

Experimental Determination of Predation Intensity in an Intertidal Predator Guild:

Dominant versus Subordinate Prey

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Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey

Sergio A. Navarrete and Juan C. Castilla

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Theoretical and empirical ecologists have long acknowledged that information about the intensity or strength of the interaction between species is crucial for an understanding of community dynamics. In communities in which predation is an important structuring process, and some predator species are commercially exploited, quantitative estimates of predation by different predator species within a guild are necessary to make even the simplest recommendations about conservation and resource management. Here, we evaluated per capita and population level components of predation intensity of three intertidal predators that feed on monospecific stands of barnacles and mussels at wave exposed sites in the rocky intertidal zone of central Chile. These prey species represent the two most distinctive stages of the mid-intertidal seascape, with mussels being competitively dominant. Our results showed that the commercially exploited gastropod *Concholepas concholepas* and the sea star *Heliaster helianthus* have similarly large per capita and population effects on the competitively dominant mussel *Perumytilus purpuratus*. Their per capita (by average size individual) and population effects on mussels were more than two orders of magnitude larger than those of *Acanthocyclus gayi* crabs and likely even larger than the effect of other predator species in this system (other crabs, whelks, birds, fish). The overall pattern of predation on barnacles was similar to that on mussels, but some differences occurred in the way different components of predation intensity were distributed across predator species. Despite the roughly similar pattern of population predation intensity between prey species, the expected consequences for the prey population, and hence the rest of the community, were acutely different for mussels and barnacles.

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Descriptions about predator-prey links in natural food webs and the statistical analysis of these links have provided important insights into the factors that may limit the structure of consumer guilds (Jaksic et al. 1993, Muñoz and Ojeda 1998) and have suggested the existence of potentially general rules of factors controlling community structure (Martinez and Lawton 1995). While these studies hold the promise of detecting general principles governing natural communities, it seems clear that the study of food web topology alone will not be sufficient to understand community dynam-

ics and to predict the consequences of the loss of particular species from these systems. Indeed, theoretical and empirical ecologists have long acknowledged that information about the intensity or strength of the links between species is necessary to progress further (MacArthur 1972, Paine 1980, Abrams 1987, Morin et al. 1988, Wilbur and Fauth 1990, Resetaarits 1991, Berryman 1993; and see Laska and Wootton 1998, Berlow et al. 1999 for reviews). In communities in which predation is an important structuring process, quantitative estimates of predation intensity by differ-

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ent predator species within a guild are necessary to understand the dynamics of the system and to make even the simplest recommendations about conservation and resource management (Bond 1993, Power et al. 1996, Yodzis 2001).

Across environmental gradients and among habitats, variation in different components of predation intensity will determine variability in the total mortality sustained by a prey species due to predators (Menge 1983). The components of predation that can vary across environmental gradients include: 1) the prey capture efficiency of a predator species of a given size, 2) the average size of a predator species, 3) the number or biomass of predators, 4) the number of species in the predator guild, and 5) patterns of interaction among predator species. Both per capita and population components of predation are important because they will determine whether a diffuse or keystone type of predation characterizes a given community (Robles and Robb 1993, Menge et al. 1994, Navarrete and Menge 1996, Persson et al. 1996, Power et al. 1996). Moreover, in many cases, predator species with apparently redundant effects within a community monopolized by competitively dominant prey can assume larger roles in an altered system, where subordinate prey species are common (see discussion in Navarrete and Menge 1996). In this study we examine the changes in the pattern of per capita and population predation intensity of a gastropod-asteroid-decapod carnivore guild feeding on two shared prey species, a competitive dominant mussel and a subordinate barnacle prey. Both prey species have the capacity of forming extensive monospecific stands that characterize the mid-intertidal seascape. All species considered in the study are generalist predators that consume a wide variety of prey, but in all cases, mussels and barnacles constitute a major component (> 60%) of their diets.

In the wave exposed rocky intertidal zone of central Chile, several species of predators coexist and feed on mussels and barnacles, generating free space available for recruitment by other invertebrate and algal species (Castilla and Paine 1987, Soto 1996). Among them, the sea star *Heliaster helianthus* and the muricid gastropod *Concholepas concholepas* have been suggested in separate studies to be keystone predators because of their effects on beds of the competitively dominant mussel in the mid-intertidal zone, *Perumytilus purpuratus* (Castilla and Durán 1985, Paine et al. 1985). The predatory crabs *Acanthocyclus gayi* and *A. hassleri* also prey on mussels and barnacles at fairly high rates under laboratory conditions and can be abundant in the mid and low intertidal zones, coexisting with *Concholepas* and *Heliaster* (Navarrete and Castilla 1988, 1990b). However, no observational or experimental studies have quantified their per capita and population effects under comparable conditions in the field. Unlike predator-prey relationships in many other intertidal systems,

neither mussels nor barnacles exhibit an absolute size escape from any of these predators (Castilla et al. 1979, Paine et al. 1985, Navarrete and Castilla 1988). Several other predators belong to this predator guild and share both sessile prey (e.g. whelks *Acanthina calcar* and *Crassilabrum crassilabrum*, birds, omnivorous fish), but their size, low abundance and/or seemingly low predation rates suggest that they might not be able to control the abundance of these sessile prey (Castilla and Paine 1987, Navarrete and Castilla 1993, Soto 1996).

