nor macrobenthic species richness (S), abundance (N) or diversity (H′) do contribute to the DistLM models explaining variation in the hyperbenthic assemblages. This suggests that the structuring effect of the reefs is indirect for the hyperbenthos. The high hyperbenthos abundances (dominated by mysida and to a lesser extent amphipods, juvenile fish and decapods, and shrimp excluding *C. crangon*) in the *L. conchilega* assemblages may be partly explained by their active migration to favourable environments (Dewicke et al., 2002). Highly motile hyperbenthos often reaches high densities in regions with a strong input of organic matter (Dauvin et al., 1994; Mees and

Jones, 1997). Therefore, the elevated amounts of TOM in the reefs, resulting from changes in the hydrodynamic regime due to the presence of *L. conchilega* tubes, were shown to sustain the high hyperbenthic abundances observed in our study. The increased *L. conchilega* density and hence the shelter against predation provided by the tubes, seems to be of a lesser importance to attract hyperbenthic animals. Notwithstanding their active, behavior-mediated transport, the hyperbenthos is subjected to passive transport mechanisms as well (Mees and Jones, 1997; Dewicke et al., 2002), limiting their reef selectivity.

In general, the macro − and epibenthic community are largely structured by biotic variables (due to tubeworm density and macrobenthic food availability respectively), while the hyperbenthos, which is the least dependent on the sea bed, is rather structured by environmental variables.

4.2. The effect of the local environment on the macro-, epi-, and hyperbenthic community

At both locations, the macrobenthic reef samples are heavily clustered, which demonstrates that although the reef areas are very patchy, their species composition remains the same on a local spatial scale. On a larger scale, the magnitude of the reef effect on the macro-, epi-, and hyperbenthos seems to be influenced by the location of the reef. For the macro- and epibenthos, the differences in the community descriptors between a reef and control area were more pronounced for Boulogne than for the BMSM (except for the epibenthic species richness). The location effect is most likely driven by the difference in *Lanice conchilega* density between both sites, as shown by the DistLM analyses. The higher tubeworm densities in Boulogne (5044 ± 589 ind m^{-2}) compared to the BMSM (1724 ± 292 ind m^{-2}) can provide a larger and more secure settlement surface of larval and postlarval benthic organisms (Qian et al., 1999; Rabaut et al., 2007). Being characterized by a higher macrofaunal abundance and species diversity, high density *L. conchilega* reefs act as feeding grounds for more mobile epibenthic animals. Nevertheless, the high density reef of Boulogne was observed to have a lower mud content (silt + clay) and lower amounts of TOM compared to the lower density reef of the BMSM. This finding is in contradiction to the higher macrofaunal abundances in the Boulogne reef, which growth is believed to be promoted by the sedimentation of organic matter (Wieking and Kröncke, 2005). Although the *L. conchilega* density is the most explaining predictor variable, the location effect is amplified by other location dependent environmental variables (e.g. grain size and Chl *a*).

Differences in the hyperbenthic community between locations were less pronounced and not attributable to the density of the tubeworm, but rather to environmental variables inherent to the location such as TOM, Chl *a* and SPM. Therefore, the hyperbenthos, which is dominated by mysids and known to feed mainly on detritus, algae and zooplankton (Mauchline, 1980), is largely structured by the availability of food.

The presence of the *Lanice conchilega* reef undoubtedly affects the abundances of all three investigated benthic communities and most notably the macrobenthic component. Moreover, our study shows that intertidal *L. conchilega* reefs do not only affect abundances and diversity but also the presence and relative contribution of species belonging to multiple trophic levels. As such, an altered predator-prey relationship in *L. conchilega* reefs versus bare sands can be presumed. Furthermore, the positive feedback of *L. conchilega* reefs on higher trophic levels of intertidal sandy beaches is shown to be applicable on locations with different environmental conditions. This outcome amplifies the current idea that *L. conchilega* reefs are important habitats under the Habitats Directive and might be crucial towards the implementation of widespread conservation measures in the future.

