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

Taormina Bastien ^{1,2,*}, Percheron Arthur ², Marzloff Martin ², Caisey Xavier ², Quillien Nolwenn ¹, Lejart Morgane ¹, Desroy Nicolas ³, Dugornay Olivier ⁴, Tancray Aurelien ⁵, Carlier Antoine ²

¹ France Energies Marines, 525 Avenue Alexis de Rochon, Plouzané 29280, France

² Ifremer, Centre de Bretagne, DYNECO - Laboratoire d'écologie benthique, ZI de la Pointe du Diable - CS 10070, Plouzané 29280, France

³ Ifremer, Laboratoire Environnement Ressources Bretagne Nord, 38 rue du Port Blanc, Dinard 35801, France

⁴ Ifremer, Centre de Bretagne, Direction de la Communication - Pôle audiovisuel, ZI de la Pointe du Diable - CS 10070, Plouzané 29280, France

⁵ Ifremer, Centre de Bretagne, Laboratoire Comportement des Structures en Mer, ZI de la Pointe du Diable - CS 10070, Plouzané 29280, France

* Corresponding author : Bastien Taormina, email address : bastien.taormina@france-energies-marines.org

Abstract :

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

1. Introduction

When submerged in seawater, hard substrates are colonised 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 *etc.*), and macroalgal (*e.g.* Chlorophyta, Rhodophyta and Ochrophyta) assemblages. Colonisation 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 colonisers are usually pioneering species, which are gradually replaced by longer-lived morphologically-complex species as the colonising 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 *etc.* ; Falace and Bressan, 2000) and local environmental conditions (*e.g.* temperature, light, pH, salinity, currents *etc.* ; Bowden et al., 2006; Falace and Bressan, 2000; Pérès and Picard, 1964) .

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 *etc.*; 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.* windfarms, 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, colonisation of MRE structures by benthic organisms is often considered 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 colonisation 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 *etc.*) 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 (Airoidi *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 Airoidi, 2005).

Although colonisation 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 characterise 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 characterising epibenthic colonisation of different MRE structures located in a high-energy hydrodynamic environment. Using four 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.

2. Methods

2.1 Study area

The study area encompasses a 15 km-long submarine power cable (8 MVA - 10 kVDC) set up in 2012 to connect the tidal test site of Paimpol-Bréhat (Brittany, France; Figure 1) managed by Electricité De France (EDF). The implantation site is characterised by major tidal currents (up to $3 \text{ m}\cdot\text{s}^{-1}$ during Spring tides) and the bottom is dominated by hard substratum (pebbles and rocks) and highly mobile shell debris and coarse sand (authors pers. obs.). Because of these characteristics, 11 km of cable are unburied and fully protected with nested cast iron half-shells (50 cm long, 15 cm diameter). The cable is also stabilised 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 colonisation of the investigated artificial reefs wasn't influenced by any potential effects of electromagnetic fields or heat emission.

2.2 Sites characterisation

The three sites span similar depth ranges (between 18 and 20 m). To characterise 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 $\text{m}\cdot\text{s}^{-1}$) were derived from a 2010-2015 climatology from simulations using the MARS3D hydrodynamic model (Lazure and Dumas, 2008) and seafloor topography was used to characterise exposure to residual current (ranging from 0° , when the seafloor is sheltered, to 180° , when it is fully exposed to dominant current).

2.3 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) 40 photographs were taken to cover both sides of each 50 cm long iron half-shell along a 10 m transect;
- ii) 16 photographs were taken to survey the 16 concrete blocks that constitute each mattress (8 units of 47x38 cm and 8 units of 47x20 cm);
- iii) a minimum of 20 photographs were taken to characterise the neighbouring natural habitat in the vicinity of the cable. Each corresponds to a 25x25 cm quadrat randomly positioned at a minimum distance of 10 m from the cable to avoid the influence of artificial structures.

The four years survey produced a total of 1,482 images (Table 1). Photographs were taken at a resolution of 37 million pixels per image with a Nikon D810 inside a Ikelite underwater housing, with a 20 mm lens and 2 Keldan LED lights (105W, 9000 lumens). All images of half shells were calibrated with a scale bar.

2.4 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 optimised based on a representative subset of the data base (Taormina *et al.*, 2020). For each

combination of habitat, site and campaign, 10 images were chosen at random among the available image set. A standardised scoring area of 625 cm² was cropped for ‘natural’ and ‘mattress’ habitat images. For half-shell images, scoring area varied between 500 to 625 cm² depending on the surface available on the original photograph. Within these cropped areas, 0.4 points.cm⁻² (*i.e.* 250 points for an area of 625 cm²) 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 were 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 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 recognisable 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). In order to analyse changes in density estimates over time for each target species (ind.m^{-2}), estimated abundances were divided by each image surface area. In total, 1,482 images were analysed for this task.

2.5 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 1). 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 characterised across habitats and campaigns using non-parametric Kruskal-Wallis tests. When significant, pairwise comparison tests using Bonferoni 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).

3. Results

3.1 Site characterisation

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

respectively). 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.

3.2 Epibenthic community dynamics

Across all pictures analysed, a total of 36 taxa (8 macroalgae and 28 animals) from 10 phyla were identified (Supplementary information 2). Benthic community composition changed significantly across all factors “Habitat”, “Campaign”, “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 colonising 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 four 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 colonising 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 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 (Figure 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 (Figure 3, Figure 5).

At the beginning of the survey, half-shells and mattresses hosted fairly similar communities characterised by high proportions of unstaked solitary ascidians and other types of ascidians (Table 3, 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 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).

3.3 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 site A and B, *C. fornicata* densities were higher on half-shell habitats than on natural habitats ($P < 0.05$; maximum mean density of $6.3 \pm 4.1 \text{ ind.m}^{-2}$ 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 $6.3 \pm 4.1 \text{ ind.m}^{-2}$ at site C during the summer of 2014) and mattress habitats (maximum mean density of $11.1 \pm 1.3 \text{ ind.m}^{-2}$ 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.

The foundation species *Laminaria sp.* presented an opposite temporal dynamic (Figure 6). Kelp density remained low ($< 1 \text{ ind.m}^{-2}$) 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 ($< 1 \text{ ind.m}^{-2}$). From summer 2015 onwards, densities were consistently higher (and reached a maximum mean density of $185.2 \pm 43.3 \text{ ind.m}^{-2}$ at site C during the summer of 2017) on mattresses than on natural and half-shell habitats ($P > 0.05$).

