



Greater functional similarity in mobile compared to sessile assemblages colonizing artificial coastal habitats

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ABSTRACT

Among anthropogenic habitats built in the marine environment, floating and non-floating structures can be colonized by distinct assemblages. However, there is little knowledge whether these differences are also reflected in the functional structure. This study compared the functional diversity of sessile and mobile invertebrate assemblages that settle over three months on floating vs. non-floating artificial habitats, in two Chilean ports. Using morphological, trophic, behavioral, and life history traits, we found differences between mobile and sessile assemblages regarding the effect of the type of habitat on the functional diversity. Compared to sessile assemblages, a greater functional similarity was observed for mobile assemblages, which suggests that their dispersal capacity enables them to balance the reduced connectivity between settlement structures. No traits, prevailing or selected in one or the other habitat type, was however clearly identified; a result warranting for further studies focusing on more advanced stages of community development.

1. Introduction

Increasing anthropogenic coastal activities around the world have resulted in the construction of numerous man-made structures in the marine environment (Firth et al., 2016; Bishop et al., 2017). These structures such as dikes, breakwaters, piers, mariculture lines, offshore platforms, stand for a major driver of change in marine environments by replacing many natural habitats (Airoldi et al., 2009; Bulleri and Chapman, 2010; Firth et al., 2016). While the rise of artificial structures in coastal and marine areas degrade, fragment, and deplete natural habitats (Bulleri and Chapman, 2010; Bishop et al., 2017), they provide new surfaces available for the settlement, reproduction, and growth of many organisms.

Novel assemblages associated with marine artificial structures however commonly differ from those found in natural habitats, and often include a large proportion of stress-resistant or opportunistic species (Connell, 2000; Perkol-Finkel et al., 2006; Aguilera et al., 2014). Because they are embedded in an expanding propagule transport network, much of these species also appear to be non-indigenous or cryptogenic species (Glasby et al., 2007; Dafforn et al., 2009; Johnston et al., 2017; Leclerc et al., 2021). Overall, artificial structures facilitate

the dispersal of a range of neocosmopolitan (sensu Darling and Carlton, 2018) species (Mineur et al., 2012; Adams et al., 2014; Airoldi et al., 2015) contributing to the homogenization of coastal biota at regional and global scales (Villéger et al., 2011, Simberloff et al., 2013, Leclerc et al., 2020a). The physical characteristics of these artificial structures (e.g., material, roughness, structural complexity, inertia vs. movement capacity), and the levels disturbance in their surroundings (Bulleri and Chapman, 2010; Airoldi and Bulleri, 2011) influence the composition of biotic assemblages (Connell, 2000; Glasby and Connell, 2001; Holloway and Connell, 2002; Firth et al., 2016).

Comparing natural vs. artificial habitats, some studies documented differing species compositions (Connell, 2000; Glasby and Connell, 2001; Holloway and Connell, 2002; Sedano et al., 2020) and contrasting functional patterns between them (Mayer-Pinto et al., 2018; Janiak and Branson, 2021). Similarly, among different types of artificial structures, differences in community composition and biotic interactions have also been shown (Connell, 2001; Firth et al., 2016; Rogers et al., 2016; Strain et al., 2018; Giachetti et al., 2020). For instance, floating structures, such as buoys, pontoons or floating longlines, present contrasting species assemblages to those found on non-floating structures, such as the pillars of piers or docks (Connell, 2001; Glasby, 2001; Holloway and Connell,

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2002), and can differ in their β -diversity across multiple spatial scales (Leclerc et al., 2020a). The various studies that have tried to understand the mechanisms behind these differences have attributed them not only to the aforementioned physical properties of the structures but also to those to which these structures are subjected (e.g., water motion, connectivity with the benthos, exposure to predators and scavengers, disturbance regimes; Glasby, 2001, Holloway and Connell, 2002, Giachetti et al., 2020). Hence, the differing conditions to which floating versus non-floating structures are subjected could act as filters for certain functional traits among the resulting assemblages (see Piola and Johnston, 2009; Zhan et al., 2015; Aronson et al., 2016; Johnston et al., 2017). For instance, the establishment of certain species in a given artificial habitat may result from specific traits that favor the recruitment of those species and increase their local fitness in this specific habitat (Beauchard et al., 2017, Córdova-Tapia and Zambrano, 2015). Traits allowing for rapid colonization of novel empty patches (e.g., high reproductive and growth rates, large dispersal ability) may notably be favored on floating structures, which are prone to physical disturbances (among others, Holloway and Connell, 2002, Johnston et al., 2017) due to their maintenance and replacement. Conversely, traits favoring competitive and defensive abilities may rather be promoted in non-floating structures, wherein stronger biotic interactions can take place (Leclerc et al., 2020b, López and Freestone, 2021).

The communities colonizing these artificial habitats are generally composed of abundant sessile species, including habitat-formers for associated mobile species. Despite the importance of the interactions among these two species groups (Sellheim et al., 2010, Thomsen et al., 2014), only few studies examined the variations in the composition of the mobile species assemblage (e.g., Karalis et al., 2003, Leclerc and Viard, 2018, Martínez-Laiz et al., 2019, Carvalho et al., 2013, Sedano et al., 2020). Thus, several questions are still unanswered, such as whether differences in the composition of sessile species and habitat formers are mirrored by changes in the composition of mobile species in the assemblage, and whether these changes are strong enough to be reflected in the functional structure of the resulting community. The few studies available suggest that the diversity and traits of habitat-forming species affect the structure of their associated sessile and mobile species (Yakovis et al., 2008, Leclerc and Viard, 2018, Sellheim et al., 2010). However, unlike sessile species, mobile species have the ability to disperse and relocate after settlement to colonize new patches of habitat (e.g. Martins et al., 2017). This ability is advantageous under stressful conditions or in variable environments, as it provides mobile species with a greater plasticity in their use of habitats or micro-habitats. Therefore, variations in the mobile species component, due to habitat types (exposed to differing conditions), are expected to be smaller than in the sessile component of these communities.

The present study examined the species diversity and functional structure of sessile and mobile invertebrate assemblages that settle on floating versus non-floating artificial habitats, off the East Pacific coast, central Chile. Using morphological, trophic, behavioral, and life history traits of sessile and mobile species, we particularly examined whether the functional differences among sessile taxa between the two habitat types are mirrored among mobile taxa. We predicted that the magnitude of the differences between habitats will be greater in the assemblages of sessile species than in those of mobile species, given the post-settlement dispersal capacity of the latter. To our knowledge, this is the first study dedicated to comparing the functional structure of communities of different types of artificial coastal habitats. The comparison of the composition, abundance, and diversity of functional traits (functional diversity) among the assemblages colonizing these artificial habitats may reveal mechanisms that determine the functional composition of these new arising man-made ecosystems (see Bremner et al., 2006; Mouchet et al., 2010; Beauchard et al., 2017). This knowledge could help predict how assemblages respond to habitat properties and aid conservation managers in the prediction of changes in ecosystem functioning related to coastal human activities.

