




## Original Article

# Succession in epibenthic communities on artificial reefs associated with marine renewable energy facilities within a tide-swept environment

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Although colonization of artificial structures by epibenthic communities is well-documented overall, our understanding of colonization processes is largely limited to low-energy environments. In this study, we monitored epibenthic colonization of different structures associated with a tidal energy test site located in a high-energy hydrodynamic environment. Using four years of image-based underwater surveys, we characterized changes through space and time in the taxonomic composition of epibenthic assemblages colonizing two kinds of artificial structures, as well as the surrounding natural habitat. Our results highlight that ecological successions followed similar trends across the two artificial habitats, but that different habitat-specific communities emerged at the end of our survey. Deployment of these artificial structures resulted in the addition of elevated and stable substrata in an environment where natural hard substrates are unstable and strongly exposed to sediment abrasion. Although epibenthic communities colonizing artificial habitats are unlikely to have reached a mature stage at the end of our survey, these supported structurally complex taxa facilitating an overall increase in local diversity. We were able to quantify how epibenthic communities can significantly vary over time in high-energy coastal environment, and our final survey suggests that the ecological succession was still in progress five years after the deployment of artificial reefs. Thus, maintaining long-term continuous survey of coastal artificial reef habitats will be key to better discriminate between long-term ecological successions and shorter-term variability.

**Keywords:** artificial reef, benthic communities, marine renewable energy, non-indigenous species, succession, underwater imagery

## Introduction

When submerged in seawater, hard substrates are colonized by epibenthic organisms, which form the so-called “biofouling”. These organisms are diverse and, following the early establishment of

microbial biofilms, they become dominated by marine invertebrates (e.g. Arthropoda, Tunicata, Bryozoa, Annelida, Porifera), and macroalgal (e.g. Chlorophyta, Rhodophyta, and Ochrophyta) assemblages. Colonization of bare substrates can be described in time as an

ecological succession, i.e. a sequence of stepwise changes in community composition until community composition eventually reaches a persistent stage, called climax (Clements, 1916; Connell and Slatyer, 1977). Early pluricellular eukaryote colonizers are usually pioneering species, which are gradually replaced by longer-lived morphologically complex species as the colonizing community evolves towards its climax (Clements, 1916). Numerous biotic and abiotic factors condition changes in community composition and hence determine epibenthic communities succession and time needed to reach climax (Falace and Bressan, 2000). Biotic factors include competition, facilitation, and trophic interactions between organisms (Connell and Slatyer, 1977) while non-biotic factors can be split between substratum properties (e.g. surface type, material, texture, slope; Falace and Bressan, 2000) and local environmental conditions (e.g. temperature, light, pH, salinity, currents; Pérès and Picard, 1964; Falace and Bressan, 2000; Bowden *et al.*, 2006).

For several centuries, humans have deployed artificial structures on the bottom of aquatic ecosystems for different purposes (Lima *et al.*, 2019). Among these artificial reefs, two main types can be differentiated: (i) those intentionally designed to mimic certain characteristics of natural reefs via provision of hard substrate and shelters to living organisms (e.g. ecosystems conservation/restoration, fish stocks enhancement/management; Thierry, 1988; Bohnsack *et al.*, 1991; Jensen *et al.*, 2000) and (ii) those deployed for another primary purpose, such as oil rigs, breakwaters, or marine renewable energy (MRE) facilities (e.g. wind-farms, tidal turbines, and wave energy converters; Wilson and Elliott, 2009; Langhamer, 2012; Lima *et al.*, 2019). Globally, the number of MRE structures has rapidly increased to meet the growing demand for renewable energy as a mitigation strategy against global anthropogenic climate change (Copping *et al.*, 2014; Lindeboom *et al.*, 2015; Coolen *et al.*, 2018). In addition to providing carbon neutral energy, colonization of MRE structures by benthic organisms is often considered as an extra positive environmental benefit (Inger *et al.*, 2009; Langhamer, 2012; Copping *et al.*, 2016). For instance, when installed on soft bottoms, MRE facilities directly increase substrate structural complexity and hence facilitate colonization by species previously absent, which leads to an overall increase in local diversity (De Mesel *et al.*, 2015). Certain epibenthic organisms can create complex tri-dimensional biogenic structures (e.g. kelps, gorgonians) that further increase habitat heterogeneity (Pickering and Whitmarsh, 1997). Moreover, epibenthic communities developing on MRE facilities can provide important food sources for commercial fish and crustacean species that also settle in artificial reefs (Pickering and Whitmarsh, 1997; Reubens *et al.*, 2011; Krone *et al.*, 2013). Conversely, deployment of artificial structures can reduce availability in natural sedimentary habitats, and hence they can modify soft-sediment-associated processes such as organic matter enrichment, biogeochemical fluxes between seawater and sediment, and sound and light attenuation. Artificial structures can also directly induce hydrodynamic changes, contamination, and they can alter biotic interactions (Heery *et al.*, 2017). Artificial structures may also facilitate the spread of non-indigenous species by creating new connectivity routes via a stepping-stone process (Mineur *et al.*, 2012; Adams *et al.*, 2014; Bishop *et al.*, 2017). For example, in the Adriatic sea, artificial structures along sedimentary coastlines were shown to harbour three times more non-indigenous ascidians than natural rocky reefs or artificial structures built close to rocky coastlines, which facilitated their spread across the whole region (Airoldi *et al.*,

2015). The high number of coastal breakwaters is also a likely cause for the massive spread of the non-indigenous green algal species *Codium fragile* ssp. *tomentosoides* in the Mediterranean sea (Bulleri and Airoldi, 2005).

Although colonization of MRE structures by epibenthic communities has been documented in several case studies (Langhamer, 2012; Sheehan *et al.*, 2020), our knowledge of ecological succession on artificial structures is limited in high-energy hydrodynamic environments (i.e. with current velocities  $>1.5 \text{ m s}^{-1}$ ), which are specifically targeted for tidal energy extraction (Copping *et al.*, 2016; Quillien *et al.*, 2018). In these tide-swept environments, physical processes can considerably influence epibenthic community structure, as organisms are exposed to high physical stress, which can dominate over interspecific biological interactions (Sousa, 1979a; Dean and Connell, 1987). Although communities associated with tide-swept environments are reportedly highly diverse (Connor *et al.*, 2004; Kregting *et al.*, 2016; O'Carroll *et al.*, 2017), only a few studies have monitored their long-term composition to characterize their variability. This is mainly due to logistical constraints of field sampling, which essentially relies on scuba diving as remote grabs are ineffective on hard substrates (Sheehan *et al.*, 2010, 2013), and diving operations are restricted to narrow time windows as they are only achievable during slack tides.