4. Discussion

Based on a four year survey using high-resolution underwater imagery, we characterise 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.

4.1 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 it prevented (Osman, 1977; Sousa, 1979a).

4.2 Patterns of ecological succession

Our survey actually started two years after deployment of half-shells and one year after deployment of concrete mattresses. Thus, the first months of bare substrate colonisation, 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 three 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 four year survey, they had gradually been replaced or overgrown by different erect macroalgae (especially on mattresses) and hydroids (especially on half-shells).

Both barnacles and ascidians are well-known to be early colonisers 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 or 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 colonised by barnacles (*i.e.* the first foundation species if only considering macro-organisms). These barnacles 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 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 colonisation 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 five and six 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 in order to better characterise 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.

4.3 Implications for non-indigenous species

Numerous examples showed that introduction of new artificial habitats in marine environments can contribute to introduction or propagation of non-indigenous species (Bulleri and Airoidi, 2005; Vaselli *et al.*, 2008; Mineur *et al.*, 2012; Airoidi *et al.*, 2015; De Mesel *et al.*, 2015). Non-indigenous species are often opportunistic and act as early colonisers 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 two or three 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. *C. 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-colonising epibenthic taxa, as reported in other locations (Lützen, 1999). *C. fornicata* early decline can thus be explained by strong competition for space for instance with barnacles and ascidians, which drastically reduce availability of bare artificial substratum. On the contrary, *S. clava*, which can settle on other species, could better persist in time as 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, 1999) while *C. fornicata* female and male individuals can reach maturity within two years and one 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 colonised new substrate before declining, their dynamics are likely specific to our study environment. Indeed, artificial substrates installed within soft-sediment environments disproportionally 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 colonisation dynamics and for instance outcompete indigenous species. For example, another study comparing trends of epibenthic communities colonisation on natural and artificial (aluminium sheet metal, polystyrene, PVC and rubber), shows a decline in the relative

abundance of native compared to non-indigenous species over a six-month survey (Tyrrell and Byers, 2007).

4.4 Towards different climaxes

Despite a common trend in terms of community succession on both artificial substrates during the first three years of the survey, epibenthic communities exhibited contrasted habitat-specific trajectories at the end of the four 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 colonising 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) :

1. First, artificial substrate type and seafloor characteristics (*e.g.* texture, complexity, composition and colour) may impact epibenthic communities colonising 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; Ushiana *et al.*, 2016).

2. Furthermore, in such high-energy environment, substratum degree of immovability largely determines the trajectory of colonising 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 destabilise 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 cm 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 colonisation 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.

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, 1979b; 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 an heterogeneous mosaic

of more or less mature species communities given that disturbances regularly interrupt successional sequences (Osman, 1977; Palmer and Palmer, 1977; Sousa, 1979a, 1979b). 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.

Acknowledgements

This work is sponsored by the Région Bretagne, France Energies Marines and the National Research Agency within the framework of Investments for the Future program under reference ANR-10-IED-0006-17. The authors would like to thank Fernando Tempera, Laura Taormina and Nicolas Job for their kind assistance.

- Adams, T. P., Miller, R. G., Aleynik, D., and Burrows, M. T. 2014. Offshore marine renewable energy devices as stepping stones across biogeographical boundaries. *Journal of Applied Ecology*, 51: 330–338.
- Airoidi, L., Turon, X., Perkol-Finkel, S., and Rius, M. 2015. Corridors for aliens but not for natives: Effects of marine urban sprawl at a regional scale. *Diversity and Distributions*, 21: 755–768.
- Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C. H. L., Stuart-Smith, R., *et al.* 2015. A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: The CATAMI classification scheme. *PLoS ONE*, 10: 1–18. <http://dx.doi.org/10.1371/journal.pone.0141039>.
- Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. *American Naturalist*, 169: 195–206.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26: 32–46. <http://libproxy.udayton.edu/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=a9h&AN=5472169&site=eds-live>.
- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62: 245–253.
- Andersson, M. H., Berggren, M., Wilhelmsson, D., and Öhman, M. C. 2009. Epibenthic colonization of concrete and steel pilings in a cold-temperate embayment: a field experiment. *Helgoland Marine Research*, 63: 249–260.
- Bishop, M. J., Mayer-Pinto, M., Airoidi, L., Firth, L. B., Morris, R. L., Loke, L. H. L., Hawkins, S. J., *et al.* 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. *Journal of Experimental Marine Biology and Ecology*, 492: 7–30. The Authors. <http://dx.doi.org/10.1016/j.jembe.2017.01.021>.
- Boero, F., and Fresi, E. 1986. Zonation and evolution of a rocky bottom hydroid community. *Marine Ecology*, 7: 123–150.
- Bohnsack, J. A., Johnson, D. L., and Ambrose, R. F. 1991. Ecology of Artificial Reef Habitats and Fishes. *In* *Artificial Habitats for Marine and Freshwater Fisheries*, pp. 61–107. ACADEMIC PRESS, INC., San Diego. <http://dx.doi.org/10.1016/B978-0-08-057117-1.50009-3>.
- Bowden, D. A., Clarke, A., Peck, L. S., and Barnes, D. K. A. 2006. Antarctic sessile marine benthos: Colonisation and growth on artificial substrata over three years. *Marine Ecology Progress Series*, 316: 1–16.
- Brault, S., and Bourget, E. 1985. Structural changes in an estuarine subtidal epibenthic community : biotic and physical causes. *Marine Ecology Progress Series*, 21: 63–73.
- Bulleri, F., and Airoidi, L. 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, 42: 1063–1072.
- Carter, J. W., Carpenter, A. L., Foster, M. S., and Jessee, W. N. 1985. Benthic succession on an artificial reef designed to support a kelp-reef community. *Bulletin of Marine Science*, 37: 86–113.
- Christie, H., Jørgensen, N. M., Norderhaug, K. M., and Waage-Nielsen, E. 2003. Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian coast. *Journal of the Marine Biological Association of the United Kingdom*, 83: 687–699.
- Clarke, K. R., and Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, 92: 205–219.
- Clements, F. E. 1916. *Plant succession; an analysis of the development of vegetation*. Carnegie

