

Ecosystem functioning of canopy- and turf-forming algae: contrasting supply of invertebrate prey to pelagic consumers

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ABSTRACT: Macroalgal canopies are declining worldwide and are being replaced by low-lying algal turfs which frequently dominate reefscape. Their loss may impact reef ecosystems in different ways, including the collapse of small canopy-dwelling invertebrates, and thus the decline of juvenile reef fish that prey on them. To evaluate this potential loss, we assessed (1) the differences between the mobile invertebrate assemblages associated with turf-forming (filamentous and articulated coralline turf) and canopy-forming (*Sargassum* spp. and *Dichotomaria marginata*) algae, and (2) the mechanisms underlying those contrasts by examining the invertebrate community assembly of filamentous turf and *Sargassum* spp. over the main canopy season. Abundance, biomass and diversity almost always differed between canopies and turfs (although not in a consistent way across sampling sites), while differences within canopy and turf algal types were nearly absent. The structure of invertebrate assemblages differed more consistently between canopies and turfs, with certain hard-bodied and soft-bodied invertebrates characterizing canopies and turfs, respectively. This divergence increased as the canopy season advanced. While no temporal changes occurred in turf invertebrate assemblages, clear temporal dynamics occurred in the invertebrate fauna associated with *Sargassum*. Brittle stars and amphipods were most abundant as early colonizers, followed by hard-shelled gastropods, bivalves and ostracods. By the end of the season, these groups became dominant and decreased diversity in the canopy habitat. As hard-shelled prey are preferred items for the main invertivore fish species in the area, results suggest that canopies may play an important role in the provisioning of trophic resources to pelagic consumers.

KEY WORDS: Ecosystem engineering · Phase-shifts · Competition · Ecological succession · Reef fish

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1. INTRODUCTION

Reef macroalgae may often grow to canopy height and play unique ecosystem functions through 'ecosystem engineering'. Notably, canopy-forming algae host a very diverse and abundant fauna of mobile benthic invertebrates that find shelter and forage on the intricate structure provided by the main algal

hosts and their epiphytes (Wikström & Kautsky 2007, Tait & Schiel 2011, Filbee-Dexter et al. 2016). Those invertebrate assemblages comprise filter-feeders, detritivores, mesoherbivores directly feeding on algal tissues, and first-order predators (Taylor 1998, Viejo 1999), interacting within self-sustained food webs. They also support pelagic carnivores (e.g. Edgar & Aoki 1993, Dubiaski-Silva & Masunari 2008), mostly

juvenile fish stages spanning up to 4 different trophic levels (Rooker et al. 2006).

However, this important benthic–pelagic link may be highly vulnerable because canopy-forming algae are more susceptible to environmental disturbance compared to low-lying algal turfs of lower physical complexity (O'Brien & Scheibling 2018). Canopy-to-turf phase shifts have been repeatedly linked to different sources of anthropogenic impact (Benedetti-Cecchi et al. 2001, Airoidi et al. 2008, Perkol-Finkel & Airoidi 2010), including the concentration of heavy metals, excessive sedimentation from coastal runoff, overfishing and eutrophication (Strain et al. 2014), as well as climate change, through ocean heat-waves and storms (Filbee-Dexter & Wernberg 2018). Although not directly linked to human action, large temperate canopies can also be severely impacted by urchin overgrazing (e.g. Estes & Duggins 1995), ceding place to more opportunistic functional groups, including turf-forming algae (Dijkstra et al. 2019, Kriegisch et al. 2019). Once established, algal turfs rapidly spread over the reef habitat and accumulate large quantities of sediments, making it an unstable substrate for the settlement of canopy-forming algae, and therefore reducing the chances for phase-shift reversals (Bellgrove et al. 2010, Alestra et al. 2014, O'Brien & Scheibling 2018).

Canopy-to-turf dynamics are much less understood in tropical and sub-tropical systems. In the subtropical Southwestern Atlantic, brown algae of the genus *Sargassum* C. Agardh are abundant on rocky reefs (e.g. Paula & Eston 1987, Széchy & Paula 2000, Jacobucci et al. 2019) and often grow to canopy size (from 5 to 50 cm). However, their growth is highly seasonal, with the height of canopy-forming thalli peaking in summer and decaying shortly after, sometimes to virtual absence by winter (Godoy & Coutinho 2002, Széchy et al. 2006). Several studies have described the distribution patterns of *Sargassum* spp. and the rich fauna associated with this group of furoid algae (e.g. Széchy & Paula 2000, Leite & Turra 2003, Jacobucci et al. 2019), and the potential role of *Sargassum* beds as nurseries for invertebrates and fish (Longo et al. 2014, Eggertsen et al. 2017), and as foraging grounds for larger pelagic consumers by delivering valuable and diversified prey (Dubiascki-Silva & Masunari 2006, 2008). However, the relative importance of the seasonal *Sargassum* canopy remains unclear because no studies have assessed how their invertebrate assemblages compare to those at alternative habitats with a less complex physical structure (e.g. algal turfs). While the vertical and intricate structure of algal canopies likely adds niche

space for benthic fauna, any attributes of invertebrate assemblages thriving in seasonal *Sargassum* canopies should develop relatively fast, over 2 to 4 mo.

Theory predicts 2 different mechanisms underlying the temporal dynamics of biological assemblages. According to the first one, most species have similar chances to first colonize newly available habitat, each founder affecting later assemblage dynamics in specific ways. Because the diversity of benthic mobile invertebrates is frequently high in the tropics, species assembly would be very uncertain and context-dependent (as in lottery models; Sale 1978, Greene & Schoener 1982). In the second one, only a reduced set of species can arrive and colonize novel habitat, but as inferior competitors they are usually replaced by late-successional species following a predictable ecological succession, as observed in other reef systems (e.g. Lubchenco & Menge 1978, Benedetti-Cecchi 2000). Given that macroalgal canopies in the region have declined over the last 40 yr (Gorman et al. 2020), and their growing seasons are probably shortening (as observed in other threatened canopy-forming macroalgae; Mendez-Sandin & Fernandez 2016, Dijkstra et al. 2019), assessing whether the dynamics of invertebrate assemblages are founder- or dominance-controlled (*sensu* Yodzis 1986) is paramount. Understanding this process is essential to predict the impacts of canopy loss on the structure and diversity of invertebrate assemblages, and therefore on the pelagic consumers they sustain.

This study was divided into 2 parts. First, we compared the mobile invertebrate assemblages associated with canopy-forming algae (*Sargassum* spp. and *Dichotomaria marginata* [Kützinger]) and algal turfs (filamentous and coralline) to assess their capacity to host abundant and diversified invertebrate communities. Specifically, we tested whether invertebrate assemblages vary between canopies and turfs, as canopies can potentially add algal habitat, and whether these differences are more important than any contrasts within the 2 functional macroalgal types. Second, we investigated the mechanisms responsible for the divergent assemblage structure found in turfs and canopies. For that, we sampled turf beds and seasonal *Sargassum* meadows at different times over the canopy season to verify whether the assemblages in *Sargassum* diverge from those in algal turfs as the canopy builds up, and whether the invertebrate assembly in canopies is determined by foundation or dominance control. Variables were always standardized by reef area, not by proxies of

substrate complexity, as we focused on whole-reef ecosystem functioning. The importance of canopies for the provision of prey to pelagic consumers is discussed.

