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## Multi-scale patterns in the structure of fish and fouling communities associated with seaweeds in marinas

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### ► To cite this version:

Jean-charles Leclerc, Maéva Gonzalez, Jean-Philippe Pezy, Aurore Raoux, Romain Crec'Hriou, et al.. Multi-scale patterns in the structure of fish and fouling communities associated with seaweeds in marinas. *Marine Ecology Progress Series*, 2024, 742, pp.1-19. 10.3354/meps14641 . hal-04760065

**HAL Id: hal-04760065**

**<https://hal.science/hal-04760065v1>**

Submitted on 30 Oct 2024

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3 **Multi-scale patterns in the structure of fish and fouling**  
4 **communities associated with seaweeds in marinas**  
5  
6

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28 **Keywords:** floating pontoons, port, hierarchical design, diversity, NE Atlantic, seaweeds, kelp,  
29 marine invertebrates, fish

30 **Running headline:** Scales of variability on floating pontoons

31 **Abstract word count:** 250

32 **Main body word count:** 7807

33 **Number of references:** 94 (3015 words)

34

35 **Conflict of interests.** The authors declare no conflict of interest.

36

37 **Author contributions:** JCL, ET, KFD and TW conceived the working hypotheses and study  
38 design. JCL, MG, JPP and AR led the sampling. JCL conducted the rapid assessment surveys,  
39 based upon preliminary list of FV, while RC, MG and AR conducted the fish survey. CH, CB,  
40 AM, SL, LS, JC, DD, MC, JBV, FS, RVP, SH and CM participated to the sample collection  
41 and processing. JCL analysed the data and led the writing. All authors critically edited  
42 manuscript drafts.

43

44 **ABSTRACT**

45           Redistribution of biodiversity represents a key challenge for understanding scales of  
46 spatial variations in natural marine communities. With increasing coastal urbanization, artificial  
47 structures are proliferating with impacts on natural habitats yet there is poor knowledge on the  
48 spatial scales of processes operating over their associated species assembly. This is exemplified  
49 by novel communities establishing along and around floating infrastructures, such as pontoons  
50 in marinas. Here we explored the multi-scale patterns in the diversity and community structure  
51 of fouling seaweeds, invertebrates and fish communities associated with pontoons in 18  
52 marinas, distributed along about 1000 km of coastline in NW France. With respect to the  
53 marina's distribution across three distinct ecoregions, we predicted that their seaweed  
54 communities would follow spatial patterns reported in native communities from rocky shores.  
55 This hypothesis was poorly supported, and the variation among ecoregions (8%) was largely  
56 explained by the abundance of nonindigenous kelps. However, as anticipated, we observed  
57 important variability among and within marinas in all response variables (e.g. richness of sessile  
58 invertebrates and fish). These variations were related to contrasting sea surface temperature  
59 regimes among marinas, along with a number of explanatory variables (e.g. distance to marina  
60 entry) As also hypothesized, fouling and fish communities covaried with kelp biomass,  
61 although covariations were strengthened at the scale of the region and at the scale of the marina  
62 and pontoon when nonindigenous and native kelp were considered, respectively. Specificities  
63 in distributions and influences of foundation species in urban environments could be worth  
64 scrutinizing for their management.

## 65 1. INTRODUCTION

66 Changes in land and sea are eroding and reshaping biodiversity at an unprecedented pace and  
67 over multiple spatial scales, where climate change and interactions with other environmental  
68 changes are pervasive (Pörtner et al. 2021, Wernberg et al. 2024). In the coastal zone, “marine  
69 urbanization” – the proliferation of diverse artificial infrastructures – has expanded rapidly over  
70 recent decades and is predicted to increase in the near future (Bugnot et al. 2020). While this  
71 phenomenon is associated with dramatic modifications of natural benthic habitats through  
72 degradation, fragmentation, sedimentation and coastal darkening [cf. declines in foundation  
73 seaweeds (Wernberg et al. 2019, de Bettignies et al. 2021)], this can also provide novel hard  
74 substrates and colonization opportunities to benthic taxa. These communities generally differ  
75 from natural systems, and there is an increasing recognition that patterns and processes  
76 operating upon these structures cannot simply be transposed to natural reefs (Bulleri &  
77 Chapman 2010, Todd et al. 2019, Airoidi et al. 2021, Aguilera et al. 2022). With no natural  
78 analogues in either composition or structure, the associated ecosystems are increasingly  
79 considered “novel” (Bulleri et al. 2020). As these systems expand together with searches for  
80 solutions and initiatives to make them more sustainable (e.g. greening grey infrastructures),  
81 there are considerable needs to understand their diversity, structure and functioning across  
82 seascapes (Todd et al. 2019, Firth et al. 2020).

83 Community assembly in urbanized marine ecosystems involves a unique suite of  
84 processes, in which human activities modulate natural environmental drivers of biodiversity  
85 (Aronson et al. 2016, Pearson et al. 2018, Bulleri et al. 2020). Urbanisation can for example  
86 affect species connectivity and distribution (Bishop et al. 2017, Touchard et al. 2023) within  
87 the limit of their physiological tolerance to multiple stressors (Wang et al. 2020). In addition,  
88 the intrinsic properties of artificial habitats – such as substrate type, roughness, microhabitats,  
89 or slope which have been heavily studied at local scales (Firth et al. 2016) – can interact with

90 processes operating at biogeographic scales (Aguilera et al. 2022, Jackson-Bué et al. 2024). For  
91 example, the lack of rock pools conferring thermal refuge on breakwater had been shown to be  
92 a stronger driver of community assembly in sessile taxa and mobile invertebrates at low than at  
93 high latitude (Aguilera et al. 2022). Conversely, several dimensions of habitat complexity (Loke  
94 & Chisholm 2022) can be greater on breakwaters (Lawrence et al. 2021, Grasselli & Airoidi  
95 2021). In specific conditions (e.g. on supralittoral habitats), the accumulation of anthropogenic  
96 marine debris can also favor the same synanthropic mammals across multiple biogeographic  
97 regions (Todd et al. 2019, Aguilera et al. 2023). In addition, depending on the seascape  
98 arrangement of sedimentary vs. rocky habitats, the simple addition of hard substrates can  
99 promote stepping-stone range expansion at meso-scale of sessile non-indigenous species,  
100 cryptogenic species or native elsewhere established (Airoidi et al. 2015, Vodopivec et al. 2017),  
101 hereafter neocosmopolitan taxa (sensu Darling & Carlton 2018). While the type of habitat  
102 (including biogenic habitat) has important effects in these open systems, it is interesting to note  
103 that processes operating at meso- to macro-scale can prevail in their influence upon biota  
104 (Sedano et al. 2020, Jackson-Bué et al. 2024). Besides these extensively studied concrete  
105 shorelines, there are so far limited empirical evidence of interactions between natural vs.  
106 human-driven processes in marine urban systems across multiple spatial scales (Firth et al.  
107 2020).

108 Marine urban systems, such as ports and marinas, are however extraordinary fertile  
109 grounds for studying genetic, taxonomic and functional homogenization on a global scale  
110 (Strain et al. 2021, Touchard et al. 2023). Embedded in a transportation network of propagules,  
111 these highly similar environments offer unique sets of experimental units spread over multiple  
112 scales. In particular, floating infrastructures are associated with a series of environmental filters  
113 hardly operating upon the communities of natural reefs (Lindgarth 2001, Holloway & Connell  
114 2002, Perkol-Finkel et al. 2006) nor upon communities of natural floating items (Thiel & Gutow

115 2005). They are particularly prone to the colonization and maintenance of fouling taxa with  
116 traits favouring colonization of floating vectors (e.g. hulls and marine debris), including non-  
117 native and cryptogenic species (Mineur et al. 2012, Johnston et al. 2017, Darling & Carlton  
118 2018, Leclerc et al. 2023). In the light of invasion theories [e.g. habitat legacy (Pyšek et al.  
119 2015)] and assembly rules (Pearson et al. 2018), finding a great prevalence of neocosmopolitan  
120 taxa upon these substrata is rather not surprising. Whether the native taxa colonizing these  
121 infrastructures follow consistent distributions to those observed in their natural habitat is a  
122 question comparatively less trivial, and still poorly documented.

123         Most of the multi-scale investigations of assemblages associated with marinas, and  
124 especially floating pontoons, have relied on settlement panels left for up to tens of months, in  
125 order to examine diversity patterns (Canning-Clode 2009, Dafforn et al. 2009, Simpson et al.  
126 2017, Leclerc et al. 2020, Pezy et al. 2021) and underlying processes (Clarke Murray et al.  
127 2014, Lavender et al. 2017, Ashton et al. 2022). Although these experimental and controlled  
128 studies have improved our understanding of community assembly patterns and rules in these  
129 habitats, they are targeting early-communities and have overlooked the influence of long-lived  
130 taxa, such as canopy forming seaweeds which can be locally common members of these  
131 systems (Pederson et al. 2005, Johnston et al. 2011, Epstein et al. 2019). The influence of  
132 biogenic habitat due to comparatively short lived sessile taxa is increasingly recognized in the  
133 early development of these assemblages (Leclerc & Viard 2018). But, to our knowledge, the  
134 influence of long-lived foundation species, such as kelps, upon marina communities has seldom  
135 been studied. In addition, examination of established assemblages upon marina pontoons are  
136 rather rare (e.g. Guerra-García et al. 2021, Hawk & Johnson 2022 for among and within site  
137 variations, respectively), which is impeding our ability to evaluate scale-dependent patterns in  
138 these expanding marine habitats.