Appendix A. Macrobenthic taxa list excluding strictly hyper-, or epibenthic organisms. Indication of the life history stage is given (ad = adult: juv = juvenile)

Taxon	Stage	Taxon	Stage
Actiniaria sp.	ad	*Macoma balthica*	ad
Ampharetinae sp.	ad	*Magelona johnstoni*	ad
Angulus tenuis	ad	*Magelona mirabilis*	ad
Aphelochaeta marioni	ad	*Malmgreniella arenicolae*	ad
Arenicola marina	ad	*Malmgreniella ljungmani*	ad
Autolytus sp.	ad	*Malmgreniella* sp.	ad
Bathyporeia elegans	ad	*Melita palmata*	ad
Bathyporeia pilosa	ad	*Monocorophium acherusicum*	ad
Bathyporeia sarsi	ad	Nematoda sp.	ad
Bivalvia sp.	juv	Nemertea sp.	ad
Capitella sp.	ad	*Nephtys caeca*	ad
Carcinus maenas	ad	*Nephtys cirrosa*	ad
Cerastoderma edule	ad	*Nephtys hombergii*	ad
Cirratulidae sp.	ad	*Nephtys kersivalensis*	ad
Corophium sp.	ad	Nereis sp.	ad
Cumacea sp.	ad	*Notomastus latericeus*	ad
Cumopsis goodsir	ad	Oligochaeta sp.	ad
Cumopsis longipes	ad	*Ophelia borealis*	ad
Donax vittatus	juv	Ophiuroidea sp.	juv
Ensis magnus	ad	*Pholoe minuta*	ad
Eocuma dollfusi	ad	*Phyllodoce mucosa*	ad
Eteone longa	ad	*Pirimela denticulata*	ad
Eumida sanguinea	ad	Polynoinae sp.	ad
Eurydice pulchra	ad	Portunidae sp.	ad
Gammarus crinicornis	ad	*Pygospio elegans*	ad
Glycera alba	ad	*Scolelepis squamata*	ad
Glycera lapidum	ad	*Scoloplos armiger*	ad
Glycera sp.	ad	*Sigalion mathildae*	ad
Glycera tridactyla	ad	Siphonoecetes sp.	ad
Harmothoe sp.	ad	*Sphaeroma monodi*	ad
Hediste diversicolor	ad	Spio sp.	ad
Hesionura elongata	ad	*Spiophanes bombyx*	ad
Heteromastus filiformis	ad	Syllidae sp.	ad
Idotea pelagica	ad	*Syllis gracilis*	ad
Idotea sp.	juv	Tanaidacea sp.	ad
Kurtiella bidentata	ad	*Urothoe poseidonis*	ad
Lanice conchilega	ad	Urothoe sp.	juv
Liocarcinus navigator	ad	*Venerupis philippinarum*	ad
Lumbrineris sp.	ad		

Appendix B. Epibenthic taxa list excluding strictly macrobenthic taxa and taxa which were more efficiently caught with the hyperbenthic sledge (i.e. small sized crustaceans such as isopods and mysids; early postlaval fish; and jellyfish). Indication of the life history stage (based on Beyst et al., 2001b) is given (ad = adult: juv = juvenile)

Taxon	Stage	Taxon	Stage
Ammodytes tobianus	ad	*Palaemon serratus*	ad
Ammodytidae sp.	juv	*Pisidia longicornis*	ad
Aphia minuta	ad	*Platichthys flesus*	ad
Atherina presbyter	ad	*Pleuronectes platessa*	ad
Cancer pagurus	ad	Pleuronectidae sp.	ad
Carcinus maenas	ad	*Pomatoschistus lozanoi*	ad
Ciliata mustela	ad	*Pomatoschistus microps*	ad
Cottidae sp.	ad	*Pomatoschistus minutus*	ad
Crangon crangon	ad	*Pomatoschistus pictus*	ad
Dicentrarchus labrax	ad	*Porcellana platycheles*	ad
Diogenes pugilator	ad	Porifera sp.	ad
Echiichthys vipera	ad	*Portumnus latipes*	ad
Eualus occulus	ad	*Psammechinus miliaris*	ad
Eualus pusiolus	ad	*Scophthalmus rhombus*	ad
Liocarcinus marmoreus	ad	*Sepia officinalis*	ad
Liocarcinus sp.	ad	*Sepiola atlantica*	ad
Liocarcinus vernalis	ad	*Solea solea*	ad
Loligo sp.	ad	*Sprattus sprattus*	ad
Loligo vulgaris	ad	*Syngnathus rostellatus*	ad
Mytilus edulis	ad	Tunicata sp.	ad

