Feeding ecology of the subantarctic sea star *Anasterias minuta* within tide pools in Patagonia, Argentina

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Received 24-VIII-2007. Corrected 06-XI-2007. Accepted 17-IX-2008.

Abstract: The feeding ecology of the brooding sea star *Anasterias minuta* within tide pools was examined in Central and South Patagonia. 8 470 observations of sea stars were made. *A. minuta* does not feed while brooding. It consumes a wide range of prey, including molluscs and crustaceans, and can be regarded as a generalist or opportunistic predator. The purple mussel *Perumytilus purpuratus* was the most abundant prey item (57.6%). Other important prey were the gastropod *Pareuthria plumbea*, the isopod *Exosphaeroma lanceolatum* and the mussels *Aulacomya atra atra* and *Mytilus edulis platensis*. The proportion of sea stars feeding on sessile prey increases with sea-star size. A significant positive correlation was found between the size of the sea star and the size of the most frequent prey. The diet was fairly constant throughout the year, but diet composition differed between sites, shore level and sea-star size. The diversity of prey consumed by *A. minuta* was highest on the semi-exposed coast of Caleta Cordova Norte during the temperate season on the infralittoral fringe. *A. minuta* does not eat prey in proportion to its abundance beneath rocks within tide pools at the infralittoral fringe. Generally, the sea star consumed *P. purpuratus* and the gastropod *P. plumbea* more than other prey, even when they were not the most abundant prey present. At the midlittoral zone of the semi-exposed coast of Caleta Cordova Norte, the sea star feeds on prey species accordingly to their abundance. Larger *P. purpuratus* and *E. lanceolatum* were eaten disproportionately more often. *A. minuta* may have an opportunistic feeding strategy, taking unattached, wave-washed mussels when available rather that attached mussels. Consequently, it may have a variable impact on the community structure. Rev. Biol. Trop. 56 (Suppl. 3): 311-328. Epub 2009 January 05.

Key words: *Anasterias*, Patagonia, Feeding ecology, *Perumytilus*, Intertidal.

The feeding ecology of sea stars, especially boreal species, has been widely studied (Feder & Christensen 1966, Mauzey *et al.* 1968, Sloan 1980). The majority of sea stars are carnivorous, and can be regarded as major predators in their habitats (Paine 1974, Menge 1982, McClintock & Lawrence 1985, Himmelman *et al.* 2005). Predation is an essential factor in the regulation of species abundance and composition in marine benthic communities (Paine 1974, Robles 1987, Gaymer *et al.* 2001). Several works (Paine 1994, and references therein) have indicated the significance of intertidal sea stars to intertidal ecology, and note that it may play an important role in the maintenance of the zonation patterns and the community stability and diversity. Ecological studies on the feeding habits of sea stars from Patagonia, Argentina are scarce (Pucheta & Urban 1989, Gil 2002, Gil & Zaixso 2007). The genus *Anasterias* includes several species of wide sub-Antarctic distribution (Perrier 1891, Fisher 1940, Bernasconi 1964, Hernández & Tablado 1985, Clark & Downey 1992, Pearse & Bosch 1994).

Anasterias minuta is an oral brooding species and the most abundant intertidal sea star in Central and South Patagonia (Salvat 1985, Bertness *et al.* 2006, Gil & Zaixso 2007). It is widely distributed along the Patagonian coast, including the Malvinas Islands, and occurs from middle intertidal zone to 80 m (Bernasconi 1964).

Although *A. minuta* is a common predator and prominent member of intertidal and shallow sublittoral communities (Gil 2002, Zaixso 2004, Bertness *et al.* 2006, Gil & Zaixso 2007), its significance in regulating the community structure is uncertain since quantitative data on diet composition and foraging behavior are lacking. Gil and Zaixso (2007) studied the relationships between predatory and brooding activities and found a seasonal feeding cycle. The maximum feeding frequency was during the austral summer and was related, at least in part, to the female brooding habits. The feeding frequency was also positively correlated with seawater temperature and sea-star size, but no differences were found along a shore-level gradient. Female *A. minuta* do not feed while brooding (Gil 2002, Gil & Zaixso 2007). According to Blankley and Branch (1984), females of the congeneric species *Anasterias rupicola*, from the sub-Antarctic Marion Island, also broods eggs orally but is unusual in feeding on prey while doing so. Cooperative prey capture behaviour is also described for *A. rupicola*, where large prey are captured by a group of sea stars (Blankley & Branch 1984).

The purpose of this study was to: (1) assess the diet of *A. minuta* in tide pool habitats, (2) evaluate temporal and spatial patterns related to diet composition, (3) evaluate the effect of body size, shore zone and food availability on diet composition, and (4) analyze the relationship between sea-star body size and prey size.

MATERIALS AND METHODS

Study area: This study was conducted from September 2000 to December 2001 on the exposed coast of the Foca Peninsula (henceforth: FP; 47º45' S & 65º50' W), located ca. 4 km northeast of Puerto Deseado (South Patagonia) and at the semi-exposed coast of Caleta Cordova Norte (henceforth: CCN; 45º43' S & 67º22' W), located ca. 21 km north of Comodoro Rivadavia (Central Patagonia). Additional observations were made during the summer and winter of 2006. Both sites were located on the east coast of Patagonia, Argentina (Fig. 1), and consist of hard bedrock platforms with extensive and numerous tide pools and rocks that provide shelter for sea stars during low tides. The rocky shore at FP is mainly composed of basaltic hard substrata, while CCN is composed of relatively soft sedimentary rock. At both sites, the intertidal shows a common zonation pattern with: (1) a high-shore fringe dominated by *Balanus glandula* and cyanobacteria, (2) a midlittoral zone dominated by dense beds of purple mussel (*Perumytilus purpuratus*), and (3) a low-shore zone (infralittoral fringe) dominated by the ribbed mussel, *Aulacomya atra atra,* and *Corallina officinalis* (Zaixso & Pastor 1977, Zaixso 2004, Cabezas *et al.* 2007, Zaixso *et al.* in press). However, some minor variations on community composition may exist between sites. For instance, the introduced barnacle *B. glandula* is more abundant at the high shore fringe at CCN than FP.

The sampling areas are subjected to a daily tidal cycle that includes two low tides and two high tides, with mean and maximal fluctuations of approximately 4 and 5.8 m, respectively. The salinity in FP is ~ 32.4 ups with some minor variation resulting from the winter flow of the Deseado River (Kuhnemann 1969). At CCN salinity fluctuates between 33.3 and 33.9 ups (Zaixso, unpublished data).

A. minuta occurs in the intertidal and sublittoral zones. Intertidal and scuba diving surveys have found that on the coast of Central Patagonia *A. minuta* is more abundant on intertidal platforms (Gil 2002) and shallow sublittoral zones (H. Marraco, pers com). In the intertidal of the studied sites, small individuals (<20 mm, arm length) are mainly hidden under the mussel matrix found on mature mussel beds or on the underside of rocks. Medium size and large individuals (≥ 20 mm, arm length) are encountered primarily on the undersides of rocks in tide pools and within crevices during low tide.