139 In this study, we explored the multi-scale patterns in the diversity and structure of  
140 seaweeds, invertebrates and fish communities associated with floating pontoons along ~ 1000  
141 km of coastline in NW France, across a biogeographic transition zone (the Brittany-Normandy  
142 continuum). Our primary objective was to identify scale-dependent patterns of diversity and  
143 community structure within and among different ecoregions. The Brittany-Normandy  
144 continuum indeed expands over three distinct ecoregions (Spalding et al. 2007), which are  
145 reflected in the seaweed and invertebrate communities of natural rocky habitats (Tempera et al.  
146 2019, de Bettignies et al. 2021), notably related with contrasting water temperature regimes  
147 (Agoumi 1982) and availability in substratum (Cabioch et al. 1977, Thouin 1983). For instance,  
148 shallow subtidal reefs in Brittany are covered by dense forests of the perennial kelp *Laminaria*  
149 *hyperborea* along the Northern coasts that are sharply replaced by the annual kelp *Saccorhiza*  
150 *polyschides* along the stratified waters of the Southern coasts (Derrien-Courtel et al. 2013).  
151 Under this premise, we postulated (hypothesis 1: H1) that seaweed fouling communities would  
152 follow regional patterns similar to those reported from natural reefs (i.e. differences among  
153 regions). Among marinas, we hypothesized (H2) that community structure would be distinct  
154 and highly variable (more than among regions) owing to contrasting specific marina attributes  
155 (openness, size, maritime activities) that are interacting with local abiotic conditions  
156 (temperature regime, water movements) and (human-aided) dispersal. At even lower scale,  
157 within marina, we hypothesized (H3) that community structure would vary across pontoons in  
158 response to known fine-scale gradients (distance) between port entry and innermost portions  
159 (e.g., Rivero et al. 2013, Gauff et al. 2022). Finally, we hypothesized (H4), that fouling and fish  
160 communities would covary with the amount of foundation kelp, however without *a priori*  
161 hypotheses about their most important scale of influence (region, marina, pontoon).



## 2. MATERIAL & METHODS

### 2.1. Sampling design and data collection

The study was performed during May-June 2022 along approximately 1000 km of Brittany and Normandy shoreline, in NW France (Fig. 1A, full names and description in Table S1). Distributed along a biogeographic province transition zone (Cabioc'h et al. 1977), this shoreline is encompassing three ecoregions based upon the biogeography of coastal and shelf areas (Spalding et al. 2007) and specific information available for subtidal natural hard substrata (Thouin 1983, Derrien-Courtel et al. 2013, Tempera et al. 2019): the bay of Biscay (part of the “South European Atlantic Shelf” in Spalding et al., 2007), the Western Channel (part of the “Celtic Seas”) and the Eastern Channel (part of the “North Sea”). Within each of the three regions, six marinas (hereafter ‘sites’), 10s km apart, and mostly dedicated to leisure boating (Table S1) were selected (Fig. 1A). All marinas were constructed at least 10 years prior to the study. Strong estuarine conditions were avoided and only sites with  $S > 30$  at 1 m (cf. e.g., Pezy et al. 2021) depth were considered. At each site, three floating pontoons, 10-100s m apart and distributed along the main navigation canal were sampled (Fig. 1B; Table S1). Surveys were done along 25 m transects located nearby this canal, therefore wherein water mixing was deemed stronger and pollutant exposure weaker (Gauff et al. 2022) to select areas with favorable conditions to seaweed growth (Fig. 1C). Along each transect (avoiding the closest 5 m edge of the canal), three stations of a linear meter were set up on both sides of the pontoon, 8-10 m apart, using weighted ropes (Fig. 1D). At each station, a series of abiotic measurements and biological community surveys were then made.

For each side of the pontoon, direct measurement of abiotic parameters included the cardinal direction ( $\pm 5^\circ$ ), the immersed height of float susceptible to colonization ( $\pm 1$  cm), the temperature ( $\pm 0.1$  °C), the salinity ( $\pm 0.01$ ), the dissolved oxygen ( $\pm 0.01$  mg L<sup>-1</sup>) and the

187 turbidity ( $\pm 0.1$  m of Secchi disc vanishment, when possible, Fig. 1D-3). Temperature, salinity  
188 and dissolved oxygen measurements were made at three positions in the water column  
189 (hereafter “position”): at 0.2 m placing the probe over the pontoon surface (i.e. within the  
190 canopy if any), at 0.2 m > 1 m away from this fouling, and at 2 m depth. The temperature and  
191 the salinity were measured using a multiparameter sensor connected to either a YSI® Pro  
192 Quatro or a HANNA® HI92192, while the dissolved oxygen was measured using a  
193 luminescent/optical dissolved dioxygen probe with built-in temperature sensor connected either  
194 to a Hach® HQ40d or a EcoSense® DO200A. An intercalibration of these probes was made *a*  
195 *posteriori* with simultaneous measurements in varying brackish to seawater conditions. For  
196 more appropriate comparisons of dissolved oxygen values, percentage dissolved oxygen  
197 saturation was calculated after accounting for temperature and salinity variations (Copin-  
198 Montegut 1996). In addition to these direct measurements, continuous records of temperature  
199 and light were made, each 15 min, using onset HOBO® Pendant Temp-Light data loggers,  
200 deployed at a depth of 0.5 m to describe the temperature regime of each site. One logger per  
201 site was deployed from the date of the sampling (Table S1) to February 2023, thus during  
202 approximately 9 months over three seasons (summer, fall and winter).

203 Biodiversity surveys included fouling (seaweed and invertebrate) and fish communities.  
204 Prior any disturbance, fish surveys were conducted by snorkel. All fish taxa were counted along  
205 a sampling unit combining both distance ( $5 \times 2$  m along the pontoon) and stationary point (2  
206 min stop at each station, i.e. at the distance transect end) samplings (Fig. 1D-1) (Leclerc &  
207 Viard 2018). Fouling seaweeds and invertebrates (comprising sessile to slowly mobile,  
208 hereafter sessile) organisms were reported using both visual and destructive samplings. On both  
209 sides of each station, a rapid assessment survey (Pederson et al. 2005) was conducted by snorkel  
210 with a time limit of 10 min (Fig. 1D-2). Each taxon was visually identified *in situ* by the same  
211 observer (JCL) and was given a score of semi-abundance from 0 to 6, according to the SACFOR

212 scale (Superabundant, Abundant, Common, Frequent, Occasional, Rare, Absent, (Hiscock  
213 1996)). At each occasion, a series of photographs were taken for reference. The taxonomic  
214 resolution generally ranged from species (small to large organisms with conspicuous attributes)  
215 to family (small to large taxa separated with microscopic criteria). Following this assessment  
216 and after measuring the vertical distance the float was immersed in water (hereafter “height”),  
217 20 cm of linear pontoons were scrapped from the surface using a scrapper and the material  
218 directly retrieved within a 500  $\mu\text{m}$  meshed sieve mounted on a floating hoop (Fig. 1D-4). This  
219 material was transferred within a plastic bag, ultimately filled with 4% formaldehyde solution  
220 and preserved in dark condition until future identification (Fig. 1D-6). The biological material  
221 associated with the remaining 80 cm of linear pontoons was collected using the same procedure  
222 and disposed on a white nylon rug for direct processing on the pontoon (Fig. 1D-5). Fouling  
223 macroorganisms were sorted into groups: foundation seaweeds separated by species, seaweed  
224 turfs separated by phyla, sessile suspension feeders separated per dominant class to phyla and  
225 grazers separated by phyla. The biomass of each group (wet weight) was measured with a  
226 precision of 1.0 g.

227

## 228 2.2.Data analyses

229 Statistical analyses were performed using R (R Development Core Team 2020) and PRIMER  
230 7 (Anderson et al. 2008). As detailed in the next subsections, scale-dependent patterns of  
231 diversity were explored separately for biomass distribution and visually assessed richness and  
232 community structures. While biomass distribution patterns in major groups (autotrophs and  
233 heterotrophs) were explored across spatial scales (*cf.* H1, H2, H3), richness and community  
234 structures were further explored for scale-dependent covariations with kelp biomass (*cf.* H4).  
235 In both cases, we relied on permutational analysis of variance (PERMANOVA, Anderson et al.  
236 2008) which provides reliable estimates of pseudo-variance components of variation associated

237 with each of our nested scales. In order to interpret these variations, abiotic conditions were  
238 compared among regions and within sites, using available temporal series and direct  
239 measurements, respectively. In addition to these multi-scale approaches, we examined further  
240 the influence of kelp biomass along with a series of environmental variables related with  
241 geographic information, biota and anthropogenic activities, using a distance-based linear  
242 modelling approach (DistLM, Anderson et al. 2008).

#### 243 *2.2.1. Temporal variations in temperature between regions*

244 Whether temporal variability in environmental conditions differed among study regions  
245 was tested by using temporal series of subsurface seawater temperature obtained with our  
246 logger data. Variability in temperature was characterized for each of four nested temporal scales  
247 (the season, the month, the day, the hour and residuals) using estimates of associated variance  
248 components from each temporal series (one per site). . This was done by implementing a  
249 random intercept univariate model with the lmerTest package, followed by the extraction of  
250 bias-corrected variance components analogous to those estimated from the mean squares of an  
251 ANOVA (Dal Bello et al. 2017). The regional variability in each variance component  
252 (separately) was latter checked using one-way (factor “region” as random) univariate  
253 PERMANOVA (Anderson et al. 2008), with 4999 permutations of raw data. Prior analysis, the  
254 homoscedasticity among regions was checked using the PERMDISP routine.

255

#### 256 *2.2.2. Variations in temperature, salinity and dissolved oxygen within sites.*

257 In order to characterize putative fine scale gradients (e.g. water stratification, distance  
258 to the port entry, *cf.* H3), a series of abiotic conditions were checked for variations within sites.  
259 Direct measurements of temperature, salinity and dissolved oxygen, at the time of sampling,  
260 were used to compare variations within each study site (i.e., variations across pontoons and  
261 positions in the water column). After examining the Q-Q plots between the response variable

262 and explanatory variables, we used permutational analyses of covariance (ANCOVA, with  
263 4999 permutations) to explore environmental gradients between pontoons at different distances  
264 to the port entry (continuous, square root transformed) among positions (random, 3 levels), after  
265 accounting for the cardinal orientation of the measurement (continuous) and sites (random, 18  
266 levels). Interactions between distances to the port entry, site and position were all included in  
267 the model. For turbidity, a similar analysis of covariance was used although it did not include  
268 the term position.