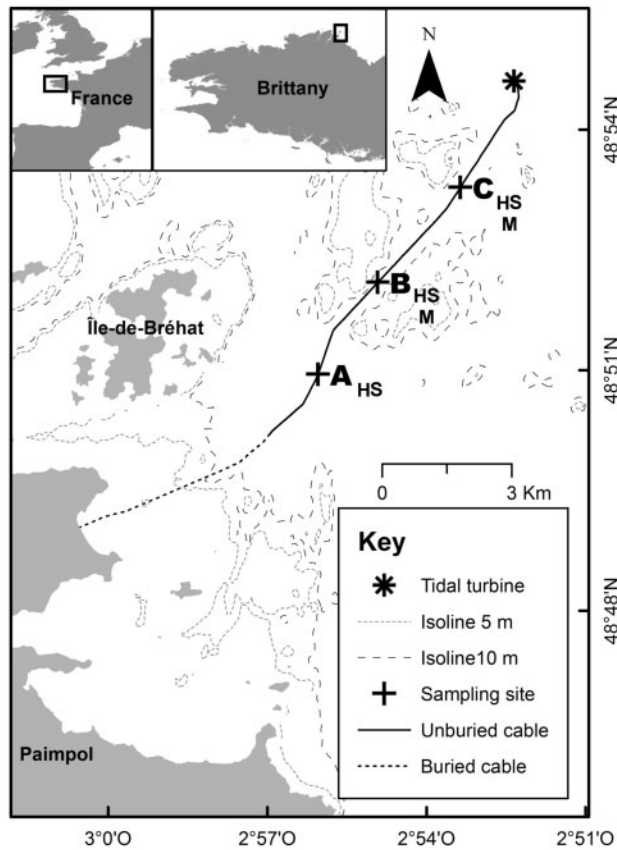
In this context, this study aims at characterizing epibenthic colonization of different MRE structures located in a high-energy hydrodynamic environment. Using 4 years of image-based underwater surveys performed by scuba divers, we specifically investigate (i) the temporal trend and (ii) composition of epibenthic communities across different natural and artificial habitats. We also specifically examine the dynamics of two different non-indigenous species and one regionally emblematic foundation species on different habitats. We test two different hypotheses: (i) that the composition and ecological succession of epibenthic communities differ across different habitats and (ii) that non-indigenous species are more present on artificial than natural habitats.

## Methods

### Study area

The study area encompasses a 15-km-long submarine power cable (8 MVA to 10 kVDC) set-up in 2012 to connect the tidal test site of Paimpol-Bréhat (Brittany, France; Figure 1) managed by Electricité De France. The implantation site is characterized by major tidal currents (up to  $3 \text{ m s}^{-1}$  during Spring tides), and the bottom is dominated by hard substratum (pebbles and rocks) and highly mobile shell debris and coarse sand (Taormina, pers. obs.). Because of these characteristics, 11 km of cable is unburied and fully protected with nested cast iron half-shells (50 cm long, 15 cm diameter). The cable is also stabilized by 120 concrete mattresses (6 m long, 3 m wide, 40 cm high, Figure 2) installed in 2013, preventing any displacement caused by high hydrodynamic conditions.

Three sites (A, B, and C) located along the cable route (Figure 1) were annually surveyed from 2014 to 2018. Sites B and C include both concrete mattresses and half-shells, while site A only had half-shells. Due to several setbacks in the commissioning progress of the tidal project, no electric current has transited through the cable during our survey. So, the benthic colonization



**Figure 1.** Map of the study area off the northern coast of Brittany in western France (top left and top centre panels), which shows the location of the three stations (A, B, and C) along the unburied section of the subsea power cable. At each site, acronyms specify which artificial habitat types were studied (i.e. HS for half-shell and M for mattress).

of the investigated artificial reefs was not influenced by any potential effects of electromagnetic fields or heat emission.

### Sites characterization

The three sites span similar depth ranges (between 18 and 20 m). To characterize the hydrodynamical characteristics of each site more thoroughly, three environmental variables were extracted based on GPS positions: mean and maximum residual current velocity above the seafloor (in  $\text{m s}^{-1}$ ) were derived from a 2010–2015 climatology from simulations using the MARS3D hydrodynamic model (Lazure and Dumas, 2008) and seafloor topography was used to characterize exposure to residual current (ranging from  $0^\circ$ , when the seafloor is sheltered, to  $180^\circ$ , when it is fully exposed to dominant current).

### Image acquisitions

Using underwater imagery collected by scuba divers, benthic communities were monitored at each site over six campaigns carried out in September 2014, March and September 2015, September 2016, September 2017, and March 2018. All sites were surveyed during each campaign, except for site A that was skipped in September 2017 due to bad weather conditions. Hereafter, September and March campaigns are referred to as

“summer” and “winter”, respectively. At each site and at each date, high-definition photographs of benthic communities were systematically taken on the two artificial habitats that protect the cable and on the neighbouring natural bottom, as follows:

- (i) Forty photographs were taken to cover both sides of each 50-cm-long iron half-shell along a 10-m transect.
- (ii) Sixteen photographs were taken to survey the 16 concrete blocks that constitute each mattress (8 units of  $47 \text{ cm} \times 38 \text{ cm}$  and 8 units of  $47 \text{ cm} \times 20 \text{ cm}$ ).
- (iii) A minimum of 20 photographs were taken to characterize the neighbouring natural habitat in the vicinity of the cable. Each corresponds to a  $25 \text{ cm} \times 25 \text{ cm}$  quadrat randomly positioned at a minimum distance of 10 m from the cable to avoid the influence of artificial structures.

The 4 years survey produced a total of 1482 images (Table 1). Photographs were taken at a resolution of 37 million pixels per image with a Nikon D810 inside an Ikelite underwater housing, with a 20-mm lens and 2 Keldan led lights (105 W, 9000 lumens). All images of half-shells were calibrated with a scale bar.