2. Materials and methods

2.1. Study area

The study area comprised two ports (separated by 30 linear km) of the Biobío Region, Chile: San Vicente (36.7591°S, 73.1551°W) and Coliumo (36.5377°S, 72.9571°W). As a sidenote, San Vicente is open to international trade, while Coliumo is only open to regional traffic (see Leclerc et al., 2018, 2020a), although maritime traffic was not the scope of our study. These two ports are located in two different bays (San Vicente and Coliumo bays) characterized by distinct biotic compositions in either natural (e.g. for intertidal mollusks; Aldea and Valdovinos, 2005) and artificial habitats, although little is known regarding soft sediment habitats in ports (but see Leclerc et al., 2018 for rapid assessment surveys of conspicuous taxa). Both ports present various types of artificial habitats that are part of the coastal infrastructure, and which were categorized for this study as: (1) non-floating habitats: those attached to the docks by rigid steel foundations/pillars and in direct contact with the benthos; and (2) floating habitats: comprising longlines or buoys that remain in the water column with a weaker, less prominent link to the benthos.

2.2. Dataset overview, study design, sampling and species identification

Our study capitalized on the sampling carried out between March and June 2017, by Leclerc et al. (2020a), who focused on sessile assemblages. In brief, the sampling consisted of the deployment of a series of 15 cm × 15 cm black polypropylene settlement plates, arranged in structures (experimental units) held by PVC tubes (for details, see Leclerc et al., 2020a). The plates were used to have a standardized substrate (surface and material) and new available surface area (which is a main limiting resource, e.g. Sellheim et al., 2010) to be colonized by sessile and mobile taxa (flora and invertebrates).

In each of the study ports and on the two types of habitats (floating vs. non-floating), two experimental units bearing plates were placed vertically, separated by 20 m to 50 m, and at approximately 3 m to 4 m depth. In the non-floating habitats of both ports, these were placed on the pillars of the pier, while in floating habitats they were attached to buoys (San Vicente) or longline (Coliumo) by ropes. Four plates per experimental unit were removed three months after installation, which is sufficient time for the settlement and growth of the sessile and mobile assemblages to take place on the plates (see Leclerc et al., 2020b, Sellheim et al., 2010). The plates were individually transferred underwater in polypropylene rubble bags (mesh size < 0.5 mm) to minimize the loss of the mobile fauna, and were kept for 4 h in a tank with seawater until they were processed in the laboratory.

In the laboratory, sessile (Leclerc et al., 2020a) and mobile taxa (this study) were identified under a dissecting microscope at the lowest possible taxonomic level. The abundance of the sessile taxa was estimated as the coverage at 100 intersection points in an area of 120 cm × 120 cm, as detailed in Leclerc et al. (2020a), while the abundance of the mobile taxa was estimated by counting the number of individuals per plate. The mobile fauna was sampled, after the identification of the sessile taxa, by washing the plate using a 500 μ m mesh sieve. The samples were preserved in 95% EtOH for later identification. Most mobile taxa were identified morphologically to the genus or family level due to a lack of taxonomic literature for the South East Pacific taxa of many abundant groups (e.g., amphipods).

2.3. Functional traits categorization

After identification, the sessile and mobile taxa were classified according to several functional traits related to their life history, behavior, and feeding habits. In this work, sessile taxa were considered to be those species with no or low mobility, those considered as habitat formers, and those which, after their settlement, do not migrate between plates. Their

functional traits were subdivided into different modalities as proposed by Bremner et al. (2003) and Beauchard et al. (2017). The information on life history traits of the individual taxa was extracted from different online sources, such as GBIF, NEMESIS, NIMPIS, MarLIN, NAS, MSIP, BIOTIC, Polytraits, as well as bibliographic sources. Each trait was categorized into three to five modalities (e.g., the trait “Larval development” was given three modalities: pelagic planktotrophic, pelagic lecithotrophic or direct benthic) obtaining a total of 11 traits and 46 modalities of traits, as detailed in Table 1. The affinity of each taxon with the modalities of each trait was assigned, so that the “total affinity” of each trait equaled 1 (Chevenet et al., 1994). This fuzzy coding allows a taxon to display modalities of a trait to different degrees (Chevenet et al., 1994). When information about a particular trait in a taxon could not be obtained, the affinity value of a similar taxon within its taxonomic group (genus or family, whichever closest available) was used as a proxy, however only whenever variations of the trait within the taxonomic group chosen had not been reported. Otherwise, an equal affinity value was assigned for all modalities of that trait for the taxon.

Functional trait data was analyzed separately for each assemblage (mobile vs. sessile). From the trait matrix (“Traits-taxon matrix”) of the

sessile and mobile assemblages, respectively, an analysis of biological traits was performed (BTA; Bremner et al., 2003, 2006). This was based on combining this matrix with the taxa abundance matrix (“Taxon-plate matrix”) by means of a canonical scalar product that transforms and weights the scores (between 0 and 1 following the fuzzy coding) of each trait modality by the abundance of each taxon. This procedure allowed for the generation of a functional trait abundance matrix (“Traits-plate matrix”), on which the subsequent functional structure analyses were based.

2.4. Data analysis

The functional diversity of the community was estimated using the functional diversity indices wFDC and FDC (Petchey and Gaston, 2006), based on the Gower similarity matrix of the FDiversity package (Casasnoves et al., 2011), in R (R Development Core Team, 2010). These indices are estimated by summing the length of the branches of a functional dendrogram of all the species from a cluster analysis, which uses profiles of multiple traits either by including their abundance (wFDC) or excluding their abundance (FDC). At the taxon level, we also estimated the richness (S) and the taxonomic diversity (Hill number 2: $1/\lambda$; Hill, 1973) of the sessile and mobile assemblages. To compare both the taxonomic and the functional diversities between the factor levels, an analysis of variance (ANOVA) was performed using the same, previously specified design. In addition, the effect size of each factor was estimated using the Omega squared index (ω^2 , Hays, 1963). Prior to each ANOVA, normality and homogeneity of variances were checked using Shapiro-Wilk and Levene's tests, respectively. The data were transformed (square root transformation) when these tests resulted significant. These analyses were performed using R version 4.0.3 (R Core Team, 2016).

The relationship between richness and functional diversity can further inform about the functional redundancy of communities (Micheli and Halpern, 2005, Córdova-Tapia and Zambrano, 2015). Instead of summarizing the associated information in a single index (e.g. van der Linden et al., 2016), we herein characterized these relationships in both habitats and compared them using the Tsutakawa and Hewett Test (Tsutakawa and Hewett, 1977) as a substitute for the ANCOVA test due to the non-fulfillment of the assumption of independence between the *Habitat* factor and the covariate richness of the species. This test allows to evaluate the equality of two populations when the observations are bivariate (XY; in this study X: Richness Y: Functional diversity) by determining whether the values of Y given X for one population dominate the other for every value of X (Williams et al., 1977). The test involved fitting a regression line (the one that best fits using the Akaike criterion (AIC); in this case, a linear regression, see results) to the entire data set, and then comparing, through a contingency table analysis (using the χ^2 distribution), the distribution of bivariate data above and below the regression line (Williams et al., 1977, Muñoz and George-Nascimento, 2008). These analyses were performed using the PAST program, version 3.14 (Hammer et al., 2001).

