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Article

Immersion Time Determines Performance of Artificial Habitats in Commercial Harbours by Changing Biodiversity of Colonising Invertebrate Assemblages

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Abstract: In highly modified coastal environments, such as commercial harbours, the installation of artificial habitats has garnered support as a means of enhancing local biological recruitment and connectivity. The success of these measures depends largely on the patterns of species colonisation. Using post-installation monitoring data, we compared the composition of assemblages of invertebrates colonising artificial habitats that were immersed for different periods (~6 vs. ~18 months) in three commercial harbours along the French Mediterranean coast. The artificial habitats were colonised by taxonomically diverse invertebrate assemblages of ecological and economic importance, including molluscs, crustaceans, and echinoids. Composition differed significantly with the immersion time of the artificial habitats, with total abundance, species richness, and evenness being significantly higher after ~18 than after ~6 months of immersion, indicating that long periods are necessary to enrich these new habitats with economically and ecologically important species. These results can inform restoration protocols and emphasise the value of post-installation monitoring programs.

Keywords: ecological community development; coastal biodiversity; species composition; artificial structures; coastal restoration



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1. Introduction

Habitat degradation and loss threaten population persistence, biodiversity, and the functioning of ecosystems [1–3]. Ecosystem managers face the challenge of implementing conservation and restoration initiatives in altered environments [4] where the effects of climate change exacerbate the impacts of coastal development [5–8]. In systems where it is determined that ecosystem thresholds have been crossed as a result of human impacts and where changes are irreversible, such as on heavily modified coastlines within large grey infrastructures (e.g., ports, harbours, commercial marinas), options for their management

as ‘novel ecosystems’ may be considered to manipulate them and fulfil desired ecological conditions or functions [4,9,10].

The installation of artificial habitats with ecologically-engineered elements has been widely advocated and implemented for replacement of lost or degraded natural habitat, ecological conservation, biodiversity enhancement, and improvement of ecosystem services [11–14]. Specific goals of artificial habitats may include supporting local biodiversity and communities of fish or invertebrates of commercial or ecological interest [12,15–19], building ecosystem resilience, and enhancing ecological connectivity [4,20–22].

Evidence shows the efficacy of these artificial habitats in attracting marine organisms at different development stages, from larvae to adults, although the patterns of colonisation are context-dependent [17,20,22–24]. These patterns can depend on processes of community assembly and succession that are determined, among others, by the timing of species colonisation and interactions among species [25–27]. It is therefore anticipated that implementing artificial habitats in degraded ecosystems can facilitate or accelerate successional processes that foster the establishment and maintenance of diverse communities [24,26,28].

Evaluating the colonisation process of artificial habitats is key for assessing their use in ecologically degraded coastal ecosystems. In this study, we examine the composition (structure and diversity) of invertebrate assemblages colonising artificial habitats after two distinct immersion periods: 5.5–7 months (Year 1), and 17.5–19.5 months (Year 2).

The artificial habitats (Dock Biohut[®]; Ecocean SAS, Montpellier, Paris) were designed to provide ecological nursery habitat within commercial harbours and marinas [17,22]. We used a subset of existing monitoring data from these artificial habitats in three spatially distinct commercial harbours along the French Mediterranean coast where post-installation sampling replication allowed for comparison of colonisation across years. We compared invertebrate assemblages found in artificial habitats in Years 1 and 2 and hypothesised that the species composition of invertebrates would differ across time periods and that abundance and taxonomic diversity would increase with immersion time.

2. Materials and Methods

2.1. Study Sites

This study uses ecological monitoring data from three large commercial harbours in the Gulf of Lion along the French Mediterranean coast, separated by distances of 29 to 204 km, namely Le Barcarès (42.7980° N, 3.0375° E), Port-Vendres (42.5190° N, 3.1089° E), and Grand Port Maritime de Marseille (43.3448° N, 5.3377° E). Each of these three harbours has >200 vessel moorings and has been operating commercially for >40 years, although the physical and environmental characteristics of each harbour vary across a range of parameters (Table 1).

