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Title

Renewable energy homes for marine life: habitat potential of a tidal energy project for benthic megafauna

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Abstract:

An increasing number of offshore structures are being deployed worldwide to meet the growing demand for renewable energy. Besides energy production, these structures can also provide new artificial habitats to a diversity of fish and crustacean species. This study characterises how concrete mattresses that stabilise the submarine power cable of a tidal energy test site can increase habitat capacity for benthic megafauna. A five-year monitoring, which relied on both visual counts and video-based surveys by divers, revealed that these mattresses provide a suitable habitat for 5 taxa of large crustaceans and fish. In particular, two commercially valuable species, i.e. the edible crab *Cancer pagurus* and the European lobster *Homarus gammarus,* showed a constant occupancy of these artificial habitats throughout the course of the project. The shape and the number of shelters available below individual mattresses largely determine potential for colonisation by mobile megafauna. Local physical characteristics of the implantation site (e.g. substratum type, topography, exposition to current *etc*.) significantly impact amount and type of shelters provided by the concrete mattresses. Thus, to characterise habitat potential of artificial structures, it is not only essential to consider (*i*) the design of the structures, but also to (*ii*) account for their interactions with local environmental conditions when deployed on the seafloor.

Keywords

Artificial habitats ; Marine renewable energy ; Crustacean ; Fish ; Habitat

Abbreviations

MRE, Marine Renewable Energy; GLMM, generalised linear mixed models; LMM, linear mixed models; PCA, principal component analysis; RDA, redundancy analysis

1. INTRODUCTION

Artificial reefs are man-made structures placed on the sea bed in aquatic habitats for different purposes, for instance to mimic characteristics of natural reefs such as substrate and/or shelter provision to associated organisms (Bohnsack et al., 1991; Jensen et al., 2000a; Thierry, 1988). Development of artificial reefs may locally increase both hard substratum availability and habitat heterogeneity (especially when deployed on soft-sediment bottoms), which can consequently lead to higher densities and biomass of fish and decapods (Bohnsack et al., 1994; Bombace et al., 1994; Langhamer and Wilhelmsson, 2009).

Enhancement of associated benthic diversity by artificial reefs depends both on reef properties and on local environmental characteristics. Colonisation success depends on artificial reef shape and size, constitutive material, orientation and degree of complexity, that directly determine habitat, and refuge availability (Charbonnel et al., 2002; Ferreira and Coutinho, 2001; Hackradt et al., 2011; Sherman et al., 2002). A range of local environmental factors (*e.g.* neighbouring habitat type, hydrological features, amplitude of seasonal variation) can significantly influence the amount and the diversity of colonising organisms (Bohnsack et al., 1991; Bombace et al., 1994; Godoy et al., 2002; Noh et al., 2017). A long-standing scientific debate persists between two dominant theories regarding the role of artificial reefs for mobile fauna: (i) the “attraction hypothesis” and (ii) the “production hypothesis” (Lima et al., 2019). The first assumes that artificial reefs only attract specimens from nearby ecological communities, without increasing overall biomass production (Bohnsack, 1989) while the latter advocates that artificial reefs increase abundance and biomass of associated species by enhancing habitat and food availability (Pickering and Whitmarsh, 1997; Polovina and Sakai, 1989). Literature shows that the two processes exist, the productive potential of artificial reef is indeed reef-dependant and varies according to an important number of factors (*e.g.* number and design of reef units, distance to natural reef, association with protected area *etc. ;* Pickering and Whitmarsh, 1997). Nevertheless, Lima et al. (2019) highlight that, despite several decades of scientific observations and experiments on the subject, separating the reef effect and the effects of changing environmental and socioeconomic conditions remains complex, impacting the assessment of artificial reefs performance.

Artificial reefs can be divided into two types: *i*) structures designed and installed specifically for their reef properties (for a variety of reasons *e.g.* ecosystems conservation/restoration, fish stocks enhancement, fisheries management *etc.*; Jensen, 2002) and *ii*) structures deployed for other purposes, such as oil platforms, breakwaters, or marine renewable energy (MRE) facilities (Langhamer, 2012; Lima et al., 2019; Wilson and Elliott, 2009). MRE facilities and associated structures (*e.g.* protection structures, submarine power cables, foundations, turbines *etc.*) are not only colonised by a variety of benthic organisms including algae, sessile epifauna and mobile macrofauna but also mobile megafauna (*i.e.* fish and decapods). A diversity of fish and large crustaceans can settle on artificial reefs deployed as part of MRE facilities (see Wilhelmsson and Langhamer, 2014 for a review). For example, commercially valuable crustacean species such as the European lobster (*Homarus gammarus*) or the edible crab (*Cancer pagurus*) can shelter around the foundations of offshore wind (Hooper and Austen, 2014; Krone et al., 2017) or wave farms (Langhamer and Wilhelmsson, 2009). Thus, such reef effects can represent an ecological benefit of MRE, since artificial structures generally host higher diversity, densities and biomass of benthic organisms than the surrounding soft bottoms (Broadhurst and Orme, 2014; Dannheim et al., 2020; Langhamer and Wilhelmsson, 2009). Wilson and Elliott (2009) estimated that in the long term, a wind-turbine facility provides 2.5 times the amount of habitat relative to the initial loss during the installation process, even though this new habitat may be of a different character to the initial one. When their deployment requires the implementation of new exclusion areas for fishing, MRE may thus act as a refuge for commercially-exploited populations, with potential spill-over benefits for adjacent stocks and fisheries (Lindeboom et al., 2015, 2011). However, the long-term reef effect associated with MRE facilities remains poorly characterised (Copping et al., 2016; Langhamer and Wilhelmsson, 2009; Lindeboom et al., 2015), especially within high hydrodynamic energy areas (as tidal energy sites; Copping et al., 2016).

The purpose of this study is to assess the role of habitat associated with MRE facilities using a French tidal energy test site as a case study. We specifically examined the habitat capacity of concrete mattresses that stabilise an unburied submarine power cable that connects the test site to the mainland. Based on a 4-year monitoring of fish and crustacean abundance on these mattresses, we (1) characterise the reef effect associated with MRE structures, and more specifically (2) how interactions between

artificial reefs and natural seafloor characteristics can determine diversity and abundance of associated megafauna.

2. METHODS

2.1 Study site

The study area consists of a 15 km-long submarine power cable (8 MVA - 10 kVDC) laid in 2012 by Electricité de France (EDF) to connect the tidal test site of Paimpol-Bréhat to the mainland (Brittany, France; Figure 1). Due to several setbacks in the project development, no electric current transited through the cable during the course of this study. An 11 km cable portion is unburied due to local seafloor characteristics (dominance of pebbles and presence of boulders; Figure 2.A) and stabilised by 120 concrete mattresses to prevent any cable displacement due to high hydrodynamic conditions. These mattresses are installed at depths ranging from 15 to 33 m and for the majority approximately 50 m apart (with some 200 m apart). The 6 m-long, 3 m-wide and 0.3 m-thick mattresses are made up of 73 concrete blocks linked together by an array of polypropylene rope, and a weight of ~10 t.

