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1 **Rapid recovery of native habitat-builders following physical disturbance on pier pilings**  
2 **offsets colonization of cryptogenic and non-indigenous species in a Chilean port.**

3

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5

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12

13 **Abstract**

14           Examining the effects of disturbances within marine urban communities can shed light  
15 on their assembly rules and invasion processes. The effects of physical disturbance, through the  
16 removal of dominant native habitat-builders, were investigated in the recolonization of  
17 disturbed patches and colonization of plates on pier pilings, in a Chilean port. On pilings,  
18 disturbance substantially affected community structure after 3 months, although it slowly  
19 converged across treatments after 10 months. On plates, cryptogenic and non-indigenous  
20 species richness increased with removal severity, which was not observed in natives.  
21 Opportunistic taxa took advantage of colonizing at an early successional stage, illustrating a  
22 competition-colonization trade-off, although indirect effects might be at play (e.g. trophic  
23 competition or selective predation). Recovery of the habitat-builders then occurred at the  
24 expense of cryptogenic and non-indigenous taxa. Whether natives could continue winning  
25 against increasing propagule and colonization pressures in marine urban habitats deserves  
26 further attention. The interactions between disturbance and biological invasions herein  
27 experimentally shown in situ contribute to our understanding of multiple changes imposed by  
28 marine urbanization in a growing propagule transport network.

29 **Keywords**

30 Biofouling, Sessile invertebrates, Succession, Invasions, Cosmopolitanism, Urban ecology,  
31 Artificial structures, SE Pacific

### 33 **Introduction**

34 Disturbances take multiple forms and regimes, and significantly affect population  
35 dynamics and community assembly (Connell and Slatyer 1977; Sousa 1979; Shea and Chesson  
36 2002; Turner 2010; Zelnik et al. 2019). Human activities influence the type, the frequency and  
37 intensity of disturbances, as well as the way they interact with each other in space and time.  
38 These disturbances can be particularly diverse and intense in urban areas (e.g., habitat  
39 modification, maintenance work, pollution, resource exploitation, and biological invasions),  
40 which are predominantly located along coastlines (Geraldi et al. 2019; Todd et al. 2019). At  
41 multiple spatial scales, marine urbanization may profoundly affect community assembly and  
42 the functioning of coastal marine and estuarine ecosystems (Dafforn et al. 2009; Duarte et al.  
43 2013; Malerba et al. 2019; Todd et al. 2019).

44 Marine urban habitats, such as ports and marinas, may have long constituted key fertile  
45 grounds for taxonomic and functional homogenization on a global scale. Indeed, they constitute  
46 highly similar (and disturbed) environments, embedded in a transportation network of  
47 propagules, and, in turn, form invasion hubs (Carlton 1996; Floerl et al. 2009; Johnston et al.  
48 2017; Darling and Carlton 2018). The multiplication of artificial structures have notably been  
49 shown to promote the intensification of gelatinous plankton blooms (Duarte et al. 2013;  
50 Vodopivec et al. 2017). In a way, this follows two twin hypotheses of invasion biology (cf.  
51 review by Enders et al. 2020), namely “human commensalism” (Jeschke and Strayer 2006) or  
52 “habitat legacy” (Pyšek et al. 2015), wherein opportunist and stress-tolerant taxa are likely to  
53 invade networks of disturbed habitats, with consistent habitat affinities between source and  
54 recipient regions. Similarly, other stress-resistant fouling taxa are widely distributed and  
55 conspicuous in ports, regardless of their non-indigenous *versus* native species status locally  
56 (Clark and Johnston 2009; Dafforn et al. 2009; Canning-Clode et al. 2011; Ferrario et al. 2020).

57 All taxa inhabiting these marine urban habitats are candidates for transport and may possess  
58 traits allowing them to overcome associated stresses (anoxia, pollutants); it is therefore of little  
59 surprise to find a high and growing prevalence of non-indigenous species (NIS) in these  
60 habitats. Although disturbance sources are diverse in marine urban systems (see Todd et al.  
61 2019 for review), it is worth noting that even the initial deployment of novel artificial structures  
62 constitutes a pulse physical disturbance (e.g. Connell and Slatyer 1977 and references therein),  
63 initiating a novel (secondary) succession sequence for this pervasive kind of marine  
64 community. In these systems, community responses to disturbances can provide important  
65 insights into assembly rules, especially in the context of ever-increasing biological  
66 introductions (Shea and Chesson 2002; Pearson et al. 2018a).

67 In the last two decades, the SE Pacific coastline has been profoundly affected by ocean  
68 sprawl (i.e. the proliferation of artificial structures at sea, Duarte et al. 2013; Bishop et al. 2017).  
69 Artificial structures have been expanding either to protect inhabited shores from storms and  
70 tsunamis or to promote economic development, through shipping, mining and aquaculture etc.  
71 (Aguilera 2018). Coastal urban communities of the SE Pacific do not only differ in composition  
72 and structure as compared to neighboring communities of natural habitats. They also suffer  
73 from diverse stressors, such as the accumulation of contaminants (plastics, pollutants, effluents)  
74 (Aguilera et al. 2019), the loss of structuring interactions (e.g. predation) across the modified  
75 seascape (Dumont et al. 2011; Leclerc et al. 2020b), the introduction and spread of NIS (Castilla  
76 and Neill 2009), and both legal and illegal fishing of a wide array of resources, including fish,  
77 benthic predators, kelp and sessile invertebrates (Siegfried et al. 1994; Aguilera et al. 2019).  
78 Despite the pressures undergone by marine urban communities, abundant populations of native  
79 species have also been found to be associated with some of these artificial habitats. Depending  
80 how they use resources (e.g. space pre-emption, predation), native species may help reduce the  
81 establishment and spread of NIS (Dumont et al. 2011; Leclerc et al. 2020a; 2020b). A

82 manipulative field experiment conducted in three ports of central Chile recently supported this  
83 scenario by bringing evidences that benthic predators (mostly invertebrates) could – as far as  
84 their diversity is maintained – efficiently regulate NIS richness and abundances, hence favoring  
85 competitive exclusion by native fouling species over succession (Leclerc et al. 2020a).  
86 Interestingly, these native fouling species constitute a three-dimensional habitat for the very  
87 same predators (Leclerc et al. 2020a), therefore habitat formation may reinforce biotic  
88 resistance in these communities. These fouling species (giant barnacles, ascidians, mussels) are  
89 also commonly fished and it is still unknown to what degree this unregulated harvesting (and  
90 subsequent disturbances for associated communities) could affect such a positive feedback.

