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1   **Title**

2   Composition of mobile invertebrate assemblages in artificial habitats determined by duration of

3   immersion in commercial harbors

4

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17

18   **Authors' contributions**

19   LR, SS, AR, GL, AG, PL conceived the ideas and designed methodology, AG, AF, LB, EA collected

20   the data. LR analyzed the data and led the writing of the manuscript. All authors contributed critically

21   to the drafts and gave final approval for publication.

22

23   **Abstract**

24   Habitat loss threatens biodiversity and ecosystem function. Managers face increasingly heterogenous

25   ecosystems composed of multiple patches in varying states of degradation from which they are

26   charged with maintaining ecosystem health, populations of species, and the provision of ecosystem

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27   goods and services. In highly modified coastal environments, such as commercial harbors, the

28   installation of artificial structures has garnered support as a means of enhancing local biological

29   recruitment, migration, and connectivity, thereby supporting ecosystem persistence. But the extent to

30   which management goals are achieved depends on biophysical processes determining the influx of

31   organisms (particularly larvae) and the process of community development. Using post-installation

32   monitoring data, we assess the capacity of artificial structures to attract and maintain biodiversity in

33   highly modified, ecologically degraded systems, and elucidate the role of habitat duration in

34   community development. We quantify differences in the composition of mobile invertebrate

35   assemblages, after immersion periods of either ca. 6 months or ca. 18 months, within artificial

36   structures across three spatially distinct commercial harbors along the French Mediterranean coast.

37   The artificial structures in these highly modified systems attracted taxonomically diverse invertebrate

38   assemblages, including molluscs, crustaceans, and echinoids of ecological and societal importance.

39   Composition changed significantly due to soak time, with total abundance and biodiversity

40   significantly higher in the second year of immersion, indicating community succession. These results

41   highlight the value of post-installation monitoring and the importance of accounting for the temporal

42   process of community development in restoration and conservation ecology where desired outcomes

43   include biodiversity, productivity, or establishment of specific species configurations.

44

45   **Keywords**

46   *Community development; ecological succession; biodiversity; species composition; artificial*

47   *structures; novel ecosystems*

48

49   **Implications**

50   • Improving biodiversity in highly modified, degraded systems such as commercial harbors

51   may be possible via local habitat enhancement, but the performance of artificial structures

52   depends on immersion duration and background levels of diversity and productivity.

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53   • Where artificial structures attract species in the regional pool that are otherwise locally

54   undetectable (i.e. absent in surveys of natural habitat), biodiversity estimates and

55   identification of invasive species may be of great value for guiding conservation, restoration,

56   and biological control.

57   • Post-installation monitoring data of artificial habitat initiatives in highly degraded systems

58   can reveal the point at which different ecological rehabilitation goals are achieved over time.

59

Introduction

61   Habitat loss and degradation threaten population persistence, biodiversity, and the functioning of

62   ecosystems (Ellison et al. 2005; Cardinale et al. 2012; Ellis et al. 2013). Ecosystem managers face the

63   challenge of implementing conservation and restoration initiatives in increasingly altered, highly

64   heterogenous, and rapidly transforming environments (Hobbs et al. 2014). Marine resource managers

65   are often charged with biodiversity conservation and ensuring the provision of ecosystem services,

66   such as food security, through sustainable fisheries, leisure and recreation, and regulation services

67   such as coastal protection from storms (Moberg & Folke 1999; Beaumont et al. 2007). However,

68   ecologically important coastal habitats are increasingly modified by urban and agricultural

69   development, the introduction of invasive species, and exacerbating impacts of climate change,

70   intensifying pressures on often overharvested communities (Beck et al. 2001; Hughes et al. 2003,

71   Thibaut et al. 2005; Townhill et al. 2017). As a result, managers must decide where and how

72   intervention in different situations will be beneficial based on the extent of ecological alteration,

73   intended management goals and likelihood of success (Hobbs & Norton 1996; Suding et al. 2004).

74   Often, restoring ecosystems to historical pre-disturbance states is not realistic (Palmer et al. 1997).

75   Nonetheless, managing whole ecosystems, including those areas in varying states of modification that

76   interact to different degrees to influence broader scale processes (such as animal migrations,

77   connectivity and nutrient flow), may increase the chances of achieving overarching management

78   objectives (Hobbs et al. 2014).

79

80   Decisions about how to conserve or restore particular areas will depend on their state of modification,

81   trajectory, interaction with other areas, their spatial scale, processes causing degradation, and the

82   intended intervention outcome (Hobbs & Norton 1996; Hobbs et al. 2014). In systems where it is

83   determined that ecosystem thresholds have been crossed as a result of human impacts and changes are

84   irreversible, such as on heavily modified coastlines within large infrastructures such as ports, harbors

85   and commercial marinas, options for their management as 'novel ecosystems' may be considered to

86   manipulate them to fulfil desired ecological conditions or functions (Hobbs et al. 2006; Hobbs et al.

87   2014; Ido & Shimrit 2015). The installation of artificial structures has been widely advocated and

88   implemented for replacement of lost or degraded natural habitat, ecological conservation, and

89   fisheries enhancement, by addressing a central issue of recruitment limitation (Grove et al. 1991; Bell

90   et al. 2006; Fabi et al. 2011). Indeed, extensive evidence demonstrates the efficacy of artificial

91   structures, from purpose-built nursery-habitat structures to large coastal defenses, in attracting

92   settlement-stage larval, juvenile, and adult marine organisms (Bouchoucha et al. 2016; Mercader et al.

93   2017a; Mercader et al. 2018; Higgins et al. 2019; Komyakova et al. 2019). So long as such structures

94   can enhance local production over and above merely attracting and concentrating fish and other

95   organisms at specific sites (Pickering & Whitmarsh 1997), they may enhance ecological conditions

96   and the functional capacity of highly modified and ecologically degraded 'novel' systems (Hobbs et

97   al. 2014; Ido & Shimrit 2015).

98

99   Specific goals of artificial habitats may include: enhancing local biodiversity for ecosystem resilience

100 (Folke et al. 2004) and social recreation (Baine 2001; Sutton & Bushnell 2007); providing ecological

101 stepping stones (i.e. facilitating species dispersal) for connectivity and ecological function (Thibaut et

102 al. 2005; Hobbs et al. 2014; Bouchoucha et al. 2016; Mercader et al. 2017a); and accumulation of fish

103 or invertebrates of commercial or social interest (Bell et al. 2006; Bell et al. 2009; Mercader et al.

104 2017b; Higgins et al. 2019). The extent and speed to which these goals are achieved will depend on

105 processes of community assembly and succession that are determined by the timing of species

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106   colonization and interactions among species (Wiggins et al. 1980; Palmer et al. 1997; Young et al.

107   2001). Communities develop and are structured over time, whereby pioneering species initially

108   colonize areas, with the abundance and composition of colonizing assemblages depending on

109   interacting factors including habitat size and connectivity, the proximity of source populations, local

110   hydrodynamics, inter-annual temporal variation in larval supply, and competitive interactions with

111   other species (Sale et al. 1984; Caffey 1985; Weiher & Keddy 2001; Young et al. 2001; Higgins et al.