To compare the functional structure between habitats of the sessile and mobile assemblages, Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001) was performed with 4999 permutations. A three-way design was applied, considering the following factors: “Habitat” (two fixed levels: floating vs. non-floating), “Port” (two random levels: Coliumo vs. San Vicente), and “Experimental unit” (two random levels nested within “Port” and “Habitat”). Separate analyses were performed for sessile and mobile assemblages to avoid violation of independency, and because abundance was not estimated in the same way. The analyses were based on the Bray-Curtis similarity matrices generated from transformed data in order to downplay the importance of the most abundant traits and homogenize multivariate dispersion. We used the fourth root for the abundance of traits of mobile taxa and the square root for that of sessile taxa. Multivariate trait data were also analyzed for their composition using a Jaccard's similarity

Table 1

Selected biological traits and categories used to describe the functional structure of sessile and mobile invertebrates assemblages in artificial marine habitats, in the Southeast Pacific, Chile.

Traits	Modality
Feeding habit	Autotroph
	Filter/suspension feeder
	Deposit feeder
	Predator
	Opportunist/scavenger
Individual/colonial size	Grazer
	1–10 mm
	10–50 mm
	50–100 mm
Body form	100–300 mm
	Flat
	Mound
	Erect
	Elongate
Sociability	Little elongate/ellipsoid
	Solitary
	Colonial
Degree of attachment	None
	Behavioral
	Temporary
Motility	Permanent
	Sessile
	Burrower
	Crawler
	Crawler-swimmer
Adult mobility	Swimmer
	None
	Low
	Medium
Lifespan	High
	<1 year
	>1–3 years
	3–5 years
Reproductive mode	>5 years
	Asexual
	Sexual (broadcast spawner)
	Sexual (planktonic larvae)
Larval development	Sexual (direct-developer)
	Pelagic planktotrophic
	Pelagic lecithotrophic
Pelagic larval duration	Direct benthic
	None
	<1 day
	1–7 days
	7–30 days
>30 days	

After Bremner et al. (2003) and Beauchard et al. (2017).

matrix (i.e., presence-absence data). The homogeneity in the dispersion of the data was verified between the levels of the factors “Habitat” and “Port”, using a Permutational Multivariate Dispersion Analysis (PERMDISP; Anderson et al., 2008). Principal coordinate analysis (PCO) and cluster analysis were performed to visualize and determine group similarity, respectively (Anderson et al., 2008). To determine if there are significant differences between the levels of each factor in certain traits of the sessile and mobile assemblages, multivariate PERMANOVAs were performed for each of the traits separately using trait modalities as response variables. The analyses were based on the Bray-Curtis similarity matrix generated from transformed data using the fourth root for the abundance of traits of mobile taxa, the square root for that of sessile taxa. All of these analyses were performed using the PRIMER 6 program (Anderson et al., 2008).

3. Results

3.1. Overall assessment of taxonomic diversity and functional traits

A total of 126 taxa were found, including 43 sessile and 83 mobile taxa (Supporting information Appendix S1). Sessile taxa were represented by 10 phyla (10 bryozoans, 9 cnidarians, 7 chordates, 6 rhodophytes, 5 mollusks, 2 arthropods, 1 annelid, 1 sponge and 1 chlorophyte, 1 ochrophyte), while mobile taxa comprised 5 phyla (43 arthropods, 24 annelids, 13 mollusks, 2 nemerteans, and 1 echinoderm). Of the sessile taxa, the most represented taxonomic groups in terms of numbers of taxa and coverage were bryozoans (10 taxa, for an average of 31% coverage per plate), followed by hydroids (9 taxa and 27% of the coverage). Of the mobile taxa, the most represented taxonomic groups in terms of numbers of taxa and abundance were amphipods (29 taxa, for an average of 54% of the total abundance per plate), followed by polychaetes (23 taxa and 21% of abundance) and gastropods (13 taxa and 5% of abundance). Oppositely, copepods, isopods, tanaidaceans, and echinoderms were the least present (only 1 or 2 taxa and less than 8% of abundance).

The sessile assemblage, regardless of the habitat (non-floating and floating), was mainly dominated in terms of numbers of taxa and cover by suspension-feeders (35 taxa and 97% of the average total coverage per plate), as compared to autotrophs (8 and 3%). These assemblages were dominated by colonial taxa (22 taxa and 67% of cover), erect taxa (23 and 81%) and smaller than 50 mm taxa (31 and 91%). These taxa had diverse reproductive modes: asexual (30 taxa and 35% of cover), sexual with spawning events (23 and 24%) or broadcasted developing larvae (22 and 41%). Most larvae were lecithotrophic (35 taxa and 86% of cover), with a pelagic larval duration most often of less than 1 day (30 taxa and 72%). The longevity of the taxa was generally less than 1 year (30 taxa and 77% of cover).

The assemblage of mobile invertebrates was equally distributed by predators (40 taxa and 32% of the average total abundance per plate), detritivores (49 and 30%) and filter-feeders (34 and 32%). Their mobility was either low (46 taxa and 48% of abundance) or moderate (42 and 42%) and associated with behavior as burrowing in micro-refuges (42 and 40%), crawling (44 and 29%) or crawling-swimming (36 and 30%). Relatively elongated individuals predominated (68 taxa), with sizes less than 10 mm (49 taxa and 77% of abundance), with a longevity less than 1 year (33 and 38%) and 1 to 3 years (77 and 53%). Different reproductive modes were observed, but most of them (51 taxa and 59% of abundance) were sexual reproduction with parental egg care and the development of juvenile phases. Most taxa developed directly in the benthos (54 taxa and 62% of abundance) and of the 38% with larval development (49 taxa), 24% had a pelagic larval duration of less than 1 day (18 taxa).

3.2. Contrasting effects of the type of habitat (floating vs. non-floating) on the taxonomic and functional diversity according to the assemblages (mobile vs. sessile)

The taxonomic and functional diversity of the two categories of assemblages (i.e., mobile vs. sessile) varied between non-floating and floating habitats, whatever the variable examined, and in the two ports (Fig. 1, Table 2). In sessile assemblages the differences between habitats were contrasting between the two ports, as evidenced by significant interactions (and associated effect sizes) *Habitat* and *Port* for all response variables (Table 2). In San Vicente, sessile richness, diversity and both functional diversity indices were higher in the non-floating habitat, while the opposite was observed in Coliumo (Fig. 1). Conversely, for mobile assemblages, the differences observed between habitats were comparatively far more consistent in the two studied ports. With the exception of wFDC that showed significant interaction, higher taxonomic and functional diversity (FDc only) of mobile assemblages were

