INDIVIDUAL- AND POPULATION-LEVEL RESPONSES OF A KEYSTONE PREDATOR TO GEOGRAPHIC VARIATION IN PREY

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Abstract. Investigating how food supply regulates the behavior and population structure of predators remains a central focus of population and community ecology. These responses will determine the strength of bottom-up processes through the food web, which can potentially lead to coupled top-down regulation of local communities. However, characterizing the bottom-up effects of prey is difficult in the case of generalist predators and particularly with predators that have large dispersal scales, attributes that characterize most marine top predators. Here we use long-term data on mussel, barnacle, limpet, and other adult prey abundance and recruitment at sites spread over 970 km to investigate individual- and population-level responses of the keystone intertidal sunstar *Heliaster helianthus* on the coast of Chile. Our results show that this generalist predator responds to changes in the supply of an apparently preferred prey, the competitively dominant mussel *Perumytilus purpuratus*. Individual-level parameters (diet composition, per capita prey consumption, predator size) positively responded to increased mussel abundance and recruitment, whereas population-level parameters (density, biomass, size structure) did not respond to bottom-up prey variation among sites separated by a few kilometers. No other intertidal prey elicited positive individual predator responses in this species, even though a large number of other prey species was always included in the diet. Moreover, examining predator–prey correlations at ~80, 160, and 200 km did not change this pattern, suggesting that positive prey feedback could occur over even larger spatial scales or as a geographically unstructured process. Thus individual-level responses were not transferred to population changes over the range of spatial scales examined here, highlighting the need to examine community regulation processes over multiple spatial scales.

Key words: bottom-up effects; community regulation; Heliaster helianthus; *open populations;* Perumytilus purpuratus; *predator–prey relationship; recruitment; rocky intertidal.*

INTRODUCTION

Investigating how food supply regulates the behavior and population structure of predators remains a central focus of population and community ecology. The nature and intensity of these responses will determine the dynamics of the predator–prey system as well as the propagation of these effects through the community (Abrams and Roth 1994, Lima et al. 2003). In the case of predators with broad diets, a common situation in natural communities (Strong 1992, Holt and Lawton 1994, Menge et al. 1994, Polis et al. 1997), a wide variety of individual responses can be expected as prey species change in abundance and productivity, potentially limiting bottom-up effects to higher trophic levels (Strong 1992, McCann et al. 1998, Arim et al. 2007). Moreover, whether individual responses lead to changes in predator populations will further depend on the net energy gains accrued by consuming prey that is directed to reproduction and the predator dispersal scales. Thus

these predator–prey systems can be complex. Yet investigating how variation in prey affects generalist predators is critical to further our understanding of key issues in predator–prey dynamics and community ecology (McCann and Hastings 1997, Menge et al. 2003, Halpern et al. 2006, Arim et al. 2007).

Variation in prey productivity should first influence behavioral responses of predators (e.g., functional and aggregative responses), as these responses generally allow predators to "track" changes in prey abundance with comparatively little delay (Kerfoot and Sih 1987, Murdoch and Bence 1987, Fairweather 1988, Eggleston 1990*a*, *b*, Robles et al. 1995, Abrams 1996). Population-level changes in predator numbers or size structure in response to varying prey productivity follow comparatively longer time courses, and the temporal and spatial scales over which such effects can be observed depend critically on predator dispersal. At spatial scales encompassing the entire metapopulation, over which the system can be treated as essentially closed, strong bottom-up as well as top-down effects have been reported (Worm and Myers 2003, Richardson and Schoeman 2004, Frank et al. 2005, Ware and Thomson 2005). At small spatial scales, from tens to hundreds of

meters, experimental information comes mostly from the study of whelk predators feeding on intertidal mussels and barnacles. These predators are direct developers lacking a pelagic larvae and are capable of responding to varying levels of prey productivity by changes in reproductive success, feeding efficiency, feeding preferences, and movement and mortality rates (Spight 1982, Wieters and Navarrete 1998, Wieters 1999, Sanford et al. 2003), leading to overall positive correlations between predator density and prey recruitment (Wieters et al. 2008). In the case of marine predators with long-lived pelagic larvae, the effects of prey on predator populations are expected to occur over spatial scales that can encompass from a few to tens or even hundreds of kilometers (Witman et al. 2003, Velázquez et al. 2005, Wieters et al. 2007), making it impossible to assess these effects through experimental manipulations. Few studies have examined predator population responses to prey variation in marine open systems at scales commensurate with predator and prey interactions as well as dispersal scales (Witman et al. 2003, White 2007, Wieters et al. 2008). Here we use spatially extensive, long-term information on multi-specific variation in prey recruitment rates and prey abundance along 970 km of the coast of central Chile to assess the potential effects on individual- and population-level variables of a keystone intertidal predator, the South American sunstar *Heliaster helianthus* over a range of spatial scales.

The system

The sunstar *Heliaster helianthus* is a keystone intertidal predator in central Chile, capable of controlling the abundance of the competitively dominant mussel *Perumytilus purpuratus* (Paine et al. 1985, Navarrete and Castilla 2003). *Heliaster* have pelagic larvae, and although their development has not been described in detail, time to metamorphosis is known to be longer than two to three months (S. A. Navarrete, *unpublished data*). Rates of recruitment are therefore expected to be uncorrelated from local feeding performance and reproduction (Gaines and Lafferty 1995, Wieters et al. 2008). However, diet composition, growth, size structure, and mortality rates of those predators that recruit to a given site should be influenced by prey productivity and composition. Since overall biomass is the result of individual sizes and their numbers, among-site variation depends on the relative changes of these variables. Yet because maximal size is a species-specific trait but numbers can be unbounded, unless body size varies widely among sites, biomass variation should largely be determined by variation in density. Studies of monthly recruitment rates of mussels and chthamaloid barnacles over the past seven years have shown persistent, orders-of-magnitude differences among sites (Navarrete et al. 2005, Navarrete et al. 2008). Intertidal abundances (cover) of *Perumytilus* and barnacles also change dramatically across the study region (Broitman et al.

2001, Navarrete et al. 2005). Since growth rates and natural mortality of barnacles and mussels vary little across sites in comparison to recruitment (Navarrete et al. 2005), prey productivity is largely determined by recruitment, and it should be independent of local predator activity (White 2007, Wieters et al. 2007). In this system, our goals were to determine whether variation in prey productivity, largely driven by recruitment from the plankton, led to (1) predictable changes in the diet of this generalist predator, (2) correlated changes in predator size, (3) concomitant changes in density (population abundance) and total biomass of this predator among sites kilometers apart, and (4) stronger positive correlations at larger spatial scales approaching the potential dispersal scales of this predator species.

MATERIALS AND METHODS

Study site

Field surveys and monitoring were carried out between 1998 and 2005 at one to three wave-exposed rocky intertidal platforms (10 to 100 m apart) at each of 16 sites dispersed over 970 km, between 28° and 34° S (Fig. 1). Three of the sites (Montemar, Estación Costera de Investigaciones Marinas [ECIM], and Quisco; Fig. 1) are marine protected areas where harvesting of invertebrates is prohibited or regulated. At ECIM we sampled two sites separated by ~300 m, with one (ECIMsur) slightly more protected from waves than the other (ECIMnor). Further description of sites, sampling methods, and patterns of community structure and recruitment can be found in Broitman et al. (2001), Navarrete et al. (2002, 2005), and Rivadeneira et al (2002). Here we focus on predator–prey relationships.