2. MATERIALS AND METHODS

2.1. Study site

Three sites were sampled along the São Sebastião Channel (SSC) on the northern coast of São Paulo State, Brazil (Guaecá: 23.822° S, 45.468° W; Pedra Montada: 23.829° S, 45.442° W; and Zimbros: 23.825° S, 45.420° W), comprising a coastline of approximately 4 km. This is a generally sheltered coastline, with the rocky shores at Guaecá and Pedra Montada closer to the Southwestern SSC end, but facing east, and thus protected from direct swell, and Zimbros further into the mid-section of the channel and facing south. From late spring to early autumn, shallow underwater reef habitats, such as those found at the selected sampling sites, are extensively covered by macroalgae of 2 different functional types; turfs and canopy-forming algae (defined here as those growing erect thalli longer than 5 cm). Turfs can be broadly separated into those formed mostly by filamentous (hereafter 'filamentous turf') or by articulated coralline algae (hereafter 'coralline algal turf'). Different algal species may build canopy habitat for several different invertebrates and fish recruits, but the furoid algae *Sargassum* spp. (mostly *S. furcatum* Kützinger, hereafter *Sargassum*) and the nemalialean alga *Dichotomaria marginata* (hereafter *Dichotomaria*) make up almost all of the canopy habitat at the study sites and were thus the focus of this study. Reduced wave action usually favors the vertical growth of macroalgae, especially *Sargassum* that may reach over 40 cm in size (Széchy et al. 2006, Veloso & de Széchy 2008), and therefore algal canopies at the study sites are taller than average in the region.

2.2. Field sampling

This study was divided in 2 main parts: the first compared invertebrate assemblages associated with different algal turfs and canopies, and tested whether main algal types can be considered separate functional habitats; the second verified whether canopy-specific invertebrates assemble in any predictable temporal way during the *Sargassum* season.

2.2.1. Canopy vs. turf comparisons

Fieldwork for the first task took place between December 2017 and March 2018, when the *Sargassum* cover was high and fronds were well developed. At all 3 sites, 4 replicate samples were collected for each of 4 algal substrates; 2 canopy-forming algae (*Sargassum* and *Dichotomaria*) and 2 algal turf types (filamentous and coralline) at shallow depths (1–5 m below mean low-tide level). Sampling units consisted of all macroalgal materials scraped off the reef from 40 × 40 cm quadrats, placed in separate (at least 5 m) and interspersed random patches of full canopy or turf cover (100%). As macroalgae were scraped off the substrate, a 38 mm hose connected to a 5.5 HP pump onboard (set at 200 l min⁻¹) suctioned all materials into a net bag (150 µm mesh). All underwater work was undertaken using SCUBA. Sample bags were immersed onboard in large plastic buckets and immediately sorted upon arrival to the laboratory.

2.2.2. Seasonal cover of canopy-forming algae

We recorded the seasonal variation of algal canopies formed by *Sargassum* and *Dichotomaria* by sampling all 3 sites monthly from October 2014 to July 2015. At each site and sampling date, video footage using a GoPro camera was taken along a 70 m transect, marked at 20 cm intervals and laid parallel to the shoreline at a depth of maximum canopy cover (1.0 to 4.0 m). Fifteen replicate frames were randomly sampled from each video to obtain estimates of algal abundance (percentage cover) on ImageJ (Rasband 1997). The average area covered by each frame was 1.902 m², but there was considerable variation among sites and sampling dates (overall SD = 1.216 m²), as long as transects were recorded at variable depth to adjust for visibility and the cross-shore width of canopy patches.

2.2.3. Temporal assembly of invertebrates

We compared the invertebrate assemblages in turfs and *Sargassum* meadows, at 3 different times during the canopy season, to verify how those assemblages diverge as canopies build up. Invertebrate assemblages were markedly similar in filamentous and articulate coralline turf (see Section 3.3), and we selected the former here as a random choice. Four replicate samples of *Sargassum* and filamentous turf were thus obtained at Pedra Montada and Zimbros in

December 2018 (early season), January (mid-season) and February 2019 (late season). Samples were obtained and transported to the laboratory as described in Section 2.2.1.

2.3. Laboratory procedures

The contents of the mesh bags were immediately placed in large buckets, washed and vigorously shaken. Suspended materials were then sieved and retained in a 1 mm mesh sieve. The whole procedure was repeated several times until invertebrates were no longer found in the sieves. Invertebrate samples were then re-suspended in seawater and sorted through a sequence of sieves of decreasing mesh size (12.5, 8.0, 6.3, 4.0, 2.8, 1.7 and 1.2 mm). The contents of each sieve were washed and rinsed into white plastic trays, and invertebrates were sorted out and preserved in 70 % ethanol. The height of filamentous and coralline turf was fairly uniform across sites and sampling dates (1–2 cm), but the thallus length of canopy-forming macroalgae was highly variable. We thus measured the length of 5 separate random fronds within each *Sargassum* and *Dichotomaria* sample to verify whether canopy height (a measure of structural complexity) may eventually affect overall metrics of invertebrate assemblages. The level of invertebrate identifications resulted from a trade-off between the need to tease apart groups with very different functional roles, and the personnel and time available to sort, count and identify several tens of thousands of invertebrates under a dissecting microscope. A total of 29 groups was considered in this study (Table S1 in the Supplement at www.int-res.com/articles/suppl/m647p079_supp.pdf).

2.4. Statistical analyses

2.4.1. Canopy vs. turf comparisons

Two-way general linear mixed models, with factors 'algae' (fixed, with 4 levels, corresponding to the 2 turf and the 2 canopy algal species tested) and 'site' (random, with 3 levels, testing for the spatial consistency of algal effects), and using 4 replicates, were first run as an omnibus procedure to obtain mean square error estimates of either 'algae' or 'algae × site'. These were used to test 3 planned contrasts, namely (1) canopy vs. turf (*Sargassum*—*Dichotomaria* vs. filamentous turf—coralline turf), (2) within canopies (*Sargassum* vs. *Dichotomaria*) and (3)

within turfs (filamentous vs. coralline). Dependent univariate metrics included abundance, the Shannon-Wiener (H') diversity index, average size and biomass (using the size-to-weight relationship obtained by Méthot et al. 2012) of mobile invertebrate assemblages. Data were square-root transformed when needed to meet variance homogeneity. The same model was used to examine assemblage structure but, as a multivariate variable, permutational analyses of variance on square-root transformed data (singletons removed, Poos & Jackson 2012) were run instead, using type I sums of squares and unrestricted permutation (9999 times) of raw data (Anderson 2017). Pairwise comparisons followed the same planned contrasts above, and similarity percentage (SIMPER) analyses were conducted, whenever comparisons proved significant, to identify the taxonomic groups that contributed the most to dissimilarities (Clarke 1993). Student's t -tests comparing the abundance of those groups between the algal habitats of interest complemented the SIMPER analyses.

