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Effects of wave exposure on the abundance and composition of amphipod and tanaidacean assemblages inhabiting intertidal coralline algae

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Peracarid crustaceans are an important component of the vagile fauna associated with coralline algal beds, which often characterize the infralittoral fringe of tropical rocky shores. Among other variables affecting faunal assemblages, sedimentation, food supply and oxygen concentration within mats or turfs of coralline algae may greatly depend on the exposure to waves. In this study, peracarid assemblages were compared at replicated rocky shores within different levels of wave exposure, along a coastline in south-eastern Brazil. Overall amphipod diversity (11 species) was much higher than tanaidacean diversity (two species). Correlation analyses did not support any biological interactions between amphipods and tanaidaceans. Habitat complexity, while apparently limiting amphipod populations, did not affect tanaidaceans at a local scale. Amphipod abundance, not assemblage structure, was positively affected by wave exposure, probably improving oxygen concentration levels and renewal of food resources. Rather than abundance, which remains fairly stable, exposure to waves determined species identity in tanaidaceans, with Zeuxo coralensis *found at exposed shores and* Leptochelia *aff.* dubia *found at sheltered shores, except for two* L. *aff.* dubia *individuals found at one of the exposed sites. Differences in the supply of sediment and the ability of these species in manipulating grains for tube building may explain such a striking pattern.*

Keywords: Species composition, peracarids, hydrodynamism, articulated coralline algae, rocky shores

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INTRODUCTION

Wave-swept habitats are prone to physical disturbance, resulting in major changes of community diversity and structure (Denny, 2006). Among other parameters, wave exposure can determine the relative biomass of dominant functional groups in intertidal areas (McQuaid & Branch, 1984), allowing composition estimates from measures of wave intensity (Burrows *et al.*, 2008; Blamey & Branch, 2009). Higher abundance of filter-feeding invertebrates such as mussels and barnacles at exposed areas contrasts with the predominance of macroalgae on more protected environments (Blockley & Chapman, 2008; Christofoletti *et al.*, 2011). Direct effects of wave impact include mortality owing to dislodgement or damage (e.g. Dayton, 1971; Paine & Levin, 1981), while indirect effects may be related to responses to enhanced flow, such as increased larval settlement (Hunt & Scheibling, 1996) and reduced sediment deposition (Kennelly, 1989).

Interstitial spaces within biogenic habitats, such as mussel beds (O'Donnell, 2008), provide shelter from wave action due to drag and water retention, and are often colonized by diverse invertebrate assemblages. Coralline algae can also provide suitable topographic complexity for the establishment of a wide array of invertebrates. Their hard calcareous branches and potential for sediment accumulation result in mechanical protection and water retention, lowering the impact of wave splash on the associated fauna. Calcium carbonate layers over cell walls, visible as a pink coating (Joly, 1967; Johansen, 1974), provide high resistance to both herbivory and hydrodynamism (Littler & Littler, 1980). As wave exposure increases, turfs tend to be more compact, thus enclosing smaller interstitial spaces and different invertebrate assemblages (Dommasnes, 1968). The upper limit of coralline habitats usually delimit the lower shore level in tropical rocky shores (Stephenson & Stephenson, 1972) and usually host diverse invertebrate assemblages including molluscs, polychaetes and crustaceans (e.g. Bussell *et al.*, 2007).

Among crustaceans, peracarids are the most common coralline dwellers (e.g. Izquierdo & Guerra-García, 2011). They undergo direct development, with the eggs being laid into the female marsupium, where they hatch and juveniles develop. Therefore, species may settle and find stable populations regardless of immigration from distant turf habitats. Also, algal turfs may be colonized by many different peracarids, because they exhibit a variety of lifestyles, even among closely related species. Within free-living and tube-building species, peracarids can be herbivorous, detritivorous,

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carnivorous or omnivorous (for review, see Guerra-García *et al.*, 2014). Frequent predation of peracarids by nearshore fish (Nelson, 1979) may constitute an important trophic link between the benthic and pelagic environments.