2.2 Target species

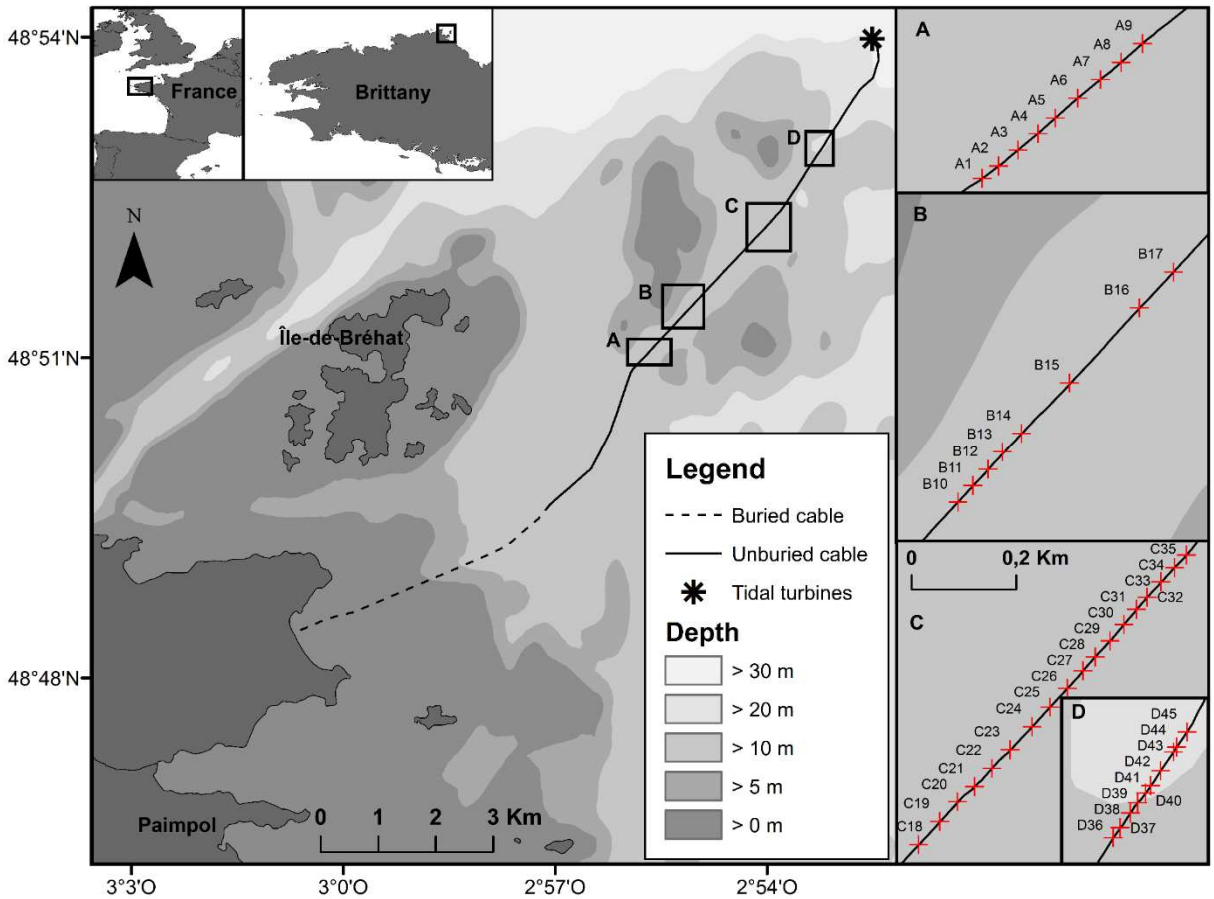

Figure 1: Map of the study area off the north coast of Brittany in Western France (top-left and top-centre panels). The thick black line represents the power cable that connects the Paimpol-Bréhat tidal test site to the mainland. Zones A, B, C and D (right) correspond to the four sites where concrete mattresses were surveyed.

A set of 5 benthic megafauna taxa easily recognisable by scuba-diving were surveyed: the crustaceans *Homarus gammarus* (European lobster) and *Cancer pagurus* (edible crab) and the benthic or demersal fish, *Conger conger* (European conger), *Labrus bergylta* (Ballan wrasse), and two species of the genus *Trisopterus: T. luscus* (whiting pout) and *T. minutus* (poor cod). These two latter species were hereafter gathered as a single taxon (*Trisopterus* spp.) since we cannot exclude that confusions of identification may have occurred.

2.3 Sampling strategy

Between June 2015 and September 2019, 45 different concrete mattresses in the 16-20 m depth range were surveyed by divers within four different zones along the cable (Zones A, B, C and D; Figure 1). These selected zones are located within a channel surrounded by several rocky shelves. A total of 45 mattresses were surveyed in June 2015, 30 in September 2015 (zone A, D and part of the zone C), 37 in June 2016 and 2017 (zone A, C and D); and only 20 in September 2019 (zone A and C Table 1). All surveys were performed at slack tides of neap tides and during daytime hours, *i.e.* between 8 am and 8 pm. During each survey, two divers inspected each mattress: the first diver moved slowly along the entire perimeter of the mattress while examining all the cavities and counting all conspicuous individuals of the 5 target species. Simultaneously, the second diver followed the first one around the mattress and recorded a video using a GoPro Hero 4® camera to provide some additional observations of the mobile fauna and the environment (substratum bottom type, frequency and forms of cavities *etc.*). Hereafter, a "sample" refers to all these pieces of information recorded for a given mattress, during a given campaign.

Campaign	Number of Mattresses	Zone
June 2015	45	A-B-C-D
September 2015	30	A-C(only C25 to C35)-D
June 2016	37	A-C-D
June 2017	37	A-C-D
September 2019	20	A-C(only C25 to C35)

Table 1: Summary of the concrete mattresses and zones surveyed during each campaign.