Appendix C. Hyperbenthic taxa list excluding strictly macrobenthic, larger epibenthic and sessile organisms. Indication of the life history stage (based on Beyst et al., 2001a) is given (ad = adult, juv = juvenile; la = larvae, me = megalopa, zo = zoeae)

Taxon	Stage	Taxon	Stage	Taxon	Stage
Abludomelita gladiosa	ad	*Dexamine spinosa*	ad	*Monocorophium sextonae*	ad
Abludomelita obtusata	ad	*Diastylis bradyi*	ad	Mysidae sp.	ad
Achelia echinata	ad	*Diastylis lucifera*	ad	*Mysidopsis gibbosa*	ad
Achelia sp.	ad	Diastylis sp.	ad	*Neomysis integer*	ad
Allomelita pellucida	ad	*Endeis spinosa*	ad	*Nototropis falcatus*	ad
Ammodytes tobianus	juv	*Eocuma dollfusi*	ad	*Nototropis guttatus*	ad
Ammodytidae sp.	juv	*Ericthonius punctuatus*	ad	*Nototropis swammerdamei*	ad
Ammothella longipes	ad	*Ericthonius* sp.	ad	Nudibranchia sp.	ad
Amphipoda sp.	ad	*Eualus cranchii*	ad	*Nymphon brevirostre*	ad
Anilocra sp.	ad	Eualus sp.	ad	Ophiuroidea sp.	juv
Anoplodactylus pygmaeus	ad	*Euphausiidae* sp.	ad	*Palaemon elegans*	ad
Aoridae sp.	ad	*Eurydice pulchra*	ad	*Palaemon serratus*	ad
Apherusa ovalipes	ad	Galathea sp.	juv	*Pariambus typicus*	ad
Apherusa sp.	ad	Galatheidae sp.	me	*Philocheras fasciatus*	ad
Apseudopsis latreillii	ad	Gammarus sp.	ad	*Philocheras trispinosus*	ad
Astacilla longicornis	ad	*Gastrosaccus spinifer*	ad	*Phoxichilidium femoratum*	ad
Asterias rubens	juv	Gobiidae sp.	juv	*Phtisica marina*	ad
Athanas nitescens	ad	*Haustorius arenarius*	ad	*Pilumnus hirtellus*	ad
Atylus sp.	ad	*Heteromysis formosa*	ad	*Pinnotheres pisum*	ad
Atylus vedlomensis	ad	Hippolyte sp.	ad	Pisces sp.	juv
Bathyporeia elegans	ad	Hippolyte sp.	juv	*Pisidia longicornis*	ad
Bathyporeia pelagica	ad	*Hippolyte varians*	ad	*Pleurobrachia pileus*	ad
Bathyporeia pilosa	ad	Hippolytidae sp.	ad	Pleuronectiformes sp.	juv
Bathyporeia sarsi	ad	*Idotea balthica*	ad	*Pontocrates arenarius*	ad
Bathyporeia sp.	ad	*Idotea linearis*	ad	Porcellanidae sp.	juv
Bodotria scorpioides	ad	*Idotea metallica*	ad	*Portumnus latipes*	juv
Bougainvilliidae sp.	ad	*Idotea pelagica*	ad	Portunidae sp.	juv + zo
Calanoida sp.	ad	Idotea sp.	ad	*Praunus flexuosus*	ad
Calliopius laeviusculus	ad	*Iphimedia obesa*	ad	*Processa edulis crassipes*	ad
Callipallene brevirostris	ad	Jaera sp.	ad	Processa sp.	ad
Caprella linearis	ad	*Jassa herdmani*	ad	*Pseudoprotella phasma*	ad
Caridea sp.	juv	*Jassa marmorata*	ad	Pycnogonida sp.	ad
Cheirocratus intermedius	ad	Jassa sp.	ad	*Schistomysis kervillei*	ad
Cheirocratus sp.	ad	*Lekanesphaera monodi*	ad	*Schistomysis ornata*	ad
Clupeidae sp.	la	*Leptomysis lingvura*	ad	Schistomysis sp.	ad
Cnidaria sp.	ad	*Leptomysis mediterranea*	ad	*Schistomysis spiritus*	ad
Corophium arenarium	ad	*Leucothoe incisa*	ad	*Sepiola atlantica*	ad
Corophium sp.	ad	*Listriella picta*	ad	Siphonoecetes sp.	ad
Corophium volutator	ad	*Maerella tenuimana*	ad	*Siriella armata*	ad
Corynidae sp.	ad	Majidae sp.	juv	*Siriella clausii*	ad
Crangon crangon	juv	*Melita palmata*	ad	*Siriella jaltensis*	ad

