



# Article Four-Year Temporal Study of an Intertidal Artificial Structure in the English Channel

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Abstract: An experimental artificial structure was deployed in March 2014 on the intertidal zone of the Bay of Seine (eastern part of the English Channel), at intervals of one year until April 2018, i.e., from February 2015 onwards, two blocks were collected in April each year. This study provides an inventory of sessile and motile invertebrates living on the artificial hard-bottom and describes the stages of colonization and succession during the four-year study. A total of 84 taxa were identified including 13 sessile and 71 motile taxa. For the sessile fauna, only two taxa Balanus crenatus and Mytilus edulis had colonised the blocks in 2014, and the Taxonomic Richness (TR) was relatively stable during the next three years (between 8 and 10 taxa). The TR of the motile fauna showed an increase between 2014 (5 taxa) and 2015 (34 taxa), and then decreased from 54 taxa in 2017 to 29 taxa in 2018. The abundance of the sessile fauna was very high in 2014 due to the rapid settlement of the barnacle Balanus crenatus, which remained the dominant species throughout the study. Another barnacle Perforatus perforatus, the blue mussel Mytilus edulis and three ascidians including two non-indigenous species Perophora japonica and Corella eumyota, and Molgula sp. were also among the dominant taxa of the sessile fauna. In April 2014, the dominant motile taxa was the decapod Carcinus maenas juvenile, then in 2015 the fauna became dominated by pioneer taxa such as the amphipod of the genus Monocorophium and the tanaid Zeuxo holdichi. A reduction of mean abundance was observed in the last three years of the study, combined with diversification of the dominant species especially those of small size such as Peracarida. The study shows that the colonization of such blocks deployed on oyster tables in the intertidal zone is efficient to test the ability of building material to be colonized in this transition zone.

**Keywords:** artificial structure; species diversity; successional change; epifaunal colonisation; motile fauna colonisation; Bay of Seine

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# 1. Introduction

Artificial Reefs (ARs) started during the second half of the past century (in Europe between 1960–1970) and their deployments were intensified over the five last decades. They have been used around the world to create, protect or restore a rich and diverse ecosystem [1,2]. Their development has been intensified to elicit several ecological responses, i.e., settlement and colonization processes, in relation to benthic community succession in response to biotic and abiotic factors [2,3]. An AR can produce up to 100 times more



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biomass than the surrounding sandy-muddy bottom [4]. Studies of ARs show an ecological succession in the mechanism of colonization; the first colonisers of ARs are benthic micro-organisms ranging from biofilms to microphytobenthos, followed by macroalgae as well as sessile and motile faunas [5–8].

Today, there are many submerged ARs of various shapes and materials [1–3,9–11]. These structures are submerged for diverse reasons such as improving fish production, as well as for the protection, conservation and restoration of habitats, or in relation to economic activities including fisheries, stock management, aquaculture, renewable energy, research and development of new materials and structures [10,12–14]. Historically, ARs have been deployed with the aim of increasing local fisheries production or protecting the coastal zone from the effects of trawling [15]. Furthermore, recent research on ARs tends to focus on variations in the community structure or composition of biota, suggesting that the purpose of AR research has shifted from improving fishery resources to restoring marine ecosystems and developing marine structures to increase biodiversity, taking into account different scopes, such as biodeterioration of archaeological remains, protection against trawling, and bioremediation role [2,10,12,16–20]. However, the presence of such artificial structures in the marine environment modifies the seabed by adding areas of hard substrate to soft-bottom habitats [10,16,17,21].

One of the scientific questions concerning ARs is to establish an inventory of the species colonizing reefs, i.e., the taxonomic richness, the temporal succession of species and taxa during the immersion phase and the growth of existing species and taxa [1,10,22,23]. Most ARs are constructed to increase the production of fishes and invertebrates of commercial interest. However, it is important to monitor species colonizing the AR community since these species control the local diversity and could be potential prey for other species including commercial crabs and fishes [24]. Moreover, the composition and heterogeneous nature, lithology, mineralogy, texture and porosity of the immersed artificial substrate play important roles during the early phases of colonization by fixed organisms [1,10,22]. Rough textures induce greater microhabitat diversity than smooth surfaces [15,22]. Furthermore, the settlement, colonisation and succession of organisms on the surface of ARs are favoured by the water retention properties of the porous artificial reef material mainly in intertidal zones, while crevices and pits protect small organisms from predators [15,25]. Many motile taxa are also associated with the fouling community, which increases the attractiveness of the reef for predators [25]. However, the nature of the substrate appears to be a determining factor in the abundance and species richness of colonizing organisms [26]. Nevertheless, most of the studies of ARs consider only the taxa composition and succession of the main groups of macroalgae or macrofauna, which are mainly sessile organisms [15,16,27-29]. Very few studies take into account all the species colonizing ARs [30,31]. Moreover, most of the studies were deployed over a short period, frequently one year [15,28,29], and only few ARs have been studied over the medium term (2–3 years) [27], or the long term (>3 years) [16,30,31]. Some studies focused on the long-term changes in polychaetes [18,32] or molluscs [33], while others compared the fauna colonizing ARs with natural rocky reefs [10,13,16,17,31–35]. Studies have also been undertaken to compare the colonization of Non-Indigenous Species (NIS) on these two types of substrate [36], or the role of ARs in the colonization by NIS [37]. In these studies, species identification was mainly carried out by divers and photographers and concerned only the megafauna and fish, while only few studies have identified the small sessile and motile macrofauna.

ARs have been deployed along the coast of metropolitan France since 1968 with the chief objective of enhancing the success and continuity of artisanal fishing mainly in the Mediterranean Sea [3,38]. Most of these ARs have been immerged recently—since 2000 and have been emplaced along the Atlantic coast, but only one AR has been deployed in the eastern part of the English Channel at Etretat [39]. Fishermen opposed to the emplacement of ARs argued that numerous wrecks in the English Channel could be considered to act as ARs. These wrecks mainly resulted from Operation Overlord in Normandy in 1944. This may explain the low number of ARs currently emplaced in the English Channel. At present, with the aim of maintaining or increasing biodiversity in coastal ecosystems including harbour basins, a new perception of ARs is spreading among the scientific community and users of the English Channel [11,39].

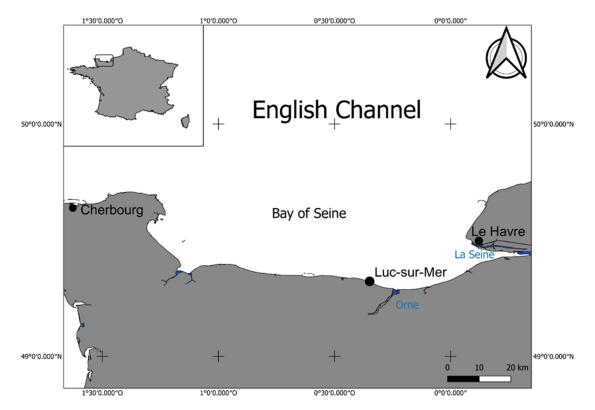
In the framework of the RECIF INTERREG project between France and the United Kingdom, concrete blocks have been deployed on the intertidal zone of the Bay of Seine (eastern part of the English Channel) since March 2014 and monitored each year at the beginning of the spring until April 2018. The objectives of our study are the first time for the English Channel, as an example of a megatidal sea with a large intertidal zone: (1) to provide a complete inventory of sessile and motile invertebrates colonizing artificial hard-bottom substrates, while most of the studies in such AR take into account only the large sessile species (megafauna), and (2) to describe the stages of colonization during the four-year study, and the succession of organisms on these blocks over the four years of the experiment, while most of the studies of AR colonization do not surpass one year.

#### 2. Materials and Methods

#### 2.1. Experimental Site and Design of Blocks

In the RECIF project we had used the incorporation of crushed seashells of the queen scallop *Aequipecten opercularis* (Linnaeus, 1758) into the substrate of concrete blocks through the development of innovative building materials for Ars [40–42]. The short-term colonization during the first year of the study up to February 2015 was previously described from observations every 15 days between 1 April 2014 and 4 February 2015, making a total of 22 sampling dates, and was not discussed in this paper (see [23,42] for results of the first phases of macroalgae and macrofauna colonisations). At the end of the first year of the experiment (2014–2015), it was decided to extend the study, with observations once a year until April 2018 to obtain a four-year temporal study of the colonization and succession of animal organisms observed on innovative intertidal ARs in the English Channel (i.e., the macroalgae did not count during this long-term study).

