

Predation on the Rocky Shores of Patagonia, Argentina

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ABSTRACT: Rocky intertidal communities of Argentinean Patagonia are exposed to harsh physical conditions caused by dry, strong southern trade winds (mean speed 45 km h⁻¹, gusts up to 140 km h⁻¹) that result in intense desiccation of intertidal organisms. Predator distributions in these communities were evaluated from April 2003 to December 2004 at two exposed headlands and six protected bays in Cabo dos Bahías (44°50'S, 65°40'W). Crabs and sea stars dominated the predator assemblage, with occasional scavenger snails and fish also present. During low tide, predators were never found in the open but were always associated with shelter (primarily within mussel beds and coralline algae), suggesting a strong predator dependency on foundation species to buffer them from physical stress. Few predators (mostly crabs) emerged from shelter at high tide. Unlike the larger predators found on Chilean rocky shores, invertebrate predators in this system are diminutive, generally < 2 cm. The lone exception was the newly discovered invasive green crab, *Carcinus maenas*. Feeding trials, gut content analyses, and visual surveys indicated that native predators feed primarily on small, soft-bodied prey. *C. maenas* fed on slow-moving and sessile animals, including the super abundant mussel *Perumytilus purpuratus*, with much greater voracity than native predators. Because native intertidal organisms are dependent on mussel beds and coralline algae for shelter from desiccation, successful invasion of *C. maenas* may lead to a significant decrease in native diversity by consuming foundation species. This study represents a preliminary survey of predator distributions and feeding habits on the rocky shores of Argentinean Patagonia and provides important baseline data to evaluate trophic linkages and predatory effects on Patagonian rocky shores.

Introduction

The importance of predation as a structuring force in natural communities has been demonstrated in a variety of marine systems, including rocky shores (Paine 1966), coral reefs (Hay 1984), seagrasses (Heck and Valentine 1995), kelp beds (Estes and Palmisano 1974), deep sea (Dayton and Hessler 1972), salt marshes (Silliman and Bertness 2002), and mud and sand flats (Peterson 1982; Eggleston et al. 1992). In rocky intertidal habitats, predators such as sea stars, crabs, drilling snails, and fish often exert top-down control on community structure by regulating rates of succession (McCook and Chapman 1993), local patterns in species diversity (Paine 1966), prey densities and distributions (Paine 1966; Behrens Yamada and Boulding 1996), and competitive interactions (Paine 1974). The relative importance of predation in regulating rocky shore community organization can depend on a wide variety of biotic and abiotic factors, including larval and nutrient supply, interaction strengths among predators and prey, food availability, wave exposure, temperature, and desiccation stress

(Menge et al. 1985; Menge and Sutherland 1987; Duffy and Hay 2000).

Most investigations of the relative role played by predators in structuring intertidal communities have taken place on temperate rocky shorelines characterized by moist air and moderate temperatures (e.g., the coasts of Maine, Washington, and Oregon, USA; central coast of Chile; New Zealand; the Atlantic coast of Europe). Less work has been done on rocky shores where desiccation stress is more intense like desert coasts and tropical and subtropical areas (but see Menge and Lubchenco 1981; Menge et al. 1985; Dungan 1986). In these systems, theory predicts that predation should be less important in structuring communities (Menge and Sutherland 1987; Schiel et al. 2004), while physical stress and positive interactions driven by the amelioration of physical conditions should be more important (Bertness and Callaway 1994).

In Argentinean Patagonia, rocky shore communities are subjected to intense physical stress due to severe climatic conditions (Bertness et al. 2006). The region is characteristic of the arid Patagonian steppe where annual precipitation is less than 200 mm, mean annual temperature is 12°C, and predominant winds are from the southwest, with wind speeds averaging 45 km h⁻¹ but gusting up to

