



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

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**ABSTRACT:** Redistribution of biodiversity represents a key challenge for understanding scales of spatial variation in natural marine communities. With increasing coastal urbanization, artificial structures are proliferating, with impacts on natural habitats, yet we have limited 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. In this study, we explored multi-scale patterns in the diversity and community structure of fouling seaweeds, invertebrates and fish communities associated with pontoons in 18 marinas, distributed along ~1000 km of coastline in NW France. With respect to the distribution of marinas across 3 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 to inform their management.

**KEY WORDS:** Floating pontoons · Port · Hierarchical design · Diversity · NE Atlantic · Seaweeds · Kelp · Marine invertebrates · Fish

## 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', i.e. the proliferation of diverse artificial infrastructures, has expanded rapidly over recent decades and is predicted to increase in the near future (Bugnot et al. 2021). 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), urbanization can also provide novel hard substrates and colonization opportunities for 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, Airoidi 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 is a considerable need 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). Urbanization 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 refuges on breakwaters is a stronger driver of community assembly in sessile taxa and mobile invertebrates at low than at high latitudes (Aguilera et al. 2022). Conversely, several dimensions of habitat complexity (Loke & Chisholm 2022) can be greater on breakwaters (Grasselli & Airoidi 2021, Lawrence et al. 2021). In spe-

cific conditions (e.g. on supralittoral habitats), the accumulation of anthropogenic marine debris can also favour the same synanthropic vertebrates 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-scales of sessile non-indigenous species, cryptogenic species or native species established elsewhere (Airoidi 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-scales can prevail in their influence upon biota (Sedano et al. 2020, Jackson-Bué et al. 2024). Besides these extensively studied concrete shorelines, there is 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, extraordinarily 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 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 not surprising. Whether the native taxa colonizing these infrastructures follow distributions consistent with 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 <2 yr, 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 underly-

ing 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 have targeted 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). However, to our knowledge, the influence of long-lived foundation species, such as kelps, on marina communities has seldom been studied. In addition, examinations of established assemblages upon marina pontoons are rather rare (e.g. see 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 3 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 to 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-Courtel 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 an even lower scale, within marinas, 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. Callier et al. 2009, 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, but without *a priori* hypotheses about their most important scale of influence (region, marina, pontoon).

## 2. MATERIALS AND METHODS

### 2.1. Sampling design and data collection

The study was performed during May and June 2022 along approximately 1000 km of shoreline in Brittany and Normandy, NW France (Fig. 1A; full names and descriptions in Table S1 in the Supplement at [www.int-res.com/articles/suppl/m742p001\\_supp.pdf](http://www.int-res.com/articles/suppl/m742p001_supp.pdf)). Distributed along a biogeographic province transition zone (Cabioch et al. 1977), this shoreline encompasses 3 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 3 regions, 6 marinas (hereafter 'sites'), 10s of km apart, and mostly dedicated to leisure boating (Table S1) were selected (Fig. 1A). All marinas were constructed at least 10 yr prior to the study. Strong estuarine conditions were avoided, and only sites with salinity > 30 at 1 m (cf. e.g. Pezy et al. 2021) depth were considered. At each site, we sampled 3 floating pontoons, 10–100s m apart and distributed along the main navigation canal (Fig. 1B; Table S1). Surveys were done along 25 m transects located near this canal, where water mixing was deemed stronger and pollutant exposure weaker (Gauff et al. 2022) to select areas with conditions favourable to seaweed growth (Fig. 1C). Along each transect (avoiding the closest 5 m edge of the canal), 3 stations of 1 linear metre 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), temperature ( $\pm 0.1^\circ\text{C}$ ), salinity