Investigating the interactive effects of physical and biological factors on peracarid assemblages may help in understanding the functioning of turf habitats. In this study, we focused on gammaridean amphipods and tanaidaceans, the most abundant peracarids in our study region. We specifically investigated the effect of hydrodynamics on abundance and assemblage structure by sampling natural habitat patches exposed to different degrees of wave action. We expected that effects of wave exposure on the physical structure of coralline habitats would result in important changes in the associated peracarid assemblages.

MATERIALS AND METHODS

Study area and sampling

In this study we focused on the structure of peracarid assemblages in the intertidal zone, where wave exposure and sedimentation are likely to be particularly relevant. Four rocky shores at Ubatuba, São Paulo, Brazil were chosen to provide spatial replication of habitats of varying wave exposure, along a 20 km coastline (Figure 1). Enseada and Itaguá are relatively protected shores formed by small boulders, while Bravinha and Praia Grande are moderately exposed areas where larger boulders and platforms make the most of the rocky habitat. Exposure categories were based on the indices reported by Bueno & Flores (2010), using the method described in Palumbi (1984). Dense coralline algal patches were found at low-shore heights on all these localities and were sampled during emersion periods. On protected sites, coralline algae form homogeneous mat-like habitats, whereas patches are sparser and turf-like on exposed shores. The most abundant algal species were *Corallina officinalis* Linnaeus, *Jania rubens* (Linnaeus) J. V. Lamouroux and *Amphiroa beauvoisii* J. V. Lamouroux (Joly, 1967). Since they usually co-occur at any given patch, and form an overall common turf habitat (although of variable height and structure), we did not identify algal species in each sample. We occasionally observed sponges *Hymeniacidon heliophila* growing among coralline fronds, especially at sheltered shores, which may affect amphipod species composition.

Fieldwork was conducted from September to November 2010, thus minimizing the influence of seasonal trends. We sampled each shore by haphazardly taking three samples, separated by an approximate distance of 20 m along shorelines, during three sampling events (22 September, 22 October and 7 November). We tested for variation among sampling events and did not find any. Therefore, we pooled samples obtained at these different times and used a sample size of nine replicates. Samples were taken at 100% coralline cover areas during diurnal low-tide periods, using a 10 cm diameter corer. Turfs were frozen and later analysed under a dissecting microscope to sort out amphipods and tanaidaceans, which were counted and identified to species level. Abundance was calculated as individuals per plot. After removing the vagile fauna and trapped sediment, habitat complexity was estimated as coralline biomass (dry weight) per plot for the two last events. For that, samples were dried at 60°C for 48 h and weighed on a precision weighing scale.

Statistical analyses

We first investigated the co-occurrence of amphipods and tanaidaceans in the coralline algae through correlation

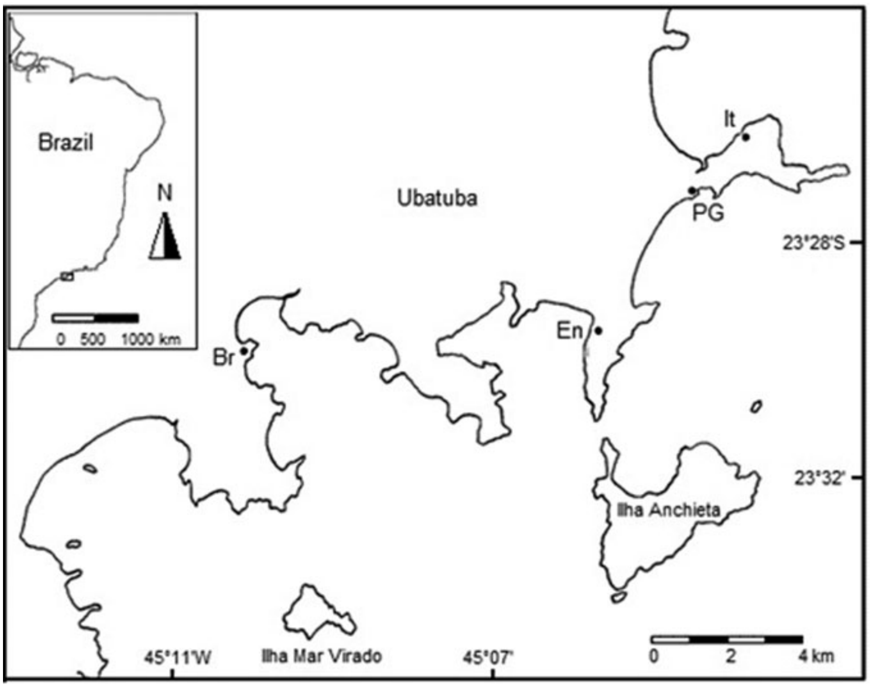

Fig. 1. Map of the study area. Rocky shores are indicated by black dots. It, Itaguá; Pg, Praia Grande; En, Enseada; Br, Bravinha.