(continued)

Taxon	Stage	Taxon	Stage	Taxon	Stage
Crangonidae sp.	juv	*Mesopodopsis slabberi*	ad	*Stenothoe marina*	ad
Ctenophora sp.	ad	Microprotus sp.	ad	*Sunamphitoe pelagica*	ad
Cyclopoida sp.	ad	*Monocorophium acherusicum*	ad	*Urothoe poseidonis*	ad
Decapoda sp.	me	*Monocorophium insidiosum*	ad		

Appendix D. Three-factor univariate Permanova main and pair-wise tests results for the environmental variables. Reef (reef vs. control), Location (BMSM vs. Boulogne) and Period (spring vs. autumn) were fixed factors. Analyses were based on an Euclidian distance resemblance matrix and performed on untransformed data (except for the total organic matter, TOM, which was fourth-root transformed). Only significant results including the factor Reef are shown. In case of significant differences ($p < 0.05$) p values are in bold.

Main test	Reef x location x Period			Reef x location			Reef x Period		
	MS	Pseudo-F	p value	MS	Pseudo-F	p value	MS	Pseudo-F	p value
Median grain size (μm)	1582.3	5.27	**0.026**	–	–	–	–	–	–
Mud content (%)	–	–	–	141.8	11.8	**0.0001**	–	–	–
MPB (μg g^{-1} sediment)	–	–	–	0.19	5.67	**0.016**	34.56	8.74	**0.0025**
SPM (mg L^{-1} water)	–	–	–	64254	16.86	**0.0012**	64254	16.86	**0.0012**
Chl$a$ (μg L^{-1} water)	–	–	–	–	–	–	272.12	4.88	**0.0375**

Main test	Reef			Location			Period		
	MS	pseudo-F	p value	MS	pseudo-F	p value	MS	pseudo-F	p value
Total organic matter (%)	0.18	17.41	**0.0001**	0.58	55.94	**0.0001**	0.07	6.44	**0.008**

Pair-wise test	Reef x location x Period				Reef x location		Reef x Period	
	BMSM – S	BMSM – a	Boul – S	Boul – A	BMSM	Boul	Spring	Autumn
Median grain size (μm)	0.0001	0.0002	0.1991	0.9474	–	–	–	–
Mud content (%)	–	–	–	–	0.0001	0.1275	–	–
MPB (μg g^{-1} sediment)	–	–	–	–	0.5298	0.0014	0.0007	0.9467
SPM (mg L^{-1} water)	–	–	–	–	0.0163	0.03	–	–
Chl$a$ (μg L^{-1} water)	–	–	–	–	–	–	0.0646	0.0096

Appendix E. Three-factor univariate Permanova main and pair-wise tests results for the macro-, epi-, and hyperbenthic community descriptors. Reef (reef vs. control), Location (BMSM vs. Boulogne) and Period (spring vs. autumn) were fixed factors. Analyses were based on an Euclidian distance resemblance matrix and performed on untransformed data (except for the macrobenthic species abundance N and the epibenthic species richness S which were fourth-root transformed). Only significant results including the factor Reef are shown. In case of significant differences ($p < 0.05$) p values are in bold.