At the beginning of the experiment (19–20 March 2014), 75 blocks ( $20 \times 20 \times 40$  cm) were placed on oyster culture tables, 0.5 m above the sea bed, used by oyster farmers in Normandy in the intertidal zone of Luc-sur-Mer ( $49^{\circ}19'15''$  N– $0^{\circ}20'55''$  W; southern part of the Bay of Seine, eastern basin of the English Channel) [23,41,42] (Figures 1 and 2). The water depth of the oyster tables is 6.5 m at high tide and the concrete blocks were accessible at low tide about 44% of the time, i.e., located in the infralitoral zone composed of coarse sand and natural rocky shores corresponding to the EUNIS (European Nature Information System) code A5. 125; *Mastocarpus stellatus* and *Chondrus crispus* habitat on very exposed to moderately exposed lower eulittoral rock [23]. At the beginning of the experiment, three types of blocks were deployed: two composed of 40% crushed queen scallop shells, using two types of porosities, and a third type with ordinary concrete made from natural aggregates [40,43].



**Figure 1.** Location of the experimental site on the intertidal zone of Luc-sur-Mer (Calvados coast, southern part of the Bay of Seine).



**Figure 2.** In situ experimental structure. At the beginning of the experiment in March 2014 (**a**) and at the end of the Experiment in April 2018 (**b**).

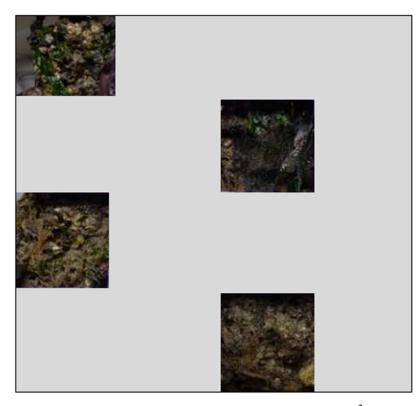
As no difference was observed in colonization according to block composition or porosity [23,42], we have studied the fauna collected on two blocks each year independently of their initial composition.

With a view to running a long-term yearly study of such ARs which was no-existent in the English Channel, two blocks were collected in April 2014 (one month), in February 2015 (11 months), April 2016 (24 months), April 2017 (36 months) and April 2018 (48 months for

end of the experiment), making a total of 10 blocks (two different blocks per year). Only the results of the long-term study and on macrofauna were analysed in our present study.

### 2.2. Laboratory Analyses of the Blocks

The total surface of colonization of each block was 0.6 m<sup>2</sup>. The sessile fauna was examined in the laboratory using three main procedures: (1) sub-sampling by scraping of unit areas of 25 cm<sup>2</sup>) delimited by a mask (Figure 3), and analyses covered approximately one quarter of the total surface area of each face (see [42] for details), (2) each face of the blocks was photographed in its entirety, and (3) an inventory was carried out of the taxa present on each block, as well as counting of individuals where this was possible (countable organisms: barnacles, mussels and some solitary ascidians were considered for quantitative analyses) while the colonial taxa were only considered for their presence (inventory of the taxa). The abundances of sessile organisms are normalized to 0.6 m<sup>2</sup>.



**Figure 3.** Photo of a block showing a mask of  $5 \times 5$  cm, i.e., 25 cm<sup>2</sup>.

After placing the blocks in bowls in stagnant conditions for at least 24 h, the seawater was then filtered on a 0.5 mm mesh sieve to collect the motile fauna. The retained material was fixed with 96% alcohol, and then identified to the most precise level of taxonomy and counted as living motile fauna associated with the blocks. For polychaetes and nemerteans, only the heads of the individuals were counted. The numbers of motile fauna counted correspond to the individuals on the entire surface of one block (0.6 m<sup>2</sup>).

#### 2.3. Statistical Analyses

To test the differences of colonization between the years, total number of taxa, i.e., taxonomic richness (TR) and total abundances (0.6 m<sup>2</sup>) for the sessile and motile fauna separately, and all taxa combined were compared by ANOVAs (ANalyse Of Variance) using R Software. The null hypothesis  $H_0$  states that there is no effect of the sampling date, and the alternative hypothesis  $H_1$  is that there an effect of the date.

A post-hoc test (Tukey) was performed if the  $H_0$  null hypothesis was rejected in favour of the  $H_1$  hypothesis. The normality and homogeneity of the variances in the distribution of the data or residuals were tested with a Shapiro test and Bartlett tests, respectively.

When one of these conditions was not meet, a non-parametric Scheirer–Ray–Hare test was applied instead of the ANOVA, followed by a post-hoc Dunn test. Table 1 presents the tests applied in each case.

| Fauna     | Variable              | Distributio      | on Normality | Variance He            | omogeneity | Tests                        |
|-----------|-----------------------|------------------|--------------|------------------------|------------|------------------------------|
| rauna     | variable              | <i>p</i> -Values | Conclusion   | <i>p</i> -Values       | Conclusion |                              |
| Conth     | Taxonomic<br>richness | 0.040            | No           | $<2.2 \times 10^{-16}$ | No         | Scheirer-Ray-Har<br>and Dunn |
| Sessile   | Abundance             | 0.002            | No           | 0.322                  | Yes        | Scheirer–Ray–Har<br>and Dunn |
| Marth     | Taxonomic<br>richness | 0.280            | Yes          | 0.960                  | Yes        | ANOVA and Tuke               |
| Motile    | Abundance             | 0.007            | No           | 0.175                  | Yes        | Scheirer–Ray–Ha<br>and Dunn  |
| Sessile + | Taxonomic<br>richness | 0.245            | Yes          | 0.921                  | Yes        | ANOVA and Tuke               |
| Motile    | Abundance             | 0.014            | No           | 0.478                  | Yes        | Scheirer–Ray–Ha<br>and Dunn  |

Table 1. Summary of the tests applied in each case.

Hierarchical Cluster Analysis (HCA) was carried out based on Sorensen's coefficient for the presence/absence of the taxa found in each of the ten blocks, along with the construction of a dendrogram using the mean grouping method (UPGMA (Unweighted pair group method with arithmetic mean)) generated from the PRIMER V6 software (PRIMER-e67 Mahoenui Valley RoadRD3, Albany, AKL, New Zealand) [44].

Considering all the macrofauna taxa (abundance matrix), the temporal changes were analysed separately by group-average sorting classification, using a hierarchical clustering procedure (CLUSTER mode) based on the Bray–Curtis similarity index with a  $Log_{(X+1)}$  transformation of abundances, followed by the construction of a dendrogram using the mean grouping method (UPGMA) [44]. To identify those species within different groups which primarily account for the observed assemblage differences, SIMPER (SIMilarity PERcentage) routines were performed using a decomposition of Bray–Curtis similarity on Log transformed abundance data [44].

#### 3. Results

#### 3.1. General Patterns of the Fauna

A total of 84 taxa were identified in the 10 blocks sampled during the study, including 13 sessile taxa and 71 motile taxa (Appendix A). One month after the immersion in 2014, the number of total taxa found on the two blocks was seven, and then the TR for two blocks increased the subsequent years to reach a maximum of 63 taxa in 2017, and decreased after in 2018 with 36 taxa. Two sessile ascidian species (*Corella euryota* and *Perophora japonica*) and two amphipod genera (*Aoroides and Monocorophium*) are Non-Indigenous Species (NIS) in Normandy.

Two taxa of sessile fauna colonized the blocks in 2014, after which the TR remained relatively stable and included between 8 and 10 taxa in 2018 (Figure 4). In 2014, the TR was significantly different compared with the following years which do not show significantly different values between themselves (Tables 2 and 3). Conversely to the number of taxa, the numbers of individuals decreased between 2014 (attaining very high abundances of the barnacle *Balanus crenatus*) and the other four years (Figure 5). In 2016, the abundances were lower but not significantly different compared with the other years (Tables 2 and 3). The abundance observed in 2014 was significantly higher than observed during the four

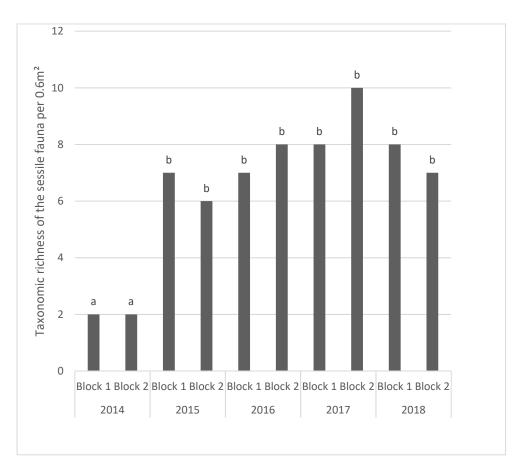
other years of the study (Tables 2 and 3). At the end of the study, in 2017 and 2018, the abundances were of the same order of magnitude for the four blocks (Figure 5).