Prey and predator abundance

Local cover of sessile species and density of small mobile species inhabiting the low and mid intertidal zones were quantified using seven to twelve 50×50 quadrats haphazardly placed along 10–20 m long transects laid down parallel to the coastline at each mid and low shore level (Appendix A). Densities of larger species (*Heliaster*, the gastropod *Concholepas concholepas*, keyhole limpets) were measured in "swept transects" along the mid and low zones of two to three platforms at each site (Appendix A). To estimate *Heliaster* biomass, we used length to wet mass ordinary least squares regressions on log–log data obtained at five sites, spanning the study region (Appendix A). As a way to summarize size structure and the relative contribution of small individuals to total biomass, we calculated the proportion of the sunstar biomass at a site that was accounted for by all individuals 50% or 25% ($L_{50\%}$ and $L_{25\%}$) the size of the maximum *Heliaster* size observed at that site. In this manner, the proportions $L_{50\%}$ and $L_{25\%}$ reflect the shape of the size structure and are independent of average size; i.e., a local population dominated by small individuals will have large $L_{50\%}$ and/or $L_{25\%}$
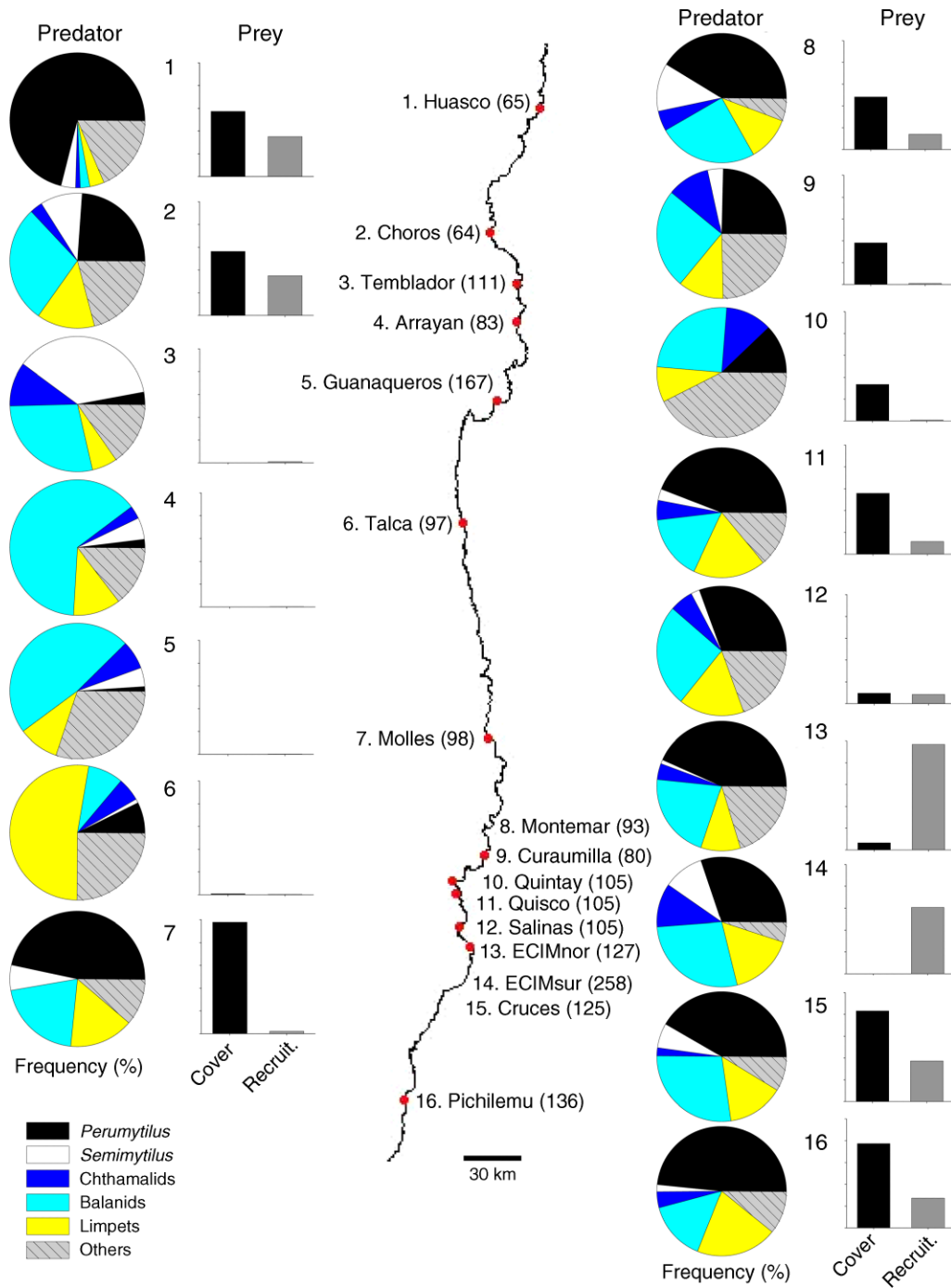
FIG. 1. Map of the study region along the coast of central Chile indicating the location of the 16 study sites. The frequency of the main prey of *Heliaster* is shown for each site (pie charts), next to the average intertidal cover (black bar) and recruitment (gray bar) of the mussel *Perumytilus purpuratus* in the accompanying histograms. The *y*-axis in all histograms ranges from 0% to 100% cover and from zero to 2.4 recruits per day. The numbers of sampled individuals eating at each site are shown in brackets.

relative to a population dominated by large individuals, regardless of the average individual size at the site.

Heliaster *diet*

To characterize *Heliaster* diet, a thorough, systematic search was conducted, and for each sunstar encoun-

tered, we recorded size, whether it was actively feeding, and the identity and size of prey. An individual was considered to be eating if the cardiac stomach was everted or prey were found in or immediately around the oral disc. If eating, all prey were removed with forceps, placed in labeled bags, and taken to the lab, where they

were identified to lowest taxa (generally to species) and measured with vernier calipers or an ocular micrometer under a dissecting microscope. All sunstars were returned to their original position in the field. Sunstars can consume several individuals of the same or different species at the same time, and therefore we calculated the mean number of prey individuals per predator as well as the frequency of predators eating a given prey species for each site, which can be >100%. Prey biomass was calculated using species-specific linear regressions of length to flesh dry mass (Appendix A).