Table 1. Characteristics of the three study sites (harbours) and Dock Biohut sampling.

Harbour	Coast Type	Distance to Rhone River Mouth (km)	Connections	Harbour Construction Date	Harbour Surface Area (ha)	Harbour Maximum Depth (m)	Mean ± SE Distance from Biohuts to Sea (m)	Mean ± SE Depth under Biohuts (m)	Biohuts Installation Date	Date of Sampling (Sample Size)	
										Year 1	Year 2
Le Barcarès	Sandy	158 (west)	Sea and lagoon	1963	81	2.5	610 ± 112	1.50 ± 0.50	1 March 2013	30 Sept–1 October 2013 (n = 9)	15 October 2014 (n = 4)
Port-Vendres	Rocky	167 (west)	Sea	1953	33	10.0	816 ± 133	5.67 ± 1.33	1 March 2013	1–2 October 2013 (n = 9)	7 October 2014 (n = 5)
Grand Port maritime de Marseille	Rocky	42 (east)	Sea	1840	400	14.5	2126 ± 152	8.25 ± 1.84	1 June 2013	14 November 2013 (n = 12)	26–27 November 2014 (n = 7)

We extracted this subset of data from a large monitoring database comprising data from Biohuts installed in 21 harbours and marinas across 19 French cities and in Monaco between 2013 and 2017 (Table S1). The subset was selected to allow for sufficient replication of artificial habitats within harbours across the years.

2.2. Sampling Unit and Protocol

Biohuts were composed of two adjoining carbon-steel alloy cages ($50 \times 80 \times 12.5$ cm; combined cages depth 25 cm) and attached to the dockside (Figure 1). One cage was filled with empty oyster shells to provide complex substrate and was positioned against the dock (2.5 cm mesh-size); the outward-facing adjoining cage was left empty (5 cm mesh size) to keep out large mobile predatory fish.

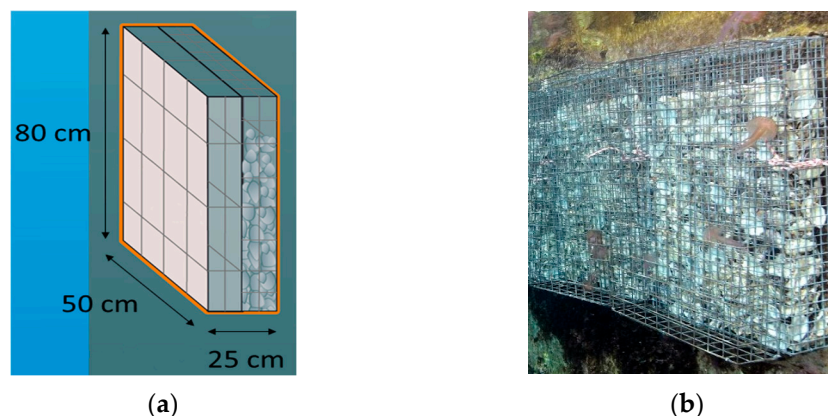


Figure 1. Dimensions (a) and image (b) of Dock Biohut structures, composed of two carbon-steel alloy cages: inner-cage filled with oyster shells (2.5 cm mesh) and empty outer-cage (5 cm mesh).

In March and June 2013, all the sampled Biohuts were installed in each harbour, submerged just below the surface of the water. Assemblages were sampled on randomly selected Biohuts at least 20 m apart, either 5.5–7 (Year 1) or 17.5–19.5 months after installation (Year 2; Table 1). Because of the number of remaining Biohuts available in Year 2, the number of sampled Biohuts were different among years. During Year 1, 30 Biohuts were sampled (9 in Le Bacarès, 12 in Marseille and 9 in Port-Vendres), whereas 16 were sampled in Year 2 (4 in Le Bacarès, 7 in Marseille, and 5 in Port-Vendres). During monitoring, the Biohuts were encased with a PVC net (2 mm mesh) by divers to prevent loss of organisms during removal and lifted from the water onto the adjoining dock. Biohuts were then disassembled, the organisms identified to the lowest taxonomic level possible, and they were counted. The sampling protocol did not allow us to sample for macroalgal cover or biomass and we focused the study on consumers.