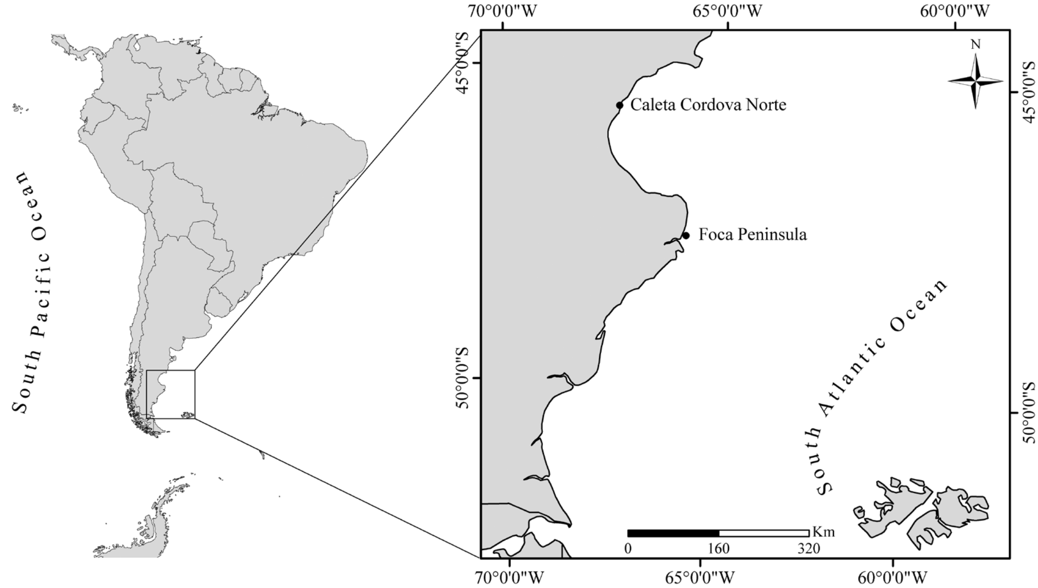

Fig. 1. Location of the two study areas, Foca Peninsula and Caleta Cordova Norte in South and Central Patagonia, Argentina.

Field survey and laboratory analysis: Surveys of sea-star activity were carried out monthly at both sites. During each survey, 200-300 sea stars encountered under rocks in tide pools were removed from the substrate, observed and left undisturbed in the same area. Both rocks and tide pools were randomly selected. The observations were made during low tide at daylight hours because of the difficulty of observing animals during high tide on the exposed rocky shore (due to high wave activity). The activity at CCN was recorded as: (1) non-feeding (e.g. inactive or brooding individuals) or (2) feeding. Shore zones were also recorded for each sea star as: (1) midlittoral zone (between 3-1.20 m of tidal range) or (2) infralittoral fringe (below 1.20 m of tidal range). Monthly variation in the feeding frequency at FP was reported by Gil and Zaixso (2007). Sea stars were regarded as feeding only if their cardiac stomach was clearly everted over prey. Prey items were identified at species level, and the predator-prey size relationship was recorded. Sea-star arm length (R) was defined as the distance from the center of the disc to the extremity of the longest arm. Prey measurements taken were: (1) anterior-posterior length for mussels, chitons, limpets and isopods, (2) columellar length for spiraled shells gastropods and (3) carapace length for crabs. Since some isopod prey were partly digested, we estimated the total length using functional relationships (Gil 2002) between anterior-posterior length against cephalic plate width and telson length. All measurements were made using calipers (0.1 mm).

To estimate the availability of prey in the environment, all potential prey within 20 randomly placed quadrats (0.25 m^2) on the underside of rocks were cleared at all sites and shore levels. All organisms within each quadrat were counted, measured and identified at the species level. We did not observe the escape of crabs and isopods during the sampling.

Data analysis: Normality of the population size structure distribution was tested with a Kolmogorov-Smirnov one-sample test (Zar 1996). A subsequent t-test was used to evaluate differences between sea-star sizes at the two sites. Correlation analysis was used to study predator-prey size relationships by means of the Pearson product-moment (r) correlation coefficient. The significance of Pearson´s correlation coefficient was estimated by 10 000 permutations (Montecarlo test of significance; Siegel & Castellan 1988).

The diet composition was assessed through a canonical correspondence analysis (CCA) (ter Braak 1986, 1995, Legendre & Legendre 1998, ter Braak & Smilauer 1998); where the diet composition was explained by environmental (explanatory) variables: sites, seasons, shore level and sea-star size. This analysis compares the percent composition of samples (ter Braak & Smilauer 1998). The explanatory variables were treated as nominal and divided into classes as follows: (1) Sites, CCN (Caleta Cordova Norte) and FP (Foca Peninsula); (2) Season, T1 ($\leq$ 8.5ºC, cold season) and T2 ($>$ 8.5ºC, temperate season), (3) Shore level, Z1 (infralittoral fringe) and Z2 (midlittoral zone), and (4) Sea star size, Sz1 (small sea stars, $R < 20$ mm) and Sz2 (medium and large sea stars, $R \geq 20$ mm). The CCA was performed using square-root transformation of the original data, preservation of the distance between species, and forward selection of significant explicative variables ($p < 0.05$).

The association between sea-star arm length and the number of individuals feeding on prey of different mobility was evaluated by a Jonckheere-Terpstra test for doubly ordered r × c contingency tables (Lehmann 1975), where sea-star arm length (R) was classified in four ordered categories ($R < 20$ mm, $20 \leq R < 27$ mm, $27 \leq R < 34$ and $R \geq 34$ mm). Prey mobility was categorized as sessile (e.g. mussels), slow moving (e.g. limpets, gastropods) or fast moving organisms (e.g. isopods, crabs).

In order to assess the diversity of prey eaten at different spatial and temporal scales, two measures of diversity were calculated: (1) total number of species preyed upon during each sampling date and shore zone and (2) Pielou's evenness measure *(*J', Pielou 1966). Differences among sites, seasons and shore zone on these measures were analysed using a factorial ANOVA. Assumptions of homoscedasticity were checked previous to each analysis using Cochran's C-test (Winer 1971). The approximate normal distribution of the within-cell deviations from the respective cell means was tested graphically by normal probability plots (Zar 1996). The dominance of prey species was studied through a partial order represented by a curve known as the intrinsic diversity profile (k-dominance curve; Clarke & Warwick 2001).

The relation between: (1) the size-frequency distribution of major prey in the diet and the size-frequency distribution available; and (2) diet composition and the prey available in the field were analysed by means of an exact Chi-square goodness of fit test (Siegel & Castellan 1988). A significance level of 5% was assumed throughout the study.