**Table 2.** Results of the ANOVA test corresponding to the interaction effect of the year on the sessile fauna found on the ten blocks sampled from 2014 to 2018 for Taxonomic Richness and abundance per  $0.6 \text{ m}^2$ . \* significant to 5%; \*\* significant to 1% and \*\*\* significant to <0.001.

| Fauna            | Factor             | <i>p</i> -Value |
|------------------|--------------------|-----------------|
| Sessile          | Abundance          | < 0.001 ***     |
| 5635116          | Taxonomic richness | 0.003 **        |
| Motile           | Abundance          | < 0.001 ***     |
| Wotne            | Taxonomic richness | < 0.001 ***     |
| Sessile + Motile | Abundance          | < 0.001 ***     |
|                  | Taxonomic richness | < 0.001 ***     |

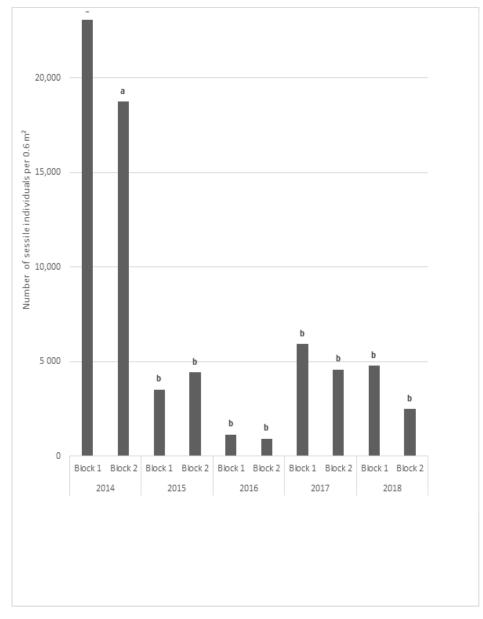
**Table 3.** Results of the ANOVA test corresponding to with the interaction effect of the year on the motile fauna found on the ten blocks sampled from 2014 to 2018 for Taxonomic Richness and the abundance per 0.6 m<sup>2</sup>.\* significant to 5%; \*\* significant to 1% and \*\*\* significant to <0.001.

|           |          | 20                    | 14          | 20                    | 15          | 20                    | 16        | 2017                  |             |  |
|-----------|----------|-----------------------|-------------|-----------------------|-------------|-----------------------|-----------|-----------------------|-------------|--|
| Fauna     | Variable | Taxonomic<br>Richness | Abundance   | Taxonomic<br>Richness | Abundance   | Taxonomic<br>Richness | Abundance | Taxonomic<br>Richness | Abundance   |  |
|           | 2015     | 0.015 *               | < 0.001 *** |                       |             |                       |           |                       |             |  |
| C '1      | 2016     | 0.006 **              | < 0.001 *** | 0.756                 | 0.459       |                       |           |                       |             |  |
| Sessile   | 2017     | 0.002 **              | 0.002 **    | 0.137                 | 0.925       | 0.464                 | 0.208     |                       |             |  |
|           | 2018     | 0.006 **              | < 0.001 *** | 0.756                 | 0.999       | 1                     | 0.556     | 0.464                 | 0.848       |  |
|           | 2015     | < 0.001 ***           | < 0.001 *** |                       |             |                       |           |                       |             |  |
|           | 2016     | < 0.001 ***           | 0.003 **    | 0.573                 | < 0.001 *** |                       |           |                       |             |  |
| Motile    | 2017     | < 0.001 ***           | < 0.001 *** | 0.043 *               | < 0.001 *** | 0.012 *               | 0.059     |                       |             |  |
|           | 2018     | 0.002 **              | 0.949       | 0.005 **              | < 0.001 *** | 0.014 *               | 0.005 **  | < 0.001 ***           | < 0.001 *** |  |
|           | 2015     | < 0.001 ***           | 0.00223 **  |                       |             |                       |           |                       |             |  |
| Sessile + | 2016     | < 0.001 ***           | < 0.001 *** | 0.910                 | 0.086       |                       |           |                       |             |  |
| Motile    | 2017     | < 0.001 ***           | 0.00158 **  | 0.036 *               | 0.965       | 0.018 *               | 0.162     |                       |             |  |
|           | 2018     | 0.002 **              | < 0.001 *** | 0.018 *               | 0.291       | 0.036 *               | 0.762     | 0.002 **              | 0.532       |  |

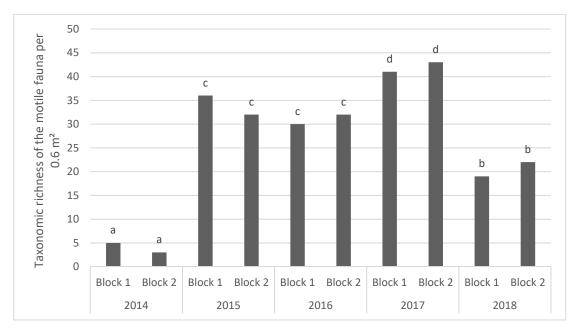


**Figure 4.** Taxonomic richness of the sessile fauna per 0.6 m<sup>2</sup> in the ten blocks sampled from 2014 to 2018, with results of the Tukey tests (superscript: same letters in adjacent columns indicate no significant statistical difference between blocks and years).

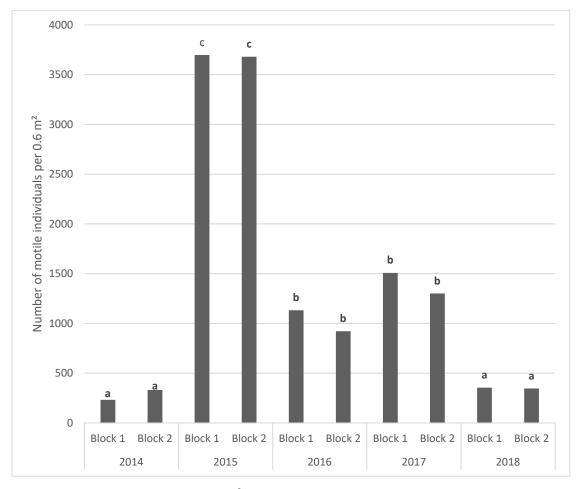
The TR of the motile fauna shows a highly significant increase between 2014 (5 taxa) and 2015 (44 taxa) (Tables 2 and 3). Then, a slight non-significant decrease occurred in 2016 (37 taxa), a significant maximum in 2017 (54 taxa), and a significant decrease during the last year of the study in 2018 with 29 taxa (Figure 6) (Tables 2 and 3). The abundance shows changes from one year to another; it increased in 2015, significantly decreased in 2016, slightly increased in 2017, and significantly decreased again in 2018 (Figure 7). The abundance of 2015 was significantly higher than observed during the other years (Tables 2 and 3).



**Figure 5.** Abundance of the sessile fauna per 0.6 m<sup>2</sup> in the ten blocks sampled from 2014 to 2018, with results of the Tukey tests (superscript: same letters in adjacent columns indicate no significant statistical difference between blocks and years).



**Figure 6.** Taxonomic richness of the motile fauna per 0.6 m<sup>2</sup> in the ten blocks sampled from 2014 to 2018, with results of the Tukey tests (superscript: same letters in adjacent columns indicate no significant statistical difference between blocks and years).



**Figure 7.** Abundance of the motile fauna per 0.6 m<sup>2</sup> in the ten blocks sampled from 2014 to 2018, with results of the Tukey tests (superscript: same letters in adjacent columns indicate no significant statistical difference between blocks and years).