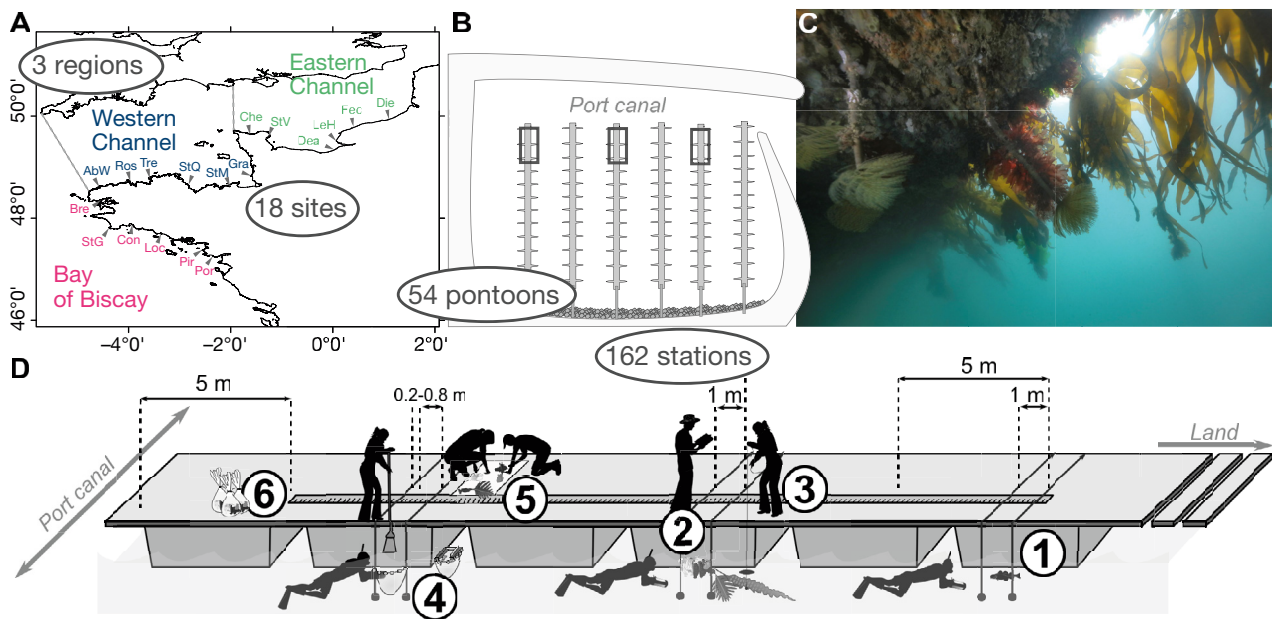


Fig. 1. (A) Locations of the study sites (full names in Table S1) within 3 biogeographic regions along the north-western part of France. (B) Sampled areas were restricted to the vicinity of the port canal, along which the selected pontoons were distributed. (D) After the stations were established on each pontoon, fish surveys took place using both distance and stationary point sampling (1). On both sides of the pontoons, fouling communities (as depicted in panel C, © Wilfried Thomas) were visually assessed by snorkelling (2) while abiotic parameters were measured by surface operators (3). After destructive sampling on vertical (but also horizontal) surfaces (4) of the pontoons, 80% percent of the scraped material was sorted by main groups and weighed (5) while the remaining material was stored in formaldehyde solution or ethanol until later processing (6). Figures by J. C. Leclerc using several diagrams taken from Ian Symbols (<http://ian.umces.edu/symbols/>)

( $\pm 0.01$ ), dissolved oxygen ( $\pm 0.01 \text{ mg l}^{-1}$ ) and turbidity ( $\pm 0.1 \text{ m}$  of Secchi depth, when possible, Fig. 1D-3). Temperature, salinity and dissolved oxygen measurements were made at 3 positions in the water column (hereafter 'position'): at 0.2 m, placing the probe over the pontoon surface (i.e. within the canopy, if present), at 0.2 m > 1 m away from this fouling and at 2 m depth. Temperature and salinity were measured using a multiparameter sensor connected to either a YSI® Pro Quatro or a HANNA® HI92192, while dissolved oxygen was measured using a luminescent/optical dissolved dioxygen probe with built-in temperature sensor connected either to a Hach® HQ40d or an 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 every 15 min using onset HOBO® Pendant Temp-Light data loggers, deployed at a depth of 0.5 m to describe the temperature regime at each site. One logger per site was deployed from the date of sampling (Table S1) to February 2023,

thus during approximately 9 mo over 3 seasons (summer, fall and winter).

Biodiversity surveys included fouling (seaweed and invertebrate) and fish communities. Prior to any disturbance, fish surveys were conducted by snorkel. All fish taxa were counted along a sampling unit combining both distance ( $5 \times 2 \text{ m}$  along the pontoon) and stationary point sampling (2 min stop at each station, i.e. at the distance transect end) (Fig. 1D-1) (Leclerc & Viard 2018). Fouling seaweeds and invertebrates (comprising sessile to slowly mobile taxa, hereafter 'sessile') were recorded using both visual and destructive sampling. 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 'Super-abundant, Abundant, Common, Frequent, Occasional, Rare, Absent' (SACFOR) scale (Hiscock 1996). On 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 pontoon surface were scraped from the surface using a scraper and the material was directly retrieved within a 500  $\mu\text{m}$  meshed sieve mounted on a floating hoop (Fig. 1D-4). This material was transferred to a plastic bag, ultimately filled with 4% formaldehyde solution and preserved in dark conditions 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 macro-organisms 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, WW) was measured with a precision of 1.0 g.

## 2.2. Data analyses

Statistical analyses were performed using R (R Core Team 2020) and PRIMER 7 (Anderson et al. 2008). As detailed in the following subsections, scale-dependent patterns of diversity were explored separately for biomass distribution and visually assessed richness and community structure. While biomass distribution patterns in major groups (autotrophs and heterotrophs) were explored across spatial scales (cf. H1, H2, H3), richness and community structure 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 (VC) 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 further examined 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 variation 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 4 nested temporal scales (season, month, day, hour and residuals) using estimates of associated variance components from each temporal series (1 per site). This was done by implementing a random intercept univariate model with the 'lmerTest' package (Kuznetsova et al. 2014), 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 later checked using 1-way (factor 'region' as random) univariate PERMANOVA (Anderson et al. 2008), with 4999 permutations of raw data. Prior to 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 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 distance to 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 position term. PERMANOVAs were followed by pairwise comparisons and p-values were estimated using a Monte Carlo (MC) procedure.