112   2019). Multiple community states can develop over time, even among sites with similar

113   environmental conditions and where a broad pool of species has equal access to communities (Young

114   et al. 2001). As community heterogeneity increases, generally so too does biodiversity (MacArthur

115   1965; Palmer et al. 1997) and therefore the capacity for ecological connectivity (Palmer et al. 1997;

116   Suding et al. 2004). By increasing the availability of habitat resources, it is therefore anticipated that

117   artificial habitat restoration can facilitate or accelerate successional processes that foster the

118   establishment and maintenance of diverse communities (Palmer et al. 1997; Hauser et al. 2006;

119   Komyakova et al. 2019).

120

121   Evaluating the efficacy of artificial structures in attracting and maintaining diverse communities of

122   marine life in ecologically degraded commercial ports and marinas is key to assessing their role in

123   conservation and management of heterogenous, highly modified coastal ecosystems. In particular,

124   elucidating temporal patterns of community development in such environments may inform the use of

125   artificial substrates as potential tools for enhancing recruitment success, biological migration and

126   connectivity, and accelerating ecological recovery. In this study, we analyze existing monitoring data

127   of artificial habitat structures, using a subset of data from three spatially distinct commercial harbors

128   along the French Mediterranean coast where post-installation sampling replication allowed for

129   temporal comparison across years. By quantifying temporal variation in community development

130   from this monitoring data, we assess the performance of these artificial structures as effective habitats

131   for mobile marine invertebrates. Specifically, we compare the biodiversity, species composition and

132   abundance of predominant classes of invertebrates found during monitoring of artificial structures

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133   after initial immersion periods of either ca. 6 months or ca. 18 months. We hypothesize that the

134   species composition, abundance and taxonomic diversity of small-bodied mobile marine invertebrates

135   found within the structures would change through time. Our overarching goal was to compare patterns

136   in the development of invertebrate species assemblages in the artificial habitats and assess processes

137   of community development to inform the application of artificial substrates for ecological restoration.

138

Methods

Study sites

141   This study analyzed ecological monitoring data from three large commercial harbors in the Gulf of

142   Lion along the French Mediterranean coast, located in Le Barcarès, Port-Vendres, and Marseille, and

143   separated by distances of 29 to 204 km (Table 1). Monitoring data were available from artificial

144   structures installed within 21 marinas in 19 cities in France and Monaco between 2013 and 2017

145   (Table S5), however, a subset was selected to allow sufficient replication of structures installed in the

146   harbors across comparable years: Le Barcarès (42.7877° N, 3.0366° E), Port-Vendres (42.5185° N,

147   3.1066° E), and Grand Port Maritime de Marseille (43.3051° N, 5.3652° E). Each of these three

148   harbors have >200 vessel moorings and have been operating commercially for >40 years, although the

149   physical and environmental characteristics of each harbor vary across a range of parameters (Table 1).

150

Sampling unit and protocol

152   Temporal variation in the species composition of mobile invertebrate assemblages was assessed using

153   data from monitoring surveys of artificial vertical structures (Dock Biohut®; Ecocean SAS,

154   Montpellier) within each harbor, sampled either within the first or second year since installation.

155   Biohuts were composed of two adjoined carbon-steel alloy cages (50 x 80 x 12.5 cm; combined cage

156   depth 25 cm), connected vertically and attached to the dockside. One cage was filled with empty

157   oyster shells to provide substrate complexity and was positioned against the dock (2.5 cm mesh-size);

158   the outward-facing adjoining cage was left empty (5 cm mesh size) (Fig. 1). In March and June 2013,

159   the 13–19 sampled Biohuts were installed in each harbor, submerged just below the surface of the

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160 water and separated by at least 20 m. Invertebrate assemblage composition was assessed during

161 monitoring on 9–12 randomly selected Biohuts 5.5–7 months after installation (Year 1), and the

162 remaining Biohuts were monitored after 17.5–19.5 months (Year 2; Table 1). During monitoring, the

163 Biohuts were encased with a PVC net (2 mm mesh) by divers to prevent loss of organisms during

164 removal, and lifted from the water onto the adjoining dock. Biohuts were then disassembled and all

165 mobile invertebrates were counted, identified to species level where possible, and the maximum

166 diameter measured (to the nearest mm).

167

168 *Data analysis*

169 Variation in the composition of surveyed invertebrate assemblages (total abundance, species richness,

170 Shannon diversity, Pielou's evenness, abundance of abundant classes and exploitable species

171 contributing to >5% of total abundance) was assessed through time with linear mixed effects models,

172 using time period (factor: years one and two) as a fixed effect, and harbor as a random effect (Le

173 Barcarès, Port-Vendres, Marseille; in *R*; R Core Team 2017). Mixed-effects models that estimate

174 parameters based on residual maximum likelihood were used due to their capacity to more

175 appropriately handle unbalanced designs (particularly with random effects) than alternative

176 approaches using observed and expected mean squares or error strata (Logan 2010). Count data

177 models of total abundance, the abundance of dominant classes of invertebrates (Bivalvia, Gastropoda,

178 Malacostraca, Ophiuroidea), and potentially exploited species (palaemonid shrimp, *Palaemon* spp.;

179 variegated scallop, *Mimachlamys varia*; FAO 2018) were fitted using negative binomial distributions

180 to accommodate alternative exponential distributions of residuals (with glmer.nb in *lme4*). Temporal

181 variation in species richness was modelled with a Poisson distribution due to exponential variance but

182 within the assumed bounds of dispersion (glmer in *lme4*). Temporal variation in Shannon diversity

183 and Pielou's evenness was assessed with Gaussian models and a constant variance structure due to

184 heteroscedasticity between time periods. Model assumptions were assessed visually using diagnostic

185 plots of Pearson residuals.

186

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187   Variation in the taxonomic composition of invertebrate assemblages through time was visualized with

188   non-metric multidimensional scaling (nMDS) based on a Bray-Curtis dissimilarity matrix of log (x+1)

189   transformed data. Clustering of surveyed Biohuts by year of sampling was then tested using a two-

190   way nested PERMANOVA (maximum permutations = 9999), with time period (fixed) and harbor

191   (random) as factors, and Monte Carlo sampling to estimate differences due to limited available unique

192   permutations (360) and unconverged permutation versus Monte Carlo P-values (Anderson et al.

193   2008). This was supported by percentage similarity analysis (SIMPER) on log (x+1) transformed data

194   to quantify mean similarity within or dissimilarity between harbors across time periods, and to

195   identify those species contributing consistently to similarity or dissimilarity (similarity or

196   dissimilarity/standard deviation ≥ 2). Multivariate analyses were performed in Primer v6 with

197   PERMANOVA+ (Clarke & Warwick 2001; Anderson et al. 2008).

198

199   **Results**

200   A total of 48 mobile invertebrate species, from 39 families, eight classes, and five phyla were

201   recorded in Biohut structures across both survey years (Table S1, S2). The maximum size of surveyed

202   species ranged from 0.3 to 14.0 cm diameter (mean ± SE: 2.2 ± 0.1 cm). All species were classified as

203   native to the Mediterranean (Palomares & Pauly 2010). Analyzing variation in the composition of

204   invertebrate assemblages in Biohuts across Year 1 to Year 2 revealed significant increases in total

205   abundance (z (1,42) = 2.36, p = 0.02), species richness (z (1,42) = 2.28, p = 0.02), and Pielou's

206   evenness (z (1,42) = 2.07, p = 0.04), but not Shannon diversity (Fig. 2; Table S3 and S4).

207

208   The taxonomic composition of invertebrate assemblages varied from Year 1 to Year 2

209   (PERMANOVA, Pseudo-f = 3.57, df = 1,40, p (MC) = 0.02, unique permutations = 360; Fig. 3).

