

UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

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

Funcionamento ecossistêmico de dosséis e tapetes de macroalgas: potencial
suprimento de presas para consumidores pelágicos

Carla Kühn de Figueiredo

Dissertação apresentada à Faculdade de
Filosofia, Ciências e Letras de Ribeirão Preto
da Universidade de São Paulo, como parte das
exigências para obtenção do título de Mestre
em Ciências, obtido no Programa de Pós-
Graduação em Biologia Comparada

Ribeirão Preto - SP

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Orientador: Prof. Dr. Augusto Alberto Valero Flores.

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1. engenharia de ecossistemas 2. mudança de fase 3. competição 4. sucessão ecológica 5. peixe de recife

Dedico esta dissertação aos meus pais
Helena e Ronaldo, por todo amor e apoio

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“Mas o amanhecer virá, mesmo que a noite seja dolorosa

Vamos superar isso, até que o futuro venha

Não vamos mais parar

Decida para si mesmo o que significa ser feliz”

Lights – BTS

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Resumo

As algas formadoras de dossel podem fornecer recursos tróficos e complexidade estrutural para uma ampla gama de invertebrados móveis, que por sua vez podem sustentar consumidores pelágicos de níveis tróficos mais altos. No entanto, os dosséis de algas estão declinando em todo o mundo e substituídos por tapetes de macroalgas menos complexos, que podem dominar as paisagens dos recifes. Aqui, comparamos primeiro associações de invertebrados móveis associadas às principais algas formadoras de dossel (*Sargassum* spp. e *Galaxaura marginata*) e algas formadoras de tapetes (filamentoso e calcário articulado) e depois avaliamos se, e como, as associações de invertebrados que habitam o dossel flutuam afastando da linha de base dos tapetes durante a estação de floração do principal habitat de dossel (*Sargassum*). Abundância, biomassa e diversidade quase sempre diferiram entre dosséis e tapetes nos locais de amostragem, enquanto as diferenças nos principais tipos de algas funcionais estavam quase ausentes. Surpreendentemente, porém, nenhuma dessas métricas gerais variou de maneira consistente nos locais de amostragem. Diferentemente, a estrutura da associação diferia consistentemente entre dosséis e tapetes, com invertebrados de exoesqueleto rígido (como gastrópodes e caranguejos braquiúros) e de corpo mole (principalmente poliquetas e platelmintos) caracterizando associações de dossel e tapete, respectivamente. A divergência entre associações de invertebrados em dosséis e tapetes aumentou à medida que a estação de floração do dossel avançava. Notavelmente, enquanto a estrutura da associação de invertebrados permaneceu inalterada nos tapetes, a sucessão rápida de ofiuróides e anfípodes foram seguidos por gastrópodes, bivalves e ostracodas de concha rígida em *Sargassum*, onde se tornaram dominantes e diminuíram a diversidade mais tarde na temporada. Como presas de exoesqueleto rígido são itens preferenciais para as principais espécies de peixes invertívoros da região, os resultados indicam que os dosséis desempenham um papel particularmente importante no fornecimento de recursos tróficos aos consumidores pelágicos.

Palavras-chave: engenharia de ecossistema, mudanças de fase, competição, sucessão ecológica, peixe de recife

Abstract

Canopy-forming algae may provide trophic resources and structural complexity for a wide array of mobile invertebrates, which in turn may sustain pelagic consumers of higher trophic levels. However, algal canopies are declining worldwide and replaced by less-complex macroalgal turfs which may dominate reefscales. Here, we first compare the assemblages of mobile invertebrates associated to main canopy-forming (*Sargassum* spp. and *Galaxaura marginata*) and turf-forming algae (filamentous and articulated coralline turf), and then assess if, and how, canopy-dwelling invertebrate assemblages drift away from the turf baseline during the blooming season of the main canopy habitat (*Sargassum*). Abundance, biomass and diversity almost always differed between canopies and turfs at sampling sites, while differences within main functional algal types were nearly absent. But, surprisingly, none of those overall metrics varied in any consistent way across sampling sites. Differently, the assemblage structure consistently differed between canopies and turfs, with hard-bodied (as gastropods and brachyuran crabs), and soft-bodied (mainly polychaetes and flatworms) invertebrates characterizing canopy and turf assemblages, respectively. The divergence between invertebrate assemblages at canopies and turfs increased as the canopy-blooming season advanced. Notably, while the invertebrate assemblage structure remained unaltered at turfs, early-successional brittle stars and amphipods were followed by hard-shelled gastropods, bivalves and ostracods in *Sargassum*, where they become dominant and decreased diversity later on within the season. As hard-shelled prey are preferred items for the main invertivore fish species in the area, results indicate that canopies play a particularly important role in the provisioning of trophic resources to pelagic consumers.

Keywords: ecosystem engineering, phase-shifts, competition, ecological succession, reef fish

General Introduction

The importance of canopy-forming macroalgae

Marine coastal environments host rich, diverse and productive biological communities, providing food, shelter, and protection for many organisms, and having been widely exploited by humans in many different ways (Lilley & Schiel 2006, Matias et al. 2015, Martins et al. 2016, Piazzini et al. 2018). Still, seascapes are highly heterogeneous and most biological diversity and productivity is concentrated at discrete hotspots, where limiting resources elsewhere can be plentiful. In rocky reef systems, several types of algae can build-up densely vegetated areas amidst rather simplified habitats, such as barren grounds or algal turf beds, being considered ‘ecosystem engineers’, sustaining important ecosystem services such as the supply of food and shelter for many other species (Schmidt & Scheibling 2007, Orlando-Bonaca & Rotter 2018).

Benthic macroalgal beds are considered very productive systems (Tait & Schiel 2011, Miller et al. 2009a), growing to canopy height, and altering the physical structure of reef shorelines, mostly from the low intertidal zone to shallow depths of marine ecosystems (Rindi et al. 2017). In warm-temperate and tropical coastal habitats worldwide, macroalgal beds are often dominant components of the benthos (Schmidt & Scheibling 2007, Strain et al. 2014), forming a three-dimensional canopy structure that affect important physical variables such as light penetration in the water column (Airoldi et al. 1995, Lilley & Schiel 2006, Martins et al. 2016), water flow (Schmidt & Scheibling 2007, O’Brien & Scheibling 2018), sediment transport and deposition (Airoldi 2003, Connel 2005) and pH (Hernández et al. 2018, Layton et al. 2019). Also, large canopy-forming algae contribute to the development of urbanized coasts providing cleaner water through the filtration of nutrients and protecting shorelines from erosion by attenuating and dissipating wave energy (Strain et al. 2014, Martins et al. 2016, Filbee-Dexter & Wernberg 2018).

Canopy-forming macroalgae are also colonized by a diverse and abundant fauna of mobile benthic invertebrates (Wikstrom & Kautsky 2007, Filbee-Dexter et al. 2016, Lutz et al. 2019), normally dominated by amphipods, isopods, gastropods and polychaetes (Tano et al. 2016), and constitute both reproduction sites and nursery habitats for many other larger species (Hinz et al. 2019), where juveniles find effective shelter from predators and adequate foraging grounds (Edgar et al. 2004, Filbee-Dexter et al. 2016). As such, canopy-forming algae constitute a semi-closed biodiversity loop, containing a self-sustained food-web, which include the main algal host and their epiphytic algal assemblages as a basal trophic level, direct mesoherbivore grazers and detritivores as intermediate levels and small fish and invertebrate predators as high within-canopy trophic levels. Different components of this so-called associated fauna assemblage may be used by an array of more or less specialized water column predators (mostly fish, but eventually swimming and crawling large

consumers, such as crabs), including commercially exploited species (Vásquez et al. 2014, Bennet et al. 2016, Filbee-Dexter & Wernberg 2018).

Phase-shifts and the replacement of algal canopies by alternative habitats of lower complexity

There is an increasing concern of the significant loss of complex habitats in both temperate and tropical coastal marine ecosystems. The decline of foundation species, namely reef-building corals, seagrass meadows and canopy-forming macroalgae, with the uprise of more opportunistic species such as mussels and turf-forming algae, preempting the newly available space, has been repeatedly reported for many different coastal areas worldwide (Benedetti-Cecchi et al. 2001, Airoidi et al. 2008, Gorman et al. 2009, Perkol-Finkel & Airoidi 2010, Piazzini & Ceccherelli 2019, Gorman et al. *in press*). Turfs, in particular, are highly tolerant to different sources of environmental stress and disturbance (Perkol-Finkel & Airoidi 2010, Schiel & Lilley 2011, Connel et al. 2014), forming a dense matrix of low-lying mat (from mm to a few cm height), composed by single or multi-species assemblages, mostly thinly filamentous, or other small species with more rigid branches (i.e. articulated coralline algae).

So far, interactions between canopy-forming and turf-forming algae were mostly examined in temperate coastal areas, and mainly addressing the loss of kelp forests. The evidence available indicates that competition between these two algal functional types works in the two directions. Large macroalgae, such as *Cystoseira* and different kelp species, may inhibit the development of turfs mostly through shading (Filbee-Dexter et al. 2016) and abrasion (whiplash; O'Brien & Scheibling 2018). Otherwise, turfs can inhibit canopy regeneration by negatively affecting early benthic stages of canopy-forming algae (Gorman & Connell 2009, Perkol-Finkel & Airoidi 2010), through negative allelopathy, sediment retention (a positive feedback mechanism; Connel et al. 2014), or even shading of propagules (Eriksson et al. 2006, Wernberg & Connel 2008). Less common, turfs can still displace large algal fronds, otherwise grown to a superior-competitor size, when their capacity to retain sediments is unusually high (O'Brien & Scheibling 2018). Much probably, however, the canopy-to-turf shift is not an outcome of the isolated effects of competition, but mostly the modulation of those biological interactions by several different anthropogenic stressors, such as heavy metal pollution, increased sediment loads, nutrient enrichment, and global climate change, including ocean warming and acidification, as well as the increased frequency and strength of storms causing large-scale detachment of canopies (Schiel & Lilley 2011, Strain et al. 2014, Filbee-Dexter & Wernberg 2018, O'Brien & Scheibling 2018). Contrary to late-successional canopies, more opportunistic algal functional types, such as turfs, actually take advantage of surplus nutrients to more rapidly colonize reef space, and are more resistant to the decay of water quality (Littler & Littler 2013, Bulleri et al. 2018, Provost et al. 2017). As such, algal turfs tend to become more dominant as environmental

stressors build up, up to a point that recovery of macroalgal canopies, including whole kelp forests, becomes unlikely. Phase-shifts to impoverished states constitute a major threat to marine diversity, directly affecting a number of important ecosystem functions (Airoldi et al. 2008). Major drivers of community dynamics, including recruitment, competition and predation (Milazzo et al. 2004), become fundamentally altered (Tait & Schiel 2011, Connel et al. 2014) paving the grounds for cascading effects leading to overall biodiversity loss (Wikstrom & Kautsky 2007, Piazzini et al. 2018) and the collapse of ecosystem services (Martins et al. 2016, Rindi et al. 2017) that had historically benefitted human settlements.



Fig. 1. Canopy- forming macroalgae in the São Sebastião Channel dominated by *Sargassum* spp. and, to a lesser extent the reddish canopy of *Galaxaura marginata*. Photo: Rafael Campos Duarte.

Sargassum beds in the SW Atlantic

In warm tropical waters, macroalgal canopies tend to be smaller (although large kelp forests do develop at depth, including in the subtropical SW Atlantic, (Joly & Oliveira Filho 1967, Marins et al. 2014), but highly speciose, potentially providing high functional redundancy from the lower intertidal to shallow waters up to 10 m. Even so, two seaweeds disproportionately provide canopy habitat in the northern coast of São Paulo State; *Dichotomaria* (= *Galaxaura*) *marginata* (Ellis & Solander) and species of the genus *Sargassum* C.Agardh (Fig. 1). During summertime, the canopy of these two groups may cover more than 70% of the available reef space in the São Sebastião Channel (see ‘Results’). Although more seasonal, the brown algae *Sargassum* spp. may be regarded as the principal canopy component of local reefs because they are more abundant during most of the

year and their thallii grow much higher (as in Fig. 2). These macroalgae are very important and, as well as canopy-forming macroalgae from temperate reefs, play an important role in the reef ecosystem. In southeast Brazil, the main blooming season takes place during spring and summer (Godoy & Coutinho 2002, Reis et al. 2003, Széchy et al. 2006), when they harbor a well-described and rich invertebrate fauna (e.g. Jacobucci & Leite 2006, Mafra & Cunha 2006, Marinho-Soriano et al. 2006, Bertagnolli et al. 2014, Jacobucci et al. 2019). During most of this season, several different species compose the majorly *Sargassum* bed as epiphytic plants (especially algae of the genera *Hypnea* J.V.Lamouroux and *Canistrocarpus* de Paula & De Clerck; Fig. 2), which increase the diversity and abundance of the overall associated fauna (Leite & Turra 2003). However, to the best of our knowledge, no studies so far had compared, in a systematic way, the assemblages of mobile invertebrates associated to *Sargassum* to those living in other canopy-forming algae, or even to other important macroalgae, notably algal turfs. Such comparisons would however be very important to assess the relative role of *Sargassum* to the overall diversity of reef systems, and their relevance to the supply of invertebrate prey to water column consumers.

