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Diversity, structures assemblages and production of benthic communities on artificial reefs, a comparative case study in the English Channel

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Abstract. In this study, the diversity and structures assemblages of benthic communities present on artificial reefs (AR) immersed for 5 years were monitoring during a full year in 2020. The comparison of two different sites Bernières in the Bay of Seine and Cherbourg in the central part of the English Channel brings innovative results on the efficiency of such structures. Benthic fauna and macroalgae communities were studied; several biotic indices like Shannon-Wiener diversity index were calculated. Benthic fauna was classified according to their trophic group and the biomass was estimated. Our results pointed out strong differences for several indicators between sites and seasons. Benthic fauna was more abundant in the Bay of Seine and more diversified than in the Bay of Cherbourg. Primary producers' diversity and biomass were higher in the Bay of Cherbourg and dominated by Rhodophyceae species. Primary production results showed that the Bay of Cherbourg was a more productive system than the Bay of Seine. This study highlighted the efficiency of such structures to create habitats and promote biomass and diversity of associated living communities. In comparable conditions, different systems were highlighted: a "primary producer reef" and a "primary consumer reef".

1. Introduction

Artificial reefs (ARs) are man-made structures emplaced in aquatic environments that serve as habitats or shelters for organisms. AR have long been used to attract fish and the development of these structures has been intensified over the three last decades [1–3]. These structures are usually expected to produce an overall increase in species richness by protecting some species, and also an increase and diversification of trophic contributions [4–6]. The improvement in habitat is generally reflected in greater food availability and more shelter against predators, as well as new recruitment areas for juveniles of various species (benthic invertebrates or fish), which explains the increase in organism biomass associated with these structures after their installation [7,8]. The ecological value of artificial



structures as habitats for native species can vary in relation to many structural and environmental factors [9–11]. In this study, the biodiversity, the trophic assemblages and the production associated to AR have been investigated. The comparison of identical structures in two different sites along the French coasts of the English Channel brings important indications on the elevated success rate of such projects in order to restore impacted ecosystems. This study also provides important understanding on the biodiversity – production relation. Moreover, the seasonal monitoring of several biological and environmental parameters over a full year after five years of immersion brings reliable data on the benthic communities (producers and consumers) associated to a stable hard substrate ecosystem.

2. Materials & Methods

2.1. Sampling sites

AR were deployed in two different macrotidal sites (Bay of Cherbourg, CHER and Bay of Seine in Bernières-sur-mer, BERN) in 2015. These AR were designed and immersed within the European project RECIF and were used as an example of artificial substrate in the European Interreg Va project MARINEFF (2018-2022). The first site CHER is characterised by a sandy bottom area while the second site BERN is characterised by sandy-rocky bottom area. In both sites, the low tide bathymetry is about 4 m. At CHER, the AR was made up of 12 modules grouped in 3 clusters to create a triangle structure and only 3 modules in BERN. Each module is 3 m long, 2 m wide and 1.35 m high (8,1 m³ each module - 32,4 m³ by cluster - 97,2 m³ in total at CHER). The modules were constructed in three levels (Figure 1), the first level was a supporting base to avoid sinking; the second level was made up of solid concrete pillars and empty concrete drains; the third level was a metal cage filled with cinder blocks. The dimensions of each cinder blocks were 0.4 m long by 0.2 m wide by 0.2 m high. These cinder blocks were made with porous concrete.

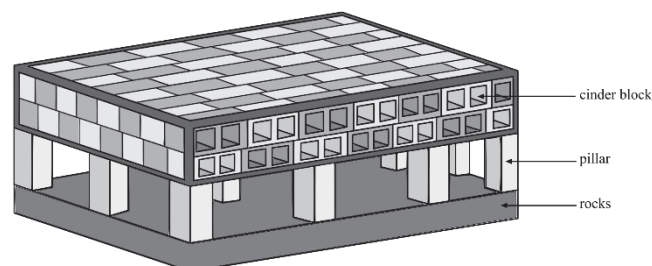


Figure 1. Representation of one AR module.