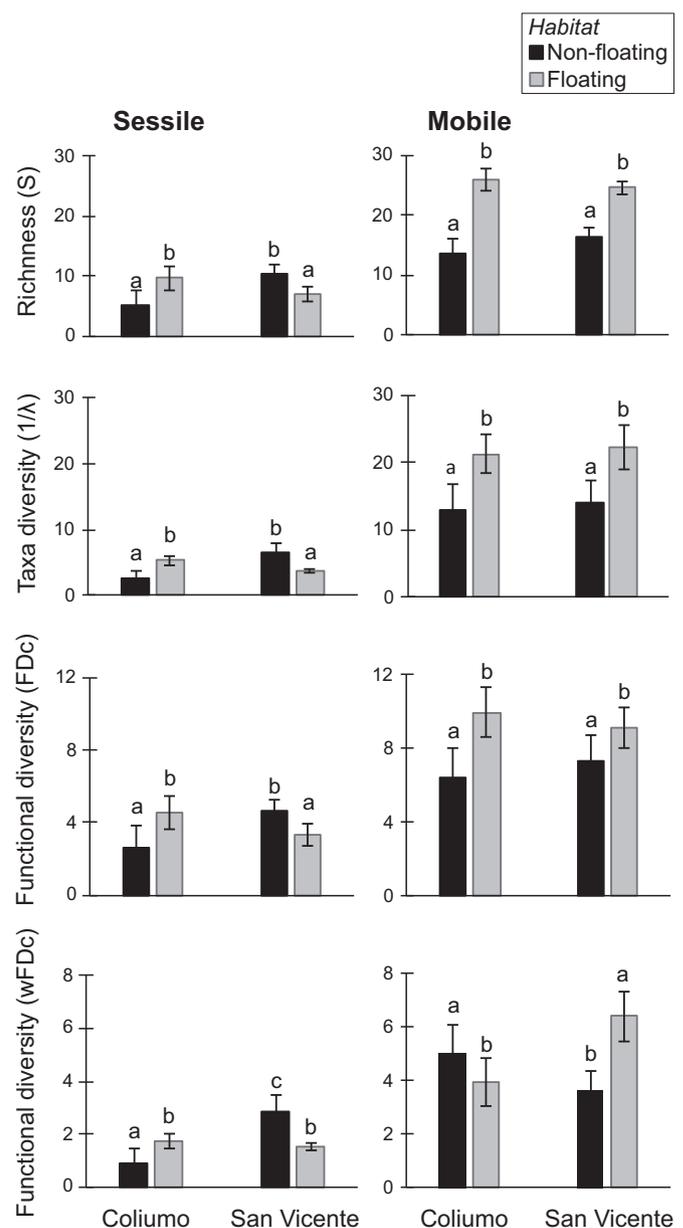


Fig. 1. Indices of taxonomic and functional diversity of the sessile and mobile assemblages associated with non-floating vs. floating habitats in the two ports: San Vicente and Coliumo, Southeast Pacific, Chile.

Table 2

Results of the ANOVA for the difference of taxonomic and functional diversity of sessile and mobile invertebrate assemblages associated to artificial marine habitats in two ports of the Southeast Pacific, Chile. The value of F and ω^2 and its significance at $\alpha = 0.05$ in bold (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$) is given for each factor (*Habitat* vs. *Port*), and their interactions. Tests of homogeneity of variances are summarized by their p values.

Response variable	ANOVA factor (df, total = 31)								Levene p
	Habitat = H		Port = P		H × P		Experimental unit		
	F	ω^2	F	ω^2	F	ω^2	F	ω^2	
Richness (S)									
Sessile	0.90	0.00	2.92	0.03	34.74***	0.49	1.20	0.05	0.64
Mobile	53.64***	0.63	0.19	0.00	2.04	0.01	0.80	0.03	0.63
Taxa diversity (1/ λ)									
Sessile (^{sqrt})	1.35	0.00	19.02**	0.10	104.9***	0.58	1.27	0.06	0.11
Mobile	45.62***	0.60	0.70	0.00	0.00	0.00	0.68	0.02	0.37
Functional diversity (FDc)									
Sessile	1.12	0.00	2.39	0.02	33.08***	0.47	1.78	0.08	0.45
Mobile	32.30***	0.60	0.02	0.00	3.76	0.04	1.62	0.08	0.51
Functional diversity (wFDc)									
Sessile	4.47	0.03	0.23	0.26	91.32***	0.44	7.83	0.14	0.07
Mobile	6.84*	0.41	2.88	0.02	33.84***	0.46	0.66	0.02	0.41

(^{sqrt}) transformation square-root.

observed in floating than in non-floating habitats in both ports (Table 2, Fig. 1).

The functional diversity in non-floating and floating habitats showed a general positive linear relationship with taxa richness for both sessile and mobile assemblages (Fig. 2), although this relationship was better supported for sessile ($r^2 = 0.58$, $p < 0.001$) than for mobile assemblage ($r^2 = 0.16$, $p = 0.023$, Fig. 2). According to the bivariate relationships between taxa richness and functional diversity, a contrasting functional redundancy between habitats for sessile assemblages was supported by the Tsutakawa and Hewett tests ($\chi^2 = 8.33$, $df = 1$, $p = 0.004$). A lower slope for the linear relationships in floating habitats than in non-floating habitats was observed (Fig. 2; non-floating: slope = 0.29, $r^2 = 0.73$; floating: slope = 0.09, $r^2 = 0.73$). On the contrary, for mobile assemblage the bivariate relationships (richness, functional diversity) suggested a similar functional redundancy between habitats ($\chi^2 = 1$, $df = 1$, $p = 0.317$), with a similar slope between floating and non-floating habitats (Fig. 2; non-floating: slope = 0.12, $r^2 = 0.22$, floating: slope = 0.04, $r^2 = 0.01$).

3.3. Stronger effects of the type of habitat on the functional structure of sessile assemblages compared to mobile assemblages

The functional compositions (presence-absence) of the sessile and mobile assemblages did not show significant differences between non-floating and floating habitats (Table 3). However, the functional structure weighted by the abundance (wFDc) showed a significant interaction between the factors, *Habitat* and *Port*, in both assemblages (Table 3). The PCO results also showed distinct clusters, for both composition and

abundance (Fig. 3). Interestingly, in the sessile assemblages, when compared to the mobile, a greater differentiation in the functional structure weighted by the abundance was observed between both habitats (cf. similarity thresholds in Fig. 3), as well as a greater similarity within and between the floating habitats of both ports. Likewise, the variation between plates in the abundance of the functional traits of the sessile assemblage was significantly greater in non-floating habitats than in floating habitats (PERMDISP F = 32.69, $p < 0.001$). In addition, nested within habitat categories, experimental units display significant (and sizable) effects only for the sessile assemblages, in their (functional composition and abundance structure; Table 3). Overall, the mobile assemblages presented higher similarity in their composition and functional abundance than the sessile assemblages, regardless of the habitat or port (80% similarity, Fig. 3).

When analyzing the functional traits of the sessile assemblage separately, no effect of the *Habitat* factor was detected on the functional structure of the traits. However, significant interactions between *Habitat* and *Port* were observed for five (out of nine examined) traits, namely body form, individual/colony size, lifespan, reproductive mode, and pelagic larval duration (Table 4). It is also noteworthy that for the feeding trait (represented by two modalities), the factor *Habitat* had a high effect size in the multivariate analysis. Although a dominance of filter-feeders was observed in both habitats and ports (Fig. 4), their absolute coverage on the plates was greater in floating habitats than in non-floating ones (Fig. S1). Among the other functional traits evaluated, although the proportions of modalities varied between habitats, the differences were not consistent between ports for which these traits did not contribute to any further differentiation between the habitats,

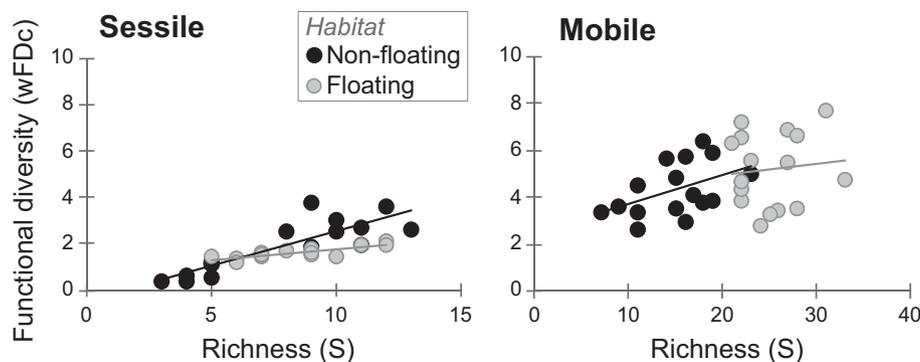


Fig. 2. Relationship between functional diversity and taxa richness of sessile and mobile assemblages in non-floating vs. floating habitats. Data are pooled across ports.