91 In the present study, we determined the effects of the removal of dominant native  
92 habitat-builders, with varying disturbance severity, on community assembly. We used a  
93 manipulative experiment to examine the recolonization of established assemblages within  
94 manipulated patches (varying surface areas were available across treatments) as well as the  
95 colonization of settlement plates (standardized for available surface areas), on pier pilings.  
96 Given the proximity of shipping traffic and prior ecological knowledge of our study site (see  
97 methods), we hypothesized (H1) that the severity of disturbance would induce contrasting  
98 colonization responses, with greater prevalence of opportunistic cryptogenic and non-  
99 indigenous species when larger patches were available. We further hypothesized (H2) that such  
100 treatment effects would be greater on plates (controlled for substrate availability) compared to  
101 pilings due to indirect effects, such as the loss of biogenic habitats used by local predators  
102 (Leclerc et al. 2020a). Post disturbance assemblages were surveyed at both early and late stages  
103 of succession to examine community composition resilience (cf. e.g. Hillebrand et al. 2018),  
104 which was hypothesized (H3) to vary negatively with the severity of the disturbance.

105

106 **Materials and methods**

107

108 Study site and associated community

109 This study was performed in the port of San Vicente Bay (36.7591°S, 73.1551°W),  
110 central-southern Chile. In this Bay, environmental conditions are fairly stable across seasons,  
111 with temperatures – averaged over 20 m depth CTD profile at its mouth (in 1996) – ranging  
112 from 10°C in the winter to 13°C in the summer (Rudolph et al. 2002), although this range tends  
113 to be greater in shallow waters (from 10 to 15°C measured at 4 m over 2016-2018 surveys,  
114 Leclerc et al. 2018 and JCL pers. obs.). Heavy metal concentrations are generally greater than  
115 in adjacent pristine locations, with an average of 16.0, 18.2 and 46.1 mg kg<sup>-1</sup> found in the  
116 sediment for copper, lead and zinc, respectively (Leclerc et al. 2018). At the edges of San  
117 Vicente Bay, water quality (organic matter, turbidity, dissolved oxygen) may be highly variable  
118 over the year, notably due to changes in the wind regime and organic matter effluents from  
119 rivers and local fishing industries (Mudge and Seguel 1999; Rudolph et al. 2002). This Bay (ca.  
120 3 × 4 km) also constitutes one of the main hotspots of maritime traffic of the conurbation of  
121 Concepción. In 2016, a total of 427 foreign commercial ships and 217 national commercial  
122 ships made stopovers, while a total of 162 fishing crafts moored in San Vicente Bay (Leclerc  
123 et al. 2020b).

124 The center of San Vicente Bay is crossed by a private, ca. 2 km long steel dock used as  
125 a gas pipeline connecting carriers with the local fuel industry (Abastible ©). Previous studies  
126 in the area (Leclerc et al. 2018; Leclerc et al. 2020a; 2020b) have shown massive fouling by  
127 large native barnacles (*Austromegabalanus psicattus*) and ascidians (*Pyura chilensis*) on the  
128 pilings of this dock (Fig. 1C). According to repeated rapid assessment surveys on established  
129 communities, these ascidians and barnacles remain common to super-abundant (SACFOR  
130 scale), respectively, all yearlong (Leclerc et al. 2018). Patterns of dominance by the same  
131 habitat-builders are actually common on artificial structures throughout the temperate SE

132 Pacific, with consistent observations up to 800 km northwards and 700 km southwards  
133 (Valdivia et al. 2005; Manríquez et al. 2014; Leclerc et al. 2020b). The relatively long life  
134 duration of these species may significantly contribute to these patterns, although cohort  
135 monitoring beyond the ages of 18-20 months are, to the best of our knowledge, lacking  
136 (Manríquez and Castilla 2005; López et al. 2008; Leclerc et al. 2020a). Multiple surveys of  
137 settlement plates in our study site over the period 2016-2018 indicated a fair convergence (with  
138 no signs of attrition) after 18 months, regardless of the timing of their deployment (winter,  
139 summer), towards the dominance of these two species along with colonial organisms growing  
140 either on the primary surface of the piling or as epibionts of these habitat builders (e.g. the  
141 hydroid *Amphisbetia operculata* and the bryozoan *Alcyonidioides mytilii*, see also Table S1)  
142 (Leclerc et al. 2020a). The seasonality of these communities is rather marked in smaller  
143 associated species (epibionts or not), showing massive recruitment and/or vegetative growth  
144 periods (e.g. the barnacle *Balanus laevis*, the hydroids *Obelia dichotoma* and *Halecium* sp. as  
145 well as filamentous turfs such as Ectocarpales or *Antithamnionella* sp., Table S1 and Leclerc et  
146 al. 2020a). Most cryptogenic and non-indigenous species are poorly-represented in the mature  
147 fouling communities of these pilings throughout the year, unless they are released from the  
148 influence of predators, either through exclusion cages (Leclerc et al. 2020a) or because of the  
149 presence of inaccessible cavities, such as those formed by the arrangement of experimental  
150 panels and plates (Leclerc et al. 2018, and JCL pers. obs.).

151

## 152 Study design and data collection

153 The manipulative experiment aimed at simulating the ‘severity’ of a physical  
154 disturbance (i.e. the effect of a disturbance event on the community), which is closely related  
155 to the disturbance ‘intensity’ (the energy associated with this event, per area per time, sensu  
156 Turner 2010). The experiment took place in December 2017 and consisted of the control (0%),



157 partial (50%), and complete (100%) removal of the dominant habitat-builders, from the surface  
158 to the seafloor (circa 8 m depth) of distinct pilings along the dock described above (Fig. 1A,  
159 B). In the partial removal treatment, dominant organisms were scraped from the pilings along  
160 45° inclined parallel strips of ca. 20 cm widths, separated by the same width. The manipulation  
161 was replicated in two areas (hereafter blocks) separated by ca. 200 m, within which one piling  
162 was randomly assigned to one of each treatment. Within each block, treatment pilings were  
163 separated by ca. 20-40 m (Fig. 1A). The removal of sessile taxa was conducted by commercial  
164 divers (Prosub Ltd) using a large customized spatula (10 cm width) welded to a 150 cm steel  
165 stick (Fig. 1B) that they commonly employ for maintenance works in the submerged  
166 infrastructures of the region. It is noteworthy that these scraping tools are also similar to those  
167 employed by fishermen to harvest the edible fouling taxa, which include the giant barnacle and  
168 ascidian habitat-builders (up to 10 cm width) that were targeted in our removal experiments.  
169 We thus simulated the realistic physical disturbance ‘intensity’ experienced by these  
170 communities through seafood harvesting. Such hard fieldwork implied, however, some  
171 imprecision in the intended disturbance effect, i.e. the ‘severity’ (Turner 2010). In fact, several  
172 species associated with the three dimensional habitat formed by these dominant species were  
173 visibly damaged or removed from the piling surface following manipulation, therefore our  
174 results may rather be interpreted as the outcome of a pulse physical disturbance on the whole  
175 community, similar to those related with ocean sprawl.

