



RESEARCH ARTICLE

Trophic ecology of the chiton *Acanthopleura echinata* on Chilean rocky shores

Ecología trófica del chitón *Acanthopleura echinata* en costas rocosas de Chile

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ABSTRACT

Polyplacophorans are common herbivores on rocky shores, but basic aspects of their ecology remain scarcely studied and their role within communities could be more complex than previously considered. Such is the case of *Acanthopleura echinata* (Barnes), one of the largest and most conspicuous chitons in the world, and at the same time, one of the least known intertidal species in the southeastern Pacific. To improve the basic ecological knowledge of this potentially important intertidal consumer, we studied the diet of *A. echinata* and its variation among sites of varying levels of coastal upwelling spread over 1000 km along the coast of northern Chile. A seasonal evaluation of diet, body size distribution and density at sites expected to vary in overall nutrient loadings, benthic algal productivity and sea surface temperature, allowed us to examine plasticity in *Acanthopleura* diet and body size. Overall, *A. echinata* consumed 85 items of algae (64.7 %, mainly fleshy and calcified encrusting thalli) and invertebrates (35.3 %, mainly barnacles). Diet was always dominated by encrusting corallines, although the proportion of algae increased with body size suggesting an ontogenetic variation in feeding habits. Although the number and occurrence frequency of dietary items varied significantly in time and space, there were no consistent seasonal patterns and the dominant items in the diet remained the same at all places. The density of *A. echinata* showed no significant spatial variation, but its body size and diet breadth correlated positively among sites and both tended to increase with latitude. Our results show that *A. echinata* is a generalist, polyphagous consumer with a high potential for affecting the space-occupancy dynamics in the intertidal system, and also that among site variation in diet bears no simple relationship with variation in sea surface temperature and upwelling intensity.

Key words: body size, intertidal, niche breadth, omnivory, upwelling.

RESUMEN

Los poliplacóforos son herbívoros comunes en costas rocosas, pero los aspectos básicos de su ecología han sido escasamente estudiados y su rol trófico dentro de las comunidades podría ser más complejo de lo considerado hasta ahora. Tal es el caso de *Acanthopleura echinata* (Barnes), uno de los chitones más grandes y conspicuos en el mundo, pero a la vez una de las especies intermareales menos conocidas del Pacífico sudeste. A fin de mejorar el conocimiento ecológico básico de este consumidor intermareal potencialmente importante, estudiamos la dieta de *A. echinata* y su variación entre sitios con distintos niveles de surgencia costera distribuidos a través de 1000 km en la costa del norte de Chile. Una evaluación estacional de la dieta, distribución de tamaño corporal y densidad en sitios con diferencias esperables en aporte total de nutrientes, productividad de algas bentónicas y temperatura superficial del mar, permitió examinar la plasticidad de la dieta y el tamaño corporal de *Acanthopleura*. Globalmente, *A. echinata* consumió 85 ítems de algas (64.7 %, principalmente algas incrustantes calcificadas y blandas) e invertebrados (35.3 %, principalmente cirripedios). Su dieta estuvo siempre dominada por coralinas incrustantes, aunque la proporción de algas aumentó con el tamaño corporal sugiriendo una variación ontogenética en sus hábitos tróficos. Aunque el número y frecuencia de ocurrencia de ítems dietarios variaron significativamente en tiempo y espacio, no hubo patrones estacionales consistentes y los ítems dominantes en la dieta fueron los mismos en todos los lugares. La densidad de *A. echinata* no varió significativamente a través del espacio, pero su tamaño corporal y su amplitud dietaria se correlacionaron positivamente entre sitios y ambos tendieron a aumentar con la latitud. Nuestros resultados muestran que *A. echinata* es un consumidor generalista y polífago con alto potencial para afectar la dinámica de ocupación del espacio en el sistema intermareal, y además que la variación dietaria entre sitios no tiene una relación evidente con la variación en intensidad de surgencia y temperatura superficial del mar.

Palabras clave: amplitud de nicho, intermareal, omnivoría, surgencia, tamaño corporal.

INTRODUCTION

Polylacophoran mollusks or chitons exhibit a wide geographic and bathymetric distribution in marine environments, and they are best known as typical herbivores of rocky intertidal communities (e.g., Boyle 1977, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Otway 1994, Markel & De Wreede 1998). Nonetheless, chitons display in fact a high trophic versatility, including detritivorous, carnivorous, herbivorous, and omnivorous species (e.g., Latshev et al. 2004), but their actual patterns of food consumption and assimilation are known in detail for a few species. The same is true for Neotropical chitons such as *Acanthopleura echinata* (Barnes), one of the largest and most conspicuous species on southeastern Pacific rocky shores, but also one of the less known.

The available ecological data on *A. echinata* are notably scarce and little precise. While several sources place its northern geographical limit at 15° S, or even at the Galapagos (though this last record has been repeatedly rejected; e.g., Kaiser 1987), the distribution of the species would range from at least 9°16' S (Punta Filomena, northern Peru; Paz et al. 2005) to 36°40' S (Punta de Parra, southern Chile; Aldea & Valdovinos 2005). In Chile, *A. echinata* is common at the lower intertidal zone on wave-exposed shores (Otaíza & Santelices 1985), and despite being considered an important herbivore, the only published information on its trophic ecology is apparently a secondary analysis included in a study by Santelices et al. (1986), based on two samplings at a single locality in central Chile. According to these authors, *A. echinata* fed mainly and selectively on non-calcified instead of coralline algae, and showed a markedly different diet than *Chiton granosus* (Frembly) in spite of having a similar radular structure, contradicting Steneck & Watling's (1982) predictions regarding the capacity of this radula for dealing with calcified algae. However, ongoing analyses of northern Chilean chitons (Camus et al. unpublished data) show that *A. echinata* share at least 55 dietary items (65 %) with *C. granosus*, including several encrusting and erect coralline algae. Indeed, the radular teeth of *A. echinata* are known for being larger than in most chiton species and for their high incorporation of biomineralized forms of iron, calcium, and phosphorus (Lee et al.