Prey recruitment

Recruitment rates of mussels, barnacles, and limpets, the main prey items consumed by *Heliaster* (see *Results*) were estimated by monthly counts of individuals settling on artificial substrates. Recruitment of chthamaloid barnacles was quantified on 10×10 cm Plexiglas plates covered with Safety-Walk (3M, Maplewood, Minnesota, USA), whereas recruitment of mussels, limpets, and chitons was quantified on 7 cm diameter scrub pads (Tuffy, Clorox Company, SOS, Oakland, California, USA). Tuffy pad collectors provided a reasonably good settlement substrate for limpets and chitons, which reached up to 47 individuals per collector during peak recruitment days. Beginning in January 1998 at 13 sites and February 2003 at Huasco and Choros, five replicate collectors and plates were deployed in the mid and high intertidal zones of each site, respectively, and replaced monthly. Complete descriptions of methods, as well as patterns of mussel and chthamaloid barnacle recruitment variation across the region, can be found in Navarrete et al. (2002, 2005, 2008). Because balanoid barnacles were an important item in the *Heliaster* diet (see *Results*), in spring–summer 2004–2005 and then again in 2005–2006, we deployed five replicate plates in the low intertidal zone of all study sites in order to quantify recruitment of the balanoid barnacle *Notobalanus flosculus*, which recruits mostly in the lower intertidal zone (Lagos et al. 2005).

Data analyses

To evaluate the association between mean prey recruitment rates and predator variables, we first calculated long-term means of prey recruitment for each site and the average of individual or population predator variables for the same sites. The frequency of a given prey was calculated as the number of *Heliaster* individuals eating that prey at a site out of the total number of individuals observed eating. The average number of prey was the average number of individuals of a given prey item found per predator. The proportion of a given prey item was calculated as the fraction of that item from the total (pooled) number of prey individuals. We used a combination of univariate and multivariate approaches to examine predator–prey relationships. For the main prey items in the diet (mussels, balanoid barnacles, and limpets), we examined whether (1) the frequency of predators consuming a given prey item and (2) the proportion of individuals of a given prey per predator were related to the abundance and/or recruitment of that species across sites. Since these relationships are similar to functional responses evaluated across sites, we explored both linear and quadratic trends, and we present the one providing the best fit to the data. Note that since individual predators regularly consume more than one prey at the time, frequencies do not add up to one and are not strictly dependent between prey species. We also investigated whether consumption of a given prey was affected by the availability (abundance and recruitment) of other prey species in the field by using simple and multiple stepwise regressions. To obtain a single measure of prey "availability" that combines both local abundance (cover, density) and renewal rates (i.e., recruitment), we used principal components analyses (PCA) for each of the three main prey species (mussels, barnacles, limpets) and examined the relationships between the second axis (PC2) with predator variables. To examine which prey species, if any, explains variation in overall diet composition, a Bray-Curtis ordination of the 12 most-frequent prey items was used to summarize *Heliaster* diet at each site. We then examined whether this multivariate representation of the diet was related to abundance and/or recruitment of prey in the field.

Simple and multiple regressions were used to examine whether individual predator size, total biomass, and predator density were related to the local abundance and recruitment of prey. In the case of regressions between predator and prey abundances, caution must be exerted in interpreting coefficients of determination, because selection of the independent variable is arbitrary. This will not be the case in the relationship between predator abundance and prey recruitment, since prey recruitment is largely independent from local predator consumption (Wieters et al. 2008). The latter assumption could be violated if predators drive prey populations to very low levels and there is a large fraction of self-recruitment in the prey, or when predator and prey settlement are spatially correlated (White 2007). In any case, the strength and significance of the regressions will be comparable to a linear Pearson correlation.

Because at sufficiently large spatial scales the dynamics of populations of marine organisms with pelagic larval stages should tend to be increasingly closed (Hughes et al. 2000, Hamilton et al. 2006, Wieters et al. 2008), we examined whether the predator population responded to changes in prey over spatial scales larger than the among-sites scale (few to tens of kilometers). We used LOcally WEighted Regression Scatterplot Smoothing (LOWESS; Cleveland 1979) to obtain spatial trends in predator and prey data. LOWESS is a nonparametric regression technique that uses a parametric local polynomial fitting to construct a nonparametric (shape-free) regression between variables (Lagos
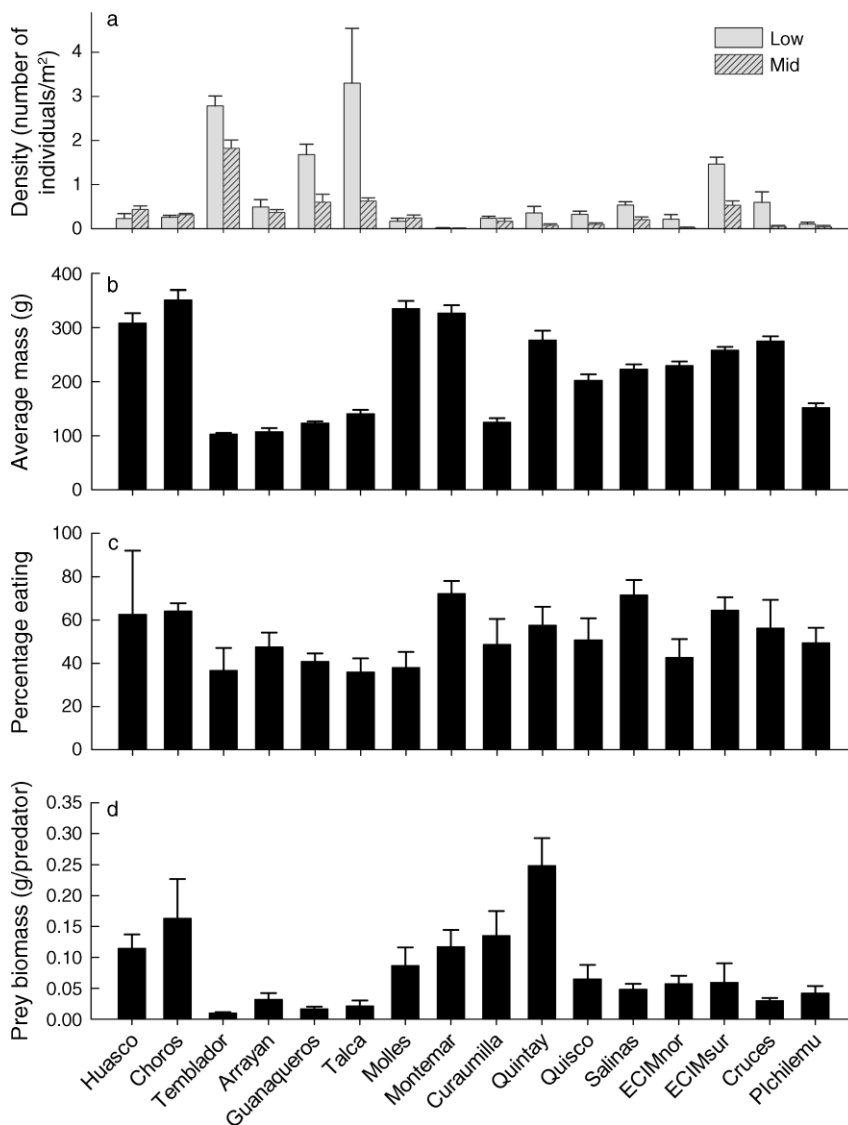
FIG. 2. (a) Mean density (individuals/m^2) by tidal level; (b) average individual mass (g); (c) frequency of predators (%) found eating at least one prey item; and (d) average prey biomass per predator (all prey items pooled) for the sunstar *Heliaster helianthus* at sites ordered from north to south. Error bars indicate +SE.

et al. 2005). We used three values of the *f*-factor or smoothing parameter (Trexler and Travis 1993), which corresponded roughly to 80, 160, and 200 km. The *f*-factors selected for analyses were those producing normal LOWESS residuals and independence from geographical distance (Kolmogorov-Smirnov tests, $P > 0.05$; Trexler and Travis 1993). Since the method keeps degrees of freedom approximately constant along the range of the *x* variable (geographic distances), the actual size of the spatial window used by LOWESS varied somewhat depending on the distribution of sites along the coast. For each LOWESS regression, we retained the predicted predator and prey variables (trends), as well as the residuals due to site variation at that spatial scale. Simple regressions were then used to

examine the predator–prey relationship between trends at the three spatial scales selected, and between residuals due to site variation at those spatial scales.