269

### 270 2.2.3. *Biomass distribution in seaweed, suspension feeders and grazers across spatial* 271 *scales*

272 The variations in the biomass and community structure (hereafter “composition”) of  
273 seaweeds, suspension feeders and grazers across spatial scales were all examined separately  
274 using a four-way PERMANOVAs with 4999 permutations under a reduced model. Spatial  
275 factors (all as random and nested within each other) were the region, the site, the pontoon and  
276 the station. In addition, the height (i.e. maximal depth of the float), affecting the surface area of  
277 the fouling, was included as a covariate. Univariate analyses were based on Euclidean distance  
278 matrices generated from either raw or transformed data, depending on the outcome of  
279 PERMDISP tests for the factor region. When no transformation allowed homoscedasticity to  
280 be achieved in univariate data, analyses were run on untransformed data using a more  
281 conservative  $\alpha$  of 0.01. Noteworthy however, we were mostly interested in the pseudo-variance  
282 components of variation associated with each term, which we extracted by setting equal the  
283 observed mean square to their expectations. When occurring, any negative estimate was set to  
284 zero and the model was adjusted by excluding the corresponding factor to re-calculate the  
285 remaining estimates. Using the same design, multivariate analyses were based on Bray-Curtis  
286 similarity matrices generated from raw data, after adding a dummy variable ( $x = 1$ ) to account

287 for the similarity in empty (e.g. disturbed) plots. When appropriate and for the highest random  
288 factor (region) only, PERMANOVAs were followed by pairwise comparisons and the  
289 respective contributions of specific variables to the multivariate structure were explored using  
290 similarity percentage analyses (SIMPER).

291

292 2.2.4. *Diversity and structure of sessile taxon and fish communities and covariations with*  
293 *kelp abundance.*

294 The variations in the richness and structure of sessile taxon and fish communities across  
295 spatial scales were all examined separately using three to four-way PERMANOVAs with 4999  
296 permutations under a reduced model. Of the four main nested factors outlined above, the station  
297 could not be included in the case of fish, in the absence of replicates at this scale. The covariate  
298 of interest for this analysis was the kelp *stricto sensu* (i.e. Laminariales) biomass, which was  
299 previously log-transformed, to ensure its appropriate dispersion in the data. Other “forest  
300 forming seaweeds”, such as Fucales were not included in this analysis, as they were only  
301 observed in 7 out of 18 sites and were poor contributors to the seaweed biomass (0.1 to 3.5%).  
302 Because we were interested in covariations in diversity and composition at multiple spatial  
303 scales, our model also included three interactions terms: “kelp biomass  $\times$  region”, “kelp  
304 biomass  $\times$  site” and “kelp biomass  $\times$  pontoon”. Owing to the limited replication within station  
305 (i.e. in the case of sessile taxa,  $n = 2$ ), the interaction of the covariate with this term was not  
306 included. Univariate analyses were based on Euclidean distance matrices generated from either  
307 raw or transformed data as detailed above. Multivariate analyses were based on Bray-Curtis  
308 similarity matrices generated from log-transformed counts of fish, and untransformed scores  
309 (from 0 to 6) for sessile taxa. Note that kelp species were dropped off from the sessile taxon  $\times$   
310 sample matrix and associated richness estimate to avoid collinearity. PERMANOVA results  
311 were supported by ordination using principal coordinate (PCoA) analyses based on the same

312 similarity matrices. In order to better understand our results with respect to biogeography and  
313 coevolution history between biota, we repeated the analyses focusing either on indigenous or  
314 nonindigenous kelp biomass as covariate.

315

#### 316 2.2.5. *Geographic and biotic variable accounting to the variability in the data clouds.*

317 In addition to our multi-scale approach, we examined further the influence of kelp  
318 biomass along with a series of environmental variables (categorical to continuous) available for  
319 either the site, the pontoon or the patch (i.e. replicate) scale (Table S1). These explanatory  
320 variables comprised (i) geographic information, such as latitude, longitude, distance to entry  
321 (square root transformed) and orientation, (ii) biotic variables, such as the fouling height and  
322 biomasses (all log-transformed to avoid skewness) of grazers, suspension feeders and kelp, as  
323 well as (iii) anthropogenic proxies, such as the number of berths (correlated with the number  
324 and size of pontoons, which were discarded from analyses), an international connection score  
325 (ranging from 0 to 2 depending on whether overseas ferry and commercial shipping coexisted),  
326 a water mixing score (depending on the number of port entries and presence of a step  $\pm$  lock)  
327 and known disturbance associated with recent ( $< 6$  mo) maintenance (e.g. clearing or pontoon  
328 section replacements). Although further detailed disturbance history was sought from port  
329 operators and users through direct interviews and questionnaires, sole this 6 mo threshold was  
330 deemed viable in all ports and parsimoniously retained. Depending on their *a priori* relevance  
331 or lack of collinearity with our response variables (e.g. abundances, richness and composition  
332 of each group), the influence of these explanatory variables were examined using a distance-  
333 based linear modelling approach (DistLM, Anderson et al. 2008) using the same matrices as  
334 described above (i.e. on the full datasets). The explained variations ( $R^2$ ) was calculated for each  
335 of these variables and the best overall model was selected according to a modified Akaike  
336 Information Criterion (AICc) following a step wise selection procedure (4999 permutations),

337 whereby conditional test associated with either the addition or removal of a given variable is  
338 done at each step (Anderson et al. 2008). Fitted models were routinely visualized by distance-  
339 based redundancy analysis (dbRDA, not presented).



### 340 3. RESULTS

#### 341 *3.1. Temporal variations in temperature do not follow ecoregional patterns.*

342 Over the same 9 months period, temporal variations in temperature at 0.5 m depth varied  
343 greatly among sites, especially among seasons (Fig. 2A, loggers retrieved in 13 out of 18 sites).  
344 The variations observed in Deauville (from 2.8°C in winter to 24.5°C in summer, Fig. 2B) were  
345 twice as much as those observed in Aber Wrac'h (from 8.3°C in winter to 19.2°C in summer,  
346 Fig. 2C). Low values in the cumulated variance components in temperature were estimated in  
347 the westernmost sites (Saint Guénolé, Brest, Aber Wrac'h and Roscoff, Fig. 1A, Fig. 2D).  
348 Contrary to our expectations, none of those variance components however differed among the  
349 three ecoregions: Season (PERMANOVA Pseudo- $F_{2,12} = 1.61$ ,  $P_{MC} = 0.242$ ), Month (Pseudo-  
350  $F_{2,12} = 1.00$ ,  $P_{MC} = 0.404$ ), Day (Pseudo- $F_{2,12} = 2.54$ ,  $P_{MC} = 0.129$ ), Hour (Pseudo- $F_{2,12} = 1.35$ ,  
351  $P_{MC} = 0.301$ ) and Residual (Pseudo- $F_{2,12} = 0.57$ ,  $P_{MC} = 0.586$ ).

352

#### 353 *3.2.A abiotic conditions generally varied according to the distance to entry although* 354 *gradients are site-dependent.*

355 Direct measurements of abiotic parameters made at the time of the sampling revealed important  
356 variations within site in abiotic conditions, especially according to the distance to the port entry  
357 (ANCOVA, Table S1). For temperature and dissolved oxygen, these gradients were position  
358 dependent although the position in the water column generally explained only a small portion  
359 of the variation in the data (sum of all terms equaling 0.2-5.4%, cf. Distance  $\times$  Site interactions,  
360 Table S2). At the time of sampling, mean site temperature varied between 14.2°C (Cherbourg)  
361 and 18.1°C (Fécamp) at 0.2 m depth along the pontoon (Table S1) and the values did not differ  
362 markedly with those obtained 2 m away from the canopy at the same depth (significantly higher  
363 by 0.1-0.2°C in only two sites, cf. Position  $\times$  Site interaction and pairwise tests in Table S2).  
364 Colder temperatures were generally observed at 2 m depth (from 13.8°C to 17.9°C in the same

365 sites, Table S1), with significant differences in 15 out of 18 sites. With oxygen concentration  
366 varying from 8.6 mg L<sup>-1</sup> (Dieppe) to 12.6 mg L<sup>-1</sup> (Trébeurden), percent oxygen was generally  
367 > 100% (up to 154.6% in Trébeurden), with the sole exception of Dieppe (95.7% at 0.2 m  
368 depth). At a depth of 2 m, salinity was also generally greater than at 0.2 m (Table S1 and cf.  
369 Position × Site in Table S2), with values ranging from 29.5 (Dieppe, on a heavy rainy day) to  
370 36.2 (Saint Guénolé). There was also a strong “distance to entry” effect with 53.2% of variation  
371 in salinity associated with the main term and 6.1% of variation associated with its interaction  
372 with positions (Table S2). A Distance × Site effect was also detected regarding turbidity as  
373 estimated by Secchi disc estimates but gradients were inconsistent across sites. It is noteworthy  
374 that our logger data revealed that up to 5.0°C of subsurface temperature variation could occur  
375 locally within a single month. We thus did not compare these direct measurement values across  
376 all spatial scales, in the absence of temporal replication.