### Image analyses

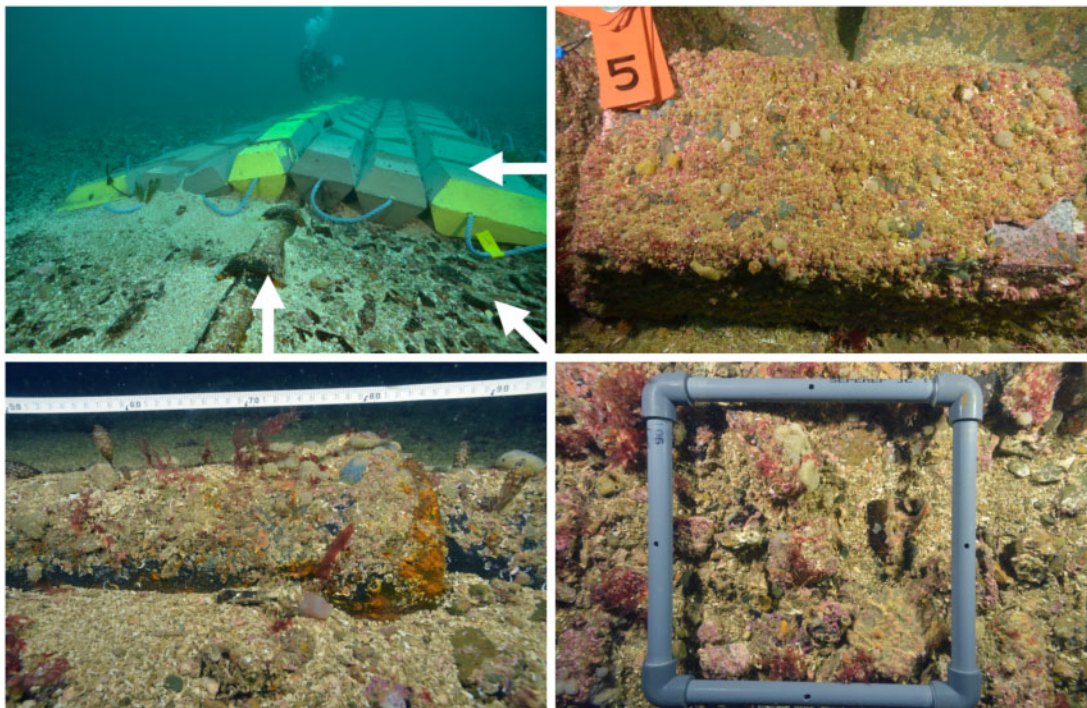
#### Benthic community

Images were described following a scoring methodology adapted from the point count method (Pielou, 1974). The protocol was preliminarily tested, validated and optimized based on a representative subset of the database (Taormina et al., 2020). For each combination of habitat, site, and campaign, ten images were chosen at random among the available image set. A standardized scoring area of  $625 \text{ cm}^2$  was cropped for “natural” and “mattress” habitat images. For half-shell images, scoring area varied between  $500$  and  $625 \text{ cm}^2$  depending on the surface available on the original photograph. Within these cropped areas,  $0.4 \text{ points cm}^{-2}$  (i.e. 250 points for an area of  $625 \text{ cm}^2$ ) were projected with the random-stratified projection method (Taormina et al., 2020). Then, each projected point was manually assigned to a benthic category (biological or substratum type). Biological categories were labelled using the highest resolution of the CATAMI (Collaborative and Automated Tools for Analysis of Marine Imagery) classification (Althaus et al., 2015). This classification combines coarse taxonomy levels and organism morphology to identify benthic taxa from underwater imagery (Althaus et al., 2015). Percentage covers were estimated as the ratio between the number of points attributed to a given category and the total number of points. Image analysis was performed using the free software PhotoQuad (Trygonis and Sini, 2012).

Some sets of images were excluded from this analysis for two reasons. Footage from the September 2016 campaign was excluded as poor image quality could have biased the analysis. Images taken on half-shells at site C from September 2015 onwards could not be analysed because the hard substrate was largely covered in coarse sand. Overall, a total number of 350 images were analysed in this study (Table 1).

#### Species of particular interest

Image scoring was adjusted for three target species so as to specifically study their temporal dynamics. These three species were



**Figure 2.** Illustration of the different substrates sampled at each survey site, namely: cast iron half-shells, a concrete mattress (freshly installed), and natural habitat (top left); close-up views of a mattress concrete unit (top right), a cast iron half-shell (bottom left), and a quadrat laid in the neighbouring natural habitat (bottom right) (courtesy: Olivier Dugornay).

**Table 1.** Summary of the total number of pictures sampled across the different sites and campaigns.

Campaign	Number of pictures sampled			Number of pictures analysed	
	A	B	C	Community study	Species of particular interest
Summer 2014	58	98	85	80	241
Winter 2015	71	114	110	80	295
Summer 2015	68	109	96	70	273
Summer 2016	61	97	97	–	255
Summer 2017	–	89	94	50	183
Winter 2018	58	90	87	70	235
Total	316	597	569	350	1 482

For each combination of site and campaign, we detail the number of pictures analysed to assess (i) community composition and (ii) species of particular interest abundance. Note that site A was not surveyed during the 2017 summer campaign due to adverse weather conditions and that for the 2016 summer campaign community composition could not be analysed due to poor image quality.

chosen both for ecological and practical reasons: (i) the slipper limpet *Crepidula fornicata* and the stalked sea squirt *Styela clava* are two non-indigenous species and the kelp *Laminaria* sp. is an important keystone species in the region and (ii) these organisms are easily recognizable from imagery because of their large size and conspicuous aspect. Contrary to the image scoring strategy described above and used to analyse the whole community, all available images across all campaigns were exhaustively analysed by counting all visible individuals belonging to these three species (Table 1). To analyse changes in density estimates over time for each target species ( $\text{ind m}^{-2}$ ), estimated abundances were divided by each image surface area. In total, 1482 images were analysed for this task.

### Data analyses

A permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) was used to determine if epibenthic community composition significantly differed across three factors: (i) sites (fixed, three modalities), (ii) campaigns (fixed, five modalities), and (iii) habitats (fixed, three modalities). Pairwise tests were used when relevant, to further explore significant community changes in space and time. Prior to the PERMANOVA, homoscedasticity was tested across all combinations of factors using PERMDISP (Anderson, 2006; Supplementary Information S1). As a complementary exploratory approach, changes in epibenthic communities were also visualized using non-metric multidimensional scaling (nMDS; Clarke and Ainsworth,

1993). All multivariate analyses were based on Bray–Curtis similarity matrices, computed without any prior transformation because no dominant taxa were present. Differences in target species densities were characterized across habitats and campaigns using non-parametric Kruskal–Wallis tests. When significant, pairwise comparison tests using Bonferroni correction were applied. We discuss statistical significance based on a probability threshold of 0.05. Mean values are given with associated standard error. Data analyses were performed using the *vegan* package (Oksanen et al., 2018) within the R environment using RStudio interface (RStudio Team, 2015). Graphics were produced using the *ggplot2* package (Wickham, 2016).

**Results**

**Site characterization**

Sites A, B, and C present similar mean current velocities (0.53, 0.57, and 0.48 m s<sup>-1</sup>, respectively) but more contrasted maximum current velocities (3.13, 3.53, and 2.83 m s<sup>-1</sup> respectively).

**Table 2.** Results of the PERMANOVA testing differences in epibenthic community composition across all sites, habitats, and campaigns.

Factor	df	SS	MS	Pseudo-F	p (perm)
Habitat	2	29.1	14.5	162.3	<b>&lt;0.001*</b>
Site	2	9.2	4.6	51.1	<b>&lt;0.001*</b>
Campaign	4	10.1	2.5	28.2	<b>&lt;0.001*</b>
Habitat:Site	3	4.0	1.3	15.0	<b>&lt;0.001*</b>
Habitat:Campaign	8	7.3	0.9	10.2	<b>&lt;0.001*</b>
Site:Campaign	7	2.2	0.3	3.6	<b>&lt;0.001*</b>
Habitat:Campaign:Site	8	2.0	0.2	2.8	<b>&lt;0.001*</b>
Residuals	301	27.0	0.1	–	–
Total	335	90.9	–	–	–

The analysis is based on Bray–Curtis similarities in community composition based on percentage cover of all surveyed taxa. The PERMANOVA tested for the effects of habitat (half-shell, mattress, and natural), site (A, B, and C), campaign (summer 2014, winter 2015, summer 2015, summer 2017, and winter 2018), and all levels of interactions. Significant values at *p* (perm) ≤ 0.05 are shown in bold and with an asterisk. MS: mean squares; SS: sum of squares.

**Table 3.** Summary of pairwise PERMANOVA tests conducted based on Bray–Curtis similarities in epibenthic taxa percentage cover (N = 595 combinations).

Pairwise comparisons					
Within natural habitat		Within artificial habitat		Artificial vs natural	
Site	<i>P</i>	Year	Comparison	<i>P</i>	<i>p</i>
Site A	<b>&lt;0.05</b>	2014S	Half-shell site B vs mattress site C	>0.05	All combinations
			All other combinations	<b>&lt;0.05</b>	
Site B	>0.05	2015S	Half-shell site B vs mattress site C	>0.05	All combinations
			Half-shell site B vs mattress site B	>0.05	
Site C	<b>&lt;0.05</b>	2015S	Half-shell site B vs half-shell site A	>0.05	All combinations
			All other combinations	<b>&lt;0.05</b>	
			2015W–2017S–2018W	All combinations	
Between sites	<b>&lt;0.05</b>	2015W–2017S–2018W	Between campaign	>0.05	All combinations
			All combinations	<b>&lt;0.05</b>	

Significant values at *p* ≤ 0.05 are shown in bold. S: Summer; W: Winter.