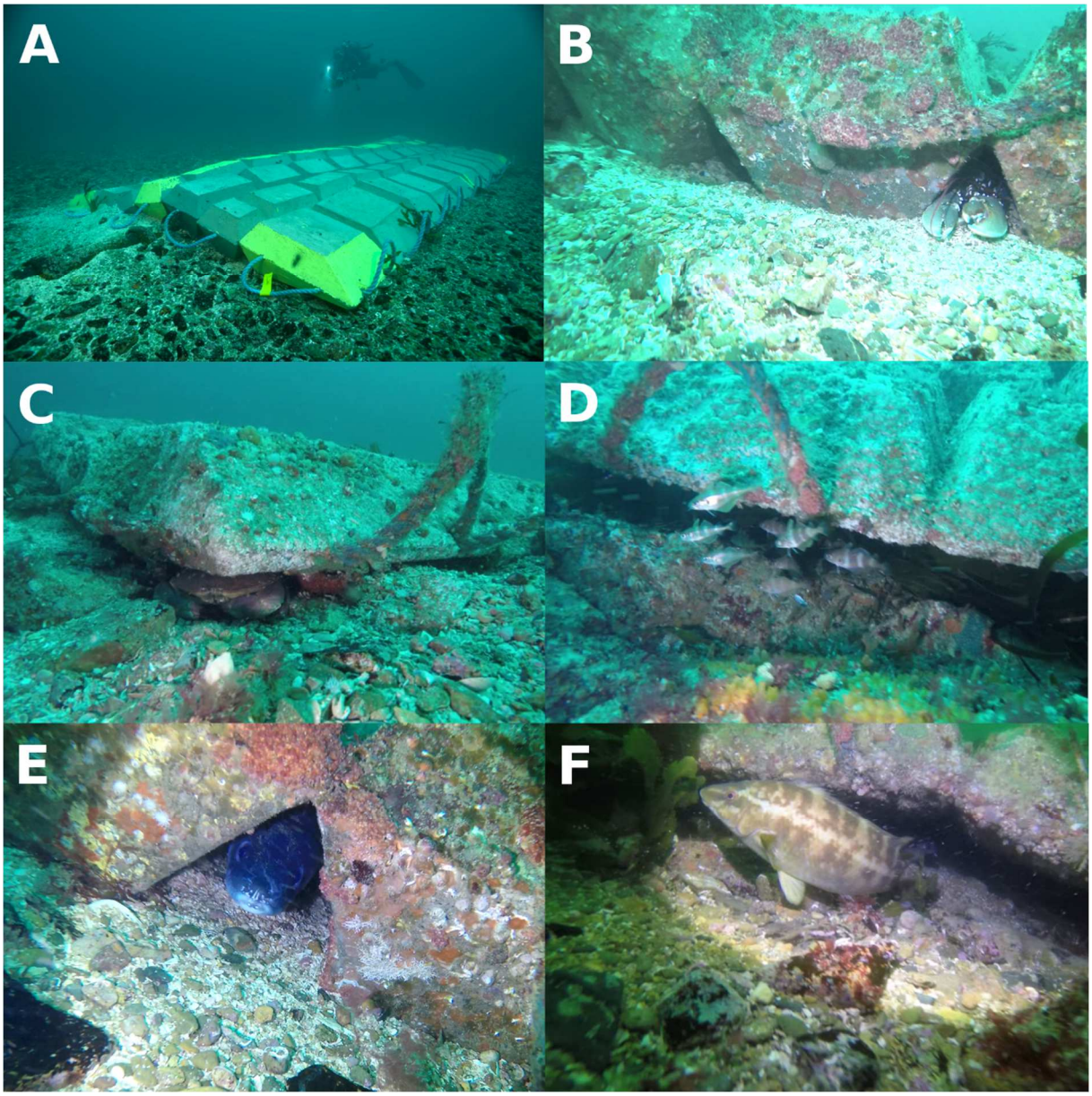

Figure 2: (A) Overall view of a concrete mattress (constituted of 73 concrete blocks) a few weeks after its installation on the power cable of the Paimpol-Bréhat tidal test site; (B) Homarus gammarus within a "hole", i.e. a small ~20 cm-wide triangular cavity between two concrete blocks; (C) Cancer pagurus within a "cave", i.e. a >10 cm high cavity formed below the mattress; (D) school of Trisopterus spp. close to a mattress "cave" ; (E) Conger conger within a "hole" ; (F) Labrus bergylta close to a mattress "cave'.

134 **2.4 Environmental variables**

135 Substratum as well as types and number of cavities associated with each mattress were estimated
136 from the video footage: each concrete block along the mattress edges (see Figure 2A) was assigned to
137 one of three substratum categories: sand, pebbles or boulders. For each mattress, substratum properties

were estimated as a proportion of these three categories across all peripheral concrete blocks (Table 2). Two different types of cavity that can provide habitats to mobile fauna underneath the mattresses were identified: "holes", which correspond to small ~20 cm-wide triangular cavities between two concrete blocks along the mattress width (Figure 2.B & E; Table 2); and "caves", which correspond to larger cavities formed below the mattress when it overhangs at least 10 cm above the seafloor (Figure 2.C, D & F; Table 2).

In addition, the following environmental variables were extracted for each mattress (Table 2): (1) bottom residual current velocity (computed from a 2010-2015 climatology extracted from the MANGA500-MARS3D hydrodynamic model); (2) seafloor facet exposure to residual current (computed using seafloor aspect and residual current direction and ranging from 0°, when the seafloor is sheltered, to 180°, when it is fully exposed to dominant current) and (3) linear distances from each mattress to the closest 5 m and 10 m depth isobaths. This final shortlist of environmental variables was defined by removing correlated variables (> 0.7) from an original selection that only included well-resolved biologically-relevant parameters.

2.5 Biological data

In addition to *in situ* abundance counts performed by divers, video counts of all visible individuals were performed for the same 5 target species (Table 2). To avoid multiple counts of single individuals of *Trisopterus* spp. given their high mobility, the maximum number of individuals occurring in a single snapshot of the full video was recorded. In order to investigate species-specific sheltering preferences, the positions of each counted individual with respect to the mattress was noted as either *i*) inside a "hole", *ii*) inside a "cave", or *iii*) free-moving outside any cavities.

For *H. gammarus*, *C. pagurus* and *C. conger*, we used *in situ* counts performed by divers for multivariate analyses (Table 2), since video counts underestimated the abundance of these three species (SI 1) due to their cryptic behaviours. For the 2 other target taxa *L. bergylta* and *Trisopterus* spp., we used video counts for multivariate analyses (Table 2) since *in situ* counts were less accurate due to the high mobility of these species and the tendency to form dense schools of *Trisopterus* spp. (SI 1). All

video analyses were performed using the Ifremer ADELIE© Software V2.0 according to the methodology developed and tested by Dufournaud (2018).

	Variable	Unit	Origin	Mean	Min	Max
Biological data	*Homarus gammarus*	count	*in situ*	1.1	0	5
	Cancer pagurus	count	*in situ*	1.5	0	5
	Conger conger	count	*in situ*	1.4	0	4
	Trisopterus spp.	count	video	3.5	0	68
	Labrus bergylta	count	video	1.1	0	6
Environmental data	Sand proportion	%	video	67%	0%	100%
	Pebble proportion	%	video	27%	0%	100%
	Boulder proportion	%	video	6%	0%	89%
	Number of holes	count	video	10.2	3	12
	Number of caves	count	video	9.2	0	28
	Bottom-current velocity	$m\ s^{-1}$	GIS	0.71	0.65	0.99
	Exposure	°	GIS	93.8	12.7	163.8
	Distance to 5 m isobath	m	GIS	500.2	149.7	791.2
	Distance to 10 m isobath	m	GIS	245.1	62	403.5

Table 2: Summary of all biological and environmental variables considered in this study, either measured in situ or from video footage, or derived from bathymetric map or from the MARS3D hydrodynamic model.

Due to poor footage quality, only 129 out of the 169 videos could be fully analysed and were used to perform multivariate analyses. To investigate specific habitat preferences, we also reported the type of cavity (either inside a "hole", inside a "cave", or free-moving out of any cavities) where each specimen was detected on the 129 videos.

2.6 Data analysis

Three main types of statistical analyses were performed, namely: *i*) generalised linear mixed models (GLMM) and linear mixed models (LMM) to explore temporal variations in megafauna abundance and diversity, *ii*) a principal component analysis (PCA) to study patterns in megafauna assemblage compositions, and *iii*) a redundancy analysis (RDA) to examine how variability in megafauna community relates to environmental conditions.