Table 3

PERMANOVA results for the differences in functional structure (composition and abundance) of the sessile and mobile assemblages. The pseudo-F of PERMANOVA and PERMDISP ($H \times P$) are given along with significance at $\alpha = 0.05$ in bold (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$) and the effect size (ω^2) of each factor.

Assemblage	Sessile						Mobile					
	Composition			Abundance			Composition			Abundance		
Transformation	None			Square-root			None			Fourth-root		
PERMDISP	$F_{1,30} = 1.09$ $p = 0.354$			$F_{1,30} = 34.01$ $p < 0.001$			$F_{1,30} = 8.23$ $p = 0.012$			$F_{1,30} = 7.47$ $p = 0.013$		
Source	df	Pseudo-F	ω^2	df	Pseudo-F	ω^2	df	Pseudo-F	ω^2	df	Pseudo-F	ω^2
Habitat = H	1	0.65	0.05	1	1.01	0.26	1	4.31	0.15	1	1.25	0.39
Port = P	1	3.02**	0.16	1	22.74**	0.50	1	6.97*	0.15	1	12.63*	0.08
$H \times P$	1	1.19	0.05	1	10.87**	0.23	1	1.61	0.01	1	50.17**	0.32
Experimental unit ($H \times P$)	4	3.17***	0.21	4	5.92***	0.07	4	1.15	0.07	4	1.01	0.02
Res.	24			24			24			24		

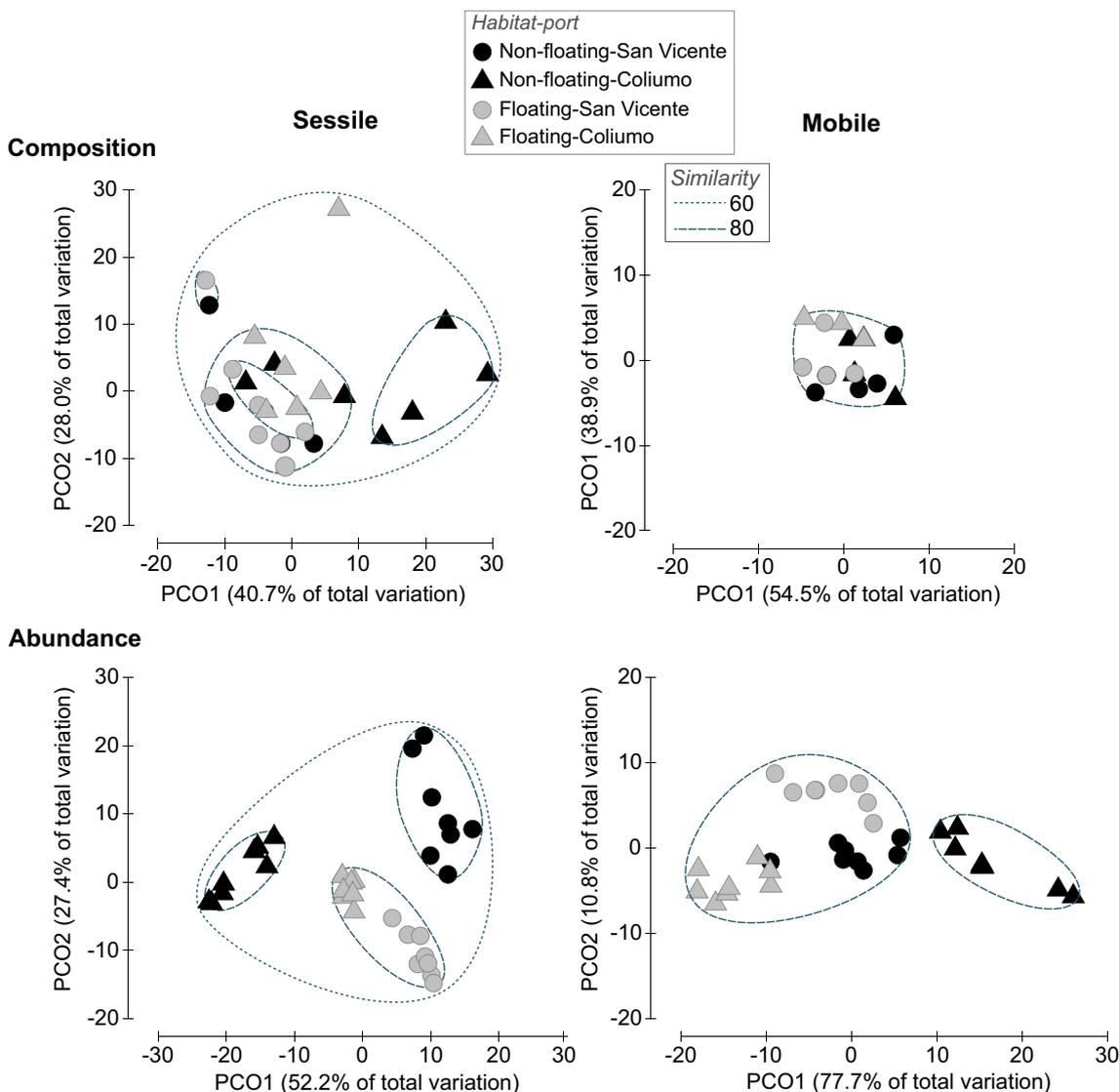


Fig. 3. Principal coordinates analysis (PCO) of the composition (presence-absence) and abundance of functional features of sessile and mobile assemblages on non-floating vs. floating habitats in two ports (San Vicente vs. Coliumo) in the Southeast Pacific, Chile.

floating vs. non-floating (Fig. 4). Consistently with the analysis of functional composition and abundance structure, significant spatial effects of the experimental units were observed on the modalities, only for the sessile assemblages (Table 4).

For the mobile assemblages, although all the traits had a high effect size of the *Habitat* factor, this effect was only significant in interaction

with the factor *Port* (Table 5). This is also illustrated by the modality proportions of abundance within each functional trait across habitats and ports (Figs. 5, S2), for which variations were observed, although these were not as marked as for the sessile assemblage.

Table 4

PERMANOVA results for the differences in the modality composition (weighted by abundances) of each functional trait of taxa of the sessile assemblages of artificial marine habitats studied in two ports of the Southeast Pacific, Chile. The pseudo-F of PERMANOVA and t value of PERMDISP (H × P) are given along with significance (in bold) at $\alpha = 0.05$ (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$) and the effect size (ω^2) of each factor.