2.2. Sample collection

2.2.1. Benthic communities and production. The sampling of benthic communities was conducted from December 2019 to September 2020. Three campaigns were performed in BERN and four at CHER. At each campaign, six cinder blocks of the upper face of the modules were sampled randomly and taken back to the laboratory for analysis. In order to prevent any loss of fauna, each cinder block was carefully disposed in a planktonic net (500 μm) then closed and brought back to the boat. Each cinder block was conserved separately in a tank until the transport to the marine station of Luc-sur-mer. Then they were conserved in their planktonic net in several large basins with an open sea water renewal. Each cinder block was first incubated in a hermetic box with controlled lighting in the large basin in order to record the cinder block production. During each incubation, photoactive radiation (PAR) was recorded with a RBR solo3 PAR logger connected to a Li-COR “Underwater Quantum Sensor” LI-192. Dissolved oxygen (mg O₂.L⁻¹) was recorded with an EXO Optical Dissolved Oxygen Sensor hermetically connected to the system. Each incubation consisted of seven different light conditions (dark 1 – PAR 1 – PAR 2 – PAR 3 – PAR 4 – PAR 5 – dark 2). Oxygen production was calculated as the slope of the linear regression of O₂ concentration against incubated time per light condition and expressed in $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$, after integration of water volume contained in the box (58.8 L) and the cinder block surface. The gross primary production (GPP) was calculated for each PAR condition as the addition of the

respiration (dark 2 condition) and the net primary production (NPP) of the selected condition. After the incubation, all macroalgae were sampled and conserved at -20°C for species identification and biomass estimation. The biomass of each species was determined and expressed Ash-Free Dry Weight (AFDW) per m^2 (loss of weight of dry organisms after 5h at 500°C). Ash Free Dry Weight biomass was converted to carbon content using a conversion factor of 0.35 [12,13]. Macroalgae species were assigned to their class (Ulvophyceae, Rhodophyceae or Phaeophyceae). Then, the cinder block was fixed in 10% formaldehyde, rinsed and scraped carefully in order to sample all organism which were preserved in 70% ethanol, identified to the lowest possible taxonomic level and counted (sieved on 0.5 mm diameter). The biomass of each taxonomic group was determined and expressed in terms of AFDW per m^2 (loss of weight of dry organisms after 5h at 500°C). Ash Free Dry Weight biomass was converted to carbon content using a conversion factor of 0.518 [14]. Benthic invertebrates were assigned to six trophic groups: grazers (Gr), filter feeders (FF), predators (Pr), scavengers – omnivorous (Scv/O), sub-surface deposit feeder (ssDF) and surface deposit feeder (sDF). The community structure analysis was based on the taxonomic richness, the Shannon-Wiener diversity index H' and the Pielou evenness index J' . The taxonomic richness corresponded to the total number of taxa recorded on the six cinder blocks sampled at each campaign. Both indices, H' and J' using \log_2 were calculated for each campaign too.

2.2.2. Abiotic parameters and inorganic nutrient analyses. In the same time, high frequency measurements using the SMILE instrumented buoy located in the Bay of Seine ($0^{\circ}19'41.00''\text{O}$ $49^{\circ}21'14.00''\text{N}$) near BERN was collected (data available doi.org/10.17882/53689). Conductivity and temperature (tetracon sensor, WTWTM), turbidity (Seapoint turbidity meter, Seapoint Sensor), oxygen (AADI Oxygen optode, Anderraa) and fluorescence (Cyclops-6K, Turner Design) were combined in an automatic NKE instrumentation (MP7, NKE Instrumentation[®]). PAR (photosynthetically active radiation) was measured with Saltanics sensor. For the inorganic nutrient analyses, a water sample was collected at each campaign in CHER and in autumn at BERN. Each sample was filtered using cellulose acetate filter (ClearLine, CA, 33mm, $0.45\ \mu\text{m}$) in 50 mL falcon tube and frozen (-20°C). Analysis were conducted using a Seal Analytical AA-3 system [15]. The limits of quantifications were $0.02\ \mu\text{mol.L}^{-1}$ for PO_4^{3-} and $0.05\ \mu\text{mol.L}^{-1}$ for NO_3^- , NO_2^- and Si(OH)_4 . NH_4^+ were analysed by fluorometric measurements according to the protocol of Oriol et al. (2014). N_{tot} was calculated as follow: $\text{N}_{\text{tot}} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$.

2.3. Data treatment and analysis

Data analysis was performed with R i386 3.5.1 [17]. The non-parametric Kruskal-Wallis test was used to find differences in benthic macrofauna between sites and seasons in terms of species richness, abundance, biomass, Pielou's evenness index J' and Shannon-Wiener diversity index H' .