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140 km h⁻¹ (Camacho 1979). On these rocky shores, the zonation pattern of organisms is striking (Bertness et al. 2006). At wave-exposed sites, the mussel *Perumytilus purpuratus* forms dense beds from the high to the low intertidal. Mussel cover decreases at the lower levels of the shore, with the coralline algae *Corallina officinalis* covering 10–15% of the available space at mid and low intertidal levels (Bertness et al. 2006). At the lowermost intertidal levels, those exposed only a few days a year, *P. purpuratus* gives way to areas dominated by bare space and a mixture of algae and invertebrates (Bertness et al. 2006). On wave-protected sites, the high intertidal is mainly unoccupied, the mid level is covered by *P. purpuratus* with approximately 50% bare substrate, and the low intertidal is almost entirely dominated by *C. officinalis* (Bertness et al. 2006). On both exposed and protected sites, the primary space holders (i.e., *P. purpuratus* and *C. officinalis*) harbor a diverse assemblage of small mobile invertebrates, which are restricted to living within these matrices buffered from the extreme desiccation stress (Bertness et al. 2006).

Because these Argentinean rocky shores have similar temperatures to their North American counterparts, but experience much greater desiccation stress (Bertness et al. 2006), they represent a good study system to examine how the relative strength of predation changes under high physical stress. There is little work on the distribution and feeding ecology of intertidal predators in this region. The recent invasion of the European green crab, *Carcinus maenas*, to Patagonia (Hidalgo et al. 2005), a global invader whose effects on natural communities have been well documented (e.g., Grosholz and Ruiz 1996; Carlton and Cohen 2003; Freeman and Byers 2006), has highlighted the need to understand the role of native predators on community dynamics so that we can assess the potential effects of a successful invasion. To determine the importance of predation on Patagonian rocky shores and how it could contribute to regulation of community dynamics, we investigated the distribution and abundance of common marine rocky intertidal predators in relation to wave exposure and tidal height, and the potential predator-prey interactions.

Materials and Methods

STUDY SITE

The study was conducted at Cabo dos Bahías (44°50'S, 65°40'W; Fig. 1), Chubut Province, in the southwestern Atlantic coast of Argentina, from April 2003 to December 2004. Rocky shores in this area are characterized by wave-exposed headlands delimited by protected bays, with a striking zonation

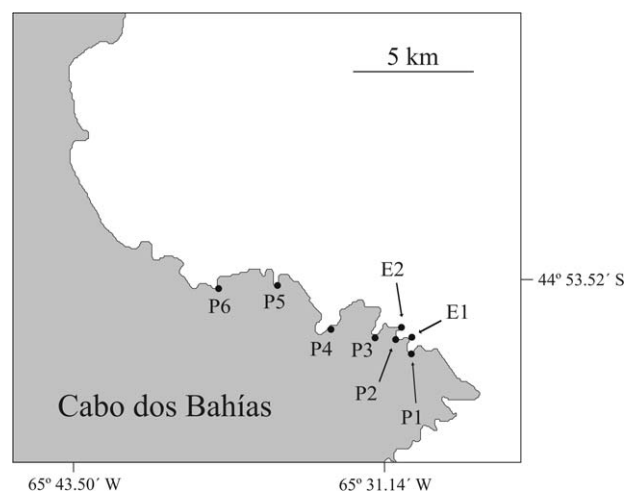


Fig. 1. The study sites at Cabo dos Bahías, in the Chubut Province, Argentina. P1 to P6: the six wave-protected shorelines selected; E1 and E2: the two wave-exposed headlands selected. P4 corresponds to Caleta Carolina, the only site where we found *Carcinus maenas* individuals.

pattern of organisms on all shorelines (see above). Average tidal amplitude in the area is 3.39 m. Two wave-exposed sites and six wave-protected shorelines were selected to evaluate predator distributions (Fig. 1).