Using count data available for each mattress surveyed during the five campaigns, (*i*) GLMMs were applied to study temporal variations in the abundance per mattress of each target species and the total community abundance across all species (with and without *Trisopterus* spp.) per mattress; and (*ii*) a LMM was apply to study temporal variation in species richness per mattress. As count estimates correspond to repeated measures through time, mattress identity was treated as a random effect and campaign date was the only categorical explanatory variable included in all models to assess temporal variation. Each GLMM was fitted assuming either a Poisson distribution (for abundances of *H. gammarus* and *C. conger*), or a negative-binomial distribution when residuals with the former were overdispersed (for abundances of *C. pagurus*, *L. bergylta*, *Trisopterus* spp. and total community abundance with and without *Trisopterus* spp.). For each model, significance of the factor "campaign" was then assessed with Chi-Squared tests for GLMMs and F-test for LMM. When appropriate, a post-hoc test using Tukey correction was performed to study pairwise differences between campaigns. We then characterised variability in megafauna composition between samples using a PCA. Finally, to relate community variability to changes in environmental variables (Table 2), we performed a Redundancy Analysis (RDA; (Legendre and Legendre, 1998)). Using a Monte-Carlo permutation test (999 permutations), a forward selection process was performed to identify environmental variables that best correlate to observed variability in community composition. In order to reduce the weight of abundant school-forming species such as *Trisopterus* spp., a logarithmic transformation was applied to the abundance data set before all multivariate analyses. Environmental variables were normalised prior to RDA analysis. Data analysis was performed with Rstudio (RStudio Team, 2015) using the *vegan* (Oksanen et al., 2018) and *ggplot2* (Wickham, 2016) packages.

3. RESULTS

3.1 Temporal variation

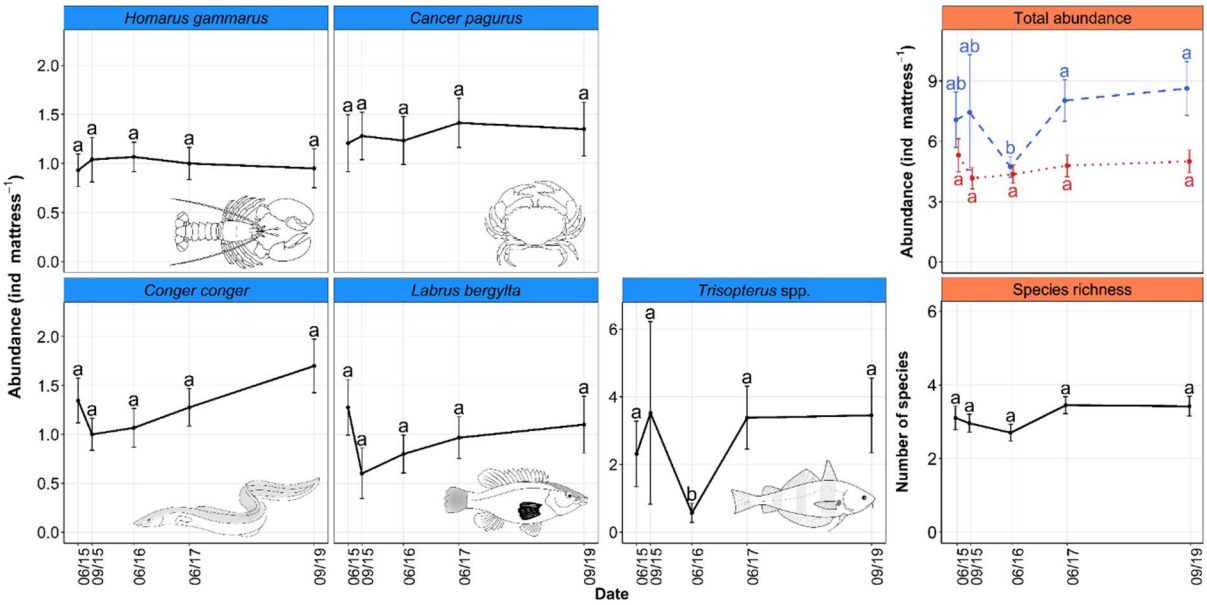

Figure 2 : Changes in mean specific abundances of the 5 target taxa (average number of individuals per mattress ± standard errors), in mean community abundance per mattress (blue dashed line when considering all species; red dotted line when excluding highly abundant Trisopterus spp.) and in mean species richness per mattress. Points labelled with different letters indicate significant differences. Only the mattresses surveyed at every campaign were considered.

Although occupancy of individual mattresses varied slightly during the different campaigns (SI 2), mean abundance estimates across all mattresses did not significantly change for *H. gammarus* (χ^2 = 0.44, df = 4, p = 0.98), *C. pagurus* (χ^2 = 0.6, df = 4, p = 0.96), *C. conger* (χ^2 = 5.42, df = 4, p = 0.25) and *L. bergylta* (χ^2 = 5.46, df = 4, p = 0.24 , Figure 3). Only *Trisopterus* spp. displayed significant abundance changes between campaigns (χ^2 = 26.42, df = 4, p < 0.001; Figure 3) due to significantly lower abundances in June 2016 relative to other campaigns. Total community abundance (across all five taxa) per mattress significantly changed between campaigns (χ^2 = 14.49, df = 4, p < 0.001 ; Figure 3) as total abundance in June 2016 was significantly lower than in June 2017 and September 2019. This is most likely due to the previously described decline in *Trisopterus* spp. abundance in June 2016. Indeed, when excluding this taxon, there was no significant temporal change in total megafauna abundance (χ^2 = 1.91,

df = 4, p = 0.75; Figure 3). Species richness per mattress did not significantly change overtime either (F = 1.78, df = 4, p = 0.14; Figure 3).

We sometimes observed co-occurrence within the same cavity of several individuals, either conspecific or from different species (Table 3). We did not quantify these co-occurrences, but observed *i*) that co-occurrence is more frequent within caves than within holes, *ii*) that mobile fish species (*i.e. L. bergylta* and *Trisopterus* spp.) frequently co-occurred with conspecifics and as well as other species, and *iii*) that individuals from sedentary species (*i.e. H. gammarus*, *C. pagurus* and *C. conger*) rarely co-occurred (Table 3).

Table 3: Observed co-occurrence within a single cavity of individuals from the different target taxa. Based on video footages, the matrix reports on whether several individuals from the same or different species co-occurred at least one time within a hole (H), or a cave (C) cavity.

	Homarus gammarus		*Cancer pagurus*		*Conger conger*		*Trisopterus* spp.		*Labrus bergylta*	
Homarus gammarus	-	-								
Cancer pagurus	-	-	-	C						
Conger conger	-	C	H	-	-	-				
Trisopterus spp.	-	C	-	C	-	C	H	C		
Labrus bergylta	-	-	-	-	-	-	H	C	H	C

Although we did not quantify their abundance (as they only marginally occurred), other species of benthic megafauna (including fish from the Blenniidae or Gobiidae families and other wrasses species such as *Labrus mixtus* and *Ctenolabrus rupestris*, and crustaceans like *Galathea sp*. and *Necora puber)* were also regularly observed.