It is difficult to evaluate rates of prey consumption in the field by simple observation of individuals, particularly when predators feed at night or high tide periods (Castilla and Guisado 1979). This is the case with *Heliaster*, *Concholepas* and *Acanthocyclus*. Alternatively, it is possible to enclose individuals in cages and observe prey survival and the release of bare rock in comparison to exclusion units. Although this method has the problem of creating "cage artifacts" by restricting the mobility of individuals (Connell 1974), it sheds light on relative consumption rates and is a good first approximation to evaluate the pattern of predation in a predator guild (Paine 1992, Osenberg and Mittelbach 1996). We follow this approach in this study. We estimate per capita (per body mass and by an average sized individual) and population level consumption rates of the three predator species on: a) monocultures of a competitively dominant species, the mussel *Perumytilus purpuratus* and on b) monocultures of the subordinate competitors that monopolize space after removal of mussels, the chthamaloid barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*. Using estimates of prey recruitment, we estimated the effect that these predator species will have on prey population within the marine reserve of Las Cruces, where densities and sizes of the commercially exploited *Concholepas* gastropod have recovered after the exclusion of humans (Castilla 1999).

Material and methods

We conducted experiments on the rocky shore of the marine reserve of Las Cruces (ECIM, 33°30'S, 71°39'W) of the Pontificia Universidad Católica de Chile in central Chile. The intertidal zonation and general community structure of the reserve has been extensively described in previous studies (Castilla and Durán 1985, Castilla 1988, 1999, Castilla and Bustamante 1989, Navarrete and Castilla 1990a). Briefly, after the exclusion of humans from the marine reserve in 1982, the density and individual size of the commercially exploited gastropod *Concholepas concholepas* increased inside the reserve. Increased predator biomass caused the virtual disappearance of beds of the competitively dominant mussel *Perumytilus purpuratus*, which

are characteristic of the mid-intertidal zone at most wave exposed sites in central Chile (Castilla and Durán 1985, Durán and Castilla 1989, Broitman et al. 2001). The mid intertidal zone inside the reserve is now dominated by the chthamaloid barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*, and fleshy crustose algae (mostly *Hildenbrandia lecanellieri*, Broitman et al. 2001).

At the site used in the predation experiments, chthamaloid barnacles covered about 65–75% of the substratum. Foliose macroalgae were scarce (< 5% cover), and coralline forms, mainly *Corallina officinalis*, formed sparse and small turfs (< 3% cover). Only small (3–15 mm long), sparse individuals of *Perumytilus* were observed among adult barnacles, never reaching more than 20% cover. Bare rock represented less than 10% of the rock surface.

In this mid-intertidal community, we quantified the intensity of predation by using inclusion cages and compared prey survival in the presence of individual predators against predator exclusions and control plots. Simple models of prey survival in the presence and absence of predators allowed us to estimate per capita and per body mass prey capture rates. Independent estimates of prey recruitment rates and predator biomass, combined with field measured prey capture rates, were used to predict prey population changes in the face of different predator species.

Predator densities

Estimates of predator densities were obtained by laying down 10- to 25-m long and 2-m wide transects in the mid- and low intertidal zones of rocky platforms distributed along ca. 100 m of coastline, encompassing the area where experiments were conducted. *Heliaster*, *Concholepas* and *Acanthocyclus* crabs were counted and measured (diameter, peristomal length and carapace width, respectively) along the transect. Densities were measured several times during the course of the experiments in 1989–1990 and then again in 1999–2000, and were expressed as number of individuals per square meter. Sizes of predators were used to estimate individual and total population predator biomass using length to wet weight regressions.

Experimental manipulations

To determine prey consumption rates of the three predators species on barnacles and mussels, we conducted two separate cage experiments. Experimental plots, 20 × 20 cm in size, were haphazardly distributed in the mid-zone of six rocky platforms with slopes between 20° and 35°. Platforms were no more than 70 m apart within an area of ca 500 m², and were sub-

jected to rough waves. Wave forces reach around 15–25 Newtons under normal weather conditions (Alvarado and Castilla 1996). As detailed below, slightly different cage dimensions and replication were used between the experiments to assess predation rates on barnacles and on mussels, but the experimental design and essential methods were the same. In both experiments, we randomly selected an experimental plot to either: 1) enclose an individual *Heliaster helianthus*, *Concholepas concholepas*, or *Acanthocyclus gayi*, using stainless-steel cages, 2) exclude all predators, using the same cages, or 3) allow predators to access plots that were permanently marked with stainless-steel screws, but otherwise unmanipulated ('controls'). These control plots were used to evaluate total mortality of prey in the presence of natural densities of all predators in the area. Experiments were monitored at the beginning and approximately every 10–15 days for the first 90 days and approximately bi-monthly thereafter.

To evaluate consumption of barnacles, we used the naturally established cover of chthamaloid barnacles, *J. cirratus* and *N. scabrosus* (> 60% cover). We set up seven replicates of predator enclosure and exclusion treatments and 24 replicates of controls in January 1989. Enclosure and exclusion of predators were accomplished by fastening circular stainless-steel cages (18–20 cm in diameter and 5 cm height with 4 × 4 mm mesh openings), to the rock with three stainless-steel screws. Throughout the experiment, cages were replaced every ca 15 days to avoid algae from growing on the mesh and reduce the light and water flow. At the beginning of the experiment, we lost two cages of *Heliaster* and *Concholepas* enclosures due to waves and rock breakage, so only five replicates for these two treatments were completed. Cover of all sessile species and bare rock were measured using a 20 × 20 cm quadrat with 100 evenly spaced points. Due to time constraints and bad weather conditions, it was not always possible to distinguish between the two species of chthamaloid barnacles in the field. On these occasions, both species were pooled together. Balanoid barnacles are easy to identify and were always evaluated separately. After about 3 months from the beginning of the experiments, too many cages and anchoring positions had been damaged by impounding waves and the experiment was terminated.

