



## Vertical differences in species turnover and diversity of amphipod assemblages associated with coralline mats



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### ABSTRACT

Environmental gradients are common in rocky shore habitats and may determine species spatial distributions at different scales. In this study, we tested whether environmental filtering affects amphipod assemblages inhabiting coralline algal mats at different vertical heights in southeastern Brazil. Samples obtained from the upper and lower zones of the infralittoral fringe were used to estimate mat descriptors (algal mass, sediment retention, organic matter contents, grain size and sediment sorting) and describe amphipod assemblages (abundance, species richness and diversity indices). Coralline algal mats and amphipod assemblages were similar between intertidal zones in several aspects. However, a more variable retention of sediment (positively related to algal mass), together with the accumulation of larger grains lower on the shore, likely provide higher habitat heterogeneity that hosts generally more diverse (both  $\alpha$ - and  $\beta$ -diversity, as well as higher species turnover) amphipod assemblages in the lower intertidal zone. Poorer assemblages in the upper intertidal zone are dominated by omnivores, while carnivorous species are more often found in richer assemblages in the lower intertidal zone, as predicted by traditional niche theory.

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### 1. Introduction

Intertidal organisms are commonly distributed in horizontal bands along rocky shores, making clear and comparable patterns across coastlines around the world (Stephenson and Stephenson, 1972; Chappuis et al., 2014). Current models suggest that physical stress and biological interactions, together with recruitment patterns and bottom-up drivers, have different relative effects along gradients of environmental stress in the intertidal (Benedetti-Cecchi and Trussell, 2014). For example, both classical and recent studies indicate the importance of desiccation and thermal stress on the determination of upper distribution limits of intertidal organisms (Connell, 1961; Lathlean et al., 2012), which can be modulated by physical factors such as wave and tidal action, substrate rugosity and shore topography (Gedan et al., 2011; Lathlean et al., 2014; Van Alstyne and Olson, 2014).

Ecosystem engineers can have strong habitat and ecological

effects by ameliorating the environmental conditions for a wide array of other organisms (Jones et al., 1997; Bertness et al., 1999). Seaweed canopies, for example, can provide thermal refuges and shelter from predators to their associated fauna (Bertness et al., 1999; Guerra-García et al., 2011; Wright et al., 2014). While clearly facilitating the occurrence of distinct invertebrate assemblages, ecosystem engineers, such as seaweed canopies and algal turfs, may not totally buffer the harsh conditions found in the rocky intertidal. Thermal and desiccation stress at these additional spatial niches within biogenic substrates still increase from lower to higher shore levels (Lilley and Schiel, 2006; Van Alstyne and Olson, 2014). Therefore, environmental limitation could constrain the range of trait values among all organisms using particular habitats, with decreasing biological diversity found in the upper intertidal zone (Carmona et al., 2012; Sasaki et al., 2014). However, biological interactions within the accompanying species assemblages and exogenous stochastic disturbance driven by large herbivores (e.g. turtles, parrotfish), or sedimentation, may be the most relevant factors affecting the community structure of assemblages associated with habitat-forming invertebrates or macroalgae (McQuaid and Dower, 1990; Prathep et al., 2003; Davidson, 2005). Episodic

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disturbance may enhance species diversity by allowing the occurrence of weaker competitors that would otherwise be eliminated by stronger ones in more stable conditions (Sousa, 1979; Paine and Levin, 1981).

Theoretical predictions on decreased diversity along stress gradients are partially supported by studies on whole rocky shore assemblages (e.g. Ingólfsson, 2005; Scrosati et al., 2011), but, as far as we are aware, trends for narrower taxonomic groups inhabiting specific biogenic habitats are still to be examined. Briefly, environmental filtering provided by harsher conditions in upper intertidal zones should limit species richness, since only a subgroup of the species pool could tolerate these conditions, resulting in lower  $\alpha$ - and  $\beta$ -diversity when compared to communities in a more benign environment (e.g. Adamidis et al., 2014). According to Baselga (2010), differences in  $\beta$ -diversity could result both from differences in nestedness (i.e., when sites with few species richness are subsets of those with higher species richness) or spatial turnover (when species are replaced by other species due to environmental sorting or spatial or temporal constraints).

We tested these hypotheses using the amphipod fauna associated with articulated coralline algae that form mat-like habitats in a sheltered rocky shore in southeastern Brazil. These mats can be relatively extensive, forming patches of several meters along the shoreline and up a shore height of a half a meter. Coralline algae are superior competitors for space and light, resistant to physical stress and have low surface-volume ratio. Also, their calcified thallus with flexible genicula confer resistance to herbivory and hydrodynamism (Littler and Littler, 1980; Stewart, 1989). At rocky shores along the Southeastern Brazilian coast, coralline algae usually trap substantial quantities of sediment (personal observations), which are known to affect invertebrate assemblages (Littler et al., 1983; Huff and Jarett, 2007). We predicted that  $\alpha$ - and  $\beta$ -diversity should be lower in upper intertidal zones due to environmental filtering, and that coralline mat physical attributes (i.e. algal mass, sediment retention, sediment sorting and organic matter content) would influence patterns of amphipod assemblage structure, possibly explaining much of the small-scale variation which is usually observed in rocky shore habitats (Underwood and Chapman, 1998).