Functional traits	PERMANOVA Factor (df, total = 31)								PERMDISP
	Habitat = H		Port = P		H × P		Experimental units		
	Pseudo F	ω^2	Pseudo F	ω^2	Pseudo F	ω^2	Pseudo F	ω^2	
Feeding habit	4.06	0.43	3.72	0.08	4.31	0.10	2.37*	0.09	4.27
Body form	1.31	0.26	7.89*	0.26	6.10*	0.20	6.41***	0.12	8.15**
Body size	0.33	0.16	14.01*	0.22	31.73**	0.49	6.47***	0.06	77.24***
Sociability	4.51	0.25	36.64**	0.60	3.38	0.05	11.86***	0.06	17.85***
Lifespan	0.64	0.14	23.69**	0.48	11.36**	0.23	7.87***	0.07	22.00***
Degree of attachment	7.14	0.59	1.16	0.03	2.44	0.07	5.91***	0.13	0.90
Reproductive mode	1.05	0.35	11.14**	0.17	21.93**	0.33	5.03***	0.06	1.13
Larval development	–	0.24	56.82**	0.68	–	0.03	5.75***	0.05	29.48***
Pelagic larval duration	0.00	0.05	106.37**	0.74	12.47*	0.08	2.30	0.03	44.92**

The data were previously transformed (square root transformation) and was used the Bray-Curtis Index to generate the similarity matrix.

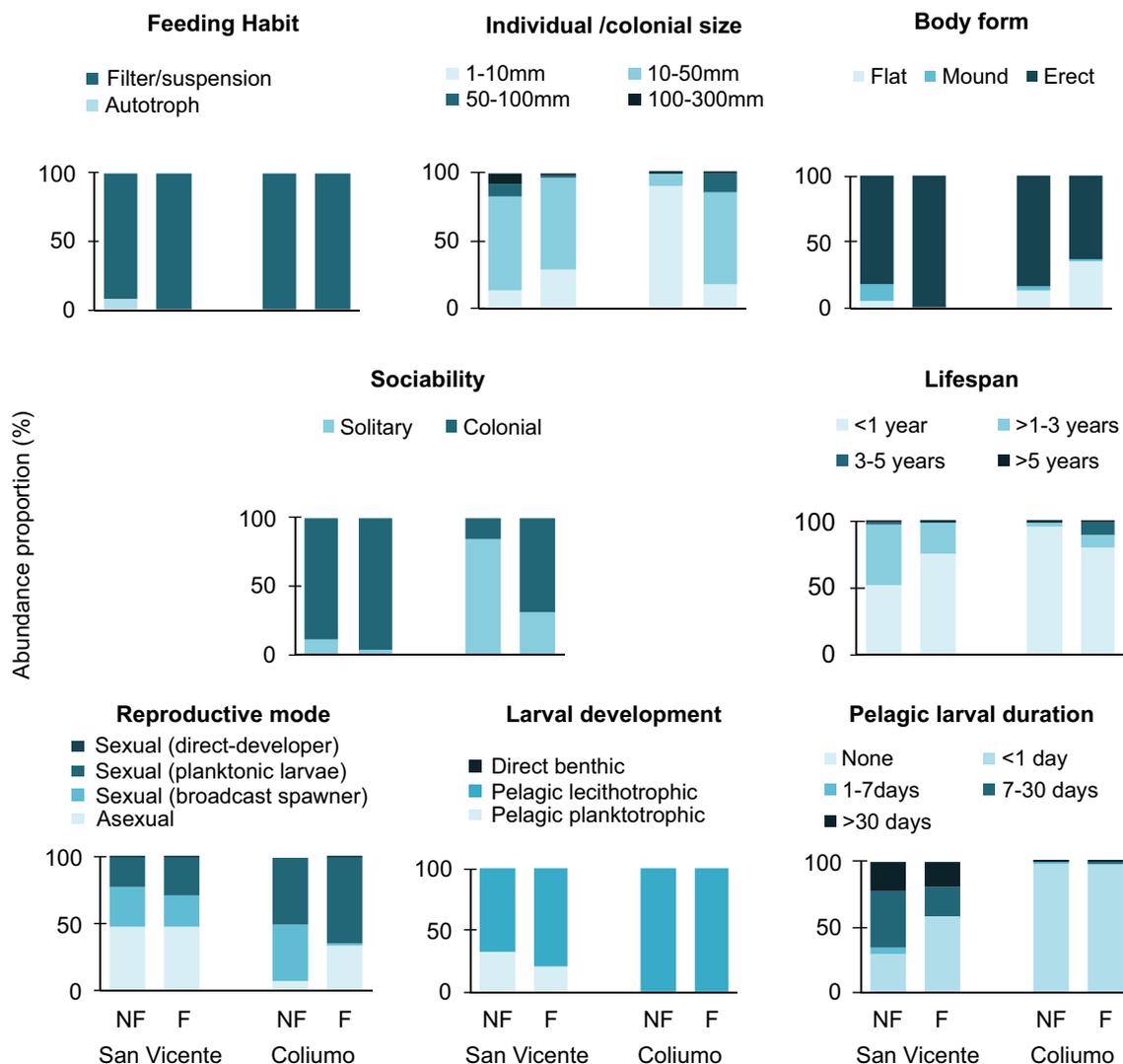


Fig. 4. Proportion of the average abundance of each category of functional traits of the sessile assemblages of two types of habitats (NF: non-floating vs. F: floating) in two ports: San Vicente vs. Coliumo, Southeast Pacific, Chile.

4. Discussion

The results of our study show that the differences reported by various authors in the community structure between different types of artificial habitats (Connell, 2001; Glasby, 2001; Firth et al., 2016; Strain et al.,

2018), including in the study area (Leclerc et al., 2020a), are also found in the functional structure of sessile and mobile marine assemblages. However, and in accordance with our predictions, these differences were not as noticeable in mobile assemblages as opposed to sessile assemblages. Our results showed that the mobile assemblages, unlike

Table 5

PERMANOVA results for the differences the functional structure (weighted by abundances) of each functional trait of the taxa of the mobile assemblages in non-floating and floating habitats. The pseudo-F of PERMANOVA and t value of PERMDISP ($H \times P$) are given along with the respective significance (in bold) at $\alpha = 0.05$ (*: $p < 0.05$, **: $p < 0.01$) and the effect size (ω^2) of each factor.

Functional traits	PERMANOVA Factor (df, total = 31)								PERMDISP
	Habitat = H		Port = P		$H \times P$		Experimental unit		
	Pseudo F	ω^2	Pseudo F	ω^2	Pseudo F	ω^2	Pseudo F	ω^2	
Feeding habit	0.95	0.36	9.41*	0.05	61.68**	0.25	0.97	0.01	0.17
Body form	1.08	0.26	26.98**	0.23	27.23**	0.24	1.05	0.03	0.21
Body size	1.73	0.44	6.49	0.04	34.90*	0.25	0.86	0.02	0.00
Mobility	1.31	0.42	6.60*	0.04	45.86**	0.32	1.07	0.02	7.64**
Adult mobility	0.93	0.34	29.36*	0.12	85.01**	0.28	0.79	0.01	0.77
Lifespan	0.96	0.38	3.30	0.01	52.75*	0.40	1.38	0.02	1.13
Degree of attachment	1.31	0.43	9.08*	0.04	55.93**	0.32	0.96	0.01	3.61
Reproductive mode	1.64	0.46	9.79*	0.05	45.65**	0.27	0.98	0.43	5.79*
Larval development	1.22	0.40	11.21*	0.06	57.85**	0.33	0.96	0.02	4.09*
Pelagic larval duration	0.00	0.38	9.40*	0.07	36.40**	0.30	1.14	0.02	5.43*