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

Variations in the biomass and community structure (hereafter 'composition') of seaweeds, suspension feeders and grazers across spatial scales were all ex-

amined separately using 4-way PERMANOVAs with 4999 permutations under a reduced model. Spatial factors (all as random and nested within each other) were region, site, pontoon and station. In addition, 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  $\alpha$  of 0.01. However, we were mostly interested in the pseudo-variance components of variation associated with each term, which we extracted by setting the observed mean square values equal to their expectations. 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 (SIMPER) analyses.

#### 2.2.4. Diversity and structure of sessile taxa and fish communities, and covariations with kelp abundance

Variations in the richness and structure of sessile taxa and fish communities across spatial scales were all examined separately using 3- to 4-way PERMANOVAs with 4999 permutations under a reduced model. Of the 4 main nested factors outlined above, 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 *sensu stricto* (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 at 7 out of 18 sites and were poor contributors to the seaweed biomass (0.1–3.5%). Because we were interested in covariations in diversity and composition at multiple spatial scales, our model also included 3 interaction 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 removed from the sessile taxon  $\times$  sample matrix and associated richness estimate to avoid collinearity. PERMANOVA results were supported by ordination using principal coordinate analyses (PCO) 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 the covariate.

#### 2.2.5. Geographic and biotic variables accounting for variability in the data clouds

In addition to our multi-scale approach, we further examined 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 (1) geographic information, such as latitude, longitude, distance to entry (square root transformed) and orientation, (2) biotic variables, such as fouling height and biomass (all log-transformed to avoid skewness) of grazers, suspension feeders and kelp, as well as (3) anthropogenic proxies, such as the number of berths (correlated with the number and size of pontoons, which were discarded from the 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, 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. abundance, richness and composition of each group), the influences 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 data sets). The explained variation ( $R^2$ ) was calculated for each of these variables, and the best overall model was selected according to Akaike's information criterion corrected for small sample size (AICc) following a stepwise selection procedure (4999 permutations), whereby a conditional test associated with either the addition or removal of a given variable is done at each step (Anderson et al. 2008).

### 3. RESULTS

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

Over the same 9 mo period, temporal variations in temperature at 0.5 m depth varied greatly among sites, especially among seasons (Fig. 2A, loggers retrieved from 13 out of 18 sites). The variations observed in Deauville (2.8°C in winter to 24.5°C in summer, Fig. 2B) were twice as much as those observed in Aber Wrac'h (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 Guérolé, Brest, Aber Wrac'h and Roscoff, Figs. 1A & 2D). Contrary to our expectations, none of those variance components differed among the 3 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. Abiotic conditions generally vary 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 2 sites, cf. Position  $\times$  Site interaction and pairwise tests in Table S2). Colder temperatures were generally observed at 2 m depth (from 13.8 to 17.9°C at the same sites; Table S1), with significant differences at 15 out of 18 sites. With oxygen concentration varying from 8.6 mg l<sup>-1</sup> (Dieppe) to 12.6 mg l<sup>-1</sup> (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  $\times$  Site in Table S2), with values ranging from 29.5 (Dieppe, on a heavy rainy day) to 36.2 (Saint Guérolé). 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  $\times$  Site effect was also detected regarding turbidity as estimated by Secchi disc, 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. Spatial variations in the biomass and community structure of seaweeds, suspension feeders and grazers 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). However, seaweed biomass varied markedly and significantly among sites (31.1% VC, aligning with 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> 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 near the port entry (e.g. ranging from 339.6  $\pm$  136.1 to 1937.0  $\pm$  973.4 gWW m<sup>-1</sup> along such gradient in Saint Quay, mean  $\pm$  SD). 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