To evaluate rates of predation on mussels, in August 1999 we transplanted a fixed number of individuals of *Perumytilus purpuratus* to experimental plots distributed over the same experimental area described above. We decided to transplant a fixed number of mussels, instead of using natural beds, in order to be able to follow the survival of individuals over time and to keep the shape, cover and density of mussel clumps homogeneous across replicates. Moreover, mussels beds inside the reserve of Las Cruces have all but disappeared from the mid intertidal zone following the exclu-

sion of humans in 1982 (Durán and Castilla 1989). Mussels were collected from sites adjacent to the marine reserve (ECIM), cleaned of all epibionts, and measured to the nearest 0.1 mm. One hundred and fifty mussels between 16 and 26 mm shell length were then transplanted to scraped clean plots, forming a monolayer of mussels that covered the entire 20 × 20 cm surface of the plot (cover > 95%). Mussels were held down using a Vexar plastic mesh (mesh opening ~ 3 × 5 mm) until they re-attached to the rock surface. The mesh was loosened two to four weeks after the initial transplant and re-applied as a dome-shaped cage that excluded predators while allowing mussels to grow freely (Menge et al. 1994, Navarrete and Menge 1996). Plots were checked approximately monthly and meshes cleaned of algae or replaced as needed to ensure adequate flow of water.

Approximately three months after mussels were transplanted and individuals had firmly re-attached to the rock, we started the predator caging experiment. To improve long-term resistance of cages to waves, we used a stronger cage design than the one used in the barnacle experiments (see above). Cages were 20 × 20 × 5 cm in size and made of stainless-steel mesh with 5 cm outward flaps at the bottom (Navarrete 1996). Eight screws through the cage flaps fastened each cage to the rock surface. All treatments were replicated five times. During each monitoring, we counted the number of live, dead and broken mussels, registered the general condition and size of the predator and the number of mobile organisms that had invaded the plots. Photographs were taken and whenever possible, maps of each mussel clump were made on transparent acetate plates to quantify changes in area covered by mussel clumps over time.

Individuals of each predator species enclosed in cages were roughly similar in size: *Acanthocyclus*, 20–37 mm carapace width (6.6–43.7 g), *Heliaster* 46–95 mm in diameter (14.4–48.7 g), *Concholepas*, 28–47 mm peristomal length (7.2–18.9 g). The sizes of crabs used in the experiment corresponded well with the average size of adults found in the field (Navarrete and Castilla 1990b). Sizes of *Concholepas* and *Heliaster* were smaller than those of an average adult (see Results), which was necessary to allow individuals to move freely inside inclusion cages.

Data analyses

Estimates of prey capture rates

In the caging experiment conducted on barnacle monocultures, we evaluated the effect of each individual predator on the rate of change in cover of barnacles, bare rock, and the most abundant sessile species that occupied the space (see Results), which accounted for more than 90% of the plots' surface. Estimates of per

capita prey capture rates from barnacle cover data in the different treatments require expressing cover changes as a function of prey population size. The proportion of area occupied by barnacles (B) at any given time t , out of the total area available (A), was represented as $B_t = (\bar{a}_t N_t / A)$, where \bar{a}_t is the area occupied by an average individual barnacle at time t , and N_t is the number of individuals (Petraitis 1995). Then, re-scaling $\bar{a}_t = \bar{a}_t / A$, and assuming no recruitment of new individuals over a short time lapse, the cover at time $t + 1$ will be $B_{t+1} = \bar{a}_t N_t + \bar{g} N_t - m \bar{a}_t N_t$, where \bar{g}_t is the growth rate (in terms of area increment per unit plot area) over that period of time and m is the per capita barnacle mortality rate. Since we tallied cover of existing (adult) barnacles and that of barnacle recruits separately, we can omit recruitment as a factor in the equation of barnacle cover changes. Besides, over the short duration of the experiment, recruits contributed little (< 4%) to overall barnacle cover. Growth of adult barnacles was minimal, particularly over summer months (S. Navarrete, unpubl.). Therefore, we assumed that individual growth did not contribute significantly to observed cover changes. Under these conditions, changes in barnacle cover in the predator exclusion cages can be expressed as $B_t = (N_0 e^{-mt}) \times \bar{a}$, and changes in the predator enclosure cages as $B_t = (N_0 e^{-(m+cP)t}) \times \bar{a}$, where c is the prey capture rate of a predator and P is the predator population size. In all our experiments $P = 1$ individuals per cage.

Ordinary least squares (OLS) regressions between $\log B$ (expressed as proportion) and time (days) from the beginning of the experiment were performed on each replicate, providing independent estimates of rates of change (slopes) under the different treatments. Subtraction of the slope in the predator exclusion from those under the predator enclosures provided an estimate of per capita prey capture rate (c) for each predator species (since $P = 1$). Standard errors were calculated using error propagation theory (Taylor 1997, Navarrete et al. 2000). To account for differences in body size of experimental predators and provide estimates of population effects (see below), we expressed prey capture rates on a 'per body mass' basis, c_w , dividing c by the body mass (W in grams) of the individuals used in the experiments. Estimates of per capita predation rates by an average size predator were obtained by multiplying c_w by mean W for each predator species.

Since we transplanted a fixed number of mussels to each experimental plot, we were able to directly follow mussel survival over time under the different treatments. For each replicate, the number of live mussels at a given time (N_t), expressed as the proportion from the original number transplanted (N_0), was regressed against time (days) using OLS regressions after log-transformation. The slope of mussel survival ($\log(N_t/N_0)$) on time provides an estimate of mussel mortality

rate, m , in the predator exclusion treatment, and of $m + cP$ in the predator enclosures (Navarrete and Menge 1996, Berlow et al. 1999). Standard errors were obtained using error propagation theory (Taylor 1997, Navarrete et al. 2000). Again, $P = 1$ in the enclosures.