Exposure to residual current increases with distance from the coast, from an exposure of 87° at site A to 97° and 113° at sites B and C, respectively.

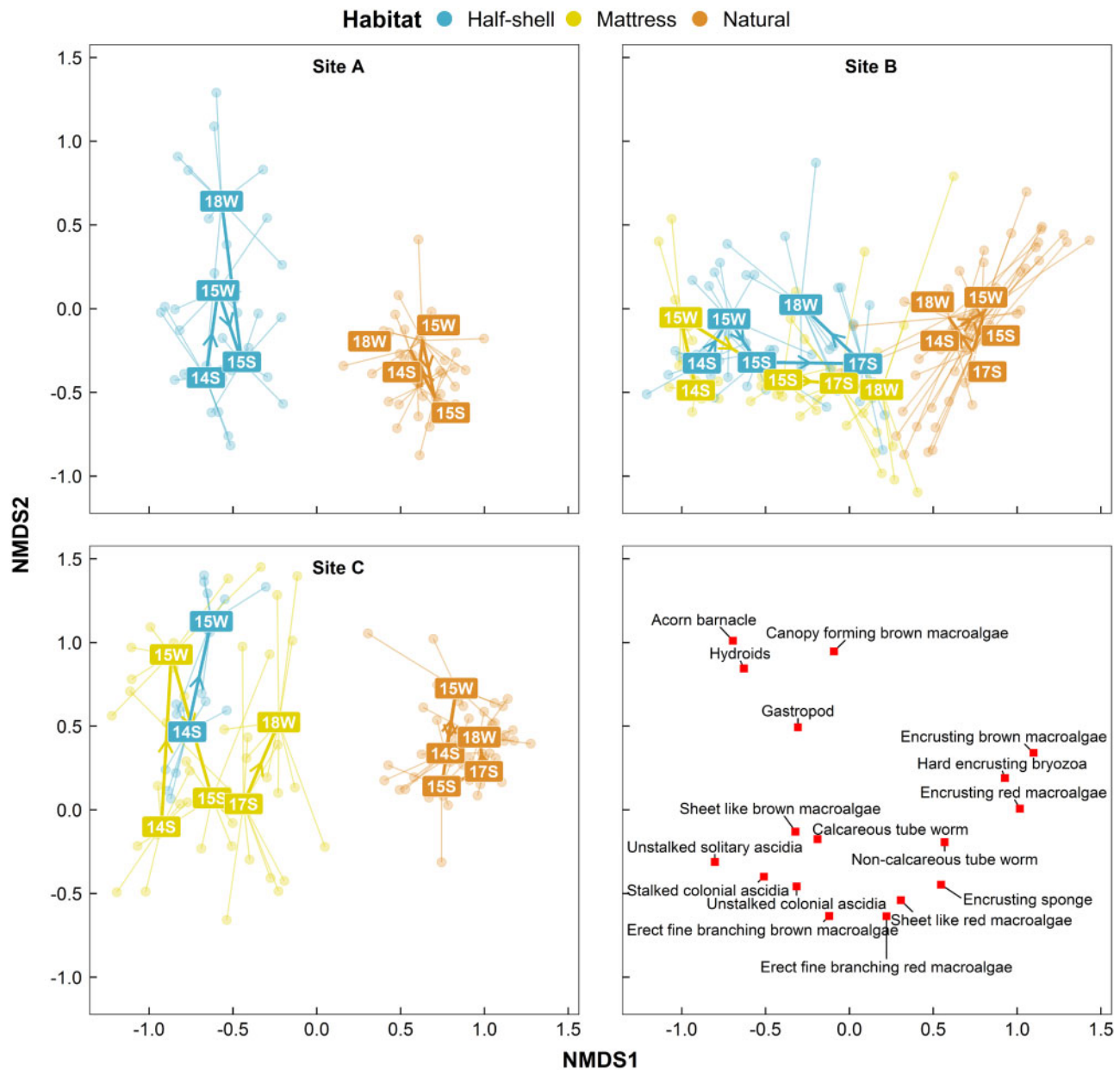
**Epibenthic community dynamics**

Across all pictures analysed, a total of 36 taxa (8 macroalgae and 28 animals) from 10 phyla were identified (Supplementary Information S2). Benthic community composition changed significantly across all factors “Habitat”, “Campaign”, and “Site”, as well as across all combinations of interactions between these factors (*p* < 0.05; Table 2). This pattern suggests that benthic communities did vary spatially throughout our survey and exhibited habitat-specific dynamics, thus validating our hypothesis i (i.e. the composition and ecological succession of epibenthic communities differ across different habitats).

Pairwise comparisons revealed significant differences in community composition across Habitats, Sites, and Campaigns (Table 3). Communities colonizing natural habitat exhibited site-specific differences throughout all campaigns (*p* < 0.05). Across all three sites, communities associated with natural habitats were always significantly different from those associated with the two artificial habitats (*p* < 0.05). Epibenthic communities on artificial substrates were significantly different between mattress and half-shell habitats (*p* < 0.05 except during the 2014 and 2015 summer campaigns). Importantly, across all sites and habitat types, community composition changed significantly over time (*p* < 0.05). Only communities on natural habitat at site B did not change significantly during the 4-year monitoring (*p* > 0.05).

Overall, these results highlight (i) clear differences in community structure between artificial and natural habitats; (ii) differences in community structure between the three sites; and (iii) larger temporal changes in communities colonizing artificial habitats relative to those found on natural hard substrates.

The MDS highlights marked differences in taxonomic composition between artificial and natural substrates (along the first axis). It also reveals a gradual change in natural communities across the three sites with clear differences in community composition at site A and site C (Figure 3): at site A, sheet-like red