3.2 Patterns in community composition / assemblage composition

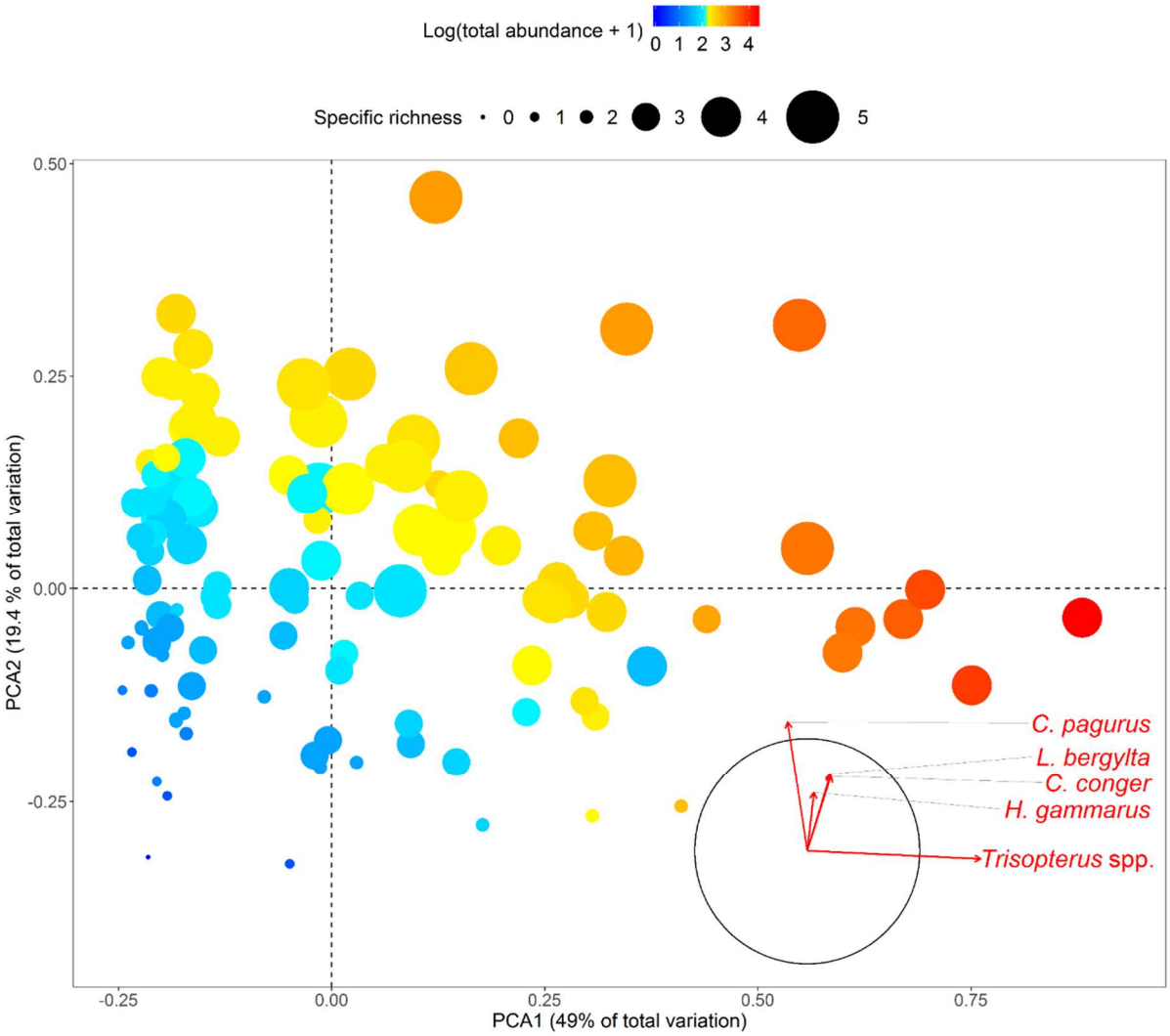

Figure 3: Principal Component Analysis (PCA) of log-transformed abundance data for the 5 target species. Each point represents a sample (i.e. a concrete mattress during a given campaign). Point size is proportional to species richness and colour indicates total megafauna abundance. Vector overlays show how species abundance correlates with the two first principal components.

Out of the 129 analysed samples, only 3 do not shelter any individuals of the target species. *Trisopterus* spp. is the most abundant species (448 individuals counted in total), followed by *C. pagurus* (196 individuals), *C. conger* (183 individuals), *L. bergylta* (145 individuals) and finally *H. gammarus* (141 individuals).

The first two PCA axes capture 68.4% of the total variation (Figure 4). Axis PCA1 (49% of total variation) is positively correlated to *Trisopterus* spp. abundance while the abundance of 4 of the 5 taxa, mainly *C. pagurus* and then *L. bergylta* and *C. conger* positively correlates with axis PCA 2 (19.4%

of total variation; Figure 4). The colour and size codes used to visualise samples on the PCA also illustrates that both species richness and total abundance per mattress are positively correlated with the two first axes (Figure 4). PCA ordination highlights a large gradient of colonisation among samples, from low-abundance and low-richness samples (in the bottom left) to samples characterised by a high level of colonisation (in the top right of the plot).

			Explained		Correlation	
Environmental variable	F-value	p-value	λ	%	RDA1	RDA2
Cave	11.01	**0.001**	0.14	14%	**0.77**	0.33
% Boulder	8.185	**0.001**	0.1	10%	**0.76**	-0.35
Exposure	4.872	**0.006**	0.06	6%	0.31	-0.39
Hole	1.794	0.146	0.02	2%	0.24	**0.71**
% Pebble	1.541	0.193	0.02	2%	0.13	**0.59**
Total			0.34	34%		

Table 4: Environmental variables selected in the RDA as well correlated to the variability in the abundance of the 5 target taxa colonising concrete mattresses at the Paimpol-Bréhat tidal test site cable (Monte Carlo permutation test in RDA with 999 permutations; $p < 0.05$). High correlation ($r > 0.5$) between environmental variables and the first two RDA axes are highlighted in bold.

In the RDA (Figure 5), the environmental variables that best correlate to variability in megafauna composition are, in order of importance, number of caves, percentage of boulders, exposure to current, number of holes and finally percentage of pebbles (Table 4). These 5 variables capture 34% of the total variability in megafauna composition (Table 4; axis 1 and axis 2 explains 21.74% and 2.63% of the total variation, respectively, Figure 5). Results of the RDA (Figure 5) are consistent with those of the PCA (Figure 4). Number of caves present below the mattresses and percentage of boulders correlate positively with RDA axis 1, while number of holes and percentage of pebbles mainly correlate positively with RDA axis 2 (Figure 5, Table 4).

