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

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43

ABSTRACT

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

1. INTRODUCTION

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

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

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

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

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

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

In this study, we explored the multi-scale patterns in the diversity and structure of seaweeds, invertebrates and fish communities associated with floating pontoons along ~ 1000 km of coastline in NW France, across a biogeographic transition zone (the Brittany-Normandy continuum). Our primary objective was to identify scale-dependent patterns of diversity and community structure within and among different ecoregions. The Brittany-Normandy continuum indeed expands over three distinct ecoregions (Spalding et al. 2007), which are reflected in the seaweed and invertebrate communities of natural rocky habitats (Tempera et al. 2019, de Bettignies et al. 2021), notably related with contrasting water temperature regimes (Agoumi 1982) and availability in substratum (Cabioch et al. 1977, Thouin 1983). For instance, shallow subtidal reefs in Brittany are covered by dense forests of the perennial kelp *Laminaria hyperborea* along the Northern coasts that are sharply replaced by the annual kelp *Saccorhiza polyschides* along the stratified waters of the Southern coasts (Derrien-Courtet et al. 2013). Under this premise, we postulated (hypothesis 1: H1) that seaweed fouling communities would follow regional patterns similar to those reported from natural reefs (i.e. differences among regions). Among marinas, we hypothesized (H2) that community structure would be distinct and highly variable (more than among regions) owing to contrasting specific marina attributes (openness, size, maritime activities) that are interacting with local abiotic conditions (temperature regime, water movements) and (human-aided) dispersal. At even lower scale, within marina, we hypothesized (H3) that community structure would vary across pontoons in response to known fine-scale gradients (distance) between port entry and innermost portions (e.g., Rivero et al. 2013, Gauff et al. 2022). Finally, we hypothesized (H4), that fouling and fish communities would covary with the amount of foundation kelp, however without *a priori* 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 (Cabioch 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 (± 1 cm), the temperature (± 0.1 °C), the salinity (± 0.01), the dissolved oxygen (± 0.01 mg L⁻¹) and the

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

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

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

2.2.Data analyses

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

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

2.2.1. Temporal variations in temperature between regions

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

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

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

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

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

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

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

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

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

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

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

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

3. RESULTS

3.1. Temporal variations in temperature do not follow ecoregional patterns.

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

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

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

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

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

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

variability in total seaweed biomass but also in their composition (Table 3, Table S4). The spatial variability in seaweed composition was rather consistent with seaweed total biomass (Table 1). Although significant differences in composition were observed among regions (Fig. 3A), the term only accounted for 8.0% of the total variation (cf. H1). It is noteworthy that more than 70% of the among-group variation (SIMPER following pairwise tests) was explained by the nonindigenous kelp *Undaria pinnatifida* (335.4 gWW m⁻¹ in the Western Channel vs. 36.9 gWW m⁻¹ in the Bay of Biscay and 165.4 in the Eastern Channel), red seaweeds (124.4 vs. 58.8 and 17.4 gWW m⁻¹) and green seaweeds (27.2 vs. 52.2 and 48.3 gWW m⁻¹). Like for the total biomass, the associated composition varied markedly among sites within region (28.8% C.V., cf. H2). Among the taxa mostly contributing to this pattern are native kelps that are confined to Brittany (*Laminaria* spp. and *Saccharina latissima*, Table S6) and more abundant in the westernmost sites of both the Bay of Biscay and the Western Channel (Fig. 3A). When present, all kelp species were major contributors of variations in seaweed biomass among pontoons (Table 1, and distance to entry in DistLM, Table 3, cf. H3). In either the total seaweed biomass or its composition, residual variability was substantial (> 40 % C.V.). The residual variability was even more pronounced with the selected DistLMs (cf. R² in Table 3)..

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

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

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

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

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

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

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

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

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

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

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

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

4. DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.4. Perspectives, limitations and concluding remarks

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

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

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

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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). ^mmarginally 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)
		Total biomass	Composition	Total biomass	Composition	Total biomass
PERMDISP Region			***	***	***	***
			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 ^m	1.1 ^m	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 ^m
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). ^mmarginally 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 ^m	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 ^mmarginally 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^2 .

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 ^m		0.9**	8	0.8		2.0***	5		
Best solution AICc			1528.2		2562.3		4666.9		2571.4		2005
Best solution R^2			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 ^mmarginally 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^2 .