Table 1. Lifestyle and feeding habits of peracarids occurring at Praia Grande, Bravinha, Enseada and Itaguá.

Order	Family	Species (N)	Lifestyle	Feeding
Amphipoda	Amphilochidae	*Hourstonius wakabarae* (1)	FL	C
	Amphitoidae	*Cymadusa filosa* (37)	TD	H
	Aoridae	*Aora spinicornis* (9)	TD	D
		Globosolembos smithi (2)	TD	D
	Hyalidae	*Apohyale media* (436)	FL	O
		Hyale niger (78)	FL	O
	Ischyroceridae	*Jassa slatteryi* (1)	TD	D
	Leucothoidae	*Leucothoe spinicarpa* (10)	I	C
	Lysianassidae	*Lysianassa tememino* (1)	FL	D
	Maeridae	*Elasmopus pectenicrus* (3)	FL	D
		Elasmopus brasiliensis (20)	FL	D
Tanaidacea	Leptocheliidae	*Leptochelia* aff. *dubia* (596)	TD	D
	Tanaididae	*Zeuxo coralensis* (535)	TD	D

N, number of individuals; FL, free-living; TD, tube-dwelling; C, carnivorous; H, herbivorous; O, omnivorous; D, detritivorous; I, inquiline; C, commensal. From Leite *et al.* (2000); Guerra-García *et al.* (2014).

analyses using the Statistica software (Stat Soft Inc., 2005). A positive correlation would suggest these groups require similar environmental conditions, clustering at favourable spots, while a negative correlation would indicate exclusion through competition or preference for different environmental conditions. No relation was expected if their occurrence is independent at the sampled local scale. Correlational trends were then tested between habitat complexity and peracarid abundance, to evaluate whether habitat size may be a limiting factor.

We applied a nested ANOVA design to test the effect of wave exposure on habitat complexity and abundance of both amphipods and tanaidaceans using the WinGMAV5 software (Underwood & Chapman, 2002). The nested design included the factors exposure (fixed, two levels: moderately exposed and sheltered) and shore (random, nested in exposure, two levels: Praia Grande and Bravinha; Enseada and Itaguá). Nesting shores within exposure levels allowed us to test the consistency of wave exposure effects. Amphipod and tanaidacean abundance data were transformed to $\ln(x+1)$ to achieve homoscedasticity when needed. Dominant amphipod species were analysed according to the degree of exposure through a one-way ANOVA.

The same nested design was used to examine changes in the assemblage structure of amphipods. In this case, PERMANOVA (Clarke & Gorley, 2006) analyses were run, using Bray–Curtis distances after 999 permutations. Singletons were removed. The SIMPER test was used to detect the main species underlying the formation of clusters. Only two tanaidacean species were found, precluding any statistical procedures. However, patterns of occurrence of these two species were strikingly different and simple numerical trends sufficed.

RESULTS

Habitat complexity was similar between moderately exposed and sheltered shores ($F = 0.01$; df = 1; $P = 0.936$). Also, we observed no variation between shores of the same exposure level ($F = 0.55$; df = 2; $P = 0.587$), suggesting a homogeneous turf at the local scale. No correlation was found between amphipod and tanaidacean abundances ($r = -0.0690$; $P = 0.690$), indicating their independent occurrence on coralline algae. Peracarid abundance, as a whole, did not show any correlation with habitat complexity ($r = 0.1074$; $P = 0.617$). Separately, we found a positive correlation between amphipod abundance and coralline complexity ($r = 0.4720$; $P = 0.020$) but no correlation for tanaidaceans ($r = 0.1119$; $P = 0.603$).