2000, Brooker et al. 2003). We thus expect that *A. echinata* is fully able to consume such hard materials as encrusting coralline thalli, which are more frequent and abundant in the low intertidal zone where it reaches greater density.

Prior analyses on northern Chilean herbivores (Camus et al. 2008, Sanhueza et al. 2008) showed that chitons such as *A. echinata*, *C. granosus*, and *Enoplochiton niger* (Barnes), have a wide dietary spectrum with a high occurrence of sessile and mobile invertebrates, including other coexisting herbivores. These chitons thus qualify as omnivores in broad terms (by eating at more than one trophic level; Pimm & Lawton 1978), and whether incidental or not, such consumption of animals could have important effects on the space occupancy patterns of algae and invertebrates in the low intertidal community (Camus et al. 2008). Nonetheless, we recently found that *C. granosus* (so far the only chiton species examined in this regard) is also a physiological omnivore, having the digestive flexibility and enzymatic capacity to digest and assimilate animal preys (Camus et al. 2009, Cid et al. unpublished data), which makes likely that other chitons exhibit similar capabilities.

The present study was thus aimed at generating a clear knowledge of the trophic habits of *A. echinata* in order to determine its trophic position and its contribution of consumer-prey links to the intertidal food web, which are needed for understanding the interplay between bottom-up and top-down processes (Bruno & O'Connor 2005, Thompson et al. 2007, Camus et al. 2008). With the goal of characterizing the variation scope of feeding patterns in relation with body size and density, we conducted a seasonal evaluation at four rocky intertidal localities from northern Chile, distributed over a 1000-km stretch of coast encompassing 40 % of the latitudinal range of *A. echinata* around its midpoint of distribution (~23° S). In addition, the selected localities differ in their proximity (near vs. distant) to localized upwelling centres bringing cold, high-nutrient water to the surface (see Thiel et al. 2007). Upwelling-driven spatial variations in nutrient supply and sea surface temperature have shown to influence herbivore feeding patterns in central Chile (Nielsen & Navarrete 2004, Wieters 2005), although in northern Chile such effects may be less clear, or less important than those from interannual

physical forcing (Thiel et al. 2007, Navarrete et al. 2008, Sanhueza et al. 2008). Upwelling was not directly assessed in this work, but its influence is inferred indirectly on the basis of sea temperature records and the proximity of the study sites to upwelling centres.

METHODS

Data collection

We selected four rocky intertidal localities (Fig. 1) distributed over 10° in latitude, only two of them located at or near to prominent upwelling centres at 23° and 30° S (see Vásquez et al. 1998, Camus & Andrade 1999, Thiel et al. 2007), assumed to experience high upwelling intensity: Río Seco (21°00'05" S, 70°09'54" W; south of Iquique, low upwelling), Caleta Constitución (23°25'23" S, 70°35'26" W; west coast of Mejillones Peninsula, high upwelling), Caleta Angosta (28°15'38" S, 71°10'23" W; north of Huasco, low upwelling), and Lagunillas (30°06'14" S, 71°22'57" W; south of Coquimbo, high upwelling).

The four localities were sampled at seasonal intervals during low tide cycles in autumn (22-28 May), winter (18-24 August) and spring (8-15 November) 2005, summer 2006 (27 January-5 February), and autumn (21-29 May) 2006. In each sampling, we evaluated the density of *A. echinata* in the intertidal zone in a total of 45 quadrats of 0.25 m², distributed in five permanent blocks (nine per

block) with georeferenced positions and spaced every 15 m. Each block included three series of quadrats located at the high, mid and low intertidal zones (three per zone), placed with ca. 1.5 and 5 m of vertical and horizontal spacing, respectively. In each sampling, we recorded the sea surface temperature (SST) with data loggers (Onset Stowaway) installed permanently at each locality (submerged 1 m below MLLW off the central sector of the sampled coastal stretch). Additionally, we obtained direct manual measurements on each day of sampling using a thermometer (± 0.1 °C) in the same place as the data logger. We provide the average value of SST estimated for each sampling date and locality.

For gut content analyses, we estimated that collecting 10 individuals per season and locality accounted for 85 to 100 % of the consumed items in all seasons (Camus et al. 2008; see also Winemiller et al. 2001). Albeit final sample sizes varied depending on the natural occurrence of *A. echinata*, we collected an average (\pm SE) number of 8.6 ± 0.6 individuals per locality and season (total = 171, $n = 43$ per locality excepting Caleta Constitución with 42). Collections were made at daytime during low tides. In order to incorporate the environmental patchiness of food resources, individuals were taken randomly from the whole area delimited by our sampling blocks. Chitons were injected with and stored in 10 % formaldehyde for preserving gut contents, which were then analyzed under microscope and stereoscope, identified to the lowest taxonomic level possible, and recorded as dietary items separately for each individual. In parallel, we estimated body size by recording the dry biomass (oven dried to constant weight at 70 °C) of each sampled individual. We failed to measure the width of shell plates as a complementary estimation, and therefore we obtained an approximate estimation by recording the maximum length of each individual (after relaxing the body for reducing biases).