Differently from different warm-temperate regions, where *Sargassum* is invasive (Stæhr et al. 2000, Strong et al. 2006, Salvaterra et al. 2013) and detached floating fronds, in addition to fully pelagic strains, can jeopardize environmental health ('golden tides', Milledge & Harvey 2016, van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019), all the 13 infrageneric *Sargassum* taxa found in São Paulo State are native (de Paula 1988). However, a recent study has showed that *Sargassum* species, overall, have been steadily declining from the 1980's to present days along the states of Santa Catarina, São Paulo and Rio de Janeiro in Brazil (Gorman et al. *in press*). The same trend has been observed in this same study for *Dichotomaria* / *Galaxaura*. A better understanding of the ecological function of canopy-forming species in the SW Atlantic, particularly in the SW coast of Brazil, is therefore urgently needed.



Fig. 2. Close view of a seaweed canopy dominated by *Sargassum* spp. (possibly *S. furcatum*) from the São Sebastião Channel. Note the abundance of associated epiphytic species, such as *Canistrocarpus cervicornis* (Kützting). Photo: Rafael Campos Duarte.

Environmental management and conservation

As declining worldwide and raising serious concerns, macroalgal canopies are presently under protection in many coastal regions and also broadly considered in management plans of many others (Airoldi et al. 2008). Undertaking such conservation policies has been driven by the now consensual view that canopy loss ultimately drives the whole ecosystem to an impoverished state, with lower physical complexity and more restricted ecosystem functioning, ultimately leading to losses of important services to humans (Strain et al. 2014, Tano et al. 2016).

Without intervention, impoverished reef-habitats may remain unaltered over decades (Strain et al. 2014). Orlando-Bonaca & Rotter (2018) advocate that any efforts to solve the problem should first consider the amelioration of environmental conditions, especially the reduction of nutrient concentrations at enclosed bays estuaries. Others, however, have successfully attempted state reversals through restoration, including the translocation of recruits and the removal of large turf areas (Connel et al. 2008, Gorman & Connel 2009, Perkol-Finkel & Airoldi 2010). In some cases,

however, reversals from turf to canopy dominated states may take enduring work over several generations of canopy-forming algae (Benedetti-Cecchi et al. 2001).

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Main Objectives

Here, the assemblages of mobile invertebrates associated to algal canopies and turfs are formally compared, and the temporal organization of canopy invertebrates at the seasonal *Sargassum* habitat is assessed with reference to the baseline turf pattern. By doing so, we assessed the potential for algal canopies to enhance the local diversity of small mobile invertebrates, and thus the supply of trophic resources to water-column consumers. We specifically asked:

- (i) Is variation among functional macroalgal types more important than variation within canopies or turf types?
- (ii) Are canopies actually capable to add additional invertebrate groups to the standard invertebrate assemblage found at less complex turf habitats?
- (iii) Do any differences among these vegetated habitats include the abundance of valuable prey for pelagic consumers, thus affecting whole ecosystem functioning?
- (iv) Do *Sargassum*-dwelling invertebrate assemblages actually drift away from the turf baseline as the canopy-blooming season advance?
- (v) Are seasonal communities associated to *Sargassum* controlled by foundation (i.e. compatible with stochastic and site-specific lottery dynamics, in which founder species influence succession) or by dominance (i.e. leading to more predictable and consistent ecological succession)?

Chapter 1. Ecosystem functioning of canopy and turf-forming algae: potential supply of invertebrate prey to pelagic consumers

Running page head: Invertebrates associated to canopies and turfs

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Abstract

Canopy-forming algae may provide trophic resources and structural complexity for a wide array of mobile invertebrates, which in turn may sustain pelagic consumers of higher trophic levels. However, algal canopies are declining worldwide and replaced by less-complex macroalgal turfs which may dominate reefscape. Here, we first compare the assemblages of mobile invertebrates associated to main canopy-forming (*Sargassum* spp. and *Galaxaura marginata*) and turf-forming algae (filamentous and articulated coralline turf), and then assess if, and how, canopy-dwelling invertebrate assemblages drift away from the turf baseline during the blooming season of the main canopy habitat (*Sargassum*). Abundance, biomass and diversity almost always differed between canopies and turfs at sampling sites, while differences within main functional algal types were nearly absent. But, surprisingly, none of those overall metrics varied in any consistent way across sampling sites. Differently, the assemblage structure consistently differed between canopies and turfs, with hard-bodied (as gastropods and brachyuran crabs), and soft-bodied (mainly polychaetes and flatworms) invertebrates characterizing canopy and turf assemblages, respectively. The divergence between invertebrate assemblages at canopies and turfs increased as the canopy-blooming season advanced. Notably, while the invertebrate assemblage structure remained unaltered at turfs, early-successional brittle stars and amphipods were followed by hard-shelled gastropods, bivalves and ostracods in *Sargassum*, where they become dominant and decreased diversity later on within the season. As hard-shelled prey are preferred items for the main invertivore fish species in the area, results indicate that canopies play a particularly important role in the provisioning of trophic resources to pelagic consumers.

Keywords: ecosystem engineering, phase-shifts, competition, ecological succession, reef fish

Introduction

Reef macroalgae may often grow to canopy height and thus play unique ecosystem functions. As such, canopy-forming algae are considered ‘ecosystem engineers’, influencing important environmental factors within the reef habitat. As physical barriers to flow over the substrate, large macroalgae may change local hydrodynamics, thereby protecting coastlines by reducing coastal surge, and retaining large quantities of sediments that host diverse biological assemblages (Eriksson et al. 2006, Schmidt & Scheibling 2007). As important primary producers, algal canopies contribute to nutrient uptake, carbon sequestration and ultimately climate control (Schmidt & Scheibling 2007, Filbee-Dexter & Wernberg 2018, Piazzini et al. 2018). Macroalgal beds also sustain additional loops to coastal trophic webs, directly sustaining different herbivores, from large browsers to grazers spanning 2-3 orders of magnitude in size (e.g. Estes & Duggins 1995, Hughes et al. 2007), providing particulate matter for filter-feeding invertebrates (Heip et al. 1995, Vizzini & Mazzola 2003), and small planktivores (Vizzini & Mazzola 2003, Metillo et al. 2016), and subsidizing terrestrial trophic webs after being detached from the substrate after storms and deposited along shorelines (Adin & Riera 2003, MacMillan & Quijón 2012).

Canopy-forming algae also add physical complexity to seascapes, hosting not only the herbivores that directly feed on plant tissues, but also a very diverse and abundant fauna of mobile benthic invertebrates that locally prey on first-order consumers and find shelter on the intricate structure formed by algal branches (Wikstrom & Kautsky 2007, Tait & Schiel 2011, Matias et al. 2015, Filbee-Dexter et al. 2016). This partially self-contained biological assemblage may in turn sustain larger demersal carnivores, linking benthic primary production to higher-order trophic levels in the pelagic ecosystem (Strain et al. 2014, Tano et al. 2016, Filbee-Dexter & Wernberg 2018). Still, this important benthic-pelagic coupling may be highly vulnerable to environmental disturbance because canopy-forming algae are generally late successional species, competing with the physically impoverished vegetated substrates formed by filamentous and articulated coralline turf (O’Brien & Scheibling 2018). The phase-shift between a state of habitat complexity, with the predominance of canopy-forming algae, to a poorer state, in which algal turfs prevail, has been repeatedly linked to different sources of anthropogenic impact (Benedetti-Cecchi et al. 2001, Airoidi et al. 2008, Gorman & Connel 2009, 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). Competition with more opportunistic seaweeds (Schmidt & Scheibling 2007, Reeves et al. 2018, Lutz et al. 2019) may further contribute to the worldwide decline of temperate macroalgal canopies, notably large fucoids (Wikstrom & Kautsky 2007, Connel & Russel 2010), which have been mostly replaced by turf-forming algae, leading to impoverished landscapes (Airoidi et al. 2008, Gorman et

al. 2009). Once established, algal turfs most often reduce the recruitment rate of canopy-forming algae through space preemption and sediment accumulation, making it an unstable substrate for settlement (Bellgrove et al. 2010, Alestra et al. 2014, O'Brien & Scheibling 2018).

Turf-to-canopy dynamics are much less understood in tropical systems, where canopy-forming algae are more diversified and relatively smaller. One important group, however, are brown algae of the genus *Sargassum* C. Agardh, 1820. In the subtropical Southwestern Atlantic, *Sargassum* spp. is very abundant on rocky reefs (Paula & Eston 1987, Széchy & Paula 2000a, Jacobucci et al. 2019), encompassing 13 different species (de Paula 1988). Altogether, their abundance is highly seasonal, peaking in summer and decaying shortly after, sometimes to virtual absence during winter (Godoy & Coutinho 2002, Széchy et al. 2006). Several studies have described the spatial distribution patterns of *Sargassum*, and the rich fauna associated to this brown weed (e.g. Széchy & Paula 2000a, Godoy & Coutinho 2002, Jacobucci & Leite 2006, Mafra & Cunha 2006, Marinho-Soriano et al. 2006, Bertagnolli et al. 2014), overall suggesting that *Sargassum* beds serve as a nursery habitat for several invertebrates and fish, and a foraging ground for pelagic consumers, by delivering valuable and diversified prey. However, the relative importance of the seasonal *Sargassum* canopy remains unclear because no studies have assessed how the invertebrate assemblages associated to this seaweed compare to those inhabiting other algal canopies, or other important vegetated substrates lacking a complex physical structure (i.e. algal turfs). Owing to its seasonal nature, with full developing fronds lasting only 2-4 months, understanding the temporal organization of mobile invertebrate assemblages in *Sargassum* beds is crucial to assess the importance of this habitat as foraging grounds for pelagic consumers. Because the diversity of benthic mobile invertebrates potentially colonizing algal canopies is immense, the determination of founder invertebrate groups, and hence later assemblage dynamics, may be uncertain and very context-dependent (e.g. lottery models; Sale 1978, Green & Schoener 1982). Alternatively, early successional invertebrates may be more predictably replaced by superior competitors, which tend to become dominant and endure for longer in the assemblage, following a pattern of ecological succession as observed in other reef systems (e.g. Lubchenco & Menge 1978, Benedetti-Cecchi 2000). This would narrow down possibilities and allow an anticipation of temporal dynamics, even for very complex and diverse assemblages such as the ones we address here. Understanding whether the temporal dynamics of invertebrate assemblages are founder or dominance-controlled (*sensu* Yodzis 1986) is thus paramount to assess the role of *Sargassum* spp. beds, which are declining in the region over the last 40 years (Gorman et al. submitted), and their blooming seasons probably shortening.

Here we first compare the mobile invertebrate assemblages associated to canopy-forming algae [*Sargassum* spp. and *Galaxaura marginata* (Kützinger)] and algal turfs (filamentous and coralline) to assess the capacity of those vegetated habitats to host abundant and diversified

communities. Namely, we asked (i) whether variation among functional macroalgal types is more important than variation within canopies or turf types, (ii) whether canopies are actually capable to add additional invertebrate groups to the standard invertebrate assemblage found at less complex turf habitats, and (iii) whether any differences found among these vegetated habitats include the abundance of valuable prey for pelagic consumers, thus affecting whole ecosystem functioning. Second, we compare the temporal dynamics of the invertebrate assemblages associated to *Sargassum* beds and filamentous turfs to (iv) test whether the invertebrate assemblages at *Sargassum* actually drift away from the turf baseline as the canopy-blooming season advances, and, according to Yodzis (1986), (v) test whether the seasonal communities associated to *Sargassum* are foundation controlled (i.e. compatible with a stochastic and site-specific lottery dynamics, in which founder species influence succession) or dominance controlled (i.e. leading to more predictable and consistent ecological succession). The underlying mechanisms controlling the temporal dynamics of invertebrate assemblages at *Sargassum* would ultimately determine whether maximum ecosystem functioning can be achieved before its seasonal decay.