3. Results

3.1. Biotic indices and structure assemblages

A total of 40 macrofauna taxa was recorded, 35 in BERN and 37 in CHER, considering all the campaigns. Results showed that Shannon-Wiener diversity index and Pielou evenness index were significantly higher in CHER than at BERN at every season. These results indicate that CHER site hosted more diversified communities than BERN, (H') even if CHER seemed more dominated by one species in comparison with BERN (J'). Contrarily, the total biomass was significantly higher in BERN than CHER for all surveys. No significant differences were measured for taxonomic richness and abundance between the two sites and the different campaigns (Tables 1 and 2). In BERN during the winter, the most abundant taxa (> 30 individuals per m^2) were Amphipoda (86 per m^2), Aphroditidae (30 per m^2), *Pilumnus hirtellus* (178 per m^2) and *Pisidia longicornis* (90 per m^2). Spring was dominated by Amphipoda (230 per m^2), Aphroditidae (268 per m^2), Caprellidae (97 per m^2), Isopoda (70 per m^2), Nemertea (46 per m^2), Ophiuridae (190 per m^2), *Pilumnus hirtellus* (148 per m^2), *Pisidia longicornis* (84 per m^2), *Porcellana platycheles* (52 per m^2), Sabellidae (79 per m^2), Serpulidae (77 per m^2), Syllidae (44 per m^2) and Tanaidacea (91 per m^2). Autumn season was dominated by Amphipoda (239 per m^2),

Aphroditidae (102 per m²), Bivalvia (140 per m²), Caprellidae (35 per m²), Isopoda (373 per m²), Lysianassidae (33 per m²), Ophiuridae (129 per m²), *Pilumnus hirtellus* (270 per m²), *Pisidia longicornis* (340 per m²), *Porcellana platycheles* (40 per m²), Sabellidae (83 per m²), Serpulidae (58 per m²), Tanaidacea (88 per m²). In CHER, winter was dominated by Bivalvia (30 per m²), Isopoda (47 per m²), Ophiuridae (53 per m²), summer by Amphipoda (42 per m²), Cirratulidae (24 per m²), Dynamenae (55 per m²), Isopoda (38 per m²), Nereidae (43 per m²), *Pisidia longicornis* (70 per m²). Autumn was dominated by Amphipoda (184 per m²), Aphroditidae (40 per m²), Ascidiacea (35 per m²), Balanomorpha (112 per m²), Bivalvia (121 per m²), Capitellidae (69 per m²), Cirratulidae (67 per m²), Dynamenae (48 per m²), Ectoprocta (96 per m²), Eunicidae (219 per m²), Gastropoda (39 per m²), Isopoda (124 per m²), Lysianassidae (49 per m²), Ophiuridae (56 per m²), Phyllodocidae (30 per m²), *Pilumnus hirtellus* (59 per m²), *Pisidia longicornis* (48 per m²), Porifera (35 per m²), Sabellidae (32 per m²) and Serpulidae (35 per m²). Finally, winter was dominated by Ascidiacea (50 per m²), Eunicidae (43 per m²), Ophiura (64 per m²) and Sabellaria (31 per m²).

Table 1. Main characteristics of macrofauna with different univariate indices for both sites and all seasons. H': Shannon-Wiener diversity index; TR: Taxonomic Richness; J': Pielou's evenness index; A: Abundance (number of individuals.m⁻²) and B: biomass (g AFDW.m⁻²). Significant differences (p-value < 0.05) are indicated by letter (a, b).

	Cherbourg (CHER)				Bay of Seine (BERN)			
		Winter	Spring	Summer	Autumn	Winter	Spring	Autumn
Macrofauna	H'	3.95 ^a	4.17 ^a	4.24 ^a	4.45 ^a	3.10 ^b	3.77 ^b	3.69 ^b
	TR	26	27	31	33	28	30	29
	J'	0.84 ^a	0.88 ^a	0.86 ^a	0.88 ^a	0.65 ^b	0.77 ^b	0.76 ^b
	A	400	374	490	1071	524	1563	2078
	B	1.49 ^a	1.06 ^a	1.62 ^a	2.39 ^a	3.75 ^b	4.6 ^b	2.5 ^b

Table 2. Results of the non-parametric Kruskal-Wallis test on five parameters between the two sites. H': Shannon-Wiener diversity index; TR: Taxonomic Richness; J': Pielou's evenness index; A: Abundance; B: biomass (g AFDW.m⁻²); Df: Degrees of Freedom; F: F-ratio score; BERN: Bay of Seine; CHER: Bay of Cherbourg.