Analyses

The following analyses are based on field and laboratory data which were processed at different levels of resolution in order to obtain a proper characterization of the *A. echinata* diet on a local and regional scale. Analysis of variance (ANOVA) was employed after checking normality and homoscedasticity assumptions, and possible correlations between means and variances, applying data transformations when necessary. Seasons and localities (non-randomly selected) were treated as fixed factors.

The density of *A. echinata* was the only variable directly assessed at the sampling blocks in each locality, and was therefore analyzed by a nested ANOVA including blocks within localities, using $\log(x+1)$ -transformed data. The occurrence of *A. echinata* was zero at high levels and near zero at mid levels, and the comparison of densities was based only on data from low intertidal quadrats. The body mass and length of the randomly collected individuals were compared among localities by means of one-way ANOVA. In addition, the relationship between body mass and length of all collected individuals was obtained by a non-linear power regression fit. The concordance in the local consumption (average occurrence frequency) of dietary items by *A. echinata* was assessed with the non-parametric, rank-based Friedman test (Fr), which is suited for comparing the relative importance of items (i.e. within-locality distribution of relative rank-orders) across localities. The number of dietary items consumed per individual was compared among localities and seasons using two-way ANOVA, applying a Tukey test for a posteriori



Fig. 1: Study localities in northern Chile, located in zones with contrasting regimes of coastal upwelling (H: high upwelling vs. L: low upwelling).

Localidades de estudio en el norte de Chile, ubicadas en zonas con regímenes contrastantes de surgencia costera (H: alta surgencia vs. L: baja surgencia).

comparisons. The relationship of the dietary richness of *A. echinata* with both SST and body mass was evaluated by means of Spearman rank correlation based on average values calculated per season and locality, considering the total number of consumed items as well as the number of algal and animal items separately.

For each group of *A. echinata* individuals collected per community and season, we estimated their niche breadth by means of Levins' index (reciprocal of Simpson's index; Levins 1968), using the richness and occurrence frequency of the recorded dietary items. On this basis, we estimated a value of niche breadth for each season and community, as well as an overall value per community by pooling seasonal data. The differences in niche breadth between communities and seasons were assessed using a two-way Friedman test and a non-parametric test for a posteriori comparisons (Siegel & Castellan 1988).

The dietary composition of *A. echinata* was preliminarily examined using a non-metric multidimensional scaling ordination (stress = 0.14), in order to infer possible spatiotemporal variations. We then evaluated such variation by means of a similarity analysis (ANOSIM; Clarke 1993), based on a Bray-Curtis similarity matrix obtained from the occurrence frequency of items per season recorded at each locality, using locality and season as factors, and applying global and pair-wise permutation tests (statistics R; $\alpha = 0.05$, corrected for multiple comparisons).

RESULTS

General aspects

The local vertical distribution of *A. echinata* in northern Chile appeared largely restricted to lower intertidal sectors (Fig. 2A): 97.4 % of individuals occurred at low tidal levels and only 2.6 % at mid levels in Caleta Constitución and Lagunillas. The absence of chitons at

high levels would not be an obvious result of sampling at low tides, as field observations before and after samplings suggest that the species would remain at lower sectors during high tides. The local population density of *A. echinata* ranged in average from 1.46 m⁻² in Caleta Angosta to 2.54 m⁻² in Río Seco (Table 1), and was not significantly different among localities ($F_{3,280} = 0.33$; $P = 0.479$) but showed a significant variation among blocks within localities ($F_{16,280} = 2.25$, $P = 0.0012$), suggesting that the spatial dispersion of chitons is controlled by local heterogeneity.

The individual body mass of *A. echinata* (Fig. 2B, Table 1) varied significantly among localities ($F_{3,167} = 24.05$; $P < 0.001$), and was larger at higher latitudes. Body mass in Lagunillas was significantly higher than in Caleta Angosta (Tukey test; $P = 0.0028$), and these two localities showed in turn significantly higher values than Río Seco and Caleta Constitución ($0.0001 < P < 0.0027$), which did not differ between them ($P = 0.96$). Likewise, the length of *A. echinata* (Fig. 2B, Table 1) varied significantly between localities ($F_{3,167} = 17.40$; $P < 0.0001$), following the same pattern of paired differences as described above for biomass (Tukey tests; $0.0001 < P < 0.0449$), with a greater length at higher latitudes. In fact, the largest individual (23.0 cm) was recorded in Lagunillas, while 50 % of chitons varied between 10 and 20 cm. In addition, the relationship between body mass (B) and length (L) of *A.*

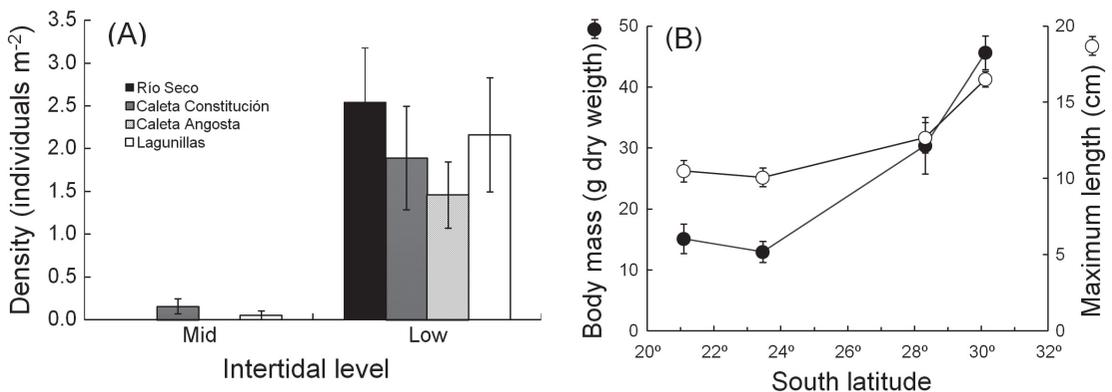


Fig. 2: Populational variation of *Acanthopleura echinata* across localities. (A) Density at the mid and low intertidal zone (the species was not found at high tidal levels). (B) Body mass and length vs. latitude: localities ordered from north (Río Seco) to south (Lagunillas). Values: mean \pm SE.