One-way ANOVA and Tukey's multiple comparison tests were used to compare prey capture rates for barnacle and mussel prey in the predator enclosures and exclusions. We used separate one-way ANOVA's to compare the rates of change in the exclusion versus control treatments, including prey adults plus recruits. We decided to perform these separate ANOVA's, instead of one test including controls and caged plots, because control plots evaluated the effects of all three experimental predator species, plus all other predators in the system. Since the second comparison was not completely independent of the first one, we used a Bonferroni corrected significance value, $\alpha = 0.025$ for these tests. Pairwise comparisons of predation rates between predator species were done with Student-t tests and sequential Bonferroni correction (Peres-Neto 1999).

Estimates of prey capture rates by predator populations and effects on prey

Predation pressure exerted by the entire predator population over a given area on the two prey species were based on per body mass capture rates, c_w , obtained from the experiments and predator biomass obtained from predator densities and sizes measured in the field. This approach has the advantage of integrating over the variability in predator body size observed in the field and facilitates estimates of total additive effects of different predator species (Osenberg and Mittelbach 1996). Thus, prey capture rates by predator populations were estimated by multiplying the total biomass of a predator species in the field (BI) by its per body mass capture rate (c_w). We calculated predator biomass as $BI = \sum W_i N_i$, where W_i is the body mass and N_i the number of predator individuals in size class i .

To determine the effect of predator consumption at the prey population level, we estimated prey recruitment during the course of the experiments by tallying new mussels and barnacles recruiting to experimental plots separately from the cover of adults. Mussel recruits were counted only when established outside the originally transplanted patch of adults, but mussels recruiting to the mussel bed matrix were not considered. Additional barnacle recruitment data were obtained from a three year-long study conducted at the same experimental site, during which barnacle recruitment was quantified on a monthly basis (Navarrete et al. 2002). Assuming that predators did not alter rates of prey recruitment, expected changes in prey population were simply calculated as the difference between recruitment input and total mortality due to predators ($c_w \times BI$) and other causes (m).

Results

Predator densities

The most abundant carnivore predators in the study site were the sea stars *Heliaster helianthus* (mean = 1.89, SE = 0.29 ind/m²), the gastropod *Concholepas concholepas* (mean = 3.30, SE = 0.67 ind/m²) and the crab *Acanthocyclus gayi* (mean = 2.70, SE = 0.42 ind/m²). The crab *Acanthocyclus hassleri* was scarce at the study site (< 0.2 ind/m²), probably as a consequence of the low abundance of mussel beds (Navarrete and Castilla 1990b). Juveniles and adults of the omnivorous clingfish *Sicyases sanguineus* were common at mid- and low tidal elevations. This fish species occasionally feeds on mussels and barnacles (Cancino and Castilla 1988). The predatory whelk *Crassilabrum crassilabrum* was found only in the very low intertidal fringe and shallow subtidal areas. The crabs *Paraxanthus barbigier* and juveniles of *Homalaspis plana* were occasionally seen in shallow subtidal areas.

Significant differences in mean body mass (W) were observed among the three predator species in the field (one-way ANOVA, $F = 523.62$, d.f. = 2, 579, $P = 0.0001$), with *Acanthocyclus* crabs being the smallest and *Heliaster* the largest. Body size distribution of *Concholepas* was approximately log-normal, while those of *Heliaster* and *Acanthocyclus* were left skewed even on a log scale (Fig. 1).

Barnacle prey

Species composition and cover of the dominant sessile species were similar among all treatments at the beginning of the experiment and separate ANOVA's for the most common species showed no significant differences. Roughly 60% of chthamaloid barnacles were *Jehlius cirratus* and 40% *Notochthamalus scabrosus*. Cover of these chthamaloid barnacles remained at about 65% in the exclusion cages throughout the experiment (Fig. 2a), with no significant trend over time (Table 1). All predators had similar negative effects on the cover of barnacles. Analysis of variance and Tukey's multiple comparison test on the slope of the regressions between log proportional barnacle cover and time showed significant differences between the exclusion and all predator enclosure treatments, but no differences among predator species (Table 2). No significant time trend in barnacle cover was observed in the control treatments to which all predators had access, while a slight but significant decrease over time was observed in the predator exclusions (Fig. 2c, Table 1). Differences between controls and exclusions were not statistically significant, however (one-way ANOVA; $F = 2.86$, d.f. = 1, 29, $P = 0.1017$).

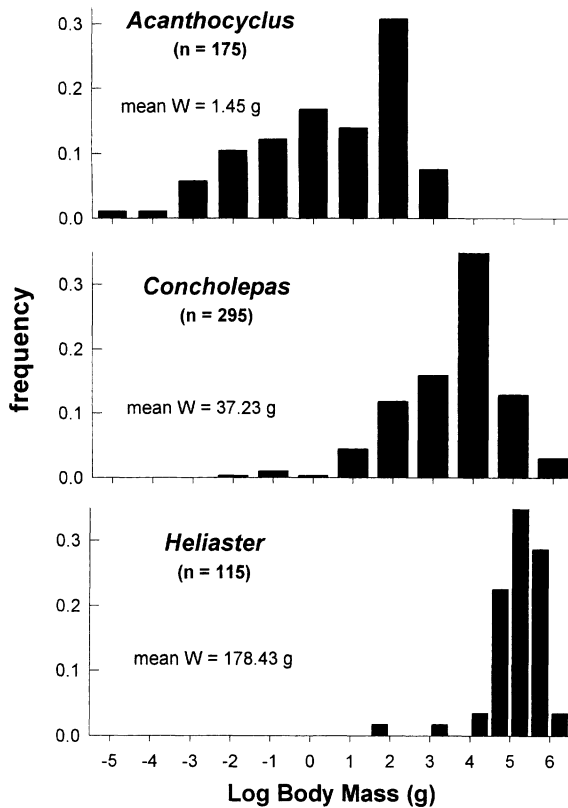


Fig. 1. Body size (W) frequency distributions in the study site for the three experimental predator species. The mean weight (in grams) and sample size is also given in each panel.