210   Changes in assemblage composition caused an increase in taxonomic similarity of assemblages

211   (average assemblage similarity: Year 1, 28%; Year 2, 37%), with an average 78% dissimilarity in

212   species composition between years. In Year 1, only the variegated scallop *Mimachlamys varia*

213   contributed consistently to assemblage similarity among Biohuts in Port-Vendres. However, in Year

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214 2, 6 species consistently characterized species assemblages in Le Barcarès and 8 species in Port-

215 Vendres (Table 2). In Marseille, no species consistently contributed to assemblage similarity in either

216 year.

217

218 There was an overall increase in abundance of Malacostraca (z (1,42) = 4.50, p < 0.0001), but not

219 Bivalvia, Gastropoda, or Ophiuroidea (Fig. 4; Table S3 and S4). Of 11 surveyed species identified as

220 potentially exploited (FAO 2018), only two contributed to >5% of the total invertebrate abundance—

221 *Palaemon* spp (palaemonid shrimp) and *M. varia*—but neither varied in abundance significantly

222 across years (Table S5). The remaining nine species (*Carcinus* crab spp; common cockle

223 *Cerastoderma edule*; black squat lobster *Galathea squamifera*; small periwinkle *Melarhaphe*

224 *neritoides*; European flat oyster *Ostrea edulis*; purple sea urchin *Paracentrotus lividus*; *Periclimenes*

225 shrimp spp; bristle worm *Polychaeta* spp; common cuttlefish *Sepia officinalis*) each accounted for

226 <2% of the total surveyed invertebrate abundance (Table S6).

227

Discussion

229 Artificial structures may enhance the ecological capacity of highly modified areas of coastline such as

230 large commercial ports and marinas by providing habitats for marine life at different stages of life-

231 history and migration (Hobbs et al. 2014; Ido & Shimrit 2015; Bouchoucha et al. 2016; Mercader et

232 al. 2017b). Examination of post-installation monitoring data found that artificial habitats (Dock

233 Biohuts®) attracted and maintained taxonomically diverse assemblages of mobile invertebrate

234 species, including molluscs, crustaceans, and echinoids of ecological, commercial, and social interest,

235 in addition to the fish species previously shown to associate with these structures (Bouchoucha et al.

236 2016; Mercader et al. 2017a). However, our results show that the abundance, composition, and

237 diversity of invertebrate assemblages in these structures varied significantly with the duration of

238 habitat immersion, such that accounting for community development in restoration or conservation

239 ecology would likely be time-dependent in achieving desired endpoints of biodiversity, productivity,

240 and species-specific configurations (Palmer et al. 1997; Suding et al. 2004). Our analyses reveal an

241 increase over ca. 12 months in the similarity in composition both within and among assemblages in

242 two of the three spatially distinct harbors, and an overall increase in abundance of crustaceans—a

243 group of ecologically important organisms due to their role in food-web dynamics (Szaniawska 2018)

244 and their influence on the behavior of settlement-stage larval organisms (Simpson et al. 2005;

245 Montgomery et al. 2006; Stanley et al. 2010; Lillis et al. 2013; Parmentier et al. 2015).

246

247 Sampling revealed taxonomically diverse assemblages of small-bodied mobile invertebrates in the

248 structures after ca. 6–18 months of immersion, indicating the capacity of artificial habitats to support

249 local biodiversity enhancement via the recruitment of organisms in highly modified harbors. Indeed,

250 114 species of mobile invertebrates have been recorded in Biohut structures installed across 21

251 harbors in France and Monaco between 2013 and 2017. Biodiversity conservation and restoration are

252 widely supported management goals (Palmer et al. 1997; Brooks et al. 2006), with species diversity

253 considered important for promoting ecosystem resilience via the maintenance of critical ecosystem

254 functioning during disturbance (due to functional redundancy and response diversity; Walker 1992;

255 Elmqvist et al. 2003). Increasingly, efforts to restore or replace nursery habitats is viewed as a key

256 component of the conservation of biodiversity and management of productive systems (Hobbs &

257 Norton 1996; Beck et al. 2001). Artificial structures such as breakwaters and jetties are known to

258 augment the availability of crevices and holes providing organisms with refuge from environmental

259 stressors and predation (Guidetti 2004; Clynick 2006; Mercader et al. 2018). In particular, the

260 availability of fine-scale structural complexity, such as is created by caged oyster shells in the focal

261 Biohut structures, can provide refugia and enhance the survival of small-bodied and/or juvenile stage

262 organisms when their risk of mortality is highest (Bouchoucha et al. 2016; Goatley & Bellwood

263 2016). Indeed, the colonization, abundance and species diversity of macroinvertebrate fauna can be

264 directly associated with availability and structural characteristics of habitats such as macroalgal-

265 dominated beds and rocky intertidal areas (García-Sanz et al. 2012), seagrass beds (Heck & Orth

266 1980; Attrill et al. 2000), coral reefs (Fabricius et al. 2014), lowland streams (O'Connor 1991; Warfe

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267 & Barmuta 2006), as well as artificial habitats (Hauser et al. 2006). The nursery capacity of artificial

268 structures in large commercial ports has previously been shown for diverse assemblages of juvenile

269 finfishes including species of Atherinopsidae, Blennidae, Gobiidea, Labridae, Mugilidae, Mullidae,

270 Serranidae, Sparidae, and Tripterygiidae, with typically higher abundance and species richness on

271 artificial habitat structures than on adjacent bare surfaces (Bouchoucha et al. 2016; Mercader et al.

272 2017a, b). Our findings, demonstrating that Biohuts promote post-larval settlement and grow-out of a

273 diverse range of invertebrates, provide supporting evidence that habitat enrichment in highly modified

274 systems may enhance the ecological function of such areas, despite severe ecological degradation.

275

276 Significant variation in composition between the invertebrate assemblages sampled ca. 6 months and

277 ca. 18 months after deployment of the Dock Biohuts highlights community development and

278 underscores the influence of habitat duration in influencing the outcome of artificial habitat

279 installation initiatives (Palmer et al. 1997; Young et al. 2001; Komyakova et al. 2019). Our results

280 revealed significantly greater total abundance, species richness, species evenness, and a significant

281 increase in abundance of crustaceans in artificial structures across the three spatially distinct harbors

282 after a longer period of immersion. Time is an established and important predictor of community

283 composition due to processes of faunal succession (Wiggins et al. 1980; Wiens 1984; Schneider &

284 Frost 1996; Young et al. 2001). Indeed, our results provide evidence of community turnover through

285 time, likely due to spatially and temporally variable colonization by different species (Wiens 1984;

286 Young et al. 2001). Species composition was highly variable in the first year across all harbors.

287 However, we observed an increase in similarity of invertebrate assemblage structure within and

288 between Port-Vendres and Le Barcarès after just ca. 18 months, with composition in the second year

289 more consistently characterized by species of mollusc, crustacean and echinoderm. The results

290 suggest that so long as artificial habitats do not simply concentrate organisms (Pickering &

291 Whitmarsh 1997), they may enhance local productivity and biodiversity in highly modified areas

292 within relatively short periods of time. Similarly, the observed assemblage turnover highlights that

293 where specific species configurations are desired endpoints for habitat restoration, understanding how

294   local communities are structured over time will likely enable pragmatic management goal setting

295   (Palmer et al. 1997; Young et al. 2001).