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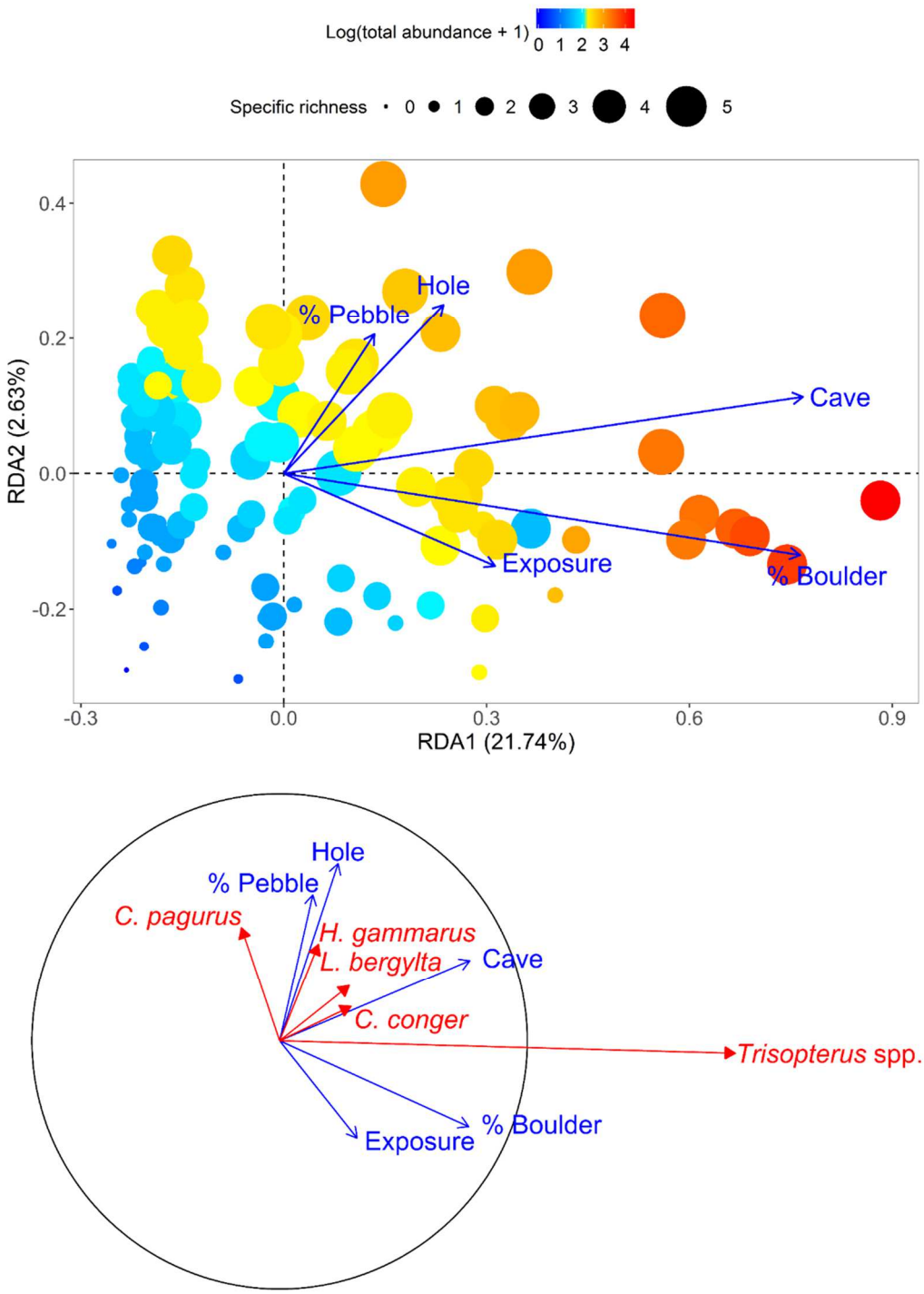

Figure 4: Redundancy analysis (RDA) ordination plots of axes 1 and 2 showing (A) samples (i.e. a concrete mattress during a given campaign, points) in relation to environmental variables (blue arrows); and (B) target megafauna species (red arrow) in relation to environmental variables (blue arrows). A different scaling was used for each panel, so environmental variables projection on the RDA should be used to reconcile both parts of the Figure. Axes 1 and 2 together explain 24.37% of the total taxonomic variation. Point size corresponds to associated species richness and point colour to associated total megafauna abundance.

Note that samples with high abundance of *Trisopterus* spp. (to the right of the RDA) are associated with relatively high numbers of caves and percentages of boulders (Figure 5). On the other hand, high abundances of *C. pagurus* and *H. gammarus* occur on mattresses with high numbers of holes and percentage of pebbles. *L. bergylta* and *C. conger* are correlated with high number of caves and holes (Figure 5). Finally, samples with low diversity and low total abundance exhibited relatively small numbers of both types of cavity (holes or caves) and low percentages of pebbles and boulders (Figure 5).

3.3 Habitat preferences

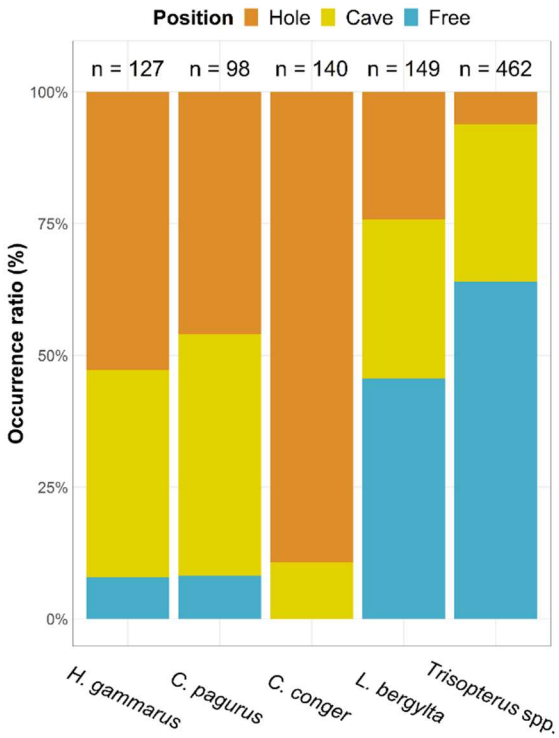

Figure 5 : Relative frequency of locations (either inside a "hole", inside a "cave", or free-moving out of any cavities) in which the 6 target species were detected, based on analyses of 169 video footages.

According to video footages, conger preferentially shelters within hole cavity (89,3% of sheltered individuals observed on videos are in holes), whereas the two species of *Trisopterus* commonly shelter within cave cavities (for sheltered individuals, 83% found in caves; Figure 6). Conversely, edible crab, European lobster and Ballan wrasse do not show any clear habitat preference as they appear to randomly shelter in either cavity types (specific proportions of individuals sheltering in caves are 50%, 42.7% and 55.6%, respectively; Figure 6).

4. DISCUSSION

By combining *in situ* visual census by divers and video analysis, our results help to characterise how MRE facilities can enhance benthic megafauna diversity by providing artificial reefs. Specifically, our findings help: (*i*) characterise the habitat potential of concrete mattresses deployed to anchor an unburied power cable; (*ii*) disentangle how interactions between artificial reef and natural substrate determine the effectiveness of the 'reef effect' and (*iii*) to a lesser extent identify fine-scale habitat preferences of the 5 target species.