	Df	p-value	Interpretation
H'	1	0.03389	BERN≠CHER
TR	1	1	BERN=CHER
J'	1	0.03389	BERN≠CHER
A	1	0.0771	BERN=CHER
B	1	0.03389	BERN≠CHER

The 40 taxa were assigned to six trophic groups. Abundance and biomass of these trophic groups on both sites and during the entire survey are represented in the figure 1. In BERN, the total abundance was higher in autumn than in the rest of the year (Figure 2A). In winter, filter feeders and predators were the most abundant trophic groups (143 and 193 individuals per m²). In spring, the most abundant group was scavengers – omnivorous benthic invertebrates (590 individuals per m²) followed by filter feeders one (296 individuals per m²). Finally, in autumn the most abundant group was the filter feeders (523 individuals per m²) immediately followed by the surface deposit feeders (507 individuals per m²). As for BERN, the total abundance of benthic invertebrates was higher in autumn for CHER (Figure 2B). The variations in term of abundance from winter to summer were non-significant in CHER. However, the abundance of filter feeders, predators and sub-surface deposit feeders reached respectively 358, 397 and 564 individuals per m² in autumn. Some significant differences could be noted between the two

sites, especially for spring were the abundances of some trophic groups like scavengers – omnivorous or filter feeders were three to six times higher in BERN. In term of biomass in BERN (Figure 2C), filter feeders were the main contributors with 56% of the total AFDW biomass in winter, 84% in spring and 76% in autumn. Predators represent 38% of the total AFDW biomass in winter, 10% in spring and 5% in autumn. Some trophic groups like scavengers – omnivorous or surface deposit feeders represent a very small part of the total AFDW biomass in comparison with their large abundances. In CHER, the main contributors were filter feeders with 27% of the total AFDW biomass in winter, 48% in spring, 56% in summer and 29% in autumn. Predators represent also a large part of the total biomass with 63% in winter, 41% in spring, 38% in summer and 17% in autumn. Moreover, sub-surface deposit feeders represented the higher percentage of total biomass in Autumn (39%) against 6% in the Bay of Seine at the same period.

A total of 18 different macroalgae species was recorded, 9 in BERN and 15 in CHER considering all campaigns. *Cryptopleura ramosa*, *Dictyota dichotoma*, *Heterosiphonia plumosa*, *Hypoglossum hypoglossoides*, *Kallymenia reniformis*, *Plocamium cartilagineum*, *Sphaerococcus coronopifolius*, *Sphondylothamnion multifidum* and *Ulva* sp. were recorded in The Bay of Seine. *Ahnfeltiopsis devoniensis*, *Bornetia secundiflora*, *Calliblepharis jubata*, *Cladophora pellucida*, *Cryptopleura ramosa*, *Halurus flosculosus*, *Hypoglossum hypoglossoides*, *Kallymenia reniformis*, *Laminaria digitata*, *Plocamium cartilagineum*, *Sargassum muticum*, *Sphaerococcus coronopifolius*, *Sphondylothamnion multifidum*, *Vertebrata byssoides* and *Vertebrata fruticulosa* were recorded in CHER. The table 3 summarise the AFDW biomass ($\text{gC}\cdot\text{m}^{-2}$) for each macroalgae class in CHER and BERN. The total biomass was higher in CHER than in BERN at each season. Macroalgae community in CHER was dominated by Rhodophyceae (between 1.253 and 1.464 $\text{gC}\cdot\text{m}^{-2}$) and some Ulvophyceae and Phaeophyceae were recorded in autumn (respectively 0.292 and 0.162 $\text{gC}\cdot\text{m}^{-2}$). In CHER, macroalgae community was also dominated by Rhodophyceae but in higher quantities (between 14.617 $\text{gC}\cdot\text{m}^{-2}$ in winter and 64.743 $\text{gC}\cdot\text{m}^{-2}$ in summer). Moreover, Phaeophyceae were recorded at each campaign and some Ulvophyceae in early winter (0.011 $\text{gC}\cdot\text{m}^{-2}$).

3.2. Primary production

The figure 3 shows the incubations results. The GPP and NPP were calculated at saturation light and the respiration was obtained from dark condition at the beginning of each incubation. The saturation light obtained for the BERN AR incubation was 933 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and 714 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for CHER. NPP incubation results were strongly different between both sites. In BERN, between spring and autumn, the total respiration was negative with -2,788 +/- 972 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ and -1,706 +/- 1,168 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ respectively. The consequence of this strong oxygen consumption in BERN was a negative GPP for all seasons. Indeed, the GPP decreased between winter and autumn from 3,512 +/- 7,205 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ to 1,165 +/- 1,659 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. There was no production measured during spring season for any of the six incubated AR. In CHER, the NPP was always positive. It showed a decrease between winter and spring from 12,907 +/- 5,958 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ to 695 +/- 2,965 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ before reached 16,344 +/- 7,632 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in summer and 13,875 +/- 4,555 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in Autumn. The total respiration was almost null between winter and spring (-1,484 +/- 371 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ and 283 +/- 93 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ respectively) and reached -3,174 +/- 769 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ and -2,336 +/- 615 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in summer and autumn. Contrarily to BERN, the GPP in CHER was always positive. Between winter and spring, it decreased from 14,391 +/- 6,256 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ to 978 +/- 2,918 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. It increased until 19,518 +/- 7,748 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in summer and stay stable at 16,212 +/- 4,735 $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in autumn.