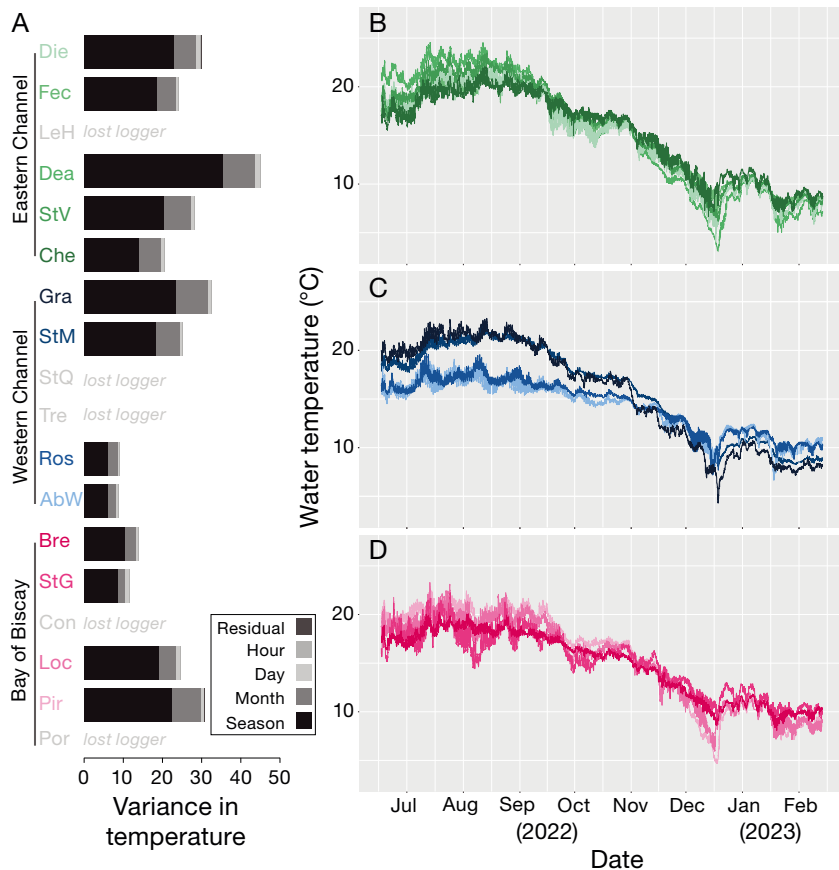


Fig. 2. Temporal variations in temperature within each study site (see Fig. 1 for site locations and Table S1 for full names). Variance components (VC) were estimated for (A) different temporal scales, based upon raw data collected every 15 min over 9 mo at each site within the (B) Eastern Channel, (C) Western Channel and (D) Bay of Biscay

composition (Table 2; 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<sup>-1</sup> in the Western Channel vs. 36.9 gWW m<sup>-1</sup> in the Bay of Biscay and 165.4 gWW m<sup>-1</sup> in the Eastern Channel), red seaweeds (124.4 vs. 58.8 and 17.4 gWW m<sup>-1</sup>) and green seaweeds (27.2 vs. 52.2 and 48.3 gWW m<sup>-1</sup>). For the total biomass, the associated composition varied markedly among sites within region (28.8% VC, cf. H2). Among the taxa mostly contributing to this pattern were 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 2, cf.

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 pseudo-variance components (VC) 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); m: marginally significant at  $\alpha = 0.07$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . Detailed results are provided in Table S3 in the Supplement

	Macroalgae		Suspension feeders		Grazers	
	Total biomass	Composition	Total biomass	Composition	(mostly <i>Patella</i> spp.) Total biomass	
PERMDISP region		***	***	***	***	
Source	df	VC	WC ≠ (BB = EC)	BB ≠ (WC = EC)	BB ≠ (WC = EC)	EC ≠ (WC = BB)
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)	



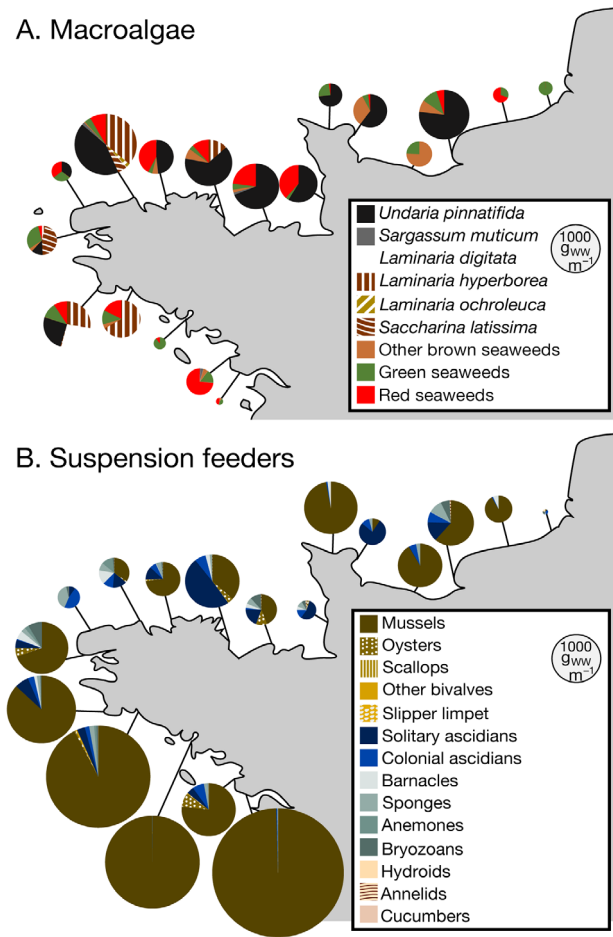


Fig. 3. Biomass (wet weight) distribution among the main (A) seaweed and (B) suspension-feeder groups at each site. For each panel, the pie size varies with the total biomass

H3). In both the total seaweed biomass and its composition, residual variability was substantial (>40% VC). The residual variability was even more pronounced with the selected DistLMs (cf.  $R^2$  in Table 2).