Variación poblacional de *Acanthopleura echinata* a través de las localidades. (A) Densidad en la zona intermareal media (Mid) y baja (Low) (la especie no fue encontrada en niveles mareales altos). (B) Masa y longitud corporal vs. latitud: localidades ordenadas de norte (Río Seco) a sur (Lagunillas). Valores: media \pm EE.

echinata was well described by the power function $B = 0.0147 L^{2.812}$ ($R^2 = 0.96$, $P < 0.001$, $n = 171$). The residuals of this relationship were homogeneous but tended to be more scattered toward largest body sizes, suggesting that smaller chitons could be less affected by environmental variations than larger ones.

Characterization of the diet

The diet of *A. echinata* in northern Chile was composed by a total of 85 items: 30 animal items including 26 invertebrate taxa (30.6 %) and four types of larvae (4.7 %), and 55 algal items including 26 Rhodophyta (30.6 %), 15 Chlorophyta (17.6 %), 10 Phaeophyta (11.7 %), two Cyanophyta (2.4 %), and two aggregated items (spores and Bacillariophyceae; 2.4 %). The identity of food items and their respective occurrence frequency (OF) at locality and overall levels are shown in Table 2. The most important algal taxa (overall OF > 25 %) were: (a) Chlorophyta: *Codium dimorphum*, *Ulva rigida*, *Pseudoulvella* sp., *Enteromorpha* sp., *Cladophora fascicularis*; (b) Phaeophyta: *Ralfsia* sp., *Ectocarpus acutus*; (c) Rhodophyta: encrusting Corallinaceae, *Hildenbrandia lecanellieri*, *Gelidium chilense*, *Amphiroa dimorpha*, *Gelidium pussillum*, *Schottera nicaensis*. Albeit Bacillariophyceae reached the highest overall OF (> 90 %), our direct observation of gut contents indicated that diatoms occurred in low relative

importance as compared to any other common item. The algal thalli most frequently ingested by *A. echinata* were encrusting forms (Table 2), and highly-calcified encrusting corallines were the dominant item (OF: 79-88 %) in all localities, although erect corallines such as *A. dimorpha* and *Corallina officinalis* were also highly important. Among invertebrate taxa, the most frequent were Cirripedia (as an aggregated item, but also recorded at the species level), Bryozoa, and Demospongiae. We highlight the potential importance of *Tegula atra* and *Scurria* sp. in its diet (in spite of their low OF), as they are common herbivores and potential competitors of *A. echinata*.

In general, the overall frequency of each algal and animal item tended to be consistently similar (either high or low) at local levels, which contributed to an obvious significant difference among items (Friedman; $Fr = 264.0$, $df = 84$, $P < 0.0001$). However, the relative importance of items (local rank order) varied significantly among localities ($Fr = 10.46$, $df = 3$, $P = 0.0151$), most likely because several items having a low overall OF (< 25 %) were ingested at a very high frequency in a single given locality. Some of these items were *C. officinalis* and *Semimytilus algosus* in Río Seco, *Hypnea cenomyce* and algal spores in Caleta Constitución, *Polysiphonia* sp. and *Blidingia minima* in Caleta Angosta, or *Erythrotrichia carnea* and *Lyngbya* sp. in Lagunillas (see Table 2).

TABLE 1

Density, body size and niche breadth (Levins' index) of *Acanthopleura echinata* in rocky shores of northern Chile. Values (mean \pm SE) were estimated by locality (averaged seasons) and for pooled localities (grand average). Niche breadth by locality was estimated also by pooling seasons (values in parentheses).

Densidad, tamaño corporal y amplitud de nicho (índice de Levins) de *Acanthopleura echinata* en costas rocosas del norte de Chile. Los valores (media \pm EE) fueron estimados por localidad (promedio estacional) y para el conjunto de localidades (gran promedio). La amplitud de nicho por localidad además se estimó agrupando las estaciones (valores en paréntesis).

	Río Seco	Caleta Constitución	Caleta Angosta	Lagunillas	Overall
Density (No. m ⁻²)	2.54 \pm 0.63	1.89 \pm 0.61	1.46 \pm 0.39	2.16 \pm 0.67	2.01 \pm 0.29
Body mass (g dry weight)	15.13 \pm 2.43	12.98 \pm 1.75	30.42 \pm 4.64	45.64 \pm 2.76	26.11 \pm 1.76
Maximum length (cm)	10.49 \pm 0.70	10.08 \pm 0.62	12.68 \pm 0.99	16.52 \pm 0.51	12.27 \pm 0.42
Niche breadth	15.72 \pm 1.25 (21.84)	16.52 \pm 3.22 (27.29)	21.72 \pm 0.96 (28.96)	21.00 \pm 2.74 (30.77)	29.62

TABLE 2

Algae and invertebrates consumed by *Acanthopleura echinata* in northern Chile, indicating their consumption frequencies (occurrence %) at a local and overall (grouped localities) level. Items are separated by taxonomic group and listed in decreasing order of their overall frequency. RS: Río Seco, CC: Caleta Constitución, CA: Caleta Angosta, LA: Lagunillas. indet: item not determined at lower taxonomic level.