Table 3. AFDW biomass in g C.m⁻² for each identified macroalgae class (Ulvophyceae, Phaeophyceae and Rhodophyceae) in the Bay of Seine (BERN) and the Bay of Cherbourg (CHER) for each campaign.

Site	Season	AFDW biomass (gC.m ⁻²)		
		Ulvophyceae	Phaeophyceae	Rhodophyceae
BERN	Winter	0	0	1.464
	Spring	0	0	1.418
	Autumn	0.292	0.162	1.253
CHER	Winter (February)	0	1.069	14.617
	Spring	0	0.283	25.360
	Summer	0	4.223	64.743
	Autumn	0	0.493	36.575
	Winter (November)	0.011	0.478	41.130

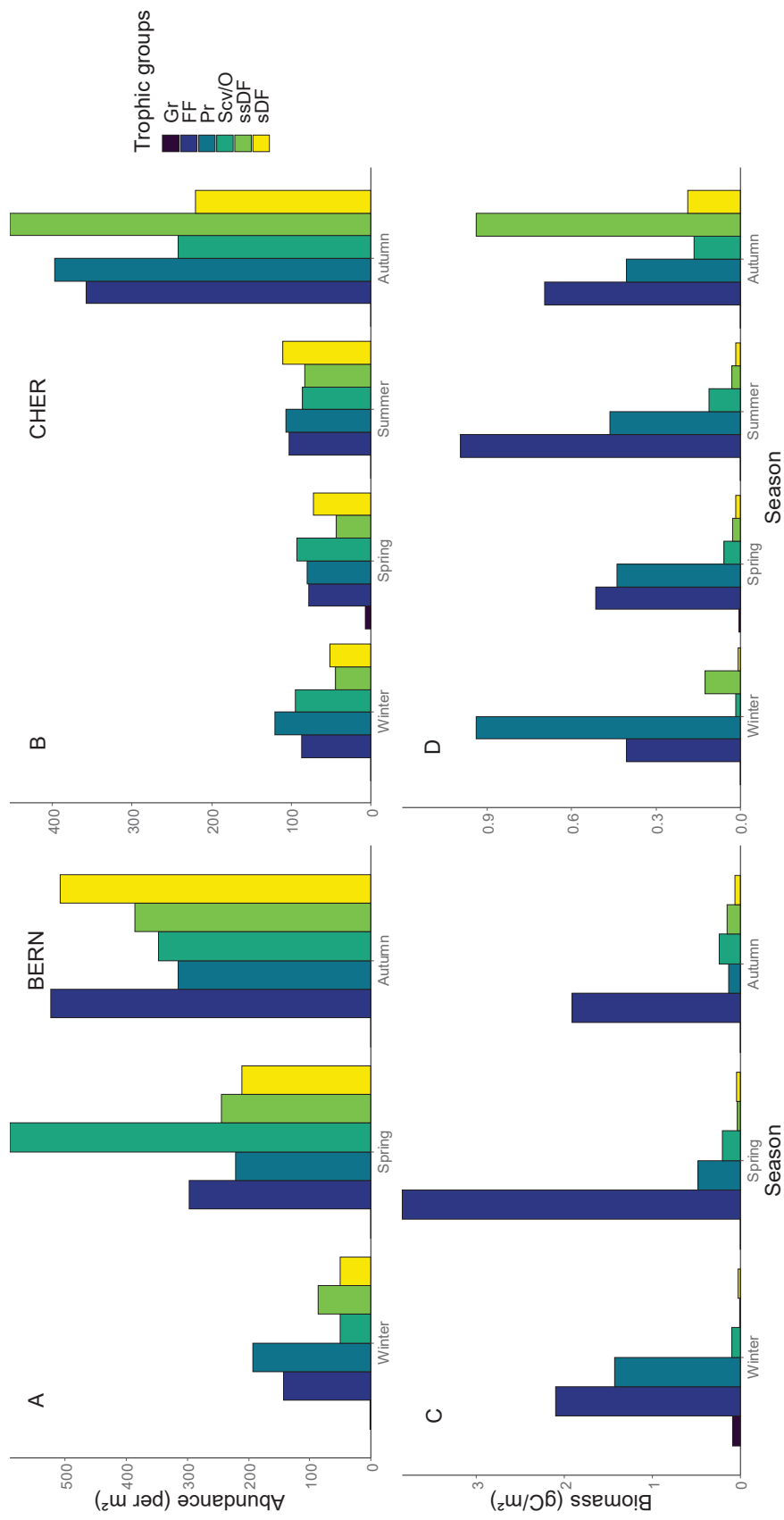