- Institution of Washington. 1-512 pp.
- Connell, J. H., and Slatyer, R. O. 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *The American Naturalist*, 111: 1119–1144.
- Connor, D. W., Allen, J. H., Golding, N., Kerry, L., Lieberknecht, L. M., Northen, K. O., and Reker, J. B. 2004. The Marine Habitat Classification for Britain and Ireland Version 15.03. [2019-09-02]. Joint Nature Conservation Committee, Peterborough. Available from <https://mhc.jncc.gov.uk/>.
- Coolen, J. W. P., van der Weide, B., Cuperus, J., Blomberg, M., Van Moorsel, G. W. N. M., Faasse, M. A., Bos, O. G., *et al.* 2018. Benthic biodiversity on old platforms, young wind farms, and rocky reefs. *ICES Journal of Marine Science*.
- Copping, A., Battey, H., Brown-Saracino, J., Massaua, M., and Smith, C. 2014. An international assessment of the environmental effects of marine energy development. *Ocean and Coastal Management*, 99: 3–13. Elsevier Ltd. <http://dx.doi.org/10.1016/j.ocecoaman.2014.04.002>.
- Copping, A., Sather, N., Hanna, L., Whiting, J., Zydlewsk, G., Staines, G., Gill, A., *et al.* 2016. Annex IV 2016 State of the Science Report: Environmental Effects of Marine Renewable Energy Development Around the World.
- Daly, M. A., and Mathieson, A. C. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology*, 43: 45–55.
- Dannheim, J., Bergström, L., Birchenough, S. N. R., Brzana, R., Boon, A. R., Coolen, J. W. P., Dauvin, J.-C., *et al.* 2020. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. *ICES Journal of Marine Science*, 77: 1092–1108.
- De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., and Degraer, S. 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia*, 756: 37–50. Springer International Publishing.
- Dean, R. L., and Connell, J. H. 1987. Marine invertebrates in an algal succession. I. Variations in abundance and diversity with succession. *Journal of Experimental Marine Biology and Ecology*, 109: 217–247.
- Di Camillo, C. G., Bavestrello, G., Cerrano, C., Gravili, C., Piraino, S., Puce, S., and Boero, F. 2017. Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests. *In* *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*, pp. 397–427. Ed. by S. Rossi, L. Bramanti, A. Gori, and O. Covadonga. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-21012-4_11.
- Falace, A., and Bressan, G. 2000. ‘Periphyton’ Colonization: Principles, Criteria and Study Methods. *In* *Artificial Reefs in European Seas*, pp. 435–449. Springer Netherlands.
- Forteach, G. N. R., Picken, G. B., Ralph, R., and Williams, J. 1982. Marine Growth Studies on the North Sea Oil Platform Montrose Alpha. *Marine Ecology Progress Series*, 8: 61–68.
- Foster, M. S. 1975. Regulation of algal community development in a *Macrocystis pyrifera* forest. *Marine Biology*, 32: 331–342.
- Glasby, T. M. 2000. Surface composition and orientation interact to affect subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, 248: 177–190.
- Hatcher, A. M. 1998. Epibenthic colonisation patterns on slabs of stabilised coal-waste in Poole Bay, UK. *Hydrobiologia*, 367: 153–162.
- Heery, E. C., Bishop, M. J., Critchley, L. P., Bugnot, A. B., Airoidi, L., Mayer-Pinto, M., Sheehan, E. V., *et al.* 2017. Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology*, 492: 31–48. The Authors. <http://dx.doi.org/10.1016/j.jembe.2017.01.020>.

- Henschel, J. R., Cook, P. A., and Branch, G. M. 1990. The colonization of artificial substrata by Marine sessile organisms in false bay. 1. Community development. *South African Journal of Marine Science*, 9: 289–297.
- Hirata, T. 1986. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan*. I. Algal succession. *Marine Ecology Progress Series*, 34: 51–61.
- Hixon, M. A., and Brostoff, W. N. 1985. Substrate characteristics, fish grazing, and epibenthic reef assemblages off Hawaii. *Bulletin of Marine Science*, 37: 200–213.
- Inger, R., Attrill, M. J., Bearhop, S., Broderick, A. C., James Grecian, W., Hodgson, D. J., Mills, C., *et al.* 2009. Marine renewable energy: Potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*, 46: 1145–1153.
- Jensen, A. C., Collins, K. J., and Lockwood, A. P. M. 2000. *Artificial Reef In European Seas*. Springer Netherlands. 508 pp.
- Kregting, L., Elsaesser, B., Kennedy, R., Smyth, D., O’Carroll, J., and Savidge, G. 2016. Do changes in current flow as a result of arrays of tidal turbines have an effect on benthic communities? *PLoS ONE*, 11: 1–14. <http://dx.doi.org/10.1371/journal.pone.0161279>.
- Krone, R., Gutow, L., Joschko, T. J., and Schröder, A. 2013. Epifauna dynamics at an offshore foundation - Implications of future wind power farming in the North Sea. *Marine Environmental Research*, 85: 1–12. Elsevier Ltd. <http://dx.doi.org/10.1016/j.marenvres.2012.12.004>.
- Langhamer, O. 2012. Artificial Reef Effect in relation to Offshore Renewable Energy Conversion: State of the Art. *The Scientific World Journal*, 2012: e386713. <http://www.hindawi.com/journals/tswj/2012/386713/abs/%5Cnhttp://downloads.hindawi.com/journals/tswj/2012/386713.pdf%5Cnhttp://www.ncbi.nlm.nih.gov/pubmed/23326215>.
- Lazure, P., and Dumas, F. 2008. An external-internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). *Advances in Water Resources*, 31: 233–250.
- Lima, J. S., Zalmon, I. R., and Love, M. 2019. Overview and trends of ecological and socioeconomic research on artificial reefs. *Marine Environmental Research*, 145: 81–96. Elsevier. <https://doi.org/10.1016/j.marenvres.2019.01.010>.
- Lindeboom, H., Degraer, S., Dannheim, J., Gill, A. B., and Wilhelmsson, D. 2015. Offshore wind park monitoring programmes, lessons learned and recommendations for the future. *Hydrobiologia*, 756: 169–180. Springer International Publishing.
- Lützen, J. 1999. *Styela clava* Herdman (Urochordata, Ascidiacea), a successful immigrant to North West Europe. *Helgoländer Meeresuntersuchungen*, 52: 383–391.
- Michaelis, R., Hass, H. C., Mielck, F., Papenmeier, S., Sander, L., Ebbe, B., Gutow, L., *et al.* 2019. Hard-substrate habitats in the German Bight (South-Eastern North Sea) observed using drift videos. *Journal of Sea Research*, 144: 78–84. Elsevier. <https://doi.org/10.1016/j.seares.2018.11.009>.
- Mineur, F., Cook, E. J., Minchin, D., Bohn, K., Macleod, A., and Maggs, C. A. 2012. Changing coasts: Marine aliens and artificial structures. *In Oceanography and Marine Biology: An Annual Review*, pp. 189–234. CRC Press.
- Norderhaug, K. M., Christie, H., and Rinde, E. 2002. Colonisation of kelp imitations by epiphyte and holdfast fauna; a study of mobility patterns. *Marine Biology*, 141: 965–973.
- O’Carroll, J. P. J., Kennedy, R. M., Creech, A., and Savidge, G. 2017. Tidal Energy: The benthic effects of an operational tidal stream turbine. *Marine Environmental Research*, 129: 277–290. Elsevier Ltd. <http://dx.doi.org/10.1016/j.marenvres.2017.06.007>.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., *et al.* 2018. *vegan: Community Ecology Package*. R package version 2.4-6.