2.3. Data Analysis

We fitted generalised linear mixed models (GLMM) with time period as fixed factor (two levels: Year 1, Year 2) and harboured a random factor [29] on univariate data. We used this structure to model the biodiversity of invertebrate assemblages (species richness, Shannon diversity, Pielou's evenness), the abundance of specific taxa (Bivalvia, Gastropoda, Malacostraca, Ophiuroidea), and the abundance of commercially exploited taxa that contributed >5% to the total invertebrate abundance (e.g., the palaemonid shrimp *Palaemon* spp.; the variegated scallop *Mimachlamys varia* [30]). Mixed-effects models that estimate parameters based on residual maximum likelihood were used due to their capacity to more appropriately handle unbalanced designs (particularly with random effects) than alternative approaches using observed and expected mean squares or error strata [31]. The count data of classes and total abundance were fitted using a negative binomial distribution to accommodate alternative exponential distributions of residuals due to evidence of overdispersion (with `glmer.nb` in *lme4*). Temporal variation in species richness was modelled with a Poisson distribution due to exponential variance, but within the assumed bounds of dispersion (`glmer` in *lme4*). Temporal variation in Shannon diversity and Pielou's evenness was assessed with Gaussian models and a constant variance structure due to heteroscedasticity between time periods. Model assumptions were assessed visually using diagnostic

plots of Pearson residuals. Variation in the multivariate taxonomic composition of invertebrate assemblages through time was tested using a two-way nested PERMANOVA (maximum permutations = 9999) and then visualised with non-metric multidimensional scaling (nMDS) based on a Bray-Curtis dissimilarity matrix of $\log(x + 1)$ transformed data. We used Monte Carlo sampling to estimate differences due to limited available unique permutations (360) and unconverged permutation versus Monte Carlo P-values [32].

Before running PERMANOVA, the homogeneity of residuals was tested using PERMDISP with time period (fixed) and harbour (random) as factors. Similarity percentage analysis (SIMPER) was also performed using Primer v6 with PERMANOVA+ [32,33]. The data were $\log(x + 1)$ transformed to quantify, (1) overall similarity across harbours across the time periods, and (2) mean similarity within or dissimilarity between harbours across time periods. SIMPER was also used to identify those species contributing consistently to similarity or dissimilarity (similarity or dissimilarity/standard deviation ≥ 2).

3. Results

A total of 48 invertebrate taxa from 39 families, 8 classes, and 5 phyla were recorded in Biohut structures across both survey periods (Tables S1 and S2). All animals were classified as native to the Mediterranean [34]. There were significant differences between Year 1 and Year 2 in total abundance ($z(1,42) = 2.36, p = 0.02$), species richness ($s(1,42) = 2.28, p = 0.02$), and Pielou's evenness ($s(1,42) = 2.07, p = 0.04$), but not Shannon diversity (Tables S3 and S4). Abundance and species richness were higher in Year 2 than Year 1 (Figure 2).