RESULTS

Heliaster population size and structure

No clear seasonal differences in *Heliaster* density were observed across study sites (mean individuals/m$^2 \pm$ SE = 0.79 ± 0.24 in summer, 0.55 ± 0.22 in fall, 0.70 ± 0.24 in winter, 0.56 ± 0.21 in spring). However, large and significant differences were observed among sites (two-way mixed ANOVA with "site" as a random factor and "tidal level" as a fixed factor, $F_{15, 178} = 6.96$; $P < 0.0001$), but with no monotonic latitudinal trend across the region (Fig. 2a). Significantly higher densities were
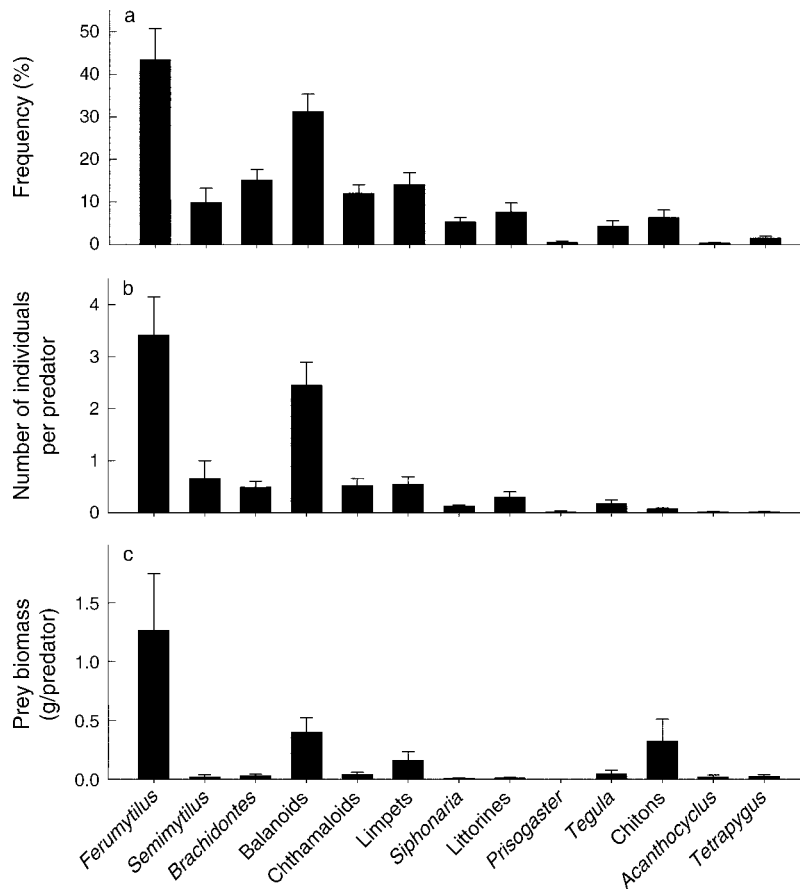
Fig. 3. (a) Frequency of *Heliaster* found eating a given prey item; (b) average number of prey individuals per predator; and (c) average prey biomass per predator for all sites pooled. Error bars indicate +SE. See Appendix B: Table B1 for a complete list of taxa.

observed in the low than in the mid intertidal zone (main effect of site, $F_{1,15} = 5.69$; $P = 0.0222$), and these differences were consistent across the region (site × tidal level, $F_{15,178} = 0.96$; $P = 0.9025$).

Mean size (maximum diameter) of *Heliaster* varied significantly among sites (Wilcoxon test, chi-square = 477.28, df = 15; $P = 0.001$). Length to mass relationships were similar among all sites (ANCOVA, $F_{3,138} = 0.509$; $P = 0.676$; Appendix C: Fig. C1); therefore average mass per site showed the same pattern as maximum diameter, with significant differences among sites (one-way ANOVA using individuals within sites as replicates, $F_{15,4382} = 114.529$; $P < 0.0001$; Fig. 2b). Sunstar population biomass per square meter (g/m^2) varied significantly among sites (one-way ANOVA based on average biomass per quadrat, $F_{15,1460} = 21.377$; $P < 0.0001$; Fig. 2). The percentage of the total biomass that was accounted for by individuals 50% of the maximum size recorded at a site was usually high across the region, between 79% and 99% of the total biomass, while biomass accounted for by individuals 25% of the maximum size varied between 16% and 97% across sites (Appendix C: Fig. C2).

Heliaster *diet*

A total of 1809 sunstars were sampled across the region, and >60 different prey items belonging to eight major taxa were observed in their diet (Appendix B: Table B1). Inspection of rarefaction curves (Gotelli and Colwell 2001) indicated that 15 to 20 individuals are necessary to represent the diversity of the diet at each site, and therefore our sample sizes per site ($n \geq 64$) should provide robust estimates of *Heliaster* diet diversity. There was no seasonal variation in feeding activity (50.7% and 54.6% of animals found feeding in spring–summer and fall–winter, respectively). There was considerable variation among sites in the average biomass of prey eaten per capita (all food items pooled) and to a lesser extent in the frequency of *Heliaster* found eating (any prey item) at the time of surveys (Fig. 2c, d), with no latitudinal trends across the region. These variables were positively correlated (Pearson $r = 0.58$; $P = 0.0190$; log-transformed data), suggesting that increased feeding activity is associated with consumption of larger, usually mobile prey. Across the region, sunstars were most frequently found preying upon the mussel *Perumytilus purpuratus* (Figs. 1, 3a), which also

TABLE 1. Regression statistics for the relationship between the frequency of *Heliaster helianthus* eating a given prey (Table 2A–C) and the proportion of prey individuals (Table 2D–F) per predator vs. prey abundance (cover of sessile species, density of mobile species) and prey recruitment rate measured in the field for the three most frequent prey species.