176 Biodiversity and community structure were determined at ca. 4 m depth for each  
177 treatment over time, using a combination of *in situ* assessment and the deployment of settlement  
178 plates using scuba diving.

179 *In situ* assessments were non-destructive and relied on percentage cover estimations of  
180 sessile biota within a flexible 0.1 m<sup>2</sup> quadrat (n = 3 per piling; 2 pilings per treatment) divided  
181 into 25 sub-quadrats. This was done by adding all of the sub-quadrats; within each an abundance

182 score from 1 to 4 was assigned to each taxon (Dethier et al. 1993). These samplings were  
183 conducted prior to- (procedural control at T0) as well as 3 and 10 months post-removals. As  
184 commonly considered for these types of communities (especially in the region), 3 and 10 month  
185 periods are appropriate to address, respectively, early and later stages of succession or recovery  
186 post- disturbances (Dafforn et al. 2009; Canning-Clode et al. 2011; Leclerc et al. 2020b). We  
187 expected colonization of pilings to be the result of both growth of remnant biota (e.g., colonial  
188 ascidians, hydrozoans, and bryozoans) and larval settlements from local and external sources.  
189 This sources include adjacent pilings of the dock (in either treatment or untouched, Fig. 1A).  
190 Considering the diversity of life history strategies in these fouling communities, the relative  
191 likelihood of larval dispersal (approximated by pelagic larval duration, Shanks 2009)) across  
192 adjacent pilings would vary across major groups and be high in barnacles (e.g. 13-23 days  
193 measured at 20°C in *Austromegabalanus nigrescens* (Egan and Anderson 1987; Pappalardo et  
194 al. 2016)) and molluscs (e.g. 15-16 days in *Crepidatella fecunda* (Chaparro et al. 2005)),  
195 intermediate for tunicates (e.g. 12-24 h for *Pyura chilensis* (Cea 1970 in ; Segovia et al. 2020))  
196 and low in hydrozoans and bryozoans (minutes to hours in shallow species (Shanks 2009)).

197         When the removal was completed, a series of plates (150 × 150 mm) were also deployed  
198 vertically, using large flexible panels (600 × 600 mm) as main frames, tied up to each piling  
199 (i.e. two panels per treatment) using ropes (Figure S1). Prior to deployment, the surface below  
200 each panel was also cleared using a crowbar. The panels were made of plastic fence (25 × 25  
201 mm mesh) – on which a total of 8 plates were attached with cable ties – and secured with PVC  
202 tubes and garden hoses (25 mm in diameter) to maintain some distance between the plates and  
203 the piling surface (Figure S1). For these reasons, we expected the colonization of plates by  
204 sessile biota to be made possible mainly by larval settlements (from local and external pools),  
205 rather than vegetative growth of remnant biota (or ‘residuals’, sensu Turner 2010) from the  
206 adjacent piling surface. Plates were made of black fluted polypropylene, mimicking most of the

207 coated dock or ship surfaces within the region. Although substrate type indeed affects early  
208 stages of colonization (e.g. Smith et al. 2014; Vaz-Pinto et al. 2014; Pinochet et al. 2020) and  
209 exacerbates differences between pilings and plates, we were only interested in differences and  
210 similarities across removal treatments for each substrate, separately. After 3 and 10 months, 4  
211 plates at random per piling (i.e. 8 per treatment) were retrieved underwater, placed in  
212 polypropylene rubble bags (< 0.5 mm mesh), and then stored in a tank filled with sea water  
213 until processing in the laboratory (located along the SW shore of San Vicente Bay).

214 In the laboratory, plates were treated as detailed in Leclerc et al. (2020b). Briefly, sessile  
215 taxa (mostly fauna, see Results) were identified under a dissecting microscope and their  
216 abundances were assessed using cover. Within a 120 × 120 mm working area (avoiding plate  
217 edges), species cover was estimated under 100 random intersection points. Any species only  
218 identified out of these intersection points was given a cover of 0.5%. Using the same procedure,  
219 cover was also determined for bare surface, grazing marks and organism remains (e.g. empty  
220 tubes or barnacle plates). On either plates or non-destructive quadrats, species layering was  
221 taken into account; therefore, the total cover frequently exceeded 100%.

222 Following a framework of criteria analogous to Chapman and Carlton (1991), the identified  
223 specimens were categorized as ‘native’, ‘non-indigenous’, ‘cryptogenic’ or ‘unassigned’. The  
224 cryptogenic species, from uncertain origin (sensu Carlton, 1996), found in this study displayed  
225 a cosmopolitan distribution, most likely resulting from historical anthropogenic dispersal  
226 (Darling and Carlton 2018) and most likely non-indigenous to the study area (Carlton and  
227 Hodder 1995; Leclerc et al. 2018; 2020b). In contrast, the unassigned category was reserved for  
228 specimens for which the taxonomic resolution and/or available information was insufficient.