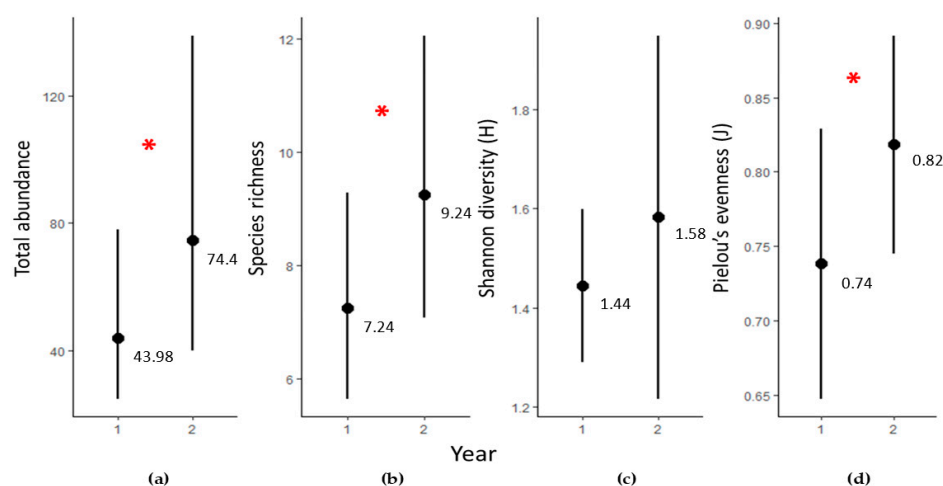


Figure 2. Temporal variation (fitted values $\pm 95\%$ confidence intervals) in: (a) the total abundance (number of individuals/ 0.1 m^3 of artificial structure); (b) species richness (number of taxa/ 0.1 m^3 of artificial structure); (c) Shannon diversity; and (d) Pielou's evenness of invertebrate assemblages in artificial Dock Biohut structures within Year 1 and Year 2 since installation. Significant differences between time periods of each metric are indicated with asterisks (red * indicates $p \leq 0.05$).

The taxonomic composition of invertebrate assemblages varied between Year 1 and Year 2. Non-metric MDS ordination showed distinct clusters between Year 1 and Year 2 (Figure 3). For both Le Bacarès and Port-Vendres, the Year 2 data were closer to each other than for the Year 1. The stress value (0.07, 0.1, and 0.08, respectively) provides a good representation of our data in reduced dimensions. PERMANOVA ($F(1,40) = 3.569; p < 0.05$) analysis revealed variation in taxonomic composition of invertebrate assemblages from Year 1 to Year 2 (Figure 3). However, PERMDISP analysis showed significant differences in the mean distance from centroids among the groups ($F(5,40) = 11.099; p < 0.001$), indicating that results from PERMANOVA should be interpreted with caution.