#### 3.2. Temporal Changes of the Fauna from 2014 to 2018

Table 4 presents the mean abundance per 0.6 m<sup>2</sup> of the eight dominant sessile countable taxa for the five years of the study. One month after the immersion of the blocks, the blocks were colonized by only two taxa, with very high abundances of the barnacle *Balanus crenatus*. This latter remained the dominant species throughout the study, with similar abundances apart from 2016 when there was a decrease in relation with the decrease abundances of barnacles. The other dominant barnacle *Perforatus perforatus* showed a regular abundance increase from 2015 to 2018 when it became the second most dominant species. A total of 11 taxa were among the eight dominant taxa, including only six taxa showing abundance higher than 100 individuals per 0.6 m<sup>2</sup>, among them two barnacles, the blue mussel, one polychaete and three ascidians including the two NIS *Perophora japonica* and *Corella eumyota*. *P. japonica* showed very high abundance in 2017, while, from 2014 to 2018, the abundance of *Mytilus edulis* ranged between 1.0 to 140.0 individuals per 0.6 m<sup>2</sup>. Finally, there was a similar composition of the dominant taxa with four dominant taxa: the barnacle *Balanus crenatus*, both NIS ascidians and the blue mussel, which colonized the blocks one year after the immersion, with a strong decrease in abundances in 2016.

**Table 4.** Mean abundance (A per  $0.6 \text{ m}^2$ ) of the eight dominant sessile species found on the two blocks sampled from 2014 to 2018 (one, two, three and four years after the beginning of the study).

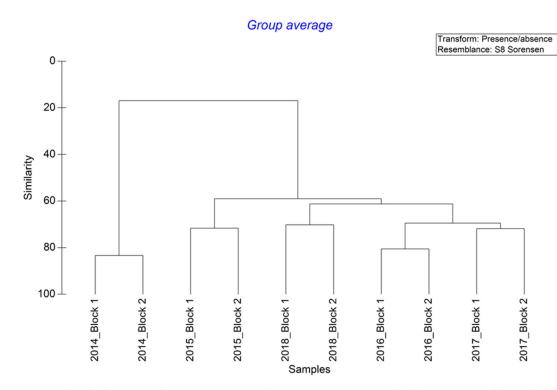
| 2014             |                  | 2015             |        | 2016                  |       | 2017                  |        | 2018                  |        |  |
|------------------|------------------|------------------|--------|-----------------------|-------|-----------------------|--------|-----------------------|--------|--|
| Species          | Α                | Species          | Α      | Species               | Α     | Species               | Α      | Species               | Α      |  |
| Balanus crenatus | 20906.0          | Balanus crenatus | 3198.0 | Balanus crenatus      | 469.0 | Balanus crenatus      | 3226.0 | Balanus crenatus      | 3284.5 |  |
| Mytilus edulis   | 1.5              | Corella eumyota  | 407.0  | Perophora japonica    | 164.0 | Perophora japonica    | 1646.5 | Perforatus perforatus | 61.5   |  |
|                  |                  | Mytilus edulis   | 160.5  | Mytilus edulis        | 139.5 | Branchiomma bombyx    | 107.5  | Mytilus edulis        | 66.5   |  |
|                  |                  | Molgula          | 109.5  | Molgula               | 105.0 | Molgula               | 90.5   | Perophora japonica    | 74.0   |  |
|                  |                  | Spirobranchus    | 85.5   | Spirobranchus         | 77.5  | Corella eumyota       | 74.0   | Molgula               | 55.5   |  |
|                  |                  | Dendrodoa        | 10.0   | Corella eumyota       | 69.0  | Perforatus perforatus | 47.0   | Spirobranchus         | 43.5   |  |
|                  |                  | Ascidia          | 4.0    | Perforatus perforatus | 6.0   | Mytilus edulis        | 41.5   | Corella eumyota       | 42.0   |  |
|                  | Perforatus perfo |                  | 2.5    | Branchiomma bombyx    | 5.0   | Spirobranchus         | 14.0   | Diadumene cincta      | 3.5    |  |

Table 5 reports the mean abundance per 0.6 m<sup>2</sup> of the ten dominant motile taxa for the five years of the study. One month after immersion of the blocks in April 2014, the dominant taxon was the decapod *Carcinus maenas* juvenile. The year 2015 was characterized by the dominance of pioneer taxa (i.e., taxa colonizing rapidly a new immerged substratum) such as amphipods of the genus *Monocorophium* and the tanaid *Zeuxo holdichi*. Subsequently, these pioneer taxa showed a decreasing abundance, while smaller taxa such as the Nematoda, the polychaetes *Pholoe* spp. and *Websterinereis glauca* became dominant but with moderate abundance. Only seven taxa showed mean abundance higher than one hundred individuals per 0.6 m<sup>2</sup>, i.e., one decapod *Carcinus maenas*, Nematoda, one amphipod *Monocorophium*, one isopod *Gnathia oxyuraea*, one tanaid *Zeuxo holdichi* and two polychaetes *Pholoe* spp. and *Websterinereis glauca* became taxa (Table 5), there was a succession of dominant species, with diverse small organisms just after the immersion in 2014. This was followed by the dominance of pioneer species one year after the immersion, and then the reduction of mean abundance combined with diversification of the 10-dominant species during the last three years of the study.

At a level of 20 % of similarity, an analysis of Sorensen similarity coefficients based on the Presence/Absence of sessile and motile taxa allows us to separate the blocks into two main groups (Figure 8): (1) blocks collected in 2014 and (2) the rest of the blocks from 2015 to 2018. Moreover, for each of the five dates, the two blocks collected show a high similar diversity indicating a low heterogeneity at the scale of a year. The second group can be divided in three sub-groups at a similarity level of 65%: 2015, i.e., one year after the beginning of the experiment, 2018, the last year of the study, and both years 2016 and 2017, with similar taxonomic richness. This first analysis shows a temporal pattern from one month of colonization (2014), the first year (2015), two and three years (2016–2017) after the block immersion and the last year (2018).

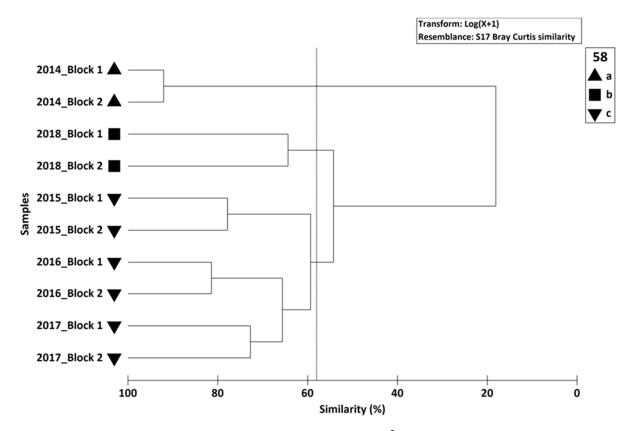
**Table 5.** Mean abundance (A per  $0.6 \text{ m}^2$ ) of the ten dominant motile taxa found on the blocks sampled from 2014 to 2018 (one, two, three and four years after the beginning of the study).

| 2014               |               | 2015                  |        | 2016                  | 2016  |                       |       | 2018                  |       |
|--------------------|---------------|-----------------------|--------|-----------------------|-------|-----------------------|-------|-----------------------|-------|
| Species            | Α             | Species               | Α      | Species               | Α     | Species               | Α     | A Species             |       |
| Carcinus maenas    | 277.0         | Monocorophium         | 1933.0 | Nematoda              | 463.0 | Pholoe                | 284.5 | Nematoda              | 131.5 |
| Venerupis          | 2.0           | Zeuxo holdichi        | 1514.0 | Monocorophium         | 102.0 | Zeuxo holdichi        | 238.5 | Websterinereis glauca | 44.5  |
| Galathea           | 1.0           | Syllidae              | 46.0   | Zeuxo holdichi        | 60.5  | Gnathia               | 217.5 | Zeuxo holdichi        | 25.5  |
| Ostracoda          | 1.0           | Gnathia               | 33.5   | Syllidae              | 59.5  | Websterinereis glauca | 198.5 | Cirratulidae          | 24.5  |
| Golfingia vulgaris | 0.5           | Websterinereis glauca | 24.5   | Gnathia               | 52.5  | Monocorophium         | 163.5 | Eulalia               | 18.0  |
|                    |               | Pholoe                | 24.5   | Pholoe                | 48.0  | Syllidae              | 64.0  | Gnathia               | 16.0  |
|                    |               | Perinereis cultrifera | 21.0   | Carcinus maenas       | 39.0  | Pilumnus hirtellus    | 34.5  | Syllidae              | 13.0  |
|                    |               | Pilumnus hirtellus    | 13.5   | Ephesiella abyssorum  | 29.5  | Eumida sanguinea      | 21.0  | Lineus                | 11.5  |
|                    |               | Dynamene bidentata    | 8.5    | Platynereis dumerilii | 25.0  | Peringia ulvae        | 20.5  | Pholoe                | 11.5  |
|                    | Tubulanus 8.5 |                       | 8.5    | Psamathe fusca        | 23.0  | Eulalia               | 18.5  | Perinereis cultrifera | 9.0   |



**Figure 8.** Hierarchical Cluster Analysis (HCA) using the mean grouping method (UPGMA) and based on Sorensen's coefficient for the presence/absence of the 84 taxa found on the ten blocks during the 2014–2018 study (superscript: same letters in adjacent columns indicate no significant statistical difference between blocks and years).

