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Spatial and temporal variation in the predation risk for hermit crabs in a subtropical bay

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ABSTRACT

Comparing the spatial and temporal dynamics of predation in turbid coastal waters can be notoriously difficult. We used a tethering approach to directly assess variation in predation risk for the intertidal hermit crab *Pagurus criniticornis* and the gastropod *Cerithium atratum* in a subtropical bay. Predation outcomes were used to test the effects of; (1) microhabitat (i.e., intertidal mud vs. intertidal fringe), (2) season (summer vs. winter), and (3) the type of domicile shell occupied (*C. atratum* vs. *Tegula viridula*). Predation varied across microhabitat for both species, with unambiguous cases more prevalent at the intertidal fringe than the mud habitat (20.6% and 11.8% greater for the hermit crab and gastropod, respectively). This pattern related to the abundance of the portunid crab predator *Callinectes danae* (~2.2 times greater in the fringe vs. mud). There was similar variation among seasons for *P. criniticornis*, with cases of predation 51.3% more prevalent in summer than winter, again matching the abundance of *C. danae* (greater in summer than winter). Closer examination of the type of shell damage suggests differences in the way that predators might access prey across spatial and temporal scales. The high prevalence of damaged shell apertures (indicative of peeling) suggests possible targeting of this species by smaller individuals or females. Although there was no seasonal difference in the size of predators, the proportion of males was greater during summer and this may constitute a driver of variable predation pressure. Lastly, the risk of predation was also related to domicile shell morphology, with crabs inhabiting *C. atratum* shells 27.3% more likely to be predated upon than those inhabiting *T. viridula* shells. Combining the outcomes of our experiments, we suggest that changes to intertidal habitat configuration (e.g., the proliferation of hard substrates through, erosion or harbor and break wall construction) as well as factors that alter the supply of appropriate domicile shells (e.g., effects of acidification on calcifying organisms) could alter predation risk for hermit crabs and other soft bottom species.

1. Introduction

Predation is a major selective force that underpins the morphological and behavioral characteristics of organisms over ecological (i.e., an individual animals lifespan) and evolutionary timescales (Lima and Dill, 1990). Hermit crabs are especially vulnerable to predation, because in the absence of a domicile shell, they have little means of protecting their soft abdominal exoskeleton (Arnott and Elwood, 2007). Predation risk thus oversees many of the complex behavioral responses exhibited by hermit crabs in their natural environments (e.g., feeding, fighting and reproduction; Gherardi, 2006; Hazlett and Rittschof, 2000, 2005, shell selection; Turra and Leite, 2004, and shell abandoning; Turra and Gorman, 2014). For many intertidal organisms, predation-based decisions are reflected in the apparent trade-offs between acquiring valuable new resources and holding existing ones (e.g., greater motivation to hold a shell in areas of high predation; Turra and Gorman, 2014). For hermit crabs, venturing into riskier habitats in order to investigate olfactory cues that may infer new shell resources (e.g., gastropod predation events; Gorman et al., 2014) may represent an appropriate trade-off that balances risk with some expected gain in fitness (Parker and Stuart, 1976; Sih et al., 2004).

While predation is a powerful driver of hermit crab behavior, there have been few empirical in-field assessments of the way in which it varies across time and space (but see Kuhlmann, 1992). This task is made difficult by the fact that many species inhabit muddy coastal environments in which direct observations are problematic and exhibit behavioral adaptations to predation and environmental perturbation (e.g., burial; Barnes, 2002; Rebach, 1974 and shell abandoning; Gorman et al., 2014; Turra and Denadai, 2003) that can further confound clear trends. Much work remains to quantify the precise nature of risk for hermit crabs and how individuals and species may respond to environmental (e.g., habitat alteration) and ecological perturbations (e.g., changes in predator abundance). One effective, though infrequently employed solution to directly assess predation risk for benthic animals in their natural environments, is tethering (for background see, Aronson and Heck, 1995). This approach is amenable for relatively slow moving intertidal invertebrates (e.g., hermit crabs) that do not range widely and are unlikely to dislodge a tether. Tethering hermit crabs offers a means of testing hypotheses related to predation risk in

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the context of spatial and temporal variability (see, Barbeau and Scheibling, 1994; Kuhlmann, 1992). Using these animals as a general model to examine variation in predation risk within intertidal environments is likely to foster a broader understanding of similar patterns for multiple marine and terrestrial taxa.