377 *3.3. The spatial variations in the biomass and community structure of seaweed, suspension*  
378 *feeder and grazer communities at multiple spatial scales are not all consistent.*

379 The magnitude of variability in seaweed biomass and composition was greater within  
380 than among regions (Table 1, Table S3). Region only accounted for 5.9% of variation in  
381 seaweed biomass and the associated effect was not significant (contrary to H1). Seaweed  
382 biomass varied however markedly and significantly among sites (31.1% C.V., aligning with  
383 H2), ranging from 21.2 gWW m<sup>-1</sup> in Pornichet (within the Bay of Biscay) to 1575.1 gWW m<sup>-1</sup>  
384 in Roscoff (Western Channel, Fig. 3A). It also varied among pontoons within sites (20.2% of  
385 variation, aligning with H3). In several of the more enclosed sites, seaweeds were indeed less  
386 abundant along the innermost pontoons as compared with pontoons located nearby the port  
387 entry (e.g. ranging from 339.6 ± 136.1 gWW m<sup>-1</sup> to 1937.0 ± 973.4 gWW m<sup>-1</sup> along such  
388 gradient in Saint Quay, ± S.D.). This result was generally confirmed by the distance based linear  
389 models (DistLMs), which ranked the “distance to entry” as the first variable explaining

390 variability in total seaweed biomass but also in their composition (Table 3, Table S4). The  
391 spatial variability in seaweed composition was rather consistent with seaweed total biomass  
392 (Table 1). Although significant differences in composition were observed among regions (Fig.  
393 3A), the term only accounted for 8.0% of the total variation (cf. H1). It is noteworthy that more  
394 than 70% of the among-group variation (SIMPER following pairwise tests) was explained by  
395 the nonindigenous kelp *Undaria pinnatifida* (335.4 gWW m<sup>-1</sup> in the Western Channel vs. 36.9  
396 gWW m<sup>-1</sup> in the Bay of Biscay and 165.4 in the Eastern Channel), red seaweeds (124.4 vs. 58.8  
397 and 17.4 gWW m<sup>-1</sup>) and green seaweeds (27.2 vs. 52.2 and 48.3 gWW m<sup>-1</sup>). Like for the total  
398 biomass, the associated composition varied markedly among sites within region (28.8% C.V.,  
399 cf. H2). Among the taxa mostly contributing to this pattern are native kelps that are confined to  
400 Brittany (*Laminaria* spp. and *Saccharina latissima*, Table S6) and more abundant in the  
401 westernmost sites of both the Bay of Biscay and the Western Channel (Fig. 3A). When present,  
402 all kelp species were major contributors of variations in seaweed biomass among pontoons  
403 (Table 1, and distance to entry in DistLM, Table 3, cf. H3). In either the total seaweed biomass  
404 or its composition, residual variability was substantial (> 40 % C.V.). The residual variability  
405 was even more pronounced with the selected DistLMs (cf. R<sup>2</sup> in Table 3)..

406         Conversely to seaweeds, suspension-feeder biomass varied markedly (cf. PERMISP and  
407 PERMANOVA) and significantly among regions (32.3% C.V., Table 1, Table S3). It is six  
408 times as great in the Bay of Biscay (3327.7 ± 2365.8 gWW m<sup>-1</sup>, ± S.D., pairwise test) as in the  
409 Western Channel (770.0 ± 480.7 gWW m<sup>-1</sup>) and Eastern Channel (361.1 ± 358.1 Fig. 3B).  
410 These differences were generally reflected in the suspension-feeder composition, although they  
411 were associated with less variation (11.8% C.V.). More than 70% of the among-group variation  
412 was explained by the mussels *Mytilus* sp. which were about approximately ten times as much  
413 abundant in the Bay of Biscay (3114.1 gWW m<sup>-1</sup>) as in the two other regions (327.7 gWW m<sup>-1</sup>  
414 <sup>1</sup> in Western Channel and 534.2 gWW m<sup>-1</sup> in the Eastern Western Channel, Fig. 3B).

415 Substantial variation was also observed among sites (ca. 26% C.V. in either total biomass or  
416 composition), with up to 7259.7 gWW m<sup>-1</sup> observed in the southernmost site of Pornichet. The  
417 selected DistLMs revealed both a latitudinal (ranking first) and longitudinal (ranking third)  
418 gradients in the biomass and composition of suspension feeders (Table 3, Table S4), recent  
419 disturbance ranking second in either case. Total biomass and composition also varied markedly  
420 among pontoons (> 12% C.V.) and among stations (> 4%). The residuals represented up to 39%  
421 C.V.

422 When occurring, macrograzers were largely dominated in composition and biomass by  
423 *Patella* spp., while other taxa such sea urchins or abalones were only observed in Concarneau  
424 and Brest (Table S6). Grazer biomass varied weakly among regions (3.2% C.V., Table S1,  
425 Table S3) but substantially (and significantly) among sites (44.3%), as also shown by the  
426 influence of geographic variables in DistLM (Table 3), and among pontoons within sites (Table  
427 1). Grazer were absent in four sites out of eighteen (Saint Quay, Granville, Deauville Dieppe)  
428 and almost absent (< 1 gWW m<sup>-1</sup>) in Pornichet and Locquiquelic, while they reached up to  
429  $97.8 \pm 75.4$  gWW m<sup>-1</sup> ( $\pm$  S.D) in Fécamp.

430

431 *3.4. The diversity and composition of sessile taxa and fish covaried with kelp biomass at*  
432 *varying spatial scales (cf. H4).*

433 By using a joint survey, we examined the covariations between fish, fouling taxa and  
434 kelp biomass. Across all sites, a total of 15 fish and 177 fouling taxa (comprising 86 seaweeds  
435 and 91 animals) were identified underwater with stationary point census and rapid assessment  
436 surveys, respectively.

437 Fish richness varied markedly among sites (18.4% C.V., Table 2), ranging for instance  
438 in the Bay of Biscay, from 0.2 species per sampling unit (2 on total per site) in Pornichet to 1.3  
439 (5 on total) in Saint Guénolé (Fig. 4A). While fish richness did not vary significantly among

440 regions, a significant interaction between region and kelp biomass was detected ( $P_{MC} = 0.039$ ,  
441 Table S7). Note that this result is to be considered with caution considering PERMDISP result  
442 with such an  $\alpha$  level ( $P_{perm} = 0.031$ ) and that no significant relationships between fish richness  
443 and kelp biomass was revealed within any of the regions (Fig. 4B). Altogether, as a main factor  
444 and interactions, kelp biomass would account for 15.6% C.V. in fish richness. Kelp biomass  
445 explained 24.2% of the total variation for fish composition (up to 16.4% for the kelp  $\times$  pontoon  
446 interaction) and its effect was significant ( $P_{MC} = 0.046$ , Table 2, Table S8) when considered  
447 alone. Fish composition varied also markedly among sites within region (17.4% C.V., Table 2).  
448 According to the principal coordinate analyses, sites were mostly discriminated by their  
449 abundances of mullets *Chelon labrosus* (axis 1) and pollocks *Pollachius pollachius* (axis 2, Fig.  
450 5A-B).

451         The richness of sessile taxa (invertebrates and seaweeds), excluding kelps, varied  
452 markedly among sites (28.1% C.V., Table 2), ranging for instance in the Bay of Biscay, from  
453 9.2 species  $m^{-1}$  (28 on total per site) in Pornichet to 22.2 (65 on total) in Concarneau (Fig. 4C).  
454 Like for fish, the sessile taxa richness did not vary significantly among regions considered  
455 alone, but a significant interaction between region and kelp biomass was detected (Table 2,  
456 Table S9). At this scale, positive and significant relationship between richness and kelp biomass  
457 were observed in the Bay of Biscay and Eastern Channel, but not in the Western Channel (Fig.  
458 4D). Altogether (as a main factor and interaction), kelp biomass would account for 30.4% C.V.  
459 in sessile taxa richness – a result consistent with DistLM ranking second this term (Table 4,  
460 Table S5). Sessile taxa richness also varied significantly among pontoons and stations, the  
461 former effect being consistent with the strong “distance to entry” effect in the DistLM (Table  
462 4). Sessile taxa composition varied significantly and generally covaried with kelp biomass at  
463 any spatial scale examined (all terms except kelp  $\times$  pontoons being significant, Table 2, S6). A  
464 significant effect of the region was detected in either position and dispersion (Table 2 and Fig.

465 5C). Indeed, a substantial variability was also detected among sites within regions (37.9%  
466 C.V.), rather well reflected in the latitude and longitude terms in retained DistLM, Table 4) and  
467 although the first axis in the PCoA discriminates the Western Channel due to diverse taxa  
468 (notably sponges, ascidians, bryozoans and red seaweeds, Fig. 5D), several sites from the  
469 Eastern Channel and the westernmost sites from the Bay of Biscay overlap in the ordination  
470 (Fig. 5C). The Bay of Biscay is however rather well discriminated from most of the other sites  
471 along the axis 2 owing notably to a greater semi-abundance in *Mytilus* mussels (Fig. 5D;  
472 Fig.3B) hence aligning with results on biomass. As a main factor and interactions, kelp biomass  
473 would account for a total of 9.5% C.V. in sessile taxa composition. Sessile composition may  
474 vary with other numerous variables, such as the distance to entry and several port characteristics  
475 (size, openness and international connection) and maintenance (Table 4).

476

### 477 *3.5. The native vs. nonindigenous origin of kelps matters for covariation scales*

478 When separating kelp by either their native or nonindigenous origin, contrasting effects  
479 of kelp biomass were observed in fish richness and composition (Table S7-S8). With  
480 nonindigenous kelps only, stronger covariations between kelp biomass and region were  
481 observed for fish richness ( $P = 0.007$ , 17.6% C.V.) or composition ( $P = 0.005$ , 14.4%). With  
482 native kelps only, total kelp contribution to the model increased but mainly at the smaller spatial  
483 scales: site (11.3% of variation in fish richness) and pontoon (12.2% of variation in fish  
484 composition). In either case, a decrease in the unexplained variability (of 7.6 to 16.4%) was  
485 observed (cf. residuals in Table S7-S8). It is noteworthy that native kelp biomass also ranked  
486 first among the explanatory variables retained in the most parsimonious – but rather powerless  
487 (cf.  $R^2$ ) – distance-based models for both the fish richness and composition (Table 4).

488 Similar results were observed for sessile taxa richness and composition (Table S9-S10).

489 While the kelp  $\times$  region interaction in richness was strengthened with nonindigenous kelps,

490 interactions remained significant when native kelps only were included, but at smaller spatial  
491 scales (site, pontoon). As for the composition, significant interactions between kelp biomass  
492 and all spatial scales were observed when only nonindigenous kelp were considered. In contrast,  
493 when only native kelps were considered, only the interactions with the scales of sites and  
494 pontoons were significant.