The analysis of the Bray Curtis similarity based on the abundance of sessile and motile taxa after  $\text{Log}_{(X+1)}$  shows (Figure 9) similar patterns to those identified by the Sorensen similarity coefficients but with the separation of 2018 at a level of 58% of similarity from the three years 2015, 2016 and 2017, which are regrouped in the same sub-group with similar pattern of abundance of the fauna (Figure 8).



**Figure 9.** Cluster dendrogram showing the pattern of abundance per 0.6 m<sup>2</sup> of the 10 blocks after  $Log_{(X+1)}$  transformation according to the Bray–Curtis similarity and using the mean grouping method (UPGMA).

SIMPER analysis shows that both species *Balanus crenatus* (52% of the contribution) and *Carcinus maenas* (33% of the contribution) characterizes the 2014 blocks. The 2018 blocks (group b) are characterised by the barnacles *Balanus crenatus* and *Perforatus perforatus*, the ascidian *Perophora japonica* and Nematoda while the 2015–2017 blocks are characterized by the barnacle *Balanus crenatus* and both motile taxa the amphipod *Monocrophium* and the tanaid *Zeuxo holdichi* and the blue mussel *Mytilus edulis* (Table 6).

**Table 6.** SIMPER analyses with respective contribution (rC) and cumulative contribution (Cc in %) of the ten top taxa of the 2018 blocks (group b) and 2015-2017 blocks (group c).

| Taxa               | Group b |       | Taxa             | Group c |       |
|--------------------|---------|-------|------------------|---------|-------|
|                    | rC      | CC    |                  | rC      | Cc    |
| Balanus crenatus   | 15.05   | 15.05 | Balanus crenatus | 9.26    | 9.26  |
| Nematoda           | 9.26    | 24.31 | Monocorophium    | 7.19    | 16.46 |
| Perophora japonica | 6.7     | 31.01 | Zeuxo holdichi   | 6.78    | 23.24 |
| Balanus perforatus | 6.41    | 37.42 | Mytilus edulis   | 6.01    | 29.25 |
| Pholoe             | 5.88    | 43.3  | Molgula          | 5.68    | 34.93 |
| Syllidae           | 5.67    | 48.97 | Corella eumyota  | 5.67    | 40.6  |
| Molgula            | 5.67    | 54.64 | Syllidae         | 5.55    | 46.15 |
| Mytilus edulis     | 5.2     | 59.84 | Gnathia          | 5.35    | 51.49 |
| Spirobranchus      | 5.2     | 65.04 | Pholoe           | 4.74    | 56.23 |
| Cirratulidae       | 4.6     | 69.64 | Spirobranchus    | 4.27    | 60.5  |

# 4. Discussion

Our experiment illustrates the colonization of concreted blocks located in the intertidal zone of a megatidal sea 'La Manche- the English Channel' during four years. To our knowledge, this experiment is unique at the scale of the north-eastern Atlantic; however, the results are based on a small number of replicates (two concrete blocks per sampling date) and should be interpreted with caution. Moreover, our study considers all the identification of sessile and motile taxa including small organisms mainly at the species level. This identification protocol is only rarely applied since numerous AR studies are concerned solely with mega-zoological groups mainly composed of sessile organisms such as sponges, cnidarians, hydrozoans, mussels, etc., or motile fauna including decapods and fishes [30,31]. However, the sampling design of our experiment with the removal of blocks at low tide prevents the capture of fishes; hence, our study is focused on invertebrate macrofauna.

During the first year of the experiment, the main colonizing organisms were barnacles, hydrozoans, mussels, tunicates, and sessile annelids [23]. Moreover, a biological succession is observed over time: a first assemblage mainly dominated by barnacles then a richer assemblage with the dominance of ascidians.

It is noteworthy that during the period of the study (2014–2018) there were no severe cold winters or warm summers. Neither there were there any floods of the Seine or Orne rivers which could have influenced the Luc-sur-Mer area during years with strong precipitation and high freshwater input (see: https://www.somlit.fr/luc-sur-mer/ (accessed on: 18 October 2021)). At the SOMLIT (Service d'Observation en Milieu Littoral) Station at Luc-sur-Mer near the block immersion site, the sea water temperature at high tide varied from a minimum of 7 °C in winter (February-March) to a maximum of 21 °C at the end of the summer (September), and the salinity ranged from a minimum of 33 (November to March depending on the year) to a maximum of 34.5 at the end of the summer in September. Thus, normal seasonality occurred during our block study, and no environmental event needs to be evoked to interpret the long-term colonization of such ARs.

A total of 84 taxa were identified during this study. This high Taxonomic Richness is due to the effort for identification of the taxa, often at species level, while considering both the sessile and motile fauna. Sessile taxa make up 15% of the recorded fauna, while the motile taxa formed 85% of the fauna with numerous small organisms (Appendix A). The most highly diversified zoological phylum is the Arthropoda (32 taxa; 38% of the fauna), then the Annelida (26; 31%), Mollusca (10; 12%), Chordata (5; 6%) and other groups (11; 13%). This taxonomic richness is on the same order that accounts for a geotextile artificial surf reef immerged at 2 m depth in the Poole Bay in the centre of the English coast in the English Channel and study during four years: 108 taxa ([10]. Due to the sampling protocols, i.e., a combination of photography, underwater video using scuba diving and a mini-ROV (Remotely Operated Vehicle), and Baited Remote Underwater Video, and image analysis the number of sessile invertebrate (67 taxa, 66%) surpasses the number of motile fauna (41 taxa, 34%), which is different to the blocks of the intertidal zone of the Bay of Seine.

One month after the immersion, only seven taxa were found on the blocks. The colonisation of the blocks was rapid and one year after the beginning of the deployment of the blocks (in April 2015) the TR of the fauna reached 52. The TR reached a maximum in 2017 with 64 taxa observed on the two sampled blocks, decreasing to 45 in 2016 and only 37 at the end of the study in 2018. Our results illustrate that the colonization by sessile and motile species was relatively rapid. One year after the immersion, the TR was established at around 50. This was followed by a relatively stability of the TR, even though the blocks sampled in 2015 showed a significant decrease.

The number of non-indigenous species remained low both for sessile and motile fauna throughout the study, while only two sessile species and two motile taxa were recorded. This new artificial structure deployed in the intertidal zone of the Bay of Seine does not favour colonization by numerous pioneers NIS. This contrasts with the situation observed in other ARs where new habitats are found to facilitate biological invasions [37]; but apart

from the amphipod *Aoroides*, the other NIS show very high abundances on blocks during the experiment.

Only one female of the amphipod *Aoroides* was recorded in 2017; two species of this Pacific genus, *Aoroides longimerus* Ren and Zheng, 1996 and *A. semicurvatus* Ariyama, 2004 were recorded in 2019 for the first time along the Normandy coast of the English Channel associated with the brown macro-algae *Sargassum muticum* as well as occurring on harbour pontoons [45]. Both *A. semicurvatus* and *A. longimerus* show low abundances and were absent during a 2015 study carried out in Normandy marinas on associated species and the extent of biofouling "reefs" formed by the NIS polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) [46]. Their introduction into Normandy waters, including the intertidal zone of Luc-sur-Mer, is probably recent.

Two NIS of the genus *Monocorophium* colonized the blocks, attaining a maximum abundance only one year after the beginning of the experiment ( $3200 \text{ ind} \cdot \text{m}^{-2}$  in 2015). Their abundance decreased rapidly thereafter and these taxa were no longer among the ten-dominant species in 2018 (Table 5). *Monocorophium acherusicum* (Costa, 1853) had been recorded at the beginning of the 20th century along the Brittany coast and identified in 1977 in Normandy in the Le Havre harbour basin [47]. *Monocorophium sextonae* (Crawford, 1937) was described from New Zealand and recorded in European waters at the middle of the 20th century and recorded in 1976 in the Bay of Seine. These two *Monocorophium* species are difficult to distinguish from each other; they are sympatric species with very high abundance and only mature males can be accurately identified. Both species were also reported in very high abundances in Normandy marinas during a two-year experiment of colonization of plates (unpublished data). *M. sextonae* was reported in Normandy harbours by [46].