4.1 Habitat potential of cable stabilizing structures

MRE structures create additional potential habitat for benthic megafauna, as shown by several studies on colonisation (Krone et al., 2017; Langhamer and Wilhelmsson, 2009; Reubens et al., 2011; Wilhelmsson and Langhamer, 2014). On the subsea power cable of Paimpol-Bréhat, concrete mattresses offer a suitable habitat for large crustaceans and fish, at least for the 5 taxa targeted during our five-year monitoring. This result corroborates with previous studies that showed that these target species are known to be attracted by a number of artificial hard substrates, either associated with MRE facilities (Krone et al., 2017; Langhamer and Wilhelmsson, 2009; Reubens et al., 2011) or with other types of man-made structures (Castège et al., 2016; Charbonnel et al., 2000; Fabi et al., 2004; Jensen et al., 2000b, 1994; Santos et al., 2005).

In our study, one mattress is on average inhabited by 1 to 2 individuals of *C. conger*, *H. gammarus* and *C. pagurus*, corresponding to species-specific density of around 0.1 individuals per m^2. By extrapolating these density estimates to all the 120 mattresses stabilising the power cable, the associated populations inhabiting these structures could be up to around 125 *H. gammarus*, 162 *C. conger*, 162 *C. pagurus*, 119 *L. bergylta* and 357 *Trisopterus* spp. These density estimates are smaller than others reported in the literature. Krone et al. (2017) showed that scour protections of a wind turbine foundation (1 m high and around 30 m diameters) in the German Bight (North Sea) were inhabited by several thousand of *C. pagurus* individuals, *i.e.* a density of ~7 ind m^{-2}. Note, however that these estimates by Krone et al. (2017) include all life stages (including juveniles, which we missed in our visual surveys). Similar scour protection devices were found to host dense schools of *T. luscus* on a Belgian wind farm (Reubens et al., 2011). With an average density estimated at 14 ind m^{-2}, total *T. luscus* population within the windfarm was estimated at about 22,000 individuals. Langhamer and

Wilhelmsson (2009) highlighted colonisation of fish and crustacean on wave energy foundations (1 m high and 3 m diameters) in the North Sea, with a mean density of around 5 edible crabs per foundation, being ~0.7 ind m^{-2}. Finally, Jensen et al. (1994) estimated that within the Poole Bay artificial reef, each reef unit (1 m high by 4 m of diameter) made up of several blocks (40 x 20 x 20 cm) sheltered between 2 and 3 *H. gammarus* individuals (*i.e.* density up to 0.25 ind m^{-2}). The fact that density values found in our study are smaller than those reported in the literature may be mainly explained by differences in surrounding natural habitats. In soft-sediment-dominated areas (*e.g.* the North sea), the number of shelters provided by natural habitat surrounding artificial reef is very low. Thus, mobile individuals are likely to find shelter in artificial reefs due to the low complexity of the natural habitat. The attraction effect is therefore likely stronger on soft-sediment bottoms relative to structurally-complex seafloor. In our case, natural hard substrate providing shelters are present in the wider area giving other options for this species. Another point can come from the basic shape of concrete mattresses, which are less complex than scour protections or wave-energy foundations.

It is noteworthy that target species abundance estimates were constant during our five-year monitoring. This absence of temporal variation suggests that *i*) colonisation of mattresses by mobile megafauna reached a plateau in less than 2 years after their deployment (first campaign was in June 2015 *i.e.* 2 years after the deployment of the mattresses) and *ii*) that target species may be permanent, rather than temporary residents of the mattresses. Our results are consistent with earlier findings of rapid colonisation of artificial reefs by megafauna: Jensen et al. (1994) showed that *H. gammarus*, *C. pagurus, T. luscus* and different species of wrasses can colonise artificial reefs within 3 weeks of their deployment. Moreover, biological traits related to mobility can to some extent support observed patterns of species-specific positioning around the mattress. Concerning *H. gammarus*, two modes of behaviour may exist: a mobile phase, with migration between different reefs, and a territorial phase where lobster individuals stay in close proximity to a chosen site/shelter (Jensen et al., 1994). *H. gammarus* can be highly loyal to its refuge, as showed by Jensen et al. (1994): 21% of lobsters caught on a reef unit stayed on it for more than 100 days. *Labrus bergylta* and other *Labridae* are also territorial species dwelling in the vicinity of an identified reef unit (Jensen et al., 1994; Villegas-Ríos et al., 2013). Results from a

332 mark-recapture programme suggest that a wide proportion of *Trisopterus luscus* individuals are bound
333 to the same artificial reef units, which serve as a "home reef" (Fowler et al., 1999).

334 The degree of colonisation of individual mattresses appears highly dependent on the number
335 and type of available shelters. Both these features condition how an artificial reef artificially enhances
336 the carrying capacity of the local environment (Bohnsack, 1989; Eggleston et al., 1992; Pickering and
337 Whitmarsh, 1997). As each species exhibits specific habitat preferences, the variety of shelters also
338 largely explains the species composition of artificial reefs (Anderson et al., 1989; Beets and Hixon,
339 1994; Chandler et al., 1985; Pickering and Whitmarsh, 1997; Smith et al., 1979). Optimisation of MRE
340 facilities through basic designs (*e.g.* with creation of manufactured holes of different sizes) has been
341 shown to enhance their attractivity for benthic species (Langhamer and Wilhelmsson, 2009). The
342 concrete mattresses of Paimpol-Bréhat were not designed to effectively provide additional habitat for
343 marine fauna but to stabilise the submarine power cable and prevent fishing gear hooking. The two types
344 of shelters we identified, namely holes and caves, present different physical characteristics: holes are
345 narrow (around 20 cm-wide) while caves can be much wider (around 1 m-wide for the biggest caves).
346 Total space availability likely explains why several individuals were more frequently observed to co-
347 occur within caves than within holes. Note, also, that the two different types of cavities also host distinct
348 groups of species. While *L. bergylta* shelters in both type of cavities, *Trisopterus* spp. show a clear
349 habitat preference for caves. *Trisopterus* spp. are known to colonise rocky habitats with numerous and
350 wide cavities such as caves, crevices or wrecks for shelters against tidal current (Jensen et al., 1994;
351 Krone et al., 2013). Consequently, they shelter to a limited extent in holes and favour wide caves that
352 can fit a whole school. This schooling behaviour conditions the species preference for larger caves, as
353 highlighted by the high correlation between *Trisopterus* spp. abundance and the number of caves
354 available below concrete mattresses. Our results also highlight that holes constitute the preferred habitat
355 for *C. conger*. This solitary species is known to shelter in narrow cavities, the holes of the mattress
356 constitute narrow and linear shelters which fit perfectly the shape of the adults, compared to the caves
357 which are too wide. Adult European lobster individuals use physical shelters to avoid predators and
358 being swept by strong tidal currents (Addison and Lovewell, 1991). Given the high tidal currents that
359 can occur at the Paimpol-Bréhat tidal site (up to 3 m s^{-1}), mattresses thus provide an adequate shelter to

360 lobsters. Lobsters typically select dark shelters that fit their body size closely (sometimes with physical
361 contact; Wahle et al., 2013). Although *H. gammarus* shows a subtle preference for mattresses with holes,
362 this species is found in both cavities in equal proportions, suggesting that narrow caves can also be
363 appealing to lobsters. Less information is available concerning sheltering behaviour and preferences of
364 *C. pagurus* but the species has been reported to compete with lobsters for shelter so it is likely to display
365 similar habitat preferences (Richards and Cobb, 1986). Contrastingly to the European lobster, *C.*
366 *pagurus* individuals are known to escape predators by rapidly burrowing themselves in sandy habitats
367 (Hudon and Lamarche, 1989). This burrowing behaviour may allow *C. pagurus* to colonise a wider
368 variety of mattresses relative to lobster, including those exhibiting high proportions of soft sediments.