Algas e invertebrados consumidos por *Acanthopleura echinata* en el norte de Chile, indicando sus frecuencias de consumo (ocurrencia %) a nivel local y general (localidades agrupadas). Los ítemes están separados por grupo taxonómico y listados en orden decreciente de su frecuencia general. RS: Río Seco; CC: Caleta Constitución; CA: Caleta Angosta; LA: Lagunillas. indet: ítem no determinado a nivel taxonómico inferior.

Dietary items	RS	CC	CA	LA	Overall
Chlorophyta					
<i>Codium dimorphum</i> Svedelius	27.91	50.00	51.16	60.47	47.37
<i>Ulva rigida</i> C. Agardh	39.53	42.86	46.51	55.81	46.20
<i>Pseudoulvella</i> sp.	37.21	26.19	55.81	23.26	35.67
<i>Cladophora fascicularis</i> (Mertens) Kützing	23.26	21.43	27.91	30.23	25.73
<i>Enteromorpha</i> sp.	11.63	21.43	25.58	44.19	25.73
<i>Blidingia minima</i> (Kützing) Kylin	11.63	14.29	25.58	9.30	15.20
<i>Chaetomorpha</i> sp.	6.98	19.05	13.95	20.93	15.20
<i>Rama novazelandiae</i> (J. Agardh) Chapman	6.98	11.90	18.60	2.33	9.94
<i>Ulvella lens</i> Crouan	2.33	7.14	16.28	11.63	9.36
<i>Rhizoclonium</i> sp.	2.33	9.52	6.98	9.30	7.02
<i>Ulothrix flacca</i> (Dillwyn) Thuret	0	7.14	4.65	9.30	5.26
<i>Urospora</i> sp.	4.65	0	4.65	2.33	2.92
<i>Chaetomorpha firma</i> Levring	0	7.14	0	2.33	2.34
<i>Enteromorpha compressa</i> (Linnaeus) Greville	2.33	0	0	0	0.58
<i>Pseudopringsheimia</i> sp.	0	0	2.33	0	0.58
Phaeophyta					
<i>Ralfsia</i> sp.	41.86	35.71	53.49	48.84	45.03
<i>Ectocarpus acutus</i> Setchell et Gardner	27.91	26.19	48.84	62.79	41.52
<i>Macrocystis integrifolia</i> Bory	4.65	4.76	4.65	6.98	5.26
<i>Petalonia fascia</i> (Müller) Kuntze	0	0	9.30	4.65	3.51
<i>Pilayella littoralis</i> (Linnaeus) Kjellman	4.65	2.38	0	0	1.75
<i>Colpomenia</i> spp.	4.65	0	0	0	1.17
<i>Glossophora kunthii</i> (C. Agardh) J. Agardh	0	2.38	2.33	0	1.17
<i>Hincksia granulosa</i> (Smith) Silva	0	0	0	4.65	1.17
<i>Endarachne binghamiae</i> J. Agardh	0	0	0	2.33	0.58
<i>Sphacelaria furcigera</i> Kützing	0	0	2.33	0	0.58
Rhodophyta					
Encrusting Corallinaceae	81.40	78.57	81.40	88.37	82.46
<i>Hildenbrandia lecanellieri</i> Harriot	76.74	66.67	74.42	44.19	71.35
<i>Gelidium chilense</i> (Montagne) Santelices et Montalva	58.14	61.90	74.42	46.51	60.23

TABLE 2. Continuation

<i>Amphiroa dimorpha</i> Lemoine	32.56	19.05	48.84	48.84	37.43
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	11.63	35.71	23.26	39.53	27.49
<i>Schottera nicaeensis</i> (Lamouroux ex Duby) Guiry et Hollenberg	18.60	26.19	16.28	41.86	25.73
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	6.98	14.29	32.56	34.88	22.22
<i>Polysiphonia</i> sp.	0	11.90	60.47	4.65	19.30
<i>Corallina officinalis</i> (Decaisne) Kützing	23.26	9.52	16.28	11.63	15.20
<i>Acrochaetium grandis</i> (Levring) Papenfuss	2.33	16.67	20.93	16.28	14.04
<i>Hypnea cenomyce</i> J. Agardh	16.28	35.71	4.65	0	14.04
<i>Hildenbrandia</i> sp.	4.65	19.05	4.65	20.93	12.28
<i>Chondrus canaliculatus</i> (C. Agardh) Greville	16.28	9.52	4.65	11.63	10.53
<i>Gelidium lingulatum</i> Kützing	0	11.90	11.63	11.63	8.77
<i>Amphiroa peruana</i> Areschoug	6.98	4.76	4.65	4.65	5.26
<i>Porphyra columbina</i> Montagne	0	7.14	6.98	4.65	4.68
<i>Ceramium rubrum</i> (Hudson) C. Agardh	0	0	9.30	2.33	2.92
<i>Polysiphonia pacifica</i> Hollenberg	0	0	4.65	6.98	2.92
<i>Centroceras clavulatum</i> (C. Agardh) Montagne	0	4.76	4.65	0	2.34
<i>Gastroclonium cylindricum</i> Santelices, Abbott et Ramirez	4.65	2.38	0	0	1.75
<i>Gigartina tuberculosa</i> (Hooker et Harvey) Grunow	0	4.76	0	0	1.17
<i>Petroglossum pacificum</i> Hollenberg	0	4.76	0	0	1.17
<i>Polysiphonia mollis</i> Hooker et Harvey	0	0	2.33	2.33	1.17
<i>Ballia callitricha</i> (C. Agardh) Kützing	0	0	0	2.33	0.58
<i>Bangia atropurpurea</i> (Roth) C. Agardh	0	0	2.33	0	0.58
<i>Montemaria horridula</i> (Montagne) Joly et Alveal	0	0	2.33	0	0.58
Cyanophyta					
<i>Lyngbya</i> sp.	6.98	33.33	16.28	27.91	21.05
Cyanophyta indet	0	0	18.60	23.26	10.53
Others					
<i>Bacilliarophyceae</i>	100	100	93.02	72.09	91.23
<i>Algal spores</i>	4.65	26.19	6.98	9.30	11.70
Invertebrates					
Cirripedia indet	74.42	64.29	51.16	81.40	67.84
Bryozoa indet	32.56	33.33	27.91	60.47	38.60
Demospongiae indet	18.60	40.48	48.84	39.53	36.84
Foraminifera indet	4.65	9.52	37.21	27.91	19.88
<i>Semimytilus algosus</i> (Gould)	25.58	2.38	9.30	11.63	12.28