RESULTS

General ecology: Individuals of *A. minuta* were found on the undersides of rocks in tide pools, under different-sized flat rocks (0.08 to 2 m^2) of the infralittoral fringe and midshore zone (usually associated with very shallow tide pools) and in crevices. A particular sea star microhabitat was discovered: small sea stars (r<20mm) were also found inhabiting spaces underneath *Perumytilus purpuratus* mussel stacks or hummocks (i.e. raised clumps of mussels) found in mature mussel beds. The hummock structure of the mussel bed occurs mainly at the low midlittoral shore zone (Zaixso, pers. obs.). All animals at tide pools were usually hidden during surveys. Mean sea-star densities on the undersides of rocks in tide pools were 103.1 ind.m^{-2} (S.E.: 69.84, n=10) at Foca Peninsula (FP) and 123.22 ind.m^{-2} (S.E.: 44.45, n=20) at Caleta Cordova Norte (CCN).

Sea stars with an arm-length between 3 and 80 mm were observed during the sampling months. There were no differences in arm length between sites (t-test, p=0.054). The overall mean arm-length was 23.55 mm (±10.86 mm). All sizes categories were well represented throughout the year at both sites.

Diet composition and foraging behavior: 8 470 sea star observations were made (4 429 for FP and 4 041 for CCN). Only 4.27% (N=362) of the animals observed were feeding. The feeding frequency was significantly higher (RxC test, $p<0.001$) at CCN than at FP (Table 1). *A. minuta* captures bivalves and large prey using the tube feet and arms, and assumes a humped feeding position to digest the prey extraorally. 86.7% of the prey were macroinvertebrates (Table 1). The rest of the animals (13.3% of feeding stars) were found with their cardiac stomach everted on the substrata. Among the macroinvertebrates, a total of 19 different items were recorded as prey of *A. minuta*. In terms of prey groups, Mollusca represented the dominant component of the diet with 13 prey items. Crustaceans followed with five prey items (Table 1).

The diet of *A. minuta* at the studied sites was dominated by a single species, the purple mussel (*Perumytilus purpuratus*) (Pielou´s evenness index, p=0.41). It occurred in 57.6% (n=181) of the feeding sea stars. The second and third most important prey were the gastropod *Pareuthria plumbea* (10.19%, n=32) and isopod *Exosphaeroma lanceolatum* (9.8%, n=31), respectively. Next were the ribbed mussel *Aulacomya atra atra* (4.8%, n=15) and the blue mussel *Mytilus edulis platensis* (4.8%, n=15). Other prey items such as the chitons *Plaxiphora aurata* and *Tonicia lebruni*, gastropods *Trophon geversianus*, *Tegula patagonica*, *Nacella* (*P.*) *magellanica*, *Fissurella radiosa* and *Turbonilla smithi*, the barnacle *Balanus glandula*, the crab *Halicarcinus planatus*, the isopod *Edotia tuberculata,* the hermit crab *Pagurus comptus*, and the polychaete *Harmothoe australis*, were relatively uncommon and occurred in no more that 3.2% of the feeding sea stars (Table 1). Predation on egg capsules of the gastropods *T. geversianus* and *P. plumbea* was observed in single cases.

Only one prey was consumed at a time. All mussels captured were already detached from the substrate and orientated by the sea star with their hinge downward. *A. minuta* is also able to pulls chiton and limpets from the rock with their tube feet. We did not observe cooperative feeding behavior. We found one purple mussel (TL: 17 mm) being consumed simultaneously by two sea stars (R: 30, 23 mm). Feeding on barnacles was accomplished by extrusion of the stomach through the aperture without damaging the outer shell and leaving the barnacle shells attached to the substrate. It is important to recognize these different prey have different mobilities. Mussels and barnacles are sessile; chitons, limpets and gastropods are slow moving; while isopods and crabs are highly mobile. In this regard, the proportion of sea stars feeding on sessile prey increases with sea-star size (Jonckheere-Terpstra Test, with Monte Carlo sampling, $p<0.0001$). No sea stars were observed feeding while brooding at either site.

A significant positive correlation was found between the size of *A. minuta* and the size of *P. purpuratus*, *P. plumbea*, *E. lanceolatum* and *P. aurata* (Fig. 2, Table 2). However, we found no significant correlation between sea-star size and the size of *A. atra atra*, *M. edulis platensis* and *T. gevesianus* (Table 2).

Spatial, temporal and sea-star size variation of diet composition: In order to evaluate for spatial, temporal and sea-star size variation on the diet composition of *A. minuta*, a canonical correspondence analysis (CCA) relating the number of sea stars feeding on individual prey species to environmental factors was performed. Variance inflation factors (VIF) in excess of 10 are suggested as an indication of multicollinearity (Chatterjee & Price 1977). In this study the VIF of the environmental variables were less than 1.02 (Canoco output), and therefore are not indicative of multicollinearity. The season was excluded because it was not significant ($p>0.32$) according to the forward variable selection.

The cumulative percentage variance on the two first axes of the general CCA explained ca. 10% of the data inertia of the species data and 81.2% of the species-environment relationship (Table 3). In the corresponding CCA joint plot (Fig. 3) of species and environmental

TABLE 1

Total and relative frequency of prey items of Anasterias minuta *at Foca Peninsula (FP) and Caleta Cordova Norte (CCN) within tidepools*

	Sites			
	FP		CCN	
Taxa	f	%	f	%
MOLLUSCA				
Polyplacophora				
Plaxiphora aurata (Spalowsky)	0	0	10	4.8
Tonicia lebruni Rochebrune	0	0	1	0.5
Gastropoda				
Fissurella radiosa Lesson	1	0.6	1	0.5
Nacella (P.) magellanica (Gmelin)	1	0.6	2	1
Pareuthria plumbea (Philippi)	25	16.2	7	3.4
Trophon geversianus (Pallas)	1	0.6	8	3.9
Turbonilla smithi Pfeffer	1	0.6	0	0
P. plumbea egg capsules	1	0.6	1	0.5
T. geversianus egg capsules	1	0.6	0	0
Tegula patagonica (d´Orbigny)	0	0	4	1.9
Bivalvia				
Aulacomya atra atra Molina	6	3.9	9	4.3
Mytilus edulis platensis d´Orbigny	0	0	15	7.2
Perumytilus purpuratus (Lamarck)	103	66.5	78	37.6
ARTHROPODA				
Crustacea				
Balanus glandula Darwin	1	0.6	1	0.5
Exosphaeroma lanceolatum (White)	14	9.1	17	8.2
Halicarcinus planatus Fabricius	0	0	2	1
Pagurus comptus White	0	0	1	0.5
Edotia tuberculata Guerin-Meneville	0	0	1	0.5
POLYCHAETA				
Harmothoe australis Kirkegaard	0	0	1	0.5
Microphage	n/a	n/a	48	23.2
Observed sea stars	4429		4041	
Observed feeding	155		207	
% feeding	3.50%		5.12%	

TABLE 2

Prey sizes and correlation coefficients between Anasterias minuta *arm length (mm) and prey size (mm) of the most important prey items*