PREDATOR DISTRIBUTION

Predator distribution in relation to wave exposure, tidal height, and presence-absence of foundation species cover were evaluated in December 2004 at two wave-exposed headlands (E1 and E2 in Fig. 1) and two wave-protected shorelines (P1 and P2). At each site, 16 quadrats (0.25 × 0.25 m) were randomly placed across the low, mid, and high intertidal levels. Intertidal heights were determined by the striking zonation pattern of organisms, clearly present at wave-protected bays. The low intertidal zone was defined as the tidal height dominated by dense coralline algal cover at wave-protected sites, approximately between 0 and 1.1 m above Chart Datum (CD). The mid intertidal zone was defined as the level covered by mussel beds at protected sites, approximately between 1.1 and 2.2 m above CD. The high intertidal zone was defined as the elevation where the bare rock dominates and mussels and barnacles are only present in crack and crevices at protected sites, approximately between 2.2 and 3.3 m above CD. Heights in relation to CD were identical at both protected and exposed sites. At each site and intertidal level, eight quadrats were randomly thrown on bare space and eight on areas occupied by primary space holders (i.e., either mussels or coralline algae), and the number of individuals of

each predator species found on the bare space or on top of or underneath primary space holders (determined by careful excavation of foundation species cover) was counted. A similarity matrix based on Euclidean distances (abundance data was 4th root transformed) was generated using the PRIMER (version 5.2.9, PRIMER-E Ltd., Plymouth, U.K.) statistical package. Two-way nested (ANOSIM) tests (Clarke and Warwick 2001), nesting height within site, were used to test for differences in predator distribution between the two wave-exposed headlands (E1 versus E2) and between the two wave-protected shorelines (P1 versus P2). Since no significant differences were found among sites with the same wave exposure, data from the two wave-exposed and wave-protected sites were pooled. A two-way crossed ANOSIM test (Clarke and Warwick 2001) was used to compare differences in predator distribution among sites with different wave exposures and intertidal levels.

To compare the relative activity of predators among wave-exposed and wave-protected sites during high tide, cylindrical minnow traps (length: 50 cm; diameter: 30 cm; mouth diameter: 7 cm) were anchored in the mid and low intertidal zones at P1, P2, E1, and E2 ($n = 4$ per site). Traps were baited with crushed mussels and attached to the substrate with stainless steel screws and straps during four periods of 2–3 d each in the summers of 2003 and 2004 (March 20–21, 2003, December 13–15, 2003, January 23–24, 2004, and February 21–23, 2004). Each day we identified, counted, and released the individuals captured, and reset the traps.

Relative abundance of predators under rocks was also recorded in protected bays (no stones were present on exposed headlands) with transect surveys in January and February 2004. Six wave-protected sites were selected along 20 km of shoreline (i.e., P1, P2, P3, P4, P5, and P6). At each site, two to eight 25-m transects were performed across the mid and low intertidal zones. Rocks (area between 0.08–0.35 m²) crossed by a line transect were overturned and the number of individuals of each predator species found underneath was recorded. To evaluate differences in the relative abundance of predators at each sampled site, a Kruskal-Wallis test was performed with post-hoc tests (Zar 1999), since the assumptions for parametric tests were not met. To confirm the presence of *C. maenas* at the study sites, one random sampling was conducted during one low tide (total sampling time ca. 1 h) in April 2004 by overturning stones along the intertidal zone in a bay (i.e., P4, named Caleta Carolina) within Cabo dos Bahías, where an established population of the invasive green crab has been reported (see Hidalgo et al. 2005). All of the individuals caught in traps

and found in the surveys were measured (i.e., carapace width for crabs, maximum length for fish and snails, and maximum distance between opposite arms for starfish).

POTENTIAL FOOD WEB INTERACTIONS OF PREDATORS

Potential food web interactions were assessed by feeding trials in aquaria, gut content analysis, field observations, and monitoring mussel mortality in the field. To evaluate potential predator-prey interactions for *C. maenas* and the native grapsid crab *Cyrtograpsus angulatus* (the larger native intertidal crab found at our study sites), feeding trials were conducted in aquaria. For each predator species, individuals representing common sizes found in the field were selected (carapace width: *C. maenas*: 65 mm; *C. angulatus*: 22 mm). Eight individuals of each species were placed in individual cylindrical plastic containers (5 l for *C. maenas* and 1 l for *C. angulatus*) inside two 500-l tanks (one for each predator species) with seawater at a temperature of 13–17°C. All animals were starved for 48 h prior to the feeding trials. Trials consisted of adding 10 individuals of each potential prey species of the more common sizes found in the field (large *P. purpuratus*: 20–25 mm; small *P. purpuratus*: 5–8 mm; the pulmonate limpet *Siphonaria lessoni*: 8 mm; the snail *Trochom geversianus*: 15 mm; the barnacle *Balanus glandula*: 8 mm; and the isopod *Exosphaeroma* sp.: 7 mm) in each individual container. After 12 h, we recorded the number of prey items consumed. One-way analysis of variance (ANOVA) was conducted to evaluate preferences of *C. maenas* for a determined prey species, by using individual containers as replicate units (Zar 1999). Preferences of *C. angulatus* were not statistically evaluated given the small number of prey consumed.