TABLE 2. Continuation

Nematoda indet	9.30	9.52	18.60	9.30	11.70
<i>Hyale</i> sp.	4.65	16.67	4.65	18.60	11.11
<i>Jehlius cirratus</i> (Darwin)	13.95	2.38	0	27.91	11.11
<i>Austrolittorina araucana</i> Orbigny	13.95	7.14	20.93	0	10.53
Hydrozoa indet	6.98	2.38	4.65	25.58	9.94
<i>Notochthamalus scabrosus</i> (Darwin)	18.60	9.52	0	11.63	9.94
Amphipoda indet	11.63	9.52	6.98	2.33	7.60
<i>Perumytilus purpuratus</i> (Lamarck)	2.33	4.76	13.95	2.33	5.85
Ostracoda indet	0	2.38	0	18.60	5.26
Tardigrada indet	6.98	2.38	2.33	0	2.92
Egg capsules of <i>Concholepas concholepas</i>	0	0	4.65	2.33	1.75
Spirorbidae indet	0	0	4.65	2.33	1.75
Acari indet	0	4.76	0	0	1.17
<i>Tegula atra</i> (Lesson)	2.33	0	0	2.33	1.17
<i>Balanus flosculus</i> Darwin	0	0	0	2.33	0.58
<i>Balanus laevis</i> Darwin	2.33	0	0	0	0.58
<i>Brachidontes granulata</i> (Hanley)	0	0	0	2.33	0.58
Isopoda indet	0	0	0	2.33	0.58
Polychaeta indet	0	2.38	0	0	0.58
<i>Scurria</i> sp.	0	0	0	2.33	0.58
Sipunculidae	2.33	0	0	0	0.58
Invertebrate larvae					
Nauplius	4.65	2.38	0	2.33	2.34
Cypris	0	2.38	0	2.33	1.17
Zoea	0	0	0	4.65	1.17
Diptera	0	0	2.33	0	0.58

Dietary richness and niche breadth

At the individual level (Fig. 3A), the dietary richness (number of consumed items) of *A. echinata* was significantly different among localities ($F_{3,151} = 12.20$, $P < 0.0001$) and seasons ($F_{4,151} = 8.32$, $P < 0.0001$), and the two factors had a significant interaction ($F_{12,151} = 3.17$, $P = 0.0005$). However, seasonal trends were not evident, and the interaction did not involve a defined covariation pattern, as most differences seemed related to the increase or decrease of dietary richness in particular localities and seasons (Fig. 3A), such as the peaks recorded at Caleta Angosta in Autumn 2005 and Lagunillas in summer-autumn 2006, or the drop at Caleta

Constitución toward spring 2005. In addition, the dietary richness averaged by locality and season ($n = 20$) was not related with mean SST ($r = 0.14$, $P = 0.57$), but showed a positive relationship with chiton body mass ($r = 0.52$, $P = 0.02$). At a closer look, however, body mass correlated positively only with the richness of algal items ($r = 0.56$, $P = 0.01$) and had no association with animal items ($r = 0.06$, $P = 0.79$), implying that the proportion of algal items in the diet increases with body mass. In fact, the average richness of animal items was nearly the same in all localities (Fig. 3B), regardless of the strong local variations in the size of *A. echinata* (Fig. 2B).

The dietary niche breadth of *A. echinata* was high in all places and dates, tending to be

wider in average at higher latitudes (Table 1), though the test showed no differences among localities ($F_r = 7.08$, $df = 3$, $P = 0.070$), likely due to the significant variation among seasons ($F_r = 10.60$, $df = 4$, $P = 0.0314$). However, a posteriori comparisons did not detect differences between particular seasons, probably because of the low relative power of the test (Siegel & Catellan 1988). As compared to seasonal averages, the overall estimates (pooled seasons) of dietary breadth were less variable among localities (Table 1), yet showing a gradual increase with latitude. In addition, the average niche breadth by locality and season was positively correlated with body mass ($r = 0.86$, $n = 20$, $P = 0.001$).

Diet composition

The taxonomic composition of the diet of *A. echinata* did not differ significantly among localities (ANOSIM; global $R = -0.025$, $P = 0.583$), but it did among seasons (global $R = 0.59$, $P = 0.001$) due to variations in the presence and/or importance of particular items. For instance, *C. fascicularis*, *C. dimorphum* or Bryozoa did not occur at all seasons but they usually reached a high OF when present, while other items were always present but showing high variations in OF, such as Cirripedia (autumn 2005: 96.4 %; autumn 2006: 17.5 %) or Demospongiae (autumn 2005: 3.8 %; autumn 2006: 68.3 %). In this context, a posteriori

comparisons between pairs of consecutive seasons showed significant differences between colder (autumn-winter 2005) or warmer (spring 2005-summer 2006) seasons ($0.32 < R < 0.97$; $P = 0.029$ in both cases), but not between contrasting seasons such as winter vs. spring 2005 ($R = 0.29$, $P = 0.086$) or summer vs. autumn 2006 ($R = 0.27$, $P = 0.200$). The above suggests that composition of *A. echinata*'s diet is little affected by seasonality.