Macrobenthos	Main test			Pair-wise test	
	Reef x location			BMSM	Boulogne
	MS	Pseudo-F	p value	p value	p value
Species abundance N	88.97	90.58	**0.0001**	**0.0001**	**0.0001**
Species richness S	361.25	47.19	**0.0001**	**0.0001**	**0.0001**
Shannon diversity index H'	5.32	27.61	**0.0001**	0.1249	**0.0001**
Pielou's eveness index J'	0.05	5.65	**0.021**	**0.0001**	**0.0001**

Epibenthos	Main test			Pair-wise test		Main test			Pair-wise test			
	Reef x Period			Spring	Autumn	Reef x location x Period			BMSM – S	BMSM – a	Boul – S	Boul – A
	MS	Pseudo-F	p value	p value	p value	MS	Pseudo-F	p value	p value	p value	p value	p value
Species abundance N	–	–	–	–	–	1.14×10^6	4.87	**0.0259**	**0.032**	0.7008	0.1993	**0.0283**
Species richness S	0.1	5.93	**0.0243**	**0.0049**	0.7291	–	–	–	–	–	–	–
Shannon diversity index H'	–	–	–	–	–	0.65	6.81	**0.0142**	0.5205	0.7038	0.2989	**0.0284**
Pielou's eveness index J'	–	–	–	–	–	0.19	9.69	**0.0056**	0.1161	0.2046	0.8062	**0.0273**

Hyperbenthos	Main test			Main test			Main test		
	Reef			Location			Period		
	MS	Pseudo-F	p value	MS	Pseudo-F	p value	MS	Pseudo-F	p value
Species abundance N	7.83×10^6	6.48	0.0107	–	–	–	–	–	–
Species richness S	–	–	–	1210.3	30.11	0.0001	463	11.52	0.0048
Shannon diversity index H'	–	–	–	–	–	–	–	–	–
Pielou's eveness index J'	0.14	4.93	0.0421	–	–	–	–	–	–

Appendix F. Sequential tests of the distance-based linear model (DistLM) analyses on the macro-, epi-, and hyperbenthic communities. Analyses were run on a Bray—Curtis resemblance matrix of fourth-root transformed data. Both environmental (grain size, mud content, TOM, MPB, Chl *a* and SPM) and biotic (*L. conchilega* density, macrobenthic N, S and H′) variables were included and (log or square-root) transformed if needed.

Variable	Adj. R^2	Pseudo-F	P	Prop.	Cumul
Macrobenthos					
L. conchilega dens.	0.14004	13,865	0.0001	0.15093	0.15093
Mud content	0.22105	9.1122	0.0001	0.08984	0.24077
Grain size	0.25631	4.6505	0.0003	0.04377	0.28455
SPM	0.28844	4.4322	0.0002	0.03992	0.32447
TOM	0.30225	2.4837	0.0112	0.02193	0.34641
Chl *a*	0.31378	2.2431	0.022	0.01948	0.36589
MPB	0.31632	1.2716	0.2434	0.011	0.3769
Epibenthos					
SPM	0.13645	5.1084	0.0002	0.16967	0.16967
Macro *H*	0.22836	3.9778	0.0029	0.11805	0.28772
Macro *N*	0.43200	9.6046	0.0001	0.20982	0.49754
Chl *a*	0.52240	5.3532	0.0001	0.09833	0.59588
TOM	0.55197	2.4521	0.0124	0.04225	0.63813
Grain size	0.58565	2.7069	0.0072	0.04313	0.68127
Hyperbenthos					
TOM	0.12465	4.4176	0.0002	0.16112	0.16112
Chl *a*	0.25446	5.0045	0.0002	0.15546	0.31658
SPM	0.43174	7.8636	0.0001	0.18619	0.50277
Grain size	0.50219	3.9719	0.0001	0.08238	0.58516
MPB	0.54569	2.915	0.0002	0.05517	0.64034
Macro *S*	0.57696	2.4043	0.0097	0.04237	0.68272
Macro *N*	0.59030	1.5861	0.1046	0.02707	0.70979

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