Figure 2. Abundance (A, B) and percentage of total AFDW biomass per season (C, D) of trophic groups in the Bay of Seine (A, C) and the Bay of Cherbourg (B, D) for every season. Trophic groups: grazers (Gr), filter feeders (FF), predators (Pr), scavengers – omnivorous (Scv/O), sub-surface deposit feeder (ssDF) and surface deposit feeder (sDF).

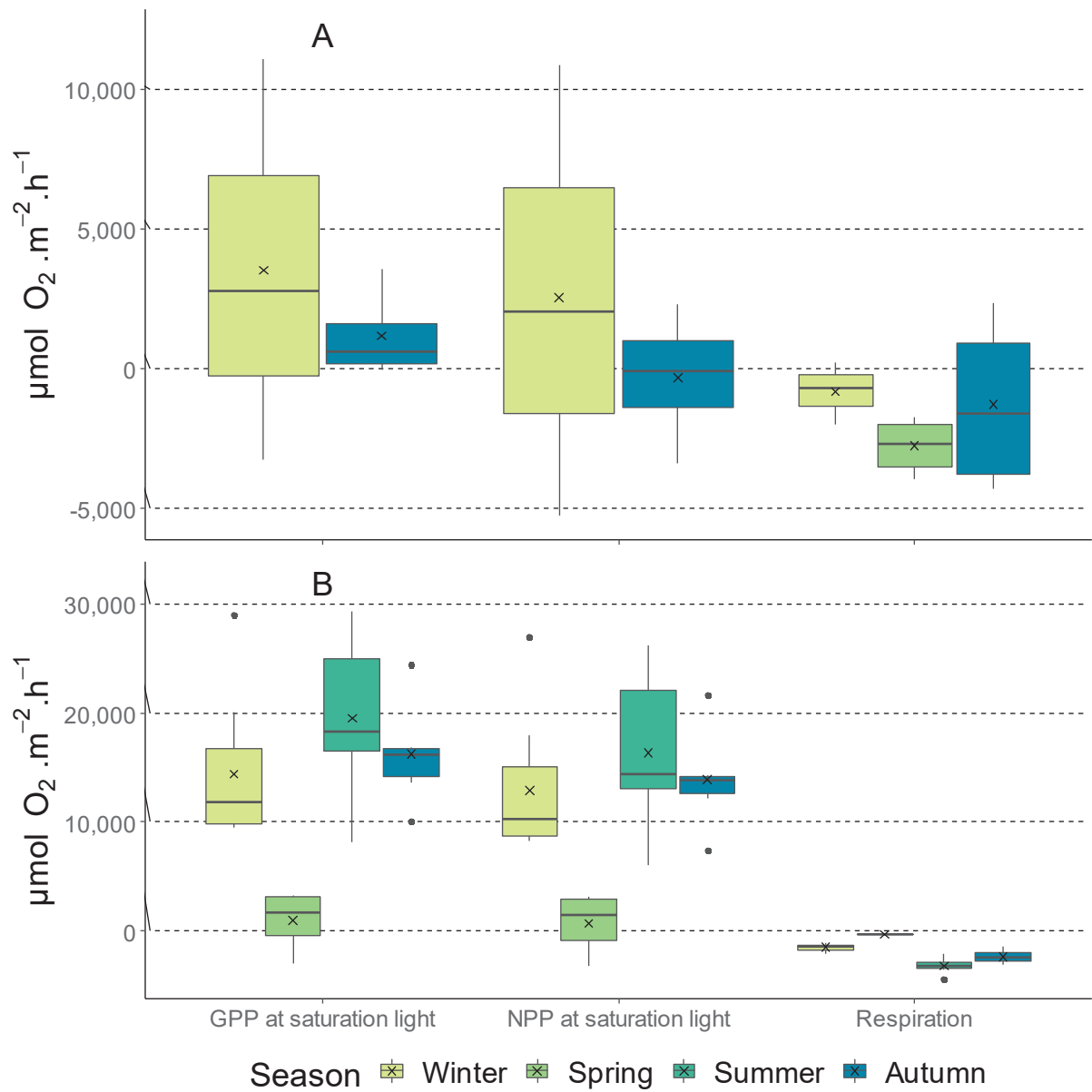


Figure 3. Gross primary production (GPP), respiration and net primary production (NPP) incubation results in $\mu\text{mol O}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ per cinder block at saturation light and at each season in BERN (A) and CHER (B).