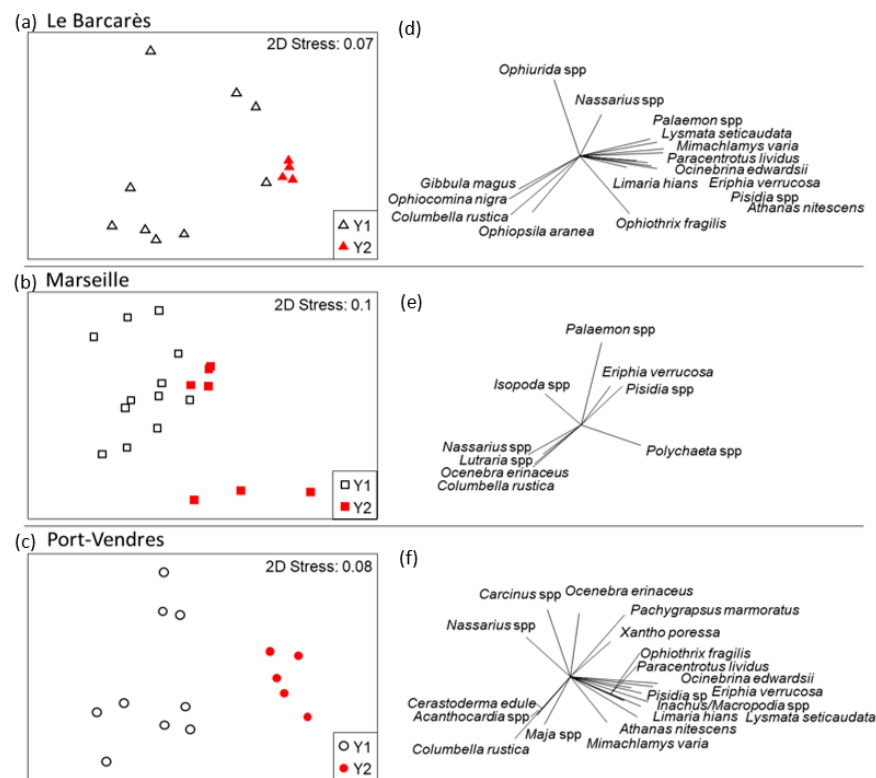


Figure 3. Non-metric multidimensional scaling analysis showing: Variation in taxonomic composition of invertebrate assemblages among surveyed Dock Biohut structures in each harbour between years (Y1 and Y2) since installation ((a–c); log x + 1 transformed data); and the relative contribution of species to variation at each harbour ((d–f); >0.5 Pearson correlation).

Changes in assemblage composition between Year 1 and Year 2 caused an overall increase in taxonomic similarity of assemblages across all harbours (average assemblage similarity: Year 1, 28%; Year 2, 37%), with an average 78% dissimilarity in species composition between years. This overall increase was likely driven largely by increased similarity in taxonomic composition of assemblages at La Bacarès (Year 1, 28%; Year 2, 72%) and Port-Vendres (Year 1, 47%; Year 2, 70%), and not Marseille where similarity decreased (Year 1, 39%; Year 2, 31%; Table 2). In Year 1, only the variegated scallop *Mimachlamys varia* contributed consistently to assemblage similarity among Biohuts in Port-Vendres. However, in Year 2, six species consistently characterised species assemblages in Le Barcarès and eight species in Port-Vendres. In Marseille, no species consistently contributed to assemblage similarity in either year.

Table 2. Similarity Percentage analysis of invertebrate assemblages in surveyed Dock Biohuts through time. Species consistently contributing to the average similarity within (sim/SD > 2), and dissimilarity between (diss/SD > 2) harbours from Year 1 (Y1) to Year 2 (Y2) identified in one-way SIMPER analysis are shown.

	Le Barcarès	Port-Vendres	Marseille
	Av. Sim: Y1: 28%; no consistent spp. Y2: 72%; <i>Ophiothrix fragilis</i> , <i>Palaemon</i> spp., <i>Pisidia</i> spp., <i>Mimachlamys varia</i> , <i>Athanas nitescens</i> , <i>Paracentrotus lividus</i> , <i>Lysmata seticaudata</i> , <i>Eriphia verrucosa</i>	Av. dissim: Y1: 77%; no consistent spp. Y2: 50%; <i>Ophiothrix fragilis</i> , <i>Ocinebrina edwardsii</i> , <i>Pisidia</i> spp., <i>Pachygrapsus marmoratus</i> , <i>Lysmata seticaudata</i> , <i>Eriphia verrucosa</i>	Av. dissim: Y1: 82%; no consistent spp. Y2: 69%; <i>Ophiothrix fragilis</i> , <i>Paracentrotus lividus</i> , <i>Lysmata seticaudata</i> , <i>Eriphia verrucosa</i>
Le Barcarès	Av. dissim. (Y1 to Y2): 75%; <i>Pisidia</i> spp., <i>Athanas nitescens</i> , <i>Lysmata seticaudata</i> , <i>Eriphia verrucosa</i>		

Table 2. Cont.

	Le Barcarès	Port-Vendres	Marseille
Port-Vendres		Av. Sim: Y1: 47%; <i>Mimachlamys varia</i> Y2: 70%; <i>Ocenebrina edwardsii</i> , <i>Lysmata seticaudata</i> , <i>Mimachlamys varia</i> , <i>Eriphia verrucosa</i> , <i>Athanas nitescens</i> , <i>Pachygrapsus marmoratus</i> Av. Dissim. (Y1 to Y2): 69%; <i>Ocenebrina edwardsii</i> , <i>Lysmata seticaudata</i> , <i>Eriphia verrucosa</i>	Av. Dissim.: Y1: 71%; no consistent spp. Y2: 76%; <i>Ocenebrina edwardsii</i> , <i>Lysmata seticaudata</i>
Marseille			Av. sim: Y1: 39%; no consistent spp. Y2: 31%; no consistent spp. Av. dissim. (Y1 to Y2): 75%; no consistent spp.