2.4.2. Seasonal cover of canopy-forming algae

In order to test whether canopy-forming algae are seasonal, and whether seasonality varied somehow among sampling sites, separate 2-way general linear mixed models were run to analyze the percent cover of each algal species (*Sargassum* and *Dichotomaria*), according to 'site' (random) and 'month' (fixed), using 15 replicate frames from the GoPro footage. The arcsine transformation solved heteroscedasticity for *Sargassum*, but not *Dichotomaria*. Nevertheless, we maintained the original procedure as datasets were balanced and replication was high (Underwood 1997). The Student-Newman-Keuls (SNK) procedure was used for post hoc comparisons among months.

2.4.3. Temporal assembly of invertebrates

Three-way general linear mixed models, with factors 'alga' (fixed, with levels '*Sargassum*' and 'filamentous turf'), 'time' (fixed, with levels 'December', 'January' and 'February') and 'site' (random, with levels 'Pedra Montada' and 'Zimbro'), and using 4 replicates, were used to examine the invertebrate assemblage metrics specified above. In the case of invertebrate assemblage structure, permutational analyses of variance followed by SIMPER analyses and complementary t -tests were carried out as specified in Section 2.4.1. Planned contrasts were in this

Table 1. Summary results of general linear mixed models comparing main parameters of invertebrate assemblages associated with algal canopies (*Sargassum* spp., *Dichotomaria marginata*) and turfs (filamentous and coralline). C: Cochran's statistic testing for variance heterogeneity; p-values in **bold** indicate statistical significance of relevant sources of variation

	df	Abundance		Diversity		Average size		Biomass	
		F	p	F	p	F	p	F	p
Alga (Al)	3	1.12	0.413	1.11	0.415	3.48	0.091	0.39	0.767
Site (Si)	2	4.59	0.017	4.37	0.02	4.57	0.017	10.05	<0.001
AlxSi	6	4.24	0.003	3.47	0.008	1.01	0.437	2.69	0.0294
Residual	36								
		√x transf. C = 0.2737; p > 0.05		Raw data C = 0.1460; p > 0.05		√x transf. C = 0.3967; p < 0.01		√x transf. C = 0.2144; p > 0.05	

case restricted to t1 vs. t2 (December vs. January: during the expected growing phase) and t2 vs. t3 (January vs. February: during the expected decaying phase), either for different 'algal' types, or within level combinations of 'alga x site'.

All general linear mixed models were run using Gmav5 and Statistica v.13 for univariate response variables, and using Primer 6 & Permanova + and Past 4.0 for multivariate response variables.

3. RESULTS

3.1. Canopy vs. turf comparisons

A total of 39987 specimens, 23321 from canopies and 16666 from turfs, encompassing 29 major invertebrate groups (details in Table S1), were recorded. All univariate metrics, except for average individual size (which responded only to site effects), varied between algal habitats (Table 1). However, differences were not consistent across sites as indicated by the significant interaction between factors 'alga' and 'site' (Table 1). Overall, planned comparisons indicated that differences between algal types, i.e. canopy vs. turf, significant in 8 out of 9 comparisons, were far more important than differences between canopies (*Sargassum* vs. *Dichotomaria*) or between turf-forming algae (filamentous vs. coralline), which were only significant in 1 out of 18 cases (Fig. 1). Overall, comparisons between the 2 main algal types do not support generalized higher carrying capacity in

algal canopies. Abundance (Fig. 1A–C) and biomass (Fig. 1D–F) of invertebrates were higher in canopy algae at Zimbro (Fig. 1C,F) and Pedra Montada (Fig. 1B,E), but higher for turfs at Guaecá (Fig. 1A,D; although not significant for abundance, Fig. 1A). Diversity was higher in algal turfs at 2 of the 3 sites (Fig. 1G–I). Shannon-Wiener diversity indices were

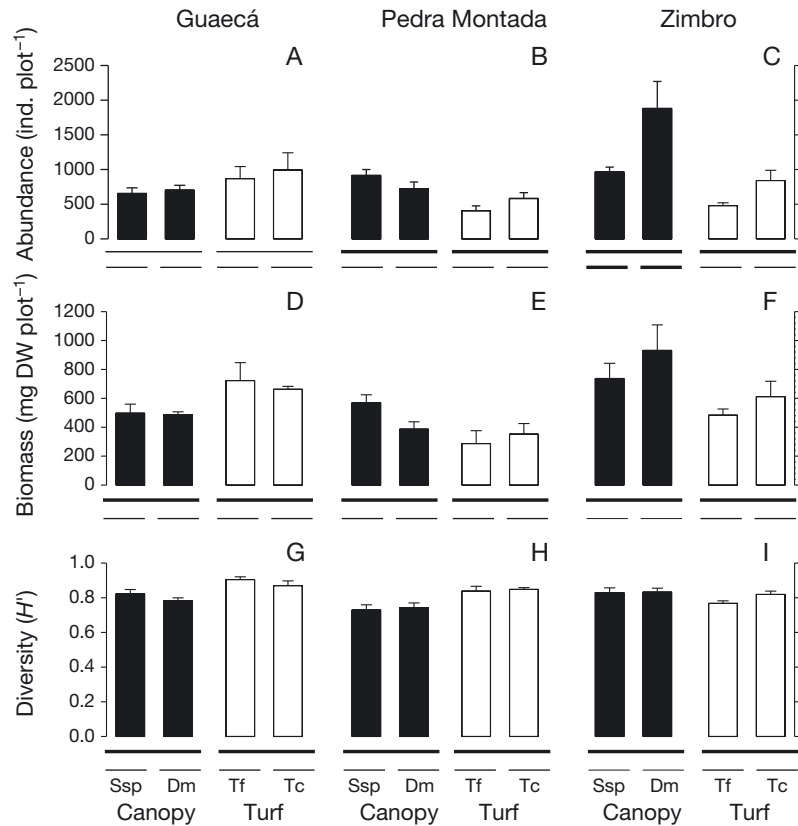


Fig. 1. (A–I) Comparisons of univariate descriptors of invertebrate assemblages between and within macroalgal habitat types at 3 sampling sites along the São Sebastião Channel, Brazil. Columns and error bars represent average values and respective SEs. DW: dry weight; Ssp: *Sargassum* spp.; Dm: *Dichotomaria marginata*; Tf: filamentous turf; Tc: coralline turf. The 3 planned comparisons are represented as underlines below each plot and significant comparisons ($p < 0.05$) are indicated in **bold**

higher for turf assemblages at Guaecá (Fig. 1G) and Pedra Montada (Fig. 1H), but not at Zimbros (Fig. 1I), where diversity for canopy assemblages was slightly (but significantly) higher for canopy assemblages. Contrasts of invertebrate assemblages within any algal functional type were restricted to canopies at Zimbros, where overall abundance was almost 2-fold higher in *Dichotomaria* compared to *Sargassum*. Average canopy height varied considerably for both species (5–18 cm for *Sargassum*, 5–14 cm for *Dichotomaria*), but such variation was not correlated with

any of the tested invertebrate parameters ($0.03 < r < 0.34$; $p > 0.30$ in all cases; Fig. S1) suggesting that additional vertical habitat did not affect assemblages in any obvious way.