We found 589 amphipods distributed on 11 species. Details on life, feeding habits and counts for all species are shown in Table 1. Higher overall amphipod abundance was observed on moderately exposed sites (Table 2, Figure 2A). We did not observe differences between shores, within each category of exposure, further suggesting that amphipod abundance is consistently higher at more exposed areas, as observed for the most abundant species *Apohyale media, Hyale niger* and *Cymadusa filosa* (Figure 3). *Apohyale media* dominated both exposed and sheltered shores, while *H. niger* and *C. filosa* occurred at lower numbers. However, differences between degrees of exposure were not significant for all three species (*A. media:* $F = 2.21$; df = 1; $P = 0.147$; *H. niger:* $F = 0.15$;

Table 2. ANOVA results for peracarid abundance at moderately exposed (Praia Grande and Bravinha) and protected sites (Enseada and Itaguá).

Source	df	*Amphipods*			*Tanaidaceans*		
		MS	F	P	MS	F	P
Exposure	1	5.67	57.33	**0.017**	0.25	0.00	0.993
Shore (Ex)	2	0.10	0.13	0.883	2247.25	1.47	0.245
Residuals	32	0.79			1529.31		
		$\ln(x+1)$; $C = 0.3442$ ns			No transformation; $C = 0.4063$ ns		

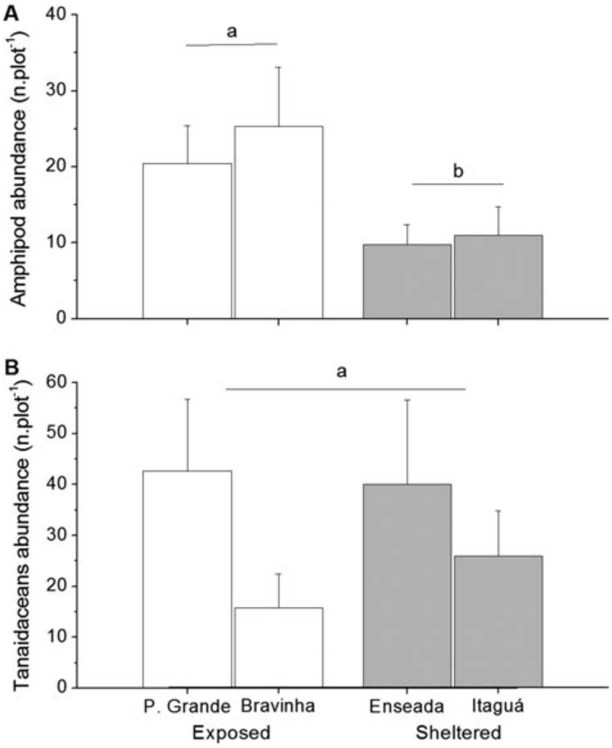

Fig. 2. Abundances at moderately exposed (Praia Grande and Bravinha) and protected sites (Enseada and Itaguá). A: amphipods. B: tanaidaceans. Bars indicate standard errors. Different letters indicate $P < 0.05$. For tanaidaceans, all individuals at exposed shores were *Zeuxo coralensis*, and all individuals at sheltered shores were *Leptochelia* aff. *dubia*, except for two *Leptochelia* individuals found at Praia Grande.

df = 1; $P = 0.703$; *C. filosa:* $F = 4.03$; df = 1; $P = 0.053$). We did not find an effect of wave exposure on the structure of amphipod species assemblages, but we did find differences between shores (Table 3). Pair-wise *post-hoc* tests showed that between-shore contrasts were significant for more exposed assemblages at Praia Grande and Bravinha ($t = 1.63$, $P = 0.048$), but not for Enseada and Itaguá ($t = 1.0492$, $P = 0.365$). Main contributors to these results were identified through SIMPER analysis and included *A. media* (60.5%), *C. filosa* (20.8%) and *H. niger* (13.1%).