495       **4. DISCUSSION**

496           By examining the diversity and structure of seaweeds, fouling invertebrates and fish  
497 communities, associated with floating pontoons, we showed that most of our working  
498 hypotheses were not supported, or only partially for some of the studied taxa. In particular,  
499 although the seaweed composition varied among regions, as expected (H1), these differences  
500 accounted for a small portion of the total variation and were due to the single nonindigenous  
501 kelp reported in our survey (i.e. *Undaria pinnatifida*). The observed spatial sea surface  
502 temperature regimes across sites also do not follow regional patterns. In addition, as  
503 hypothesized (H2), the diversity, biomass, and structure in all study communities were highly  
504 variable among sites, but the sites accounted for much more variability than region, with a  
505 single exception (i.e., suspension feeder biomass). We note however that our results support  
506 our third hypothesis (H3). Community structure was indeed highly variable among pontoons.  
507 This result was strengthened by a “distance to entry” effect in distance-based models, although  
508 this pattern was stronger for fouling than for fish communities. Finally, several covariations  
509 between diversity and structure of fish and sessile communities with kelp biomass were  
510 observed, as hypothesized (H4), but the scale of these covariations differed whether they are  
511 examined with native or nonindigenous kelps.

512

513       4.1. *Biodiversity and composition varied at large scale but not as expected from natural*  
514       *biogeographic patterns.*

515           Embedded in port environments, floating pontoons represent unique habitats opened to  
516 the colonization by novel sessile assemblages in which singular environmental filters and  
517 dispersal pathways may prevail upon processes acting in natural environments and delineating  
518 natural biogeographic patterns (Holloway & Connell 2002, Dafforn et al. 2009, Mineur et al.



519 2012, Rogers et al. 2016, Bishop et al. 2017, Leclerc et al. 2020). In our study, the effect of the  
520 region on biomass, richness or compositions was generally weak, if any. Moreover, the pattern  
521 observed in our study did not follow biogeographic patterns reported from natural rocky reefs  
522 (Thouin 1983, Derrien-Courtel et al. 2013, Tempera et al. 2019). In particular, we did not  
523 observe a shift in the contribution of long-lived native kelps, such as *Laminaria hyperborea*,  
524 between Northern and Southern Brittany (i.e. opposing the Western Channel to the Bay of  
525 Biscay). In our study, the main contributor to seaweed biomass composition was the  
526 nonindigenous kelp *Undaria pinnatifida*, which is disproportionally abundant in marinas as  
527 compared to other kelps (Fig. 3) in Brittany, wherein it is cultivated since the early 1980's  
528 (Floc'h et al. 1996), and compared to natural reefs in the English Channel (Epstein & Smale  
529 2018 and references therein). Unlike other kelps, this species is widespread across the three  
530 study regions (Fig. 3). This pattern is consistent with its strong ability to human-mediated  
531 dispersal through hull fouling (Mineur et al. 2012, South et al. 2017, Guzinski et al. 2018), its  
532 ability to quickly establish dense populations in marinas (Salamon et al. 2020), and its broad  
533 environmental tolerance (Epstein & Smale 2017, Murphy et al. 2017). In particular, although  
534 gametogenesis is constrained by mild temperatures and light levels, both *U. pinnatifida*  
535 sporophytes and gametophytes can survive for months to years at temperatures ranging between  
536  $-1$  and  $30^{\circ}\text{C}$ , and this ranges fits within that observed over the temperature survey at 0.5 m  
537 depth in all sites (Fig. 2). In contrast, while culture gametophytes of the native kelp *Saccharina*  
538 *latissima*, *Laminaria digitata* and *Laminaria hyperborea* are rather resistant and perform well  
539 under  $0^{\circ}\text{C}$  exposure (Sjötun & Schoschina 2002), they can hardly survive more than two weeks  
540 above 23, 22-23 and  $21^{\circ}\text{C}$ , respectively (Bolton & Lüning 1982). According to our 9 mo  
541 temperature survey, these maxima (99<sup>th</sup> percentile) would make 9 out of 13 sites wherein  
542 loggers were deployed suboptimal for native kelp. Prolongation of temperature above these  
543 values for periods of more than a week (up to ten weeks) in a raw further suggests that that 6 of

544 these sites are unsuitable for native kelp to renew their population, regardless of *a priori* defined  
545 regions. Native kelps are herein rather confined to the Western- and Northwesternmost sites of  
546 Brittany, which are, along with the tip of the Cotentin Peninsula (e.g. Cherbourg wherein a  
547 young *Laminaria hyperborea* was also recorded), under the influence of a so far permanent  
548 cold water body (Gallon et al. 2014). Although further processes certainly contribute to the  
549 local and regional distributions of these kelp species in their natural environments [e.g. turbidity  
550 and substratum availability (Thouin 1983, Derrien-Courtel et al. 2013, Robuchon et al. 2017)],  
551 our observations strongly suggest that temperature variations (which is herein not related to *a*  
552 *priori* defined regions) experienced by these organisms under floating pontoons is a barrier to  
553 their establishment and fate upon these novel substrates (cf. Wang et al. 2020). Besides human  
554 altered dispersal across biogeographic boundaries as exemplified by *Undaria pinnatifida*,  
555 several processes operating at smaller scales and detailed in the next subsections, may  
556 contribute to this novel biodiversity redistribution over broad scales.

557

558 *4.2. Overlapping processes may explain the substantial variations in diversity and structure*  
559 *from micro- to meso-scales.*

560 Although not taking into account for the known nested structure, distance-based models  
561 give hints into the influence of various factors such as port openness (water mixing, adding to  
562 the distance entry effect), port maintenance (recent disturbance), port size (number of berths),  
563 anthropogenic connectivity (international connection) as well as latitude, longitude and grazer  
564 biomass.

565 Site-to-site variations were substantial for all response variables considered in our study.  
566 Among the explanatory variables available at the scale of site, both the number of berths and  
567 the international connection score were ranked among the first terms in selected distance-based

568 models on seaweed and sessile invertebrate structure. Both these proxies are related to the  
569 degree of human aided connectivity as well as the size of the habitat (i.e. the port along with its  
570 artificial substrates). Neither these proxies however were retained in the selected model on  
571 sessile richness (visually assessed). Besides other anthropogenic pathways of dispersal which  
572 could hardly be scored for the models (e.g. aquaculture, Table S2), this result could reflect some  
573 complex balance between the colonization pressure (richness of putative colonizers) and the  
574 propagule pressure of the most performant and/or dominants organisms which may be sorted  
575 by other abiotic and biotic processes.

576       Regarding abiotic environment, port openness came out within selected models on seaweed  
577 and suspension feeder biomass or composition, and notably came along with the distance to  
578 entry (measured at the pontoon scale) for seaweeds. This result is consistent with water  
579 movement requirements of foundation seaweeds to directly perform photosynthesis (by  
580 disrupting the diffuse boundary layer accumulating at the surface of thallus (Hurd 2000)) or  
581 indirectly avoiding its inhibition, which could results from local and within-site accumulations  
582 of contaminants (e.g. Copper) (Connan & Stengel 2011, Johnston et al. 2011, Guerra-García et  
583 al. 2021). The strong relations (general and site-dependent) also observed between our direct  
584 measurements of salinity and the distance to entry also suggest that spatiotemporal variations  
585 in salinity within these novel marine assemblages can also be important (Dafforn et al.  
586 2009)(but see Saloni & Crowe 2015). Regarding biotic processes, it is noteworthy that the  
587 biomass of macrograzers, which was measured at the scale of plot, displayed substantial site-  
588 to-site variations. This variable was also retained in selected models on seaweed and sessile  
589 taxon compositions. Predation *sensu lato* might thus be an important process to investigate in  
590 further details. Such as in natural reefs (Leclerc 2018), we indeed observed empty to crustose  
591 coralline dominated patches that were filled with radula marks marking a vertical limit of  
592 epibiota. Although similar patterns have been described and causality demonstrated elsewhere

593 (Cole et al. 2005), they were herein pervasive in some sites but absent in others. They may  
594 interact with other biotic disturbance, such as seagull predation upon suspension feeders  
595 (Holman et al. 2019). We did observe conspicuous signs of seagull predation, such as feces and  
596 seashells remaining upon the pontoon floor. While we did not anticipate a way to address this  
597 effect, identifying proxies for predation by higher order taxa would certainly provide valuable  
598 information on spatial variation between sites.

599 Another singularity of marinas is the disturbance level due to surface cleaning and pontoon  
600 replacement. Maintenance practices in marinas are well known to impact sessile fauna  
601 assemblages (O'Shaughnessy et al. 2020). Since these disturbances reinitiate succession, it is  
602 of little surprise to find this term ranking among the first explanatory variables in either  
603 biomass, richness or composition of seaweeds, suspension feeders and overall sessile taxa.  
604 Noteworthy, and as observed in our study (Table S1) such maintenance can be practiced at the  
605 scales of patch (marina users on their will), the pontoon (replacements) and the site (depending  
606 on local operator policy) and a broad range of spatial scales, and this has certainly produced  
607 much variations across all the study spatial scales. Neither of these practices are however carved  
608 into stone. As a side note indeed, while the questionnaire filled in by some of the operators did  
609 not allow to trace back detailed history of each port or pontoon (cf. work of Aguilera et al. 2022  
610 on breakwaters), it revealed – surprisingly (O'Shaughnessy et al. 2020) – that many experienced  
611 port operators tend to favor the natural development of diverse sessile assemblages at the  
612 expense of annual cleaning facilitating the development of fast-growing taxa. Considering the  
613 ongoing rush towards environmental labelling in marine urban systems, there are pressing needs  
614 to evaluate the effect of changing maintenance or eco-engineering practices on biodiversity at  
615 multiple spatial scales (Firth et al. 2020, Airoidi et al. 2021, Gauff et al. 2023).