The aim of this study was to compare predation risk for hermit crabs and gastropods inhabiting intertidal environments over relevant spatial (i.e., microhabitats) and temporal scales (i.e., seasonality). A broad literature review returned no comparable studies contrasting the risk of predation for these animals in mud habitats (but compare a study done on vegetated seafloors; Rossi and Parisi, 1973). This is surprising given that predation underpins many of the processes governing the behavior of individuals and the functioning of intertidal ecosystems (Menge, 2000; Ruiz et al., 1993). To address this deficiency, we utilized a common and responsive hermit crab *Pagurus criniticornis* and its preferred shell donor, the gastropod *Cerithium atratum*, to test the null hypotheses; (1) that there would be no difference in the incidence of predation across microhabitats (mud vs. intertidal fringe); and (2) for the hermit crab only, across consecutive seasons (summer vs. winter). In order to investigate the relationship between predation risk and predator abundance, we compared the patterns above with the abundance of the key portunid predator *Callinectes danae*. Finally, given that predation risk for hermit crabs has been associated with domicile shell morphology (Turra et al., 2005), we tested a separate hypothesis; (3) that there would be no difference in the incidence of predation on *P. criniticornis* inhabiting different gastropod shell types (*C. atratum* vs. *T. viridula*).

2. Material and methods

2.1. Subjects and study area

This study involved the common hermit crab *P. criniticornis* (Dana 1852), the gastropod *C. atratum* (Mörch 1876) and the portunid crab *C. danae* (Smith 1869). The hermit crab is common throughout the intertidal and shallow subtidal waters of the western Atlantic (Forest and Saint Laurent, 1967; Turra et al., 2000) where it preferentially uses empty shells of *C. atratum* as a domicile shell. The swimming crab *C. danae* is a voracious predator extending over the same habitat range (Pinheiro et al., 1997) and has been shown to prey on both the crab and gastropod species examined (Branco and Verani, 1997; Turra et al., 2005). Hermit crabs and gastropods of uniform shell size were collected from the intertidal zone of Araçá Bay, São Sebastião (Fig. 1) two days prior to experiments. Collected individuals were maintained in aerated aquaria at the Centro de Biologia Marinha of the Universidade de São Paulo where they were provided with a large number of high quality shells (i.e., having no perforations or aperture/apex breaks) to standardize shell adequacy (sensu Vance, 1972). Prior to deployment in the field, all test subjects had a 50 cm long stainless steel trace attached to their shells using 'Super Bonder' cyanoacrylate instantaneous glue (Ellsworth Adhesives, Germantown, U.S.A.).

Predation risk for both hermit crabs and gastropods was assessed using tethers that allowed subjects to move as they would naturally, albeit within a limited range. The approach is similar to mark and recapture techniques (see, Lebreton et al., 1992) but is especially suited to situations where marking or recapture is hampered by the behavior (e.g., burial) and physiology (e.g., molting) of animals or by certain environmental characteristics of the study area (e.g., muddy water), salient features of *P. criniticornis* and Araçá Bay. Similar approaches have been used successfully in the past to assess the relative rate of predation by crabs in the field (Borjesson and Szelistowski, 1989; Kuhlmann, 1992). Tethering results were allocated into the following possible outcomes; (a) animals present, (b) animals absent with no evidence of predation, and (c) animals absent with unambiguous evidence of predation (i.e., broken and damaged shells). Since *P. criniticornis* readily abandon shells in response to a range of environmental cues (e.g., high