229

230 Statistical analyses

231 For both *in situ* and plate surveys, univariate patterns in species richness and abundance  
232 were examined with a three-way design using PERMANOVAs with 4999 permutations.  
233 Factors included ‘treatment’ (fixed, 3 levels: control, 50% removal and 100% removal), ‘time’  
234 (fixed) and ‘block’ (random). The number of levels of ‘time’ differed between *in situ* and plate  
235 surveys. By using standardized plates in the latter, time before-removal (T0) had no variation  
236 associated with any response variable. By including the blocking term in the model, part of the  
237 total variance was attributed to differences between our two working areas within the study site,  
238 thereby reducing the residual unexplained variation (Quinn and Keough 2002). In order to  
239 further improve the statistical power of the model, non-significant interactions at  $\alpha = 0.25$  were  
240 excluded and the model was run again (Underwood 1997). Univariate analyses were based on  
241 Euclidean distance matrices (analogous to the ANOVA) generated from either raw or  
242 transformed data. The homogeneity in univariate dispersion was checked for the main factor of  
243 interest, that is ‘treatment’, using PERMDISP (Anderson et al. 2008). When no transformation  
244 (square-root, fourth root, log, arcsine) allowed homoscedasticity to be achieved in univariate  
245 data (herein the case of biomass), analyses were run on untransformed data (Underwood 1997).  
246 PERMANOVAs were followed by pairwise comparisons and *P*-values were estimated using a  
247 Monte Carlo procedure. For the plate survey, univariate analyses were performed either on all  
248 taxa combined (including unassigned taxa), native species or cryptogenic and non-indigenous  
249 species combined.

250 Multivariate patterns in community structure were analyzed using the same PERMANOVA  
251 designs described above. All multivariate analyses were based on Bray-Curtis similarity  
252 matrices generated from fourth root-transformed data, in order to downplay the importance of  
253 the most abundant species and homogenize multivariate dispersion (which was checked using  
254 PERMDISP). PERMANOVA results were supported by ordination (Anderson et al. 2008;  
255 Anderson et al. 2017) using principal coordinate (PCO) analyses based on the same similarity

256 matrices. In addition, the main taxa or abiotic variables (e.g., bare surface, grazing marks, dead  
257 biota) explaining differences among treatments were identified according to their correlation to  
258 PCO axes. From this first ordination, distances among centroids for each combination of  
259 treatment  $\times$  time were determined in a second stage and their temporal trajectories were  
260 visualized using non-metric multidimensional scaling (nMDS). All analyses were performed  
261 using PRIMER 7 (Anderson et al. 2008).

262

## 263 **Results**

264 A total of 38 taxa, including 6 non-indigenous and 9 cryptogenic taxa were identified  
265 across *in situ* and plate surveys over time (cf. Table S1 for complete list and authorities). Prior  
266 to the experiment, neither the percentage of cover of fouling habitat-builders on pilings (average  
267 cover of live individuals:  $75\% \pm 14$ , SD; Fig. 1C) nor community structure varied across the  
268 pilings (pairwise comparisons in Table 1, Fig. 2). As expected, the experimental removal of  
269 habitat-builders (*Austromegabalanus psiccatus* and *Pyura chilensis*) on pier pilings had  
270 substantial effects (Fig. 1C, Table 1), which are detailed below.

271

272 Effect of the removal on pier piling communities.

273 The effect of removal (i.e. severity of disturbance, (Turner 2010)) on these habitat-  
274 builders was detectable (and significant, Table 1) after 3 months, wherein habitat-builders  
275 covered ca. 30 % and  $< 5$  % of the piling surface in the 50% and 100% removal treatments,  
276 respectively (Fig. 2D). Although the actual values must be compared to the procedure control  
277 prior to the treatments (average cover of 75%), we note a discrepancy observed after 3 months  
278 between expected (e.g. 37.5% in the 50% removal treatment) and observed (30%) covers, which  
279 may be due to post-manipulation die-off following neighbor removals. Considering Turner's

280 framework (2010), a given energy of a disturbance event per area (i.e. the disturbance intensity)  
281 can indeed conceptually induce a larger effect (i.e. its severity) than expected.

282         Along with decreasing cover (and contribution) of habitat-builders, there was an  
283 increasing contribution of various animals to the community structure (cf. first axis of PCO,  
284 Fig. 2A), including native (*Balanus laevis*), cryptogenic (*Alcyoniodioides mytilii*) and non-  
285 indigenous taxa (*Bougainvillia muscus*, *Bugulina flabelatta*), as well as various unassigned  
286 algae, including turf (*Antithamnionella* sp. and Ectocarpales) and foliose forms *Ulva* sp. Most  
287 of these taxa were already present on pilings prior to treatments. Nonetheless, after 10 months,  
288 the contribution of these taxa decreased as habitat-builders recuperated their cover to 30 and  
289 50% of the piling surface in the complete and partial removal treatments, respectively. These  
290 values were statistically similar across manipulated assemblages, though still lower than  
291 controls (pairwise comparisons in Table 1). After 10 months (discriminated from 3 month-  
292 samples along axis 2), the community structure converged among treatments (see both PCO  
293 and nMDS in Fig. 2A), although significant differences were still present between the complete  
294 removal treatment and the other two (Table 1, Fig. 2A). Abundant hydroid colonies of *Halecium*  
295 sp. (unassigned status) were found in the complete removal treatments, as illustrated along the  
296 second axis of the PCO.

297         Effect of the removal on community development on plates

298         Major shifts in community structure were observed between 3 and 10 months post-  
299 deployment of the plates (ca. 52% explained variation according to PCO, Fig. 2B, significant  
300 time effect in Table 2), but these shifts were not influenced by the experimental manipulations  
301 (removal) of the fouling assemblages on pilings, according to the PERMANOVA (i.e. no  
302 interaction ‘time × treatment’, Table 2). Independent of age, the community structure differed  
303 statistically across all treatments (Table 2), with an increase in the contribution of one native  
304 ascidian (*P. chilensis*) and two cryptogenic taxa (the bryozoan *Amathia* cf. *gracilis* and the

305 hydroid *Plumularia cf. setacea*) to community structure when the partial removal was  
306 compared to control treatments (Fig. 2B). This was further pronounced in the complete removal  
307 treatment.

308 In the complete removal treatment, biomass increased significantly (about twice as  
309 heavy) compared to other treatments after 10 months (Table 2, Fig. 3A). Interestingly, neither  
310 the cover nor the richness of native taxa differed across treatments at any time post-deployment  
311 (Table 3, Fig. 3B-E). This result contrasts with cryptogenic and non-indigenous taxa, which  
312 displayed an increasing mean richness with removal severity, although cover remained  
313 unaffected (Table 3). This pattern of increased colonization was particularly strong after 3  
314 months, when the average richness of these taxa was greater than after 10 months (Table 3, Fig.  
315 3F, G) In total, 1, 2 and 4 non-indigenous and 5, 7 and 8 cryptogenic taxa were recorded in  
316 control, partial and complete removal treatments , respectively (Fig. 3B).

