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Predation on competing mussel species: Patterns of prey consumption and its potential role in species coexistence

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ABSTRACT

Theoretical and empirical studies have demonstrated that predators can modulate coexistence between prey species and can modify broad patterns of community structure. Although the keystone predator effect (i.e., local coexistence and species diversity mediated by predator consumption) is commonly reported, negative effects of predators on species coexistence are also common. The balance depends critically on the asymmetry of competition, predator preferences for different prey, and the effective mortality rates exerted by predator populations on prey per capita growth rates. Here we studied the role of predation on two competing mussels, the dominant competitor *Perumytilus purpuratus* that dominates in abundance at most shores, and the subordinate *Semimytilus algosus*, which is common, but persistently abundant only at a smaller set of shores. We examined the potential for keystone effects by quantifying and evaluating the patterns of mussel consumption rates of sea star (*Heliaster helianthus*) and crab (*Acanthocyclus gayi*) predators in laboratory experiments, and under natural field conditions. Field sites with contrasting mussel abundance and recruitment (i.e., different local prey population growth rates) were chosen. Laboratory experiments showed that crabs would first consume *Semimytilus* over *Perumytilus* in mixed mussel clumps, while the larger sea star predators made no distinction between mussel species. Regardless of the order in which mussel species were first ingested, consumption rates of the two mussel species through the experiment were not different for either predator species. A similar temporal pattern was partly observable in the field through specific differences in the order of mussel consumption; however, experimental mussels of both species where consumed after the first two months of exposure to predators at both sites. Thus, in this system predation could not foster coexistence between mussel species and it may instead favor the occurrence of local extinction of the subordinate competitor, especially at sites where the smaller and more selective crab predators are relatively more abundant and recruitment of the subordinate species is low. Existing patterns of locally abundant *Semimytilus* beds are probably related to high site-specific recruitment rates of this species and should be further explored.

1. Introduction

The role of predators in modifying broad patterns of community structure has been the focus of many theoretical, observational and experimental studies. These studies show that one of the manners in which predators alter local communities is through modifying the outcome of competitive interactions among prey species and, therefore, the possibilities for species coexistence or co-occurrence within defined habitats (Slobodkin, 1961; Van Valen, 1974; Abrams, 1977; Kotler and Holt, 1989; Chesson and Huntley, 1997; Chase et al., 2002; Chesson and Kuang, 2008; Kuang and Chesson, 2008; Rius et al., 2017). Whether predators favor, decrease, or outright impede the possibility of local coexistence among prey depends on fundamental components of the predator-prey interaction (e.g., attributes of the limiting resource, prey behavioral responses to predators, predator foraging strategies, prey preferences, etc.), as well as characteristics of the physical environment, such as overall productivity or habitat heterogeneity (Chase et al., 2002; Peckarsky et al., 2008; Guariento et al., 2014; Menge et al., 2016). Probably the most commonly reported effect of predators on competing prey species in natural communities, especially in marine benthic habitats (Menge, 1995), but also in terrestrial and aquatic habitats (Dungan, 1987; Brown and Heske, 1990; Fauth and Resetarits Jr., 1991), is the one in which predators facilitate local coexistence through preventing competitive exclusion of weaker competitors by a dominant

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competitor for the limiting resource, which in marine habitats usually is space (Menge et al., 1994). This "keystone effect" (Paine, 1966, 1969) requires the existence of deterministic competitive hierarchies. Predator preference and effective consumption rates on particular prey species (i.e., the predator effect on prey per capita population growth rates) are critical components that largely determine whether or not predation favors species coexistence. If predators prefer or, in some way, impact more negatively the per capita growth rate of the competitively dominant species, they can promote the maintenance of the subordinate species, even if these are also consumed, which is usually the case in marine habitats where generalist predators are common (Paine, 1966; Menge et al., 1994; Castilla and Duran, 1985; Paine et al., 1985; Menge et al., 1994; Navarrete and Menge, 1996; Robles et al., 1995). In contrast, if predators have a stronger effect on the subordinate competitor, predation can increase the rate of exclusion (Lubchenco, 1978; Menge and Lubchenco, 1981) and eventually lead to the local extinction of the inferior competitor; this event could be particularly possible if predation is intense and renovation rates (i.e., recruitment) of the inferior competitor are low.

Because of the difficulties encountered when trying to perform high frequency observations in the field, predator prey-preference experiments are commonly conducted under laboratory conditions, where experimental arenas attempt to reproduce predator-prey encounters. Logistic constraints approximating natural conditions can limit the insight gained from these laboratory trials and restrict conclusions to the selections made by predators over small spatial scales, when the different prey are in close proximity. Moreover, the different body sizes, movement rates and feeding modes employed by different predators interact with the size of the experimental arenas and make it difficult to compare across predator species. Thus, while predator preferences and predation rates estimated solely from laboratory studies can provide valuable insight into the role of predation on competing prey species, they may lead to misleading estimates of the intensity of predator preference, the strength of mortality rates exerted on different prey, and ultimately, the consequences of predation for the coexistence of species that compete asymmetrically. Field manipulations, on the other hand, may better reproduce natural encounters between predators and prey and provide more realistic estimates of predation rates. However, logistical constraints, such as the frequency of observations and the number of treatments and/or experimental units, can lead to the use of simple experimental designs, which might limit our ability to determine the specific identity of the predator(s) responsible for observed prey mortality, except in enclosures (e.g., Navarrete and Castilla, 2003) or through direct observations when environmental and habitat conditions permit (e.g., Robles, 1987; Novak and Wootton, 2008). In this study, we use a combination of laboratory and field experiments to estimate predator preferences and predation rates on two competing mussel species and assess the potential role of predation in mediating coexistence.