Conversely to seaweeds, suspension-feeder biomass varied markedly (cf. PERMDISP and PERMANOVA) and significantly among regions (32.3% VC, Table 1; Table S3). It was 6 times as great in the Bay of Biscay (mean  $\pm$  SD:  $3327.7 \pm 2365.8$  gWW  $m^{-2}$ , pairwise test) as in the Western Channel ( $770.0 \pm 480.7$  gWW  $m^{-2}$ ) and Eastern Channel ( $361.1 \pm 358.1$  gWW  $m^{-2}$ , Fig. 3B). These differences were generally reflected in the suspension-feeder composition, although they were associated with less variation (11.8% VC). More than 70% of the among-group variation was explained by the mussels *Mytilus* spp. which were approximately 10 times as abundant in the Bay of Biscay ( $3114.1$  gWW  $m^{-2}$ ) as in the 2 other regions ( $327.7$  gWW  $m^{-2}$  in Western Channel and  $534.2$  gWW  $m^{-2}$  in the Eastern Channel, Fig. 3B). Substantial variation was also observed among sites (ca. 26% VC in either total biomass or composition), with up to  $7259.7$  gWW  $m^{-2}$  observed at the southernmost site of Pornichet. The selected DistLMs revealed both a latitudinal (ranking first) and longitudinal (ranking third) gradient in the biomass and composition of suspension feeders (Table 2; Table S4), with recent disturbance ranking second in either case. Total biomass and composition also varied markedly among pontoons (>12% VC) and among stations (>4%). The residuals represented up to 39% VC.

When occurring, macrograzers were largely dominated in composition and biomass by *Patella* spp.,

Table 2. 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- $F$  (m: 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 Akaike's information criterion corrected for small sample size (AICc) and total  $R^2$

Variable	Scale	Macroalgae				Suspension feeders				Grazers	
		Total biomass Prop.	Rank	Composition Prop.	Rank	Total biomass Prop.	Rank	Composition Prop.	Rank	Total biomass 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 connection 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 ( $\sqrt{}$ )	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 $R^2$			0.207		0.226		0.458		0.226		0.156

while other taxa such as sea urchins or abalones were only observed in Concarneau and Brest (Table S6). Grazer biomass varied weakly among regions (3.2% VC; Tables S1 & S3) but substantially (and significantly) among sites (44.3%), as also shown by the influence of geographic variables in DistLM (Table 2), and among pontoons within sites (Table 1). Grazers were absent at 4 of the 18 sites (Saint Quay, Granville, Deauville, Dieppe) and almost absent (<1 gWW m<sup>-1</sup>) in Pornichet and Locmiquelic, while they reached up to 97.8 ± 75.4 gWW m<sup>-1</sup> in Fécamp.

**3.4. Diversity and composition of sessile taxa and fish covary 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% VC, Table 3); for example, in the Bay of Biscay, it ranged from 0.2 species per sampling unit (2 in total per site) in Pornichet to 1.3 (5 in total) in Saint Guérolé (Fig. 4A). While fish richness did not vary significantly among regions, a significant interaction was detected between region and kelp biomass (p<sub>MC</sub> = 0.039; Table S7). Note that this result is to be consid-

ered with caution, considering the PERMDISP result with such an α level (p<sub>perm</sub> = 0.031) and that no significant relationships between fish richness and kelp biomass were revealed within any of the regions (Fig. 4B). Altogether, as a main factor and in interactions, kelp biomass accounted for 15.6% VC in fish richness. Kelp biomass explained 24.2% of the total variation for fish composition (up to 16.4% for the kelp × pontoon interaction) and its effect was significant (p<sub>MC</sub> = 0.046, Table 3; Table S8) when considered alone. Fish composition also varied markedly among sites within region (17.4% VC, Table 3). According to the PCO, sites were mostly discriminated by their abundances of mullets *Chelon labrosus* (axis 1) and pollacks *Pollachius pollachius* (axis 2, Fig. 5A,B).

The richness of sessile taxa (invertebrates and seaweeds), excluding kelps, varied markedly among sites (28.1% VC, Table 3); for example, in the Bay of Biscay, it ranged from 9.2 species m<sup>-1</sup> (28 in total per site) in Pornichet to 22.2 (65 in 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 3; Table S9). At this scale, positive and significant relationships 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 in interactions), kelp biomass accounted for 30.4% VC in sessile taxa richness—a result consistent with DistLM ranking this term second (Table 4;

Table 3. 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, the pseudo-variance component (VC) 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); m: marginally significant at α = 0.07, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001. The factor 'Station' was not considered in the fish models due to the lack of replication

Variable	Fish		Sessile taxa	
	Richness	Composition	Richness	Composition
PERMDISP region	*	**	***	*
	EC ≠ (WC = BB)	EC ≠ (WC = BB)	BB ≠ (WC = EC)	(WC ≠ BB) = (WC ≠ <sup>m</sup> EC)
	df	VC	df	VC
Kelp biomass = Ke	1	2.7 <sup>m</sup>	1	17.5**
Region = Re	2	1.3	2	5.9
Site(Re) = Si	15	18.4**	15	28.1***
Ke × Re	2	13.0*	2	7.5**
Pontoon(Si(Re)) = Po	36	0	36	13.6***
Ke × Si(Re)	10	0	10	0.8
Station(Po(Si(Re)))	—	—	108	4.8
Ke × Po(Si(Re))	23	0	23	4.6
Residuals	72	64.6	126	17.3
Total	161		323	
Pairwise test for region:			WC ≠ <sup>m</sup> (BB = EC)	WC ≠ (BB ≠ <sup>m</sup> EC)