Bare rock remained low and constant in the exclusion treatment (ca. 6%) but rapidly increased in the presence of predators (Fig. 3). Analysis of variance

and Tukey's multiple comparison test showed that rates of increase in bare rock cover were similar among all predator enclosure treatments and significantly different from the exclusion (Table 2). Other sessile species intermixed within the barnacle matrix never occupied more than 17% of the plot area. Sparse juveniles of *Perumytilus* mussels presented a slight but significant increase (from 12 to 17%) in total cover over the course of the experiment in the absence of predators (Table 1). In the presence of individual predators (enclosures), as well as in controls, cover of mussels slightly decreased over time, but the trends were not significant (Table 1). Other sessile invertebrate and algal species were scarce and exhibited no clear trends over time or among treatments.

Mussel prey

After transplanted and reattached to the rock surface, mussel survival remained high (>90%) under the predator exclusion treatment but decreased significantly under all predator inclusion treatments (Fig. 2b, Table 3). Transplanted mussels in predator exclusions were still alive a year after concluding the experiment. Significant differences in mussel survival rates were found between predator exclusion and all predator enclosures, as well as among predator species (Table 4, and see below for comparisons among predators). Mortality of mussels in the control plots, in the presence of natural densities of all predators in the study area, was significantly higher than in the exclusion (Fig. 2d, $F = 27.25$, d.f. = 1, 8, $P = 0.0008$).

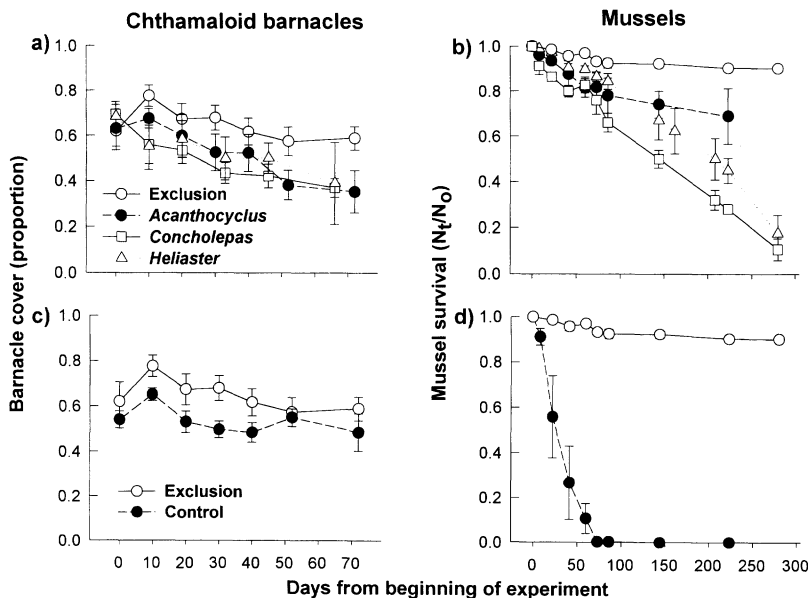


Fig. 2. Changes in barnacle cover (a and c) and mussel survival (b and d) in the different predator enclosures and exclusion treatments as well as in the control plots under natural predator densities. For clarity, predator enclosures and exclusions are presented in the top panels (a and b) and exclusions and controls are presented in the bottom panels (c and d).

Table 1. Summary of ordinary least square regressions of log cover (proportion) versus time performed on each replicate of the experiments conducted in barnacle beds under the different treatments. a) Chthamaloid barnacles, b) bare rock, and c) small *Perumytilus* (intermixed in barnacle beds). a = average intercept; b = average slope; t = value of Student' t test for the null hypothesis that b = 0; P = probability of t value. The standard errors for the slopes (based on independent replicates) are given in parenthesis. Boldface indicates significance at $\alpha = 0.05$.

Treatment	a	b	t	P
a) Barnacles				
Control	-0.680	-0.00214 (0.0013)	1.60	0.1338
Exclusion	-0.379	-0.00271 (0.0009)	3.00	0.0240
<i>Acanthocyclus</i>	-0.419	-0.0107 (0.0018)	5.86	0.0011
<i>Concholepas</i>	-0.465	-0.0096 (0.0004)	21.24	0.0001
<i>Heliaster</i>	-0.476	-0.0070 (0.0015)	4.58	0.0102
b) Bare rock				
Control	-2.622	0.0073 (0.0036)	2.04	0.0622
Exclusion	-3.015	-0.0059 (0.0078)	0.75	0.4805
<i>Acanthocyclus</i>	-2.506	0.0222 (0.0062)	3.58	0.0116
<i>Concholepas</i>	-2.195	0.0243 (0.0026)	9.44	0.0007
<i>Heliaster</i>	-2.235	0.0264 (0.0089)	2.96	0.0414
c) sparse <i>Perumytilus</i>				
Control	-2.083	-0.0030 (0.0031)	0.85	0.4100
Exclusion	-2.374	0.0084 (0.0025)	3.37	0.0150
<i>Acanthocyclus</i>	-2.051	-0.0030 (0.0025)	1.20	0.2752
<i>Concholepas</i>	-2.001	-0.0000 (0.0002)	0.02	0.9855
<i>Heliaster</i>	-1.919	-0.0058 (0.0056)	1.03	0.3610

Prey capture rates

The rates at which predators consumed barnacles, expressed as individuals captured by a predator of unit body mass (c_w), were similar across predator species (Fig. 4a); i.e. gram for gram, all predators consumed barnacles at similar rates (Table 5). This pattern changed when predators fed on mussels, where differences among predator species in their specific efficiency of mussel consumption were significant (Fig. 4b, Table 5). The gastropod *Concholepas* presented the highest predation rate on mussels per gram of predator, followed by *Heliaster* and finally *Acanthocyclus* (Fig. 4b).