- <https://CRAN.R-project.org/package=vegan>.
- Osman, R. W. 1977. The Establishment and Development of a Marine Epifaunal Community. *Ecological Monographs*, 47: 37–63.
- Palmer, T. J., and Palmer, C. D. 1977. Faunal distribution and colonization strategy in a Middle Ordovician hardground community. *Lethaia*, 10: 179–199.
- Pérès, J. M., and Picard, J. 1964. Nouveau manuel de bionomie benthique de la Mer Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, 31: 1–137.
- Pickering, H., and Whitmarsh, D. 1997. Artificial reefs and fisheries exploitation: A review of the 'attraction versus production' debate, the influence of design and its significance for policy. *Fisheries Research*, 31: 39–59.
- Pielou, E. C. 1974. *Population and Community Ecology : Principles and Methods*. Gordon and Breach Science Publishers, New-York, Paris and London. 432 pp.
- Quillien, N., Lejart, M., and Damblans, G. 2018. *Bibliographical atlas of biofouling : Along the French Coasts in the Context of Offshore Renewable Energy*. France Energies Marines Editions, Plouzané. 76 pp.
- Reubens, J. T., Degraer, S., and Vincx, M. 2011. Aggregation and feeding behaviour of pouting (*Trisopterus luscus*) at wind turbines in the Belgian part of the North Sea. *Fisheries Research*, 108: 223–227. Elsevier B.V. <http://dx.doi.org/10.1016/j.fishres.2010.11.025>.
- Richard, J. 2005. *Crepidula fornicata : un modèle biologique pour l'étude du rôle de la variabilité des caractères phénotypiques (reproduction, croissance et nutrition) sur les processus de colonisation en milieu marin*. Université de Genève. 370 pp.
- RStudio Team. 2015. *RStudio: Integrated Development for R*. RStudio, Inc., Boston.
- Russ, G. R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology*, 42: 55–69.
- Sheehan, E. V., Stevens, T. F., and Attrill, M. J. 2010. A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS ONE*, 5.
- Sheehan, E. V., Gall, S. C., Cousens, S. L., and Attrill, M. J. 2013. Epibenthic assessment of a renewable tidal energy site. *The Scientific World Journal*, 2013.
- Sheehan, E. V., Cartwright, A. Y., Witt, M. J., Attrill, M. J., Vural, M., and Holmes, L. A. 2020. Development of epibenthic assemblages on artificial habitat associated with marine renewable infrastructure. *ICES Journal of Marine Science*, 77: 1178–1189.
- Sousa, W. P. 1979a. Disturbance in Marine Intertidal Boulder Fields : The Nonequilibrium Maintenance of Species Diversity A. *Ecology*, 60: 1225–1239.
- Sousa, W. P. 1979b. Experimental Investigations of Disturbance and Ecological Succession in a Rocky Intertidal Algal community. *Ecological Monographs*, 49: 227–254.
- Taormina, B., Marzloff, M. P., Desroy, N., Caisey, X., Dugornay, O., Metral Thiesse, E., Tancray, A., *et al.* 2020. Optimizing image-based protocol to monitor macroepibenthic communities colonizing artificial structures. *ICES Journal of Marine Science*, 77: 835–845.
- Thierry, J. M. 1988. Artificial reefs in Japan - A general outline. *Aquacultural Engineering*, 7: 321–348.
- Trygonis, V., and Sini, M. 2012. PhotoQuad: A dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *Journal of Experimental Marine Biology and Ecology*, 424–425: 99–108. Elsevier B.V. <http://dx.doi.org/10.1016/j.jembe.2012.04.018>.
- Tyrrell, M. C., and Byers, J. E. 2007. Do artificial substrates favor nonindigenous fouling species over native species? *Journal of Experimental Marine Biology and Ecology*, 342: 54–60.

- Ushiyama, S., Smith, J. A., Suthers, I. M., Lowry, M., and Johnston, E. L. 2016. The effects of substratum material and surface orientation on the developing epibenthic community on a designed artificial reef. *Biofouling*, 32: 1049–1060.
- Vaselli, S., Bulleri, F., and Benedetti-Cecchi, L. 2008. Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. *Marine Environmental Research*, 66: 395–403. Elsevier Ltd. <http://dx.doi.org/10.1016/j.marenvres.2008.06.002>.
- Vogel, S. 1994. *Life in moving fluids: the physical biology of flow*. Princeton University Press. 467 pp.
- Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Marine Ecology Progress Series*, 58: 175–189.
- Whomersley, P. P., and Picken, G. B. O. 2003. Long-term dynamics of fouling communities found on offshore installations in the North Sea. *Journal of the Marine Biological Association of the UK*, 83: 897–901.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <http://link.springer.com/10.1007/978-0-387-98141-3>.
- Wilson, J. C., and Elliott, M. 2009. The habitat-creation potential of offshore wind farms. *Wind Energy*, 12: 203–212.
- Yakovis, E., and Artemieva, A. 2017. Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. *Scientific Reports*: 1–11. Springer US. <http://dx.doi.org/10.1038/s41598-017-00260-2>.
- Yakovis, E. L., Artemieva, A. V, Shunatova, N. N., and Varfolomeeva, M. A. 2008. Multiple foundation species shape benthic habitat islands. *Oecologia*, 155: 785–795.