296

297   We observed an overall increase in abundance of Malacostraca, while abundance of other

298   predominant classes (gastropods, bivalves, and brittle-stars) remained consistent, carrying

299   implications for efforts targeting ecological restoration (Palmer et al. 1997; Parmentier et al. 2015;

300   Szaniawska 2018). Crustaceans are key components of the diets of a range of finfish and other

301   macroinvertebrates (Szaniawska 2018), such that an increase in their abundance may have

302   implications for local food-web dynamics (Leitão et al. 2007). Similarly, crustaceans can create a loud

303   and acoustically complex biophony, producing acoustic cues used by settlement-stage larvae of fish

304   and invertebrates that likely further enhances community development (Simpson et al. 2004, 2005;

305   Montgomery et al. 2006; Stanley et al. 2010; Lillis et al. 2013; Parmentier et al. 2015). For example,

306   the estimated detection distance of snaps of the shrimp, *Athanas nitescens*, characteristic of Biohut

307   invertebrate assemblages in Le Barcarès and Port-Vendres by Year 2, can be up to 40 m (Coquereau

308   et al. 2016). As such, shifts towards greater abundance of crustaceans may have a disproportionate

309   role in the maintenance, development, and function of locally diverse ecological communities (Palmer

310   et al. 1997; Szaniawska 2018), and may point towards opportunities for passive acoustic monitoring

311   of community development where intrusive survey techniques are less desirable (Nedelec et al. 2015;

312   Coquereau et al. 2016; Gervaise et al. 2019). Many species of crustaceans are also highly valued

313   commercial and recreational fisheries resources (FAO 2018). Where artificial structures can enhance

314   rather than relocate local productivity, they may provide opportunities for harvesting species in

315   support of fisheries enhancement initiatives (Bell et al. 2005; Bell et al. 2006), for the live-trade of

316   ornamental organisms (Bell et al. 2009), or for aquaculture (Hair et al. 2002).

317

318   As mounting human impacts push coastal ecosystems to a variety of highly modified, novel

319   ecological states, the use of artificial habitat structures may serve to increase ecological thresholds and

320   ecosystem function (Hobbs et al. 2006; Hobbs et al. 2014). Similarly, where artificial structures can

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321   attract and accumulate species in the regional pool that are present but otherwise locally undetectable

322   (i.e. absent in estimates of natural habitat-specific species pools), they may serve to refine biodiversity

323   estimates for guiding conservation and restoration (Lewis et al. 2017; Moeslund et al. 2017).

324   Investigating existing ecological monitoring data, our results provide insights into the short-term

325   capacity of artificial structures to attract and maintain diverse assemblages of invertebrates, and the

326   role of habitat duration in community development and the establishment of biodiversity and

327   productivity in highly modified commercial harbors. That artificial structures can host diverse and

328   abundant assemblages of molluscs, crustaceans and echinoderms in large and commercially active

329   harbors, provides promise for their capacity in ecological enhancement. However, we note that where

330   post-installation monitoring practices allow, assessing changes in community structure in additional

331   locations and with additional temporal replication would add greater generality to these findings.

332   Furthermore, longer temporal studies comparing the performance of artificial habitats against

333   background levels of diversity and productivity would enable greater understanding of their capacity

334   to augment the ecological function of modified systems (Pickering & Whitmarsh 1997). This includes

335   improving our understanding of their role as ecological stepping stones for enhanced connectivity,

336   and the ecological processes determining positive feedbacks and alternative states across degraded

337   systems (Folke et al. 2004; Suding et al. 2004). Finally, given the ecological importance of

338   invertebrates in trophic dynamics and community development (Lillis et al. 2013; Szaniawska 2018),

339   experimental research considering the influence of variation in invertebrate assemblage composition

340   on the recruitment of teleost fishes may aid understanding of the capacity for complementary acoustic

341   ecological enhancement programs (Mukhin et al. 2008; Parmentier et al. 2015; Moeslund et al. 2017).

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Running head: Duration determines artificial habitat performance

1   **Figures and Tables**

2   **Table 1** Characteristics of the three study sites (harbors) and Dock Biohut sampling.

Harbor	Coast type	Distance to Rhone river mouth (km)	Connection(s)	Harbor construction date	Harbor surface area (ha)	Harbor maximum depth (m)	Mean ± SE distance from Biohuts to sea (m)	Mean ± SE depth under Biohuts (m)	Biohut 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	01 Mar 2013	30 Sept – 01 Oct 2013 (*n*=9)	15 Oct 2014 (*n*=4)
Port-Vendres	Rocky	167 (west)	Sea	1953	33	10.0	816 ± 133	5.67 ± 1.33	01 Mar 2013	01 – 02 Oct 2013 (*n*=9)	07 Oct 2014 (*n*=5)
Grand Port maritime de Marseille	Rocky	42 (east)	Sea	1840	400	14.5	2126 ± 152	8.25 ± 1.84	01 June 2013	14 Nov 2013 (*n*=12)	26 – 27 Nov 2014 (*n*=7)

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Running head: Duration determines artificial habitat performance

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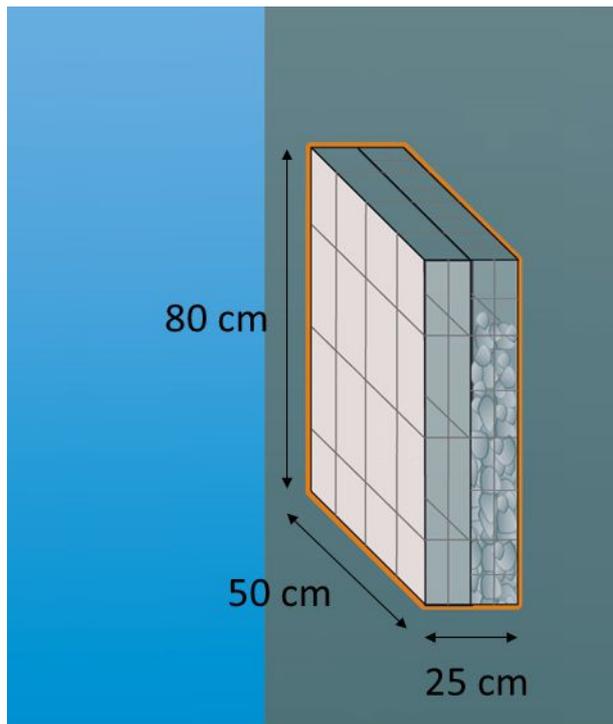2 **Figure 1** Dimensions of Dock Biohut structures, composed of two carbon-steel alloy cages: inner-cage

3 filled with oyster shells (2.5 cm mesh), and empty outer-cage (5 cm mesh).