Prey	N	r (95% CI)	p-value	Predator size Mean (±SE)	Prey size		
					Mean (±SE)	Max	Min
P. purpuratus	202	0.41 (0.31–0.52)	<0.0001	29.14 (12.5)	18.63 (5.2)	33	6
P. plumbea	32	0.40 (0.15–0.65)	0.027	27.35 (11.6)	17.14 (4.9)	22.3	6
E. lanceolatum	31	0.49 (0.13–0.83)	0.007	22.08 (12.3)	12.43 (4.9)	22	5.5
M. edulis platensis	22	0.12 (-0.37–0.60)	0.598	34.01 (8.0)	32.55 (7.1)	50	22.5
A. atra atra	15	0.13 (-0.51–0.77)	0.656	39.22 (16.2)	31.02 (9.7)	48	13
T. geversianus	12	0.42 (0–0.85)	0.170	29.47 (4.8)	23.60 (4.8)	31	16
P. aurata	9	0.87 (0.74–1)	0.002	21.61 (6.8)	13.86 (6.3)	22	6

TABLE 3

Summary of canonical correspondence analysis ordination

Axes	1	2	3	4	Total inertia
Eigenvalues	0.216	0.162	0.088	0.694	3.837
Species-environment correlations	0.712	0.604	0.502	0.000	
Cumulative percentage variance of:					
species data	5.6	9.9	12.1	30.2	
species-environment relation	46.5	81.2	100.0	0.0	
Sum of all unconstrained eigenvalues					3.837
Sum of all canonical eigenvalues					0.466

factors, the resulting data structure indicates that *Perumytilus purpuratus* was an important prey in all circumstances. It was preyed upon by both large and small sea stars at both sites and was eaten to a slightly greater extent in the midlittoral zone. This general pattern is observed in the CCA joint-plot, where *P. purpuratus* is situated close to the center of coordinates (Fig. 3). The CCA analysis indicated differences in diet composition between sites (p<0.005) and shore level (p<0.005). The diet of *A. minuta* at CCN was associated mainly with the molluscs *Perumytilus purpuratus, M. edulis platensis*, *A. atra atra*, *T. geversianus*, *Plaxiphora aurata aurata* and *Tegula patagonica* and the crab *Halicarcinus planatus*. At FP the diet of *A. minuta* was associated with *Pareuthria plumbea, Perumytilus purpuratus* and *Balanus glandula*. On the infralittoral fringe, *A. minuta* fed mainly on *P. aurata aurata*, *T. patagonica*, *H. planatus*, *E. lanceolatum*, *A. atra atra* and *F. radiosa.* The most representative preys in the midlittoral zone were *P. plumbea*, *P. purpuratus, B. glandula* and *N. magellanica.* The diet of small sea stars also differed significantly (p<0.005) from medium and large sea stars. In the CCA joint-plot (Fig. 3), the diet composition of small sea stars consisted largely of the isopod *Exospaheroma lanceolatum* and the keyhole limpet *Fissurella radiosa.* In contrast, the diet of medium and large sea

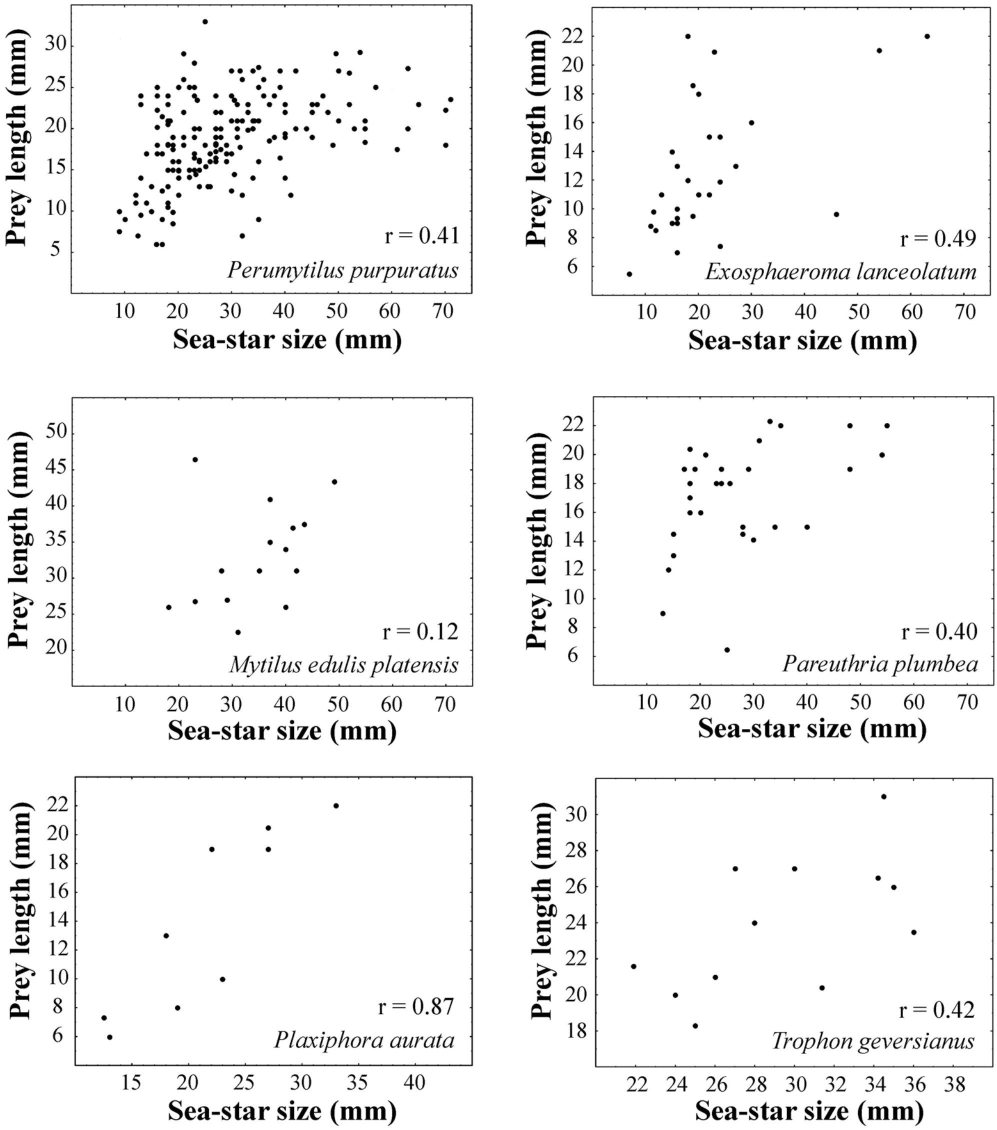

Fig. 2. The relationship between *Anasterias minuta* size and prey length (see Table 2).

stars consisted of the gastropods *Trophon geversianus* and *Nacella magellanica* and the mussels *Aulacomya atra atra* and *Mytilus edulis platensis* (Fig. 3).

Diversity of prey eaten: The ANOVA factorial analysis carried out on the number of species (S) eaten by the sea star showed that only site, season and shore zone were highly significant ($p<0.005$). The diversity of prey consumed by *A. minuta* was higher at the semi-exposed coast of CCN and on the infralittoral fringe of both sites during the temperate season (Fig. 4). Differences were apparent between the k-dominance curves of abundance (Fig. 5) for the two sites, shore zones and seasons and are consistent with the differences observed on the number of prey species eaten.