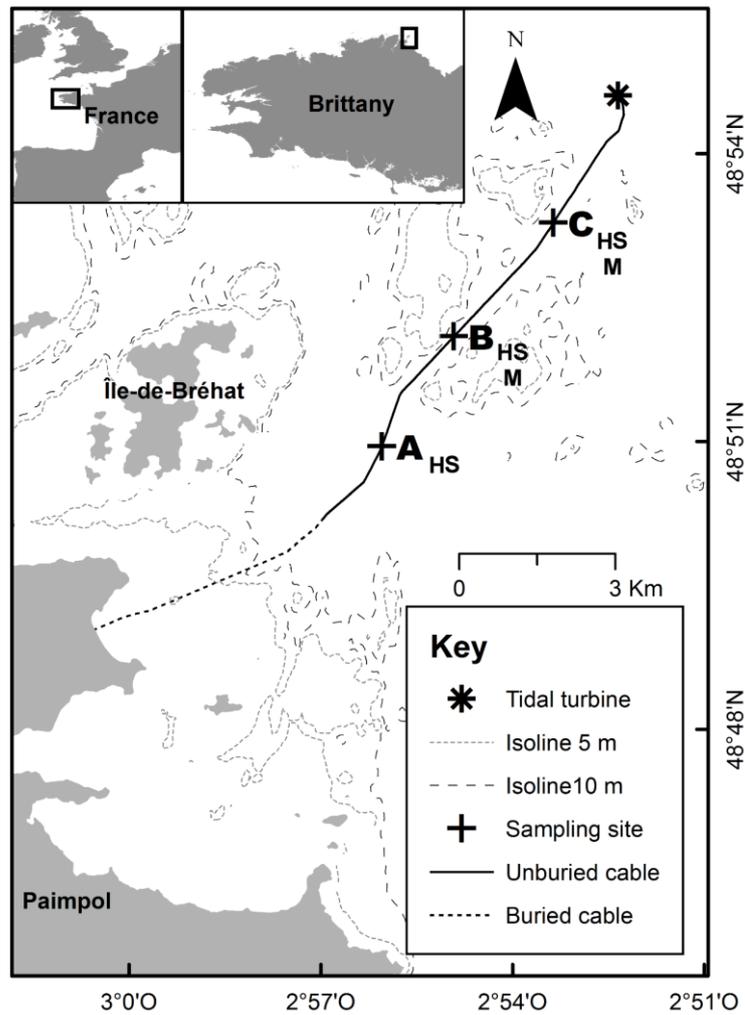


Figure 1: Map of the study area off the northern coast of Brittany in western France (top-left and top-centre panels), which shows the location of the three stations (A, B and C) along the unburied section of the subsea power cable. At each site, acronyms specify which artificial habitat types were studied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

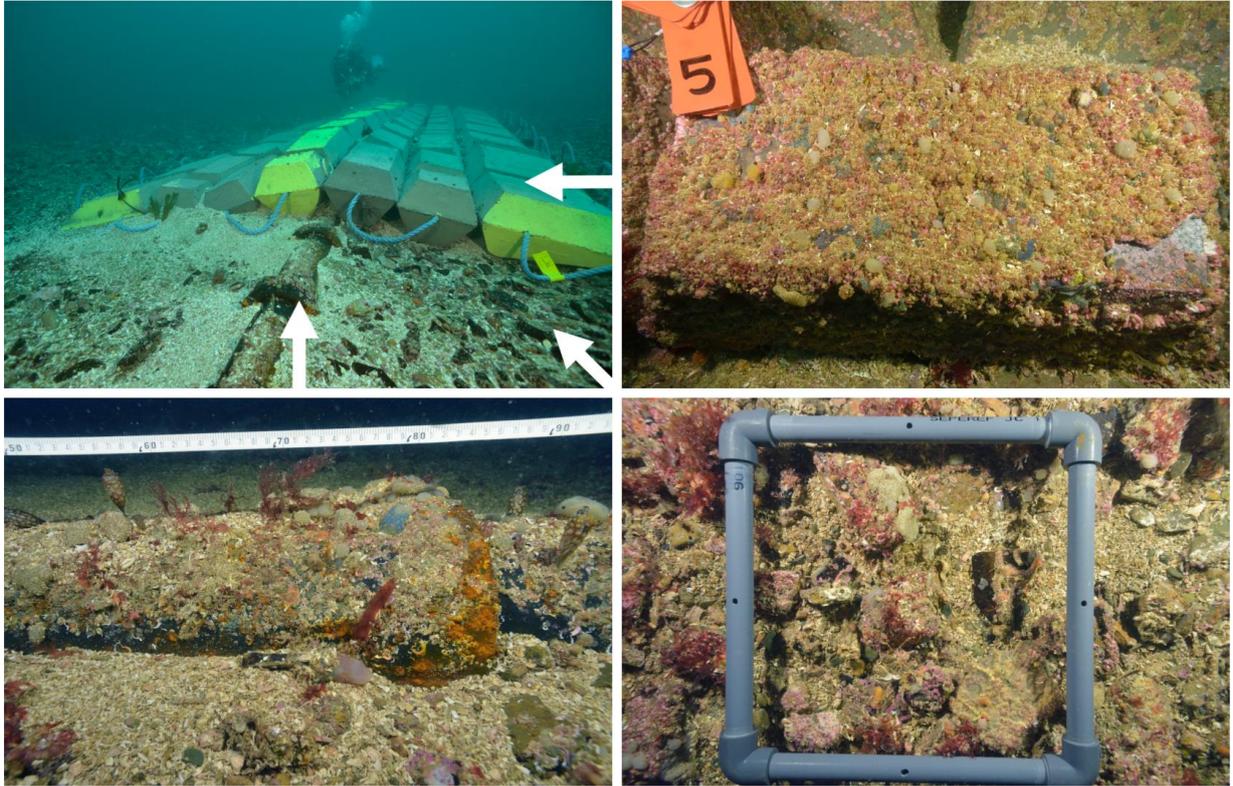


Figure 2: Illustration of the different substrates sampled at each survey site, namely: cast-iron half-shells, a concrete mattress (freshly installed) and natural habitat (top-left); Close-up views of a mattress concrete unit (top-right), a cast-iron half- shell (bottom-left), and a quadrat laid in the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

Table 1: Summary of the total number of pictures sampled across the different sites and campaigns. For each combination of site and campaign, we detail the number of pictures analysed to assess (i) community composition and (ii) target species 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.