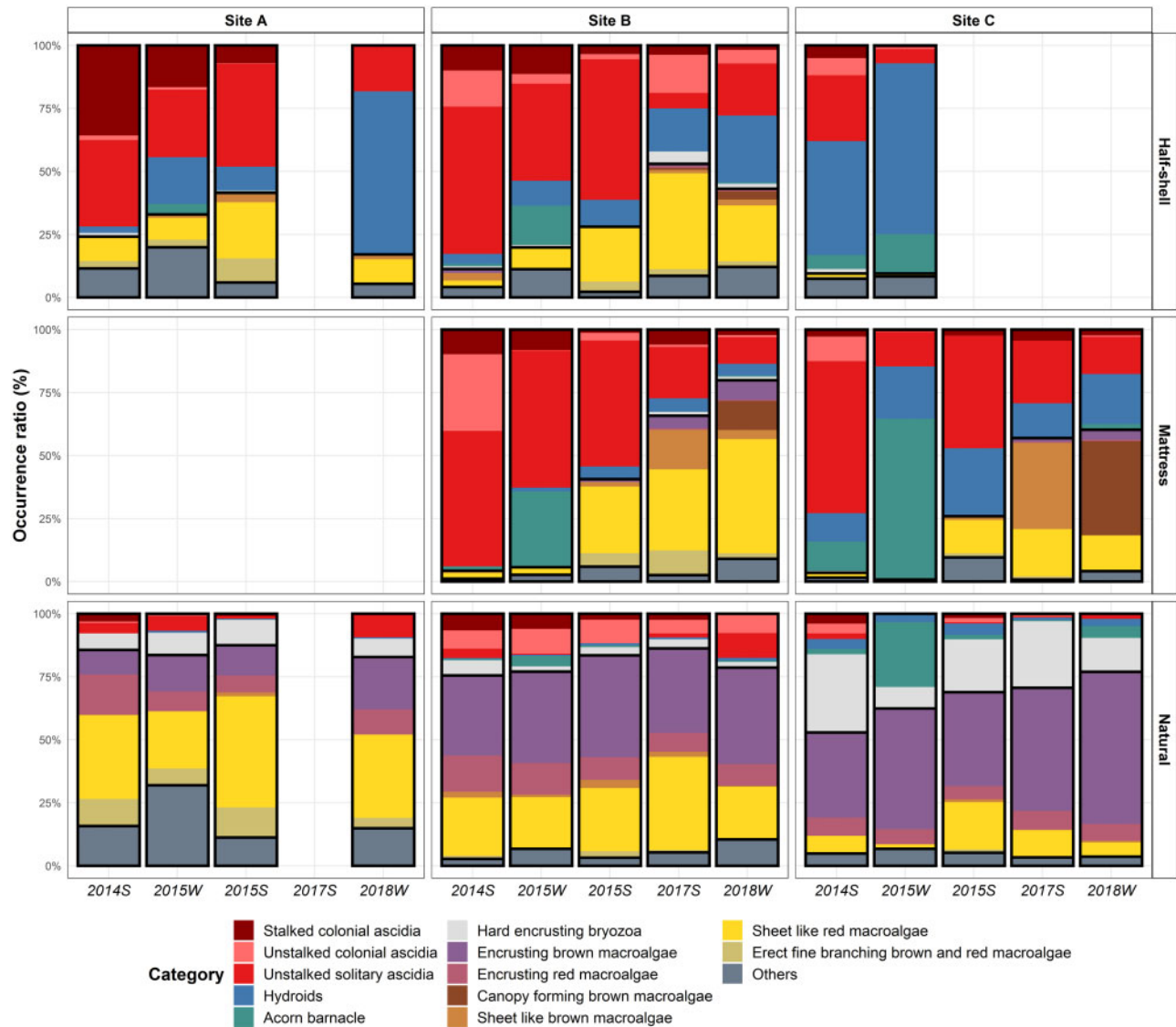


**Figure 3.** nMDS based on Bray–Curtis similarities in community composition between samples. Each point represents an image, and thin lines connect all images scored from the same “Habitat, Site, and Campaign” combination to their centroid; bold lines and arrows show the mean temporal trajectories for each site and habitat. For clarity purposes, the nMDS is shown independently for each survey site (A, B, and C). The 50% most frequent epibenthic taxa and the 70% best fitting with the axes were displayed in the bottom right panel. 2D stress = 0.18; S: summer; W: winter.

macroalgae dominated natural habitats; conversely, encrusting algae (mainly brown) and encrusting bryozoans dominated at site C (Figure 4); at site B, natural substrate hosted both sheet-like red algae and encrusting brown algae in similar proportions (Figure 4). Natural habitat communities varied significantly through time at sites C and A, but these changes were marginal relative to those observed within communities on artificial habitats (Figures 3 and 4).

Across all sites, the first axis of the MDS clearly distinguishes between artificial and natural habitats (Figure 3). Taxonomic similarity between artificial and natural habitats increased with time at site B but remained low at sites A and C (Figures 3 and 5).

At the beginning of the survey, half-shells and mattresses hosted fairly similar communities characterized by high proportions of unstalked solitary ascidians and other types of ascidians (Table 3 and Figures 3 and 4). Note that if the point count method does not quantify understory organisms, we observed from the imagery that this matrix of ascidians mainly developed on top of barnacle mats during the summer of 2014. From the summer 2015 campaign onwards, community composition started to diverge between the two artificial habitats (Figure 5). Indeed, the cover of the different ascidians declined in both habitats but were essentially substituted by sheet-like red macroalgae and hydroids on half-shells, whereas mattresses were mostly



**Figure 4.** Temporal changes in mean relative percentage cover estimates for epibenthic taxa per habitat (half-shell, mattress, and natural) and at each sites (A, B, and C). Only taxa with mean relative cover percentage >5% were displayed, all others were agglomerated as “Others”. Black lines delineate algal from animal taxa as well as “Others”. S: summer; W: winter.

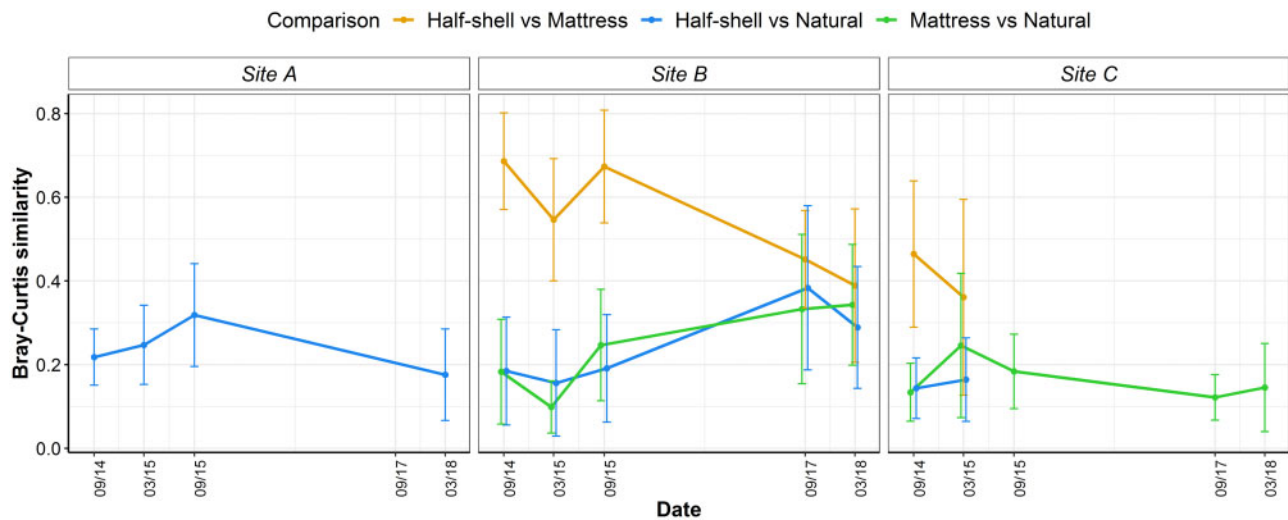
overgrown by diverse types of macroalgae. Canopy-forming algae (i.e. kelps) started to appear only on mattresses, and to a lesser extent on half-shells, during the last campaign (Figure 4). It should be noted that during the winter 2015 campaign, a massive settlement of barnacles was recorded on both artificial habitats at sites B and C and natural habitat at site C, but the population was not observed during the following campaigns (Figure 3).

### Target species dynamics

On natural habitat, densities of the three target species were constant throughout the period except for *C. fornicata*, which density decreased over time at site C (Figure 6).