Material and Methods

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 Zimbro: 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 Zimbro 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 two different functional types; turfs and canopy-forming algae. Turfs can be broadly separated in those formed mostly by filamentous (hereafter “filamentous turf”) or articulated coralline algae (“coralline algal turf”). Several different species may build canopy habitat for several different invertebrates and fish recruits, but the brown weed *Sargassum* spp. and the red alga *Galaxaura marginata* are particularly common at the study sites and were thus target of this study. Reduced wave action usually favors the vertical growth of algal canopies, especially *Sargassum* (Széchy et al. 2006, Veloso e Széchy 2008), and therefore algal canopies at the study sites are expected to be more luxurious than average in the region.

Field sampling

This study is divided in two main tasks; the first to compare invertebrate assemblages associated to algal turfs and canopies, and test whether those algal substrates can be considered single functional habitats, and the second to verify whether canopy-specific invertebrates assembly in any predictable temporal way during the blooming season of *Sargassum*.

Canopy vs turf comparisons - Fieldwork for the first task took place between December 2017 to March 2018, when the *Sargassum* cover is high and their fronds well-developed. At all three sites, four replicate samples were taken for each of four algal substrates; 2 canopy-forming algae (*Sargassum* spp. and *Galaxaura marginata*) and 2 algal turf types (filamentous and coralline) at shallow depth (1-5 m below mean low-tide level). Sampling units consisted of all macroalgal materials scrapped within 40 x 40 cm PVC squares, placed at separate (at least 5 m) and interspersed random patches of full canopy or turf cover (100%). As macroalgae were scrapped off the substrate, a 38 mm hose connected to a 5.5 HP pump onboard (set at $12 \text{ m}^3 \cdot \text{h}^{-1}$) suctioned all materials to a net bag (150 μm). All underwater work was undertaken using SCUBA. Sample bags were immersed onboard on large plastic buckets and immediately sorted out upon arrival to the laboratory.

Temporal assembly of invertebrates associated to canopy-forming algae - This task was divided in two stages. First we reported the seasonal variation of algal canopies formed by *Sargassum* spp. and *Galaxaura marginata* by monthly sampling all three sites from October 2014 to July 2015. At each site and sampling date, video footage was taken along a 70 m ruled transect, laid parallel to the shoreline at the depth of maximum canopy cover, to allow a record of virtually all canopy cover. Fifteen replicate frames were randomly sampled out from each footage to obtain estimates of abundance (percentage cover) on ImageJ (Rasband 1997). The average area covered by each frame was 1.902 m^2 , but there was considerable variation among sites and sampling dates (overall SD = 1.216 m^2) owing to several environmental conditions, such as tide level, visibility and the extent of the long-shore canopy width. The second stage of this temporal sampling task aimed the identification of any assembly patterns during the development of seasonal algal canopies (*Sargassum*) that drifted invertebrate assemblages away from the turf baseline. For that, we obtain four replicate samples of *Sargassum* spp. and filamentous turf at Pedra Montada and Zimbros during three different moments within the main canopy season (December 2018, January and February 2019). The sampling procedure followed exactly the one described above.

Laboratory procedures

The contents of 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 on sieves. Sampled materials 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 thickness of filamentous and coralline turf was fairly constant 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 separate five random fronds within each *Sargassum* and *Galaxaura* sample to verify whether canopy height (a measure of structural complexity) may eventually affect overall metrics of invertebrate assemblages. All invertebrates were identified into large taxonomic groups (within a total of 29) and counted under a dissecting microscope.

Statistical analyses

Canopy vs turf comparisons - One-way omnibus general linear models were used to test whether invertebrate assemblages differed between canopy-forming algae and algal turfs, and whether differences are also found within these major habitat types. For that, we used mean square error estimates obtained from the main procedure to test the three respective planned contrasts, namely (i) canopy vs turf (*Sargassum* – *Galaxaura* vs filamentous turf – coralline turf), (ii) within canopies (*Sargassum* vs *Galaxaura*), and (iii) within turfs (filamentous turf vs coralline turf). Dependent univariate metrics included overall abundance, the Shannon-Wiener (H') diversity index, average size and overall biomass (using the size-to-weight relationship obtained by Méthot et al. 2012). 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) were run instead, using type I sums of squares and unrestricted permutation (9,999 times) of raw data. Pairwise comparisons followed the same contrasts above, and similarity percentage analyses were conducted, whenever comparisons proved significant, to identify the taxonomic groups that contributed the most for dissimilarities.

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* spp. and *Galaxaura marginata*), according to 'site' (random) and 'month' (fixed), using 15 replicate observations. The

arc-sin transformation solved heteroscedasticity for *Sargassum*, but not *Galaxaura*. Still, we maintained the original procedure as datasets were balanced and replication was high (Underwood 1997). The SNK procedure was used for post-hoc comparisons among months.

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’) were used to examine the invertebrate assemblage metrics specified above. Statistical significance of the two-order interaction ‘alga*time’, would indicate habitat-dependent temporal change of invertebrate community structure, as predicted, while significance of the three-order interaction ‘alga*time*site’, would also point to divergent assembly of invertebrate groups between algal types, with drifting patterns, however, dependent on idiosyncratic conditions at sampled sites. Equivalent permutational analyses of variance were carried out to examine invertebrate assemblage structure, as above. Planned contrasts were restricted to t1 vs t2 (December vs January) and t2 vs t3 (January vs February), either for different ‘algal’ types, or within level combinations of ‘alga*site’.

Results

Canopy vs turf comparisons

A total of 39,987 specimens, 23,321 from canopies and 16,666 from turfs, encompassing 29 major invertebrate groups (details in Table S1), were recorded. All univariate metrics, except for average individual size, responding only to site effects (Table 1), indicate significant differences of invertebrate assemblages associated to the sampled algal habitats. 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 different canopies (*Sargassum* vs *Galaxaura*) or between turf-forming algae (filamentous vs coralline), which were only significant in 1 out 18 occasions (Fig. 1).

Table 1. Summary results of general linear mixed models comparing main parameters of invertebrate assemblages associated to algal canopies (*Sargassum* spp., *Galaxaura 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.

	<i>df</i>	Canopy vs Turf									
		Abundance		Diversity		Biomass		Average size		Structure	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	pseudo- F	<i>P</i>
Alga: Al	3	1.12	0.413	1.11	0.415	0.39	0.767	3.48	0.091	8.49	0.001
Site: Si	2	4.59	0.017	4.37	0.020	10.05	< 0.001	4.57	0.017	7.68	0.001
Al*Si	6	4.24	0.003	3.47	0.008	2.69	0.0294	1.01	0.437	2.97	0.001
Res.	36										
		√x transf. <i>C</i> = 0.2737; <i>p</i> > 0.05		Raw data <i>C</i> = 0.1460; <i>p</i> > 0.05		√x transf. <i>C</i> = 0.2144; <i>p</i> > 0.05		√x transf. <i>C</i> = 0.3967; <i>p</i> < 0.01		√x transformed -	

However, metrics were much less favorable to canopy-forming algae than anticipated. Abundance (Fig. 1 A-C) and biomass (Fig. 1 D-F) were higher for canopies at Zimbros (Fig. 1 C, F) and Pedra Montada (Fig. 1 B, E), but higher for turfs at Guaecá (Fig. 1 A, D; although not significant for abundance, Fig. 1A). The trends for diversity are actually more favorable to algal turfs (Fig. 1 G-I). Average Shannon-Wiener diversity was 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 invertebrates assemblages within any algal functional type were restricted to canopies at Zimbros, where overall abundance was almost

2-fold higher at *Galaxaura* compared to *Sargassum*. Although with average frond size varying from 5 to 18 cm for *Sargassum*, and 5 to 14 cm for *Galaxaura*, no correlation was observed between any of the tested parameters and canopy height ($0.03 < r < 0.34$; $p > 0.30$ in all cases; Fig. S1), suggesting that additional complexity, such as surface plant area and whole interstitial volume, did not affect assemblages in any obvious way.

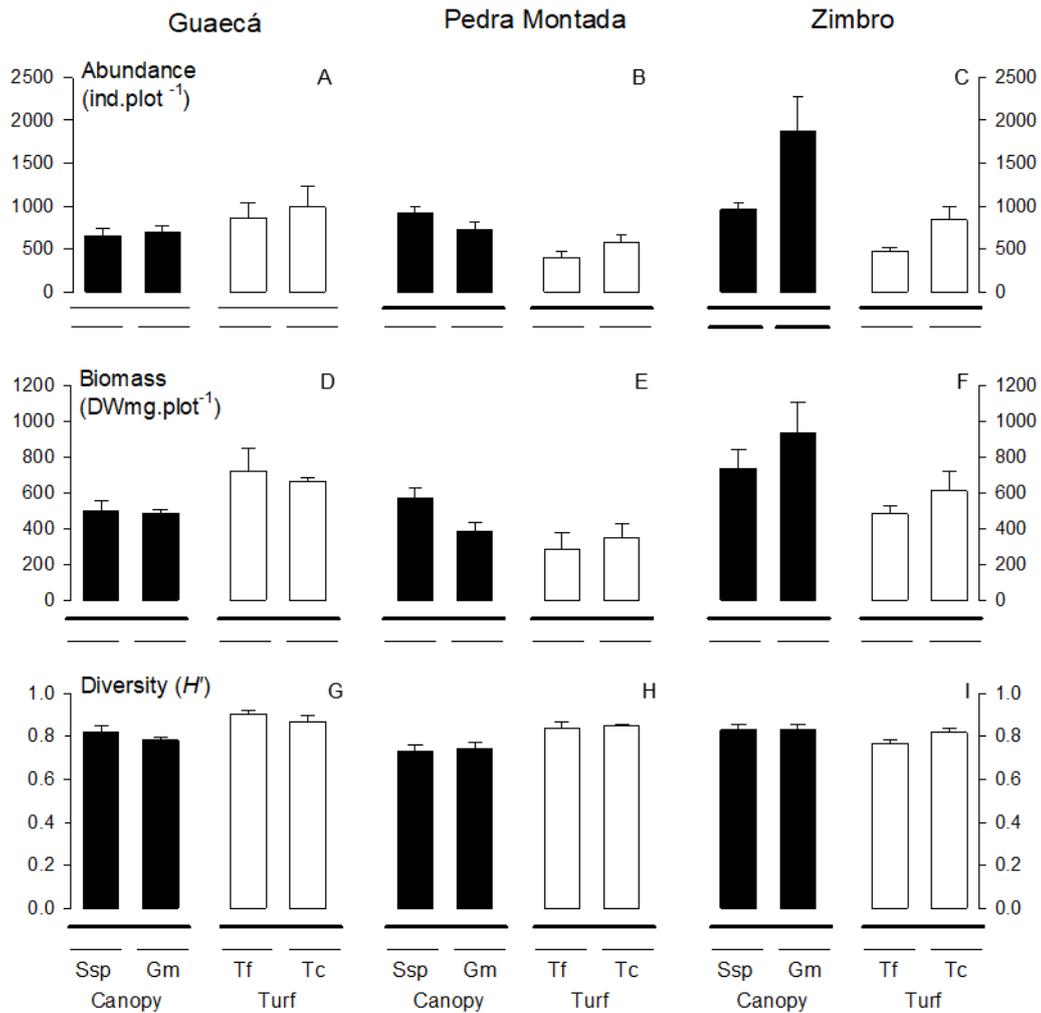


Fig. 1. Comparisons of univariate descriptors of invertebrate assemblages between and within macroalgal habitat types at sampling sites (A-I). Columns and error bars represent average values and respective SEs. Ssp: *Sargassum* spp., Gm: *Galaxaura marginata*, Tf: Filamentous turf, Tc: Coralline turf. Significance planned comparisons ($p < 0.05$) are indicated with bold underlines.