317

## 318 **Discussion**

319 The removal of the dominant habitat-builders affected community assembly in the  
320 recolonization of established assemblages and the colonization of novel substrata on pier  
321 pilings. As hypothesized (H1), the patches made available by the substrate clearing offered  
322 colonization opportunities for novel assemblages, including cryptogenic and non-indigenous  
323 species (NIS) otherwise less abundant, rare or absent locally (i.e. at the scale of the focal piling),  
324 with contrasting contributions to community structure across treatments. Interestingly, even  
325 while initially offered the same free surface for colonization, the richness (but not the  
326 abundance) of cryptogenics and NIS on settlement plates increased significantly with the  
327 severity of the disturbance experienced by the surrounding assemblages. As hypothesized (H2),  
328 the contrasting response on pilings and plates could indicate indirect effects decoupled from

329 spatial competition at the patch scale. As for natives, neither their richness nor their abundance  
330 varied across treatments in the colonization of plates. Although none of the cryptogenics and  
331 NIS are new in this highly frequented, principal regional port, contrasting responses to  
332 treatments among natives versus cryptogenics and NIS could reflect differences in life history  
333 traits and distinct legacies of these two species pools. Finally, regarding H3, although habitat-  
334 builders did not recover their initial (control) occupied surface in any of the treatments,  
335 community structure on pilings generally converged across treatments after 10 months;  
336 differences were only detected between complete removal and other treatments. As these native  
337 dominants bounced back rapidly, cryptogenic and non-indigenous taxa decreased in their  
338 contribution on pilings.

339 *1. Direct effect of physical disturbance: decreasing spatial competition*

340 One way in which physical disturbance directly influences community assembly is by  
341 providing open substratum for remote and local colonizers (e.g. Levin and Paine 1974; Connell  
342 and Slatyer 1977; Sousa 1979; Shea and Chesson 2002). When propagule and colonization  
343 pressures are high in the long-term, local disturbances can increase the probability of the  
344 establishment of more abundant and diverse NIS (Davis et al. 2000; Clark and Johnston 2009;  
345 Blackburn et al. 2020), including their possible impacts (being intimately linked with their  
346 proliferation, Geraldi et al. 2019). Here, the piling-scale removal of the dominant native space-  
347 occupiers (*Austromegabalanus psicattus* and *Pyura chilensis*) – both of which are harvested  
348 along the SE Pacific – has generally led to a greater contribution of diverse native, cryptogenic  
349 and non-indigenous species (as well as unassigned turf algae) to the community structure (as  
350 hypothesized, H1), but only at an early post-disturbance stage (i.e. hereafter 3 months).

351 The observed early colonizers are either stress resistant (to the physical disturbance),  
352 opportunistic or both. Withstanding stress in this context implies that live remnant colonies (or  
353 'residuals', sensu Turner 2010) are capable of rapid vegetative growth, permitting the



354 colonization of vacant patches (Sousa 1979; Valdivia et al. 2005; Hiebert et al. 2019). In spite  
355 of the limited larval dispersal of shallow water hydroids (over a few meters in a few minutes,  
356 Shanks 2009), such spreading capabilities are notably found in vines and runners (through  
357 stolonal expansion, Greene and Schoener 1982; Schuchert 2007), such as *Bougainvillia muscus*  
358 and *Clytia linearis* (see disturbed pilings in Fig. 2). Opportunism can involve a greater diversity  
359 of traits (e.g., reproductive output), but it generally implies a low rank in the competitive  
360 hierarchy (i.e., along an inter-specific competition-colonization trade-off, Greene and Schoener  
361 1982; Chesson 2000; Valdivia et al. 2005; Wernberg et al. 2020). For instance, although  
362 barnacle larvae may disperse over kilometers in several weeks (Shanks 2009; Pappalardo et al.  
363 2016), small species such as *Balanus laevis* (see Fig. 2) are unable to secure the primary  
364 substratum when competing with larger ones, such as *A. psicattus* (Leclerc et al. 2020a, this  
365 study). The prevalence of cryptogenic and non-indigenous species fitting into these categories  
366 may illustrate the legacy of the disturbance regimes typical of artificial habitats. These species,  
367 most of which could be considered neocosmopolitan (sensu Darling and Carlton 2018), have  
368 been frequently and rapidly observed on settlement plates deployed at various ports in the  
369 region (Leclerc et al. 2018; Leclerc et al. 2020b). Over their natural history, they have likely  
370 colonized diverse artificial habitats (e.g. ship hulls, debris, port infrastructures), selecting for  
371 traits conducive of the fouling network that these habitats compose. Although this hypothesis  
372 is beyond the scope of this study, we note that this phenomenon is akin to trait biases observed  
373 within terrestrial plants and the legacy of ruderal habitats (Catford et al. 2012; Hufbauer et al.  
374 2012; Pearson et al. 2018b). The expansion of novel artificial structures (ocean sprawl), almost  
375 independent of further co-varying stresses (Todd et al. 2019) is likely to worsen future invasions  
376 across novel or intensifying pathways (Dafforn et al. 2009; Aguilera 2018; Geraldi et al. 2019;  
377 Sardain et al. 2019).

378           While the contrasting contribution of cryptogenic and non-indigenous species to  
379 community structure across treatments on pilings was probably driven by varying amounts of  
380 open surface, the same hypothesis hardly stands for the patterns observed on settlement plates,  
381 which had standard open surfaces (see H2). Beyond the competition for free surface, removal  
382 of the dominant habitat-builders of our system probably influenced community assembly by  
383 additional and more indirect mechanisms discussed in the following sections.