Results of the permutational analysis of variance indicated that differences among algal habitats were not fully consistent across sampling sites, as the interaction term proved significant (pseudo- $F_{\text{alxsi}} = 2.97$, $p = 0.001$; Fig. 2). Planned pairwise comparisons showed that dissimilarities were almost restricted to canopy vs. turf comparisons ($4.62 < \text{pseudo-}F <$

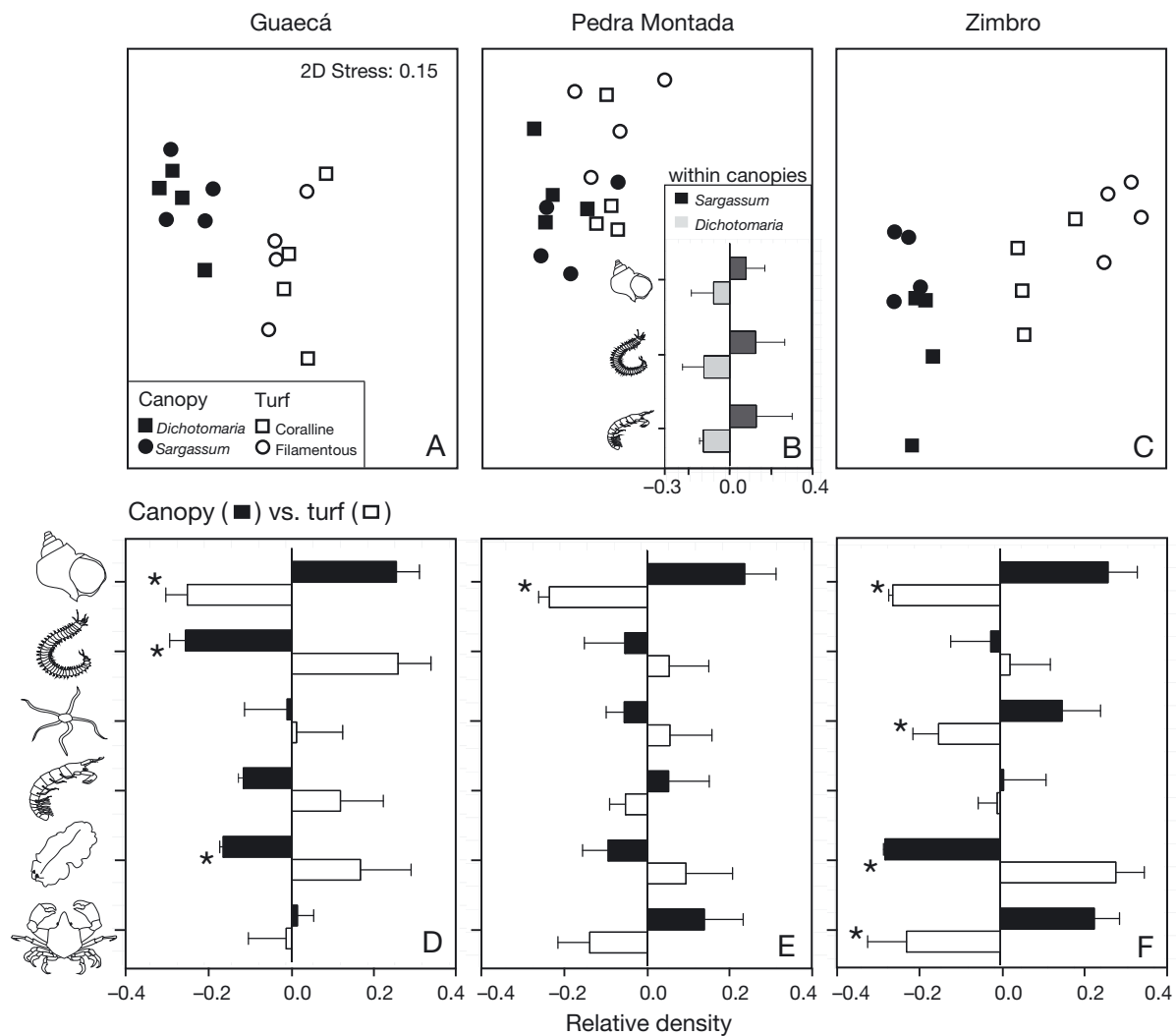


Fig. 2. Comparisons of the invertebrate assemblage structure between and within macroalgal habitat types at 3 sampling sites. Pairwise comparisons after the omnibus permutational analysis of variance indicated significant canopy vs. turf contrasts at all sites, and significant contrasts within canopy-forming algae at Pedra Montada (*Sargassum* vs. *Dichotomaria*). (A–C) Spatial ordinations extracted from the whole-data non-metric multi-dimensional scaling (nMDS) plot showing sample clusters at Guaecá, Pedra Montada and Zimbros. The average relative densities of invertebrate groups contributing the most to dissimilarities between canopy-forming algae (B), and (D–F) between the pools of canopy-forming and turf algae, were obtained from normalized and mean-subtracted raw data (ind. plot⁻¹). Drawings represent, from top to bottom, gastropods, polychaetes, tanaids (B), and gastropods, polychaetes, brittle stars, tanaids, flat worms and brachyuran crabs (D–F). Error bars represent SE and asterisks indicate statistical significance (t -tests, $p < 0.05$)

13.60; $0.0001 < p < 0.028$; Fig. 2A–C), with more clear differences at Guaecá and Zimbros (overall dissimilarities 33.24 and 39.96 %, respectively, Fig. 2A,C), compared to Pedra Montada (28.64 %, Fig. 2B). No differences were found between turfs, and differences between canopies were restricted to Pedra Montada (pseudo- $F = 2.21$, $p = 0.028$; Fig. 2B). SIMPER analyses indicated that 6 invertebrate groups contributed the most to differences between the assemblage structure of invertebrates at canopies and turfs (Table S2), namely sea snails (hereafter gastropods), polychaetes, brittle stars, tanaids, flat worms and brachyuran crabs (Table S2, Fig. 2D–F). Not all 6 groups contributed to 7 % or more of dissimilarities at sampling sites, with flat worms and brachyuran crabs comprising only 3.86 and 1.76 %, and 3.33 and 5.31 % at Guaecá and Pedra Montada, respectively; and tanaids only 5.67 and 5.77 % at Pedra Montada and Zimbros (Table S2). Still, all of these invertebrate groups were considered in further analyses for all sites. The most consistent trend was the much higher abundance of gastropods in canopies than in turfs (Table S1, Fig. 2D–F), confirmed by t -tests for all 3 sites. Brachyuran crabs were also more abundant in canopies than in turfs at all sites, but this difference was only significant at Zimbros (Fig. 2F). Groups that were otherwise more abundant in turfs than in canopies were polychaetes and flat worms (with statistical support found at Guaecá for the former, and Guaecá and Zimbros for the latter, Fig. 2D,F). Two other groups varied in a less consistent way, but a statistically significant difference was found at Zimbros for brittle stars (more abundant with canopies, Fig. 2F) and at Guaecá for tanaids (more abundant in turfs, Fig. 2D). The dissimilarities between algal canopies found at Pedra Montada were driven by a higher abundance of gastropods, polychaetes and tanaids in *Sargassum* compared to *Dichotomaria*, but separate t -tests for these groups did not reveal any significant differences.