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 ^m		2.5***	8
International connexion score	Site	0		0.6	4	0		2.7***	3
Latitude	Pontoon	4.6**		1.5 ^m		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 ^m		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^2			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

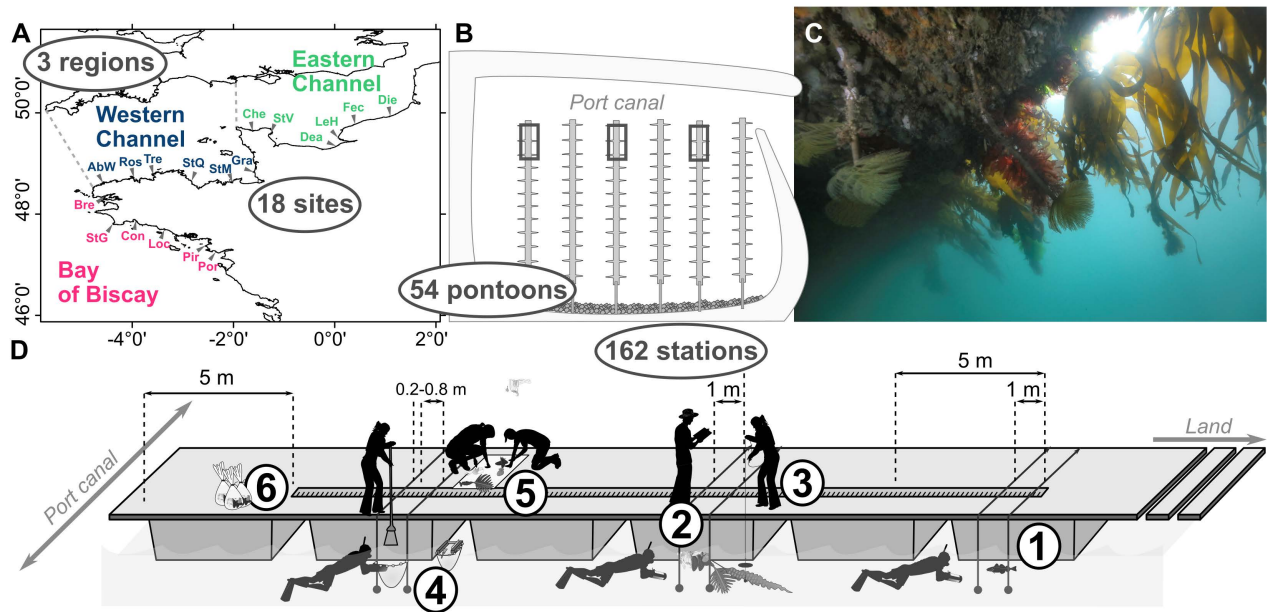


Fig. 2

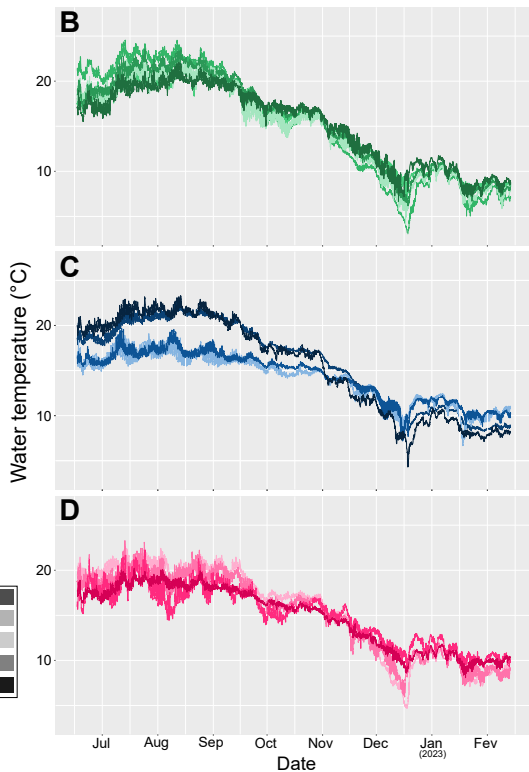
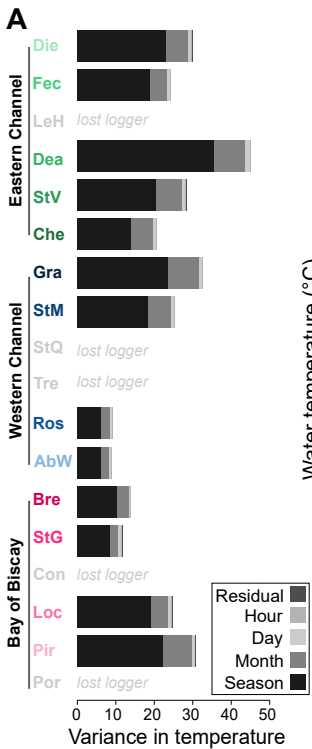
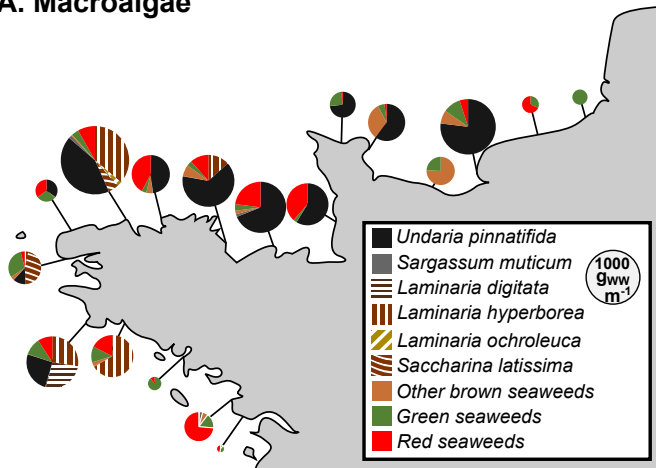