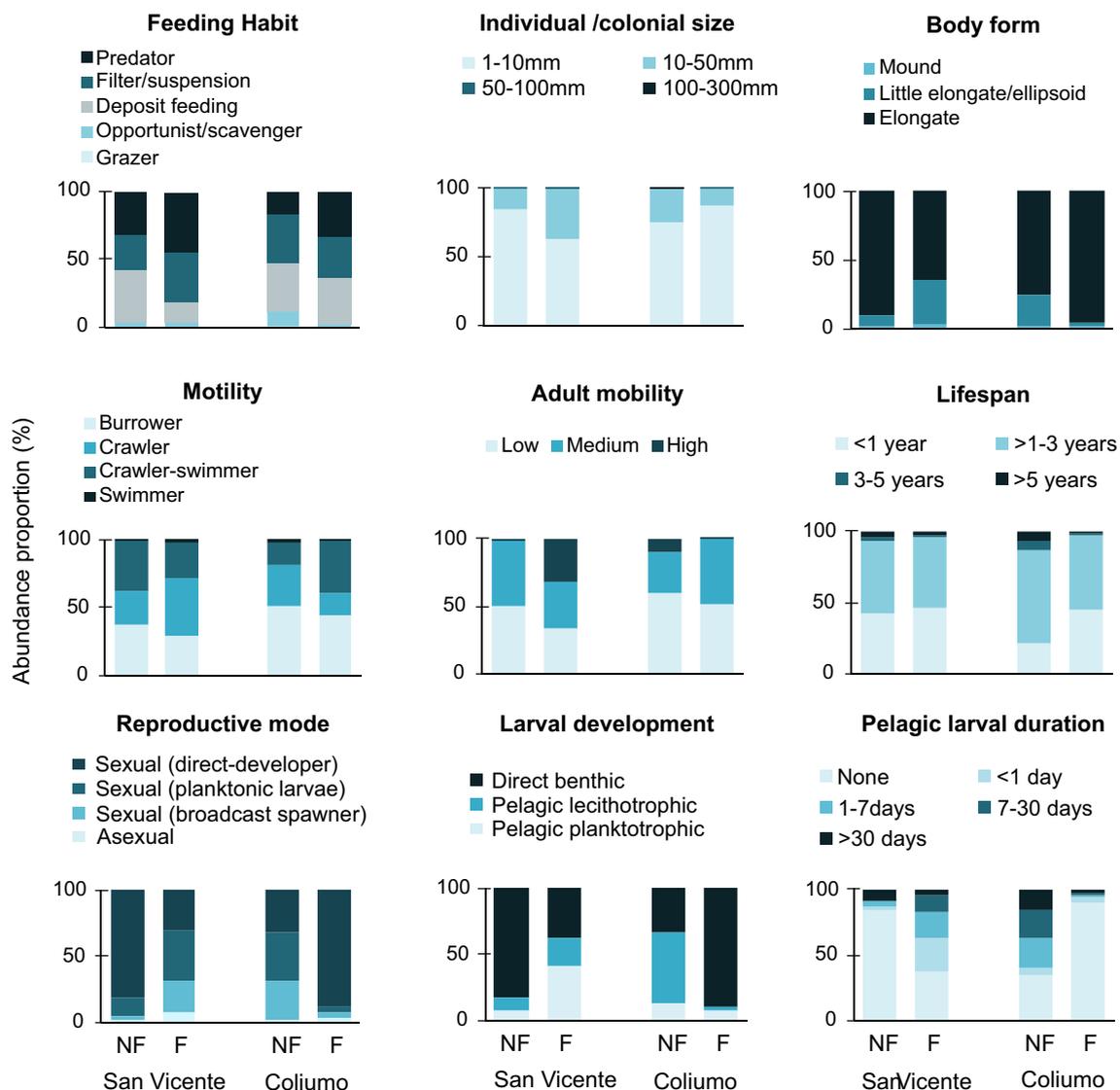


Fig. 5. Proportion of the average abundance of each category of functional traits of the mobile assemblages of two types of habitats (NF: non-floating vs. F: floating) in two ports: San Vicente vs. Coliumo, Southeast Pacific, Chile.

sessile ones, present a compositional structure and abundance of functional traits more similar than that of sessile assemblages, suggesting that the functional structure of these mobile assemblages is less affected

by the type of artificial coastal structures (floating vs. non-floating) than that of sessile assemblages.

Floating and non-floating man-made marine structures have the

potential to create habitats that attract diverse organisms, including habitat-formers that develop on the empty foundations of these structures (Connell, 2000, Holloway and Connell, 2002, Leclerc and Viard, 2018). These habitat-forming organisms, most often sessile, facilitate the recruitment and the subsequent establishment of diverse sets of other species that use these taxa as a source of food and/or shelter (see Bruno and Bertness, 2001, Karalis et al., 2003, Sellheim et al., 2010). Given these biotic interactions, changes in the species composition of sessile assemblages may further determine the composition and changes of the associated mobile assemblages (Sellheim et al., 2010, Sueiro et al., 2011, Leclerc et al., 2020b). For example, on floating structures, Leclerc et al. (2020b) found correlations between the richness and abundance of mobile fauna and the volume of interstices created by the sessile fauna. Other studies in ports however only reported few correlations between the compositions of the sessile and mobile assemblages (see Birdsey et al., 2012, Lavender et al., 2017), and variables such as habitat cover, identity, and functional diversity of sessile assemblages did not predict the variation of the associated mobile assemblages (Birdsey et al., 2012). In our study, contrasting patterns were observed between sessile and mobile assemblages. In sessile assemblages, the functional structure varied between habitats within each port, and among experimental units (plots), with contrasting abundance of the functional traits. This pattern could be explained because sessile assemblages may be influenced by local settlement dynamics (e.g. Hedge and Johnston, 2012; Leclerc et al., 2021), especially where taxa with propagules displaying short pelagic duration (notably lecithotrophic larvae) dominate, as upon our settlement plates. Conversely, in the mobile assemblages, the functional structure was more similar and the modalities of the traits showed similar proportions of abundance in habitats and ports, and seldom varied among experimental plots. Considering the prominent role of species abilities to post-settlement dispersal on the community structure of novel habitats (Palmer et al., 1996; Martins et al., 2017), the intrinsic capability of movement among taxa is likely to be a critical factor explaining the observed greater functional similarity between habitats in mobile compared to sessile assemblages.

Moreover, while we observed complex variations in the richness and diversity (taxonomic and functional) of the sessile assemblages between habitats and ports, the mobile assemblages showed more consistent results, with the greatest richness and diversity found in the floating habitats at both ports. This indicates that despite the putative lower connectivity with the benthos of the floating habitats for many groups (especially non-swimming taxa), a substantial dispersal of mobile species towards floating habitats and between them is warranted. Considering that 60% of the taxa has a direct development in these habitats, dispersal of these mobile species is likely due to the migration of adults and juveniles. However, larval dispersal and recruitment of post-larval stages, either from nearby benthic habitats or from other artificial habitats (see Susick et al., 2020, Leclerc et al., 2020b) is likely to play an important role for benthic-pelagic or holo-pelagic species (Hudson et al., 2016). In our experiments, the plates were deployed over 3 months, a time long enough for colonization by mobile species (including tube-dwelling taxa) from rocky subtidal habitats, especially during summer (Norderhaug et al., 2002; Waage-Nielsen et al., 2003). Additionally, these mobile assemblages can redistribute after settlement, colonize new patches of habitat in interconnected or nearby areas, becoming more diverse and abundant in areas further away from their source habitat/reef (Virnstein and Curran, 1986; Martins et al., 2017).