#### 384           2. *Indirect effect of physical disturbance: decreasing competition for other resources*

385           Although open space is generally considered as the main limiting resource for sessile  
386 invertebrates in fouling assemblages (Osman and Whitlatch 1995a; Stachowicz et al. 2002),  
387 there is mounting evidence that competition for trophic resources can also influence community  
388 assembly in such systems, even at local scales (Buss 1979; Svensson and Marshall 2015). Using  
389 *in situ* experiments, Svensson and Marshall (2015) demonstrated that the nature, diversity and  
390 abundance of planktonic resources can influence the richness and structure of sessile  
391 assemblages, at least at an early stage (1 month). In our experiment, we cannot rule out that the  
392 varying amount of sessile fauna left in place across treatments led to contrasting trophic  
393 competition between these organisms and the new recruits, even those which colonized  
394 settlement plates with standardized free surfaces. Although certainly not exclusive (e.g.,  
395 predation on larvae by neighbour adults, Young and Gotelli 1988; see also next section),  
396 competition for food resources could actually constitute a solid hypothesis explaining the  
397 significant difference across treatments observed in biomass on fully covered plates after 10  
398 months (Ctrl = 50% removal < 100% removal, Fig. 3A). Escaping such competition, recruiting  
399 organisms may indeed have been promoted for growth between sampling periods in the full  
400 removal treatment, as compared to their counterparts in control and partial removal treatments.  
401 The ability of species to secure phytoplankton resources could thus mediate competition for  
402 space (Buss 1979). Considering such a possibility, assessing individual growth and post-

403 recruitment survival on a series of focal species could be valuable in future research to  
404 disentangle diverse interacting processes at a micro-scale, such as propagule pressure,  
405 competition for food and/or space, and predation.

### 406 3. *Indirect effect of physical disturbance: partially releasing incomers from predation*

407 Habitat-builders often provide shelter to the predators of their own competitors (and  
408 predators); therefore, their removal can have side effects. Previous work carried out in three  
409 ports of the region indicated that benthic predators had an overall stronger effect on most non-  
410 indigenous species than on native species at an early stage of development on settlement plates  
411 (Leclerc et al. 2020a). Results varied across sites and predator types (separated by size) but, in  
412 general, predator exclusion led to an increase in cryptogenic and non-indigenous richness,  
413 categories of which 18% and 36% taxa, respectively, were observed only under predator  
414 exclusion. These results mirror the differences herein observed for richness among treatments  
415 (Figs. 3B, 3F). Although benthic predators were not quantified, local loss of some of them, due  
416 to the removal of habitat-builders, is very likely (Hernández et al. 2001; Sepúlveda et al. 2003).  
417 This was also supported by our observations of macro-predators ( $> 2$  cm) *in situ*, seemingly  
418 associated with complex biogenic habitats made up by well-developed fouling communities  
419 (Fig. 1D, JCL, pers. obs., Leclerc et al. 2018) (see also Coleman and Connell 2001). Such a loss  
420 in predator diversity may have contributed to the observed differences in community structure  
421 across treatments. Along with other studies (Dumont et al. 2011; see also Dias et al. 2020), the  
422 experiments mentioned above also demonstrated that an important predation on most of the  
423 non-indigenous and cryptogenic ascidians gave a competitive advantage to their native,  
424 dominant and less predated counterpart, namely *Pyura chilensis*, one of our habitat-builders.  
425 This effect, measured by percentage of cover reduction after 4 months in a settlement panel  
426 experiment, was, however, not consistently detected by the exclusion of macro-predators  
427 (Leclerc et al. 2020a). According to further exclusion treatments, the authors found that micro-

428 predators (ranging between 2 mm and 2 cm) largely contributed to the biotic resistance  
429 described above, by controlling post-settlement survival (see also Osman and Whitlatch 1995b;  
430 Oricchio et al. 2016). Considering the turn-over, dispersal abilities and rapid colonization of  
431 many micro-invertebrates across diverse habitats (dispersing 10s m within a few days to weeks  
432 (Waage-Nielsen et al. 2003; Martins et al. 2017), many micro-predators may have rapidly  
433 recolonized disturbed pilings from adjacent ones, throughout the recovery of sessile  
434 assemblages, even at an early stage of biogenic habitat formation (see also Leclerc and Viard  
435 2018). As in other marine systems (e.g. Waage-Nielsen et al. 2003; Freestone et al. 2011),  
436 diverse and abundant assemblages of micro-invertebrates may have strong influences on the  
437 structure and dynamics of associated communities, as well as their responses to anthropogenic  
438 influences, which would be worth further considering in future studies.

#### 439 4. Implications, perspectives and concluding remarks

440 Regardless of the precise mechanism explaining differences in biomass on plates across  
441 treatments, and although we did not follow a strict functional approach, our results most likely  
442 illustrate that the distribution of traits conferring high efficiency in exploiting and maintaining  
443 resources in the native community may be critical not only for its biotic resistance (Davis et al.  
444 2000; Bulleri et al. 2008), but also for its resilience after a physical disturbance (see H3). In our  
445 system, the native habitat-builders largely recovered from removal within a few months.  
446 Opportunist taxa, such as those characterizing most non-indigenous fouling species established  
447 in our region, are indeed poorly efficient in securing resources and inhibiting overgrowth by  
448 native dominants (Valdivia et al. 2005; Cifuentes et al. 2010). Although experimental outcomes  
449 at an early stage of succession would certainly vary with the timing and regime of the  
450 disturbance (e.g. Chesson 2000), the convergence in community structure shown here has been  
451 observed across multiple succession trials in this very site (Leclerc et al. 2020a) and in nearby  
452 regions (Valdivia et al. 2005; Cifuentes et al. 2010).

453        Nonetheless, this rather deterministic hypothesis overlooks the variations in propagule and  
454        colonization pressures characterizing port areas. The observed outcome at later stages of  
455        succession are indeed undermined by an “ecological roulette” (sensu Carlton and Geller 1993),  
456        related to the diversity of traits in the non-indigenous species pool and niche similarities with  
457        natives, in recipient communities (Davis et al. 2000; Catford et al. 2019; Zelnik et al. 2019). In  
458        the framework of a competition-colonization trade-off, for instance, disturbed communities  
459        could be greatly susceptible to profound and perennial changes in native community structure  
460        depending on standoff, self-organization, and competitive traits in successful settlers (Sebens  
461        1986; Catford et al. 2018; Bertolini et al. 2019; Catford et al. 2019). Strong competitive traits  
462        are common in widespread sessile marine invaders, such as seagrasses, seaweeds, oysters and  
463        mussels, which are known to affect ecosystems through habitat engineering, resource use and  
464        nutrient cycling (Paine 1974; Thomsen et al. 2014; Bailey et al. in press). As elsewhere,  
465        successful introduction and establishment of such highly competitive space-occupiers have  
466        been common throughout the SE Pacific (Castilla and Neill 2009; Villaseñor-Parada et al.  
467        2018). Many of them are still being transported due to little regulated human activities (e.g.  
468        Cardenas et al. 2020), which are showing alarming signs of expansion across the planet  
469        (Seebens et al. 2018; Sardain et al. 2019). Altogether, our results reveal, on the one hand, that  
470        the dominant native fouling species of the study region display a series of traits and competitive  
471        abilities conferring their population with rapid recovery post-disturbance and the potential  
472        sustainability of well-managed localized fisheries. On the other hand, the currently unregulated-  
473        harvesting practices certainly deserve further attention, most notably in a context of marine  
474        urbanization and expanding shipping networks.