There was an overall increase in the abundance of Malacostraca ($z(1,42) = 4.50$, $p < 0.0001$), but not in Bivalvia, Gastropoda, or Ophiuroidea (Figure 4; Tables S3 and S4). Of 11 surveyed taxa identified as potentially commercially exploited [30], only two contributed to >5% of the total invertebrate abundance—*Palaemon* spp. (palaemonid shrimp) and *M. varia*—but neither varied in abundance significantly across years (Table S5). The remaining nine species (*Carcinus* spp.; common cockle *Cerastoderma edule*; black squat lobster *Galathea squamifera*; small periwinkle *Melarhaphé neritoides*; European flat oyster *Ostrea edulis*; purple sea urchin *Paracentrotus lividus*; *Periclimenes* spp. shrimp; bristle worm Polychaeta spp.; common cuttlefish *Sepia officinalis*) each accounted for <2% of the total surveyed invertebrate abundance (Table S6).

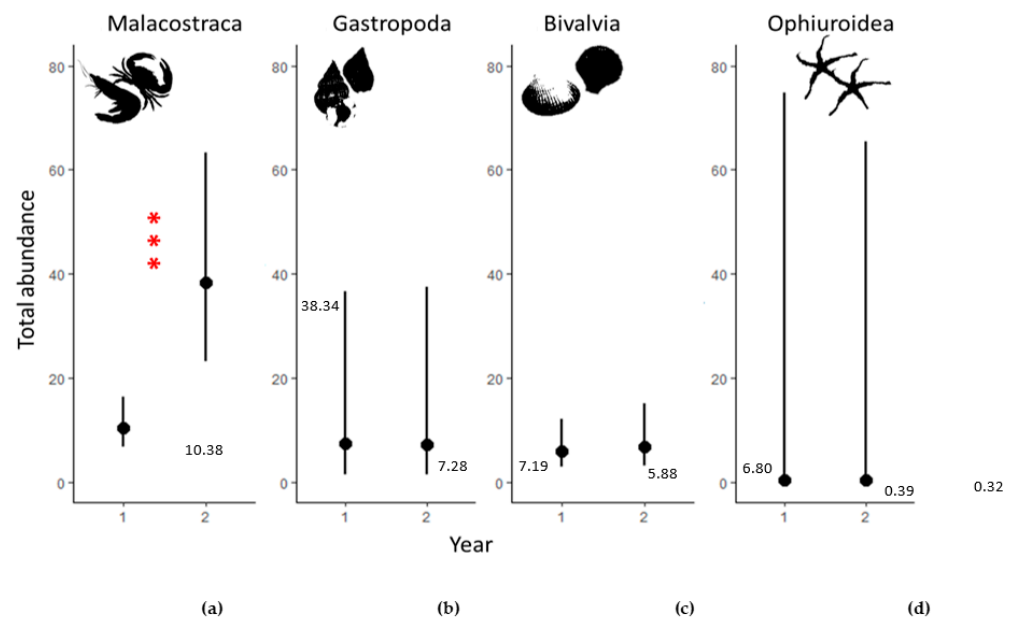


Figure 4. Temporal variation (fitted values \pm 95% confidence intervals) in the total abundance (number of individuals/0.1m³ of artificial structure) of (a) Malacostraca; (b) Gastropoda; (c) Bivalvia; and (d) Ophiuroidea in surveyed Dock Biohut structures within Year 1 and Year 2 since installation. Significant differences between time periods are indicated with asterisks (red *** $p < 0.001$).