616

617 4.3. *Diversity covary with kelp biomass but the scale of covariation depends on native vs.*  
618 *nonindigenous origin of kelps.*

619 Understanding the role of foundation species in artificial infrastructures is critical to get  
620 fundamental knowledge on biodiversity and ecosystem functioning (Airoldi et al. 2021, Leclerc  
621 et al. 2021). In our work, we did not examine causal links (Anderson et al. 2008) but made a  
622 preliminary exploration of the specific role of Laminarian kelps through a series of co-  
623 variations analyses in order to give support and provide guidance for future experimental work.  
624 Overall, we observed important covariations between kelp biomass and the diversity and  
625 structure of either fish and sessile taxa, with both scale- and origin-dependent effects. Kelp  
626 biomass was for instance one of the main explanatory variables in fish diversity and community  
627 structure. Both DISTLM and PERMANOVA showed the importance of native kelps in this  
628 pattern at the scale of the site and pontoons, which is consistent with their restricted distribution  
629 in the study regions. This effect mainly involved the distribution of *Pollachius* juvenile schools  
630 known to use regional kelp forests (Norderhaug et al. 2020). In contrast, synanthropes to  
631 beneath pontoon habitat, such as the *Chelon* mullets (Leclerc & Viard 2018), varied  
632 independently of kelps. We did not detect further effect of sessile biota (e.g. suspension feeders)  
633 on fish, conversely to what has been reported in SE Australia in other artificial habitats such as  
634 pilings (Coleman & Connell 2001, Clynick et al. 2007). As for sessile taxa, interactions at  
635 smaller spatial scales (site, pontoon) remained significant only when nonindigenous kelp were  
636 excluded. Co-occurrences between diverse categories of organisms (e.g., understory or  
637 epiphytes, native or nonindigenous) and conspicuous foundation species, such as seaweeds and  
638 mussels, would be worth to be scrutinized in further work.

639 When considering variations at the regional scale, results on fish composition concur with  
640 findings on sessile taxa: Sessile taxa richness and composition varied (positively) with kelp  
641 biomass in two regions out of three (Fig. 4B), but both DISTLMs and separate PERMANOVAs

642 revealed that this effect may mostly be due to the nonindigenous kelp *Undaria pinnatifida*, in  
643 particular, which was widespread but strongly varied in abundance. Although some species  
644 interactions can drive patterns across broad biogeographic scales (Coleman et al. 2006, Ashton  
645 et al. 2022), it is certainly premature to attribute this result to some form of facilitation between  
646 this annual kelp and sessile taxa. We nonetheless note that literature on the topic suggests that  
647 *Undaria* invasions in new localities have mostly been accompanied by neutral to positive  
648 effects on understory richness depending on local conditions and recipient assemblages (South  
649 et al. 2017). Interestingly, there is considerable evidence in the mostly invasion-driven literature  
650 that some sessile taxa (e.g. turfs, ascidians) can facilitate *Undaria* for the above mentioned  
651 provision of substrate to either sporophyte and the gametophytes (Thompson & Schiel 2012,  
652 Arcángel et al. 2022). It is also likely that *Undaria* and several nonindigenous species, most of  
653 which generally sharing traits conducive to hull fouling, cooccur wherein they share  
654 environmental tolerance.

#### 655 *4.4.Perspectives, limitations and concluding remarks*

656 By investigating in concert several components of fouling (seaweeds and sessile  
657 invertebrates and fish along floating pontoons at scales ranging from 1-10s cm to 100s km, our  
658 study constitutes a unique – but easily transferable – exploration of the patterns, and putative  
659 drivers, of diversity and structure of these communities in marine urban habitats. Interestingly,  
660 substantial intra-station and residual variability herein revealed are consistent with findings in  
661 either intertidal and subtidal natural hard substrata (Fraschetti et al. 2005). We note for instance  
662 that shading and disturbances associated with frequently observed seaweed and anthropogenic  
663 rafts may be highly variable in time (accidental pollution, tide, season) and space and likely  
664 interact with the position of boats, catways and pontoon orientation. We also clearly showed a  
665 strong effect of the “distance to entry” variable, but we would like to stress out the limitation  
666 of our sampling that certainly did not captured all stress gradients elsewhere described (Gauff

667 et al. 2022, Hawk & Johnson 2022), and which could influence foundation species and  
668 associated communities. Expanding our work on nearby natural reefs would also be of strong  
669 interest, as it may allow to examine putative interactions between artificial and natural habitats,  
670 for example the effect of surrounding habitats on fish (Franzitta & Airoidi 2019). Repetition of  
671 this type of study in time should also help strengthening our understanding of drivers of mobile  
672 communities, such as fish, for which the substantial residual variability may partly be due to  
673 the one-shot nature of our study. Another limitation is the taxonomic identification that could  
674 be achieved, notably during our rapid assessment surveys (RAS). RAS were critical to  
675 characterize the structure of sessile communities across multiple spatial scales but they are  
676 limited in their accuracy due to the impossibility to assign all specimens to species, unless  
677 additional time are dedicated to specimen collection and/or multiple experts are gathered  
678 (Carlton & Schwindt 2024). Of the 177 taxa identified *in situ*, 63 displayed criteria conspicuous  
679 enough to ascertain identification at the species level while others would have required  
680 microscopic examination. Because of this limitation, the native vs. nonindigenous status of  
681 many taxa could not be assigned. Overcoming such issue, for instance by enhanced taxonomic  
682 training (Carlton & Schwindt 2024) and/or indirect tools (e.g., metabarcoding; Couton et al.  
683 2022), would be extremely valuable, especially to further investigate how invasion processes  
684 interact with urbanization in reshaping biogeography (McKinney 2006, Marchini & Cardeccia  
685 2017, Darling & Carlton 2018). As shown elsewhere, our results however showed that a  
686 reasonable degree of taxonomic sufficiency, especially coupled with biomass, can depict  
687 consistent large-scale patterns (Anderson et al. 2005, Guerra-García et al. 2021), embrace  
688 functional attributes and underpin associated processes (Bustamante & Branch 1996, Ashton et  
689 al. 2022). In particular, we report a rather striking latitudinal gradient in suspension feeder, and  
690 more specifically in *Mytilus*, biomass echoing kelp-to-mussel shifts in natural reefs of the  
691 southernmost region (de Bettignies et al. 2021) for which the complex causes and functional

692 consequences of such changes from local (Ratmaya et al. 2019), regional (Gallon et al. 2014)  
693 to broader scales (Malerba et al. 2019) are far from being fully elucidated.

694

695 **Acknowledgements.** We are grateful to all port operators for granting us access to the study  
696 sites, and for their kind help with logistics. We are indebted to Laurent Lévêque for his seminal  
697 work and shared expertise on the fouling communities of the region, which notably helped  
698 building the rapid assessment surveys up. We also thank Claire Daguin-Thiébaud, Yuna Tauzia,  
699 Clara Duval and Basile Robbe for their assistance with fieldwork. We are grateful to the  
700 handling editor and three anonymous reviewers, whose comments helped greatly to improve  
701 the manuscript. This work is licensed under CC BY 4.0. JCL received funding from the  
702 European Union's Horizon 2020 research and programme under the Marie Skłodowska-Curie  
703 grant agreement No 899546. This is publication ISEM 202X-XXX. TW and KFD were  
704 supported by the Australian Research Council (DP220100650) and the Norwegian Research  
705 Council (335371).

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## TABLES

Table 1. Summary of PERMANOVA tests for differences in the biomass and composition of seaweeds, suspension feeders and grazers, among levels of the tested factors (height, region, site, pontoon and station), and associated component of variation expressed as a percentage (C.V.). PERMDISP results and pairwise tests are summarized for the factor region: Bay of Biscay (BB), Western Channel (WC) and Eastern Channel (EC). <sup>m</sup>marginally significant at  $\alpha = 0.07$ , \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001. Detailed results are provided in Table S3

		Macroalgae		Suspension feeders		Grazers ( <i>Patella</i> spp. mostly)
PERMDISP Region		Total biomass	Composition	Total biomass	Composition	Total biomass
			***	***	***	***
			WC ≠ (BB = EC)	BB ≠ (WC = EC)	BB ≠ (WC = EC)	EC ≠ (WC = BB)
Source	df	C.V.	C.V.	C.V.	C.V.	C.V.
Height = He	1	0	0.3	7.4 <sup>m</sup>	1.1 <sup>m</sup>	0
Region = Re	2	5.9	8.0**	32.3**	11.8**	3.2
Site(Re) = Si	15	31.1***	28.8***	26.6***	26.2***	44.3***
Pontoon(Si(Re)) = Po	36	20.2***	10.4***	12.6***	14.8***	23.4***
Station(Po(Si(Re)))	108	0	0.8	4.8	7.2***	3.7 <sup>m</sup>
Residuals	161	42.8	51.6	16.3	39	25.3
Total	323					
Pairwise test for Region:			WC ≠ (BB = EC)	BB ≠ (WC = EC)	BB ≠ (WC = EC)	



Table 2. Summary of PERMANOVA tests for differences in the richness and composition of fish and sessile taxa, among levels of the main factors (kelp biomass, region, site, pontoon and station) and their interactions. For each term (C.V.), the component of variation is expressed as a percentage. PERMDISP results and pairwise tests are summarized for the factor region: Bay of Biscay (BB), Western Channel (WC) and Eastern Channel (EC). <sup>m</sup>marginally significant at  $\alpha = 0.07$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

Variable	Fish			Sessile taxa		
	Richness	Composition		Richness	Composition	
PERMDISP Region	*	**		***	*	
	EC $\neq$ (WC = BB)	EC $\neq$ (WC = BB)		BB $\neq$ (WC = EC)	(WC $\neq$ BB) = (WC $\neq^m$ EC)	
	df	C.V.	C.V.	df	C.V.	C.V.
Kelp biomass = Ke	1	2.7 <sup>m</sup>	2.1*	1	17.5**	3.5**
Region = Re	2	1.3	2.6	2	5.9	8.1**
Site(Re) = Si	15	18.4**	17.4***	15	28.1***	37.9***
Ke $\times$ Re	2	13.0*	6.1*	2	7.5**	1.6***
Pontoon(Si(Re)) = Po	36	0	9.6***	36	13.6***	12.6***
Ke $\times$ Si(Re)	10	0	0	10	0.8	3.7***
Station(Po(Si(Re)))	-	-	-	108	4.8	1.6*
Ke $\times$ Po(Si(Re))	23	0	16.4	23	4.6	0.7
Residuals	72	64.6	45.7	126	17.3	30.2
Total	161			323		
Pairwise test for Region:				WC $\neq^m$ (BB = EC)		WC $\neq$ (BB $\neq^m$ EC)

Table 3. Summary of DISTLM outputs for relationship between available environmental (geographic, biotic) variables and the biomass and composition of seaweeds, suspension feeders and grazers. Marginal tests are summarized by Pseudo-*F* (with <sup>m</sup>marginally significant at  $\alpha = 0.07$ , \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001) and explained variation (Prop. In %), while sequential tests are summarized for the best solution model by the rank of each variable, its AICc and total R<sup>2</sup>.