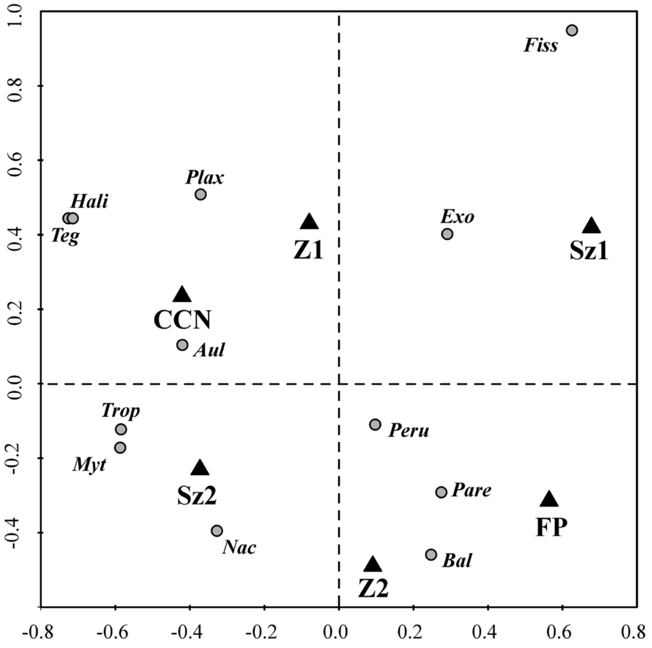

Fig. 3. Canonical correspondence analysis (CCA) joint plot of prey species and explanatory variables. Explanatory variables: CCN (Caleta Cordova Norte), FP (Foca Peninsula), Z1 (infralittoral fringe), Z2 (midlittoral zone), Sz1 (small sea stars) and Sz2 (medium and large sea stars). Prey species: Aul (*Aulacomya atra atra*), Bal (*Balanus glandula*), Exo (*Exosphaeroma lanceolatum*), Fiss (*Fissurella radiosa*), Hali (*Halicarcinus planatus*), Myt (*Mytilus e. platensis*), Nac (*Nacella magellanica*), Pare (*Pareuthria plumbea*), Peru (*Perumytilus purpuratus*) Plax (*Plaxiphora aurata*), Teg (*Tegula patagonica*) and Trop (*Trophon geversianus*).

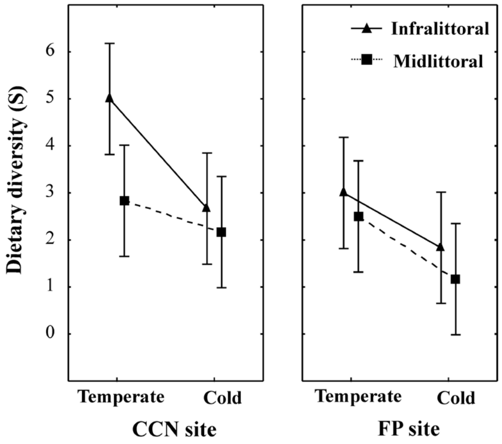

Fig. 4. Diversity of prey eaten by *Anasterias minuta* at different seasons (temperate and cold), shore level (infralittoral fringe and midlittoral zones) and sites (CCN and FP).

Diet and prey availability: The relative abundances of prey in the diet and the amount available in the habitat are shown in Figure 6. The study site CCN has a higher number of available prey species than FP (S=21 and 13, respectively).

At Foca Peninsula (FP), the exact Chi-square goodness of fit test found significant differences on the frequency of prey eaten in relation to their relative abundance at the infralittoral fringe ($p<0.0001$), and at the midlittoral zone ($p<0.0001$). In the midlittoral zone of FP, the isopod *E. lanceolatum* was eaten less in proportion to its relative abundance while the mussel *P. purpuratus* and the gastropod *P. plumbea* were consumed by the sea star more often than their relative abundance in the field

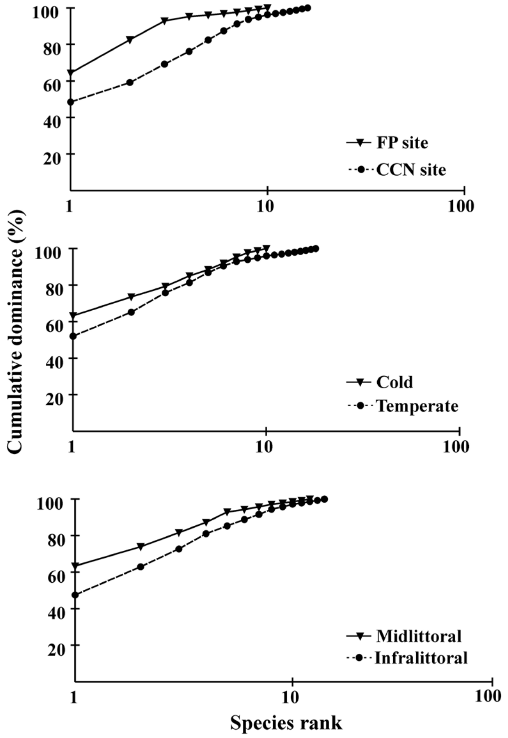

Fig. 5. K-dominance curves of preyed species abundances at different seasons (temperate and cold), shore level (infralittoral fringe and midlittoral zones) and sites (CCN and FP).

(Fig. 6). At the infralittoral fringe of FP, *P. purpuratus* and *P. plumbea* were eaten in high proportion compared to their relative abundance. *E. lanceolatum* was the most abundant prey in the field but was not often eaten. *A. atra atra* was taken almost proportionately to its relative abundance.

At Caleta Cordova Norte, we found differences in the diet and relative abundance of prey in the infralittoral fringe (p<0.0001) but not in the midlittoral zone (p>0.05). The diet composition in the midlittoral zone was dominated by the mussels *P. purpuratus* and *M. edulis platensis*, which were the most abundant and available prey species in the field. The ribbed mussel *A. atra atra* was also captured at this shore zone in low numbers (Fig. 6), even though there were no ribbed mussels growing in this shore level and the observed available mussels were already detached and enmeshed in coralline algae. At the infralittoral fringe, *P. purpuratus*, *E. lanceolatum, M. edulis platensis and A. atra atra* were the dominant prey items although *P. purpuratus* and *M. edulis platensis* had a low relative abundance. The mussel *A. atra atra* was consumed proportionally to its