4. Discussion

The examination of post-installation monitoring data found that artificial habitats (Dock Biohut) hosted taxonomically diverse assemblages of invertebrate species, including molluscs, crustaceans, and echinoids of ecological, commercial, and social interest. Our analysis aims to complement the already-existing studies focused on the fish species associated with artificial habitats [17–19,22]. Communities develop and are structured over time, whereby pioneering species initially colonise areas, with the abundance and composition of colonising assemblages depending on interacting factors including habitat size and connectivity, the proximity of source populations, local hydrodynamics, inter-annual temporal variation in larval supply, and competitive interactions with other species [20,27,35–37].

Community development in restoration or conservation ecology would likely be time-dependent in achieving desired endpoints of biodiversity, productivity, and species-specific configurations [26,38]. The immersion time of artificial habitats is a known, influential predictor of community composition due to processes of faunal succession [25,27,39,40]. In our study, the results indicated that community changes through time, likely due to spatially and temporally variable colonisation by different species [27,39]. The results showed differences in the colonisation and recruitment of organisms in the Biohuts between Year 1 and Year 2 of immersion, indicating the capacity of artificial habitats to support local biodiversity enhancement via the recruitment of organisms in highly modified harbours.

We found significantly greater total abundance, species richness, species evenness, and abundance of crustaceans in artificial habitats across the three spatially distinct harbours after a longer period of immersion. Multivariate analysis of our data also showed differences in artificial habitats assemblages between Year 1 and Year 2. Indeed, significant variation in composition between the invertebrate assemblages sampled in Year 1 and Year 2 after deployment of the Dock Biohuts indicates the processes of community development and highlights the role of habitat soak-time in determining the outcome of artificial habitat installation initiatives [24,26,27].

Our analyses revealed an increase in the similarity in composition both within and among assemblages in two of the three spatially distinct harbours between Year 1 and Year 2, and an overall increase in abundance of crustaceans—a group of ecologically important organisms due to their role in food-web dynamics [41]—and their influence on the behaviour of settlement-stage larval organisms [42–46]. Species composition was highly variable in the first year across all harbours, but in Year 2, assemblage structure became similar within and between Port-Vendres and Le Barcarès, with the dominance of molluscs, crustaceans, and echinoderms. These similarities and the differences with Marseille harbour could be explained by the environmental characteristics of Marseille harbour, which is the largest and the deepest harbour of this study, and it is not directly influenced by outflow from the Rhone River, which delivers organic matter and sediment into the other two study harbours. Furthermore, the Biohuts of the Marseille harbour were positioned at a greater distance from the harbour entrance than those of the other two harbours. Finally, the differences in species assemblages could also be due to the local availability of species, e.g., the ecological concept of species pool [47,48]. We observed an overall increase in abundance of Malacostraca, while the abundance of other predominant classes (gastropods, bivalves and brittlestars) remained consistent, carrying implications for efforts targeting ecological restoration [26,41,46]. Crustaceans are key components of the diets of a range of macroinvertebrates and finfish [41], and an increase in their abundance may have implications for local food-web dynamics [49]. Similarly, crustaceans can create a loud and acoustically complex biophony, producing acoustic cues used by settlement-stage larvae of fish and invertebrates that likely further enhances community development [42–46,50]. For example, the estimated detection distance of snaps of the shrimp, *Athanas nitescens*, characteristic of Biohut invertebrate assemblages in Le Barcarès and Port-Vendres by Year 2, can be up to 40 m [51]. As such, shifts towards greater abundance of crustaceans may have a disproportionate role in the maintenance, development, and function of locally diverse ecological communities [26,41], and may point towards opportunities for passive

acoustic monitoring of community development where intrusive survey techniques are less desirable [51–53].