The orange-tipped sea squirt *Corella eumyota* (Traustedt, 1882) is a solitary tunicate native to the Southern Hemisphere and has been known in Normandy waters since 2007 in the Havre harbour basins and recorded along the Luc-sur-Mer intertidal zone in 2013 [47]. It is known to be invasive and shows abundances higher than 680 ind  $\cdot$ m<sup>-2</sup> in 2015; although its abundance subsequently decreased, the species remained among the most dominant sessile species on the blocks (Table 4). The other tunicate *Perophora japonica* (Oka, 1927) is a colonial sea squirt native to the North Indo-Pacific realm. It has colonized several other parts of the world including the south coast of England, France, the Netherlands and the west coast of the United States [48], and was reported since 1982 in Normandy waters and later observed in 2013 at Luc-sur-Mer [47]. Its abundance increased regularly from 2015 to 2017 when its abundance reached a maximum of 2750 ind  $\cdot$ m<sup>-2</sup>, then decreased in 2018 (Table 4).

The tanaidacean *Zeuxo holdichi* (Bamber, 1990) was described from the Bay of Arcachon in the south of the Bay of Biscay, France. Since its description, this small species (<6 mm total length) has been recorded in European waters, from the Iberian Peninsula to Germany [49]. Along the French coast of the English Channel, *Z. holdichi* remained rare at most of the locations where it was recorded except at Luc-sur-Mer where the species was very abundant in the blocks deployed during this experiment (Foveau et al., 2018). The reason for the high abundances (more than 100,000 individuals collected; up to 2500 ind  $\cdot$ m<sup>-2</sup> in 2015) at this location remains enigmatic. *Z. holdichi* can be considered as a pioneer invasive species. Since its first record in 2013 in Normandy waters in the Rade de Cherbourg [49], it has become present in all soft-bottom and hard bottom habitats in Normandy (unpublished data). This shows that this species is ubiquitous in spite of its holobenthic development limiting its natural dispersal, which highlights its efficiency in engendering an abundant population in few months. Foveau et al. (2018) [49] hypothesized that the spread of *Z. holdichi* is in relation to aquaculture activities.

Depending on the fauna, two distinct patterns can be identified.

A rapid colonization by the pioneer barnacles was observed, favoured by the heterogeneous surface of the blocks [42]. It is known that the complexity of the colonised surface influences micro-habitat selection and favours the settlement of barnacle cyprids [13,22,26,50]. Subsequently, the sessile fauna became characterized by a low biodiversity, with only few taxa colonizing the blocks, mainly barnacles and ascidians. These taxa show high abundances and great ability to cover the entire surface of the blocks, thus monopolizing the surface and preventing the establishment of other sessile taxa but favouring the presence of small motile organism. Such low biodiversity (one to four taxa according to the site) was also observed in Normandy marinas [46], with the dominance of the NIS polychaete *Ficopomatus enigmaticus* and the barnacle *Balanus improvisus* (Darwin, 1854) with maximum densities reaching 10,000 ind·m<sup>-2</sup>. The abundance of Balanus *crenatus* in our blocks reached 33,000 ind·m<sup>-2</sup> in April 2014, then varied between 800 and 5500 ind·m<sup>-2</sup> from 2015 to 2018.

As regards the motile fauna, the opportunist amphipods and tanaids dominated the fauna in 2015, reaching a maximum abundance of around 5800 ind  $\cdot$ m<sup>-2</sup>. Similarly, to the sessile fauna, the diversified motile fauna shows temporal fluctuations, with the lowest abundances observed during the last year of the study.

In summary, our experiment shows a very rapid colonisation of sessile fauna onto blocks deployed on oyster tables in the intertidal zone of the Bay of Seine, taking place over a period of one month. The colonization of motile fauna was also rapid, but took place over a period of one year. The type of observation used in this study was designed to test the efficiency of building materials favouring the colonisation of artificial structures on the lower part of the intertidal zone. Since this zone is accessible at each spring tide, it is easier to study than the subtidal zone, where the mobilization of divers needed to sample the blocks is dependent on the meteorological conditions. Two years after the beginning of the experiment, the blocks showed a relative stability. This process of colonisation is also observed on the geotextile artificial reef on the south coast of England, where the natural rock substrate where rare in the Poole Bay near the immersion zone of Boscombe (Herbert et al. 2017). At Luc-sur-Mer, the presence of natural hard substratum is not a limiting factor for the block colonisation by both sessile and motile surrounding macrofauna. An analysis of the main environmental factors controlling settlement, colonization and competition between species during the first year (2014–2015) of the block's colonization shows that the dominant factors explaining biological processes are light plus hydrodynamics and larval behaviour [23,41,42]. The main factor affecting the long-term pattern of colonisation is a biological pattern with succession of sessile taxa from pioneer and opportunist species such as the barnacles (100% of block cover), and then the settlement of the blue mussel, and ascidians and those of motile fauna with both pioneer taxa the amphipod Monocorophium and the tanaid Zeuxo holdichi, and a taxonomic diversity associated with a drastic reduction of abundance at the end of the study in 2018.

To our knowledge, the single study which had examined the faunal succession of artificial structure colonization in the English Channel were those of Herbert et al. (2017) and Taormina et al. (2020) [10,51]. Herbert et al. (2017) [10] observed different stages in colonisation beginning with bryozoans and green algae which are replaced by red algae, hydroids and ascidians. Taormina et al. (2020) [51] monitored the epibenthic colonization of artificial structures in a subtidal (18–20 m depth) high-energy hydrodynamic environment in the western part of the English Channel at a site planned for the deployment of a tidal turbine. Using four years of image-based underwater studies, they identified a rich fauna (28 taxa) and characterized changes of the epibenthic communities which reached a mature stage at the end of their study. However, their study suggested that the ecological succession was still in progress five years after the deployment of artificial structures.

However, it was difficult to compare the colonization of intertidal and subtidal structures with different designs and influences, because of the size of the blocks, i.e., it was known that for the sessile organisms the surface of potential colonised substrates was a limiting factor. However, it appeared noticeable differences in the colonisation patterns of intertidal and subtidal zones, with low diversity and rapid colonization in the intertidal zone, and high diversity and low colonization of subtidal artificial structures. It should be useful to measure the biomass of the colonizing fauna to estimate the role of artificial structures in the secondary production of artificial hard bottoms and compare them with natural hard bottoms, and thus assess their potential for increasing biodiversity in coastal ecosystems.

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# Appendix A

**Table A1.** List of the collected taxa with their abundance per  $0.6 \text{ m}^2$  for the ten blocks analysed from 2014 to 2018. \* Non-Indigenous Taxa.