Variable	Scale	Macroalgae				Suspension feeders				Grazers	
		Total biomass		Composition		Total biomass		Composition		Total biomass	
		Prop.	Rank	Prop.	Rank	Prop.	Rank	Prop.	Rank	Prop.	Rank
Mixing score	Site	4.3***	4	2.6***	6	6.5***	4	2.1***	6	0.3	4
Number of berths	Site	0		4.0***	4	0.1	5	1.1**		0.6	
International connexion score	Site	0	5	4.2***	3	0.2		3.4***	4	0.4	6
Latitude	Pontoon	0.1	3	3.3***	2	32.3***	1	6.3***	1	7.4***	1
Longitude	Pontoon	2.4**		2.1***	7	5.0***	3	2.5***	3	6.1***	5
Distance to entry (√)	Pontoon	6.9***	1	5.0***	1	4.4***		2.7***	7	1.6*	3
Orientation	Station	1.7*		0.8**		0		0.2		0	
Recent maintenance	Station	2.3**	2	1.3***	5	2.9**	2	4.2***	2	0.3	
Fouling height	Station	1.3*		1.6***		10.5***	6	2.6***		1.2*	2
Grazer biomass (Log)	Station	1.2 <sup>m</sup>		0.9**	8	0.8		2.0***	5		
Best solution AICc			1528.2		2562.3		4666.9		2571.4		2005
Best solution R <sup>2</sup>			0.207		0.226		0.458		0.226		0.156

Table 4. Summary of DISTLM outputs for relationship between available environmental (geographic, biotic) variables and the richness and composition of fish and sessile taxa. Marginal tests are summarized by Pseudo-*F* (with <sup>m</sup>marginally significant at  $\alpha = 0.07$ , \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001) and explained variation (Prop. In %), while sequential tests are summarized for the best solution model by the rank of each variable, its AICc and total R<sup>2</sup>.

Variable	Scale	Fish				Sessile taxa			
		Richness		Composition		Richness		Composition	
		Prop.	Rank	Prop.	Rank	Prop.	Rank	Prop.	Rank
Mixing score	Site	2.7*		2.2*	5	7.7***		2.7***	9
Number of berths	Site	1.2		1.8*		1.1 <sup>m</sup>		2.5***	8
International connexion score	Site	0		0.6	4	0		2.7***	3
Latitude	Pontoon	4.6**		1.5 <sup>m</sup>		3.1**	4	5.1***	2
Longitude	Pontoon	6.6**		3.6**	6	23.5***	3	5.4***	4
Distance to entry (v)	Pontoon	7.5**	2	3.3**	3	25.3***	1	6.4***	1
Orientation	Station					3.4***	6	0.8***	
Recent maintenance	Station	0		0.3		0.7		3.0***	7
Fouling height	Station					5.0***		3.3***	11
Grazer biomass (Log)	Station					1.8*	8	2.5***	6
Suspension feeders biomass (Log)	Station	2.3 <sup>m</sup>		0.9					
All kelp biomass (Log)	Station	6.0**		4.8***		22.1***	2	5.9***	10
Native kelp biomass (Log)	Station	7.8**	1	7.0***	1	13.1***	7	2.5***	12
Non-indigenous kelp biomass (Log)	Station	3.4*		3.3***	2	11.3***	5	5.2***	5
BEST SOLUTION AICC			-22.8		1079.4		983.1		2473.7
BEST SOLUTION R <sup>2</sup>			0.115		0.158		0.427		0.324

## FIGURE CAPTIONS

Figure 1. Location of the study sites (Full names in Table S1) within three biogeographic regions (A) along the north-western part of France. Sampled areas were restricted to the vicinity of the port canal, along which were distributed the pontoons selected (B). After the stations were materialised on each pontoon (D), fish surveys took place using both distance and stationary point sampling (1). On both sides of the pontoons, fouling communities (as depicted on C, © Wilfried Thomas) were visually assessed by snorkelling (2) while abiotic parameters were measured from surface operators (3). After a destructive sampling on vertical surfaces (4, but also horizontal) of the pontoons, 80% percent of the scrapped material was sorted per main groups and weighted (5) while the remaining material was stored in formaldehyde solution or ethanol until later processing (6).

Figure 2. Temporal variations in temperature within each study sites. Variance components were estimated for different temporal scales (A), based upon raw data collected each 15 min over 9 months at each site within the Eastern Channel (B), the Western Channel (C) and the Bay of Biscay (D).

Figure 3. Biomass (Wet weight) distribution among the main seaweed (A) and suspension-feeder groups (B) at each site. For each panel, the pie size varies with the total biomass.

Figure 4. Taxonomic richness of fish and sessile taxa at each study site (A, C) and its variation with kelp biomass (log scale) within each region (B, D). Around the median (horizontal line), the box plots (A, C) show the quartiles, the 95% confidence intervals (whiskers) and the outliers, with backward coloured bars indicating cumulative richness values across all

replicates. Significant linear regressions ( $p < 0.05$ ) are depicted with filled lines while non-significant regressions are dotted (with 95% CI).

Figure 5. Principal coordinate analyses describing fish (A) and sessile taxa (C) community structure. Vector plots of variable correlated with the PCO axes are indicated for fish ( $r > 0.4$ , B) and sessile ( $r > .4$ , D), respectively. Centroids (determined from the PCO) were ordinated using non-metric multidimensional scaling (right inserts).