The invertebrate assemblage structure between algal substrates was markedly different at all sampling sites (Table 1). Planned comparisons showed that sound dissimilarities are almost restricted to canopy vs turf comparisons for all sites ($4.62 < \text{Pseudo-}F < 13.60$; $0.0001 < p < 0.028$; Fig. 2 A-C), with more clear differences at Guaecá and Zimbro (overall dissimilarities 33.24 and 39.96%, respectively, Fig. 2A, C), compared to Pedra Montada (28.64%, Fig. 2B). No differences were ever found between turfs, and differences between canopies were restricted to Pedra Montada (pseudo- $F = 2.21$, $p = 0.028$; Fig. 2B). Similarity percentage analyses indicated that six invertebrate groups contributed the most to differences between the assemblage structure of invertebrates at canopies and turfs (Table S2), namely gastropods, polychaetes, brittle stars, tanaids, flat worms and brachyuran crabs (Table S2, Fig. 2 D-F). Not all six contributed to 7% or more of dissimilarities at sampling sites, with flat worms and brachyuran crabs making 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 Zimbro (Table S2). Still, all these invertebrate groups were considered in further analyses for all sites. The most consistent trend was the much higher abundance of gastropods at canopies than at turfs (Table S1, Fig. 2 D-F), confirmed by t -tests for all three sites. Brachyuran crabs were also numerically more abundant at canopies than at turfs at all sites, but this difference was only significant at Zimbro (Fig. 2F). Groups that were otherwise more abundant at turfs than at canopies were polychaetes and flat worms (with statistical support found at Guaecá for the former, and Guaecá and Zimbro for the latter, Fig. 2 D, F). The abundance variation for the other two groups was more inconsistent, but a statistically significant difference was found at Zimbro for brittle stars (more abundant at canopies, Fig. 2F) and at Guaecá for tanaids (more abundant at turfs, Fig. 2D). The dissimilarities between algal canopies found at Pedra Montada accounted mostly for a higher abundance of gastropods, polychaetes and tanaids at *Sargassum* compared to *Galaxaura*, but no statistical significances were observed for separate comparisons of the abundance of these groups between canopies.

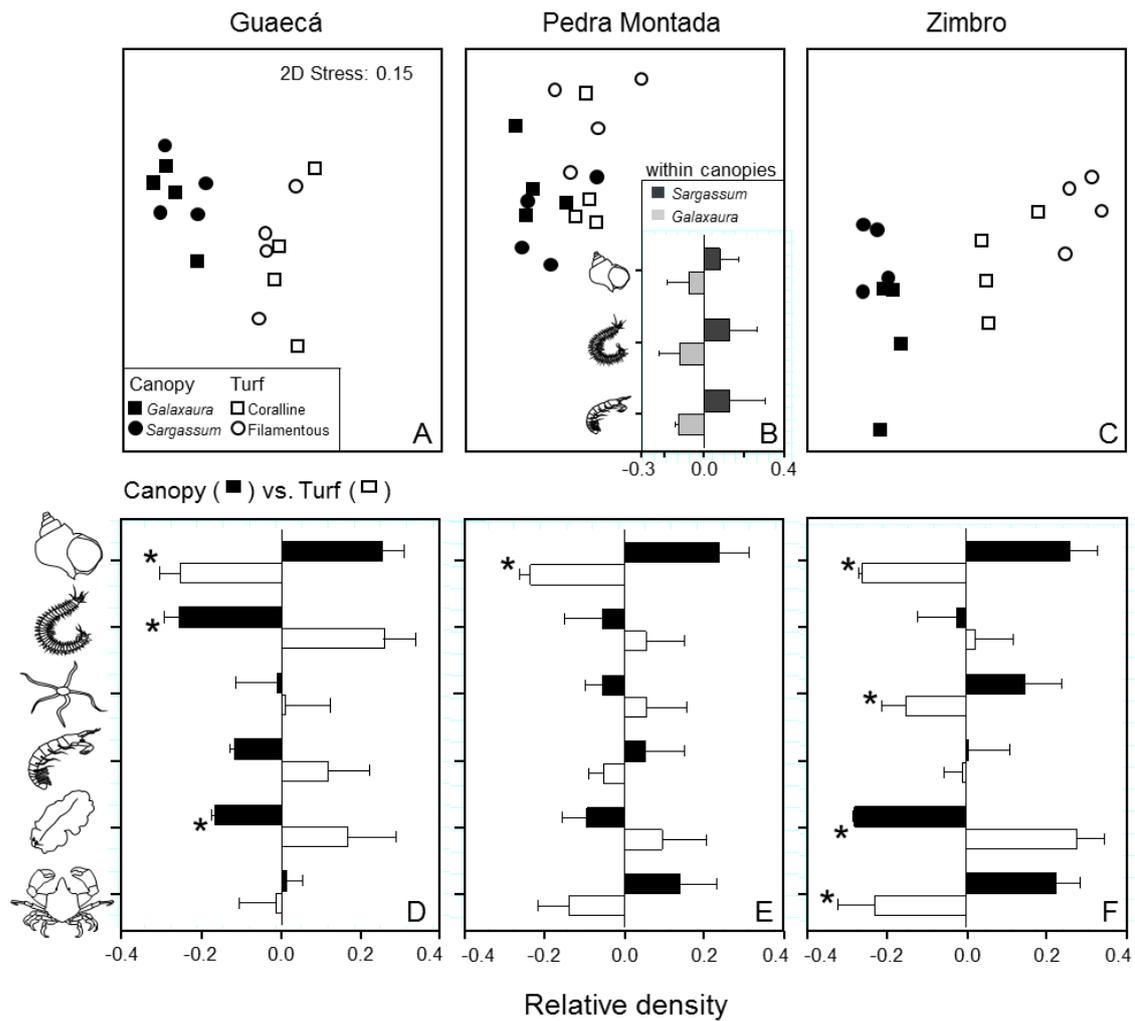


Fig. 2. Comparisons of the invertebrate assemblage structure between and within macroalgal habitat types at sampling sites. Pairwise comparisons after the omnibus permutational analysis of variance indicated significant canopy vs turf contrasts at all sites, and significant contrasts within canopy-forming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

Seasonal cover of canopy-forming algae and the assembly of invertebrates

The seasonal cover of *Sargassum* spp. and *Galaxaura* were nearly inversely related, especially at Guaecá and Pedra Montada (Fig. 3 A,B). Altogether, the cover of these two canopy-forming algae can make up most 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. 3 A-C). *Sargassum* spp. reached a much higher cover and showed a clearer seasonal variation compared to *Galaxaura* at all sites. Strong 'site*month' interactions were found for both canopy-forming weeds (*Sargassum*: $F_{s*m} = 4.48$; *Galaxaura*: $F_{s*m} = 5.63$; $p < 0.0001$ in both cases; Fig. 3A-C). *Sargassum* abundance was highest from January to February at Guaecá, December to February at Pedra Montada and December through May at Zimbros (SNK post-hoc tests, $p < 0.05$). The trend for *Galaxaura* is less clear, with higher substrate cover from October to November, and then from April to July in Guaecá, and single peak abundances at July and December observed at Pedra montada and Zimbros, respectively (SNK post-hoc tests, $p < 0.05$; Fig. 3A-C).

Because the overall abundance was higher and the seasonal trend clearer at *Sargassum* spp., we used this vegetated habitat to examine the temporal assembly patterns of mobile invertebrates associated to algal canopies, namely from December 2018 to 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 to *Sargassum* spp. and filamentous turfs, respectively, encompassing 27 major invertebrate groups (Table S3).

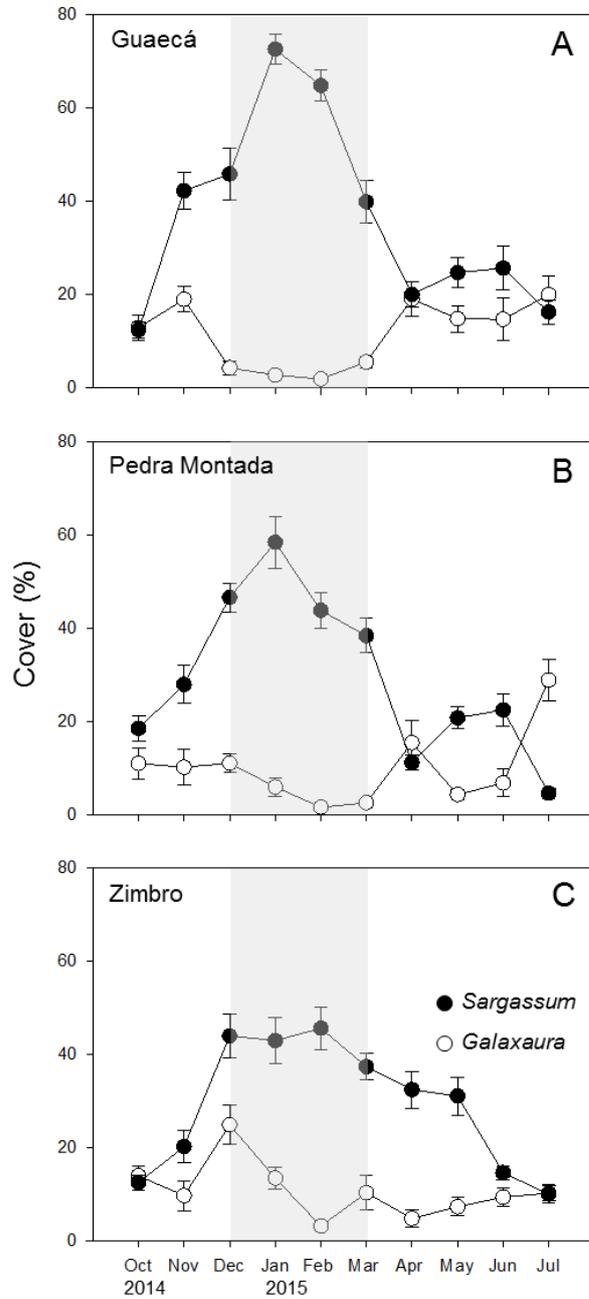


Fig. 3. Seasonal variation of the abundance of canopy-forming algae, as percent cover, at sampling sites Guaecá (A), Pedra Montada (B) and Zimbro (C). The seasonal peak abundance, from December to February, is shown in gray shade. Scatter dots and error bars stand for average values and respective SEs.

Of all metrics examined in this study, only diversity and assemblage structure showed algal-type dependent temporal trends, although site-specific (as significant three-order interactions ‘alga*time*site’; Table 2). Diversity was overall higher at filamentous turfs compared to the *Sargassum* canopy, but showed quite variable temporal variation depending on algal type and site (Fig. 4). At Pedra Montada, diversity dropped from December to January, and remained low until February in *Sargassum* (Fig. 4A), but persisted high and stable in filamentous turf (Fig. 4B). At Zimbros, the trends in *Sargassum* and in filamentous turfs were inverted (Fig. 4 C-D), decreasing in the canopy habitat and increasing in the turf one through time. Statistical differences were only observed between January and February at both sites (SNK post-hoc tests, $p < 0.05$).