Campaign	Number of pictures sampled			Number of pictures analysed	
	Site			Community study	Species of particular interest
	A	B	C		
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	1482

Table 2: Results of the PERMANOVA testing differences in epibenthic community composition across all sites, habitats and campaigns. 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 $P(\text{perm}) \leq 0.05$ are shown in bold.

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

Table 3: Summary of pairwise PERMANOVA tests conducted based on Bray Curtis similarities in epibenthic taxa percentage cover (N= 595 combinations). Significant values at $P \leq 0.05$ are shown in bold. S = Summer; W = Winter.

Pairwise Comparisons				
Within natural habitat		Within artificial habitat		Artificial vs natural
	<i>P</i>		<i>P</i>	<i>P</i>
Site A		2014S		All combinations <0.05
All combinations	<0.05	Half-Shell site B vs Mattress site C	>0.05	
Site B		All other combinations	<0.05	
All combinations	>0.05	2015S		
Site C		Half-Shell site B vs Mattress site C	>0.05	
All combinations	<0.05	Half-Shell site B vs Mattress site B	>0.05	
		Half-Shell site B vs Half-Shell site A	>0.05	
Between sites		All other combinations	<0.05	
All combinations	<0.05	2015W-2017S-2018W		
		All combinations	<0.05	
		Between campaign		
		All combinations	<0.05	

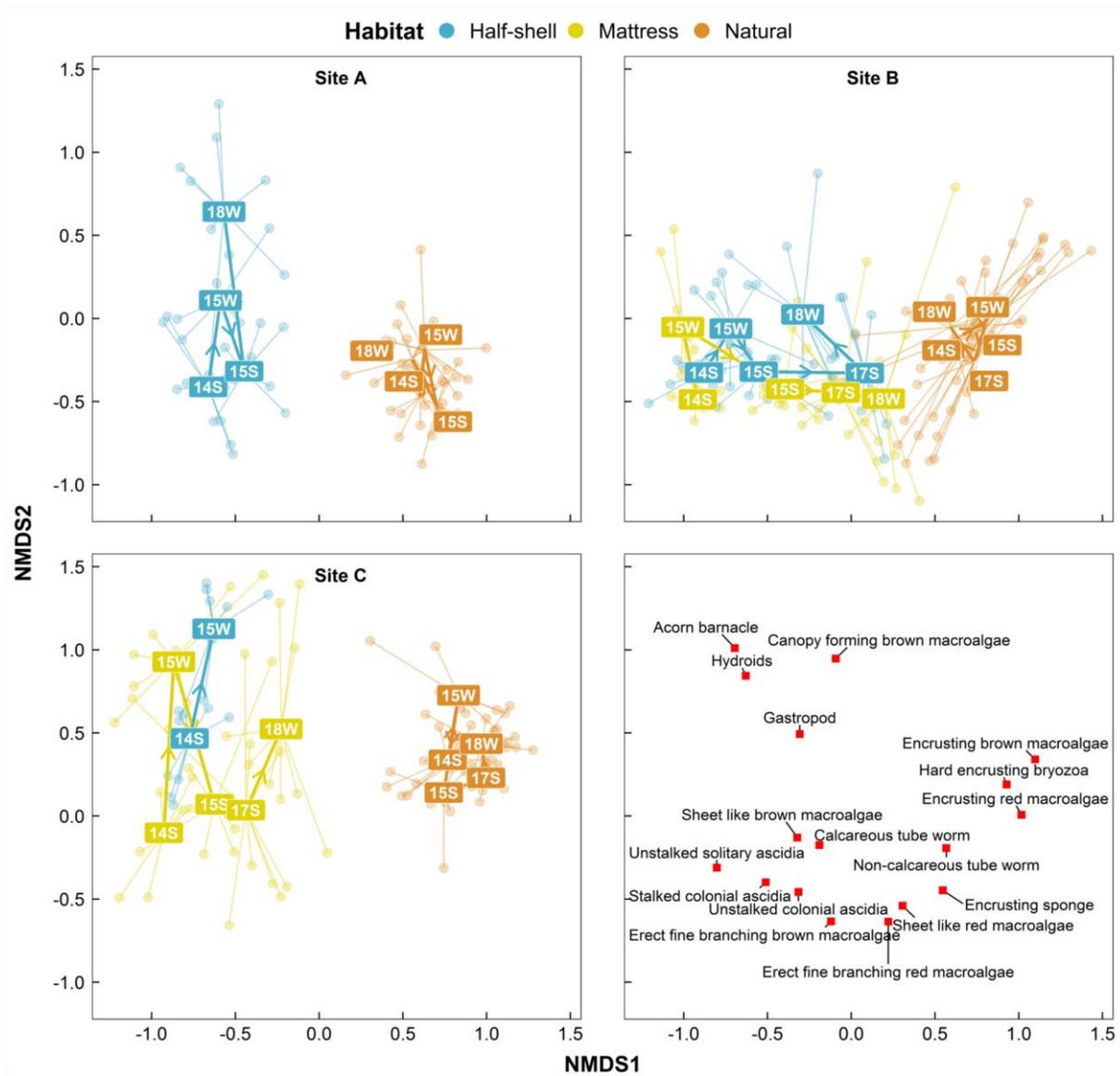


Figure 3: Non-metric Multidimensional Scaling (nMDS) based on Bray-Curtis similarities in community composition between samples. Each point represents an image, and thin lines connect all images scored from the same ‘Habitat, Site and Campaign’ combination to their centroid; bold lines and arrows show 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.