475

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490

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747 **Tables**

748 Table 1: Results of PERMANOVA tests for differences in habitat-builders cover (HB, %) and  
 749 community structure on pier pilings among levels of the main fixed (experimental treatment,  
 750 time) and random (block) factors, as well as their interactions. Non-significant interaction terms  
 751 at  $\alpha = 0.25$  were removed (as indicated by “-”) and the model was run again. Significant *P*-  
 752 values are in bold. Pairwise tests are summarized, with T0 indicating the moment of removal;  
 753 T3 and T10 indicate 3 and 10 months post-removal, respectively; and Ctrl, 50%r, 100%r  
 754 indicate control, partial and complete removals, respectively.

755

756

Transformation	HB cover (%)			Community structure	
	None			Fourth-root	
Dispersion	$F_{8,45} = 2.17$	$P = 0.111$		$F_{8,45} = 1.84$	$P = 0.157$
<i>Main test</i>					
Source	df	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>
Treatment (Co)	2	45.39	< <b>0.001</b>	1.59	0.203
Time (Ti)	2	10.64	0.122	7.25	0.066
Block (Bl)	1	0.16	0.684	2.37	<b>0.038</b>
Co x Ti	4	12.45	< <b>0.001</b>	2.84	< <b>0.001</b>
Co x Bl	2	-	-	1.96	<b>0.037</b>
Ti x Bl	2	2.15	0.128	1.62	0.096
<i>Pairwise comparisons:</i>					
T0:		Ctrl = 50%r = 100%r		Ctrl = 50%r = 100%r	
T3:		Ctrl > 50%r > 100%r		Ctrl ≠ 50%r ≠ 100%r	
T10:		Ctrl > 50%r = 100%r		Ctrl = 50%r ≠ 100%r	

757

758

759 Table 2: Results of PERMANOVA tests for differences in biomass (g) and community structure  
 760 on settlement plates among levels of the main fixed (experimental treatment, time) and random  
 761 (block) factors, as well as their interactions.. Significant *P*-values are in bold. Abbreviations  
 762 are the same as in Table 1.

763

	Biomass (g)			Community structure	
Transformation	None			Fourth-root	
Dispersion	$F_{5,45} = 6.11$ <b><i>P</i> = 0.004</b>			$F_{5,42} = 7.04$ <b><i>P</i> &lt; 0.001</b>	
<i>Main test</i>					
Source	df	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>
Treatment (Co)	2	4.20	0.024	4.42	< <b>0.001</b>
Time (Ti)	1	39.30	< <b>0.001</b>	13.35	<b>0.011</b>
Block (Bl)	1	1.81	0.190	2.25	<b>0.041</b>
Co x Ti	2	3.78	<b>0.029</b>	1.41	0.171
Ti x Bl	1	-	-	4.08	< <b>0.001</b>
<i>Pairwise comparisons:</i>					
		T3: Ctrl = 50%r = 100%r		Ctrl ≠ 50%r ≠ 100%r	
		T10: Ctrl = 50%r < 100%r			

764

765 Table 3: Results of PERMANOVA tests for differences in richness (S) and cover (%) of native, cryptogenic and non-indigenous species on  
 766 settlement plates among levels of the main fixed (experimental treatment, time) and random (block) factors, as well as their interactions.  
 767 Significant *P*-values are in bold. Abbreviations are the same as in Table 1.

768

	Native				NIS + Cryptogenics				
	Richness		Cover (%)		Richness S		Cover (%)		
Transformation	None		None		None		None		
Dispersion	$F_{5,42} = 1.68$ $P = 0.203$		$F_{5,42} = 2.9$ $P = 0.107$		$F_{5,42} = 1.63$ $P = 0.268$		$F_{5,42} = 0.43$ $P = 0.937$		
<i>Main test</i>									
Source	df	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>
Treatment (Co)	2	1.48	0.400	1.74	0.191	13.03	< <b>0.001</b>	2.49	0.099
Time (Ti)	2	0.97	0.333	6.27	0.236	18.61	< <b>0.001</b>	2.93	0.340
Block (Bl)	1	1.61	0.213	0.41	0.516	0.02	0.890	2.37	0.127
Co x Ti	2	0.35	0.747	0.27	0.787	2.01	0.146	2.28	0.116
Co x Bl	2	1.67	0.194	-	-	-	-	-	-
Ti x Pl	1	-	-	5.19	<b>0.029</b>	-	-	7.07	<b>0.013</b>
Co x Ti x Bl	2	2.94	0.073	3.25	0.053	-	-	-	-
<i>Pairwise comparisons:</i>									
						Ctrl < 50%r < 100%r			

769

770

771 **Figures**

772 Figure 1: Experimental design and habitat-builders cover, before and after removal treatment,  
773 upon pier pilings at the study location. Within each block (A), experimental treatments  
774 consisted of the removal (partial ca. 50%, 100% vs. control, B) of native fouling habitat-builders  
775 (*Austromegabalanus psicattus*, *Pyura chilensis*), commonly inhabited by various macro- (e.g.  
776 *Romaleon setosum*, *Homalaspis plana*) and micro-predators (e.g. *Hypsoblennius sordidus*  
777 inhabiting empty barnacle shells, and *Palaemon* sp. crawling among epibiotia) that are  
778 highlighted here by the white arrows in the pictures (C, photos are courtesy of Mauricio  
779 Altamirano). For each sampling occasion (before, after removal), letters indicate significant  
780 differences in the cover of habitat-builders among treatments (D, n = 6). Around the median  
781 (horizontal line), the box plots are bounded by the quartiles, the 95% confidence intervals  
782 (whiskers) and the outsiders.