Tanaidaceans occurred at higher numbers, summing up 1131 animals belonging to two species, *Leptochelia* aff. *dubia* (after Bamber, 2010) and *Zeuxo coralensis* (Table 1). Segregation of these two species according to levels of wave exposure was virtually absolute. *Leptochelia* was restricted to sheltered areas (Enseada and Itaguá), except for two animals recorded at Praia Grande, while *Zeuxo* was only found at exposed shores (Figure 2B). These two species apparently fulfil the tanaidacean niche, since whole tanaidacean abundance did not vary according to exposure levels, nor between shores within the same level (Table 2).

Table 3. PERMANOVA results for amphipod species composition at moderately exposed (Praia Grande and Bravinha) and protected sites (Enseada and Itaguá).

Source	df	MS	Pseudo-F	P(perm)
Exposure	1	5610.7	1.24	0.319
Shore (Ex)	2	4542.2	1.84	**0.048**
Residuals	32	2473.6		

DISCUSSION

The occurrence of amphipods and tanaidaceans at a very local scale, within turf samples of less than 80 cm^2, was unrelated, suggesting no substantial interactions between these two major groups, neither positive or negative, nor any meaningful similarity (or divergence) of habitat preferences. Despite no apparent differences of habitat complexity between the tested exposure levels, and our rather restricted sampling effort (two shores in each exposure level), the peracarid community in our study region is clearly affected by wave action, suggesting that other factors than habitat structure may affect these assemblages. Because we found mostly changes in abundance for amphipods and species composition for tanaidaceans, effects of wave exposure are apparently complex and group-specific.

Amphipods were far less abundant than tanaidaceans but much more diverse, as observed for Masunari (1982) for turfs dominated by the coralline alga *Amphiroa beauvoisii.* We found 11 amphipod species with different lifestyles and feeding modes, suggesting they may exploit a wide array of resources within the turf habitat. Habitat complexity, which did not differ between turfs exposed to different wave action, but did vary considerably within any given shore (52%), positively affected overall amphipod abundance. Habitat features can influence hydrodynamics at small scales (Madsen *et al.*, 2001) and more physically complex patches may supply several different microhabitats. It would allow resource partitioning, as observed for *Corallina officinalis*, where six species of copepods are specialized on the use of different resources, probably mitigating interspecific competition (Hicks, 1977).

Higher overall abundance of amphipods on more exposed shores could be related to more frequent water renewal. This could enhance oxygen saturation, a factor correlated to higher abundance of several Eastern Atlantic caprellid and gammarid species (Izquierdo & Guerra-García, 2011), and supply of suspended food particles (Fenwick, 1976), which could be used by the prevailing omnivore species (*Apohyale media*). Also, amphipods are highly mobile species which may rapidly return to their algal hosts after being dislodged (Fenwick, 1976; Norderhaug *et al.*, 2012), thus possibly overcompeting more sedentary invertebrates. Wave exposure would likely benefit in a similar manner all amphipod species since it did not affect assemblage composition, in contrast to the results obtained by Lancellotti & Trucco (1993) for Chilean rocky shores. It should be noted, however, that a greater gradient of wave exposure was sampled by these latter authors. Shores within similar conditions of exposure to wave action may however host distinct amphipod assemblages, as noted here for the communities sampled at Bravinha and Praia Grande. Therefore, any processes operating at spatial scales of a few km may drive substantial environmental change and alter the composition of the turf-dwelling amphipod fauna. Among many possible factors, the identity of accompanying epiphytic algae (e.g. Schmidt & Scheibling, 2006; Jacobucci & Leite, 2014), and patterns of sedimentation (Whorff *et al.*, 1995; Boström & Bonsdorff, 2000) may play important roles. The effects of these and other possible

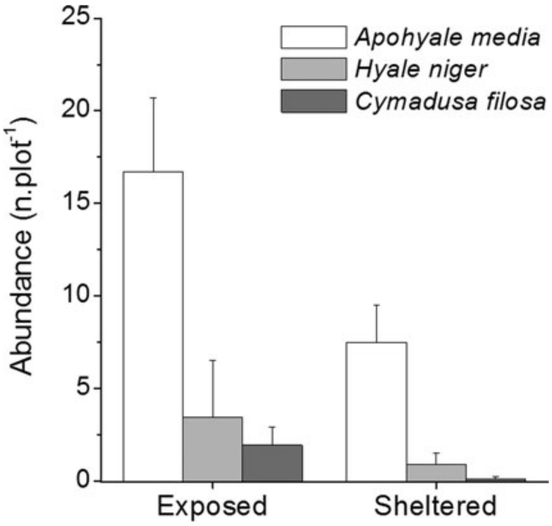

Fig. 3. Abundance of dominant species *Apohyale media, Hyale niger* and *Cymadusa filosa* at exposed and sheltered rocky shores. Bars indicate standard errors.

factors cannot be advanced here and should be addressed in future experimental work.