3.2. Seasonal cover of canopy-forming algae

The seasonal cover of *Sargassum* and *Dichotomaria* was nearly inversely related, especially at Guaecá and Pedra Montada (Fig. 3A,B). Together, these 2 canopy-forming algae dominate cover of available reef habitat in the region, as observed in January at Guaecá (75.4 %) and Pedra Montada (64.2 %), and in December at Zimbros (68.7 %; Fig. 3A–C). *Sargassum* reached a much higher cover and showed a clearer seasonal variation com-

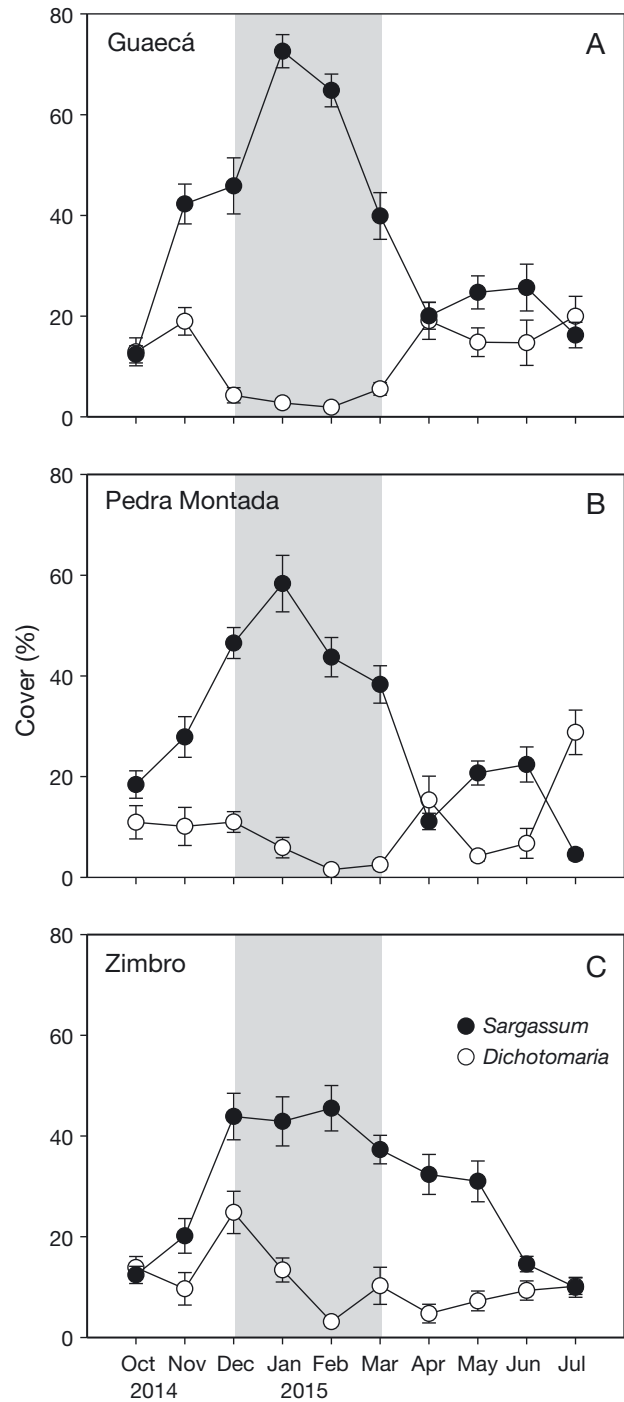


Fig. 3. Mean \pm SE seasonal variation in the abundance of canopy-forming algae, as percent cover, at 3 sampling sites: (A) Guaecá, (B) Pedra Montada and (C) Zimbros. The seasonal peak abundance, from December to February, is shown in gray

pared to *Dichotomaria* at all sites (Fig. 3). Strong ‘site \times month’ interactions were found for both canopy-forming algae (*Sargassum*: $F_{s \times m} = 4.48$; *Dichotomaria*: $F_{s \times m} = 5.63$; $p < 0.0001$ in both cases;

Table 2. Summary results of general linear mixed models comparing main parameters of invertebrate assemblages associated with the canopy-forming algae *Sargassum* spp. and filamentous turfs over time (December 2018 to February 2019). The random factor 'Site' tests the spatial consistency of any divergent patterns characterizing the temporal assembly of major invertebrate groups at the sampled algal habitats. C: Cochran's statistic testing for variance heterogeneity; p-values in **bold** indicate statistical significance of relevant sources of variation

	df	Abundance		Diversity		Biomass		Average size	
		F	p	F	p	F	p	F	p
Algal (Al)	1	5.19	0.263	464.31	0.030	1.00	0.500	7.52	0.223
Time (Ti)	2	1.54	0.394	13.98	0.067	26.64	0.036	<0.01	0.999
Site (Si)	1	0.30	0.584	5.40	0.026	0.16	0.689	<0.01	0.964
Al×Ti	2	0.39	0.719	1.54	0.394	7.15	0.123	15.88	0.059
Al×Si	1	1.77	0.192	0.10	0.754	3.66	0.064	2.50	0.123
Ti×Si	2	1.36	0.269	0.20	0.822	0.13	0.880	2.25	0.120
Al×Ti×Si	2	0.41	0.669	8.07	0.001	0.54	0.587	0.92	0.408
Residual	36								
		Raw data C = 0.2388; p > 0.05		Raw data C = 0.1788; p > 0.05		Raw data C = 0.2328; p > 0.05		Raw data C = 0.2128; p > 0.05	

Fig. 3A–C). *Sargassum* abundance was highest from January to February at Guaecá, December to February at Pedra Montada and December through May at Zimbro (SNK post hoc tests, $p < 0.05$). The trend for *Dichotomaria* was less clear, with higher cover from October to November, and then from April to July in Guaecá, and single peak abundances in July and December observed at Pedra Montada and Zimbro, respectively (SNK post hoc tests, $p < 0.05$; Fig. 3A–C).