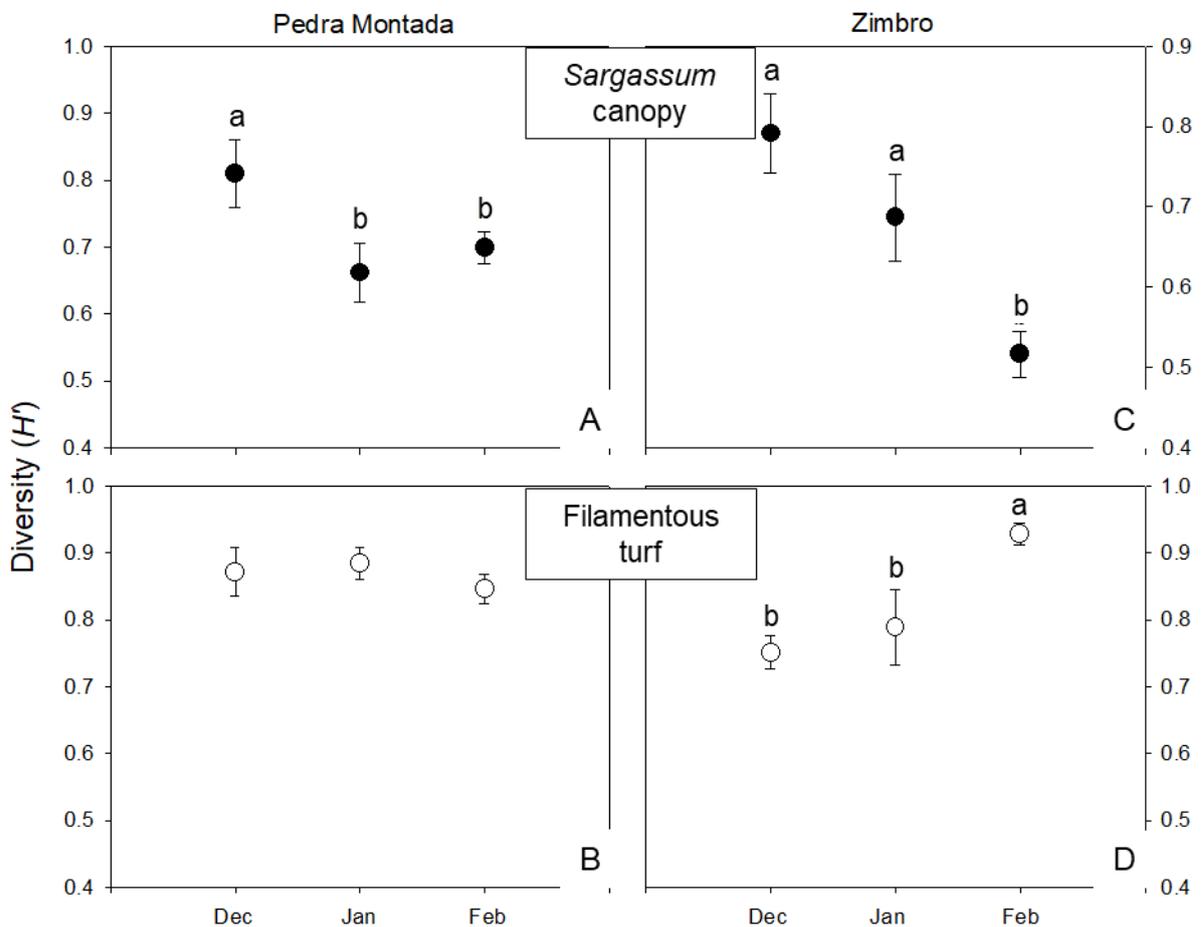


Fig. 4. Shannon-Wiener diversity estimates (H') for invertebrate assemblages associated to *Sargassum* canopy and filamentous turf from December 2018 to February 2019 at Pedra Montada (A-B) and Zimbros (C-D). Scatter dots and error bars stand for average values and respective SEs. For each individual plot, diversity estimates sharing the same letter are not statistically different (SNK post-hoc tests, $p > 0.05$).

The three-order significant interaction of the model tested through permutational analysis of variance, examining the temporal change of assemblage structure (Table 2), is explained by the observations that (i) temporal changes were restricted to *Sargassum* spp., but (ii) more extensive at Zimbrow, especially from t2 (January) to t3 (February; Fig. 5 A-B). In both cases, the invertebrate assemblage structure at *Sargassum* drifted from the turf baseline through time. Still, the divergence was more pronounced at Zimbrow than at Pedra Montada, with overall dissimilarities from t1 (December) to t2 (41.72 compared to 31.48%) and from t2 to t3 (30.65 compared to 23.76%) higher at Zimbrow than at Pedra Montada (Table S4, Fig. 5A,B). Pairwise comparisons were however significant for both sites (Zimbrow - t1 vs t2: pseudo $F = 2.59$, $p = 0.029$; t2 vs t3: pseudo $F = 2.43$, $p = 0.030$; Pedra Montada - t1 vs t2: pseudo $F = 1.95$, $p = 0.027$; t2 vs t3: pseudo $F = 1.55$, $p = 0.028$).

Table 2. Summary results of general linear mixed models comparing main parameters of invertebrate assemblages associated to the algal-forming canopy *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.

<i>Sargassum</i> vs filamentous turf over time											
	<i>df</i>	Abundance		Diversity		Biomass		Average size		Structure	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>Pseudo-F</i>	<i>p</i>
Algal:	1	5.19	0.263	464.31	0.030	1.00	0.500	7.52	0.223	12.80	0.170
Al											
Time: Ti	2	1.54	0.394	13.98	0.067	26.64	0.036	< 0.01	0.999	5.10	0.015
Site: Si	1	0.30	0.584	5.40	0.026	0.16	0.689	< 0.01	0.964	3.33	0.017
Al*Ti	2	0.39	0.719	1.54	0.394	7.15	0.123	15.88	0.059	0.93	0.534
Al*Si	1	1.77	0.192	0.10	0.754	3.66	0.064	2.50	0.123	2.20	0.072
Ti*Si	2	1.36	0.269	0.20	0.822	0.13	0.880	2.25	0.120	2.56	0.016
Al*Ti*Si	2	0.41	0.669	8.07	0.001	0.54	0.587	0.92	0.408	2.11	0.043
Res.	36										
		Raw data		Raw data		Raw data		Raw data		√x transformed	
		<i>C</i> = 0.2388; <i>p</i> > 0.05		<i>C</i> = 0.1788; <i>p</i> > 0.05		<i>C</i> = 0.2328; <i>p</i> > 0.05		<i>C</i> = 0.2128; <i>p</i> > 0.05		-	

Eight different invertebrate groups were found to account for 7% or more of overall dissimilarities considering all four comparisons, with 4-5 particularly relevant at each specific comparison (Table S4). Wider oscillations of the temporal abundance of those eight invertebrate groups were found at Zimbrow (Fig. 5D), but numerical trends are rather consistent between sites. Brittle stars and amphipods were early groups found mostly at t1 and declining afterwards at t2 and t3. This trend is statistically reinforced at Zimbrow through separate one-way comparisons, followed by SNK post-hoc tests ($p > 0.05$). Gastropods, bivalves, and ostracods were later groups, with additional statistical

evidence indicating a steady increase of gastropods at Zimbro, a steady increase of bivalves at Pedra Montada, and a more clear increase of the abundance of bivalves and ostracods from t2 to t3 at Zimbro (SNK post-hoc tests, $p > 0.05$; Fig. CD). Although contributing to dissimilarities of invertebrate assemblage structure through time, polychaetes and hermit crabs did not show temporal variation in any consistent way.

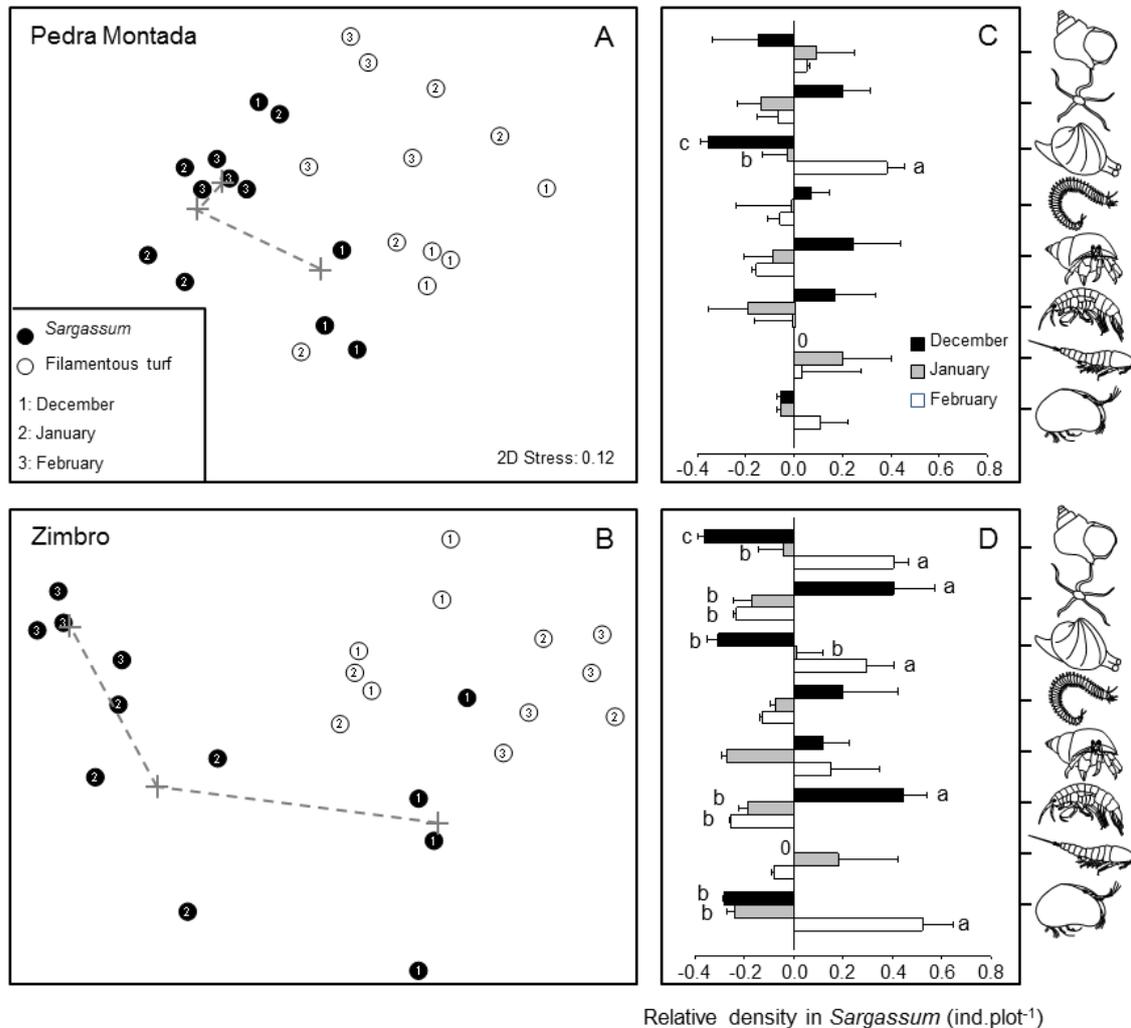


Fig. 5. Comparisons of the structure of invertebrate assemblages associated to *Sargassum* canopies and filamentous turfs at Pedra Montada and Zimbro, from December 2018 to February 2019. A-B: Spatial ordination figures extracted from the whole-data nMDS plot showing sample clusters at t1 (December), t2 (January), and t3 (February) for each site. Planned contrasts evidenced temporal changes of invertebrates assemblage structure at *Sargassum* canopies but not at filamentous turfs. Assemblage drift from the turf baseline is marked 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 and error bars stand for averages and respective SEs. Relative density estimates sharing the same letter are not statistically different ($p > 0.05$). Drawings represent gastropods, brittle stars, bivalves, polychaetes, hermit crabs, amphipods, copepods and ostracods from the upper to the lower end of plots.

Discussion

In this 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 of overall diversity, abundance and biomass between the mobile fauna found at canopies and turfs were not consistent, and therefore the hypothesis that canopies simply expanded niche space, providing resources for a new set of invertebrate groups, does not hold. 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 Guaecá and Pedra Montada. Otherwise, the lower wave exposure at Zimbrow may provide more stable conditions, explaining the larger number of mobile invertebrate groups found thriving in canopy habitats at that site (especially *Galaxaura*). This mechanism, however, remains uncertain because we had sampled different sites as a means to draw generality of any differences between canopies and turfs, not to test any additional 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 such a test.

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) had also no effect on invertebrate size (not any overall assemblage metric), we conclude that morphological attributes of these vegetated substrates play no major role in determining size-related functional traits. Still, despite the absence of size differences, and the inconsistent variation of diversity, overall abundance and biomass, the assemblage structure of mobile invertebrates was strikingly and rather consistently different between canopies and turfs. Most notably, hard-shelled groups (mostly gastropods and crabs) were more frequently associated to canopy-forming algae, while soft-bodied invertebrates (mainly polychaetes and flatworms) were more abundant in turfs. 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 *Bittiolum* Cossmann, and 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). Differently, 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. In turn, divergent invertebrate assemblages at canopies and turfs may subsidize more diversified pelagic consumers through trophic niche partitioning (e.g. Ross 1986). Since the average size of potential prey is around 2.0 - 3.0 mm, trophic subsidies would more likely impact small cryptobenthic fish species (such as blennies and gobbies; e.g. Depczynski & Bellwood 2003), or juvenile stages of larger species that use vegetated substrates as nursery grounds. We predict that whether or not those small consumers are able to prey on hard-shelled invertebrates may be a critical issue determining the distribution of pelagic consumers over the reef habitat. At our study coastline, some of the most abundant reef fishes are invertivores consuming mobile prey. Five of them are particularly abundant; the grunts *Haemulon aurolineatum* Cuvier and *H. steindachneri* (Jordan & Gilbert), the silver porgy *Diplodus argenteus* Valenciennes, the sergeant major *Abudefduf saxatilis* (Linnaeus) and the blenny *Parablennius pilicornis* (Cuvier) (Gibran & Moura 2012). Except for the blenny that feeds mostly on polychaetes (Nieder 1997), all other species tend to feed on hard-shelled prey especially during the juvenile phase, as in *Haemulon* spp., which feed mostly on copepods and amphipods, moving to polychaetes and other fish when they grow to adults (Pereira et al. 2014). Seemingly, the silver porgy feeds mostly on copepods and mussels when juveniles, but shifts to a more omnivorous diet when adults, largely feeding on macroalgae and decapod crustaceans (Dubiascki-Silva & Masunari 2006). Compared to other damselfishes that are mostly planktivores, *Abudefduf* spp. feeds mostly on benthic prey (Aguilar-Medrano & Barber 2016). The sergeant major *A. saxatilis*, in particular, is an omnivore, feeding 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 (beyond plant resources, especially turf-forming filamentous algae), but also that algal canopies may be particularly relevant as they supply target prey for a larger fraction of the common invertivores fishes found in the area.