DISCUSSION

Characteristics of Acanthopleura echinata as a consumer

The trophic habits of *A. echinata* in northern Chile showed four noteworthy aspects. First, a high and regular consumption of encrusting and erect thalli of strongly-calcified coralline algae, agreeing with Steneck & Watling's (1982) predictions regarding to the high versatility and excavating capacity of the polyplacophoran radula, and with the larger size and strong mineralization of the teeth of *A. echinata* among chiton species (Lee et al. 2000). Second, a wide dietary spectrum (a total of 85 items) reflecting a generalist behavior of the species over space and time. The number of algal items consumed by *A. echinata* increased with its body size, but the breadth and composition of its diet (integrating the study period) did not

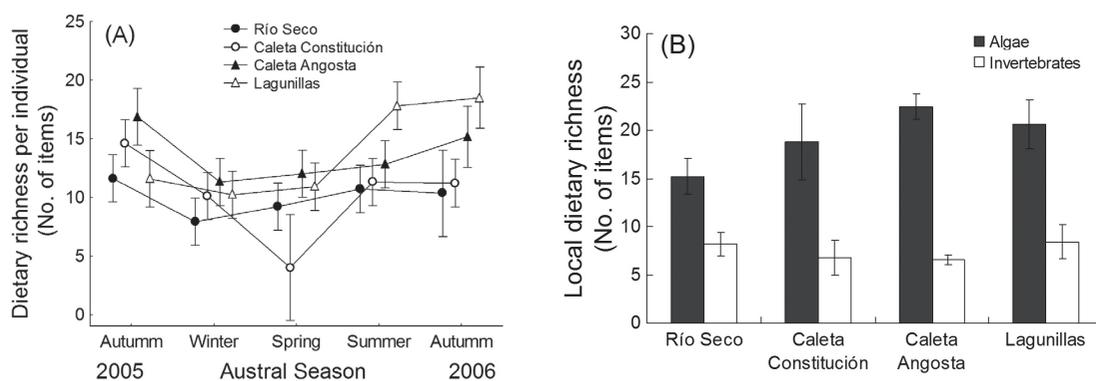


Fig. 3: Dietary richness (average number of consumed items) of *Acanthopleura echinata* in the study localities. (A) Temporal variation at the individual level including all items. (B) Spatial variation (averaged seasons) at the population level for algal and animal items separately. Values: mean \pm 95 % confidence interval.

Riqueza dietaria (número promedio de ítemes consumidos) de *Acanthopleura echinata* en las localidades de estudio. (A) Variación temporal a nivel de individuos incluyendo todos los ítemes. (B) Variación espacial (estaciones promediadas) a nivel poblacional para ítemes algales y animales por separado. Valores: media \pm intervalo de confianza 95 %.

differ significantly among the study localities. Third, the capacity of consuming taxa with a wide variation in structure, morphology, size, hardness and growth form, which can be a supplementary advantage for a species displaying a generalist conduct. However, future studies should evaluate whether microscopic food sources, such as periphyton or epiphytes, could be a primary target for *A. echinata* when grazing on larger taxa. In a wider scope, a recent analysis of herbivore species in Río Seco (Dragon & Camus, unpublished results) suggested that the generalist behavior of *A. echinata* involves both opportunistic and selective components, although such question was not directly assessed in this paper (an evaluation of the offer vs. consumption of resources for northern Chilean herbivores will be presented elsewhere). In this regard, Santelices et al. (1986) suggested that *A. echinata* fed selectively on some algal groups in a central Chilean locality. Nonetheless, our results did show that even though the most consumed items were virtually the same everywhere, the local rank-order importance of items was different among localities because several species were consumed at very high frequency only in a single given locality. The above thus suggests that *A. echinata* could take advantage of local variations by consuming the most common resources at each locality, as expected from an opportunistic behavior.

The fourth key aspect was the permanent presence of invertebrates in the gut contents of *A. echinata*, belonging to diverse phyla of intertidal (mostly sessile) organisms, which can be separated into two groups: (a) common taxa such as barnacles, sponges, bryozoans, hydrozoans and mussels, consumed at high frequency in all localities, and (b) miscellaneous taxa, consumed at low frequency only in some localities. Some of these animals, particularly from the second group, were likely ingested passively by *A. echinata* during grazing, and the possibility exists that they may be digested to a greater or lesser extent. However, molluscs are capable of fine discrimination between different food types (e.g., Franz 1990), and it is likely that other animals may be targeted as food sources and ingested actively by *A. echinata*. In fact, several supposedly herbivorous chitons have proved to be physiological omnivores or carnivores,

and some of them even change their trophic status seasonally or throughout the ontogeny (e.g., Latyshev et al. 2004, Kang et al. 2008). Consequently, we suggest that the frequent consumption of invertebrates by *A. echinata* (and other intertidal herbivores in northern Chile; Aguilera 2005, Camus et al. 2008, Navarrete et al. 2008, Sanhueza et al. 2008, Camus et al. 2009), is actually an evidence of physiological omnivory. Nonetheless, the proportion of algal (vs. animal) taxa ingested by *A. echinata* increased with its body size, suggesting some ontogenetic variation of omnivorous vs. herbivorous habits which should be taken into account in future studies.