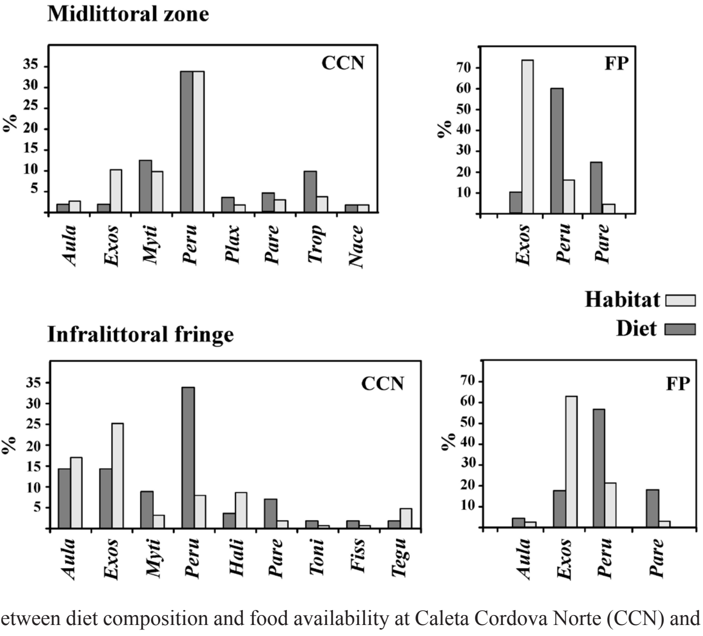

Fig. 6. The relation between diet composition and food availability at Caleta Cordova Norte (CCN) and Foca Peninsula (FP) at different shore levels. Prey species are abbreviated based on the first four letters of the genus (see Table 1).

abundance. Finally, *E. lanceolatum* was again the most abundant prey in the field but was not eaten much by the sea star (Fig. 6).

The size-frequency distribution of the prey mussel *P. purpuratus* and the isopod *E. lanceolatum* were significantly different (p<0.0001, on both cases) from the size-frequency distribution available in the field (Fig. 7). Larger *P. purpuratus* and *E. lanceolatum* were eaten more often than expected. On the other hand, the size-frequency distribution of the mussels *A. atra atra* and *M. edulis platensis* and the gastropod *P. plumbea* were not significantly different (p=0.51, p=0.12, p=0.12, respectively) from the prey size-frequency distribution available in the field (Fig. 7).

DISCUSSION

This study described the feeding habits at tide pools habitats of *A. minuta,* a dominant brooding sea star in the intertidal and shallow subtidal system of Central and South Patagonia, Argentina. Although its diet is dominated by the purple mussel *P. purpuratus*, it consumes a wide range of prey, including molluscs and crustaceans and can be regarded as a generalist or opportunistic predator.

The sea star adopts the characteristic humped-up pose when feeding on mussels, suggesting that pulling is often used to open this prey. The insertion of a portion of the stomach through a small opening or natural gap as described by Feder (1955) for *Pisaster ochraceus* may also apply to some extent to *A. minuta*. We observed a few cases (~ 3%) where the stomach was inserted at the byssus opening when feeding over *P. purpuratus*.

The high relative frequency of the isopod *E. lanceolatum* as prey indicates that *A. minuta* is also able to capture motile prey but only under circumstances in which the isopods might have a reduced motility (e.g. high densities or aggregations). The ability to capture motile prey was also described for the congeneric species *Anasterias perrieri* at the Kerguelen Islands (McClintock 1985), which feeds mainly on the motile crab *Halicarcinus planatus*.

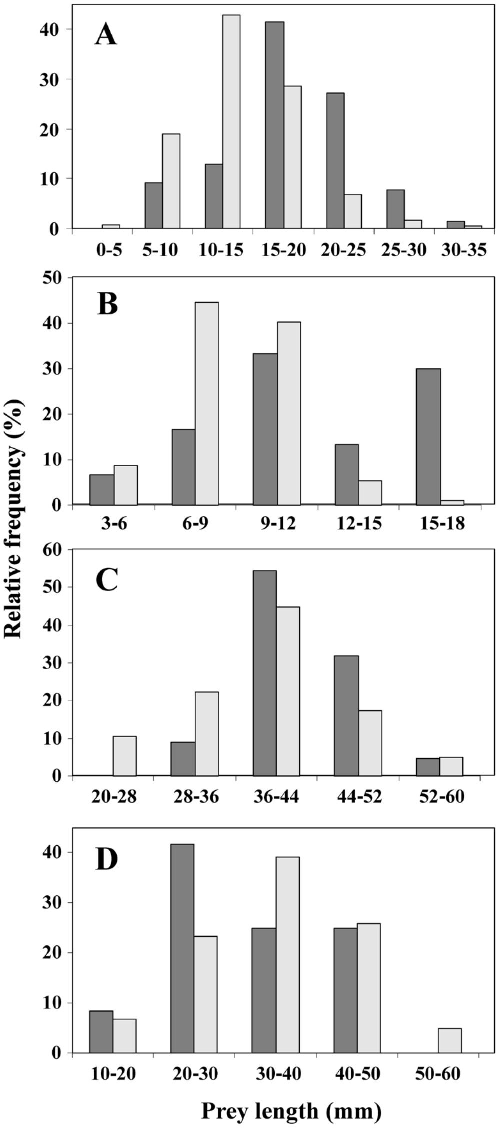

Fig. 7. Relative frequency (%) of various sizes of prey eaten by *Anasterias minuta* (dark grey bar) and the expected relative frequency in the field, based on their availability under rocks at tide pools (light grey bar). A. *Perumytilus purpuratus*, B. *Exosphaeroma lanceolatum*, C. *Mytilus edulis platensis*, D. *Aulacomya atra atra*.

A. minuta has not been observed using the cooperative feeding behavior method described for *Anasterias rupicola*, in the sub-Antarctic Marion Islands (Blankley & Branch 1984).

Sea stars and limpets are dominant members of shallow inshore communities of the sub-Antarctic Marion Islands (Blankley 1984, Blankley & Grindley 1985). Predation of limpets by solitary *A. rupicola* is size-limited but they can feed in groups, thereby circumventing this size limitation (Blankley & Branch 1984). Simpson (1976) also noted that *Anasterias directa* and *Anasterias mawsoni* formed feeding clusters on their two largest species of molluscan prey. *A. minuta* does not show this specific behavior when feeding over larger prey (*M. edulis platensis*, *A. atra atra* and *Nacella magellanica*) since the most important prey, *P. purpuratus*, dominates the intertidal mid-shore community and is size-accessible for the sea star. Nevertheless, we observed two sea stars (~ 1.2%) feeding on one purple mussel.