The two non-indigenous species *C. fornicata* and *S. clava* exhibited quite similar temporal dynamics on artificial habitats. Their densities were higher on artificial habitats relative to natural habitats during the first years of the survey before declining to levels similar to those on natural habitats (Figure 6). At sites A

and B, *C. fornicata* densities were higher on half-shell habitats than on natural habitats ( $p < 0.05$ ; maximum mean density of  $6.3 \pm 4.1$  ind  $m^{-2}$  at site C on half-shell during the summer of 2014) until winter 2015. Then, mean densities dropped below 1 ind  $m^{-2}$ , which corresponds to population density estimates on natural habitats ( $p > 0.05$ ). Across all sites, *S. clava* densities were initially higher on half-shell (maximum mean density of  $6.3 \pm 4.1$  ind  $m^{-2}$  at site C during the summer of 2014) and mattress habitats (maximum mean density of  $11.1 \pm 1.3$  ind  $m^{-2}$  at site C during the summer of 2015) than on natural habitat ( $p < 0.05$ ) before converging towards similar densities, from summer 2016 onwards and from winter 2018 onwards for mattress and half-shell habitats ( $p > 0.05$ ), respectively. Our hypothesis ii (i.e. “non-indigenous species are more present on artificial than natural habitats”) is thus validated for both non-indigenous species targeted but only during the first years of the survey.



**Figure 5.** Temporal evolution of mean Bray–Curtis similarities in epibenthic assemblage composition between the different habitats. Mean similarities were computed based on all possible image combinations for each pair of habitat types (colour coded as per the legend above the figure), for each campaign and survey site (A, B, and C). Error bars represent standard deviation.

The foundation species *Laminaria* sp. presented an opposite temporal dynamic (Figure 6). Kelp density remained low ( $<1$  ind  $m^{-2}$ ) on natural and half-shell habitats at all sites throughout the survey whereas it steadily increased over time on mattress habitat. At the beginning of the survey (i.e. summer 2014 and winter 2015), *Laminaria* sp. was scarce on mattresses ( $<1$  ind  $m^{-2}$ ). From summer 2015 onwards, densities were consistently higher (and reached a maximum mean density of  $185.2 \pm 43.3$  ind  $m^{-2}$  at site C during the summer of 2017) on mattresses than on natural and half-shell habitats ( $p > 0.05$ ).

## Discussion

Based on a 4-year survey using high-resolution underwater imagery, we characterize habitat-specific changes through space and time in the taxonomic composition of epibenthic communities in a tide-swept environment. In particular, we describe the ecological succession on two kinds of artificial habitats. Our results specifically highlight an overall similar trend in the ecological successions across both artificial habitats. However, significant habitat-specific differences in community composition emerged during the final campaigns.

### Spatial heterogeneity

While the three study sites are only 2.5 km apart and located at similar depths, they host significantly different benthic communities on natural habitat (pebbles and rocks). Encrusting organisms dominated at site C, as opposed to erect taxa at site A while community composition was intermediate at site B. This spatial pattern may be explained by the relative exposure to residual currents that increases from site A to site C. This suggests that a physical stress gradient influences epibenthic communities along the cable route, from the coast to open sea. Our observations are in line with those made concerning the SeaGen tidal test site in the Strangford Narrows, where encrusting communities are found to be associated with high-energy hydrodynamic locations, while erect communities dominated in more sheltered areas (O’Carroll *et al.*, 2017). Indeed, because of their morphology, encrusting taxa are less exposed to shear stress and abrasion,

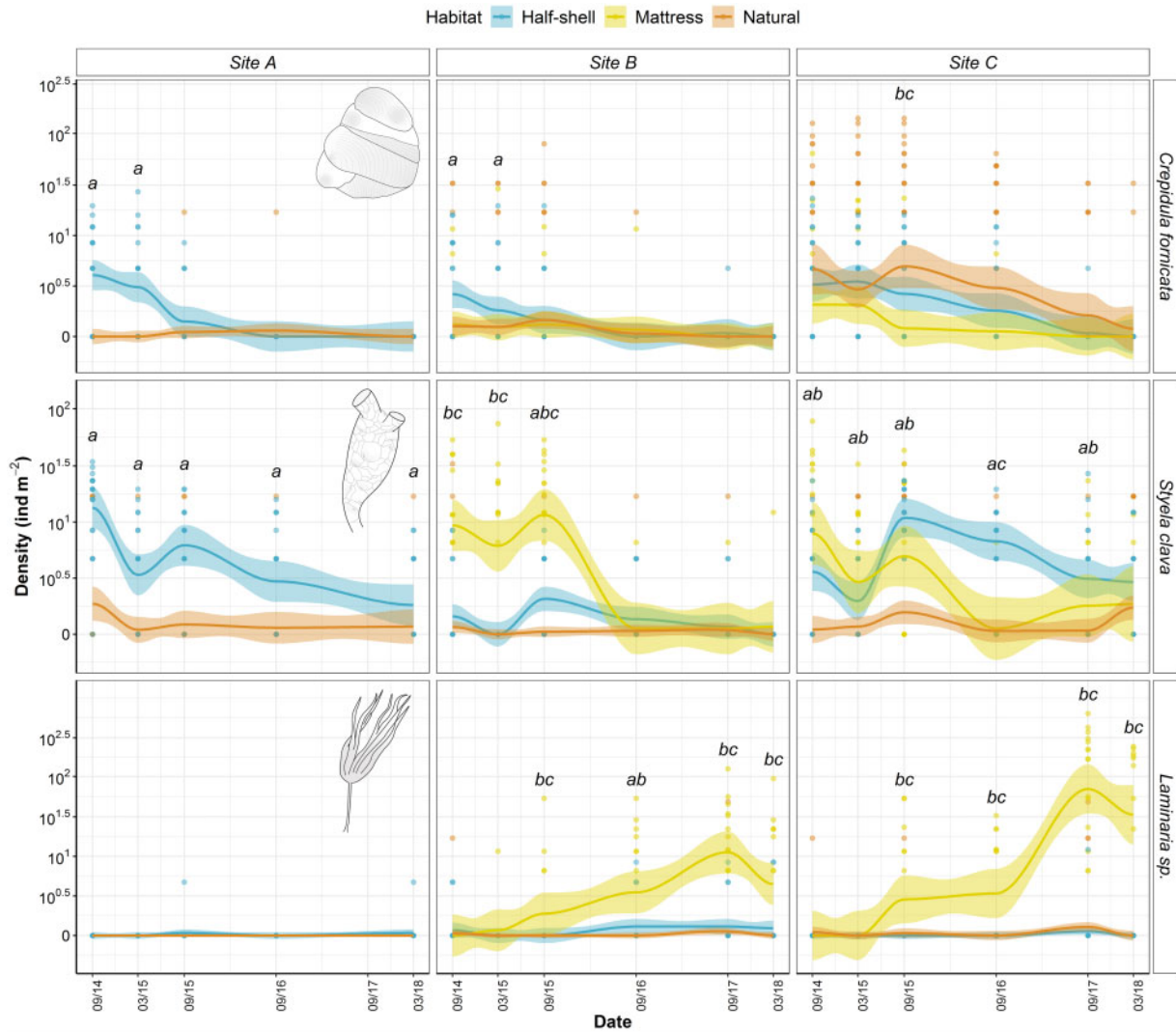
compared to erect taxa that protrude into the water column and have a reduced point of attachment to the substratum (Vogel, 1994). They are consequently more easily swept away by high frictional flow or abrasion via mobile sediments (Daly and Mathieson, 1977; Palmer and Palmer, 1977; Vogel, 1994). Hydrodynamic conditions, in addition to cause abrasion and direct removal of epibenthic taxa, alter the stability of the pebbles, which serve as substrate for these taxa, thus increasing the overall stress. Indeed, when the overturn frequency of the substratum (i.e. pebbles and boulders) is high, development of erected taxa is prevented (Osman, 1977; Sousa, 1979a).