In the study area, *Sargassum* and *Galaxaura* combined take, on average, 39 to 48% of the reef available space throughout the year, reaching together a maximum of 64 to 75% in December – January. *Sargassum* not only develops to a much taller canopy, but its average cover is nearly 3-fold that of *Galaxaura* (varying from 2.72 to 3.17), making it a particularly valuable habitat. However, the *Sargassum* cover is highly seasonal, and a point was made here that invertebrate assemblages would probably not have the time to reach an equilibrium state, limiting important community traits such as abundance (or carrying support) and diversity, but results do not support this hypothesis. We did confirm that turf assemblages are temporally more stable, that can be used as a reference to evaluate the temporal change of assemblages in *Sargassum* (as they drifted from the turf baseline as the blooming season advances), but we observed no canopy-specific increases in overall abundance or biomass. More importantly, we had observed an inverse temporal trend of diversity in turfs and

canopies, especially at Zimbro, with a *decline* (not an increase) of invertebrate diversity in *Sargassum* and an increase of diversity in filamentous turfs. Combined, these results indicate that some species had somehow become more dominant at *Sargassum* through the blooming season, with some spillover of less common groups to turfs. Multivariate analyses during this second part of the study reinforced the notion that hard-shelled invertebrates tend to prevail in canopies, and that assemblage divergences between canopies and turfs become clearer because those invertebrate groups become dominant later on during the *Sargassum* season, reducing whole-community diversity. Interestingly, the overall temporal dynamics of invertebrate communities at canopies were rather consistent and can be predicted, with peak diversity early in the *Sargassum* season, sustained in part by a large number of opportunistic species, as brittle stars and amphipods, which later on cease space to other groups (namely gastropods, bivalves and ostracods) that can more efficiently exploit resources and dominate assemblages. The life history and functional ecology of these relevant invertebrate groups explain the observed successional pattern. Most brittle stars in our samples belong to the small invasive species *Ophiotela mirabilis* Verrill, which is an emblematic generalist, very abundant in the region and 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 they do not firmly attach to the substrate or defend themselves by any known means. Likewise, 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 2006) tend to remain near their foraging grounds, in the *Sargassum* case very likely their fronds where very small epiphytic algae and organic debris tend to accumulate as plants get older. Rather than optimizing the use of food resources, filter-feeding bivalves may become dominant because they 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).

Like in many other coastal areas, the subtropical SW Atlantic is experiencing the loss of canopy-forming macroalgae at least over the last 40 yr. So far, the cover of *Sargassum* spp. may have shrunk in almost 90%, while the abundance of other canopy-forming algae (e.g. *Galaxaura*) may have been reduced in more than 20% (Gorman et al. *in press*). This is a very worrying trend because different important ecosystem services – which remain largely unknown - may be at stake. Here we suggest that the coexistence of different algal substrates at any reef site would favor the maintenance of abundant and diversified assemblages of mobile invertebrates, and much probably indirectly benefit several invertivore and omnivore fish species that are abundant in the study area. Owing to

their local abundance and because they supply reef fish with generally preferred prey types, declines in canopy-forming algae may cascade to serious socio-economic challenges led, for instance, by the collapse of small-scale artisanal fisheries. Conservation policies mitigating the environmental stressors that negatively impact algal canopies, as well as other complex coastal habitats, are therefore urgently needed.

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Supplementary material

Table S1. Overall abundance of major invertebrate taxonomic groups, as individuals per plot, associated to algal canopies (*Sargassum* spp., *Galaxaura marginata*) and turfs (filamentous and coralline) from December 2017 to March 2018. NI: non-identifiable individuals.

Groups	<i>Sargassum</i> sp						<i>Galaxaura marginata</i>					
	Guaecá		P. Montada		Zimbro		Guaecá		P. Montada		Zimbro	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Gastropods	240,0	24,7	463,5	58,9	380,0	41,4	261,0	24,1	363,3	69,4	650,5	81,5
Bivalves	93,8	20,9	67,5	12,6	102,3	21,0	137,8	12,7	50,8	11,1	247,5	95,6
Polichaetes	45,5	11,3	110,5	29,3	104,3	18,6	62,3	28,9	58,0	21,7	326,8	84,6
Brachyuran crabs	47,3	5,1	29,0	6,5	105,8	14,4	49,3	8,7	31,3	7,5	94,5	8,8
Amphipods	24,0	4,1	39,5	4,4	58,0	17,1	13,8	2,1	36,3	2,8	127,5	27,8
Tanaids	24,8	9,7	70,8	28,9	41,3	10,9	23,8	12,7	28,0	3,0	177,8	62,4
Hermit crabs	22,8	2,3	21,0	4,9	15,0	5,7	17,3	5,0	28,3	7,1	18,0	2,3
Caridean shrimps	3,3	1,8	0,3	0,2	1,5	0,3	2,3	0,5	4,5	1,7	1,8	0,5
Chitons	0,8	0,2	0,0	0,0	0,3	0,2	0,8	0,4	1,3	0,2	0,5	0,3
Brittle stars	121,5	35,4	71,0	11,6	84,5	17,6	98,3	33,7	96,5	12,9	141,0	37,6
Isopods	6,3	4,6	1,8	0,6	6,0	2,3	0,8	0,2	0,5	0,4	7,8	2,2
Sea spiders	10,3	1,8	9,8	4,6	37,3	11,0	9,5	1,6	3,3	0,7	12,3	2,1
Sipunculids	1,5	0,6	3,8	1,3	0,8	0,4	1,5	1,0	0,3	0,2	1,5	1,0
Limpets	7,5	3,2	11,3	2,0	6,3	1,4	5,8	1,6	14,0	6,6	14,0	2,2
Flat worms	0,3	0,2	0,3	0,2	0,5	0,3	0,8	0,4	0,5	0,4	0,8	0,4
Nemertines	0,3	0,2	0,5	0,4	0,3	0,2	0,0	0,0	0,0	0,0	0,5	0,4
Copepods	0,0	0,0	5,8	4,7	0,8	0,6	11,5	10,0	0,0	0,0	13,3	7,2
Ostracods	0,5	0,3	1,0	0,4	9,3	7,4	0,3	0,2	0,0	0,0	26,3	10,6
Foraminiferans	1,0	0,6	2,5	1,1	4,3	2,3	0,8	0,4	0,0	0,0	12,0	5,8
Oligochaetes	0,3	0,2	0,3	0,2	0,5	0,4	0,0	0,0	0,3	0,2	0,3	0,2
Cumaceans	0,0	0,0	0,0	0,0	0,3	0,2	1,0	0,9	0,0	0,0	0,8	0,6
Echiurans	0,0	0,0	0,0	0,0	0,8	0,4	0,8	0,4	0,3	0,2	1,0	0,4
Sea urchins	0,0	0,0	0,0	0,0	1,3	0,5	0,3	0,2	1,0	0,6	0,3	0,2
Sea stars	1,0	0,4	0,3	0,2	0,0	0,0	1,3	0,4	1,0	0,6	0,0	0,0
Sea hares	0,3	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Nudibranchs	0,0	0,0	1,0	0,4	0,0	0,0	0,0	0,0	0,0	0,0	1,3	0,6
Onchidella sp	1,0	0,4	1,0	0,5	0,3	0,2	0,5	0,4	0,0	0,0	0,3	0,2
megalopae	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Fish	0,3	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
NI	0,0	0,0	0,8	0,6	1,3	0,8	0,8	0,2	2,0	1,5	1,3	1,1

Table S1 – Continued

Groups	<i>Filamentous turf</i>						<i>Coralline turf</i>					
	Guaecá		P. Montada		Zimbros		Guaecá		P. Montada		Zimbros	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Gastropods	114,5	24,5	87,8	19,7	15,3	3,9	67,3	13,8	132,0	21,9	43,5	14,8
Bivalves	72,8	8,7	63,3	26,9	57,8	9,1	79,0	20,3	49,8	11,6	92,3	32,9
Polychaetes	241,5	41,1	79,5	20,7	126,3	27,2	286,5	47,8	134,0	28,1	360,8	79,4
Brachyuran crabs	60,5	20,0	13,8	6,7	3,8	1,1	29,3	4,6	17,3	4,5	67,8	14,0
Amphipods	63,8	21,6	16,3	7,8	63,0	10,0	64,3	18,5	21,5	5,3	78,0	10,9
Tanaids	134,0	40,1	28,5	11,0	148,0	11,1	240,8	132,8	35,5	5,9	59,0	12,3
Hermit crabs	18,0	5,4	10,3	3,6	1,5	1,0	17,0	4,9	18,5	5,5	5,0	1,7
Caridean shrimps	3,5	1,3	1,3	1,1	0,3	0,2	2,8	1,1	0,5	0,4	1,5	0,6
Chitons	15,0	3,5	5,8	3,8	0,0	0,0	13,8	3,6	2,8	0,4	4,3	3,1
Brittle stars	97,0	38,5	79,3	20,4	6,3	3,7	133,8	35,3	138,0	35,3	71,0	20,3
Isopods	0,8	0,6	0,0	0,0	0,0	0,0	0,5	0,3	0,3	0,2	1,3	0,6
Sea spiders	7,5	1,3	7,0	1,6	1,0	0,4	12,0	2,2	9,5	1,1	4,0	0,6
Sipunculids	2,8	0,6	2,3	1,2	0,3	0,2	5,0	0,9	4,8	2,7	0,5	0,4
Limpets	17,0	5,0	4,3	0,5	9,3	1,1	12,5	3,4	8,5	1,1	6,8	1,8
Flat worms	5,5	3,2	1,3	0,8	40,5	8,3	15,3	5,6	1,0	0,4	36,5	4,1
Nemertines	0,3	0,2	0,3	0,2	0,3	0,2	0,3	0,2	0,0	0,0	0,3	0,2
Copepods	0,0	0,0	0,0	0,0	0,8	0,4	0,3	0,2	0,0	0,0	0,5	0,4
Ostracods	2,0	0,4	1,3	1,1	0,3	0,2	1,3	0,5	1,3	0,4	0,0	0,0
Foraminiferans	1,3	0,8	0,3	0,2	0,0	0,0	0,0	0,0	0,8	0,4	0,0	0,0
Oligochaetes	2,5	1,6	0,0	0,0	1,5	0,6	2,0	0,9	1,0	0,5	1,3	0,5
Cumaceans	0,3	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Echiurans	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,2
Sea urchins	3,8	1,5	1,3	0,8	0,3	0,2	4,8	1,5	2,5	0,8	0,3	0,2
Sea stars	0,5	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,2	0,0	0,0
Sea hares	0,3	0,2	0,0	0,0	0,3	0,2	0,0	0,0	0,0	0,0	0,0	0,0
Nudibranchs	0,3	0,2	0,0	0,0	0,0	0,0	0,3	0,2	0,5	0,3	0,3	0,2
Onchidella sp	1,0	0,6	0,3	0,2	0,3	0,2	0,0	0,0	0,0	0,0	1,3	0,8
Megalopae	0,3	0,2	0,0	0,0	0,3	0,2	0,0	0,0	0,0	0,0	0,0	0,0
Fish	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,2	0,0	0,0	0,0	0,0
NI	0,8	0,4	2,0	1,0	1,8	1,0	5,0	2,4	1,8	0,5	4,3	1,2

Table S2. Canopy vs turf - Similarity percentage (SIMPER) analyses identifying the invertebrate groups that contributed the most (> 7% dissimilarity, in grey shade) to statistically significant planned contrasts following the omnibus permutational analysis of variance (see ‘material & methods’ and figure 2). NI: non-identifiable individuals.