Since gram for gram predators consumed barnacles at similar rates, per capita predation rates by an individual of average size were different among predator species because of differences in predator body sizes (Fig. 4c). The highest per capita predation rates on

barnacles were observed in *Heliaster* followed by *Concholepas*, and these two species had significantly higher per capita rates on barnacles than *Acanthocyclus* (Student $t = 3.03$, $p = 0.01044$ and $t = 2.93$, $p = 0.01259$ for pairwise comparisons with 12 d.f. and sequential Bonferroni corrected α 's = 0.017 and 0.025). Per capita predation rates on mussels by an average size predator were similar between *Concholepas* and *Heliaster*, and both were significantly higher than those of *Acanthocyclus* (Fig. 4d, $t = 32.73$, $p < 0.0001$ and $t = 3.12$, $p = 0.01416$, for pairwise comparisons with 8 d.f. and sequential Bonferroni corrected α 's = 0.017 and 0.025).

Prey capture rates by predator populations and effects on prey

Estimates of prey capture rates by the entire predator populations (based on total predator biomass) showed a similar pattern to per capita predation rates among predator species (Fig. 4e, f). In this case, total predation rates on barnacles were not different between *Heliaster* and *Concholepas* and both were an order of magnitude higher than the expected rates of predation by *Acanthocyclus* on barnacles (Fig. 4e). The same pattern among predator species was magnified when predators fed on mussels, with similar rates between *Heliaster* and *Concholepas*, and predation rates two orders of magnitude lower for *Acanthocyclus* (Fig. 4f).

The mean barnacle recruitment observed in caged plots during the course of the experiment was 0.95 (SE = 0.74) individuals per 400 cm² per day, which was slightly higher than the recruitment rate of 0.34 (SE =

Table 2. Results of one way ANOVA's comparing rates of change (slopes presented in Table 1) of a) barnacles, b) bare rock, and c) sparse *Perumytilus* (intermixed in barnacle bed) among the different enclosures (three predator species) and exclusion treatments. Boldface indicates significance at $\alpha = 0.05$.

Source of variation	d.f.	SS	F	P
a) Barnacles				
Treatment	3	0.3805	10.78	0.0002
Residual	20	0.2352		
b) Bare rock				
Treatment	3	0.8096	9.62	0.0004
Residual	20	0.5610		
c) <i>Perumytilus</i>				
Treatment	3	0.1048	2.66	0.0764
Residual	20	0.2633		

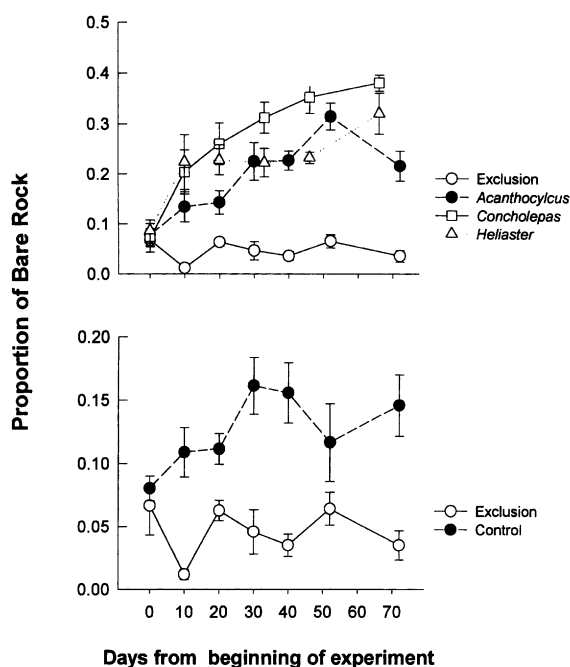


Fig. 3. Cover of bare rock in the experiments conducted in barnacle monocultures under a) the different predator enclosures and exclusion treatments, and b) exclusion and control.

Table 3. Summary of ordinary least square regressions of mussel survival ($\log(N_t/N_0)$) over time performed on each replicate of the experiments conducted in mussel monocultures. a = average intercept; b = average slope; t = value of Student's t test for the null hypothesis that b = 0; P = probability of t value. The standard errors for the slopes (based on independent replicates) are given in parenthesis. Boldface indicates significance at $\alpha = 0.05$.

	a	b	t	P
Control	0.234	-0.0360 (0.0068)	5.29	0.0061
Exclusion	-0.014	-0.0005 (0.0000)	8.00	0.0013
<i>Acanthocyclus</i>	-0.045	-0.0019 (0.0004)	4.78	0.0174
<i>Concholepas</i>	0.149	-0.0052 (0.0012)	4.17	0.0140
<i>Heliaster</i>	0.153	-0.0078 (0.0013)	5.79	0.0044

Table 4. Results of one-way ANOVA comparing mussel survival rate among the different enclosures (three predator species) and exclusion treatments. Analysis was based on slopes of the regressions between $\log(N_t/N_0)$ versus time for each independent replicate. Boldface indicates significance at $\alpha = 0.05$.

Source of variation	d.f.	MS	F	P
Treatment	3	0.000053	11.35	0.0004
Residual	15	0.000005		

0.19) individuals per 400 cm² area per day observed at the same study site over the course of the entire year (Navarrete et al. 2002). We used this latter, more conservative estimate of barnacle recruitment under natural conditions to determine the expected change in

barnacle prey population in the presence of predators. This calculation showed that barnacles could sustain positive population growth in the presence of any single predator species (Fig. 5a). If total predation on barnacles by the three predator species was additive (e.g. no interference among predators), barnacles would not be able to maintain significant positive population growth at this level of recruitment (Fig. 5a); growth rate in presence of all predators was not significantly different from zero.