The coexistence of *A. minuta* and prey underneath rock during low tides may also explain the capture of motile prey such as isopods, small crabs and snails. Blankley (1984) pointed out that fast moving amphipods and isopods were captured by *Anasterias rupicola* when seeking shelter underneath the sea star. However, the significance of dense aggregation of prey underneath rock was not discussed in detail. *A. minuta* could benefit from different sources of food found on the underside of rocks at intertidal pools: (1) reproductive or behavioral responses (i.e. light avoidance, desiccation stress, etc.) aggregations of motile prey under rocks and, (2) unattached or wave-washed sessile prey that may also accumulate on this habitat. All mussels captured by *A. minuta* were detached from the substrate. This could support the idea that sea stars removed the mussel prior to digestion or could suggest feeding on self-detached or washed-out animals that are accumulated underneath rocks. Dolmer (1998) pointed out that *Asterias rubens* detaches the majority of blue mussel prey before ingestion. Feeding over *A. atra atra* on the midlittoral zone at Caleta Cordova Norte could only be explained if mussels were torn from the substrate by turbulent conditions from the infralittoral fringe. Feder (1959) also found that *Mytilus californianus* was used as food by *P. ochraceus* on occasion in one area even though there were no mussels growing in the area. He suggests that the specimens eaten were probably washed in from an adjacent rocky island. The self-detaching behaviour and moving ability in mytilids is known for different species (White 1937, Harger 1968, Senawong 1970, Zaixso *et al.* 1978, Seed & Suchanek 1992, Feder *et al.* 2003). Chapman (2005) found in a study of occurrence of molluscs and echinoderms under boulders that the individual taxa were highly variable in abundance through time under boulders. If the latter scheme is applied to *A. minuta*, it would suggest that some sea stars might crawl upwards on rocks during high tides and disperse in tide pools if food species under rocks were limited. Others could remain on the underside of rocks if availability of food species was high.

A low percentage of feeding *A. minuta* was seen with their stomach everted over the substrata, thereby indicating an auxiliary feeding mode. They may feed on detritus or may consume small organisms (microphage). Flagellary-mucous feeding on detrital material has been described for other extraoral feeding sea stars (Mauzey 1963, Mauzey *et al.* 1968, Pearse 1965, Jangoux 1982, McClintock 1985).

The diet spectrum of *A. minuta* was fairly constant throughout the year. Gil and Zaixso (2007) found a clear feeding cycle related to a low-water temperature. Brooding females did not feed during the winter and early spring at Foca Peninsula and Caleta Cordova Norte. In contrast, brooding females of *Anasterias rupicola,* feed during the last phase of the brooding period (Blankley & Branch 1984). Gil and Zaixso (2007) pointed out that the late spring and summer periods are probably critical in terms of nutrient accumulation for gonad development for both sexes in *A. minuta*. In this context, the high dietary diversity during this period may be the result of the high feeding activity observed in summer, but not enough to change the overall composition of the diet (e.g. the dominance of *P. purpuratus* as the major prey). Town (1980) noted that the foraging strategy of the sea star *Astrostole scabra* within the intertidal region did not change seasonally, and was independent of fluctuating physical factors and small seasonal variations in prey community composition. Seasonal variations of diet in the intertidal sea star *P. ochraceus* in Puget Sound, Washington were described by Mauzey *et al*. (1968), and he suggested this was related to migration of the sea stars lower in the intertidal zone in winter where different prey were available. However, the more southerly *P. ochraceus* along the coast of Central California in Monterey Bay did not show a seasonal feeding periodicity (Feder 1970). The Monterey Bay sea stars were living at higher temperatures than the northern sea stars, and were continuously in the presence of the same food organisms throughout the year. The northern population of *P. ochraceus* feeds largely on mussels during summer when they are in the higher intertidal (Mauzey 1966, Paine 1974), but the California sea stars do not migrate and are in the presence of mussels year round (Feder 1970). The ochre sea stars were found living in irregular boulder and cave areas quite unlike our rocky area. *A. minuta* did not migrate seasonally and mussels were available all year.

Changes on the diet of sea stars with size were reported for many species (Hancock 1955, Feder 1959, Mauzey *et al.* 1968, Menge & Menge 1974, Town 1981, Blankley 1984, Himmelmann & Dutil 1991, Frid 1992, Day *et al.* 1995, Ganmanee *et al.* 2003). If we compare the diet of *A. minuta* as a function of sea-star size, *P. purpuratus* is the major prey species but there is a slight shift in diet composition between juveniles (<20 mm, arm length) and medium/large sea stars (≥ 20 mm, arm length). Juveniles were found to prey more often on isopods and keyhole limpets while large sea stars preyed upon large mussels (*M. e. platensis, A. a. atra*) and gastropods. Differences in the diet of small and large *A. minuta* may be due to variations in the size range of their prey. Consequently, small sea stars may feed on a narrow size range of prey, while large sea stars may feed on a broader size range, reaching more nutritionally valuable prey that are not available for small sea stars. This suggests that the gain from feeding on isopods and small limpets decreases with increasing body size and, consequently, there is a change in dietary preference for larger prey. This result is supported by the fact that large sea stars feed more on sessile prey. Feeding on isopods on the undersides of rocks by small sea stars may indicate that: (1) the availability of mussels with accessible sizes is low, (2) the availability of a preferred prey species is low or (3) small sea stars stay more often under rocks than large sea stars, coexisting with dense patches of isopods. Feder (1959) and Frid (1992) suggested that the diet of *Pisaster ochraceus* and *Marthasterias glacialis* is more a function of the availability of prey of a size that the sea star is able to consume than being determined by the size or age of the sea star. Blankley (1984) also found that small *A. rupicola* were mostly found under rocks where they live in association with a community of amphipods, isopods and polychaetes. Although our work does not include the diet of recently recruited sea stars (R ~ 4 mm) a defined shift on diet might be more apparent with the very small stars. Small and medium sized *A. rupicola* fed almost exclusively on amphipods, pelecypods, chitons, polychaetes and isopods, whereas larger sea stars fed mostly on the limpet *Nacella delesserti* (Blankley 1984).

The observed differences in diet between study sites can be attributable to the differences in prey availability resulting from the opportunistic feeding strategy. The gastropod *Tegula patagonica* is absent in FP but it is eaten at CCN where it occurs at high densities. The mussels *Aulacomya atra atra* and *Mytilus edulis platensis* and the gastropod *Trophon geversianus* are more abundant at CCN and are therefore used by the sea star as food. Branch (1978) found that if the preferred prey of *Marthasterias glacialis* is rare or absent, a wider range of species is eaten more or less in relation to their abundance in the field. In the intertidal sea stars *Pisaster ochraceus* and *Astrostole scabra,* the diet varies markedly by habitat (Feder 1959, Mauzey *et al.* 1968, Town 1980). *A. minuta* has a higher feeding frequency (5.2%) on the semi-exposed coast of CCN than at the exposed intertidal of FP (3.5%). In the same way, Feder (1970) found that *P. ochraceus* fed much less in relatively unprotected intertidal areas than in areas better protected from wave action. The diet of *A. minuta* at different shore levels seems to also be correlated with the pattern of the abundance of the prey species in the different areas. Purple mussels, small gastropods (*P. plumbea*), barnacles, and limpets are most important in the midlittoral zone and isopods, crabs and large mussels (*A. atra atra*, *Mytilus edulis platensis*) in the infralittoral fringe. A clear variation of diet with depth was observed for *Leptasterias hexactis* (Mauzey *et al.* 1968).

The availability of prey to predators depends not only on their population density, but also on exposure, activity, and escape or defense responses (Feder & Christensen 1966, Sloan 1980). *A. minuta* does not eat prey in proportion to their abundance on undersides of rocks in both sites at the infralittoral fringe. Generally, it consumed *P. purpuratus* and the gastropod *P. plumbea* more than other prey, even when they were not the most abundant prey species.