Prey variable	Frequency eating prey			Number of prey in diet		
	Trend	r^2	P	Trend	r^2	P
Perumytilus						
Cover	Q	0.31	**0.0249**	Q	0.50	**0.0114**
Recruitment	Q	0.54	**0.0091**	Q	0.54	**0.0088**
PC2	L	0.75	**<0.0001**	L	0.74	**<0.0001**
Balanus						
Cover	L	0.02	0.6003	Q	0.04	0.7961
Recruitment	Q	0.14	0.1845	L	0.05	0.4218
PC2	L	0.07	0.3864	L	0.10	0.2864
Limpet						
Density	L	0.16	0.1611	L	0.05	0.4809
Recruitment	L	0.05	0.4238	L	0.10	0.5683
PC2	L	0.01	0.7332	L	0.06	0.4086

Notes: PC2 is the multivariate representation of prey abundance and recruitment. Only statistics for the best of linear (L) or quadratic (Q) fits are given. In all cases $n = 16$ sites, except for limpets because the site Talca ($n = 15$) was an outlier and had to be omitted to avoid spurious relationships. Boldface indicates statistical significance.

dominated per capita prey intake, both in terms of numerical abundance (Fig. 3b) and biomass (Fig. 3c). However, at sites between Choros and Molles (~400 km) *Perumytilus* was nearly absent from the diet, as well as from the intertidal zone (Fig. 1). The second most important prey was balanoid barnacles (primarily *Notobalanus flosculus*) (Figs. 1, 3), which was particularly common in the diet at northern sites (Fig. 1). Limpets were also frequently consumed at most sites. Chthamaloid barnacles were not among the most common or most numerous prey items (Fig. 3), but they reached almost 20% frequency at a site in ECIM and about 15% frequency at Temblador (Fig. 1). In general, there was good agreement between the frequency of predators consuming a given prey and the number of individual prey per predator across the region (Pearson $r = 0.92$; $P < 0.0001$; Fig. 3a, b), and weaker but significant correlations between these and their contribution to total prey biomass (between number of prey and biomass $r = 0.56$; $P = 0.0443$; between frequency and biomass $r = 0.54$; $P = 0.0517$). For instance, while limpets and the mussels *Brachidontes granulata* and *Semimytilus algosus* were frequent and numerous in the diet, they contributed little to overall prey biomass. In contrast, relatively few chitons were consumed less frequently, but contributed significantly to overall prey biomass due to their large size.

Prey availability and Heliaster *individual and population variables*

At sites with higher cover of *Perumytilus* in the mid intertidal zone, *Heliaster* individuals consumed a greater proportion of *Perumytilus* (numbers), and a higher frequency of individual predators consumed this species (Table 1, Fig. 4a), suggesting that sunstars concentrated on mussels when their intertidal abundance was high.

Exceptions did occur, however. For example, the abundance of *Perumytilus* in the intertidal zone was low (<2% cover), yet the proportion in the *Heliaster* diet was high (>60%) at ECIM (Fig. 1). This is apparently explained by the high mussel recruitment at this site and the fact that *Heliaster* can sit on algal turf (mostly *Gelidium chilense*) and consume small mussel recruits before they overgrow the turfs and become visible in field surveys (Wieters 2005). Consequently, there were highly significant correlations between the proportion of *Perumytilus* in the diet, the frequency of *Heliaster* eating this mussel, and mussel recruitment rate across sites (Table 1). A principal components analysis (PCA) multivariate representation of *Perumytilus* cover and recruitment across sites (PC2–*Perumytilus*) explained >74% of the variation in frequency and numbers of this mussel species in the *Heliaster* diet (Table 1, Fig. 4b, c). In contrast to *Perumytilus*, inclusion of balanoid barnacles in the diet was not correlated with their intertidal cover, recruitment, or a multivariate combination of both (Table 1, Fig. 4d–f). Similarly, the inclusion of limpets in the *Heliaster* diet was not significantly related to variation in limpet density or recruitment across sites (Table 1, Fig. 4g–i). On the other hand, the total (pooled) consumption of balanoid and chthamaloid barnacles and limpets per predator was significantly and negatively related to PC2–*Perumytilus* (Fig. 4j).

Results of multiple stepwise regressions (Table 2) were concordant with patterns observed using single-prey variables. The cover and/or recruitment of *Perumytilus* across sites were the only significant variables explaining not only the inclusion of this species in the diet, but also the degree to which *Heliaster* fed on barnacles and limpets (Table 2). The only exception was the number of
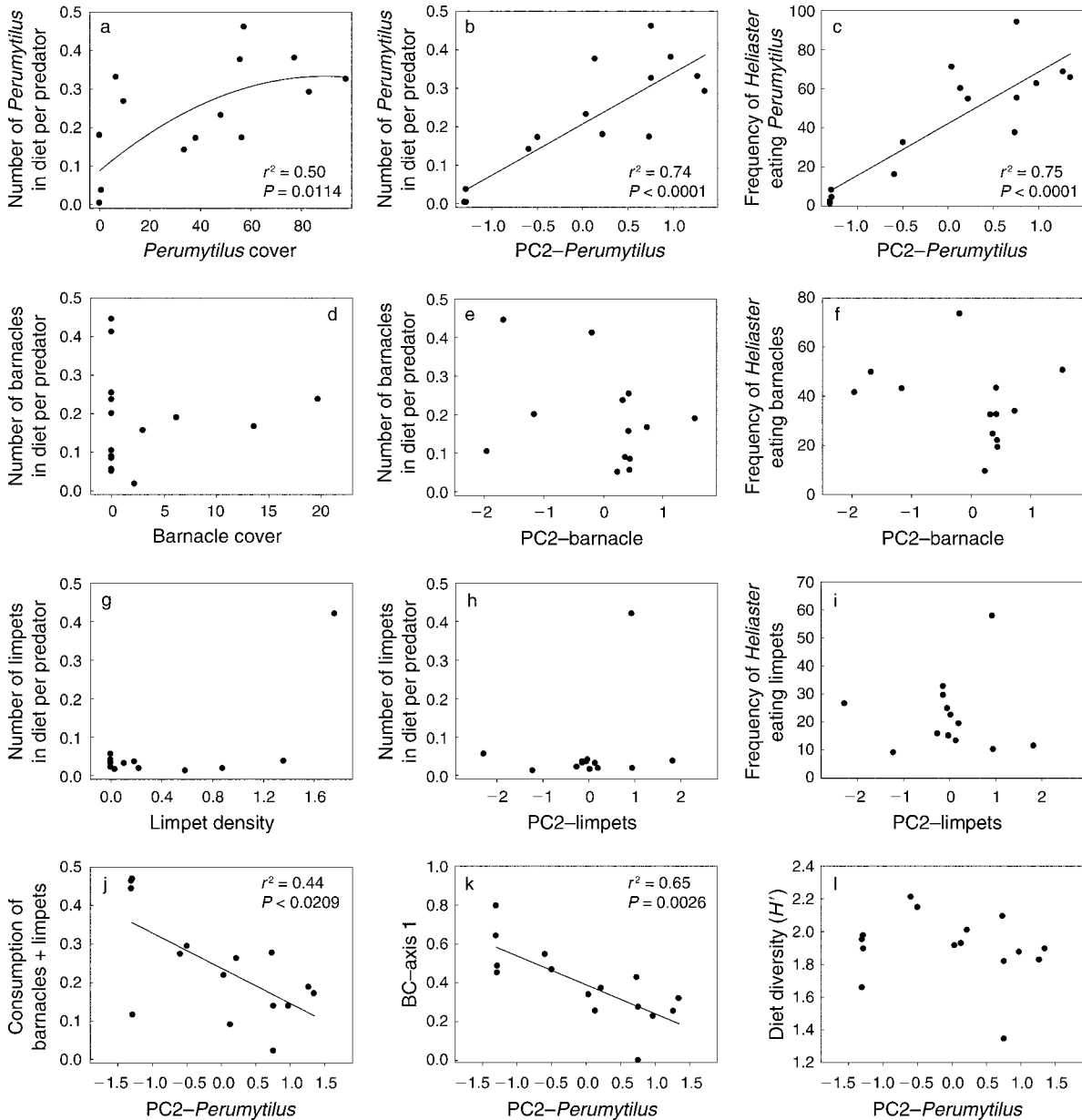
FIG. 4. The relationship between the availability of the main prey and the diet of *Heliaster* across sites. In all cases, "PC2" followed by a prey item refers to the multivariate representation of prey availability given by the second axis of principal components analysis considering intertidal abundance (cover of barnacles or mussels, density of limpets) and long-term recruitment rate (individuals per month) across sites. Panels a, d, and g show the relationship between the average number of prey in the diet per individual predator and the intertidal abundance of that prey species. Panels b, e, and h show how numbers in the diet change according to simultaneous variation in prey intertidal abundance and recruitment (PC2). Panels c, f, and i show changes in the frequency of individuals of the local predator population consuming a given prey and the multivariate representation of prey availability. The bottom three panels show the relationship between the availability of *Perumytilus* in the field and (j) consumption of barnacles and limpets, (k) multivariate composition using Bray-Curtis ordination for the 12 most frequent prey items, and (l) diversity (breadth) of the diet. Whenever the relationship was significant, the best linear or quadratic fit is shown in each panel.