4

5
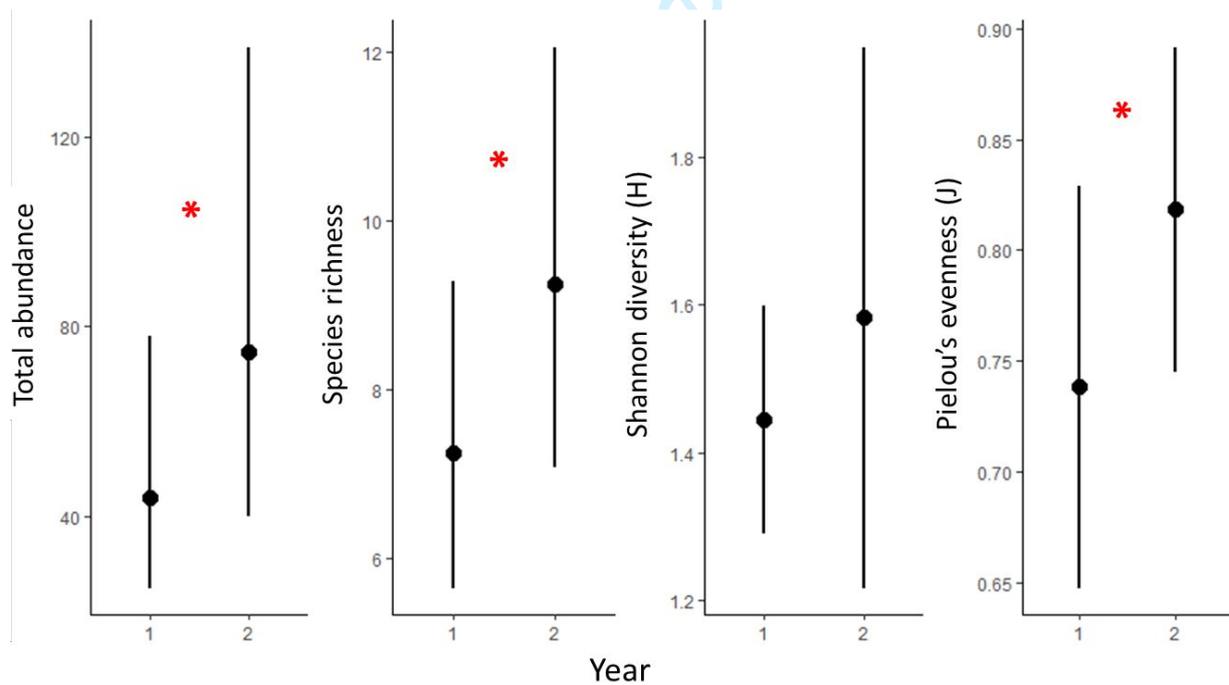
6 **Figure 2** Temporal variation (fitted values ±95% confidence intervals) in the total abundance, species

7 richness, Shannon diversity, and Pielou's evenness of mobile invertebrate assemblages in artificial

23

1   Dock Biohut structures within Year 1 and Year 2 since installation. Significant differences between

2   time periods of each metric indicated with asterisks (red * indicates $p \leq 0.05$).

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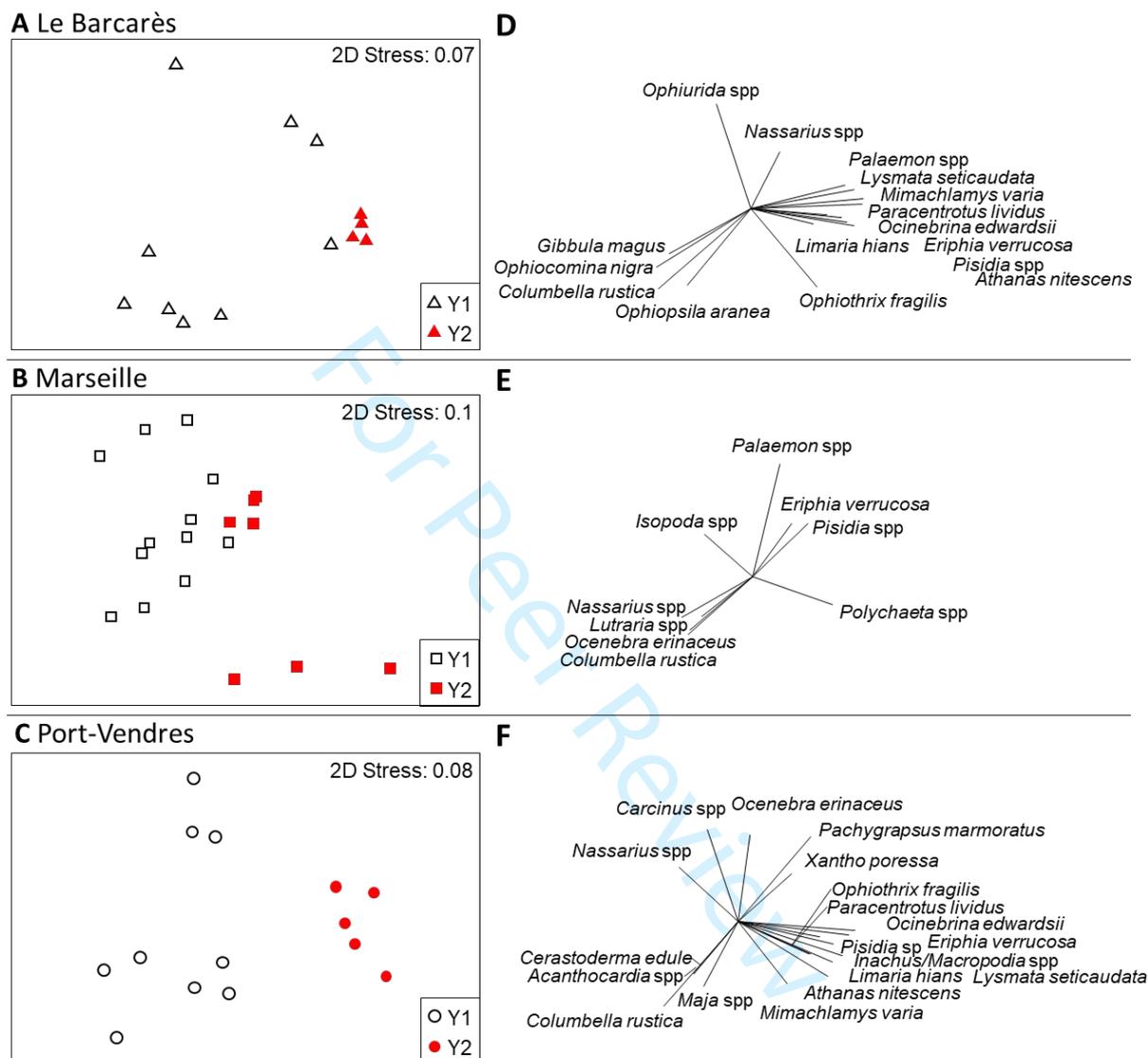
5   **Figure 3** Non-metric multidimensional scaling analysis showing: Variation in taxonomic composition

6   of mobile invertebrate assemblages among surveyed Dock Biohut structures in each harbor between

7   years (Y1 and Y2) since installation (A–C) (log x+1 transformed data); and the relative contribution of

8   species to variation at each harbor (D–F; >0.5 Pearson correlation).

9

10

1 **Table 2** Percentage similarity analysis of mobile invertebrate assemblages in surveyed Dock Biohuts

2 through time. Species consistently contributing to the average similarity within (sim/SD >2; grey shaded

3 boxes), and dissimilarity between (unshaded boxes; diss/SD >2) harbors from Year 1 (Y1) to Year 2

4 (Y2) identified in one-way SIMPER analysis are shown.