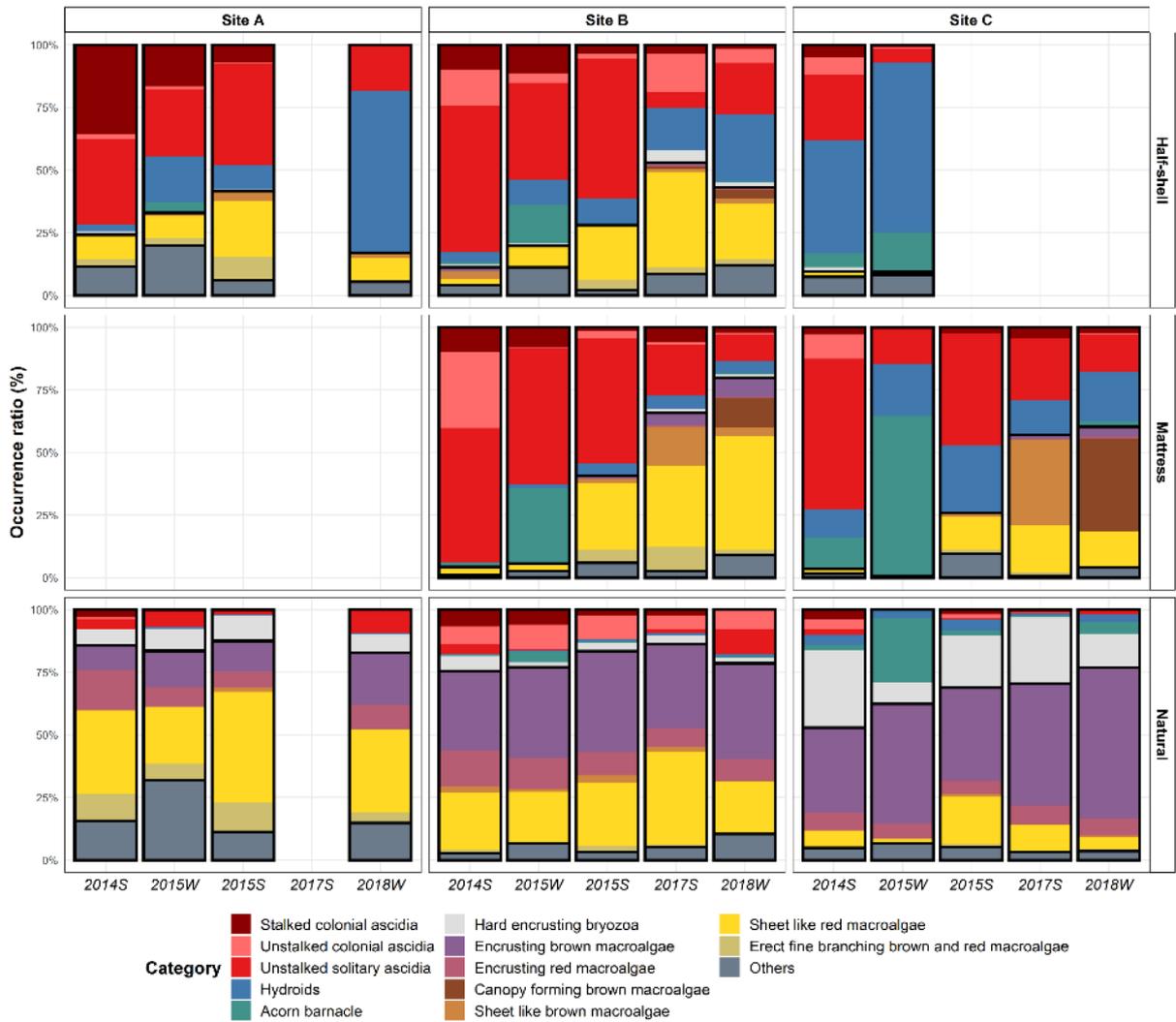


Figure 4: Temporal changes in mean relative percentage cover estimates for epibenthic taxa per Habitat (Half-Shell, Mattress and Natural) and at each sites (A, B and C). Only taxa with mean relative cover percentage > 5% were displayed, all others were agglomerated as “Others”. Black lines delineate algal from animal taxa as well as “Others”. S = Summer; W = Winter.

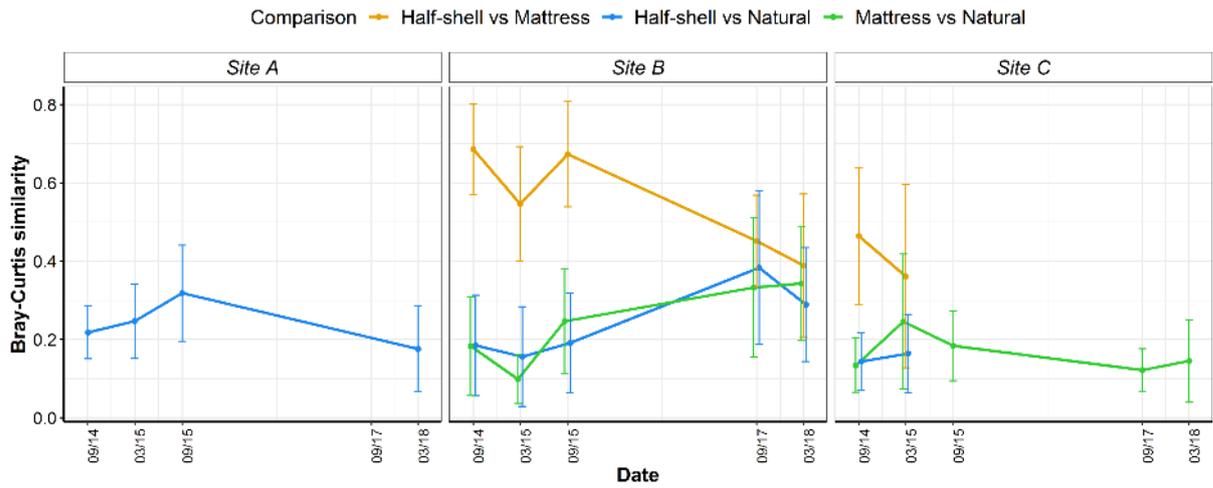


Figure 5: Temporal evolution of mean Bray-Curtis similarities in epibenthic assemblage composition between the different habitats. Mean similarities were computed based on all possible images combinations for each pair of habitat types (colour-coded as per the legend above the figure), for each campaign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