limpet individuals found per predator, which was negatively related to the barnacle recruitment rate across sites. Moreover, recruitment and cover of *Perumytilus* were the only prey variables that singly or in combination (PC2–*Perumytilus*) were significantly associated with variation in diet composition, as summarized by the first axis of Bray-Curtis ordination of the 12 most-frequent prey items in the diet (Table 2, Fig. 4j). While *Perumytilus* recruitment and cover caused significant changes in *Heliaster* diet composition, neither diet richness nor diversity showed correlations with any prey variable (Fig. 4k, l).

TABLE 2.   Results of multiple stepwise regressions.

Regression parameter	Significant variables in best model	r^2	P
A) Frequency eating *Perumytilus*	+PC +PR	0.85	<**0.0001**
B) Frequency eating *Balanus*	−PC	0.33	**0.0306**
C) Frequency eating limpets	−PR	0.45	**0.0235**
D) Number *Perumytilus* in diet	+PC +PR	0.90	<**0.0001**
E) Number of *Balanus* in diet	−PC	0.32	**0.0269**
F) Number of limpets in diet	−BR	0.41	**0.0175**
G) BC-scores 12 prey	−PC −PR	0.63	**0.0064**
H) Average *Heliaster* size	+PC +BR	0.62	**0.0052**
I) *Heliaster* density	−PC	0.62	**0.0003**
J) *Heliaster* biomass	No variable selected		

Notes: (A–C) the frequency of *Heliaster helianthus* eating a given prey, (D–F) the average number of prey individuals per predator, (G) multivariate Bray-Curtis composition of diet for 12 most frequent prey (BC-Scores 12 prey), (H) average predator size, (I) predator density, and (J) total predator biomass against prey abundance (cover of sessile species, density of mobile species) and prey recruitment in the field of mussels, barnacles, limpets, and chitons. Variables included in models are PC, *Perumytilus* cover; PR, *Perumytilus* recruitment; BC, *Balanus* cover; BR, *Balanus* recruitment; LD, limpet density; LR, limpet recruitment; ChD, chiton density; ChR, chiton recruitment; SC, *Semimytilus* cover; and SR, *Semimytilus* recruitment. The sign indicates whether the relationship with prey was positive or negative. The coefficient of determination (r^2) and significance (P) for the best model selected (simple or multiple) are also shown. Boldface indicates statistical significance.

Cover of *Perumytilus* explained 44% of the variance in average *Heliaster* size across the entire region (Fig. 5a). Stepwise multiple regression selected *Perumytilus* cover and balanoid barnacle recruitment as the only variables explaining significant (62%) variation in *Heliaster* size (Table 2). In contrast, the total biomass of *Heliaster* was not significantly correlated with mussels or any other prey variable (Fig. 5b, Table 2). Size structure, as summarized by $L_{50\%}$ and $L_{25\%}$ (Appendix C: Fig. C2) was not correlated with either abundance or recruitment of mussels or barnacles ($P > 0.05$; Fig. 5c). There was a highly significant but negative relationship between predator density and intertidal mussel cover (Fig. 5d), suggesting that *Heliaster* control mussel abundance at
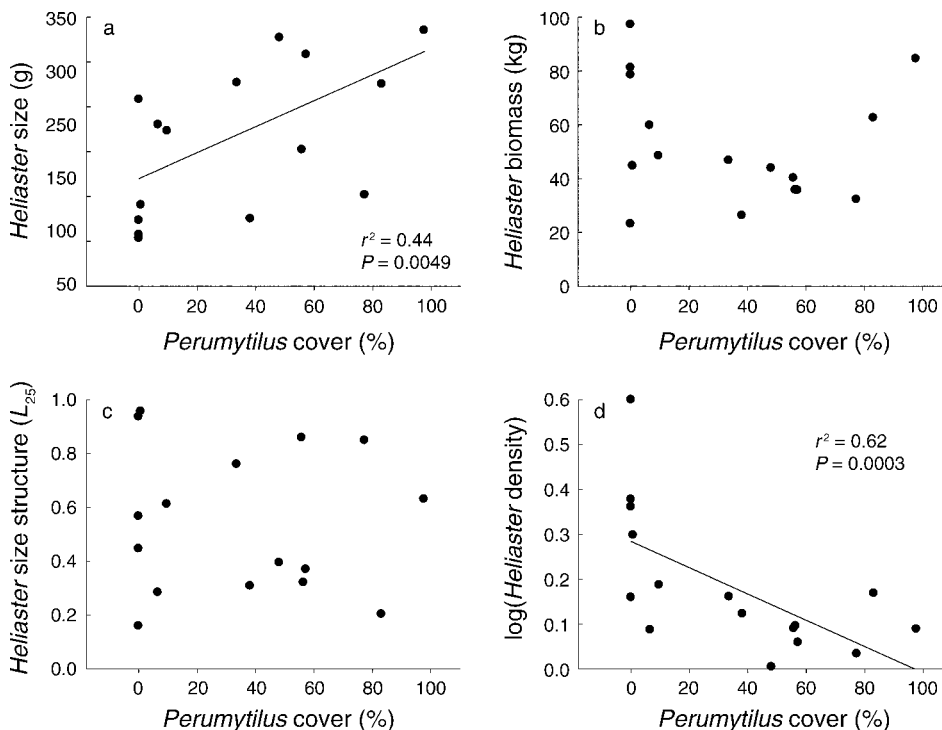