Fig. 1

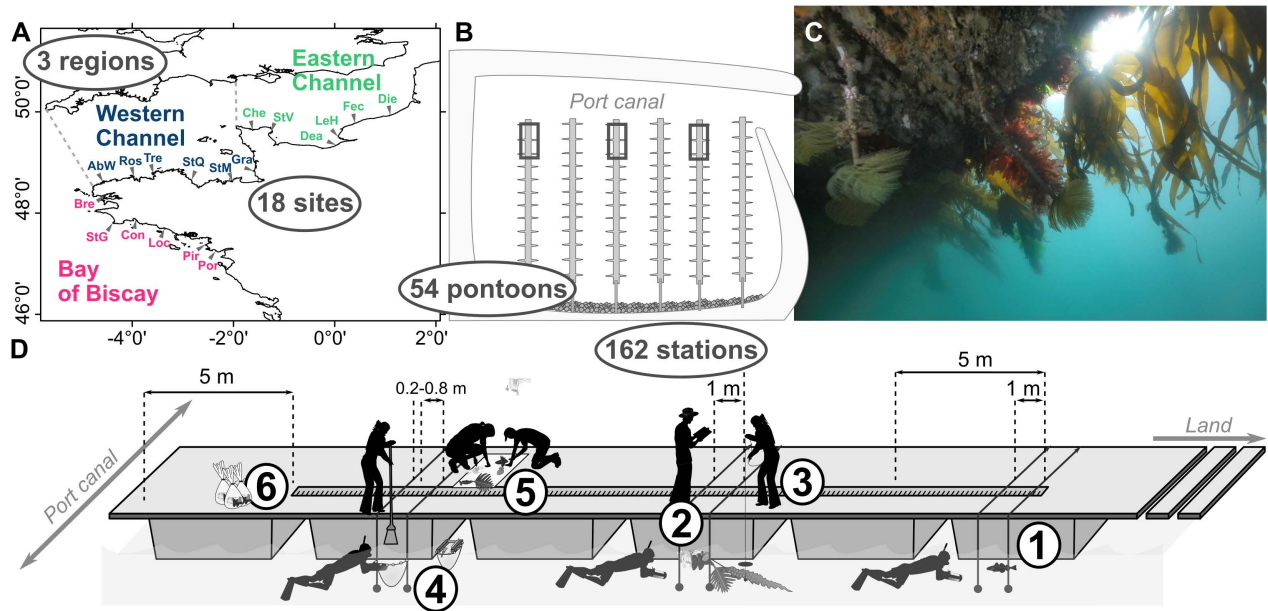


Fig. 2

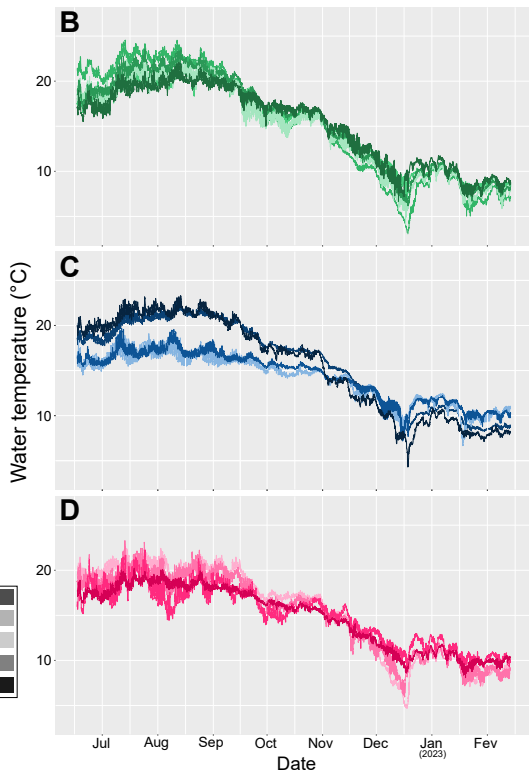
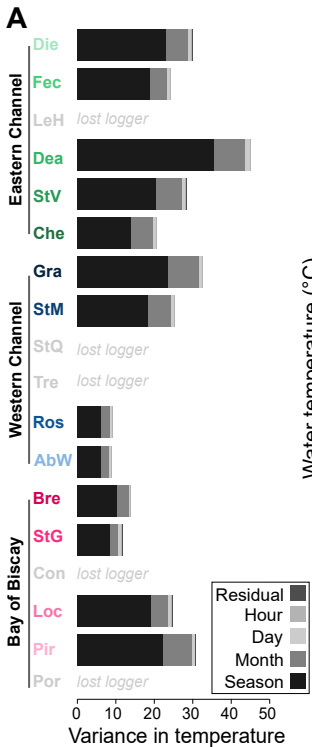
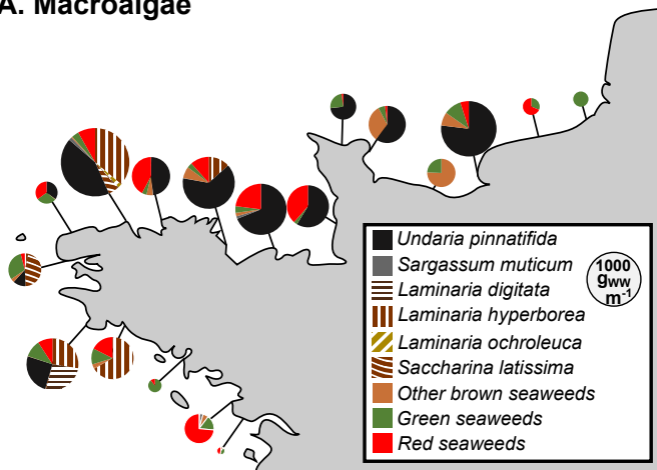


Fig. 3

## A. Macroalgae



## B. Suspension feeders

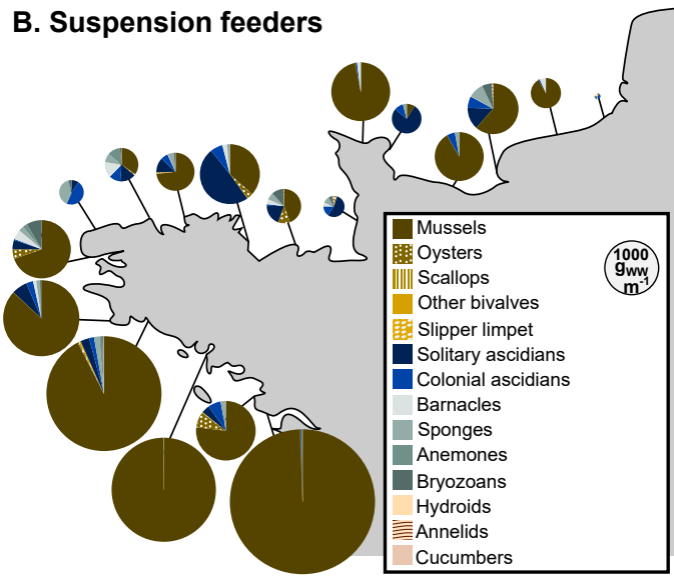




Fig. 4

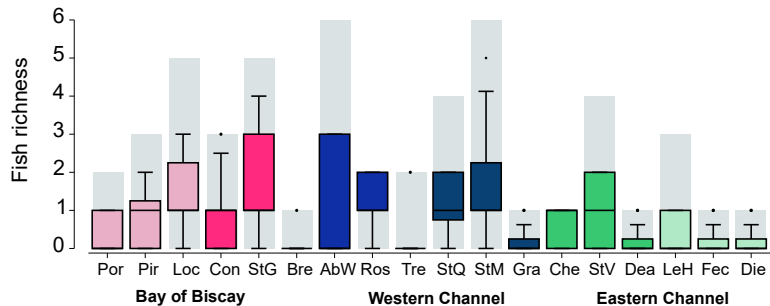
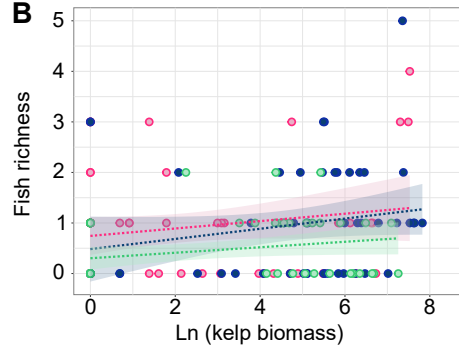
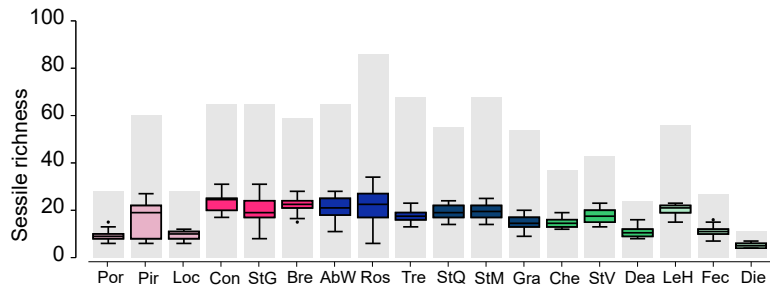
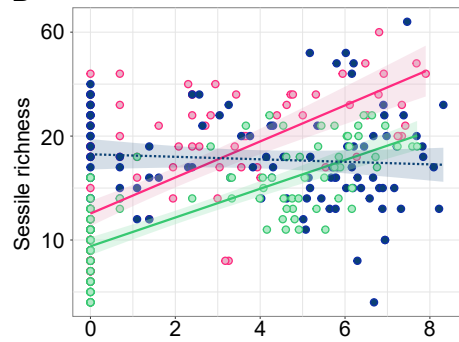
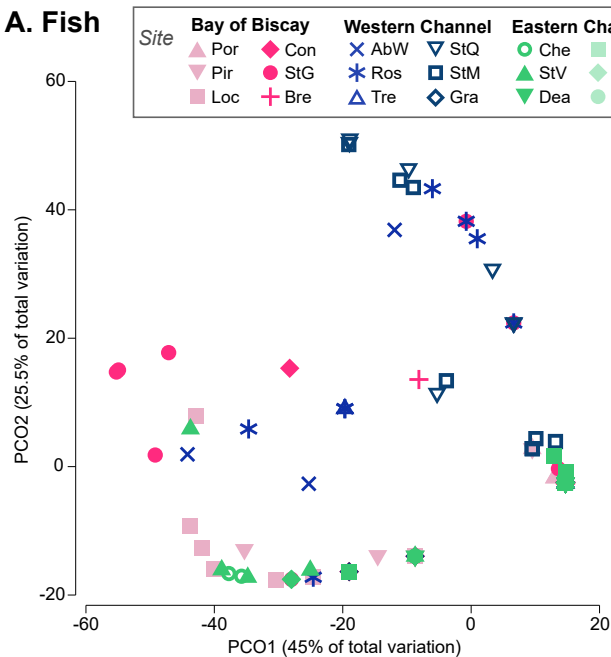
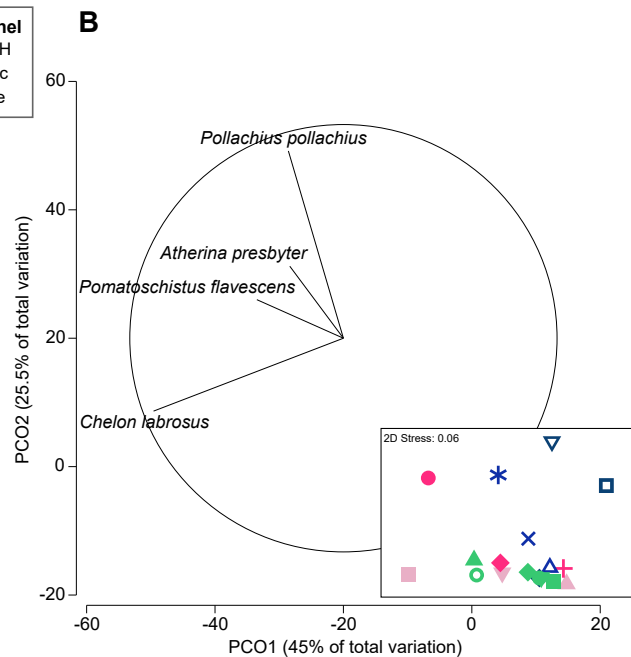
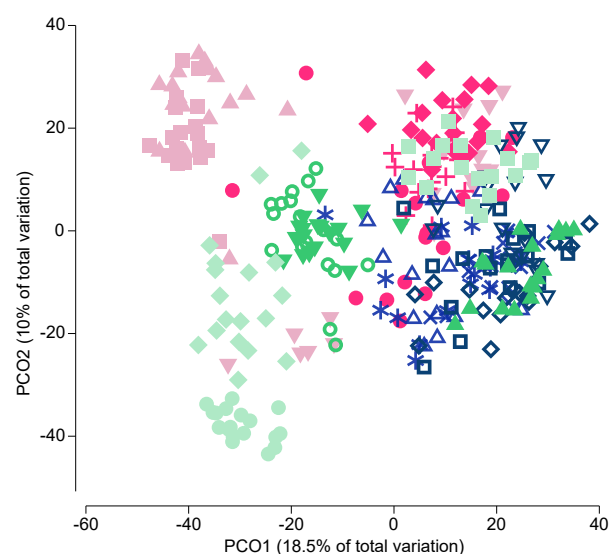
**A. Fish****B****C. Sessile taxa****D**

Fig. 5

**A. Fish****B****C. Sessile taxa****D**