|                        |                         |               |                | 20         | 14         | 20         | 15         | 20         | 16         | 2017       |            | 20         | 18         |
|------------------------|-------------------------|---------------|----------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
|                        |                         |               |                | Block<br>1 | Block<br>2 |
| Motile fauna           |                         |               |                |            | -          |            |            | -          |            | -          |            | -          | -          |
| Acanthochitona crinita | (Pennant, 1777)         | Mollusca      | Polyplacophora | 0          | 0          | 0          | 0          | 0          | 0          | 1          | 2          | 0          | 0          |
| Achelia                | Hodge, 1864             | Arthropoda    | Pycnogonida    | 0          | 0          | 1          | 1          | 7          | 4          | 2          | 10         | 1          | 1          |
| Ampelisca spinipes     | Boeck, 1861             | Arthropoda    | Malacostraca   | 0          | 0          | 0          | 0          | 0          | 0          | 1          | 0          | 0          | 0          |
| Amphipholis squamata   | (Delle Chiaje,<br>1828) | Echinodermata | Ophiuroidea    | 0          | 0          | 1          | 0          | 0          | 0          | 9          | 1          | 0          | 2          |
| Aonides oxycephala     | (Sars, 1862)            | Annelida      | Polychaeta     | 0          | 0          | 0          | 1          | 0          | 0          | 0          | 0          | 0          | 0          |
| Aoroides *             | Walker, 1898            | Arthropoda    | Malacostraca   | 0          | 0          | 0          | 0          | 0          | 0          | 1          | 0          | 0          | 0          |
| Apseudes talpa         | (Montagu, 1808)         | Arthropoda    | Malacostraca   | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 2          | 0          | 0          |
| Arenicolides ecaudata  | (Johnston, 1835)        | Annelida      | Polychaeta     | 0          | 0          | 0          | 1          | 18         | 16         | 1          | 10         | 0          | 1          |
| Bodotria scorpioides   | (Montagu, 1804)         | Arthropoda    | Malacostraca   | 0          | 0          | 0          | 1          | 0          | 0          | 0          | 0          | 0          | 0          |
| Cancer pagurus         | Linnaeus, 1758          | Arthropoda    | Malacostraca   | 0          | 0          | 3          | 1          | 1          | 0          | 0          | 0          | 0          | 0          |
| Carcinus maenas        | (Linnaeus, 1758)        | Arthropoda    | Malacostraca   | 226        | 328        | 1          | 0          | 53         | 25         | 8          | 3          | 5          | 3          |
| Cirratulidae           | Ryckholt, 1851          | Annelida      | Polychaeta     | 0          | 0          | 0          | 0          | 11         | 4          | 9          | 0          | 6          | 43         |
| Monocorophium *        | Latreille, 1806         | Arthropoda    | Malacostraca   | 0          | 0          | 2152       | 1714       | 74         | 130        | 151        | 176        | 7          | 0          |
| Doto pinnatifida       | (Montagu, 1804)         | Mollusca      | Gastropoda     | 0          | 0          | 0          | 0          | 0          | 0          | 1          | 0          | 0          | 0          |
| Dynamene bidentata     | (Adams, 1800)           | Arthropoda    | Malacostraca   | 0          | 0          | 2          | 15         | 0          | 0          | 0          | 11         | 0          | 6          |
| Emplectonema gracile   | (Johnston, 1837)        | Nemertea      | Hoplonemertea  | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 6          | 0          | 0          |
| Ephesiella abyssorum   | (Hansen, 1878)          | Annelida      | Polychaeta     | 0          | 0          | 0          | 0          | 4          | 55         | 0          | 0          | 0          | 0          |
| Eulalia                | Savigny, 1822           | Annelida      | Polychaeta     | 0          | 0          | 0          | 0          | 13         | 6          | 11         | 26         | 36         | 0          |
| Eumida sanguinea       | (Örsted, 1843)          | Annelida      | Polychaeta     | 0          | 0          | 2          | 3          | 22         | 11         | 26         | 16         | 1          | 0          |
| Eupolymnia nebulosa    | (Montagu, 1819)         | Annelida      | Polychaeta     | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 2          | 0          | 0          |
| Galathea               | Fabricius, 1793         | Arthropoda    | Malacostraca   | 1          | 1          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          |
| Gammaropsis            | Lilljeborg, 1855        | Arthropoda    | Malacostraca   | 0          | 0          | 1          | 0          | 0          | 0          | 1          | 0          | 0          | 0          |

|   |   |                         |                              |              |        |         |              |         |              |             |          | 2018    |       |
|---|---|-------------------------|------------------------------|--------------|--------|---------|--------------|---------|--------------|-------------|----------|---------|-------|
|   |   |                         |                              | 20:<br>Block | Block  | Block   | )15<br>Block | Block   | 016<br>Block | 20<br>Block | Block    | Block   | Block |
| Martha Garage   |   |                         |                              | 1            | 2      | 1       | 2            | 1       | 2            | 1           | 2        | 1       | 2     |
| Motile fauna<br>Gnathia                               | I                                       |                         | Malagastra                   | 0            | 0      | 42      | 24           | 27      | (8           | 151         | 204      | 27      | 5     |
| Gnathia<br>Golfingia (Golfingia)<br>vulgaris vulgaris | Leach, 1814<br>(de Blainville,<br>1827) | Arthropoda<br>Sipuncula | Malacostraca<br>Sipunculidea | 0<br>1       | 0<br>0 | 43<br>0 | 0            | 37<br>1 | 68<br>0      | 151<br>10   | 284<br>0 | 27<br>0 | 2     |
| Harmothoe   | Kinberg, 1856                           | Annelida                | Polychaeta                   | 0            | 0      | 0       | 2            | 0       | 0            | 3           | 2        | 0       | 0     |
| Idotea pelagica                                       | Leach, 1816                             | Arthropoda              | Malacostraca                 | 0            | 0      | 0       | 0            | 0       | 0            | 0           | 5        | 0       | 0     |
| Jasmineira elegans                                    | Saint-Joseph,<br>1894                   | Annelida                | Polychaeta                   | 0            | 0      | 1       | 4            | 13      | 1            | 7           | 0        | 0       | 0     |
| Jassa falcata   | Montagu, 1808                           | Arthropoda              | Malacostraca                 | 0            | 0      | 1       | 2            | 0       | 1            | 8           | 2        | 0       | 0     |
| Lepidonotus squamatus                                 | (Linnaeus, 1758)                        | Annelida                | Polychaeta                   | 0            | 0      | 3       | 5            | 4       | 3            | 5           | 1        | 0       | 6     |
| Leucothoe spinicarpa                                  | (Abildgaard,<br>1789)                   | Arthropoda              | Malacostraca                 | 0            | 0      | 3       | 2            | 0       | 0            | 0           | 0        | 0       | 0     |
| Limacia clavigera                                     | (O. F. Müller,<br>1776)                 | Mollusca                | Gastropoda                   | 0            | 0      | 1       | 3            | 0       | 6            | 0           | 0        | 0       | 0     |
| Lineus  | Sowerby, 1806                           | Nemertea                | Pilidiophora                 | 0            | 0      | 1       | 0            | 2       | 0            | 1           | 1        | 18      | 5     |
| Lumbrineris latreilli                                 | Audouin and<br>Milne Edwards,<br>1833   | Annelida                | Polychaeta                   | 0            | 0      | 0       | 0            | 0       | 0            | 4           | 2        | 0       | 0     |
| Lysidice unicornis                                    | (Grube, 1840)                           | Annelida                | Polychaeta                   | 0            | 0      | 1       | 0            | 0       | 0            | 0           | 0        | 0       | 0     |
| Lysianassidae   | Dana, 1849                              | Arthropoda              | Malacostraca                 | 0            | 0      | 6       | 10           | 1       | 1            | 3           | 1        | 0       | 0     |
| Paucibranchia fallax                                  | (Marion and<br>Bobretzky, 1875)         | Annelida                | Polychaeta                   | 0            | 0      | 0       | 0            | 0       | 0            | 0           | 2        | 0       | 0     |
| Melita palmata  | (Montagu, 1804)                         | Arthropoda              | Malacostraca                 | 0            | 0      | 1       | 1            | 0       | 0            | 0           | 0        | 0       | 0     |
| Microdeutopus anomalus                                | (Rathke, 1843)                          | Arthropoda              | Malacostraca                 | 0            | 0      | 0       | 3            | 0       | 0            | 6           | 1        | 0       | 0     |
| Nassarius   | Duméril, 1805                           | Mollusca                | Gastropoda                   | 0            | 0      | 0       | 0            | 0       | 0            | 1           | 0        | 0       | 0     |
| Necora puber  | (Linnaeus, 1767)                        | Arthropoda              | Malacostraca                 | 0            | 0      | 1       | 0            | 0       | 0            | 0           | 0        | 0       | 0     |
| Nematoda  | ,                                       | Nematoda                |                              | 0            | 0      | 7       | 0            | 559     | 367          | 17          | 1        | 49      | 214   |
| Nemertea  |   | Nemertea                |                              | 0            | 0      | 0       | 0            | 0       | 3            | 3           | 1        | 0       | 0     |
| Notomastus latericeus                                 | Sars, 1851                              | Annelida                | Polychaeta                   | 0            | 0      | 0       | 7            | 0       | 0            | 0           | 0        | 0       | 0     |
| Nototropis<br>swammerdamei                            | (H. Milne<br>Edwards, 1830)             | Arthropoda              | Malacostraca                 | 0            | 0      | 1       | 8            | 0       | 2            | 6           | 7        | 0       | 0     |
| Nucella lapillus                                      | (Linnaeus, 1758)                        | Mollusca                | Gastropoda                   | 0            | 0      | 0       | 0            | 0       | 0            | 3           | 0        | 0       | 0     |
| Tryphosa nana   | (Krøyer, 1846)                          | Arthropoda              | Malacostraca                 | 0            | 0      | 6       | 6            | 0       | 0            | 0           | 6        | 0       | 0     |
| Ostracoda   | Latreille, 1802                         | Arthropoda              | Ostracoda                    | 2            | 0      | 0       | 0            | 8       | 1            | 0           | 2        | 0       | 3     |
| Perinereis cultrifera                                 | (Grube, 1840)                           | Annelida                | Polychaeta                   | 0            | 0      | 27      | 15           | 1       | 2            | 14          | 2        | 18      | 0     |
| Peringia ulvae  | (Pennant, 1777)                         | Mollusca                | Gastropoda                   | 0            | 0      | 0       | 0            | 0       | 2            | 25          | 16       | 0       | 1     |
| Pholoe  | Johnston, 1839                          | Annelida                | Polychaeta                   | 0            | 0      | 20      | 29           | 84      | 12           | 359         | 210      | 11      | 12    |
| Phoxichilidium<br>femoratum                           | (Rathke, 1799)                          | Arthropoda              | Pycnogonida                  | 0            | 0      | 0       | 0            | 0       | 0            | 1           | 0        | 0       | 1     |
| Phyllodoce  | Lamarck, 1818                           | Annelida                | Polychaeta                   | 0            | 0      | 1       | 3            | 0       | 0            | 0           | 27       | 6       | 2     |
| Pilumnus hirtellus                                    | (Linnaeus, 1761)                        | Arthropoda              | Malacostraca                 | 0            | 0      | 9       | 18           | 24      | 4            | 22          | 47       | 2       | 5     |
| Pinnotheres pisum                                     | (Linnaeus, 1767)                        | Arthropoda              | Malacostraca                 | 0            | 0      | 1       | 0            | 0       | 1            | 0           | 3        | 0       | 0     |
| Pisidia longicornis                                   | (Linnaeus, 1767)                        | Arthropoda              | Malacostraca                 | 0            | 0      | 1       | 4            | 0       | 0            | 0           | 1        | 0       | 0     |
| Platyhelminthes                                       | Minot, 1876                             | Platyhelminthes         |                              | 0            | 0      | 1       | 0            | 0       | 4            | 1           | 0        | 0       | 0     |
| Platynereis dumerilii                                 | (Audouin and<br>Milne Edwards,<br>1833) | Annelida                | Polychaeta                   | 0            | 0      | 0       | 0            | 14      | 36           | 5           | 0        | 10      | 0     |
| Polititapes rhomboides                                | (Pennant, 1777)                         | Mollusca                | Bivalvia                     | 0            | 0      | 0       | 1            | 7       | 3            | 5           | 5        | 0       | 0     |
| Polynoe scolopendrina                                 | Savigny, 1822                           | Annelida                | Polychaeta                   | 0            | 0      | 0       | 0            | 0       | 0            | 0           | 0        | 0       | 7     |
| Porcellana platycheles                                | (Pennant, 1777)                         | Arthropoda              | Malacostraca                 | 0            | 0      | 0       | 3            | 2       | 0            | 2           | 5        | 0       | 0     |
| Psamathe fusca  | Johnston, 1836                          | Annelida                | Polychaeta                   | 0            | 0      | 2       | 0            | 10      | 36           | 0           | 2        | 0       | 0     |
| Schistomeringos                                       | Jumars, 1974                            | Annelida                | Polychaeta                   | 0            | 0      | 1       | 0            | 1       | 0            | 0           | 0        | 0       | 0     |
| Sphaerodoridium<br>claparedii                         | (Greeff, 1866)                          | Annelida                | Polychaeta                   | 0            | 0      | 0       | 0            | 9       | 2            | 13          | 5        | 0       | 0     |
| Sunamphitoe pelagica                                  | (H. Milne<br>Edwards, 1830)             | Arthropoda              | Malacostraca                 | 0            | 0      | 0       | 0            | 0       | 0            | 0           | 1        | 0       | 0     |
| Syllidae  | Grube, 1850                             | Annelida                | Polychaeta                   | 0            | 0      | 48      | 44           | 61      | 58           | 36          | 92       | 10      | 16    |
| Tritaeta gibbosa                                      | (Spence Bate,<br>1862)                  | Arthropoda              | Malacostraca                 | 0            | 0      | 0       | 0            | 0       | 1            | 0           | 0        | 0       | 0     |
| Trivia monacha  | (da Costa, 1778)                        | Mollusca                | Gastropoda                   | 0            | 0      | 0       | 0            | 1       | 0            | 0           | 0        | 0       | 0     |
| m 1 1   | Renier, 1804                            | Nemertea                | Palaconomortoa               | 0            | 0      | 12      | 5            | 11      | 14           | 0           | 2        | 11      | 5     |
| Tubulanus   | Kenner, 1004                            | Nemeriea                | Palaeonemertea               | 0            | 0      | 12      | 5            | 11      | 14           | 0           | 0        | 11      | 5     |