Our results indicate that provided that the artificial habitats do not simply concentrate organisms, they may enhance local productivity and biodiversity in highly modified areas within relatively short periods of time [54]. Similarly, the observed differences in assemblage composition through time suggests that where specific species configurations are desired endpoints for habitat restoration, understanding how local communities are structured over time will likely enable pragmatic management goal setting [26,27]. Many species of crustaceans are also highly valued commercial and recreational fisheries resources [30]. Where artificial habitats can enhance rather than relocate local productivity, they may provide opportunities for harvesting species in support of fisheries enhancement initiatives [12,55,56], for the live-trade of ornamental organisms [18], or for aquaculture [57].

Artificial habitats can enhance the ecological capacity of highly modified areas of coastline such as large commercial ports and marinas by providing habitats for marine life at different stages of life-history and migration [4,10,19,22]. The nursery capacity of artificial habitats in large commercial ports has been shown previously for diverse assemblages of juvenile finfishes, with typically higher abundance and species richness on artificial habitat structures than on adjacent bare surfaces [17,19,22]. The availability of fine-scale structural complexity, such as is created by caged oyster shells in the focal Biohut structures, can provide refugia and enhance the survival of small-bodied and/or juvenile stage organisms when their risk of mortality is highest [22,58]. Furthermore, the colonisation, abundance and species diversity of macroinvertebrate fauna can be directly associated with availability and structural characteristics of habitats [28,59–64]. Investigating existing ecological monitoring data, our results provide insights into the relatively short-term capacity of artificial habitats to attract and maintain diverse assemblages of invertebrates. Moreover, our results highlight the role of habitat duration in community development and changes, and the establishment of biodiversity in highly modified commercial harbours. Our results also suggest that the environmental and physical characteristics of the harbours equipped with artificial habitat structures can also facilitate the colonisation by specific invertebrate assemblages. Furthermore, longer temporal studies comparing the colonisation of artificial habitats against background levels of diversity and productivity would enable greater understanding of their capacity to augment the ecological function of modified systems [54]. This includes improving our understanding of their role as ecological steppingstones for enhanced connectivity, and the ecological processes determining positive feedbacks and alternative states across degraded systems [15,38].

Biodiversity conservation and restoration are widely supported management goals [26,65,66], with species diversity being considered important for promoting ecosystem resilience via the maintenance of critical ecosystem functioning during disturbance (due to functional redundancy and response diversity [67,68]). Increasingly, efforts to restore or replace nursery habitats are viewed as a key component of the conservation of biodiversity and management of productive systems [5,69]. Our results indicate that periods longer than 7 months are necessary to enrich these artificial habitats of economically and ecologically important species. Finally, given the ecological importance of invertebrates in trophic dynamics and community development [41,45], experimental research considering the influence of variation in invertebrate assemblage composition through time on the recruitment of teleost fishes may aid in the understanding of the capacity for complementary acoustic ecological enhancement programs [46,70,71].

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15040505/s1>, Table S1: Surveyed species recorded in Biohut structures in Le Barcarès (BA), Port-Vendres (PV), and Grand Port maritime de Marseille (MA) in 2013 and 2014; Table S2: Invertebrate species surveyed between 2013 and 2017 in artificial structures (Dock Biohut: D; Pontoon Biohut, P) installed within 21 harbours, in 19 cities in France and Monaco during monitoring (total = 115 spp.); Table S3: Temporal comparisons (with 95% confidence intervals: CI) of invertebrate assemblages in Dock Biohut across harbours (random factor) in Year 1 to Year 2 (linear mixed effects models). Significant metrics shown in bold; Table S4: Mean \pm SE total abundance, biodiversity, and abundance of classes of invertebrates surveyed within Biohut structures in year 1 and year 2 since installation; Table S5: Temporal comparisons (with 95% confidence intervals: CI) of potentially exploited species surveyed contributing > 5% of the total abundance of invertebrate assemblages in surveyed Biohuts in Year 1 and Year 2 (linear mixed effects models) [30]; Table S6: Mean \pm SE total abundance of commercially exploitable species in surveyed Dock Biohut structures in Year 1 and Year 2 [30].

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