As observed in previous studies (Navarrete and Castilla 1990a), mussels rarely recruited to the bare rock that was generated by predators which had preyed on adult mussels. Throughout the experiment, few mussels recruited in small crevices and around the perimeter of the mussel patch, usually on the lateral walls of previously established barnacles, rendering an average mussel recruitment rate of 0.0067 (SE = 0.0022) individuals per plot and day. Under these low mussel recruitment rates on primary substrate (mussels recruited at higher rates to the mussel matrix and artificial pads), predation by *Concholepas* or *Heliaster* alone is expected to cause significant declines in mussel population (Fig. 5b). Predation by *Acanthocyclus* alone is not expected to cause a significant decline of mussel population, but their effect could prevent the mussels from attaining significantly positive population growth (Fig. 5b).

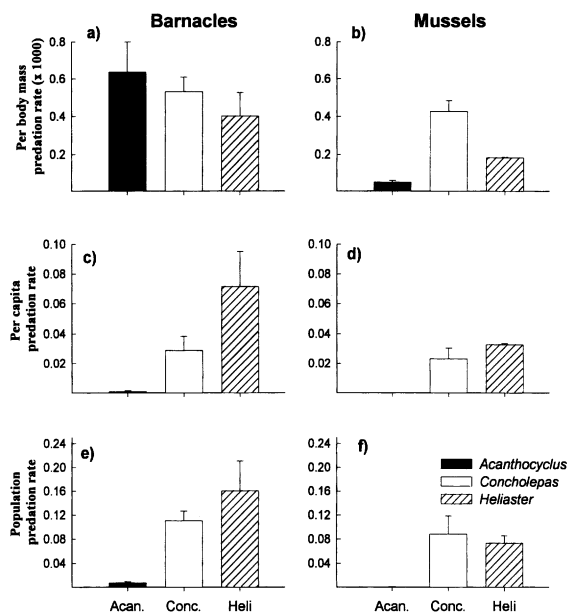


Fig. 4. Components of predation intensity by the three predator species feeding on barnacles and mussels. a) and b) predator efficiency expressed as number of prey captured per unit body mass of predator per unit of time, c) and d) per capita prey capture rates by a predator of average body size, e) and f) population predation intensity.

Table 5. Pairwise comparisons of prey capture rates per gram of predator (c') between predator species feeding on a) barnacles and b) mussels. Sequential Bonferroni corrected significance levels (corrected alpha) were used to judged significance of each comparison, which are arranged in order of the magnitude of differences between means (see text). t = Student-t test statistic, P = probability of t value with 12 and 8 degrees of freedom for barnacles and mussels, respectively.

Comparison	t	P	Corrected alpha	Significance
a) Barnacles				
<i>Heliaster</i> vs <i>Acanthocyclus</i>	1.15	0.273609	0.017	No
<i>Heliaster</i> vs <i>Concholepas</i>	0.88	0.393973	0.025	No
<i>Concholepas</i> vs <i>Acanthocyclus</i>	0.58	0.570341	0.050	No
b) Mussels				
<i>Heliaster</i> vs <i>Acanthocyclus</i>	12.27	0.000002	0.017	Yes
<i>Concholepas</i> vs <i>Acanthocyclus</i>	6.33	0.000226	0.025	Yes
<i>Heliaster</i> vs <i>Concholepas</i>	4.22	0.002930	0.050	Yes

Discussion

Our results showed that in the rocky intertidal zone of central Chile, juveniles of the gastropod *Concholepas concholepas* and of the sea star *Heliaster helianthus* have similarly large per capita and population effects on the competitively dominant mussel *Perumytilus purpuratus*. Their per capita (by an average size individual) and population effects on mussels were more than two orders of magnitude larger than those of *Acanthocyclus gayi* crabs and likely even larger than the effect of other predator species in this system, agreeing well with previous claims that *Heliaster* and *Concholepas* play keystone roles on the structure of intertidal communities (Castilla and Durán 1985, Paine et al. 1985). A roughly similar pattern of population predation intensity was observed when predators fed on barnacles, but the expected consequences for the prey population, and hence the rest of the community, were acutely different to those on mussels.

Mussel and barnacle monocultures represent two very distinctive and persistent states in the rocky intertidal community of central Chile (Durán and Castilla 1989). The mussel *Perumytilus* is the dominant competitor for space at mid-tidal elevations, while barnacles readily colonize and dominate the space when mussels are removed (Paine et al. 1985, Durán and Castilla 1989, Navarrete and Castilla 1990a). In areas where humans had reduced the average size, biomass and

density of the commercially exploited gastropod *Concholepas*, experimental manipulations of *Heliaster* by Paine et al. (1985), showed that the sea star can severely reduce the abundance of mussels.

A separate study showed that following the exclusion of humans from the marine reserve of Las Cruces in 1982, the biomass of *Concholepas* increased dramatically inside the reserve (due to increases in average size and density), leading to the virtual elimination of the mussel bed from the entire reserve (Castilla 1999). While *Acanthocyclus gayi* and *A. hassleri* can consume mussels at fairly high rates (Navarrete and Castilla 1988), they are less efficient mussel consumers per gram of body mass than *Heliaster* and especially *Concholepas*. Moreover, their relatively small size and comparatively low biomass per square meter leads to small or negligible per capita and population effects on mussels. Other mussel predator species in this system (Castilla and Paine 1987), including whelks, other crabs, birds and fish, most likely have even weaker per body mass or per capita effects than *Acanthocyclus* and/or their population effects are low due to low abundance. Thus, the pattern of predation intensity in this intertidal predator guild is highly right skewed, i.e. two strong and several weak effects. This skewed distribution of 'interaction strength' (sensu Paine 1992, Navarrete and Menge 1996) resembles the one reported by Paine (1992) for the herbivore guild at Tatoosh Island, Washington, the carnivore guild at wave exposed intertidal areas of Santa Catalina island, California (Robles and Robb 1993) and the carnivore guild at mudstone habitats of the Ythan River estuary (Raffaelli and Hall 1996).