	Le Barcarès	Port-Vendres	Marseille
Le Barcarès	<u>Av. sim</u>: **Y1**: 28%; no consistent spp **Y2**: 72%; *Ophiothrix fragilis, Palaemon* spp, *Pisidia* spp, *Mimachlamys varia, Athanas nitescens, Paracentrotus lividus, Lysmata seticaudata, Eriphia verrucosa* <u>Av. dissim. (Y1 to Y2)</u>: 75%; *Pisidia* spp, *Athanas nitescens, Lysmata seticaudata, Eriphia verrucosa*	<u>Av. disssim</u>: **Y1**: 77%; no consistent spp **Y2** 50%; *Ophiothrix fragilis, Ocinebrina edwardsii, Pisidia* spp, *Pachygrapsus marmoratus, Lysmata seticaudata, Eriphia verrucosa*	<u>Av. disssim</u>: **Y1**: 82%; no consistent spp **Y2**: 69%; *Ophiothrix fragilis, Paracentrotus lividus, Lysmata seticaudata, Eriphia verrucosa*
Port-Vendres		<u>Av. sim</u>: **Y1**: 47%; *Mimachlamys varia* **Y2**: 70%; *Ocinebrina edwardsi, Lysmata seticaudata, Mimachlamys varia, Eriphia verrucosa, Athanas nitescens, Pachygrapsus marmoratus* <u>Av. dissim. (Y1 to Y2)</u>: 69%; *Ocinebrina edwardsii, Lysmata seticaudata, Eriphia_verrucosa*	<u>Av. disssim.</u>: **Y1**: 71%; no consistent spp **Y2**: 76%; *Ocinebrina edwardsii, Lysmata seticaudata*
Marseille			<u>Av. sim</u>: **Y1**: 39%; no consistent spp **Y2**: 31%; no consistent spp <u>Av. dissim. (Y1 to Y2)</u>: 75%; no consistent spp

5

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Running head: Duration determines artificial habitat performance

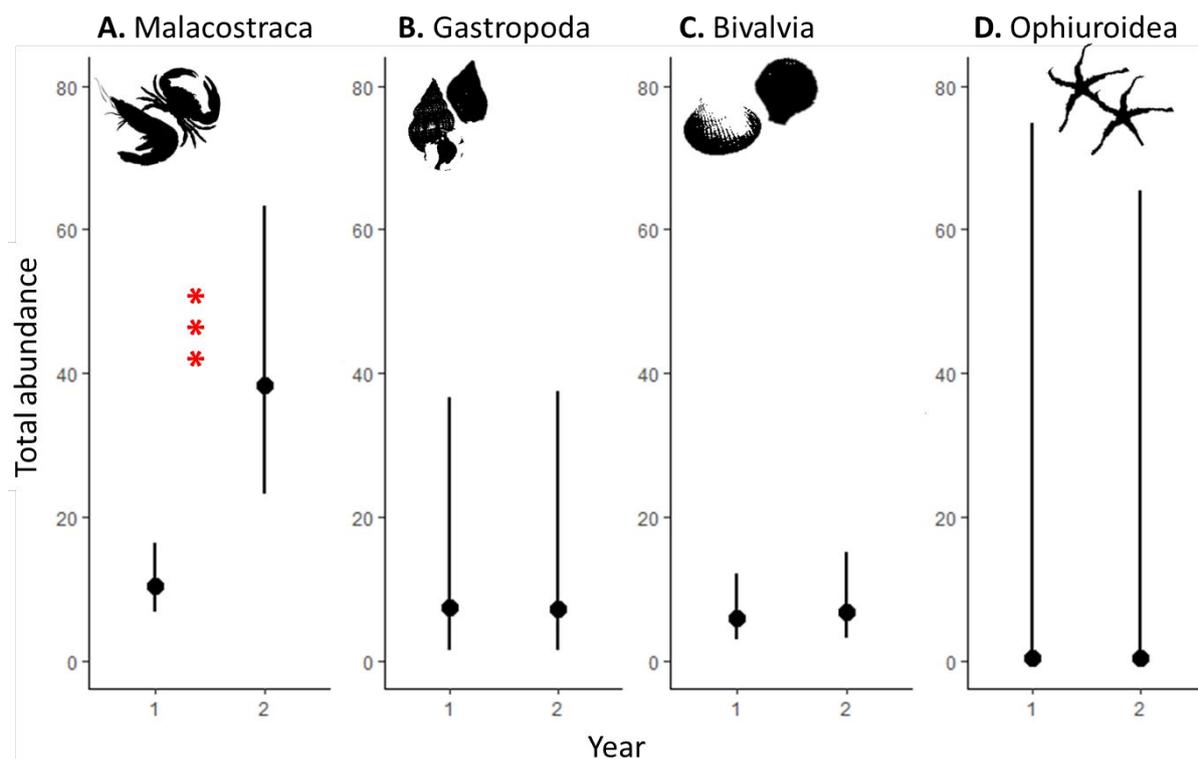**Figure 4** Temporal variation (fitted values ±95% confidence intervals) in the total abundance of Malacostraca (A), Gastropoda (B), Bivalvia (C), and Ophiuroidea (D) in surveyed Dock Biohut structures within Year 1 and Year 2 since installation. Significant differences between time periods indicated with asterisks (red *** $p < 0.001$).

Composition of mobile invertebrate assemblages in artificial habitats determined by duration of immersion in commercial harbors

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Supplementary material

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.

Phylum	Class	Family	Species	Location(s) recorded
Annelida	Polychaeta	-	*Polychaeta* spp	BA, MA
Arthropoda	Malacostraca	Alpheidae	*Athanas nitescens*	BA, MA, PV
Arthropoda	Malacostraca	Carcinidae	*Carcinus* spp	BA, PV
Arthropoda	Malacostraca	Galatheidae	*Galathea squamifera*	MA
Arthropoda	Malacostraca	Grapsidae	*Pachygrapsus marmoratus*	MA, PV
Arthropoda	Malacostraca	Hippolytidae	*Lysmata seticaudata*	BA, MA, PV
Arthropoda	Malacostraca	Inachidae	*Inachus/Macropodia* spp	BA, MA, PV
Arthropoda	Malacostraca	-	*Isopoda* spp	BA, MA, PV
Arthropoda	Malacostraca	Majidae	*Maja crispata*	BA
Arthropoda	Malacostraca	Majidae	*Maja* spp	MA, PV
Arthropoda	Malacostraca	Eriphiidae	*Eriphia verrucosa*	BA, MA, PV
Arthropoda	Malacostraca	Palaemonidae	*Palaemon* spp	BA, MA, PV
Arthropoda	Malacostraca	Palaemonidae	*Periclimenes* spp	MA
Arthropoda	Malacostraca	Porcellanidae	*Pisidia* spp	BA, MA, PV
Arthropoda	Malacostraca	Xanthidae	*Xantho poressa*	BA, PV
Echinodermata	Echinoidea	Echinidae	*Paracentrotus lividus*	BA, PV
Echinodermata	Ophiuroidea	Amphiuridae	*Amphipholis squamata*	BA
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiocomina nigra*	BA
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiopsila aranea*	BA
Echinodermata	Ophiuroidea	Ophiodermatidae	*Ophioderma longicauda*	BA
Echinodermata	Ophiuroidea	Ophiothricidae	*Ophiothrix fragilis*	BA, PV
Echinodermata	Ophiuroidea	-	*Ophiurida* spp	BA, PV
Mollusca	Bivalvia	Anomiidae	*Anomia ephippium*	MA, PV
Mollusca	Bivalvia	Cardiidae	*Acanthocardia* spp	PV
Mollusca	Bivalvia	Cardiidae	*Cerastoderma edule*	BA, MA, PV