Gut content analyses were conducted to evaluate the diet of fish found at the study sites. As the number of fish captured during the surveys to evaluate predator distribution was too small to perform this analysis, several extra specimens ($n = 105$) were collected by hand at the six wave-protected sites by overturning stones in the intertidal zone during daytime low tides from September 2003 to April 2004. Fish were killed and placed in a cooler box with ice immediately after collection and were preserved whole in 10% formalin within 1 h after capture (see Baldó and Drake 2002; Declerck et al. 2002; Layman and Silliman 2002). In the lab, the gut was dissected and the prey items consumed were counted and identified under a dissection microscope to the lowest possible taxonomic category. Dietary composition was assessed by mean numerical percentage (%N) and occurrence percentage (%O) of each prey taxa (Hyslop 1980). Only stomachs with food

TABLE 1. Mean sizes (mm) of all the predators found during our samplings in Cabo dos Bahías. Data presented was pooled along all sampling methods and dates. Measurements taken were: carapace width for crabs, total length for fish, shell length for snails, and maximum distance between the extremes of opposite arms for starfish. n is the total number of individuals measured.

Species	Mean size (SD) (mm)	n
<i>Anasterias minuta</i> (Starfish)	18.7 (6.8)	132
<i>Bovichtus argentinus</i> (Fish)	70.0	1
<i>Carcinus maenas</i> (Crab)	73.0 (8.2)	6
<i>Cyrtograpsus altimanus</i> (Crab)	9.3 (2.5)	617
<i>Cyrtograpsus angulatus</i> (Crab)	22.0 (6.8)	206
<i>Halicarcinus planatus</i> (Crab)	5.7 (2.5)	99
<i>Paraeuthria plumbea</i> (Snail)	10.5 (4.2)	8
<i>Patagonotothen cornucola</i> (Fish)	95.7 (13.9)	105

were included in %O. Fish caught in traps were not included in diet examination.

To quantify predation on natural mussel beds, 100 intermediate sized mussels (1 cm shell length) were marked with a dot of nontoxic paint along a straight line in the mid intertidal zone of the two wave-exposed (E1 and E2) and two wave-protected (P1 and P2) sites. The number of marked mussels was counted at every visit to the study sites, identifying individuals that were alive, dead (categorized as open, drilled, or crushed), or missed. Throughout the study period, we also recorded instances when we observed predators eating prey during our samplings of predator abundance underneath rocks and foundation species.

Results

PREDATOR SIZES AND DISTRIBUTION

No more than eight predator species were found in the sampling conducted at Cabo dos Bahías, and most were small in size (< 2 cm; Table 1). In the sampling conducted at the two wave-exposed (E1 and E2) and wave-protected (P1 and P2) sites, all of the animals were found underneath foundation species cover and were never found in the open. There were no differences in predator distribution between the two wave-exposed (E1 versus E2; two-way nested ANOSIM, $R = 0.67$, $p = 0.2$) and the two wave-protected sites (P1 versus P2; two-way nested ANOSIM, $R = 0$, $p = 1$); data from sites with the same wave exposure were pooled. With the pooled data, predator distribution was different between wave-exposed and wave-protected sites and among intertidal heights (ANOSIM analysis, Tables 2 and 3). The starfish *Anasterias minuta* and the crab *Halicarcinus planatus* were the only species present at wave-exposed sites, and were more abundant at mid and low intertidal elevations (Table 3). In the low intertidal of protected bays the more abundant species was the crab *Cyrtograpsus altimanus*, with *H. planatus*, *A. minuta*, and the snail *Paraeuthria plumbea*

TABLE 2. Results of the two-way ANOSIM test to compare differences in predator distribution among wave exposed and protected sites and intertidal levels.