# Table A1. Cont.

|                       |                      |            |              | 20         |            | 20    |            | 20    |            | 20    |            |            | 18         |
|-----------------------|----------------------|------------|--------------|------------|------------|-------|------------|-------|------------|-------|------------|------------|------------|
|                       |                      |            |              | Block<br>1 | Block<br>2 | Block | Block<br>2 | Block | Block<br>2 | Block | Block<br>2 | Block<br>1 | Block<br>2 |
| Motile fauna          |                      |            |              | 1          |            | -     | 4          | -     |            | -     | -          | -          |            |
| Websterinereis glauca | (Claparède,<br>1870) | Annelida   | Polychaeta   | 0          | 0          | 13    | 36         | 0     | 0          | 225   | 172        | 84         | 5          |
| Zeuxo holdichi        | Bamber, 1990         | Arthropoda | Malacostraca | 0          | 0          | 1321  | 1707       | 79    | 42         | 349   | 128        | 51         | 0          |
| Sessile fauna         |                      |            |              |            |            |       |            |       |            |       |            |            |            |
| Actinothoe sphyrodeta | (Gosse, 1858)        | Cnidaria   | Anthozoa     | 0          | 0          | 0     | 0          | 0     | 0          | 0     | 1          | 0          | 0          |
| Ascidia               | Linnaeus, 1767       | Chordata   | Ascidiacea   | 0          | 0          | 0     | 8          | 0     | 0          | 0     | 0          | 0          | 0          |
| Balanus crenatus      | Bruguière, 1789      | Arthropoda | Hexanauplia  | 23,060     | 18,752     | 2862  | 3534       | 468   | 470        | 3160  | 3292       | 4505       | 2064       |
| Perforatus perforatus | (Bruguière,<br>1789) | Arthropoda | Hexanauplia  | 0          | 0          | 5     | 0          | 8     | 4          | 25    | 69         | 71         | 52         |
| Branchiomma bombyx    | (Dalyell, 1853)      | Annelida   | Polychaeta   | 0          | 0          | 0     | 0          | 0     | 10         | 200   | 15         | 0          | 0          |
| Corella eumyota *     | Traustedt, 1882      | Chordata   | Ascidiacea   | 0          | 0          | 404   | 410        | 80    | 58         | 102   | 46         | 4          | 80         |
| Dendrodoa             | MacLeay, 1824        | Chordata   | Ascidiacea   | 0          | 0          | 20    | 0          | 0     | 0          | 0     | 0          | 0          | 0          |
| Diadumene cincta      | Stephenson,<br>1925  | Cnidaria   | Anthozoa     | 0          | 0          | 0     | 0          | 0     | 0          | 0     | 0          | 7          | 0          |
| Lanice conchilega     | (Pallas, 1766)       | Annelida   | Polychaeta   | 0          | 0          | 0     | 0          | 0     | 0          | 0     | 4          | 0          | 0          |
| Molgula               | Forbes, 1848         | Chordata   | Ascidiacea   | 0          | 0          | 62    | 157        | 143   | 67         | 72    | 109        | 40         | 71         |
| Mytilus edulis        | Linnaeus, 1758       | Mollusca   | Bivalvia     | 1          | 2          | 113   | 208        | 144   | 135        | 24    | 59         | 29         | 104        |
| Perophora japonica *  | Oka, 1927            | Chordata   | Ascidiacea   | 0          | 0          | 0     | 0          | 207   | 121        | 2337  | 956        | 64         | 84         |
| Spirobranchus         | Blainville, 1818     | Annelida   | Polychaeta   | 0          | 0          | 56    | 115        | 86    | 69         | 10    | 18         | 56         | 31         |

#### Table A1. Cont.

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