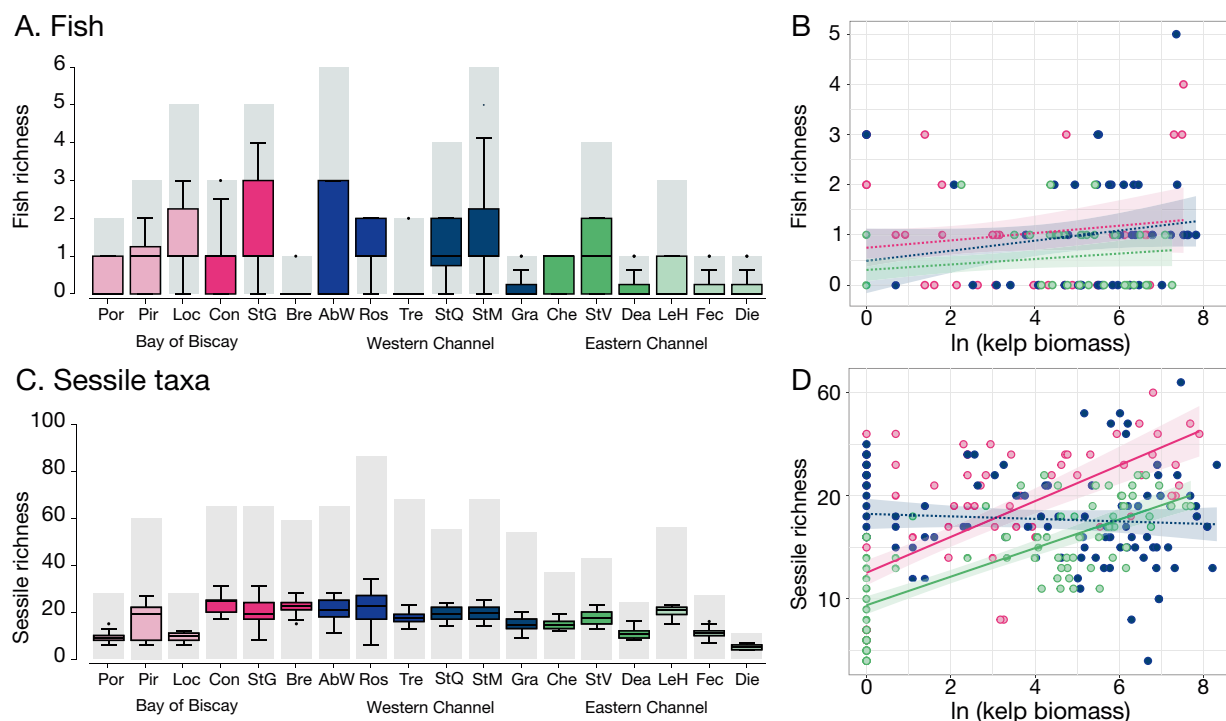


Fig. 4. (A,C) Taxonomic richness of fish and sessile taxa at each study site (see Fig. 1 for locations and Table S1 for full names) and (B,D) its variation with kelp biomass (log scale) within each region. Around the median (horizontal line), the box plots (A,C) show the quartiles, the 95% confidence intervals (whiskers) and the outliers (dots), with light gray bars indicating cumulative richness values across all replicates. In panels B and D, significant linear regressions ( $p < 0.05$ ) are depicted with solid lines while non-significant regressions are illustrated with dashed lines (shaded areas indicate 95% CI)

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 3; Table S6). A significant effect of region was detected in both position and dispersion (Table 3, Fig. 5C). Indeed, a substantial variability was also detected among sites within regions (37.9% VC), rather well reflected in the latitude and longitude terms in retained DistLM (Table 4). Although the first axis in the PCO 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). However, the Bay of Biscay is rather well discriminated from most of the other sites along axis 2, owing notably to a greater semi-abundance in *Mytilus* mussels (Figs 3B & 5D), hence aligning with results on biomass. As a main factor and in interactions, kelp biomass accounted for a total of 9.5% VC 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. Native vs. nonindigenous origin of kelps matters for covariation scales

When separating kelps by either their native or nonindigenous origin, contrasting effects of kelp biomass were observed in fish richness and composition (Tables S7 & S8). With nonindigenous kelps only, stronger covariations between kelp biomass and region were observed for fish richness ( $p = 0.007$ , 17.6% VC) and 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 low-power; cf.