Guaecá			Pedra Montada			Zimbro					
Canopy vs Turf			Canopy vs Turf			Between canopies: <i>Sargassum</i> vs <i>Galaxaura</i>			Canopy vs Turf		
Taxon	%	Cum %	Taxon	%	Cum %	Taxon	%	Cum %	Taxon	%	Cum %
Polychaetes	15.51	15.51	Gastropods	23.45	23.45	Gastropods	11.66	11.66	Gastropods	23.28	23.28
Tanaids	13.32	28.84	Polychaetes	8.65	32.09	Polychaetes	11.04	22.70	Brittle stars	8.08	31.36
Gastropods	11.68	40.52	Brittle stars	7.21	39.30	Tanaids	8.82	31.52	Flat worms	7.63	38.99
Brittle stars	7.71	48.23	Bivalves	6.28	45.58	Bivalves	5.95	37.46	Brachyuran crabs	7.50	46.50
Amphipods	5.69	53.92	Tanaids	5.67	51.24	Brittle stars	5.27	42.73	Polychaetes	7.37	53.86
Chitons	5.07	58.99	Amphipods	5.41	56.66	Caridean shrimps	4.79	47.52	Bivalves	5.91	59.77
Bivalves	4.95	63.94	Brachyuran crabs	5.31	61.97	Brachyuran crabs	4.56	52.09	Tanaids	5.77	65.53
Flat worms	3.86	67.80	Hermit crabs	4.96	66.93	Hermit crabs	4.34	56.42	Sea spiders	4.58	70.12
Brachyuran crabs	3.33	71.13	Sea spiders	3.08	70.01	Limpets	4.28	60.70	Ostracods	3.91	74.02
Sea urchins	3.03	74.16	Sipunculids	3.06	73.07	Sea spiders	4.22	64.92	Amphipods	3.83	77.85
Limpets	2.79	76.95	Limpets	3.05	76.12	Sipunculids	4.16	69.08	Hermit crabs	3.52	81.37
Hermit crabs	2.65	79.60	Chitons	2.85	78.97	Copepods	3.58	72.65	Isopods	2.82	84.19
Sipunculids	1.97	81.57	Caridean shrimps	2.79	81.76	Foraminiferans	3.40	76.06	Foraminiferans	2.77	86.96
Isopods	1.95	83.52	Unidentified	2.51	84.27	Chitons	3.02	79.07	Copepods	2.07	89.02
Unidentified	1.84	85.35	Sea urchins	2.25	86.52	Isopods	2.83	81.90	Unidentified	1.64	90.67
Caridean shrimps	1.82	87.17	Ostracods	1.82	88.34	Unidentified	2.68	84.58	Oligochaetes	1.19	91.85
Oligochaetes	1.78	88.95	Isopods	1.77	90.11	Nudibranchs	2.42	87.00	Limpets	1.17	93.02
Ostracods	1.59	90.54	Flat worms	1.76	91.87	Ostracods	2.31	89.30	Caridean shrimps	1.09	94.11
Copepods	1.48	92.02	Foraminiferans	1.71	93.58	Amphipods	2.09	91.39	Chitons	1.05	95.16
Sea stars	1.32	93.34	Copepods	1.48	95.06	Onchidella sp	1.89	93.28	Sipunculids	0.91	96.07
Sea spiders	1.29	94.63	Sea stars	1.16	96.22	Sea stars	1.81	95.09	Echiurans	0.90	96.97
Foraminiferans	1.24	95.87	Nudibranchs	1.14	97.36	Sea urchins	1.79	96.88	Sea urchins	0.80	97.77
Onchidella sp	1.17	97.04	Oligochaetes	1.07	98.43	Flat worms	1.25	98.13	Onchidella sp	0.73	98.50
Cumaceans	0.59	97.63	Onchidella sp	0.96	99.39	Oligochaetes	0.99	99.13	Nemertines	0.57	99.07
Echiurans	0.55	98.18	Nemertines	0.61	100.00	Nemertines	0.87	100.00	Nudibranchs	0.53	99.61
Nemertines	0.53	98.71						Cumaceans	0.39	100.00	
Nudibranchs	0.51	99.22									
Sea hares	0.40	99.62									
Fish	0.38	100.00									
Overall average dissimilarity		33.24			28.64			22.55			39.96

Table S3. Overall abundance of major invertebrate taxonomic groups, as individuals per plot, associated to the algal-forming canopy *Sargassum* spp. and filamentous turfs over time (December 2018 to February 2019), from December 2018 to February 2019. NI: non-identifiable individuals.

Groups	<i>Sargassum</i> sp											
	P. Montada						Zimbrow					
	Dezembro		Janeiro		Fevereiro		Dezembro		Janeiro		Fevereiro	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Gastropods	305,3	152,7	494,0	123,2	461,0	9,5	67,8	15,0	268,3	61,8	548,3	39,3
Bivalves	29,3	11,9	147,3	37,0	297,0	26,4	29,0	8,9	92,8	20,7	149	22,8
Polychaetes	103,3	21,5	82,3	63,9	68,8	13,3	196,3	127,5	40,5	12,6	9,5	5,1
Brachyuran crabs	20,8	3,9	13,5	3,1	9,3	1,7	28,5	9,2	11,5	2,5	27,5	4,5
Amphipods	67,3	15,1	26,8	6,9	49,3	14,4	122,8	16,2	15,3	6,7	3	0,7
Tanaids	22,0	8,0	51,8	18,9	30,0	8,7	25,5	10,1	24,8	3,1	6,75	2,4
Hermit crabs	93,8	35,5	34,8	21,1	22,5	3,1	9,8	2,4	0,8	0,5	10,5	4,6
Caridean shrimps	1,5	0,6	0,0	0,0	0,5	0,5	0,3	0,3	0,3	0,3	0	0,0
Chitons	0,5	0,3	0,8	0,5	14,3	14,3	10,3	5,6	0,0	0,0	0	0,0
Brittle stars	95,5	15,6	48,3	13,4	58,5	12,4	181,8	45,4	23,5	20,2	6,5	2,6
Isopods	0,0	0,0	0,0	0,0	1,5	0,9	2,5	0,5	0,8	0,5	0	0,0
Sea spiders	5,0	2,4	8,0	2,9	14,0	3,4	13,5	4,1	14,0	6,8	6,75	3,1
Sipunculids	2,0	0,7	0,0	0,0	1,8	0,9	0,3	0,3	0,0	0,0	0,25	0,3
Limpets	16,0	5,2	8,3	2,6	1,0	0,4	5,3	2,2	9,0	3,2	18,5	2,4
Flat worms	0,5	0,5	0,0	0,0	0,3	0,3	1,8	1,4	0,0	0,0	0	0,0
Nemertines	0,3	0,3	0,0	0,0	0,0	0,0	0,8	0,5	0,0	0,0	0	0,0
Copepods	0,0	0,0	18,0	8,3	11,0	10,0	0,0	0,0	13,0	11,1	1	0,4
Ostracods	1,3	0,6	1,5	0,6	8,3	4,6	0,8	0,3	2,8	1,4	37	5,6
Foraminiferans	2,5	1,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0	0,0
Oligochaetes	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,3	0,0	0,0	0	0,0
Cumaceans	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0	0,0
Echiurans	0,0	0,0	0,0	0,0	0,0	0,0	1,8	1,4	0,0	0,0	0	0,0
Sea urchins	6,0	1,8	6,3	1,3	1,0	0,4	1,5	0,6	2,5	1,8	2,75	1,1
Sea stars	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0	0,0
Sea hares	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,3	0,0	0,0	0	0,0
Nudibranchs	0,5	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0	0,0
Onchidella sp	0,3	0,3	0,0	0,0	0,0	0,0	0,3	0,3	0,0	0,0	0,25	0,3
Megalopae	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0	0,0
Fish	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0	0,0
NI	0,0	0,0	0,0	0,0	0,3	0,3	0,5	0,5	0,0	0,0	3,75	1,9

Table S3. Continued.

Groups	Filamentous turf											
	P. Montada						Zimbro					
	Dezembro		Janeiro		Fevereiro		Dezembro		Janeiro		Fevereiro	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Gastropods	52,25	9,1	98,3	37,1	254,3	75,0	42,3	15,3	88,8	37,2	158,8	14,5
Bivalves	34	6,9	193,3	124,6	491,5	157,3	22,0	4,6	142,0	57,2	284,0	73,5
Polychaetes	228,3	76,3	327,8	128,0	305,0	54,3	458,5	81,0	418,8	207,0	340,5	64,9
Brachyuran crabs	20,5	8,5	16,5	4,6	32,5	6,0	18,5	2,8	14,0	1,9	42,0	6,7
Amphipods	168,3	17,5	150,8	64,2	46,3	14,7	445,8	66,3	115,3	39,7	115,8	17,6
Tanaids	83,25	34,6	93,3	13,6	105,8	38,3	88,5	14,9	112,8	28,2	99,5	36,0
Hermit crabs	21	7,9	18,0	5,8	66,3	20,6	14,3	8,2	11,3	7,7	13,3	4,1
Caridean shrimps	2,75	1,4	1,3	0,8	5,8	1,9	2,5	1,0	0,8	0,5	4,0	2,0
Chitons	5,5	1,3	7,0	3,8	0,5	0,3	2,8	0,8	4,0	2,1	3,0	0,6
Brittle stars	122,5	39,8	148,5	40,8	99,8	23,7	101,5	10,0	128,5	59,2	113,3	30,8
Isopods	2,75	1,0	3,3	2,0	3,0	1,1	13,0	3,8	1,5	0,9	1,8	0,6
Sea spiders	9,5	3,1	9,0	4,0	11,3	1,3	5,3	1,4	4,0	1,3	15,8	9,4
Sipunculids	2,75	1,4	4,3	2,2	2,3	1,9	0,3	0,3	1,0	0,4	0,0	0,0
Limpets	1,75	0,8	15,0	5,3	9,3	2,3	8,8	1,8	12,5	8,8	11,3	3,1
Flat worms	4,75	1,0	15,0	8,1	4,5	1,9	34,8	7,4	21,5	10,0	21,0	10,1
Nemertines	0,75	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,8	0,8	2,0	1,7
Copepods	3,25	1,3	1,8	1,4	1,5	0,5	16,8	8,4	2,8	1,3	2,5	1,2
Ostracods	3,25	0,8	25,8	12,5	32,0	12,7	1,3	0,5	4,5	2,0	54,5	18,7
Foraminiferans	0,5	0,3	0,0	0,0	18,5	7,3	0,0	0,0	0,0	0,0	10,0	5,1
Oligochaetes	0	0,0	0,3	0,3	1,8	1,0	8,0	4,8	1,3	0,8	3,5	2,5
Cumaceans	0,25	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Echiurans	0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Sea urchins	2	0,7	6,0	1,6	4,0	1,3	1,5	0,3	3,8	2,4	17,3	9,7
Sea stars	0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Sea hares	0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Nudibranchs	0,75	0,5	0,0	0,0	0,3	0,3	1,0	1,0	0,5	0,5	1,0	0,7
Onchidella sp	0,25	0,3	0,0	0,0	0,0	0,0	2,0	2,0	0,3	0,3	0,3	0,3
Megalopae	0,5	0,3	0,0	0,0	0,3	0,3	0,3	0,3	0,5	0,5	0,0	0,0
Fish	0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
NI	0,25	0,3	2,0	1,7	2,5	1,0	1,5	1,5	0,3	0,3	4,3	3,1

Table S4. *Sargassum* canopy vs filamentous turf overtime - Similarity percentage (SIMPER) analyses identifying the invertebrate groups that contributed the most (> 7% dissimilarity, in grey shade) to statistically significant planned contrasts following the omnibus permutational analysis of variance (see 'material & methods' and figure 2). NI: non-identifiable individuals. t1: December, t2: January, t3: February.