Fig. 3

A. Macroalgae



B. Suspension feeders

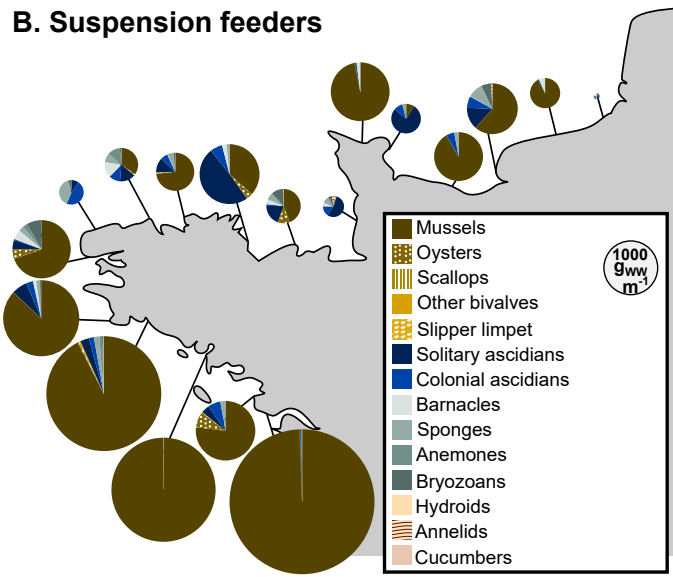


Fig. 4

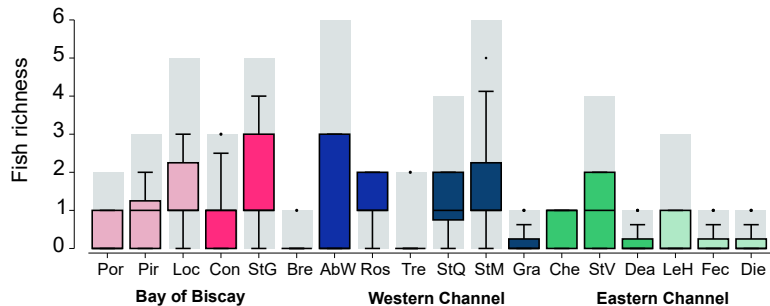
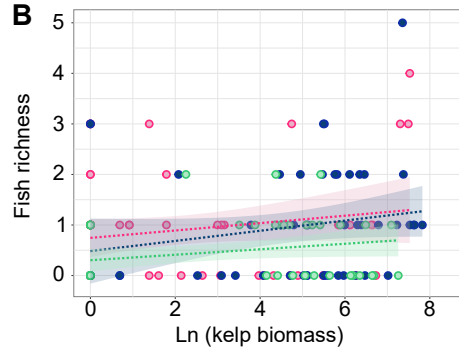
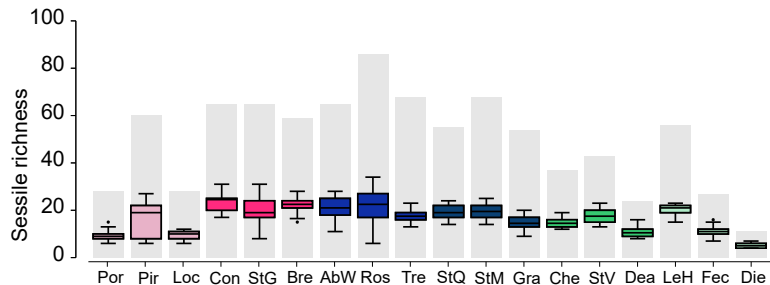