Regardless of omnivory, though, the ingestion of animals by herbivores may be a relevant factor in the dynamics of the intertidal food web. Northern Chilean consumers, including *A. echinata*, exhibit a high dietary overlap (up to 80 % in some cases; Camus et al. 2008), and their combined action could cause important per capita effects on other animal populations. In addition, such phenomenon contributes a high number of weak links to the food web, which could have positive effects on its stability (e.g., Neutel et al. 2002).

Variations in niche breadth and body size in space and time

The variation in body mass of *A. echinata* on a local scale, closely related with niche breadth and algal dietary richness, appeared as the main factor accounting for the variation of its diet on a geographical scale. In this regard, our data show that both body mass and niche breadth increase with latitude, apparently matching the classic Bergmann's rule and niche-latitude hypothesis (but see Rhode 1992, Blackburn et al. 1999). However, such trends might also be a by-product of local and/or mesoscale variations, and the lack of published data on the mean size of *A. echinata* prevented us to confirm any trend outside northern Chile (only Aldea & Valdovinos 2005 reported a single small individual 5.86 cm in length at 36°40' S, which was insufficient for comparison). In addition, prior studies in the same localities showed that other important herbivores exhibit very different patterns. For instance, the large chiton *Enoplochiton niger* showed a negative size-latitude relationship but no trend in niche

breadth (Sanhueza et al. 2008), while the black urchin *Tetrapygyus niger* (Molina) showed no trend in size but a positive niche-latitude relationship (Navarrete et al. 2008). Thus, the factors relating latitude with niche breadth are likely more complex than envisaged in early views, and we do not discard that they may involve some structural array of interspecific interactions (see Vasquez & Stevens 2004).

Additionally, none of our results suggested a direct relationship between upwelling intensity and dietary patterns of *A. echinata*. In spite of the alternate latitudinal location of our high- and low-upwelling sites (mirroring the spatial scattering of upwelling centres on the Chilean coast; Nielsen & Navarrete 2004, Thiel et al. 2007), the niche breadth of *A. echinata* (correlated with dietary richness and body size) followed a latitudinal trend and showed indistinctly high and low values under the two upwelling regimes. Being possible that our criterion of proximity of localities to upwelling centres failed to reflect the actual occurrence of upwelling, this latter could also be tracked by SST as upwelling is typically signaled by low SST values (Thiel et al. 2007), though even so dietary richness showed no relation with SST. Nonetheless, the above results do not necessarily imply that upwelling has no influence on intertidal consumers. In central Chile, for instance, the variation in nutrient supply related with upwelling has demonstrated to exert differential effects on the diversity, abundance, and succession of algal functional groups affecting in turn the consumption patterns of herbivore consumers (see Nielsen & Navarrete 2004, Wieters 2005). The above studies did not consider fleshy and calcified encrusting algae, which were the main dietary items of *A. echinata*, all of them consumed at high frequencies at all localities. We nonetheless extrapolate the suggestion that spatial variations in upwelling might affect the availability of encrusting vs. non-encrusting algae, or of fleshy vs. calcified encrusting algae, as a useful context for assessing opportunistic or selective responses in future studies. When faced to a higher abundance and diversity of algal foods, consumers such as *A. echinata* (which would be able to feed on any kind of algal thalli) are expected to increase their dietary spectrum. However, it is also possible that they may focalize on resources that are

more abundant or frequent, such as other consumers seem to do during El Niño events (Navarrete et al. 2008, Sanhueza et al. 2008), or on those more readily accessible from refuge microhabitats, as suggested by the short-range foraging excursions made by *Chiton granosus* from crevices (Aguilera & Navarrete 2007).

We finally remark some additional factors not included in our study but relevant to the scope of this paper. In northern Chilean rocky shores, the bottom-up influences of upwelling on the intertidal biota have not been clearly established so far (e.g., Vásquez et al. 1998, Camus & Andrade 1999), albeit they might be comparatively less important than the effects derived from interannual SST variations (Thiel et al. 2007, Camus et al. 2008), particularly during warm episodes of the El Niño-Southern Oscillation. While our analysis on *A. echinata* covered a period without significant SST anomalies, the prior occurrence of the 2004-05 El Niño in northern Chile revealed noticeable effects (regardless of upwelling) on the consumption patterns of other intertidal herbivores (Navarrete et al. 2008, Sanhueza et al. 2008), including the chiton *E. niger* which shows similar trophic characteristics than *A. echinata*. Thus, the results herein could have been very different if obtained during an El Niño event, although likely with local variations because upwelling, by bringing cold water to the surface, might also play a key role in counteracting local thermal impacts of SST anomalies (see Camus 2008). In addition, Nielsen & Navarrete (2004) noted that, in central Chile, upwelling regimes affected the trajectory of algal succession in previously cleared plots, though such effect revealed only after six months or more, suggesting a slow development of bottom-up influences. In this regard, the temporal species turnover resulting from the interplay among local secondary succession (subsuming upwelling-driven effects), metacommunity dynamics and large-scale disturbances (e.g., El Niño), could be another factor affecting resource availability and herbivore feeding patterns. This factor is seldom considered in trophic studies, but in our study localities, the local species turnover estimated on a seasonal basis (winter 2004-summer 2007; Camus 2008) ranged in average from 40 to 50 %, which may help to explain why *A. echinata* and most northern

Chilean herbivores are not trophic specialists (Camus et al. 2008), and why most of them seem to be opportunistic consumers.

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