FIG. 5.   Ordinary least squares regression between the cover of *Perumytilus* (measured as a percentage of the substratum) and (a) average individual size (mass), (b) total biomass, (c) a measure of the contribution of small individuals to total biomass (L_{25}), and (d) density of the sunstar *Heliaster helianthus*.
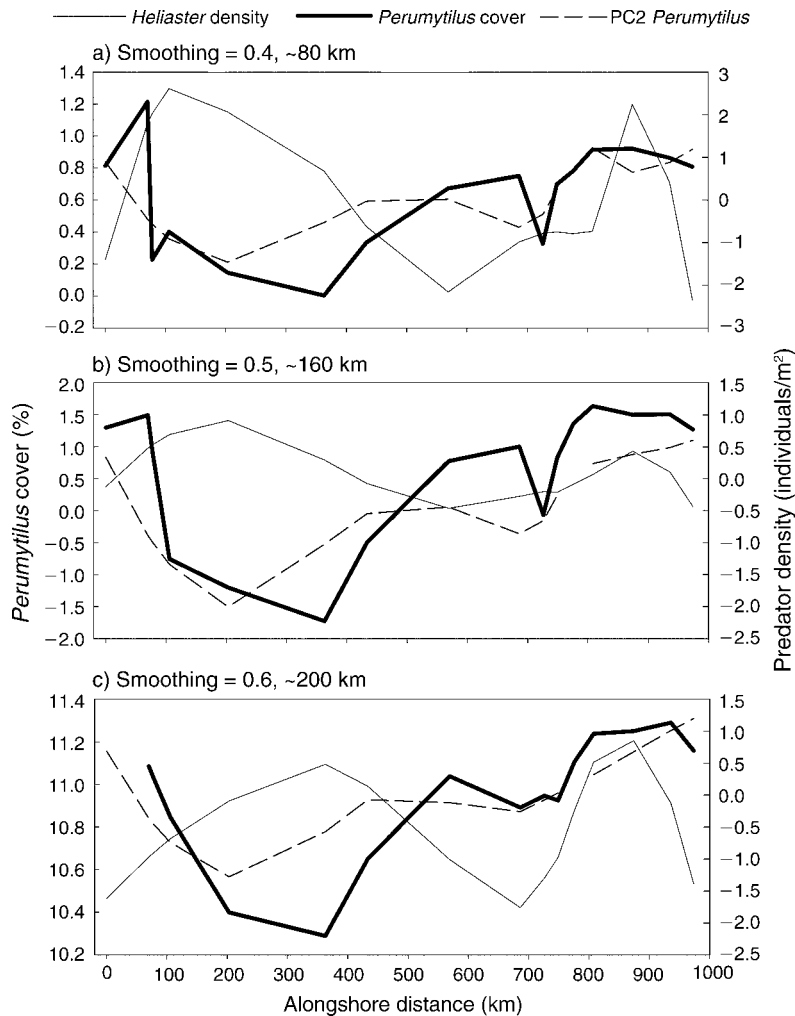
FIG. 6.   Results from LOWESS regressions across the region using three different smoothing parameters that correspond roughly to spatial scales of (a) 80 km, (b) 120 km, and (c) 200 km. The trends in *Perumytilus* cover and *Heliaster* density are shown in each panel.

sites across the region. No other prey variable was selected in stepwise regressions (Table 2).

Predator–prey correlation over increasing spatial scales

Using LOWESS smoothing we examined correlations between prey productivity and predator abundance over spatial scales of ~80, 160, and 200 km. As prey variables we tested mussel cover, mussel recruitment, and the PC2 combining cover and recruitment, but in all cases increasing the spatial scale of analysis did not change the general pattern observed; i.e., we found no evidence of bottom-up effects of prey on predator population variables (Appendix B: Table B2). Negative correlations between residuals (due to sites after removing larger spatial trends) were generally strengthened. As an example, Fig. 6 presents the trends in *Heliaster* density, *Perumytilus* cover, and PC2–*Perumytilu*s at the three different spatial scales. The LOWESS smoothing also suggested the existence of two separate subregions at

about half the domain of the study site (Fig. 6), with weakly negative correlations over the northern section of the study area (~0–700 km) and slightly positive correlations over the remainder. This change in trends across central Chile corresponded well with regional discontinuities in mussel recruitment and oceanographic regimes reported in previous studies (Navarrete et al. 2005). However, the domain and resolution of our study is not sufficient to resolve trends over regional scales.

DISCUSSION

Our results show that despite the broad diet of *Heliaster helianthus*, this generalist keystone predator responds to changes in supply of one apparently preferred prey, the competitively dominant mussel *Perumytilus purpuratus*. Individual-level parameters (diet composition, per capita prey consumption, predator size) responded to mussel abundance and recruitment, whereas population-level parameters (density,

biomass, size structure) did not respond to bottom-up factors. Examining predator–prey correlations at ~80, 160, and 200 km did not change this pattern. Thus predator abundance in this system appears to be not influenced by local prey abundance, presumably because of the dispersal scales of the predator with long-lived pelagic larvae. Here we discuss the consequences of these results for the ecology of rocky shore communities and our understanding of predator–prey relationships in the marine environment.

As suggested by previous studies at one site in central Chile (Cruces; Paine et al. 1985), the dominant mussel *P. purpuratus* was the most important and apparently preferred species of this keystone predator across the region. Across sites where recruitment and/or cover of *Perumytilus* was high, *Heliaster* individuals increased the consumption of this species in a form resembling a linear or Type II functional response. The reported preference for the mussel *Semimytilus algosus* over *Perumytilus* at a site in Peru, >2000 km to the north (Tokeshi 1989), could reflect differences in mussel availability at these sites and/or behavioral differences fixed in the predator population. Our results also showed that the second most important prey species reported by Paine et al. (1985) at Las Cruces, chthamaloid barnacles, was common in the *Heliaster* diet only around this locality but not when examined over a larger number of sites. Across the region, the second most important prey items of *Heliaster*, in terms of frequency and biomass, were balanoid barnacles and limpets, which are therefore expected to make a larger contribution to the maintenance of predator populations. However, *Heliaster* did not show any measurable responses to among-site changes in abundance (cover, density) or renewal rates (recruitment) of these prey species, even after statistically controlling for changes in *Perumytilus* availability. Moreover, regardless of their local abundance, consumption of barnacles and limpets decreased with increasing recruitment and cover of *Perumytilus* in the field. These results suggest a pattern of complex individual responses to prey variation in this sunstar species, which seems to characterize other generalist predators (Rutz and Bijlsma 2006, Arim et al. 2007).

The negative correlation between *Perumytilus* abundance and/or recruitment and the consumption of balanoids, chthamaloids, and limpets suggests there is potential for indirect effects between prey species mediated through the predator (Holt 1977, Abrams et al. 1998). Since there are no measurable numerical responses by *Heliaster* to increased prey productivity, a positive effect of *Perumytilus* on barnacles and limpets could be observed: at sites where recruitment or cover of *Perumytilus* is high, per capita predation pressure exerted by *Heliaster* on limpets and barnacles should be lower. Since recruitment of *Perumytilus* is largely controlled by physical transport processes and is independent from local predation pressure (Navarrete et al. 2005, Navarrete et al. 2008, Wieters et al. 2008),

persistent physical oceanographic processes could ultimately control the intensity of indirect interactions between prey species. Further experiments could evaluate this type of indirect interaction, comparing predation pressure across different sites while accounting for potential direct interactions between prey species (e.g., competition) within sites. A theoretical context for such studies can be provided by metacommunity models (Leibold et al. 2004, Holt and Hoopes 2005), which deserve more attention by marine ecologists.