Global test	R	P
Wave exposure	0.924	0.001
Intertidal level	0.539	0.001
Pairwise comparisons		
High versus mid	0.981	0.001
High versus low	0.902	0.001
Mid versus low	0.108	0.002

less abundant (Table 3). *C. altimanus* and *P. plumbea* were also present in the mid intertidal zone of wave-protected sites (Table 3).

The relative abundance of predator species under rocks varied among sites (Kruskal-Wallis test, $p < 0.01$ in all of the cases, Fig. 2). In general, *C. altimanus* was the most abundant, but *A. minuta* and *C. angulatus* were also quite abundant at some sites. Only one *C. maenas* individual was found during our transect survey of wave-protected sites (i.e., P4), and was not included in this analysis. *C. altimanus*, and to a lesser extent *C. angulatus* and the fish *Patagonotothen cornucola*, were also caught by traps at protected bays (Table 4). Only one individual, the fish *Bovichtus argentinus*, was trapped at the exposed sites. During our low-tide sampling at Caleta Carolina, five extra *C. maenas* individuals were found by overturning rocks, confirming its presence in the area.

POTENTIAL FOOD WEB INTERACTIONS

Feeding trials showed that *C. maenas* preyed upon all of the prey offered, with the exception of the highly mobile isopod *Exosphaeroma* sp. (Table 5), with no preferences for the species consumed (one-way ANOVA, $F_{4, 35} = 1.75$, $p = 0.16$). *C. angulatus* only ate a few small *P. purpuratus* and *B. glandula*. Gut content analysis showed that polychaetes and small crustaceans (e.g., isopods and amphipods) were the more important prey items of *P. cornucola*, in terms of occurrence (Table 6). Isopods showed the highest values in terms of number, but polychaetes and amphipods were also relatively important. During sampling in the mussel matrix, we also saw the starfish *A. minuta* preying on *P. purpuratus* and on the key-hole limpet *Fissurella* sp., and the snail *P. plumbea* was observed feeding on dead mussels. These observations accounted for < 1% of the encounters with these animals. No marked mussels were found dead at either exposed or in the protected sites after 2 mo of weekly visits to the sites. By this time, the paint started to peel off, making marked mussels difficult to find and monitoring was stopped.

TABLE 3. Predator densities (number of individuals 0.0625 m^{-2}) (SD) underneath foundation species cover at wave-exposed and wave-protected sites at three heights of the intertidal area. Data from the two wave-exposed (E1 and E2) and the two wave-protected (P1 and P2) sites were pooled. No animals were found above foundation species cover. No samples were taken at the high intertidal level of wave-protected sites, given the low foundation species cover at this zone.

	Exposed			Protected	
	High	Mid	Low	Mid	Low
<i>Anasterias minuta</i> (Starfish)	0.06 (0.25)	4.81 (2.01)	4.19 (2.53)	0	0.12 (0.34)
<i>Halicarcinus planatus</i> (Crab)	0.19 (0.75)	3.68 (3.22)	2.31 (1.81)	0	0.31 (0.60)
<i>Paraeuthria plumbea</i> (Snail)	0	0	0	0.06 (0.25)	0.56 (0.73)
<i>Cyrtograpsus altimanus</i> (Crab)	0	0	0	0.37 (0.62)	2.56 (2.50)

Discussion

Our surveys of the rocky shores of Argentinean Patagonia revealed that most of the intertidal predators are small in size, with the exception of the invasive green crab *C. maenas*. During low tide, all predators were found underneath foundation species or rocks, but at high tide some can emerge to forage. Native predators did not prey heavily on primary space holders but preferred small-sized and less abundant prey. *C. maenas*, foraged on larger prey and on the most important foundation species in the community (i.e., mussels).