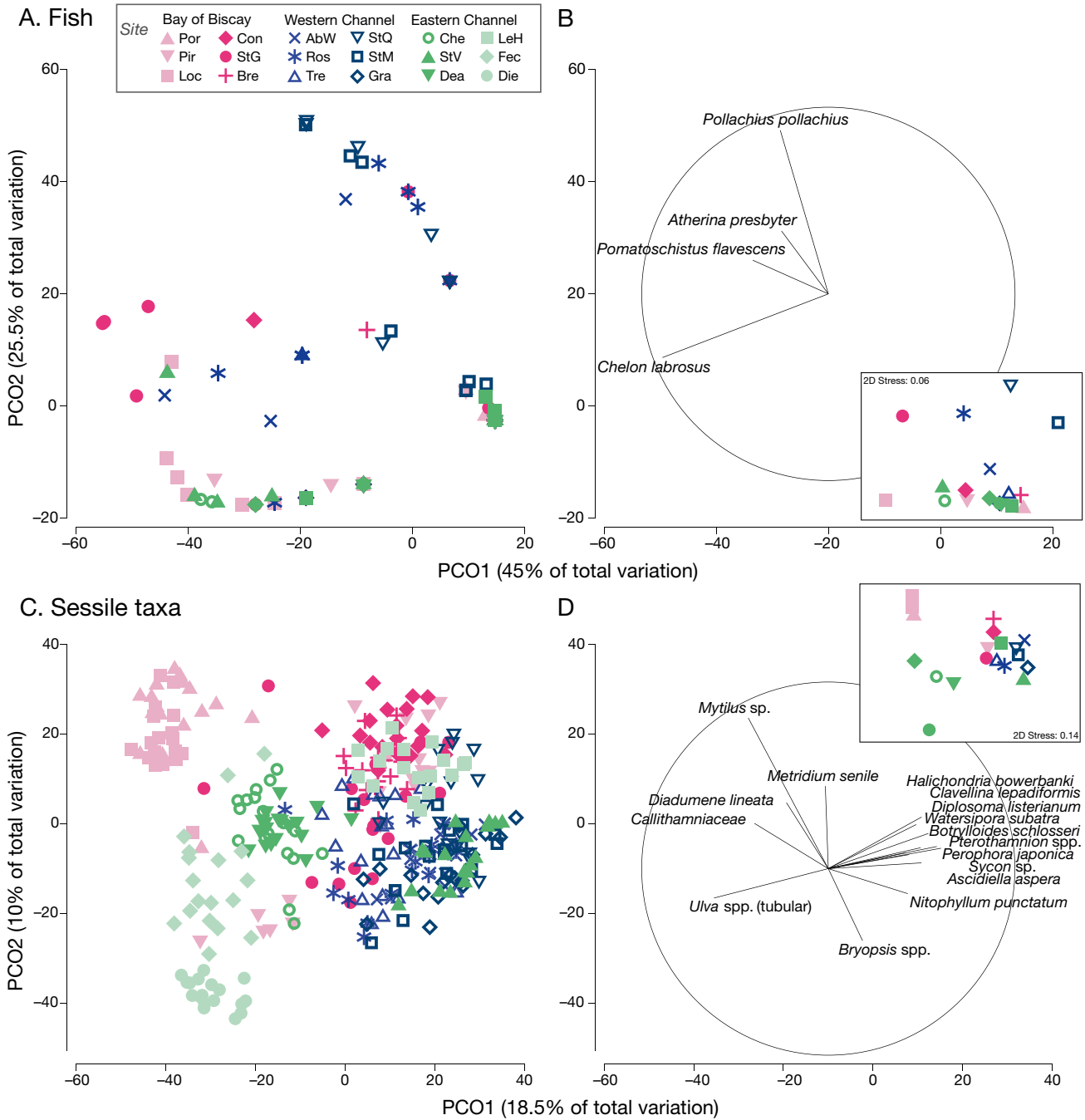


Fig. 5. Principal coordinate analyses (PCO) describing community structure of (A) fish and (C) sessile taxa. Vector plots of variables correlated with the PCO axes are indicated for (B) fish ( $r > 0.4$ ) and (D) sessile taxa ( $r > 0.4$ ); insets show centroids (determined from the PCO), ordinated using non-metric multidimensional scaling

$R^2$ ) distance-based models for both fish richness and composition (Table 4).

Similar results were observed for sessile taxa richness and composition (Tables S9 & S10). While the kelp  $\times$  region interaction in richness was strengthened with nonindigenous kelps, interactions remained significant when only native kelps were included, but at

smaller spatial scales (site, pontoon). As for composition, significant interactions between kelp biomass and all spatial scales were observed when only non-indigenous kelp were considered. In contrast, when only native kelps were considered, only the interactions with the scales of sites and pontoons were significant.

Table 4. Summary of DistISTLM 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- $F$  (m: 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  $R^2$

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 <sup>m</sup>		2.5***	8
International connection 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 ( $\sqrt{}$ )	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 feeder 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 $R^2$			0.115		0.158		0.427		0.324

#### 4. DISCUSSION

By examining the diversity and structure of seaweed, fouling invertebrate 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 only a small portion of the total variation and were due to the single non-indigenous kelp reported in our survey (i.e. *Undaria pinnatifida*). The observed spatial sea surface temperature regimes across sites also did 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 covari-

ations differed depending on whether they were examined with native or nonindigenous kelps.