### Patterns of ecological succession

Our survey actually started 2 years after the deployment of half-shells and 1 year after the deployment of concrete mattresses. Thus, the first months of bare substrate colonization, which are often associated with rapid changes in benthic macrofauna communities (Wahl, 1989), were not monitored.

The two artificial habitats (i.e. half-shells and mattresses) showed similar ecological succession patterns over the first 3 years of our survey and then exhibited different communities. In the summer of 2014, ascidian matrices covering dead barnacle mats dominated in both artificial habitats. Six months later, in winter 2015, ascidian communities had almost entirely disappeared from both artificial and natural habitats and were replaced by newly settled mats of barnacles. This “community reset” is probably due to natural decay of initial barnacle mats (and associated ascidians) and/or because of intense abrasion due to harsh winter conditions (i.e. storms). Since ascidians often grow inside barnacle orifices (Russ, 1980; Yakovis *et al.*, 2008), ascidian overgrowth may have contributed to barnacles death and subsequent unattachment. From summer 2015 onwards, barnacles did not dominate on artificial habitats. Ascidians (especially unstalked and solitary ones) persisted initially but, by the end of the 4-year survey, they had gradually been replaced or overgrown by different erect macroalgae (especially on mattresses) and hydroids (especially on half-shells).





**Figure 6.** 2014–2018 temporal changes in densities of the three target species (*C. fornicata*, *S. clava*, and *Laminaria sp.*) at each site (A, B, and C) for each habitat (half-shell, mattress, and natural). Points represent single image density estimates and curves represent mean habitat-specific trends smoothed out using a loess (local polynomial regression fitting). Greyed envelopes indicate 95% confidence intervals. Note that we used a logarithmic scale for clarity. Letters indicate significant differences in target species density during a given campaign based on pairwise comparisons between habitats, namely between half-shell and natural habitats (a), between mattress and natural habitats (b), and between half-shell and mattress habitats (c).

Both barnacles and ascidians are well known to be early colonizers on a wide variety of artificial hard substrates (Brault and Bourget, 1985; Henschel et al., 1990; Hatcher, 1998; Andersson et al., 2009; De Mesel et al., 2015). On the other hand, kelps are commonly described as a characteristic species of late stages of ecological succession (Carter et al., 1985; Hirata, 1986) while hydroids can occur both as a transient and as a permanent species in epibenthic communities (Forteath et al., 1982; Boero and Fresi, 1986; De Mesel et al., 2015). Ecological successions described on both mattresses and half-shells in our study are classic in the sense that epibenthic communities are initially dominated by pioneering taxa (i.e. barnacles and ascidians), which are then gradually outcompeted by long-lived and morphologically complex taxa (i.e. macroalgae and hydroids). This succession likely results from a facilitation cascade (Altieri et al., 2007), which can be viewed as a chain of foundation species involved in a hierarchy of positive interactions (e.g.

mutualism or facilitation). In our study, the “primary” substratum (i.e. freshly deployed artificial substrate) gets colonized by barnacles (i.e. the first foundation species if only considering macro-organisms). These barnacle mats form a “secondary” substratum that facilitates settlement for a wide diversity of taxa (Brault and Bourget, 1985; Henschel et al., 1990), including a variety of ascidians that then create a “tertiary” substratum. Ascidians, together with remaining barnacles, then allow for the settlement of more complex and long-lived taxa, such as kelp or hydroids. A similar facilitation cascade dynamics, involving the same taxa (i.e. barnacles, ascidians, and macroalgae), is described on cockle shells of the White sea (Yakovis et al., 2008; Yakovis and Artemieva, 2017). While we stopped our survey after these first signs of colonization by kelp and hydroids, we can expect that these complex habitat formers will also facilitate settlement for a new range of taxa (Norderhaug et al., 2002; Christie et al., 2003; Di Camillo et al., 2017).

Temporal changes in community composition on mattresses and half-shells during winter 2018 indicated that ecological successions had still not reached an equilibrium state, although these two artificial substrates had been in place for 5 and 6 years, respectively. This is consistent with epibenthic communities reaching climax after up to 11 years in calm environments (Whomersley and Picken, 2003). Our study highlights the need to maintain long-term surveys of coastal artificial reef habitats to better characterize ecological successions and short-term variability benthic communities. Nevertheless, taxa considered as indicators of late stages of ecological successions dominated the community of our artificial habitats at the end of our survey, giving an idea of the characteristics of their future potential climax states.

### Implications for non-indigenous species

Numerous examples showed that introduction of new artificial habitats in marine environments can contribute to the introduction or propagation of non-indigenous species (Bulleri and Airoldi, 2005; Vaselli *et al.*, 2008; Mineur *et al.*, 2012; Airoldi *et al.*, 2015; De Mesel *et al.*, 2015). Non-indigenous species are often opportunistic and act as early colonizers of new artificial habitats, which directly contribute to their invasive success (Mineur *et al.*, 2012; De Mesel *et al.*, 2015). In this study, the densities of the two non-indigenous species *C. fornicata* and *S. clava* were higher on both artificial habitats than on the natural habitat during the first years of the survey. Nevertheless, their densities decreased after 2 or 3 years of survey down to similar levels than in natural habitats, with slight differences across species (*C. fornicata* or *S. clava*) and sites. Although the two species show early temporal dynamics typical of pioneer species on artificial habitats, we noted slightly different installation strategies. *Crepidula fornicata* settled rapidly on freshly installed mattresses, on half-shells and on conspecific individuals but was never observed to settle onto other epibenthic species. Conversely, *S. clava* was able to settle on “secondary substratum” formed by early-colonizing epibenthic taxa, as reported in other locations (Lützen, 1998). *Crepidula fornicata* early decline can thus be explained by strong competition for space for instance with barnacles and ascidians, which drastically reduce the availability of bare artificial substratum. On the contrary, *S. clava*, which can settle on other species, could better persist in time as the availability of primary substratum is not a limiting factor. Nevertheless, its density eventually decreased due to spatial competition processes with other species of the community.

Although the densities of these two species on artificial habitats decreased within a few years, they possibly persisted long enough for individuals to become sexually mature and reproduce. Indeed, *S. clava* can reach sexual maturity within 10 months (Lützen, 1998) while *C. fornicata* female and male individuals can reach maturity within 2 years and 1 year post-settlement, respectively (Richard, 2005). Consequently, we showed that such artificial habitats can act as stepping stones, allowing non-indigenous species to settle and successfully reproduce even if they do not persist locally in the long term. In our case, however, there is no risk of a stepping-stone effect since (i) *C. fornicata* and *S. clava* are present on surrounding biogeographic areas for decades (Mineur *et al.*, 2012) and (ii) the presence of hard substratum is not a limiting factor in our study area (see rocky shelves on Figure 1). Nevertheless, we still largely lack a mechanistic understanding of how artificial structures can act as stepping stones