At the midlittoral zone the situation is different at the two sites. At the exposed coast of FP, the isopod *E. lanceolatum* occurs at high densities but is not often taken by the sea star. It feeds more on the purple mussel and *P. plumbea*, although they are not the most abundant prey species present. Interestingly, at the semi-exposed coast of CCN, the sea star feeds on prey species accordingly to their abundances in the field. Thus, it appears that differences in wave exposure between sites may affect foraging behaviour of *A. minuta*. In the case of the semi exposed site of CCN, *A. minuta* was found amongst debris and unattached mussels that had accumulated under rocks. The relatively high abundance of *P. purpuratus* in this condition is fed upon by the sea star according to its abundance. In contrast, at FP the high wave activity might prevent the accumulation of debris, resulting in a low abundance of detached mussels under rocks.

The relative preference of *P. purpuratus* as prey despite its low abundances on the undersides of rocks in PF and the infralittoral fringe of CCN, could be explained by: (1) *A. minuta* crawl upward during hide tide, capture mussels and move under rocks to digest them, or (2) self-detached or wave-washed-out mussels are selected among prey species under rocks. The purple mussel dominates the intertidal area but is relatively scarce within tide pools (under and on the top of rocks), so it appears that the second explanation it is more likely to occur for *P. purpuratus*. In the case of the gastropod *P. plumbea,* the relative preference could indicate an active selection of prey or, that *A. minuta* could capture the gastropod when it is aggregated under rocks during low tides. We observed cases of aggregation of various *P. plumbea* close to *A. minuta* which may also increase the chance of encounter. The low incidence of predation on the isopod *E. lanceolatum*, the small crab *H. planatus* and the gastropod *T. patagonica* in relation to their relative abundance in the habitat suggests effective avoidance and escape behaviours. Several authors have reported escape responses of various species to sea stars (e.g. Feder & Christensen 1966, Feder 1967, 1972, McClintock 1985, Harvey *et al.* 1987, Markowska & Kidawa 2007). As recommended by Fairweather and Underwood (1983), field prey analysis might provide a biased reflection of dietary choices if the time spent feeding on different prey varies, so we must be careful when assuming preference relationships. However, it is also stated that *in situ* studies are a useful technique for the study of predatory behavior in sea stars (Sloan 1980).

An optimum predator-prey size relationship with regard to efficiency in food uptake is apparent for *A. minuta* when it feeds on the most important prey species. These results are in agreement with the observations reported by Feder and Christensen (1966), showing that large specimens of *Pisaster ochraceus* were seldom seen to feed on very small prey and vice versa. The lack of correlation between predator-prey size relationship on the large mussels *A. a. atra* and *M. e. platensis* and the gastropod *T. geversianus* could be due to small sample size and/or a low sea-star size range of feeding sea stars since these prey species were captured mainly by large sea stars. Many authors describe situations in which prey species achieve an escape in size from sea stars (e.g. Feder & Christensen 1966, Menge & Menge 1974, Paine 1976, Lawrence 1987). However this strategy would not occur for the most important prey species *P. purpuratus*, since larger purple mussels were eaten more often than expected from the prey size-frequency distribution available in the field. In the case of the mussels, *A. a. atra* and *M. e. platensis* we did not observe an escape in size since the size-frequency distribution on diet was not different from the expected. However, this relationship could be different at subtidal habitats where larger mussels are present.

Bertness *et al.* (2006) pointed out that predation of *A. minuta* at Central Patagonia is not strong enough to limit mussels in most of the intertidal zone and that sea stars are only able to live in the presence of mussels ameliorating physical stress. However, there is no data to support the ameliorating hypothesis, and the significance of intertidal tide pools as sea-star habitats were not considered. The sea star *A. minuta* may depend on the amelioration of desiccation offered by the mussel matrix but this can only be applied exclusively in the case of small sea stars that inhabit the mussel matrix. However, this is just one intertidal habitat where this species occurs. Since *A. minuta* at tide pools may depend on the availability of wave-washed mussels or may actively forage undersides or upsides of rocks or on the margin of the surrounding mussel beds, we could consider that predation is not a general structural factor over the entire intertidal community, unless the landscape is dominated by tide pools and flat rocks. However, the significance of sea stars living within and under the mussel hummocks may be different. In this particular microhabitat, feeding on attached mussels could weaken the mussel matrix and produce gaps during storms. Bertness *et al.* (2006) did not observe natural gaps on Cabo Dos Bahías (~180 km northeast from CCN) during heavy storms, but in our study sites there have been major intertidal disturbances (e.g. bare patches, detachment of large areas, sliding and turn over of medium and large sized boulders and flat rocks). Nevertheless, intertidal disturbance may have other different sources (e.g. storms, human activity). *A. minuta* within tide pools is mainly a scavenger and opportunistic forager, taking unattached, wave-washed mussels when available rather that attached mussels. Consequently, it may have a variable impact on the community structure.

ACKNOWLEDGMENTS

The authors are grateful to Silvina Rosales, Paula Stoyanoff, Marcelo Sosa, Javier Tolosano and Belen Reartes for their kind assistance in the fieldwork. Marcelo Sosa also edited the map for us. We wish to express our gratitude to Howard Feder, James B. McClintock and two anonymous referees for their quality-improving contributions and suggestions.

RESUMEN

Se estudió la ecología trófica de la estrella de mar incubadora *Anasterias minuta* en ambientes de pozas intermareales en el centro y sur de Patagonia. Para tal fin, se realizaron un total de 8 470 observaciones de individuos. *A. minuta* no se alimenta mientras incuba y consume una gran diversidad de presas, como moluscos y crustáceos, y puede definirse como una especie depredadora oportunista o generalista. El mejillín *Perumytilus purpuratus* fue la presa mas frecuente (57.6%). Otras presas importantes fueron el gasterópodo *Pareuthria plumb*ea, el isópodo *Exosphaeroma lanceolatum* y los mitílidos *Aulacomya atra atra* y *Mytilus edulis platensis*. La proporción de estrellas de mar que se alimenta de presas sésiles aumenta con el tamaño de la estrella. Se encontró una correlación significativamente positiva entre el tamaño de la estrella y el tamaño de las presas mas frecuentes. La dieta no cambio a lo largo del año, pero su composición difirió entre los sitios, los horizontes intermareales, y el tamaño de la estrella. Se encontró una mayor diversidad de presas consumidas en el infralitoral de la costa semi expuesta de Caleta Cordova Norte, durante la estación templada. *A. minuta* podría ser considerada oportunista al consumir mitílidos sueltos, desprendidos por las olas y acumulados en las pozas intermareales cuando están disponibles, por consecuencia, podría tener un impacto variable en la estructura de las comunidades intermareales patagónicas.

Palabras clave: *Anasterias*, Patagonia, Alimentación, *Perumytilus*, Intermareal.

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