Mollusca	Bivalvia	Limidae	*Limaria hians*	BA, MA, PV
Mollusca	Bivalvia	Mactridae	*Lutraria* spp	BA, MA, PV
Mollusca	Bivalvia	Mytilidae	*Modiolarca subpicta*	BA
Mollusca	Bivalvia	Ostreidae	*Ostrea edulis*	MA
Mollusca	Bivalvia	Pectinidae	*Lissopecten hyalinus*	BA
Mollusca	Bivalvia	Pectinidae	*Mimachlamys varia*	BA, MA, PV
Mollusca	Cephalopoda	Sepiidae	*Sepia officinalis*	PV
Mollusca	Gastropoda	Calliostomatidae	*Calliostoma zizyphinum*	PV
Mollusca	Gastropoda	Cerithiidae	*Bittium reticulatum*	BA, PV
Mollusca	Gastropoda	Columbellidae	*Columbella rustica*	BA, MA, PV
Mollusca	Gastropoda	Facelinidae	*Cratena peregrina*	BA
Mollusca	Gastropoda	Fissurellidae	*Diodora graeca*	PV
Mollusca	Gastropoda	Littorinidae	*Melarhaphe neritoides*	MA
Mollusca	Gastropoda	Muricidae	*Hexaplex trunculus*	BA
Mollusca	Gastropoda	Muricidae	*Ocenebra erinaceus*	BA, MA, PV
Mollusca	Gastropoda	Muricidae	*Ocinebrina edwardsii*	BA, PV
Mollusca	Gastropoda	Muricidae	*Thophonopsis muricatus*	PV
Mollusca	Gastropoda	Nassariidae	*Nassarius incrassatus*	BA, MA, PV
Mollusca	Gastropoda	Nassariidae	*Nassarius* spp	BA, MA, PV
Mollusca	Gastropoda	Plyceridae	*Polycera quadrilineata*	BA
Mollusca	Gastropoda	Trochidae	*Gibbula magus*	BA, PV
Platyhelminthes	Turbellaria	Discocelidae	*Discocelis tigrina*	MA, PV
Platyhelminthes	Turbellaria	Euryleptidae	*Pseudoceros maximus*	MA

Table S2 Mobile invertebrate species surveyed between 2013 and 2017 in artificial structures (Dock Biohut: D; Pontoon Biohut, P) installed within 21 harbors, in 19 cities in France and Monaco during monitoring (total = 115 spp) (www.ecocean.fr).

Phylum	Class	Family	Species	Biohut type
Annelida	Echiura	Bonelliidae	*Bonellia viridis*	D, P
Annelida	Polychaeta	Arenicolidae	*Arenicola* spp	P
Annelida	Polychaeta	Eunicidae	*Leodice harassii*	P
Annelida	Polychaeta	Eunicidae	*Leodice torquata*	P
Annelida	Polychaeta	Hesionidae	*Hesione pantherina*	D, P
Annelida	Polychaeta	Nereidae	*Nereis* spp	P
Annelida	Polychaeta	-	*Polychaeta* spp	D, P
Arthropoda	Malacostraca	Alpheidae	*Alpheus macrocheles*	D, P
Arthropoda	Malacostraca	Alpheidae	*Athanas nitescens*	D, P
Arthropoda	Malacostraca	-	*Brachyura* spp	P
Arthropoda	Malacostraca	Carcinidae	*Carcinus aestuarii*	D, P
Arthropoda	Malacostraca	Carcinidae	*Carcinus* spp	D, P
Arthropoda	Malacostraca	Dromiidae	*Dromia personata*	D, P
Arthropoda	Malacostraca	Galatheidae	*Galathea* spp	P
Arthropoda	Malacostraca	Galatheidae	*Galathea squamifera*	D
Arthropoda	Malacostraca	Gammaridae	*Gammarus* spp	P
Arthropoda	Malacostraca	Grapsidae	*Pachygrapsus marmoratus*	D, P
Arthropoda	Malacostraca	Hippolytidae	*Hippolyte* spp	P

Arthropoda	Malacostraca	Hippolytidae	*Lysmata seticaudata*	D, P
Arthropoda	Malacostraca	Inachidae	*Inachus/Macropodia spp*	D, P
Arthropoda	Malacostraca	-	*Isopoda spp*	D, P
Arthropoda	Malacostraca	Leucosiidae	*Ebalia spp*	D
Arthropoda	Malacostraca	Majidae	*Macropodia spp*	P
Arthropoda	Malacostraca	Majidae	*Maja crispata*	D
Arthropoda	Malacostraca	Majidae	*Maja spp*	D, P
Arthropoda	Malacostraca	-	*Malacostraca spp*	P
Arthropoda	Malacostraca	Eriphiidae	*Eriphia verrucosa*	D, P
Arthropoda	Malacostraca	Mysidacea	*Mysidacea spp*	P
Arthropoda	Malacostraca	Paguridae	*Pagurus anachoretus*	D
Arthropoda	Malacostraca	Palaemonidae	*Palaemon spp*	D, P
Arthropoda	Malacostraca	Palaemonidae	*Periclimenes spp*	D
Arthropoda	Malacostraca	Polybiidae	*Liocarcinus spp*	D
Arthropoda	Malacostraca	Porcellanidae	*Pisidia longicornis*	P
Arthropoda	Malacostraca	Porcellanidae	*Pisidia longimana*	P
Arthropoda	Malacostraca	Porcellanidae	*Pisidia spp*	D, P
Arthropoda	Malacostraca	Porcellanidae	*Porcellana platycheles*	P
Arthropoda	Malacostraca	Processidae	*Processa spp*	D, P
Arthropoda	Malacostraca	Sphaeromatidae	*Sphaeromatidae spp*	P
Arthropoda	Malacostraca	Xanthidae	*Xantho poressa*	D
Echinodermata	Asteroidea	Asteriidae	*Marthasterias glacialis*	D
Echinodermata	Asteroidea	Asterinidae	*Asterina gibbosa*	D, P
Echinodermata	Asteroidea	Astropectinidae	*Astropecten irregularis*	D
Echinodermata	Crinoidea	Antedonidae	*Antedon spp*	P
Echinodermata	Echinoidea	Echinidae	*Gracilechinus acutus*	P
Echinodermata	Echinoidea	Echinidae	*Paracentrotus lividus*	D, P
Echinodermata	Holothuroidea	Holothuroiidea	*Holothuria forskali*	P
Echinodermata	Holothuroidea	Holothuroiidea	*Holothuria spp*	D, P
Echinodermata	Ophiuroidea	Amphiuridae	*Amphipholis squamata*	D, P
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiocomina nigra*	D
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiopsila aranea*	D, P
Echinodermata	Ophiuroidea	Ophiodermatidae	*Ophioderma longicauda*	D, P
Echinodermata	Ophiuroidea	Ophiothricidae	*Ophiothrix fragilis*	D, P
Echinodermata	Ophiuroidea	-	*Ophiurida spp*	D
Mollusca	Bivalvia	Anomiidae	*Anomia ephippium*	D, P
Mollusca	Bivalvia	Arcidae	*Arca noae*	D, P
Mollusca	Bivalvia	-	*Bivalvia spp*	P
Mollusca	Bivalvia	Cardiidae	*Acanthocardia spp*	D, P
Mollusca	Bivalvia	Cardiidae	*Cerastoderma edule*	D, P
Mollusca	Bivalvia	Cardiidae	*Cerastoderma glaucum*	P
Mollusca	Bivalvia	Cardiidae	*Parvicardium scriptum*	D, P
Mollusca	Bivalvia	Donacidae	*Donax spp*	D, P
Mollusca	Bivalvia	Limidae	*Lima lima*	P
Mollusca	Bivalvia	Limidae	*Limaria hians*	D, P
Mollusca	Bivalvia	Mactridae	*Lutraria spp*	D, P
Mollusca	Bivalvia	Mytilidae	*Modiolarca subpicta*	D, P