##### 4.1. Biodiversity and composition vary at the large scale, but not as expected from natural biogeographic patterns

Embedded in port environments, floating pontoons represent unique habitats open to 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, if any, of region on biomass, richness or composition was generally weak. Moreover, the pattern observed in our study did not follow biogeographic patterns reported from natural rocky reefs (Thouin 1983, Derrien-Courtel 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 non-indigenous kelp *Undaria pinnatifida*, which is disproportionately abundant in marinas compared to other



kelps (Fig. 3) in Brittany, where it has been cultivated since the early 1980s (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 3 study regions (Fig. 3). This pattern is consistent with its strong affinity for 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  $30^{\circ}\text{C}$ , and this range fits within that observed over the temperature survey at 0.5 m depth at all sites (Fig. 2). In contrast, while cultured gametophytes of the native kelp *Saccharina latissima*, *Laminaria digitata* and *L. hyperborea* are rather resistant and perform well at  $0^{\circ}\text{C}$  (Sjötun & Schoschina 2002), they can hardly survive more than 2 wk above 23, 22–23 and  $21^{\circ}\text{C}$ , respectively (Bolton & Lüning 1982). According to our 9 mo temperature survey, these maxima (99<sup>th</sup> percentile) would make 9 out of 13 sites where loggers were deployed suboptimal for native kelp. Prolongation of temperature above these values for periods of more than 1 wk (up to 10 wk) in a row further suggests that that 6 of these sites are unsuitable for native kelps to renew their populations, regardless of *a priori* defined regions. In our study, native kelps were relatively confined to the western- and northwesternmost sites of Brittany, which, along with the tip of the Cotentin Peninsula (e.g. Cherbourg where a young *L. hyperborea* was also recorded), are under the influence of a 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-Courtel et al. 2013, Robuchon et al. 2017), our observations strongly suggest that temperature variations (which were not related to *a priori* defined regions) experienced by these organisms under floating pontoons are 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 *U. 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 in diversity and structure from micro- to meso-scales

Although not accounting for the known nested structure, distance-based models give hints about the influence of various factors such as port openness (water mixing, adding to the distance-to-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 of 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 of these proxies, however, was retained in the selected model on richness of sessile taxa (visually assessed). Besides other anthropogenic pathways of dispersal which could not 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 fittest (in terms of survival and resource acquisition) and/or the most dominant organisms which may be sorted by other abiotic and biotic processes.

Regarding the abiotic environment, port openness emerged as an important variable within selected models on seaweed and suspension feeder biomass or composition, 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 the thallus; Hurd 2000) or indirectly avoiding its inhibition, which could result 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) observed between our direct measurements of salinity and the distance to entry 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 macrograzer biomass, 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 detail. As in the natural reefs of the region (Leclerc 2018), we 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), in our study, these patterns were pervasive at some sites but absent in others. This likely macrograzer predation may interact with other biotic disturbances, such as gull predation on suspension feeders (Holman et al. 2019). We did observe conspicuous signs of gull predation, such as faeces 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 primary explanatory variables in either biomass, richness or composition of seaweeds, suspension feeders and overall sessile taxa. Of note, and as observed in our study (Table S1), such maintenance can be practiced at the scales of patch (by marina users' choices), pontoon (replacements) site (depending on local operator policy) and a broad range of spatial scales, which has certainly produced much variation across all of the studied spatial scales. However, none of these practices are carved in stone. As a side note, while the questionnaires completed by some of the operators did not allow tracing back a detailed history of each port or pontoon (cf. Aguilera et al. 2022 on breakwaters), it revealed — surprisingly (O'Shaughnessy et al. 2020) — that many experienced port operators tend to favour 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 covaries 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 obtain fundamental knowledge on biodiversity and ecosystem functioning (Airolidi 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-variation analyses in order to support and provide guidance for future experimental work. Overall, we observed important covariation between kelp biomass and the diversity and structure of fish and sessile taxa, with both scale- and origin-dependent effects. For example, kelp biomass was 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 schools of juvenile *Pollachius*, which are known to use regional kelp forests (Norderhaug et al. 2020). In contrast, synanthropes in habitat beneath pontoons, such as the *Chelon* mullets (Leclerc & Viard 2018), varied independently of kelps. We did not detect further effects 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). Regarding 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 scrutinizing in further work.

When considering variations at the regional scale, results on fish composition concur with findings on sessile taxa. Richness and composition of sessile taxa varied (positively) with kelp biomass in 2 out of the 3 studied regions (Fig. 4B), but both DistLMs and separate PERMANOVAs revealed that this effect may be due mostly to the nonindigenous kelp *U. 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 sporophytes or gametophytes (Thompson & Schiel 2012, Arcángel et al. 2022). It is also likely that *Undaria* and several nonindigenous species, most of which generally share traits conducive to hull fouling, co-occur where 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 several centimetres to hundreds of kilometres, 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 revealed herein are consistent with findings in either intertidal or subtidal natural hard substrata (Fraschetti et al. 2005). We note, for example, 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, finger docks and pontoons. We also clearly showed a strong effect of the 'distance to entry' variable, but we stress the limitation of our sampling that certainly did not capture all stress gradients described elsewhere (Gauff et al. 2022, Hawk & Johnson 2022), and which could influence foundation species and associated communities. Expanding our work to nearby natural reefs would also be of strong interest, as it may allow examining 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 strengthen 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. Such surveys 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 is dedicated to specimen collection and/or multiple experts come together (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 this 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 also reported elsewhere, our results 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) and functional attributes that underpin associated processes (Bustamante & Branch 1996, Ashton et al. 2022). In particular, we report a rather striking latitudinal gradient in the biomass of suspension feeders, and more specifically in *Mytilus*, 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) and regional (Gallon et al. 2014) to broader scales (Malerba et al. 2019) are far from being fully elucidated.

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