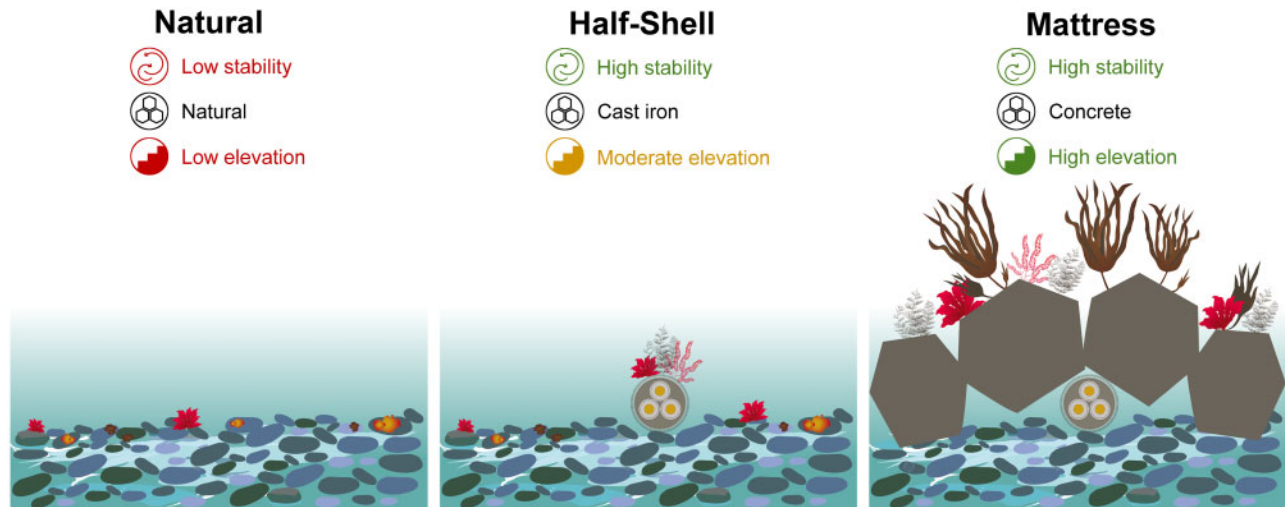
that enhance the spread of invasive species (Mineur *et al.*, 2012; Copping *et al.*, 2016; Dannheim *et al.*, 2020). This question constitutes a research priority where artificial structures are installed (i) in soft-sediment areas, where hard substratum is limiting and (ii) at the edge of invasive species biogeographical distribution.

While *C. fornicata* and *S. clava* rapidly colonized new substrate before declining, their dynamics are likely specific to our study environment. Indeed, artificial substrates installed within soft-sediment environments disproportionately favour non-indigenous over native species (Airoldi *et al.*, 2015). Also, note that we only target these two species because they were easily recognizable on underwater images. Other non-indigenous species could exhibit different colonization dynamics and for instance outcompete indigenous species. For example, another study comparing trends of epibenthic communities colonization on natural and artificial (aluminium sheet metal, polystyrene, polyvinyl chloride and rubber) shows a decline in the relative abundance of native compared to non-indigenous species over a 6-month survey (Tyrrell and Byers, 2007).

### Towards different climaxes

Despite a common trend in terms of community succession on both artificial substrates during the first 3 years of the survey, epibenthic communities exhibited contrasted habitat-specific trajectories at the end of the 4 years survey. During the two last campaigns, high proportions of hydroids taxa dominated on half-shells while erect macroalgae, especially *Laminaria* sp., were dominant, alongside with hydroids, on mattresses. These observations suggest colonizing communities gradually evolve towards different habitat-specific mature stages. In particular, final communities on both artificial substrates differ from each other, as well as from community climax observed in the surrounding natural habitat. A combination of drivers can explain these distinct habitat-specific trajectories (Figure 7):

Thus, deployment of artificial structures in tide-swept areas, such as the Paimpol–Bréhat tidal test site, contributes additional stable and sheltered substrata in an exposed and stressful environment (Sousa, 1979a, b; Dean and Connell, 1987). In these environments, epibenthic community structure is more likely influenced by physical processes than by biological interactions (Dean and Connell, 1987; Sousa, 1979a). Physical disturbances regularly free space for recolonization, as observed in our study during the winter 2015 campaign. Climax stage for epibenthic communities in such environment corresponds to a heterogeneous mosaic of more or less mature species communities given that disturbances regularly interrupt successional sequences (Osman, 1977; Palmer and Palmer, 1977; Sousa, 1979a, b). We must indeed keep in mind that climax stage is context dependent and corresponds to the most mature and most persistent community stage given local conditions. Deployment of stable artificial habitats in such dynamic environment creates a potential for epibenthic species communities to reach more mature ecological stages than communities developing on natural habitats. As these stable artificial habitats allow for mature structurally complex epibenthic communities to flourish, they likely increase local species diversity given the lack of such stable hard substrates in the natural environment.



**Figure 7.** Conceptual diagram of the epibenthic colonization of the three different habitats of the Paimpol–Bréhat tidal test site at the end of our survey. Natural habitats (left) are dominated by unstable pebbles and are highly exposed to sediment scouring; the epibenthic community is thus characterized by encrusting taxa. Half-shells (middle) constitute a stable cast iron habitat moderately exposed to sediment scouring due to moderate elevation; the epibenthic community is thus characterized by erect taxa with moderate structural complexity (e.g. hydroids). Mattresses (right) constitute a stable concrete habitat marginally exposed to sediment abrasion as their anchor point is high above adjacent sediments; the epibenthic community is characterized by various erect taxa with complex morphology (e.g. kelps).

- (1) First, artificial substrate type and seafloor characteristics (e.g. texture, complexity, composition, and colour) may impact epibenthic communities colonizing artificial habitats (Hixon and Brostoff, 1985; Glasby, 2000). Concrete and steel, which, respectively, constitute mattresses and half-cast in our study, are reported host different epibenthic communities (Andersson *et al.*, 2009). Concrete surface roughness can to some extent mimic natural rocky surfaces (Foster, 1975; Sousa, 1979b). On the contrary, steel smoother surface can make species settlement more challenging (Andersson *et al.*, 2009; Ushiyama *et al.*, 2016).
- (2) Furthermore, in such high-energy environment, substratum degree of immovability largely determines the trajectory of colonizing epibenthic communities. At the three sites, the natural habitat is essentially composed of pebbles with only a few boulders. Strong tidal currents in the area can regularly destabilize these pebbles making them a highly unstable habitat for benthic macrofauna and preventing the development of erect and complex taxa (Osman, 1977; Sousa, 1979a). On the other hand, the artificial habitats considered in this study are massive and cannot be displaced by currents, offering more stability and allowing the development of more complex communities.
- (3) In addition to stability, habitat elevation above the natural bottom directly determines local exposure to sediment abrasion. For instance, the presence of epifaunal organisms somehow depends on the size and elevation of stones in the subtidal German Bight, where large boulders are overall more colonized than cobbles (Michaelis *et al.*, 2019). According to Michaelis *et al.* (2019), these differences are due to high abrasion and burial by mobile sediments on small hard substrates with low elevation. Thus, the higher the habitat, the more sheltered the epibenthic communities from sediment abrasion. Half-shells and mattresses sit, respectively, at ~15 and ~40 cm above natural habitats. As explained previously, erect taxa are less adapted than

encrusting organisms to this frictional stress caused by abrasion (Vogel, 1994). Natural habitats, which are more exposed to abrasion, showed higher proportions of encrusting organisms than the two artificial habitats. Conversely, erect taxa are more abundant on more sheltered (i.e. elevated) habitats such as moderately elevated half-shells, and even more abundant on concrete mattresses. The high colonization of hydroids, mainly *Sertularia* sp., at the apex of the half-shells is linked to the tolerance of these taxa to periodic submergence and scouring by sand (Connor *et al.*, 2004). Mattress habitats are the least exposed to abrasion and consequently housed the most complex communities including large canopy-forming algae.

### Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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