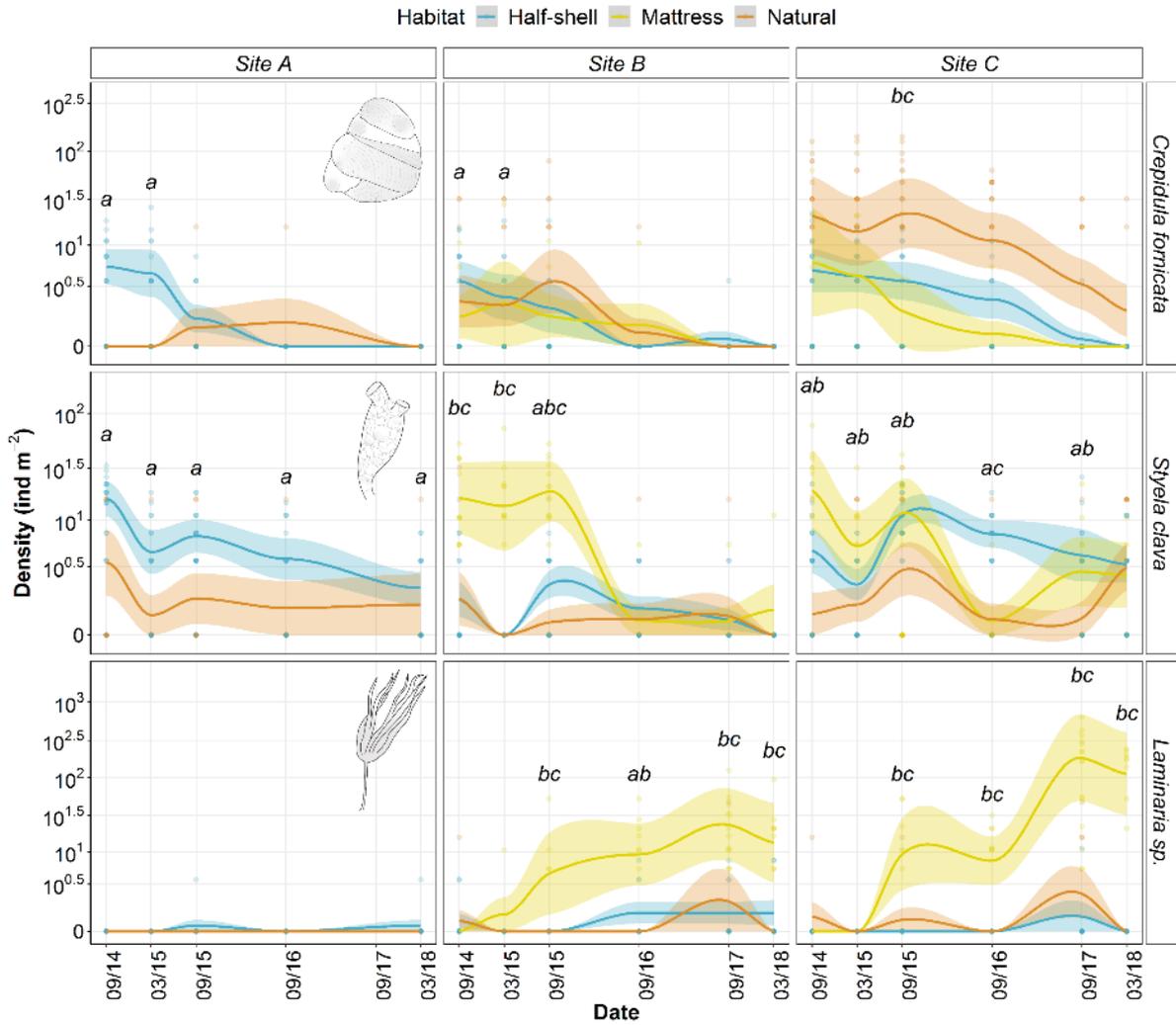


Figure 6: 2014–2018 temporal changes in densities of the three target species (*C. fornicata*, *S. clava* and *Laminaria sp.*) at each site (A, B and C) for each habitat (Half-Shell, Mattress and Natural). Points represent single image density estimates and curves represent mean habitat-specific trends 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).

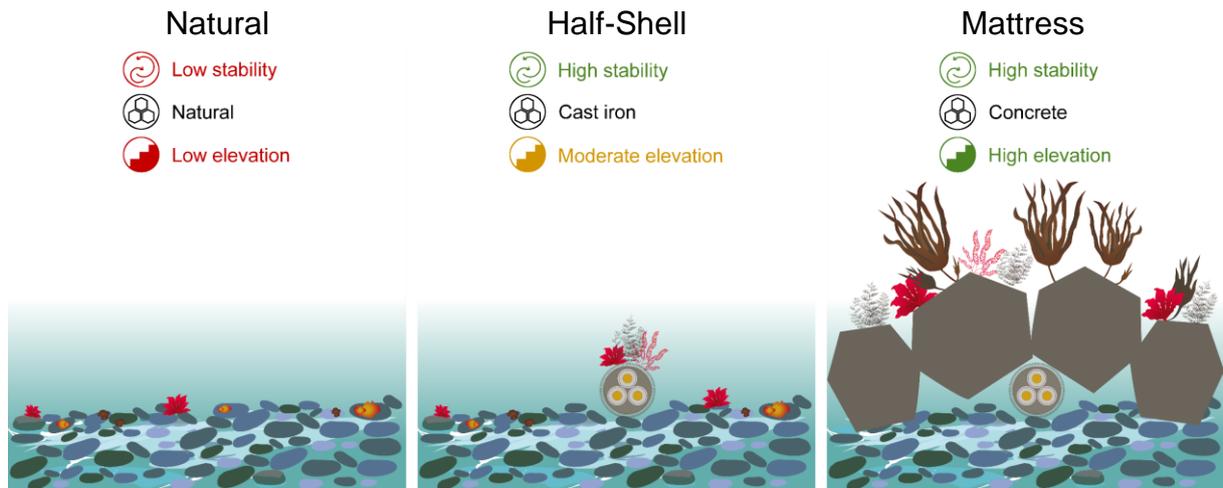


Figure 7: Conceptual diagram of the epibenthic colonisation of the three different habitats of the Paimpol-Bréhat tidal test site at the end of our survey. Natural habitats (left) are dominated by unstable pebbles and are highly exposed to sediment scouring; the epibenthic community is thus characterised 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 characterised 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 characterised by various erect taxa with complex morphology (*e.g.* kelps).