Interestingly, increased representation of *Perumytilus* in the diet did not lead to a decrease in diet breadth (richness or diversity). This is probably explained by the idiosyncratic feeding mechanism of *Heliaster* and other sunstars and the fact that a large number of invertebrate species live in the mussel beds (Prado and Castilla 2006). When *Heliaster* feed on mussels, they also consume individuals of other species found in the mussel matrix. Apparently sunstars cannot physically reject these "accidental prey" once in the oral region, or the cost of rejecting them and selecting only the mussels is too high. Therefore, increasing mussel consumption does not prevent them from also consuming other prey, sometimes in large numbers.

Determining whether predators respond to variation in prey productivity, and over which spatial and temporal scales, remains central to understanding the relative influences of top-down and bottom processes in community regulation (Power 1992, Menge et al. 2003, Witman et al. 2003, Halpern et al. 2006). The typically large dispersal scales of most marine species with pelagic larval stages (Kinlan and Gaines 2003, Siegel et al. 2003) imposes additional conceptual and logistic difficulties, since the gains accrued from consuming local prey are mostly exported to other locales, making experimental manipulations nearly impossible. Robles et al. (1995) attempted one of the largest manipulations of prey conducted in rocky shores. They added mussels *Mytilus californianus* to 0.4×6 m plots to simulate areas of increased prey recruitment and observed the response of the seastar *Pisaster ochraceus*, which rapidly aggregated to the experimental prey additions. However, although such rapid responses will likely have positive effects on individual growth and reproduction of predators, they are better understood as spatial rearrangement or aggregative responses to prey patches rather than as persistent changes at the population level. Our results show that at the scale of sites a few kilometers apart, individual-level responses of *Heliaster* do not generate changes in local populations (density, biomass, size structure). Because populations of species with pelagic larval stages become increasingly closed as we increase the spatial scale of observation (Gaines and Lafferty 1995, Witman et al. 2003, Hamilton et al. 2006, Wieters et al. 2008), the positive effect of prey on predators should arise as one approaches dispersal scales of the predator species. However, our statistical analyses of mesoscale trends using nonparametric regressions

showed no evidence of bottom-up effects on the predator for any of the prey species examined singly or pooled. Considering that *Heliaster* appears to have a long-lived larval stage (>90 days), it is possible that spatial scales >~200 km must be examined to encompass demographic effects induced by prey productivity. Indeed LOWESS smoothing suggested the existence of two separate subregions at scales of hundreds of kilometers (Fig. 6c), with changes in the direction of correlations at ~32° S (~700 km in Fig. 6). Although we could not resolve this break due to the limited domain and resolution of our study, it is interesting that it coincides well with regional discontinuities in mussel recruitment and oceanographic regimes that occur about this latitude in central Chile (Navarrete et al. 2005).

Besides studies based on fisheries or basin-scale type of data (Frank et al. 2005, Ware and Thomson 2005), a few studies have examined predator population responses to prey variation in marine open systems over scales commensurate with predator and prey interactions as well as dispersal scales. Unfortunately, there are large differences in spatial and temporal scopes as well as methods used in different studies, making it difficult to compare results directly. For instance, Menge et al. (1994) and Navarrete and Menge (1996) found positive correlations between bottom-up prey input, predator biomass, and top-down control by seastar and whelk predators on mussel prey at two sites 70 km apart in Oregon, USA. But a more extensive spatial study on this same predator–prey system, including >20 sites between Oregon and California over 2100 km, showed no correlations between prey abundance or recruitment and the population density of seastars (Wieters et al. 2008). Wieters et al. (2008) provide a theoretical model to explain their results and suggest that positive correlations could be observed at some sites, whenever predator and prey recruitment rates covary over space, which does not seem to occur across the Oregon–California region. A pattern of positive association in predator and prey recruitment has been observed in tropical fish across sites on St. Croix Island (White 2007). Probably the most insightful study on the bottom-up effects of prey recruitment on open predator populations conducted over a large spatial scale (120 km) is the work by Witman et al. (2003) who investigated the effects of a single massive recruitment event of *Mytilus edulis* on *Asterias* spp. seastars and other mussel predators on the coast of New England, USA. The authors found positive bottom-up effects of prey recruitment on seastar and crab abundances across 17 sites a few months following the massive prey input. Two to three years after the recruitment event, mussels had been consumed at most sites, and seastar abundances had declined throughout the region. While apparently contradictory with our results, which show no bottom-up effects of prey when averaging over several years, we believe results actually are strikingly similar and coherent with the view that local and regional-scale processes simultaneously influence the dynamics of benthic communities. As discussed by Witman et al. (2003), one of the mechanisms driving positive among-sites correlation is local aggregation (behavioral) responses triggered by "masting" mussel recruitment. Indeed, the positive predator density response was an all/nothing type of effect observed most clearly between sites that received massive prey recruitment and those that did not (Witman et al. 2003; Fig. 4a). After two to three years the positive predator–prey correlation had all but disappeared as seastar density declined to the low levels observed during the previous 16 years. Our study was not designed to evaluate temporal changes following prey recruitment, and no such massive mussel recruitment events have been observed in nearly 10 years (Navarrete et al. 2008), but such time responses could very well occur. On the coast of Maine, increased prey recruitment caused population-level responses of seastars, which were observed as increased predator reproductive output and augmented seastar recruitment within the entire region. A biophysical fluid dynamic model and empirical data (Witman et al. 2003) show that positive bottom-up effects are observed across the entire 120-km region studied, and probably over an even larger section of the coast. Thus averaging responses over longer periods of time will lead to no among-site predator–prey correlations, unless seastar and mussel settlement are spatially correlated. Yet periodic massive prey recruitment, as they seemed to reoccur on New England (J. Witman, *personal communication*) could have great effects on the predator metapopulation. Our failure to find a positive correlation between predators and prey, even when examining trends over ~200 km, could be due to the apparently much longer larval duration of *Heliaster* (more than two to three months; S. Navarrete, *unpublished data*) than *Asterias* (two to five weeks; Witman et al. 2003) and the limited power of our analysis at those scales. But it could also suggest that positive feedback from prey to predators occurs in a geographically diffuse manner at all but the entire metapopulation scale.

In summary, the strong top-down control exerted by this predator species on the competitively dominant mussels, as demonstrated experimentally (Paine et al. 1985, Navarrete and Castilla 2003), is clearly reflected in the tight negative correlation between *Heliaster* density and mussel cover we observed among sites throughout the region. Functional responses and changes in predator size can be observed as responses in availability of a single preferred prey, despite the continuous inclusion of a large number of prey species. However, these individual-level responses were not transferred to population changes over the range of spatial scales examined here, highlighting the need to examine community regulation processes over multiple spatial scales.

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APPENDIX A

A description of field methods used to quantify prey abundance, prey biomass, and length to wet mass of *Heliaster helianthus* (*Ecological Archives* E089-116-A1).

APPENDIX B

Tables showing prey items consumed by *Heliaster helianthus* in central Chile and statistics from LOWESS regressions on *Heliaster* density and prey abundance (*Ecological Archives* E089-116-A2).

APPENDIX C

Figures showing the relationship between the maximum diameter and wet mass of *Heliaster helianthus* and size distributions and cumulative seastar biomass at all study sites (*Ecological Archives* E089-116-A3).