The table 4 showed the monitored environmental parameters during the survey.

Table 4. Environmental parameters at each site during the survey.

	BERN			CHER			
	Winter	Spring	Autumn	Winter	Spring	Summer	Autumn
Temperature (°C)	10	14	20		14	16	17
Salinity	33.36	33.26	33.39	33.40	34.30	34.60	34.56
PAR ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	8	134	43				
pH	7.97	7.99	7.88				
Turbidity (NTU)		5.00	88.40			0.70	0.60
Dissolved oxygen (mg/L)	6.23	6.45	5.24				
MES (mg/L)	13.80	4.43	1.57				
Chlorophyll <i>a</i> ($\mu\text{g/L}$)	0.66	4.36	1.05		1.33	1.54	0.87
NO _{TOT} ($\mu\text{mol/L}$)	24.88	9.00	2.16	11.81	2.20	0.17	3.31
PO ₄ ³⁻ ($\mu\text{mol/L}$)	0.81	0.75	0.12	0.53	0.03	0.03	0.30
SiOH ₄ ($\mu\text{mol/L}$)	15.64	1.09	6.11	5.30	1.52	1.41	3.39
NH ₄ ⁺ ($\mu\text{mol/L}$)	1.36	0.94	0.80				

4. Discussion

Firstly, experimental sites showed high environmental differences such as hydrodynamism, tide amplitude, currents velocity or water turbidity. Indeed, CHER is a much more protected area than BERN due to the long dike. One of the consequences of this manmade structure is that the hydrodynamism and the tide influence on local currents is completely different and reduced in comparison with the open bay of Seine. Secondly, the water parameters were also very different between both sites. BERN is located in the bay of Seine under rivers influence where abiotic parameters showed important variations. The water turbidity is much higher in BERN than in CHER, inorganic nutrients concentration is also strongly higher in BERN than in CHER. Considering these disparities, the comparison of several biotic variables on identic AR immersed in both sites since 2015, it is interesting to study the benthic communities' assemblages and successions. Several structural factors such as depth, orientation, age and surface complexity may influence the structure and the diversity of benthic communities [1,11,18,19]. In order to eliminate some of these factors like orientation, the sampling was carried out on each artificial reef cluster in both sites.

The benthic fauna recorded in CHER showed a more diverse community than in BERN (H'). The total biomass was significantly higher in BERN than in the CHER. In order to have a functional approach, benthic fauna was assigned to several trophic groups. For both sites, the maximal of abundance was reached in autumn as illustrated by the figure 2. In term of biomass, they were high differences between sites and seasons. Indeed, in BERN, the total biomass per season was always dominated by filters feeders and, in smaller proportions, predators in winter. In CHER, the benthic fauna was also dominated by filters feeders and predators in spring and summer. The benthic community was dominated by sub-surface deposit feeders in autumn (followed by filters feeders and predators) and by predators in winter. These results indicated that the trophic webs in both sites were very different with a more complex system with distinct seasonal successions in CHER. Moreover, at the same season, the dominant trophic groups were different between both sites. For example, in autumn, the benthic fauna community in BERN was completely dominated by filters feeders and in CHER, a more diversified structure was assessed with sub-surface deposit feeders, filters feeders and predators. These ecosystems were

considered as stable because of the long immersion time of the AR (from 2015). The only two different ways to avoid over-competition between marine organisms is the food source separation and habitat specialisation. Considering that the immersed structures were the same, the recorded differences of fauna trophic structure between sites may be induced by abiotic factors (hydrodynamism, salinity, temperature...) and surrounding communities present before the artificial reef immersion. Water temperature is known to influence the metabolism of a large part of marine organisms and may explained the lower abundance for every trophic groups recorded on both sites in winter [20–22]. These results tend to confirm the efficiency of such structures to create novel habitats and restore hard substrate communities. Indeed, our results showed high similarities with natural reef investigations in this region indicating that AR immersion reproduced natural reef ecosystem [23].