Pedra Montada						Zimbro					
Sargassum t1 vs Sargassum t2			Sargassum t2 vs Sargassum t3			Sargassum t1 vs Sargassum t2			Sargassum t2 vs Sargassum t3		
Taxon	%	Cum %									
Gastropods	17.11	17.11	Bivalves	14.34	14.34	Brittle stars	16.97	16.97	Gastropods	18.87	18.87
Bivalves	13.48	30.59	Polychaetes	12.18	26.52	Gastropods	14.51	31.49	Ostracods	11.85	30.72
Polychaetes	11.87	42.45	Gastropods	11.62	38.14	Amphipods	13.54	45.03	Polychaetes	8.82	39.54
Hermit crabs	10.02	52.48	Copepods	7.18	45.32	Polychaetes	10.47	55.50	Bivalves	7.72	47.26
Copepods	7.46	59.93	Tanaids	6.69	52.00	Bivalves	8.14	63.64	Brittle stars	6.76	54.02
Brittle stars	6.46	66.39	Hermit crabs	6.05	58.05	Copepods	4.68	68.32	Tanaids	6.27	60.29
Amphipods	6.05	72.44	Amphipods	5.80	63.85	Chitons	4.40	72.72	Hermit crabs	6.07	66.36
Tanaids	6.03	78.47	Chitons	5.33	69.18	Hermit crabs	4.26	76.98	Copepods	5.59	71.95
Limpets	3.31	81.78	Brittle stars	5.16	74.33	Brachyuran crabs	3.87	80.85	Amphipods	4.88	76.83
Foraminiferans	2.53	84.31	Ostracods	4.69	79.02	Tanaids	2.73	83.58	Sea spiders	4.79	81.61
Sea spiders	2.39	86.70	Limpets	4.61	83.63	Sea spiders	2.59	86.17	Brachyuran crabs	4.79	86.40
Brachyuran crabs	2.36	89.06	Sea urchins	3.94	87.57	Limpets	2.34	88.51	Ni	3.90	90.30
Sipunculids	2.35	91.40	Sea spiders	3.21	90.78	Ostracods	1.82	90.33	Limpets	3.81	94.11
Caridean shrimps	2.00	93.40	Sipunculids	2.82	93.60	Isopods	1.78	92.11	Sea urchins	2.46	96.56
Ostracods	1.40	94.80	Isopods	2.23	95.83	Sea urchins	1.68	93.79	Isopods	1.52	98.08
Sea urchins	1.40	96.20	Brachyuran crabs	2.06	97.88	Flat worms	1.44	95.23	Caridean shrimps	0.67	98.75
Chitons	1.18	97.37	Caridean shrimps	0.86	98.74	Echiurans	1.43	96.66	Sipunculids	0.62	99.38
Nudibranchs	0.96	98.34	Ni	0.65	99.39	Nemertines	0.95	97.61	Onchidella sp	0.62	100.00
Flat worms	0.66	99.00	Flat worms	0.61	100.00	Caridean shrimps	0.65	98.25	Flat worms	0.00	100.00
Onchidella sp	0.53	99.53	Megalopae	0.00	100.00	Ni	0.51	98.76	Megalopae	0.00	100.00
Nemertines	0.47	100.00	Onchidella sp	0.00	100.00	Sipunculids	0.44	99.20	Nudibranchs	0.00	100.00
Ni	0.00	100.00	Nudibranchs	0.00	100.00	Oligochaetes	0.44	99.64	Echiurans	0.00	100.00
Megalopae	0.00	100.00	Echiurans	0.00	100.00	Onchidella sp	0.36	100.00	Oligochaetes	0.00	100.00
Isopods	0.00	100.00	Oligochaetes	0.00	100.00	Megalopae	0.00	100.00	Foraminiferans	0.00	100.00
Echiurans	0.00	100.00	Foraminiferans	0.00	100.00	Nudibranchs	0.00	100.00	Chitons	0.00	100.00
Oligochaetes	0.00	100.00	Nemertines	0.00	100.00	Foraminiferans	0.00	100.00	Nemertines	0.00	100.00
			Oligochaetes	0.00	100.00						
Overall											
average dissimilarity		31.48			23.76			41.72			30.65

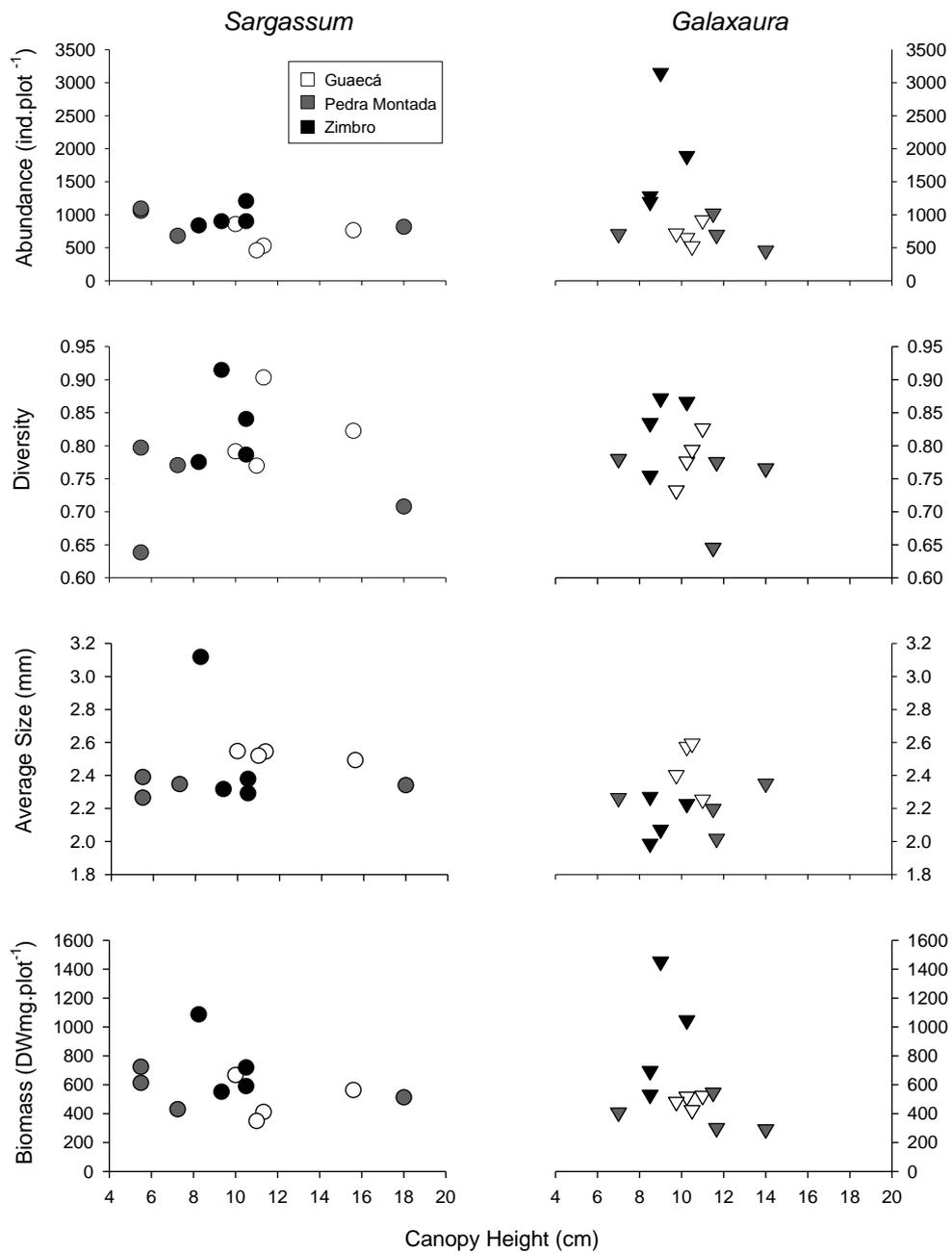


Fig S1. Relationships between canopy height and univariate metrics of invertebrate assemblages associated to *Sargassum* spp. and *Galaxaura marginata* at sampling sites Guaecá, Pedra Montada and Zimbro. Correlation coefficients ($0.03 < r < 0.34$) were never significant ($p > 0.30$ in all cases). The values of canopy height correspond to averages ($n = 5$) of thallus height within samples.

Concluding Remarks

The overall results obtained in this study show that the mobile invertebrate assemblages associated to algal turfs (filamentous and coralline) and algal canopies (*Sargassum* and *Galaxaura*) are clearly different, while the assemblages within each of these algal functional types were almost always remarkably similar. Against our expectations, we found a high invertebrate abundance and diversity at turfs, at times higher than at canopies. This finding contrasts to other reports in the literature, which indicate more severe effects of canopy loss. In these latter studies, however, a single canopy species was considered, such as monospecific kelp forests, or the important Mediterranean algal canopy formed by *Cystoseira* C. Agardh, and many of them were conducted at coastal areas where canopies were already dramatically reduced to very low cover. Despite the overall declining trend of algal canopies in the SW Atlantic, algal canopies are still a major component of the benthic seascape in the São Sebastião Channel (SCC), and therefore the migration of faunal groups from canopies to turfs, as suggested here, may in part explain why our study differs from others.

Maybe more important than concluding on the relative abundance and diversity of mobile invertebrates associated to different vegetated reef habitats, in this case turfs and canopies, would be addressing how heterogeneous reefs harboring a mosaic of complex biogenic substrates compare to more homogeneous seascapes, counting with only a single major ecosystem engineering plant or animal. By providing different subsets of the potential pool of small mobile invertebrates in the area, we conclude that canopies and turfs, together, may sustain a larger diversity (and perhaps abundance) of pelagic consumers that specialize in either type. At present, however, we anticipate a more prominent role of algal canopies as they contribute mostly to sustain large populations of hard-bodied invertebrates, which are preferred prey for 4 out of 5 of the most abundant invertivore reef fish in the study area. It is important however that the diet of the reef fish addressed here was mostly based on visual counts of stomach contents, and therefore the consumption of soft-bodied invertebrate groups may be underscored. Visual censuses of fish interactions with the different algal substrates, combined with experimental trials to verify actual feeding preferences would be key to sort out this intriguing and important question.

We also stress that our focus here was on a single ecosystem function of algal habitats – the provision of prey for water-column consumers – and further work on other roles of macroalgal substrates are urgently needed. Closely aligned with this study, further investigations should look at the importance of larger herbivores capable to graze on whole-canopy fronds or scrapping turf areas to barren grounds. Macro-herbivores of this kind include larger browsing fish, such as scarids and kyphosids, or green turtles which are relatively less frequent than most small consumers, but that may play a keystone effect in the area, together with grazing sea-urchin fronts that were observed to leave behind large extensions of bare rock at different places in the SSC and nearby coastal islands.

Also, the large abundance and diversity observed near complex reef habitats (such as complex vegetated grounds) may not necessarily reflect consumption pressure. Many fish may actually use algal canopies as shelter from their predators. Particularly small fish recruits may find shelter, or concealment, within different algal canopies, and still forage while protected from visual ambush predators. As such, algal canopies may be critical habitats as nursery grounds, a role that has seldom be investigated in structured algal canopies other than kelp forests.

Because of their abundance and structural complexity, the seasonal nature of canopies formed by the brown weed *Sargassum* spp. deserves further attention. We report an interesting temporal succession of the invertebrate assemblages associated to *Sargassum*, suggesting that gastropods, bivalves and ostracods outcompete early colonizers as the canopy-blooming season advances. By February, the invertebrate assemblages at *Sargassum* were already quite distinct from those observed at turfs, now dominated by hard-shelled groups that are apparently preferred by higher-order consumers. This leaves a rather narrow temporal window for this important ecosystem service, as canopy decay would be already in course shortly after during May and April. This opens two important and pending research lines. First, specific experimental research should aim a better understanding the processes underlying the invertebrate assembly during the short *Sargassum* blooming season. While we had advanced some starting evidence for competition as an overall interaction driving succession, there might be well other sort of biological interactions playing an important role, including within-canopy predation. Second, it is important to understand the mechanisms behind the seasonality of *Sargassum* in the region, especially the role of small epiphytes growing on the fronds, which accumulate over the season and could reduce photosynthesis to a critical threshold, and any effects of environmental stressors that could modulate such plant-plant interactions. The current decline of canopies in the SW Atlantic is very worrying and any efforts to detect its causes and propose solutions are certainly welcome. There is clearly an undisputable demand for more qualified work on the dynamics of complex vegetated habitats in the region, preferably uniting professional scientists, management planners and decision takers to attempt reverting habitat loss and bring back such important ecosystems to a healthy state.