3.3. Temporal assembly of invertebrates

Because the overall abundance was higher and the seasonal trend clearer for *Sargassum*, we focused on this habitat to examine the temporal assembly patterns of mobile invertebrates associated with algal canopies, between December 2018 and February 2019 (corresponding to the area shaded in grey in Fig. 3). During this period, 19 274 and 28 430 mobile individuals were found associated with *Sargassum* and filamentous turfs, respectively, encompassing 27 major invertebrate groups (Table S3). Of all metrics examined in this study, only diversity and assemblage structure showed algal-type dependent temporal trends (Table 2). These, in turn, were also prone to spatial variation to some extent.

Diversity trends were markedly different for the 2 algal habitats, consistently decreasing in *Sargassum*, but remaining stable or increasing in filamentous turfs (Fig. 4), thus explaining the significant third-order interaction alga × site × time (Table 2). At Pedra Montada, the diversity of invertebrate assemblages in *Sargassum* dropped from December to January, remaining low until February (Fig. 4A), but persisted at high and stable levels in filamentous turfs (Fig. 4B).

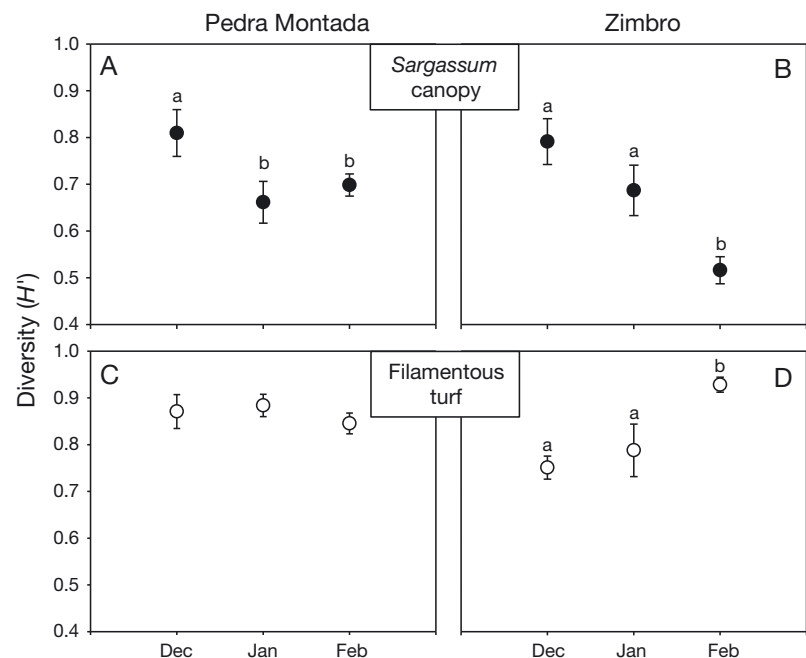


Fig. 4. Mean \pm SE Shannon-Wiener diversity estimates (H') for invertebrate assemblages associated with (A,B) *Sargassum* canopy and (C,D) filamentous turf from December 2018 to February 2019 at (A,C) Pedra Montada and (B,D) Zimbro. For each individual plot, diversity estimates sharing the same lower-case letter are not statistically different (SNK post hoc tests, $p > 0.05$)

At Zimbro, diversity decreased in *Sargassum* (Fig. 4C) and increased in filamentous turfs (Fig. 4D), with estimates obtained in December and January contrasting with February in both cases (SNK post hoc tests, $p < 0.05$).

The trends for assemblage structure were also complex, as indicated by the significance of the third-order term of the tested model (Pseudo- $F_{al \times six \times ti} = 2.11$, $p = 0.043$). Substantial temporal change was restricted to *Sargassum*, and the extent of such change varied between sites (Fig. 5A,B). Pairwise comparisons between sampling times were never significant for turfs ($1.15 < pseudo-F < 1.54$; $0.121 < p < 0.290$) but always significant for *Sargassum*

($1.55 < pseudo-F < 2.59$; $0.027 < p < 0.030$). At both sites, the assemblages in *Sargassum* diverged from those in turfs through time, but temporal changes (i.e. percent dissimilarities between times) were more pronounced at Zimbro (Dec. vs. Jan.: 41.72%; Jan. vs. Feb.: 30.65%) than at Pedra Montada (Dec. vs. Jan.: 31.48%; Jan. vs. Feb.: 23.76%) (Table S4, Fig. 5A,B). Four to 5 groups accounted for 7% or more of the overall dissimilarity in each specific comparison. Considering all comparisons together, 8 invertebrate groups were found to be relevant (Table S4). Numerical trends were rather consistent between sites, but the temporal changes in the density of those groups were less pronounced at Pedra Mon-