## 2. Materials and methods

### 2.1. Study area and sampling

Fieldwork was conducted during the spring of 2011 at Enseada (23°30'00"S 45°05'02"W), a sheltered rocky shore in Ubatuba, São Paulo state, Brazil, at two distinct occasions within the same season. As in several other locations in the region, dense coralline mats occupied the infralittoral fringe and the most abundant algal species were *Corallina officinalis* Linnaeus, *Jania rubens* (Linnaeus) J. V. Lamouroux and *Amphiroa beauvoisii* J. V. Lamouroux (Joly, 1965). These three species composed our all samples but no attempts were made to separate algal species within samples and calculate algal species compositions. Results therefore refer to the morpho-functional group of articulated corallines.

Near-vertical mats were sampled, which extended over a vertical range of 45 cm, on average, and thus encompassed a substantial part of the whole intertidal range at our study region (c.a. 1.1 m during spring tides). Mats were sampled within a shoreline of 50 m in both periods. Within each of those mats and at each sampling period, three samples were taken at random from both the upper half (upper zone) and the lower half (lower zone) of mats. Samples consisted of mat discs (10 cm diameter) scrapped off the rock surface. Sampling independence was certainly met, since fauna associated with macroalgae generally present high

turnover rates at small time scales (Howard, 1985; Tanaka and Leite, 2004). Samples were first processed by separating algae and fauna. The remaining material was separated for sediment analysis. Algae were dried at 60 °C for 48 h and weighed. Amphipods were counted and identified under a stereomicroscope. Sediment analyses consisted in drying the material at 60 °C for 48 h and adding 10% hydrochloric acid to remove all calcium carbonate. In order to remove the organic contents, samples were ashed in a furnace oven at 500 °C for 45 min, and then weighed. Grain size distribution was obtained by sieving the remaining material through a series of 12 sieves with the aid of a shaker, following the Wentworth scale, and weighing each fraction separately.

### 2.2. Statistical analyses

Because of low amphipod abundance in mat samples (with total absence in 9 samples, i.e. 25%), and also because we were not interested in specifically testing differences between sampling dates (but rather include temporal variability in the analysis), both samples within mats and sampled dates were pooled, for a total of six replicates per tidal height. Amphipod assemblage structure was described using abundance, species richness estimated by the Chao 1 estimator and diversity using the Shannon-Weaver and the Gini-Simpson indices (Magurran, 2013). The Chao 1 estimator was used to estimate  $\alpha$ -diversity accounting for differences in abundance among replicates. This method provides minimum asymptotic estimates of species richness for each sample (Chao, 1984). Total species richness was estimated in each intertidal zone using both the Chao 1 and the second-order jackknife estimators, to evaluate if adequate sampling was carried out (Canning-Clode et al., 2008). Coralline algal mat descriptors included algal mass, sediment mass, organic matter mass, mean grain size (mm) and sediment sorting (standard deviation of mean grain size). Grain size distribution was analyzed using the SEDMAR software to obtain mean grain size and sorting (Folk and Ward, 1957).

Univariate comparisons between zones were carried out using a 1-way fixed factor ANOVA ( $n = 6$ ). To evaluate possible relationships between algal mass and biotic and abiotic variables, ordinary least-squares linear regressions for each zone were adjusted. The natural log (ln) transformation was used when homoscedasticity was not supported.

Amphipod species composition was analyzed using an equivalent one-way PERMANOVA model (Anderson, 2001). Analyses were carried out on similarity matrices calculated with both the Sorensen and the Bray-Curtis index to evaluate the effects of relative abundance on amphipod assemblage composition (Clarke, 1993). Differences were tested with unrestricted permutation of raw data, with 999 permutations (Anderson, 2001), and assemblages were ordinated with non-metric multidimensional scaling (n-MDS). The SIMPER test was used to determine which species contributed most to the differences between zones (Clarke, 1993). To determine if multivariate patterns were associated with coralline mat characteristics, each axis of the MDS was regressed against algal mass.  $\beta$ -diversity was estimated using both the Sorensen and Jaccard indices, and partitioned  $\beta$ -diversity into nestedness and turnover components following Baselga (2010). Diversity indices were calculated with the 'vegan' package (Oksanen et al., 2013) in R (R Core Team, 2014), whereas partitioning of  $\beta$ -diversity was carried out with the 'betapart' package (Baselga and Orme, 2012). Multivariate analysis were carried out using PRIMER/PERMANOVA v. 6.0 (Anderson et al., 2008), and univariate analysis were carried out with Systat 13.0.

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