The restricted distribution of predators, living embedded in foundation species or underneath rocks, only emerging to feed during high tide, suggests a strong dependence on refuge from desiccation stress. In many temperate zone intertidal systems, the major activity of marine predators in the intertidal zone is during high tide, as this temporal activity pattern is a mechanism that both prevents desiccation stress and results in avoidance of terrestrial predators such as birds (e.g., Bertness et al. 1981; Hunt and Scheibling 1998). Despite the potential for bird predators to limit the activity of marine predators to high tide, our suggestion that

the dependence of predators to the refuge provided by foundation species is supported by a recent examination of Patagonian rocky shores (see Bertness et al. 2006). This study showed that this system is physically more harsh than any other rocky intertidal area studied, even those of warmer lower latitude subtropical and tropical sites such of southern California, Australia, and Central America. This highly stressful physical environment restricts the assemblage of mobile invertebrates (including the small native predators) to live inside the mussel matrix, otherwise they die within 15 min of air exposure (Bertness et al. 2006). The results of the trap sampling revealed that crabs and fish can emerge from refuges to feed during high tide only at wave-protected sites. Starfish did not appear in traps even when present under foundation species cover at both exposed and protected sites. This might be because they do not forage outside the protection of foundation species cover even during high tide, but can also be due to less ability to climb into the traps or because the bait type (i.e., crushed mussels) was not attractive for them. At exposed headlands the strong wave action common at our study sites (see Bertness et al. 2006) likely further limits predator movements and foraging (e.g., Leonard et al. 1998), restricting distributions to the cover of foundation species. One *B. argentinus* individual fell in the traps deployed at wave-exposed sites, indicating that different predator species can be using habitats with contrasting wave exposures. It must be acknowledged that using only one trap design and one type of bait may bias captures, and

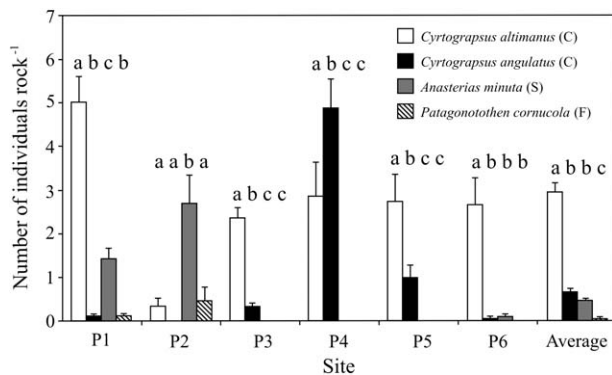


Fig. 2. Relative abundance of predators under rocks at six wave-protected sites. Bars are the mean (\pm SE) number of individuals found under rocks. Site codes (P1, P2, P3, P4, P5, and P6) refer to the six wave-protected sites sampled along 20 km of coastline. Different letters indicate differences at $p < 0.05$ (Kruskal-Wallis post-hoc test) in the relative abundance of predators at each sampled site. C = crab, S = starfish, F = fish.

TABLE 4. Density of predators captured by baited traps (number of individuals $\text{trap}^{-1} \text{d}^{-1}$) (SD) at exposed and protected sites. Data from the two wave-exposed (E1 and E2) and the two wave-protected (P1 and P2) sites, and that of all trapping dates, were pooled.

Species	Exposed	Protected
<i>Bovichtus argentinus</i> (Fish)	0.02 (0.13)	0
<i>Cyrtograpsus altimanus</i> (Crab)	0	3.97 (6.72)
<i>Cyrtograpsus angulatus</i> (Crab)	0	0.68 (2.96)
<i>Patagonotothen cornucola</i> (Fish)	0	0.07 (0.32)

TABLE 5. Total number of prey individuals consumed by *Carcinus maenas* and *Cyrtograpsus angulatus* in feeding trials. Numbers between parentheses are the mean, SE in 8 replicates with 10 prey individuals of each prey species.