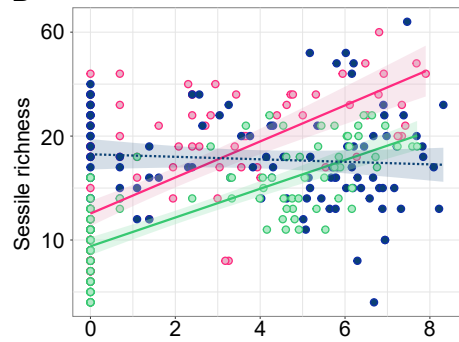
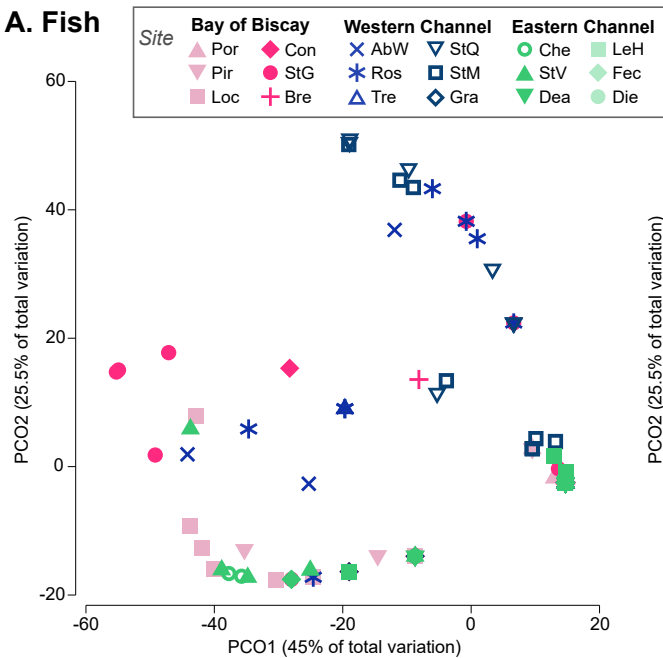
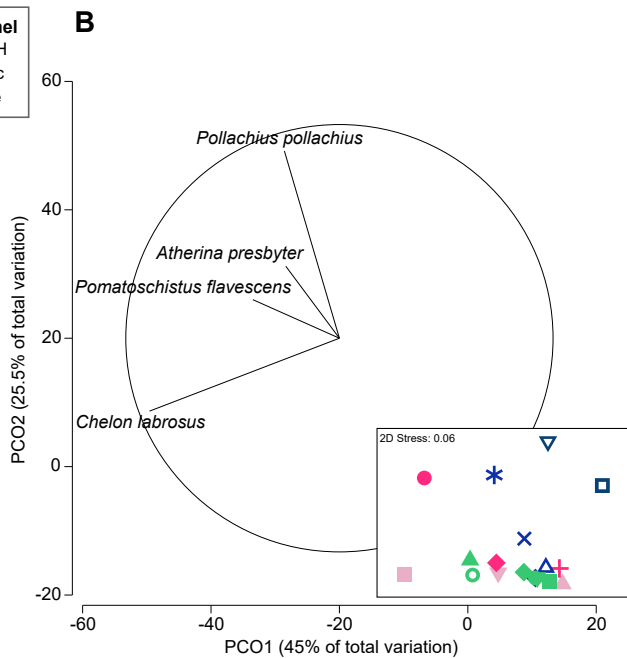
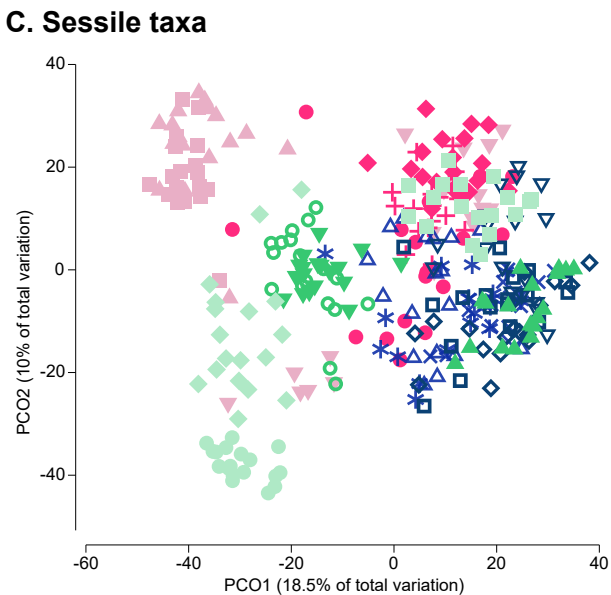
A. Fish**B****C. Sessile taxa****D**

Fig. 5

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