The investigation of relations between benthic fauna and macroalgae in AR systems have been poorly investigated [24]. The results obtained on macroalgae communities showed a significant higher diversity in CHER than in BERN (15 against 8 species in total). In BERN, the diversity and total biomass were higher in autumn in comparison with the rest of the year. Ulvophyceae and Phaeophyceae species were recorded only in autumn on this site. In CHER, total biomass and diversity were higher in summer, Ulvophyceae species were recorded only in winter. Moreover, *Sargassum muticum*, an invasive species, was recorded almost all the year in CHER and never in BERN. These results indicated that CHER AR supports a more diversified primary producers' community as for the benthic fauna. The structural differences between macroalgae communities on both sites may be explained by abiotic factors like turbidity, available PAR or inorganic nutrient availability. As for benthic fauna communities, macroalgae may be influenced by the structure, material and surface heterogeneity of the AR which cannot be the case here because of the AR homogeneity between sites [25,26]. However, even if the inorganic nutrient concentration especially N_{tot} were higher BERN than in CHER, the higher biomass and diversity were recorded in CHER. These results may be explained in part by the elevated water turbidity in the BERN and by the strong tidal currents in comparison with CHER [27,28]. Macroalgae communities were strongly dominated by *Cryptopleura ramosa* for BERN AR and by *Kallymenia reniformis* and *Sphaerococcus coronopifolius* for CHER. Several species recorded during the monitoring, such as *Calliblepharis jubata*, *Heterosiphonia plumosa* or *Sacchoriza polyschides* in CHER correspond to protected area indicative species of Atlantic reef ecosystems. However, the dominant ones correspond to exposed area indicative species of Atlantic reef ecosystem (i. e. *Kallymenia reniformis*) [23]. The large majority of these species corresponds to hard substrates habitat species; however, CHER is an area dominated by sandy seabed and a strong proportion of the macroalgae recorded in this study were not considered before as determinant species for this area. These original results for this area needed to be considered for future environmental assessment in CHER and dominant species recorded in this study may be considered as determinant ones. Generally, these results tend to confirm the good efficiency of these structure to restore or create novel habitats because recorded macroalgae communities corresponds to those observed in near rocky areas [29]. Non-indigenous species establishment in AR associated ecosystem have been largely studied and the immersion of such structures may promote their colonization [30,31]. *Sargassum muticum* is originated from Asia and already well implanted in the English Channel [32,33]. Its presence all the year at CHER and its absence in BERN was surprising and difficulted to explain because of its abundance along the English Channel coast.

The primary production results obtained by incubations (at saturation light) showed significant differences between sites and seasons. Not surprisingly because of the higher macroalgae biomass, AR in CHER were the most productive ones. In CHER, the higher production was recorded during the summer. This result corresponds to the season with higher macroalgae biomass and diversity on this site. The GPP reached $19,518 \pm 7,748 \mu\text{mol O}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ in summer in CHER, in comparison the maximal GPP in BERN was reached in autumn and was negative. The maximal respiration was recorded in summer in CHER and also correspond to the most productive season on this site. The autumn in CHER showed also a high GPP and high oxygen consumption. However, a relatively low macroalgae diversity

was recorded in autumn on this site (3 different species). The higher respiration results recorded in summer and autumn for CHER corresponded to the seasons with the higher diversity index (H') and total benthic fauna biomass. These results showed that the associated AR ecosystem in CHER was more productive than BERN for each season. The relatively poor macroalgae biomass in the BERN was not sufficient to compensate the consumed oxygen, especially during the winter season where the NPP and respiration were strongly negative. The lower saturation light for CHER incubations ($714 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) in comparison with BERN ($933 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) indicated that CHER communities were more able to realise the photosynthesis at lower PAR. These results may be induced by the important Rhodophyceae community in CHER, indeed, these macroalgae are known for high photosynthetic efficiency at low light levels and may contribute to the high oxygen production measured for this site [34,35]. These results suggested a better photoacclimatation of CHER primary producers' communities and the needed of higher PAR quantity for BERN. In the same sea, at the same depth, in the same area, but in different water masses, two types of AR functioning were highlighted: One is a "primary producer reef" rich in macroalgae, CHER, and the second is a "primary consumer reef" where production is based on phytoplankton resources, BERN.

5. Conclusion

This study provided innovative results on the biodiversity and the trophic structure associated to AR immersed since several year in two different ecosystems of the English Channel. Our results showed important and diverse benthic fauna communities for both AR sites. The Bay of Cherbourg showed higher diversity and biomass of primary producers, dominated by Rhodophyceae macroalgae. However, the BERN AR showed a more diversified and abundant benthic fauna community than CHER. Primary production results showed significant differences between site; indeed, AR in CHER were more productive than BERN possibly because of the Rhodophyceae abundance on this site. In comparable conditions, two different ecological functioning were highlighted for identical AR structures, indeed, a strong "primary producer AR" were described in CHER and a "primary consumer AR" BERN. More generally, our results showed the great efficiency of such structures to create or restore habitats and promote biomass and diversity of associated living communities.

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