Prey species	<i>Carcinus maenas</i>	<i>Cyrtograpsus angulatus</i>
Large mussel (<i>Perumytilus purpuratus</i>) (20–25 mm)	15 (1.87, 2.17)	0
Small mussel (<i>Perumytilus purpuratus</i>) (5–8 mm)	14 (1.75, 2.05)	4 (0.50, 0.92)
Limpet (<i>Siphonaria lessona</i>) (~8 mm)	35 (4.37, 3.78)	0
Snail (<i>Trophon geversianus</i>) (~15 mm)	30 (3.75, 2.76)	–
Barnacle (<i>Balanus glandula</i>) (~8 mm)	13 (1.62, 2.67)	1 (0.12, 0.35)
Isopod (<i>Exosphaeroma</i> sp.) (~7 mm)	0	0

does not provide a complete picture of the activity of predators during hide tide.

There were also differences in the relative abundance of predators underneath rocks in wave-protected bays. While *C. altimanus* was on average the most abundant predator, *C. angulatus* and *A. minuta* were also abundant at other sites. These differences might be related to site specific variation in physical properties that were not measured, such as the slope of the beach, the proximity of tide pools, or the type of substrate where rocks were deposited. The accumulation of water on gently sloped sites may increase the abundance of less physiologically resistant animals, such as starfish and fish. *C. angulatus* could be more abundant under rocks deposited on muddy substrate, where they find shelter in burrows dug in the sediment (e.g., Iribarne et al. 2003); while structurally more complex microhabitats such as between-rocks cavities or rocks placed on hard bottom might have higher densities of *C. altimanus* (e.g., Spivak 1997).

Our aquarium feeding trials indicated that even the largest native crab *C. angulatus* had a low consumption rate on shelled prey, as they only ate a small number of small mussels and barnacles. They can consume smaller or soft-bodied organisms, since polychaetes and other crabs have been found in their stomachs, suggesting an omnivorous diet (Olivier et al. 1972). Feeding trials showed that *C. maenas* have the potential to be a voracious predator of native mollusks and crustaceans, as it ate most of the prey offered and in higher proportion than *C. angulatus*. This suggestion is supported by prior studies showing diverse and strong food web interactions of green crabs within their native range (e.g., Ebling et al. 1964; Flach 2003) and successfully invaded coastal environments (e.g., Mc Donald et al. 2001; Walton et al. 2002). While feeding trials give information on potential effects, they tend to overestimate the effects of predators on prey populations, since they do not account for actual predators' densities and

TABLE 6. Occurrence percentage (%O), numerical percentage (%N), and length range (mm) of prey items in *Patagonotothen cornucola* gut. %O is the number of stomachs containing that prey item divided by the total number of stomachs containing food $\times 100$. %N is the total number of a particular prey item divided by the total number of prey items $\times 100$. Total number of stomach analyzed = 105. Total number of stomachs containing food = 61.

Prey item	%O	%N	Length range (mm)
Polychaetes (total)	72.13	16.92	
<i>Eunice</i> sp.	6.65	1.23	
<i>Nereis</i> sp.	14.75	4.31	
Unidentified polychaetes	50.82	11.38	
Sphaeromatids isopods	62.29	57.54	2–12
Amphipods (total)	39.34	16.61	2–12
Caprellidea	1.64	0.61	
Gammaridea	32.79	14.46	
Hyperiidea	4.92	1.54	
Crabs (total)	14.75	3.38	4–7
<i>Cyrtograpsus altimanus</i>	6.55	1.54	
<i>Halicarcinus planatus</i>	3.28	0.61	
Unidentified crabs	4.92	1.23	
Fish eggs	11.47		
Fish larvae	1.64	0.92	1
Unidentified crustacean larvae	9.84	2.15	4
Unidentified crustaceans	6.56	1.23	
Algae	6.56		
Chironomidae larvae	3.28	0.61	6
Cephalopods	1.64	0.31	
Gastropods	1.64	0.31	2

natural foraging behavior (e.g., Ruesink 2000). *C. maenas* may be voracious in laboratory feeding trials, but more selective in the field, consuming the more profitable prey in order to maximize the net energy intake per unit foraging time (Elner and Hughes 1978). The effect of *C. maenas* may be more subtle than that expected by the results of feeding trials.