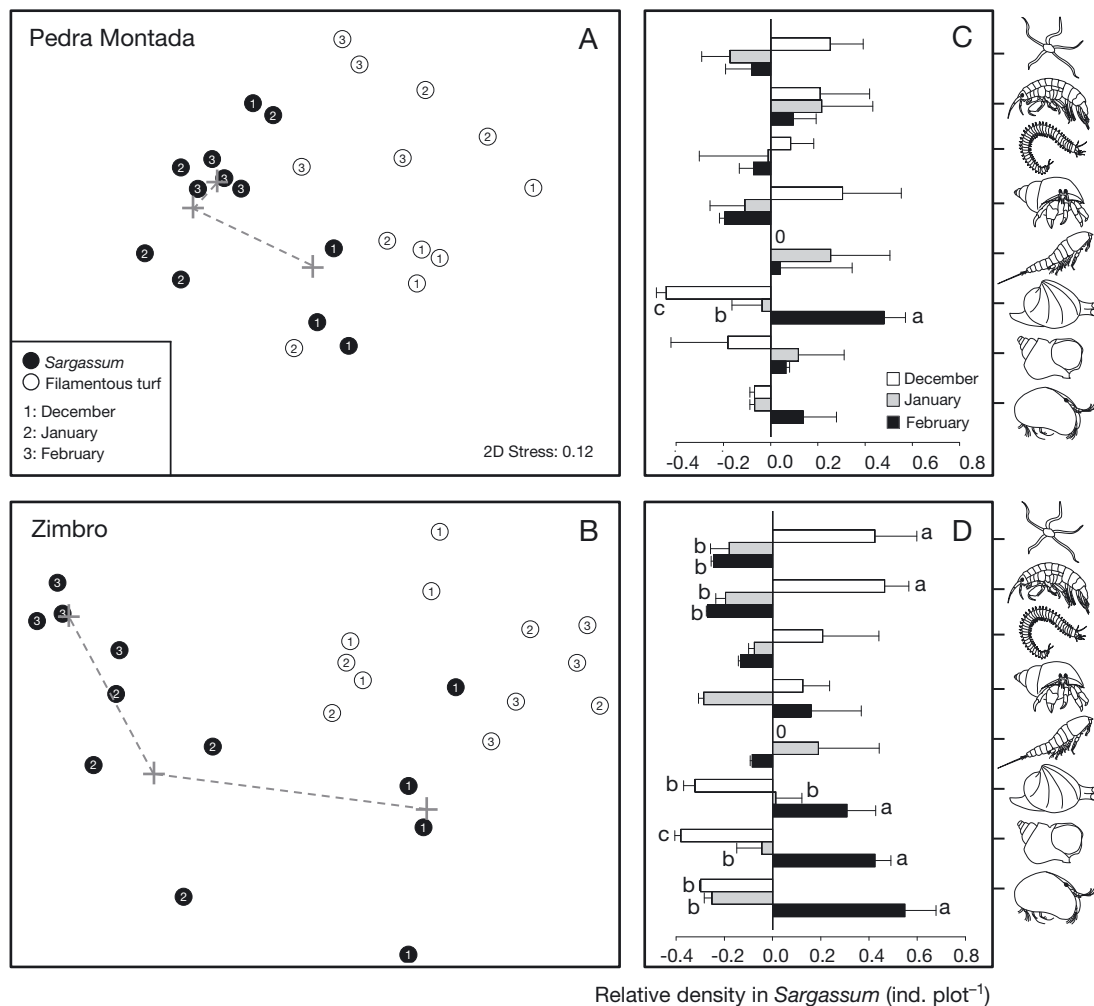


Fig. 5. Comparisons of the structure of invertebrate assemblages associated with *Sargassum* canopies and filamentous turfs at Pedra Montada and Zimbro, from December 2018 to February 2019. (A,B) Spatial ordinations extracted from the whole-data nMDS plot showing sample clusters at t1 (December), t2 (January) and t3 (February) for each site. Temporal changes in assemblages, restricted to *Sargassum*, are highlighted with dashed grey lines connecting centroids at t1, t2 and t3. (C,D) Changes in the relative density of invertebrate groups contributing the most to temporal change. Columns represent mean, error bars indicate SE. Relative density estimates sharing the same lowercase letter are not statistically different ($p > 0.05$). Invertebrates are ordered from early (top) to late successional groups (bottom): brittle stars and amphipods (early); polychaetes, hermit crabs and cumaceans (undefined); bivalves, gastropods and ostracods (late)

tada (Fig. 5C) compared to Zimbro (Fig. 5D). Clearly, there were 2 sets of invertebrate groups, which followed opposite temporal trends. The abundance of brittle stars and amphipods declined from December to January–February (Fig. 5C,D). This trend was statistically reinforced at Zimbro through separate 1-way comparisons, followed by SNK post hoc tests ($p < 0.05$; Fig. 5D). In contrast, the abundance of gastropods, bivalves and ostracods increased over the season (Fig. 5C,D). Further statistical support (SNK post hoc tests, $p < 0.05$) was obtained for the steady increase in the abundance of bivalves at Pedra Montada (Fig. 5C) and gastropods at Zimbro (Fig. 5D), and for an increase in the abundance of bivalves and ostracods from December–January to February at Zimbro (Fig. 5D). Although contributing to dissimilarities among invertebrate assemblages through time, polychaetes, hermit crabs and cumaceans did not show temporal variation in a consistent way.

4. DISCUSSION

In the present study, we show that algal canopies and turfs host clearly different assemblages of mobile invertebrates, while differences within each of these functional algal habitats are much less important. However, differences in overall diversity, abundance and biomass between the mobile fauna found in canopies and turfs were not consistent, and therefore the hypothesis that canopies simply expanded niche space, providing resources for an additional set of invertebrate groups, does not hold. Rather, we document generalized species turnover from turf to canopies, especially over the *Sargassum* season. While canopies obviously facilitate specific frond-dwelling invertebrate groups, the understory space they provide is, for some reason, apparently not equivalent to the canopy-devoid turf habitat. One possibility is that any invertebrates remaining close to the rock surface will be continuously exposed to the whiplash of canopy fronds (which is absent in turfs), thus reducing the numbers of more vulnerable species and restraining diversity (e.g. Beermann et al. 2013, Petrowski et al. 2016), as observed at Guacá and Pedra Montada. Otherwise, the lower wave exposure at Zimbro may provide more stable conditions, explaining the larger number of mobile invertebrate groups found thriving in canopy habitats at that site (especially *Dichotomaria*). This mechanism, however, remains uncertain because we had sampled different sites aiming to test for generality of any given differences between canopies and turfs, not to

test for the effects of specific environmental conditions. A properly designed study, including replication of sites within different levels of exposure to wave action, would be needed for that purpose.

By supplying larger interstitial space among branches (e.g. Gee & Warwick 1994), we also expected that the average size of invertebrates would be higher in canopy- compared to turf-forming algal habitats, but this difference was not observed. Added to the fact that canopy height (a measure of substrate complexity) also had no effect on invertebrate size (or on any other overall assemblage metric), we conclude that morphological attributes of these vegetated substrates play no fundamental role in determining size-related functional traits. It should be noted, however, that the largest invertebrates found in samples, chiefly spider crabs, were much more frequent in canopies. Because they were relatively uncommon compared to other groups, they contributed less to overall estimates of mean size. As key herbivores in algal habitats (Hines 1982) and potential prey for larger consumers, their role in whole-reef trophic webs may be disproportionately high.

Despite the absence of average size differences, and the inconsistent variation in diversity, overall abundance and biomass, the assemblage structure of mobile invertebrates was strikingly and consistently different between canopies and turfs. Most notably, hard-shelled groups (i.e. gastropods and crabs) were more frequently associated with canopy-forming algae, while soft-bodied invertebrates (i.e. polychaetes and flatworms) were more common within turf habitat. Resource supply at the sampled habitats may well explain the differences observed on the abundance of these groups. Small gastropods, chiefly the very abundant genera *Eulithidium* Pilsbry and *Bittiolium* Cossmann, as well as specialized canopy-dwelling spider crabs, are grazing animals that feed directly on the main algal host, or on their epiphytic algae (Hines 1982, Reynolds et al. 2015). In contrast, decaying organic particles and interstitial meiofauna in turf-retained sediments may be easily accessed by soft-bodied flatworms and polychaetes (e.g. Majdi et al. 2016, Melero et al. 2017), which may easily squeeze amongst sediment grains while foraging, giving them a competitive advantage in the turf habitat.