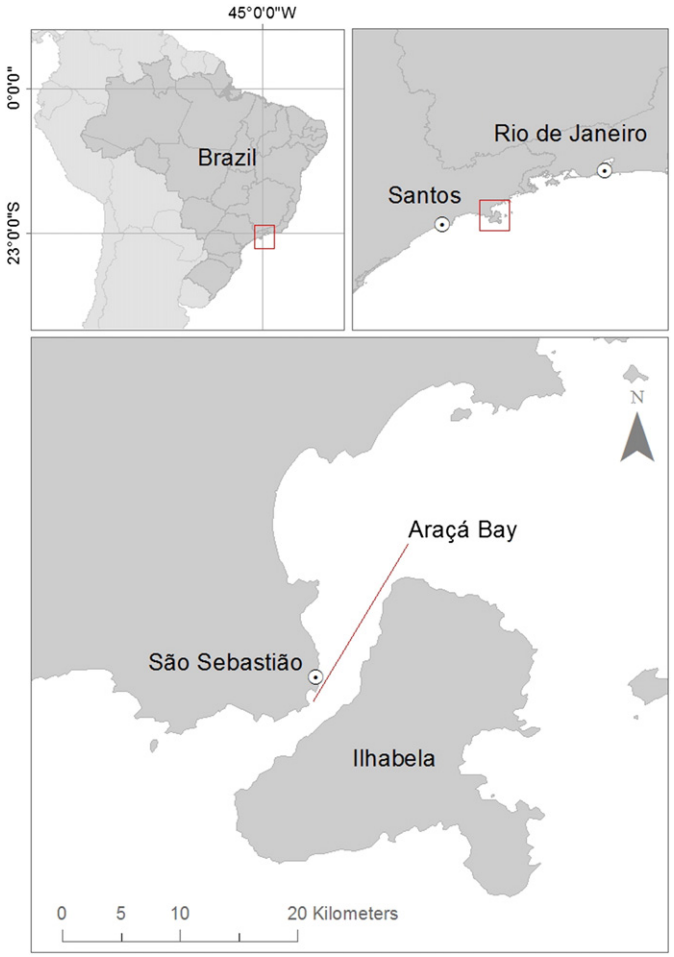

Fig. 1. Map showing the location of Araçá Bay, situated on the Atlantic coastline of São Paulo state, South-eastern Brazil.

temperatures, burial and entrapment; Gorman et al., 2014; Turra and Gorman, 2014), the absence of an individual does not necessarily infer a predation event. Likewise, we acknowledge that predation may have occurred with no perceivable damage to the shell, e.g., possible with small *C. danae* that are able to extract prey without causing shell damage (Turra et al., 2005). As a result, we recorded incidences of predation only where there was direct physical damage to the shell, and in this way our results provide a more conservative measure of predation. In an effort to better understand the nature of predation events, we also recorded the allocation of shell damage to the aperture and apex of shells in which predation was deemed to have occurred.

2.2. Spatial and temporal variation in predation risk

Tethering experiments were designed to assess variation in predation risk over both spatial (i.e., microhabitat) and temporal (i.e., seasonal) scales. The spatial assessment was done during summer (February) to coincide with anecdotal reports of high predation due to large abundances of *C. danae* (Chacur and Negreiros-Fransozo, 2001) and involved replicate trials within two predominant microhabitats of Araçá Bay; (1) intertidal mud, and (2) the intertidal fringe. Mud habitats dominate but there is a clear transition in substrate type with proximity to the intertidal fringe, where the presence of boulders, pebbles and mangrove pneumatophores increase the harness of the substratum. The design incorporated five replicate blocks comprising 4 individuals ($n = 20$ crabs and gastropods) within each of the two microhabitat types. The seasonal effect was not orthogonal to microhabitat but was based on comparisons between summer (above) and the following