783

784 Figure 2: Community structure (principal coordinate analysis, PCO) across treatments on  
785 settlement plates (A) and on surrounding assemblages (piling, B) before and after experimental  
786 removal of habitat-builders (3 and 10 months). Vector plots of variables correlated with the  
787 PCO axes are indicated, with  $r > 0.4$  and  $0.6$  for pier piling and plate assemblages, respectively.  
788 Taxa are in bold with the color code indicating the status: unassigned (black), native (blue),  
789 cryptogenic (orange) and non-indigenous (red) species. Temporal trajectories of the centroids  
790 (determined from PCO) axes for each combination of treatment  $\times$  time are ordinated using non-  
791 metric multidimensional scaling (right insets).

792

793 Figure 3: Biomass (g), richness (S) and cover (%) on settlement plates after 3 and 10 months  
794 following experimental removal. The total biomass is given (A), while richness (B, D, F) and

795 cover (C, E, G) values are given for all, native, NIS and cryptogenic taxa. Richness values are  
796 either given as cumulated over (bar charts in B, C) or averaged (box plots in D, F) across  
797 replicate plates per combination of treatment  $\times$  time ( $n = 8$  plates). Around the median  
798 (horizontal line), the box plots are bounded by the quartiles, the 95% confidence intervals  
799 (whiskers) and the outsiders.

800

801



Figure 1

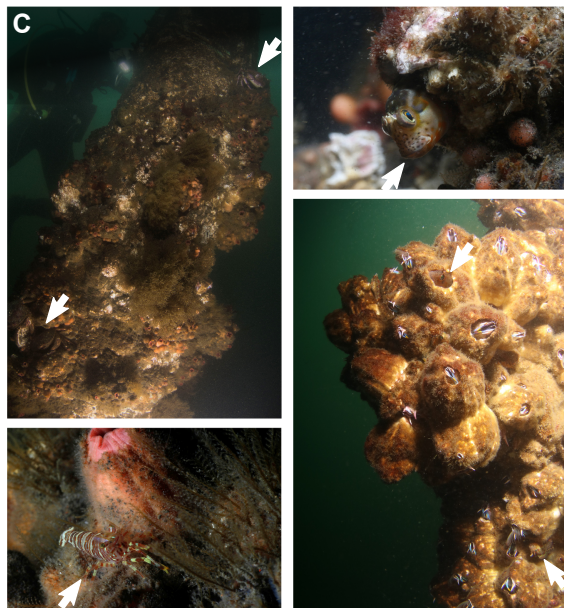
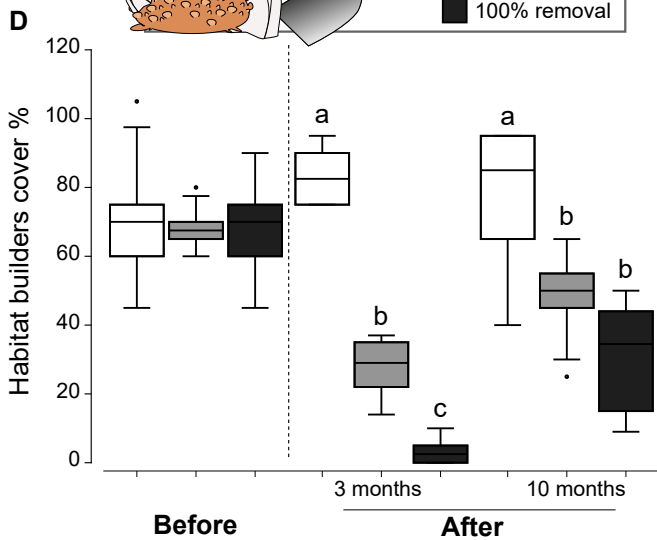
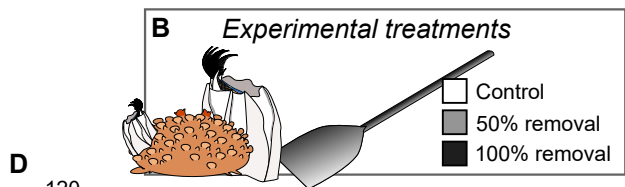
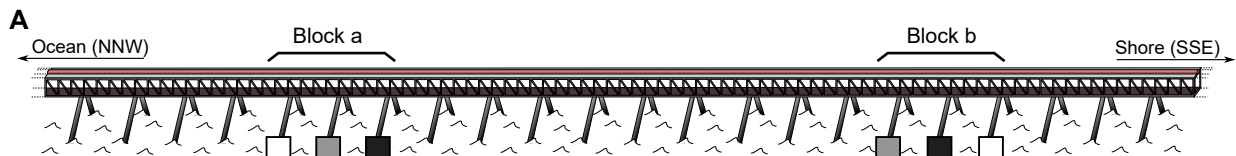
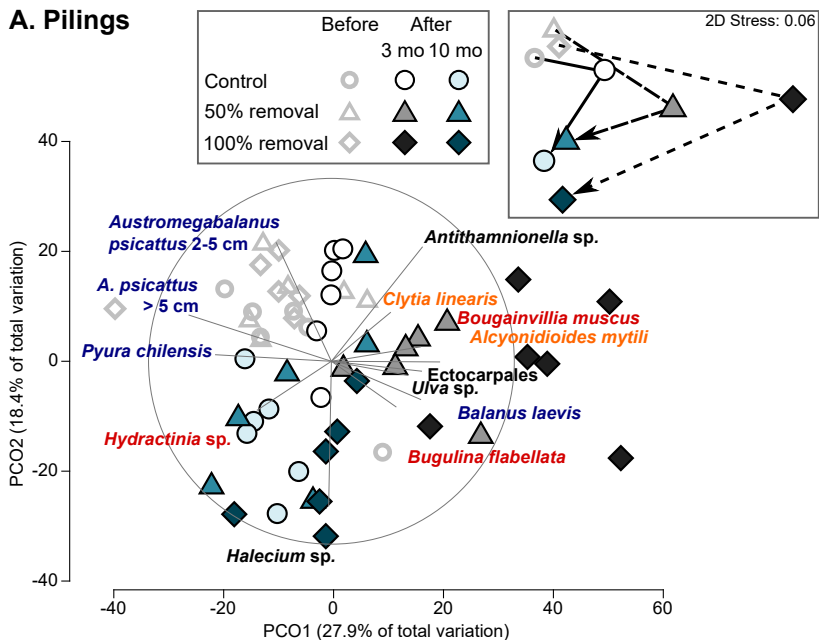


Figure 2

## A. Pilings



## B. Plates