We found both free-living and tube-dwelling amphipods. Among the free-living species, hyalids prevailed, especially *Apohyale media*. Hyalids are omnivorous and resistant to desiccation, thus capable of colonizing intertidal habitats spanning a considerable vertical height on rocky shores (Wieser, 1952; Tararam *et al.*, 1986; Chavanich & Wilson, 2000). Tube-building species are usually more patchily distributed than free-living animals (Tanaka & Leite, 2003). They are more sedentary, and juveniles build their tubes near their parents, resulting in aggregated patterns, as observed for *Cymadusa filosa* (Appadoo & Myers, 2003). This species was the most abundant tube-dwelling amphipod in this study. It occurred mostly at the exposed shore Bravinha, with no animals found at Praia Grande. Distribution of *C. filosa* was clearly patchy, since we found samples containing 10 and 14 animals, which together make up 65% of the whole sample. We also found *Leucothoe spinicarpa*, a species frequently associated with sponges and ascidians (Thiel, 2000). Although at low numbers (N = 10), its presence was probably related to the co-occurring sponge *Hymeniacidon heliophila*, a structuring organism associated with coralline algae mainly at sheltered shores.

Tanaidaceans were far more abundant than amphipods, but much less diverse (only two species recorded). Overall densities were similar in exposed and sheltered shores, but species were segregated in these two environmental conditions, with turf habitat being colonized by *Leptochelia* aff. *dubia* at sheltered shores and *Zeuxo coralensis* at moderately exposed sites. Spatial segregation of intertidal tanaidaceans according to water motion was also reported by Kitsos & Koukouras (2003) in the Greek coast. Although the authors measured water flux, not wave exposure, they observed *Leptochelia savignyi* and *Pseudoleptochelia anomala* at lower hydrodynamism, and two species of *Tanais*, belonging to the same family of *Zeuxo* (Tanaididae), at sites where higher hydrodynamism prevailed. However, substrates varied from coralline algal turfs to mussel beds, as sites varied from low to high hydrodynamic intensity (Kitsos & Koukouras, 2003), making it hard to separate the effects of hydrodynamism and habitat type. Unlike amphipods, the abundance of tanaidaceans was not related to habitat complexity. The distribution of tanaidaceans may be more directly linked to sediment trapping in coralline algal turfs, since they use grains to build their housing tubes and feeding. Krasnow & Taghon (1997) observed the behaviour of *L.* aff. *dubia* and noted that this species manipulates sediment particles using their mouth parts and pereopods. Individuals may thus obtain food from biofilms adhered to sand grains as they build up their tubes. Our ongoing research is investigating the role of trapped sediment in the distribution of tanaidaceans, and preliminary data suggest that coralline algal turfs in sheltered areas contain higher organic contents due to sediment retention. It is thus possible that the functional morphology of mouth and thoracic appendages will determine the habitat type and niche breadth in these abundant peracarids.

Wave exposure is an important environmental variable affecting the distribution of animals and plants on rocky shorelines. Regarding wave exposure and peracarid lifestyles, our results challenged the general notion that tube-building provides protection against dislodgement (Dommasnes, 1968; Fenwick, 1976). In spite of a diverse amphipod assemblage, constituted of both free-living and tube-dwelling species, we found no differences in composition structure suggesting a higher occurrence of the latter group in more exposed shores. Accordingly, both tanaidacean species build tubes using mucus and sand grains, and, if this was the single most important trait determining distribution patterns, we would expect *L.* aff. *dubia* and *Z. coralensis* to be equally distributed in sheltered and exposed habitats. Clearly, further observational and experimental studies should advance alternative hypotheses underlying distribution patterns of peracarids in intertidal algal habitats.

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