369 Among our target species, three groups can be discerned based on their habitat use on artificial
370 reefs: (*i*) solitary and nocturnal species found in shelters during the day, such as *C. conger*, *H. gammarus*
371 and *C. pagurus*; (*ii*) solitary and diurnal species found in shelters during the night, such as *L. bergylta*;
372 and (*iii*) gregarious species that display a nocturnal activity, such as the two species of *Trisopterus*.
373 Because of these overlaps in their biological traits, the three solitary and nocturnal species (*i.e. C.*
374 *conger*, *H. gammarus* and *C. pagurus*) are likely to compete with each other for available artificial
375 shelters. Although we did not directly observed competition between them, the rare co-occurrence
376 within a single cavity of individuals from these three species could be the result of their competition for
377 similar shelters. The different diel behaviours of the target species suggest a possible day/night shift in
378 mattresses occupancy, as observed for other artificial (Santos et al., 2002) and natural reefs (Mallet et
379 al., 2016; Myers et al., 2016). This day/night shift may introduce a bias in our counting procedure.
380 Considering that all diving surveys occurred during the daytime, counts of diurnal species can be
381 underestimated due to their temporary absence in the vicinity of the mattresses during the surveys. On
382 the contrary, counts of nocturnal species are likely more accurate because individuals were mostly found
383 motionless within mattresses cavities during the day. Furthermore, *Trisopterus* spp. proceeds to tidal
384 migration in addition to day/night cycle, which may be another source of bias when evaluating its
385 occupancy rate. Schools of *T. luscus* are found to be more congregated and closer to artificial reef units
386 during high current speeds (>0.3 m s^{-1}), and to be more dispersed and further from the reef during low
387 current speeds (<0.1 m s^{-1}; Fowler et al., 1999). Considering that all diving surveys occurred during

388 slack tides (*i.e.* low speed currents), *Trisopterus* spp. abundance is possibly underestimated. In order to
389 study in greater detail these community changes at the mattress scale resulting from the activity rhythms
390 of the different megafauna species, the use of continuous video recording over several tide and day/night
391 cycles could be useful (Aguzzi et al., 2013; Mallet et al., 2016; Weiss et al., 2009). Furthermore, the use
392 of continuous video recording could help characterise biological interactions between the different
393 megafauna species, such as competition for shelter associated with these artificial structures (Weiss et
394 al., 2009).

395 **4.2 Interaction of artificial reef with local environment**

396 Differences in megafauna colonisation originate from the variability in local environmental
397 conditions around each mattress: interaction between mattress and heterogeneous natural bottom
398 directly influences the number and types of cavities available. Previous studies showed that
399 environmental variables, such as bottom types, depth, hydrodynamic conditions, sediment dynamics or
400 distance to natural reef, significantly impact the colonisation of artificial reefs (Ambrose and Swarbrick,
401 1989; Bohnsack et al., 1991; Bombace et al., 1994; Foster et al., 1994; Godoy et al., 2002; Noh et al.,
402 2017).

403 Our results reveal that the higher the proportion of boulders, which is positively correlated with
404 high hydrodynamic conditions, the higher the number of caves. Indeed, the presence of boulders creates
405 an irregular seafloor topography and prevent the edges of mattress from fitting flush with it, thus creating
406 overhanging space under the mattresses *i.e.* caves. Alexander et al. (2013) showed that seafloor
407 complexity underneath a flat concrete block plays an important role as it directly impacts the volume
408 available for colonisation. On the other hand, the number of holes available increases with the
409 percentage of pebbles. However, in the presence of pebbles, caves do not form under the mattresses, but
410 holes remain as open cavities between the adjacent concrete blocks. Although less colonised than
411 mattress with caves, these holes provide shelters to *C. pagurus*, *H. Gammarus*, *C. conger* and *L.*
412 *bergylta*. Finally, when the seafloor is dominated by sand and shell debris, the number of cavities is very
413 low because, *i*) the flatness of the seafloor prevents the creation of caves, and *ii*) accretion of sand and
414 shell debris caused by the presence of the mattress often fills up existing holes. To summarise, holes
415 constitute a narrow and deep cavity inherent to the way mattress is manufactured, but its availability can

be impacted by the degree that it is filled by the sediment, which depends on local sediment dynamics. Caves constitute more or less narrow cavities with large openings, which only originate from the interaction between mattress and the local topography of the site. Here, we only differentiated these two types of cavities, but a more precise description of their physical features (*e.g.* through the use of quantitative criteria such as depth, size and shape of the entrance) would help better quantify mattress reef properties (Alexander, 2011).

Colonising an artificial reef also depends on distance to closest natural reefs (Ambrose and Swarbrick, 1989; Jessee et al., 1985). The closer to existing natural hard habitat, the higher the probability for artificial reefs to attract transient species (Campos and Gamboa, 1989; Potts and Hulbert, 1994). When deployed closely to existing natural reefs, artificial reefs essentially extend the amount of hard habitat with direct benefits for hard-substrate species recruitment (Danner et al., 1994). In our case, it is unlikely that distance to natural reefs influences mobile megafauna composition on mattresses. Since mattresses are installed between large shallow rocky shelves, their distance to natural rocky habitat are considered as low (less than 1km) and therefore relatively homogeneous. Computing precise distances between each mattress and the nearest natural reef would be difficult due to the very complex shape of the 10 m and 5 m isobaths in this area.

Finally, these structures associated with submarine power cables are not a classic artificial reef in the sense that the current transiting through cables generates electromagnetic fields. A lack of knowledge still exists concerning the impact of these anthropogenic electromagnetic fields on marine fauna (Taormina et al., 2018). This can potentially impact species capable of electroreception and/or magnetoreception through effects on predator/prey interactions, avoidance/attraction behaviour, navigation/orientation capabilities or induce physiological and developmental effects (Copping et al., 2016; Hutchison et al., 2020). Over the course of this study, no electric current transited through the cable and the mattresses thus acted as a classic artificial reef, but further investigations should be conducted once electrical current passes through.

5. Conclusion

Although the concrete mattresses deployed to anchor the submarine power cable were not specifically designed to act as a refuge for marine fauna, a five-year monitoring study (*both in situ* and

using videos) shows that they offer a suitable and stable habitat for at least 5 benthic megafauna species. Interactions between local seafloor and hydrodynamic characteristics (substratum type, topography, exposition to current *etc*.) and artificial reef units directly condition the variety and the availability of shelters. In our study, these two factors, *i.e*. shelters shape and availability, largely determine the degree of colonisation by mobile megafauna. Consequently, in order to finely characterise the habitat potential for megafauna of MRE structures, it is critical to both, optimise the design of the artificial structures, and anticipate how they will interact with local environmental site characteristics.

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