In rocky intertidal communities along the shore of central Chile (between 29°S and 35°S), the mid intertidal zone at most sites is dominated by beds of the mussel *Perumytilus purpuratus*, which at sites where recruitment rates are high can reach high densities and even expand this dominance to the low intertidal zone, overgrowing other sessile species such as chthamalid and balanid barnacles (Castilla and Duran, 1985; Paine et al., 1985; Alvarado and Castilla, 1996; Navarrete et al., 2005). Also present, but less abundant, the mussel *Semimytilus algosus* is found at most intertidal sites and in some subtidal habitats (Fernández et al., 2000; Urriago et al., 2011). Although individual *Semimytilus* are frequently found interspersed in beds of *Perumytilus*, they do not commonly form multispecific patches, or grow to form dense beds because they usually are outcompeted by *Perumytilus*. Indeed, experimental manipulations at a site in central Chile show that *Semimytilus* survives well and grows at similar or even higher rates than *Perumytilus* (Navarrete and Venegas, *unpublished*), and competition experiments conducted at multiple sites, in absence of predators, demonstrated that interspecific competition for space is highly asymmetrical, with *Perumytilus* dominating and excluding *Semimytilus* at all sites (Caro, 2009). Yet, at some sites, *Semimytilus* can also form monospecific beds in the mid and low intertidal zones that can persist for > 15 years (personal observations), despite the presence of the dominant competitor. One such site is Guanaqueros, selected for our field experimental manipulations reported here.

Both *Semimytilus* and *Perumytilus* are consumed by a suite of common predators, such as the sea star *Heliaster helianthus*, the commercially exploited muricid gastropod *Concholepas concholepas*, and crabs of the genus *Acanthocyclus*. We explored whether the natural variation in the predator assemblage across sites could favor the persistence of *Semimytilus* at Guanaqueros through a keystone effect. Each of these taxonomically distinct predators exhibit different foraging strategies, which may have important consequences for prey preference and have different effects on patterns of mussel abundance. *Heliaster*, like many predatory sea stars, has the ability to manipulate tens to hundreds of prey individuals in a single feeding event (Tokeshi et al., 1989; Navarrete and Manzur, 2008; Castilla et al., 2013), which probably makes them less selective within heterospecific aggregations of mussels, but they could select between different monospecific mussel patches or mussel bed clumps. In contrast, *Acanthocyclus* spp. and *Concholepas* manipulate one item at a time (Navarrete and Castilla, 1988; Caro et al., 2008) and they could select within mixed species clumps and potentially among mussel clumps. Laboratory studies conducted in central Chile (Mendez and Cancino, 1990) and Peru (Tokeshi et al., 1989) suggest that both *Heliaster* and *Concholepas* prefer *Semimytilus* over *Perumytilus*, but the conclusion of these studies are elaborated with results obtained in classic predator-preference laboratory approaches. No field experiments quantifying relative survival rates to predators have been conducted so far at any location.

Among the most important mussel predators present in rocky shores of central Chile (Castilla and Paine, 1987; Navarrete and Castilla, 2003), we considered the sea star *Heliaster helianthus* and the crabs *Acanthocyclus* in our laboratory trials. We did not include the gastropod *Concholepas concholepas*, one of the keystone predators in marine reserves (Castilla and Duran, 1985) because at our study sites (see Results) and at most sites open to fisheries in central Chile, this species is heavily exploited by humans (Castilla and Duran, 1985; Castilla, 1999) and its populations have been reduced to very low densities and, particularly at the intertidal zone, most observed individuals are small and unable to consume adult mussels (Caro et al., 2008). Field experiments considered the entire natural guild of predators. Thus, we combined laboratory and field experiments to answer the question whether predator species can exert differential predation on mussel species and if this difference can also be observed in the field, in order to determine the role of predators in facilitating the persistence of the subordinate *Semimytilus* species in the face of the dominant *Perumytilus* species.

2. Materials and methods

2.1. Characterization of the study sites

Field experiments were carried out during the austral summer of 2012 at two sites on the coast of central Chile (Fig. 1), Guanaqueros (30°10′ S, 71°27′ W) and Las Cruces, about 400 m south of the ECIM marine reserve (33°30′ S, 71°37′ W). Sites were selected based on information provided by spatially extensive studies that have quantified patterns of abundance in intertidal communities (Broitman et al., 2001, 2011; Navarrete et al., 2005; Wieters et al., 2008), and long-term studies on recruitment of marine intertidal invertebrates (Martinez and Navarrete, 2002; Navarrete et al., 2005, 2008). These studies show the existence of a large regional break in abundance and recruitment of the dominant mussel *Perumytilus purpuratus*, with much lower abundance and recruitment north of about 30°S. Abundance and recruitment of