Altogether, divergent invertebrate assemblages in canopies and turfs may thus subsidize a large number of roving predators through trophic niche partitioning (e.g. Ross 1986). Based on the average individual size of these invertebrates (2.0–3.0 mm), potential consumers would mostly comprise small

cryptobenthic fishes (such as blennies and gobies; e.g. Depczynski & Bellwood 2003), or juvenile stages of larger species that use vegetated substrates as nursery grounds. At our study coastline, some of the most abundant reef fishes are invertivores consuming mobile prey (Gibran & Moura 2012). There are no studies on their specific diets at our sampling sites, but studies undertaken elsewhere, within their geographic distribution ranges, indicate that the 5 most abundant invertivore fishes in our area, except for the blenny *Parablennius pilicornis* (Cuvier) which feeds mostly on polychaetes (Nieder 1997), prey preferably on hard-shelled invertebrates, especially during the juvenile phase: juvenile grunts *Haemulon aurolineatum* Cuvier and *H. steindachneri* (Jordan & Gilbert) feed mostly on copepods and amphipods, moving to polychaetes and other fish when they grow to adults (Pereira et al. 2015); the silver porgy *Diplodus argenteus* Valenciennes first preys on copepods and mussels, shifting to a more omnivorous diet when adult, including mostly macroalgae and decapod crustaceans (Dubiascki-Silva & Masunari 2006); and, finally, the sergeant major *Abudefduf saxatilis* (L.), the second most abundant fish species in the area, feeds mostly on copepods and filamentous algae during the juvenile phase (Pimentel et al. 2018, Mendonça et al. 2019). We thus conclude that, at the whole-reef level, the combination of canopy and turf habitats may indeed contribute to reef-fish diversity by supplying a wider array of potential invertebrate prey, but also that algal canopies may be particularly relevant as they supply target prey for a larger share of the common reef fishes found in the area.

Along our sampled coastline, *Sargassum* and *Dichotomaria* combined take on average 39 to 48% of the available reef space throughout the year, together reaching a maximum of 64 to 75% in December–January. *Sargassum* not only develops to a taller canopy, but its average cover is nearly 3-fold that of *Dichotomaria*, making it a very relevant habitat in the area. However, the *Sargassum* cover is highly seasonal, and therefore the time for the associated fauna to reach an equilibrium state is short, which could limit the capacity of canopy algae to provide valuable foraging grounds. This hypothesis was not supported by our results. We found that *Sargassum* assemblages steadily diverged from the invertebrate assemblages associated with the turf habitat, but the increasing dominance of some hard-shelled groups over the season did not result in higher overall invertebrate abundance or biomass in the canopy habitat. Whether this was an effect of recruitment limitation or an outcome of resource shortage within the can-

opy habitat remains an open question. The opposite temporal trends of diversity in the 2 algal habitats suggest late-season spillover of less common invertebrate groups from canopies to turfs, which could provide some support for the second alternative. Specific experimental work would be required to test this process.

Interestingly, the overall temporal dynamics of invertebrate communities in canopies were rather consistent between sites, with peak diversity early in the *Sargassum* season, sustained in part by a large number of opportunistic invertebrates (i.e. brittle stars and amphipods), followed by other groups later in the season (i.e. gastropods, bivalves and ostracods), which may efficiently exploit resources and dominate assemblages. Changes in the abundance of those invertebrate groups were dramatic. At both sites combined, the abundance of brittle stars and amphipods declined 15 and 22 times, while the abundance of bivalves, gastropods and ostracods increased 8, 5 and 26 times, respectively, over the canopy season. The life history and functional ecology of the main invertebrate groups explain the observed successional pattern. Most brittle stars in our samples belong to the exotic species *Ophiotela mirabilis* Verrill, which is very abundant in the region and is a typical generalist, colonizing several different biogenic substrata, such as octocorals, sponges, cnidarians, ascidians, echinoderms, algae and bryozoans (Mantelatto et al. 2016). Once established, *O. mirabilis* can become locally abundant very fast through asexual reproduction (i.e. fission, Tavares et al. 2019), but would hardly compete for space as it is a very small species that does not monopolize space or stand against larger, hard-shelled invertebrates that forage over the fronds. Likewise, another early group in our samples, amphipods, can locally build up large populations because they are direct-developers, lacking a larval stage, with mothers releasing benthic juvenile individuals (Munguia et al. 2007). However, as very highly mobile organisms, amphipods tend to flee rather than engage in direct competition with more sedentary species (Neideman et al. 2003). Conversely, gastropods (as grazers; Reynolds et al. 2015) and ostracods (as deposit feeders; van Oevelen et al. 2006), two of the late functional groups detected in this study, would likely benefit from very small epiphytic algae and organic debris which accumulate on *Sargassum* fronds as plants get older. Gastropods, which were by far the most abundant invertebrates in our samples, reaching an average density of 548 ind. plot⁻¹ (over 3400 ind. m⁻²), were very likely

facilitated by the growing supply of secondary trophic subsidies over the season, possibly excluding other groups through exploitative competition. Rather than optimizing the use of food resources, filter-feeding bivalves, the third group which became increasingly abundant over the season (reaching 297 ind. plot⁻¹, or over 1850 ind. m⁻²), may effectively clump to each other and remain attached to the substrate by different means, including the production of byssal threads (e.g. Morello et al. 2004, Khalaman & Lezin 2015). Strong attachment precluding dislodgment by currents (e.g. Bell & Gosline 1996, Bouhleb et al. 2017) and a steady supply of food (as suspended particles, e.g. Gili & Coma 1998) explain the dominance of bivalves, especially mussels, in late-successional, undisturbed, environmental conditions (Carroll & Highsmith 1996, Paine & Trimble 2004). The ecological succession of invertebrate groups in canopy-forming *Sargassum* thus resembles textbook examples of dominance-controlled communities, and not the more stochastic temporal patterns observed in founder-controlled assemblages.

Like in many other temperate coastal areas, the subtropical SW Atlantic is experiencing the loss of canopy-forming macroalgae, as reported over the last 40 yr for which data are available (Gorman et al. 2020). Namely, the cover of *Sargassum* may have shrunk by almost 90%, while the abundance of other canopy-forming algae (e.g. *Dichotomaria*) may have been reduced by more than 20%. The extent of these losses is very worrying, as canopy-to-turf transitions may correspond to phase shifts between alternative stable states, making any restoration efforts even more challenging (Benedetti-Cecchi et al. 2015, Rindi et al. 2017). Important ecosystem functions delivered by healthy marine canopies, which remain largely unknown, may thus be at stake. Benedetti-Cecchi et al. (2015) showed that biomass loss of *Cystoseira amentacea* canopies beyond 75% leads to the collapse of understory sessile assemblages, and thus of any ecological roles they may play in the system. Our results indicate that the diversity of foundational algal habitats leads to the diversification of mobile invertebrate assemblages, potentially sustaining several invertivore and omnivore fish species. Declines in canopy-forming algae may ultimately cascade to serious socio-economic challenges, as they appear to be a major source of preferred prey to pelagic consumers, and thus are a link to reef trophic networks that sustain small-scale artisanal fisheries in the region. Although beyond the scope of this study, it should also be considered that *Sargassum* fronds constitute important allochthonous inputs

away from the reef habitat, as they can break off and remain afloat for a long time, subsidizing complex trophic webs that include several rafting fish and invertebrates (Thiel & Gutow 2005), and eventually strand ashore, fueling complex semiterrestrial networks (Spiller et al. 2010). Conservation policies are thus urgently needed to mitigate the environmental stressors that negatively impact shallow-reef algal canopies, and potentially jeopardize important ecosystem functions across coastal habitats.

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