Mollusca	Bivalvia	Ostreidae	*Ostrea edulis*	D, P
Mollusca	Bivalvia	Ostreidae	*Ostreidae* spp	P
Mollusca	Bivalvia	Pectinidae	*Lissopecten hyalinus*	D
Mollusca	Bivalvia	Pectinidae	*Mimachlamys varia*	D, P
Mollusca	Bivalvia	Thraciidae	*Thracia* spp	P
Mollusca	Bivalvia	Veneridae	*Chamalea gallina*	P
Mollusca	Bivalvia	Verenidae	*Callista chione*	P
Mollusca	Cephalopoda	Sepiidae	*Sepia officinalis*	D
Mollusca	Gastropoda	Buccinidae	*Buccinum humphreysianum*	D
Mollusca	Gastropoda	Calliostomatidae	*Calliostoma zizyphinum*	D, P
Mollusca	Gastropoda	Cerithiidae	*Bittium reticulatum*	D, P
Mollusca	Gastropoda	Cerithiidae	*Cerithium vulgatum*	D
Mollusca	Gastropoda	Columbellidae	*Columbella rustica*	D, P
Mollusca	Gastropoda	Dorididae	*Doris verrucosa*	D
Mollusca	Gastropoda	Epitonidae	*Epitonium clathrus*	P
Mollusca	Gastropoda	Facelinidae	*Cratena peregrina*	D, P
Mollusca	Gastropoda	Fissurellidae	*Diodora graeca*	D
Mollusca	Gastropoda	Flabellinidae	*Flabellina* spp	P
Mollusca	Gastropoda	-	*Gastropoda* spp	D
Mollusca	Gastropoda	Goniodorididae	*Goniodoris castanea*	P
Mollusca	Gastropoda	Haliotidae	*Haliotis tuberculata*	D
Mollusca	Gastropoda	Haminoeidae	*Haminoea* spp	D
Mollusca	Gastropoda	Hydrobiidae	*Peringia ulvae*	P
Mollusca	Gastropoda	Littorinidae	*Melarhaphe neritoides*	D
Mollusca	Gastropoda	Muricidae	*Bolinus brandaris*	D
Mollusca	Gastropoda	Muricidae	*Hexaplex trunculus*	D
Mollusca	Gastropoda	Muricidae	*Ocenebra erinaceus*	D
Mollusca	Gastropoda	Muricidae	*Ocinebrina edwardsii*	D, P
Mollusca	Gastropoda	Muricidae	*Thophonopsis muricatus*	D, P
Mollusca	Gastropoda	Nassariidae	*Nassarius corniculum*	D, P
Mollusca	Gastropoda	Nassariidae	*Nassarius incrassatus*	D, P
Mollusca	Gastropoda	Nassariidae	*Nassarius* spp	D, P
Mollusca	Gastropoda	Nassariidae	*Tritia* spp	D, P
Mollusca	Gastropoda	Naticidae	*Euspira* spp	D
Mollusca	Gastropoda	Patellidae	*Patella* spp	D, P
Mollusca	Gastropoda	Plyceridae	*Polycera hedgpethi*	D, P
Mollusca	Gastropoda	Plyceridae	*Polycera quadrilineata*	D, P
Mollusca	Gastropoda	Trochidae	*Gibbula magus*	D, P
Mollusca	Gastropoda	Trochidae	*Gibbula umbilicalis*	D, P
Mollusca	Gastropoda	Trochidae	*Jujubinus gravinae*	D
Mollusca	Gastropoda	Trochidae	*Jujubinus striatus*	D, P
Mollusca	Gastropoda	Trochidae	*Trochidae* spp	D
Mollusca	Gastropoda	Turritellidae	*Turritella communis*	D
Platyhelminthes	Turbellaria	Discocelidae	*Discocelis tigrina*	D, P
Platyhelminthes	Turbellaria	Euryleptidae	*Oligocladus sanguinolentus*	P
Platyhelminthes	Turbellaria	Euryleptidae	*Prostheceraeus moseleyi*	P
Platyhelminthes	Turbellaria	Euryleptidae	*Pseudoceros maximus*	D, P

| Platyhelminthes | Turbellaria | Pseudocerotidae | *Thysanozoon brocchii* | D, P |
| Platyhelminthes | Turbellaria | Stylocomoplanidae | *Comoplana agilis* | P |

Table S3 Temporal comparisons (with 95% confidence intervals: CI) of mobile invertebrate assemblages in Dock Biohuts across harbors (random factor) in Year 1 to Year 2 (linear mixed effects models). Significant metrics shown in bold.

Response	Contrast	Lower CI	Upper CI	Test stat	*df*	*p*
Total abundance	**1.69**	**1.08**	**2.66**	**2.36**	**1,42**	**0.02**
Species richness	**1.28**	**1.03**	**1.58**	**2.28**	**1,42**	**0.02**
Shannon (H)	0.14	-0.26	0.54	0.70	1,42	0.48
Pielou's evenness (J)	**0.08**	**0.002**	**0.16**	**2.07**	**1,40**	**0.04**
Malacostraca abundance	**3.69**	**2.06**	**6.63**	**4.50**	**1,42**	**<0.0001**
Bivalvia abundance	1.16	0.60	2.24	0.45	1,42	0.66
Gastropoda abundance	0.99	0.54	1.80	-0.04	1,42	0.97
Ophiuroidea abundance	0.84	0.27	2.66	-0.31	1,42	0.76

Table S4 Mean ± SE total abundance, biodiversity, and abundance of classes of mobile invertebrates surveyed within Biohut structures in year 1 and year 2 since installation.

	Year 1	Year 2
Total abundance	46.30 ± 7.93	75.38 ± 11.25
Species richness	7.20 ± 0.42	9.13 ± 1.15
Shannon diversity (H)	1.44 ± 0.08	1.58 ± 0.18
Pielou's evenness (J)	0.74 ± 0.03	0.82 ± 0.02
Malacostraca abundance	10.97 ± 1.90	39.00 ± 5.81
Bivalvia abundance	6.33 ± 1.53	8.13 ± 2.07
Gastropoda abundance	13.70 ± 3.83	17.50 ± 6.16
Ophiuroidea abundance	14.73 ± 7.15	7.50 ± 3.79

Table S5 Temporal comparisons (with 95% confidence intervals: CI) of potentially exploited species surveyed contributing >5% of the total abundance of mobile invertebrate assemblages in surveyed Biohuts in Year 1 and Year 2 (linear mixed effects models) (FAO 2018).

Response	Contrast	Lower CI	Upper CI	Test stat	*df*	*p*
Palaemon spp abundance	1.81	0.81	4.07	1.49	1,42	0.14
Mimachlamys varia abundance	1.10	0.52	2.31	0.25	1,42	0.80

Table S6 Mean ± SE total abundance of commercially exploitable species in surveyed Dock Biohut structures in Year 1 and Year 2 (FAO 2018).

	Year 1	Year 2
Carcinus spp	0.47 ± 0.23	0.00 ± 0.00
Cerastoderma edule	0.17 ± 0.07	0.00 ± 0.00
Galathea squamifera	0.13 ± 0.08	0.19 ± 0.14
Melarhaphe neritoides	0.03 ± 0.03	0.00 ± 0.00
Mimachlamys varia	5.63 ± 1.50	6.63 ± 1.70
Ostrea edulis	0.03 ± 0.03	0.00 ± 0.00
Palaemon spp	4.60 ± 1.50	7.81 ± 2.00
Paracentrotus lividus	0.30 ± 0.16	2.63 ± 1.06
Periclimenes spp	0.00 ± 0.00	0.75 ± 0.44
Polychaeta spp	0.00 ± 0.00	0.56 ± 0.30
Sepia officinalis	0.07 ± 0.05	0.00 ± 0.00

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