The efficiency of predation on barnacles, expressed as prey capture rates by a predator of unit body mass, was similar across predator species, with slightly higher capture rates for *Acanthocyclus* than *Heliaster* and *Concholepas*. In contrast, large differences in the per body mass efficiency of mussel removal were observed among predator species. An individual *Concholepas* can remove mussels 2.3 times faster than a sea star and 7.4 times faster than a crab of similar body size. These

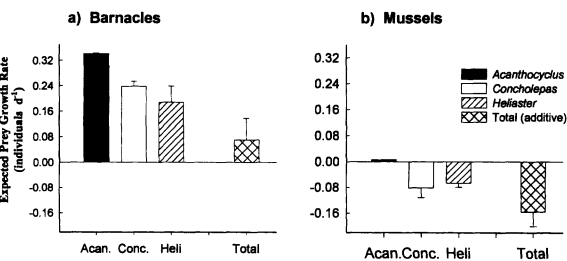


Fig. 5. Expected effects of predation by each predator species on barnacle and mussel population growth rates based on independent estimates of prey recruitment rates. The cross-hatched bar labeled 'Total' corresponded to the expected effect of the three predator species, if they were additive.

differences are probably related to the different feeding mechanisms used by these predators. All predators remove individual barnacles or groups of individuals from the rock surface, generating bare rock patches of varying sizes (Navarrete and Castilla 1990a). When feeding on mussels, crabs select and remove individuals from the bed, sometimes selecting smaller mussels not directly attached to rock surface (Navarrete and Castilla 1990, authors personal observations). In contrast, *Heliaster* usually sit over a clump of mussels, extruding the stomach and removing several individuals at a time (Paine et al. 1985). While *Concholepas* usually feed on only one individual mussel at any given time, they usually remove several mussels in the clump by bulldozing away the mussel-bed and creating bare rock halos (Castilla and Guisado 1979), therefore, they have the largest effect per gram bodyweight in the intertidal zone.

Given the differences in mean and modal body size among predator species and similar predation efficiency per gram of predator, the sea star appears to be the most important barnacle predator on a per capita basis, consuming 2.5 times more barnacles per unit time than a *Concholepas* and 77.4 times more than an *Acanthocyclus* crab of average size. In contrast, differences in predation efficiency on mussels between *Heliaster* and *Concholepas* were compensated by differences in mean body mass. These two species had similar per capita effects on mussels, which were between 277 and 393 times higher than per capita predation by an average size *Acanthocyclus*. Thus, given the predator body size distribution observed at the marine reserve of Las Cruces, average size *Heliaster* and *Concholepas* are equivalent and strong predators on mussels. These estimates do not consider potential intra- or inter-specific interference among predators, which could substantially reduce these estimates (Abrams 1993). However, while interference among predators could reduce the estimated total effect on prey, it is unlikely that interference would substantially alter the observed pattern of predation between the two prey species.

Predation by all predator species in control plots quickly eliminated all mussels transplanted, while survival was high in predator exclusions, evidencing the strong effect of predators on mussels. This strong predation effect agrees well with the expected effect on mussel growth rate (individuals per day) estimated from the difference between recruitment and mortality attributable to predation and other causes (Fig. 5b). Either *Concholepas* or *Heliaster*, by themselves, can produce significant negative growth of mussel populations, which means that any of these predators can control mussel beds in the mid-intertidal zone. In contrast, the crabs *Acanthocyclus* by themselves are not expected to control mussel population growth, as mussels could still maintain positive growth in the presence of these predators.

Unlike the strong effect of predators on mussel growth rates, exclusion of all predators in the system did not have a significant effect on barnacles. Lack of overall effects of predators on barnacles was probably produced by two factors. First, there was a slight but significant increase in the cover of mussels in predator exclusion cages, which probably thwarted the response of barnacles to the release from pressure of predation. Second and unlike mussels, barnacles can recruit directly to bare rock as the rock is being released by predation. Indeed, high barnacle recruitment rates is expected to allow barnacles to sustain positive population growth even in the presence of any single predator species in this intertidal community (Fig. 5a). Additive predation pressure of all three predator species considered in our experiments would be able to control barnacle growth. Assuming interference among predators does not substantially reduce total predation pressure. However, compared to rocky benches in the marine reserve of Las Cruces where this study was conducted, with relatively high barnacle recruitment rates, many sites in central Chile have lower barnacle recruitment (Navarrete et al. 2002) and predators could therefore have more significant effects on barnacles at those sites.

We show that expressing predation on a per body mass basis allows us to estimate population effects using predator biomass (see also Osenberg and Mittelbach 1996). Unlike mean consumer densities or mean population sizes, consumer biomass integrates across the consumer body size spectrum and therefore estimates of population effects become independent of the particular body size distribution of different consumer species. More refined estimates of population predation rates can be obtained by knowing how consumption rate scales with consumer body size. Since this sort of data are difficult to obtain, the scaling of metabolic rate with body size could be used as a proxy for the consumption rate scaling (Peters 1983). By adjusting our estimates of per body mass interaction strength by the common scaling of metabolic rates of 0.75 (Kleiber 1962), was reduced the expected population predation by all predators. This did not substantially change the pattern of predation, however.

Until these investigations, no studies have evaluated the pattern and strength of interactions among predator species in the Chilean rocky intertidal zone. The possibility of interspecific competition or intraguild predation among predator species (Navarrete et al. 2000), especially between *Heliaster* and *Concholepas*, and its consequences for prey populations, should be explored experimentally. Since outside the marine reserve of Las Cruces, humans reduce average individual size and biomass of *Concholepas*, the only de facto keystone predator in the human-dominated Chilean intertidal system is the sea star *Heliaster helianthus*. This same situation makes it difficult to study the full strength of the interaction between these predators, except within human exclusion areas.

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