The small size of native intertidal predators further suggests that predators likely do not have strong impacts on community structure (see Williams and Martínez 2000). While we did not examine the feeding habits of the other native crabs (i.e., *C. altimanus* and *H. planatus*), their small size indicates that they would not have the mechanical advantage and claw strength necessary to crack exoskeletons of adult mussels and barnacles (e.g., Juanes 1992) and must forage on more accessible and smaller species. This is supported by past observations (e.g., Scelzo and Lichtschein de Bastida 1978) noting that *C. altimanus* feeds on a wide range of non-shelled organisms, from diatoms and protozoa, to copepods, amphipods, worms, bryozoans, and hydrozoa. Gut analysis of *P. cornucola* indicated that it feeds mainly on small crustaceans and polychaetes, while foundation species or hard shelled organisms were not found in their stomachs. Our mussel marking experiment revealed no evidence of mussel mortality due to predation (or other factors) over a 2-mo period, further indicating that predation on foundation species are negligible. While the sea star *A. minuta* can consume adult mussels, our observations in the field and more extensive and long-term caging and tethering experiments conducted at the same sites (Bertness et al. 2006; Silliman unpublished data) showed negligible consumer effects on mussels and associated biota, further indicating that native predators likely do not have significant effects on community structure and diversity. Our conclusion that predation effects are small and not primary forces controlling this community contrasts starkly with studies carried out at the same latitude but along the Chilean coast (Castilla and Durán 1985; Paine et al. 1985). These studies have shown that predation by Chilean starfish and gastropods maintain a low abundance of the competitively dominant mussel *P. purpuratus*, leading to a pattern of increasing species diversity of large space holders. The dominant feature of monocultures of mussels in Argentinean Patagonia rocky shores suggests that effective predators that could potentially control these space holders are evolutionary absent.

While lab feeding preferences alone can not tell us if predation on these prey species can control their abundance and distribution, the lack of other predators and the extremely slow recovery rate of disturbed patches of foundation species (see Bert-

ness et al. 2006), suggest that a successful invasion by *C. maenas* could have the potential to strongly affect community composition in several ways. First, *P. purpuratus* beds provide associated organisms (> 90% of native intertidal organisms) with shelter from lethal desiccation stress (Bertness et al. 2006) and their removal by *C. maenas* could lead to significant declines in local diversity. Second, *C. maenas* is able to indirectly affect soft substrate communities by disturbing the sediment during their feeding activities (Schratzberger and Warwick 1999), and has the potential to decimate other intertidal species as a by-product of their foraging activity on the other foundation species in this system, *C. officinalis* (see Bertness et al. 2006). Given the extreme physical stress that shapes these Patagonian coasts, it would be reasonable to expect that this force may also limit the activity and potential effects of *C. maenas*. Contrarily to the native predators that are mainly restricted to the intertidal, *C. maenas* can also live in the subtidal (e.g., Jamieson et al. 1998), giving them potential advantages over native predators, e.g., allowing them to escape the harsh physical stressors during exposed low tides.

This work combined with other recent studies indicates that native predators do not play a large ecological role in regulating community structure in Patagonian rocky shores. Physical factors appear to be the dominating structuring force in these communities and are likely evolutionarily and ecologically responsible for weakening the effects of consumers (Bertness et al. 2006). It is acknowledged that this study represents a preliminary survey of predator distribution and feeding habits on the rocky shores of Argentinean Patagonia and that this work by no means provides a complete picture of trophic structure in the community. This study does provide important baseline data for future investigation. To further elucidate food web links, future work should include isotopic analysis of potential food web components, species-specific predator exclusion and inclusion experiments in the field, and evaluation of the potential for intraguild predation and competition among predator species, taking into account seasonal variations in predator abundance and prey availability. In order to evaluate potential predatory effects, estimation of individual and population predation rates on a broad range of sizes and age stages of the main components of the intertidal fauna, and evaluation of indirect effects of the removal of non-shelled, soft-bodied prey organisms, would also be valuable. Special attention should be taken to focus these analyses in the lowest intertidal levels that are exposed only one or twice a month, where physical conditions are less severe and predation is expected

to be more important (Menge and Sutherland 1987).

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