Floating habitats, being less accessible to non-swimming species, in particular non-swimming predators, show a lower predation pressure (Dumont et al., 2011, Rogers et al., 2016, Leclerc et al., 2020a), which may in turn influence the diversity and structure of the community. For instance, in temperate marinas, low predation pressure by benthic predators in floating habitats had been shown to increase the biotic complexity of sessile assemblages, which in turn could favor colonization by mobile species (Leclerc and Viard, 2018). In our study, the sessile assemblage had a 40% greater coverage on the floating structures than

on the non-floating ones, and we also found a higher percentage of empty patches in the settlement plates deployed on the non-floating structures. Although the present dataset does not allow to evaluate the relationship between the richness/diversity of the mobile assemblage and the functional composition of the sessile assemblage, it is likely that a greater coverage of the sessile assemblage favors the associated mobile assemblage of floating habitats by providing an increased availability of microhabitats and refuges, decreasing predator-prey encounters for mobile species (Grabowski, 2004, Scyphers and Powers, 2013, Leclerc and Viard, 2018). Nonetheless, other mechanisms to the aforementioned, such as differences of the biotic and abiotic stress gradients among habitats, may be responsible for the richer and more functionally diverse mobile fauna we measured on floating structures, for which further investigation is required. It is noteworthy that although remarkable differences in taxonomic diversity and functional richness were found for mobile assemblages between habitats, no difference in the functional structure could be detected when abundances (here the number of individuals) were considered. As suggested elsewhere (e.g. Hillebrand et al., 2018, Boyé et al., 2019), this result warrants caution regarding blind uses of diversity metrics and encourages more comprehensive analyses incorporating species identity and the influence of their traits on the system dynamics to detect changes in biodiversity and ecosystem functioning.

Floating habitats differ from their non-floating counterparts in a considerable number of abiotic and biotic conditions (e.g., connection/link with the benthos, exposure to predators and scavengers, orientation to currents, and disturbance regimes). These conditions could act as a filter for certain functional traits (e.g., r-selected traits and/or tolerance to disturbance, see Piola and Johnston, 2009, Zhan et al., 2015, Johnston et al., 2017, Leclerc et al., 2020a). When the filters are characteristic to a certain environment, then through similar selective processes, large scale patterns in the composition and functions of the assemblages of these environments may arise (Poff, 1997; Statzner et al., 2004). However, among most of the traits considered in this study, more differences were found among structures or harbors than between habitats, and this may suggest that there was no differential selection of particular traits between the types of habitats studied. However, our results showed a high percentage of taxa with traits characteristics of early successional stages such as small sizes (sessile: 79% <50 mm, mobile: 60% <10 mm), short longevity (sessile 70% <1 year, mobile: 93% <3 years) and short pelagic larval duration (70% sessile <1 day, mobile 69% none or <1 day) (Giangrande et al., 1994, Odum, 1969). Thus, the early stage of maturity of the study communities or the broad array of putative processes influencing spatial patterns in coastal biodiversity (see Benedetti-Cecchi, 2001; Fraschetti et al., 2005; Chang and Marshall, 2016) could also generate such results. Hence, considering that a greater complexity of interactions could occur in more advanced successional stages (e.g. Aguilera and Navarrete, 2012), evaluating changes in functional traits later during succession may give a better approximation of the functional structure of these communities.

The dissimilarity of the relationships between the functional diversity of sessile taxa and their richness suggests that floating habitats present a functional redundancy superior to that of non-floating ones. Likewise, our results showed a greater functional similarity of the sessile assemblages among the plates of the floating habitats and a greater multivariate dispersion among those of the non-floating habitats. In general, disturbed environments can favor the establishment of species with more similar combinations of traits (Poff, 1997; Leibold et al., 2004; Statzner et al., 2004; Valdivia et al., 2017; Leclerc, 2018). However, our results do not allow us to know whether or not the environmental conditions in floating habitats, may be responsible for the similarity we found among the traits of these habitats. For example, the greater variability in the composition of traits among the plates of non-floating habitats could possibly be linked to the more intense predation pressure reported in these types of habitats (see Díaz and McQuaid, 2011; Valdivia et al., 2017). In these habitats, important variation in the

effect of predation among patches and pillars had been previously reported (Leclerc et al., 2020b). As any other disturbance (Sousa, 1984; Connell and Slatyer, 1977; Sousa, 1979), predation at the microhabitat scale (within a single plate) on the one hand can reduce the richness and abundance of species (and proportionally the functional diversity of the community/assembly), while on the other hand, the freed space on the plates, caused by predation, can increase the richness and abundance of species by repeatedly opening new patches/substrate available for the colonization by new species.

Likewise, it should be considered that greater similarities in the community structure of sessile assemblages in floating versus non-floating habitats have been reported (Holloway and Connell, 2002; Leclerc et al., 2020a), including on a regional scale (Leclerc et al., 2020a). According to many authors, floating structures have assemblages of particular species, where there is generally a greater abundance and richness of non-native species compared to non-floating structures (Holloway and Connell, 2002, Glasby et al., 2007, Dafforn et al., 2009, Johnston et al., 2017, Leclerc et al., 2020a). The susceptibility to invasion and to biotic homogenization of these floating structures (Leclerc et al., 2020a) might explain the greater similarity in the functional structure, diversity and redundancy, of the sessile assemblages in floating habitats, a hypothesis to be further tested, for instance by distinguishing native and non-native taxa at broader scales.

To conclude, our data showed that the functional structure of both sessile and mobile assemblages varies between floating and non-floating artificial habitats. However, such variations are minor among mobile assemblages as opposed to sessile ones. Dispersal ability of mobile species is likely to be a major determinant of this pattern. Our results suggest that despite the (almost) absence of any physical link between floating habitats and the benthos, the dispersal capacity of much mobile species leads to richer and more diverse assemblages than expected in these habitats. In this study, we however did not find a clear suite of functional traits prevailing in one or the other habitat type, in either assemblages. As we only examined functional traits at an early successional state of these communities, we recommend evaluating their composition in more advanced stages of the community's development to evaluate 1) whether the low functional differences in the mobile assemblage are maintained, and 2) whether there is a selection over time of certain functional traits that differs between the types of habitats, floating vs. non-floating.

CRedit authorship contribution statement

JCL, NF, FV and AB conceived the working hypotheses and designed the study. JCL led the fieldwork, sample collection and conducted the taxonomic analyses of the sessile assemblages. NF realized the taxonomic analyses of the mobile assemblages. NF did literature research to fill in the trait matrices and conducted all data analyses (taxonomic and functional diversities, statistics). NF led the writing, with substantial contributions from the other co-authors. All authors critically revised and edited the manuscript drafts.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

Some of the data are provided in the supplementary material associated with the manuscript. Detailed data will be made publicly available in the Dryad repository.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112844>.

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