

Geographical variation in the use of intertidal rocky shores by the lizard *Microlophus atacamensis* in relation to changes in terrestrial productivity along the Atacama Desert coast

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Summary

1. The movement of materials and organisms between ecosystems is a common process in nature.
2. In the present study we investigate the hypothesis that the movement of consumers between ecosystems depends not only on the differences in productivity between ecosystems and prey availability, but also on these animals' biological characteristics.
3. To address this hypothesis we investigated the changes in abundance, habitat utilization and diet of the lizard *Microlophus atacamensis* along its geographical range on the coast of the Atacama Desert. Within this range, intertidal rocky shore communities do not show important variations in their species composition and abundance, but terrestrial communities show a steep gradient of productivity associated with the increase in rainfall from north to south.
4. Our results show that the use of intertidal habitats and the consumption of intertidal prey by *M. atacamensis* change within its geographical range: in the North, the species uses intertidal areas and behaves as an herbivore consuming mostly algae, whereas in the South it spends most of the time in terrestrial habitats as a carnivore mainly of arthropods.
5. Our study gives new evidence for cross-ecosystem connections created by consumer movement between habitats of contrasting but variable productivity levels.

Key-words: green algae, linear mixing models, stable isotopes, habitat use, thermoregulation, reptiles, primary productivity

Introduction

The movement of materials and organisms between ecosystems is a common process in nature (Heatwole 1971; Lord & Burger 1984; Bustamante, Branch & Eekhout 1995; Polis & Hurd 1995, 1996; Anderson & Polis 1998; Nakano & Murakami 2001; Fariña *et al.* 2003; Fariña, Castilla & Ojeda 2003; Ellis, Fariña & Witman 2006). These movements can be categorized into three major groups: (a) transport of nutrients, organisms and materials exerted by physical agents such as water or wind, (b) transport of nutrients and materials

by biotic or biogenic agents and (c) movement of prey and consumers between habitats (Polis, Anderson & Holt 1997). Recently, Polis *et al.* (Polis 1991; Polis & Hurd 1996; Huxel & McCann 1998; Huxel, McCann & Polis 2002) generated the theoretical framework and generalizations for these phenomena, although the exchanges have been noted in both terrestrial and aquatic communities since the work of Elton (1927). This group, working in the desert island ecosystems of the Sea of Cortez, described that terrestrial food webs on the islands were subsidized by the input of marine materials and predicted that if two ecosystems differ greatly in their levels of productivity, nutrients would move from the less to the more productive habitat. In spite of this the logical counterpart, that consumers should move from the less to the more productive habitat, one of the core predictions of the optimal foraging theory (Parker & Stuart 1976), was not considered explicitly in the model.

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Several studies show that terrestrial mammals (Navarrete & Castilla 1993; Rose & Polis 1998; Stapp *et al.* 1999; Sleeman *et al.* 2001; Delibes *et al.* 2004), terrestrial reptiles (Quijada-Mascarreñas 1992; Grismer 1994; Catenazzi & Donnelly 2006) and terrestrial birds (Sabat 2000; Sabat *et al.* 2006) effectively consume marine prey on desert islands. Indeed, Carlton & Hodder (2003) recognized that the phenomenon of terrestrial mammals entering into intertidal areas to consume prey occurs on all continents (except in Antarctica). To describe these mammals, they proposed the term 'maritime mammals' to define the 'predators that utilize living intertidal energy resources and transfer these to the land'.

In most of the above-mentioned studies it has been postulated that the inclusion of marine prey in the consumers' diet, referred to as trophic broadening, occurs in response to the low availability of resources in terrestrial habitats (energetic explanation) or to the improved nutrition of marine prey (nutritional explanation, for details see Polis *et al.* 1997). These two factors (availability and nutritional quality of prey) vary in both time (e.g. seasonally) and space (e.g. geographically) and it is expected that the food preference of consumers will track this variation. For example, deer in Alaska and foxes near the Bering Sea visit intertidal areas only during the winter season (Fay & Stephenson 1989; O'Clair & O'Clair 1998). On the British Columbian Islands, before the arrival of marine birds (or if the density of nesting birds is reduced), rodents usually expand their trophic spectra to include intertidal prey (Drever *et al.* 2000). In spatial terms, Stapp, Polis & Sanchez-Piñero (1999) showed that due to the reduced precipitation on the islands of Baja California, rodents usually consume more intertidal prey on islands where the vegetation cover is almost null or extremely low. During the El Niño Southern Oscillation (ENSO) years on these islands, precipitation increased substantially (almost 200%) and in response to the associated increase in plant vegetation, rodents shifted towards granivory, depending exclusively on terrestrial foods (Anderson & Polis 1998). Thus in coastal areas, the consumption of marine food by terrestrial consumers is a dynamic phenomenon that can be affected by the spatio-temporal variability of productivity. Specifically, it is expected that the inclusion of marine food in the diet of terrestrial consumers occurs more frequently in sites or seasons where terrestrial productivity is lower than marine productivity.

The Atacama and Peruvian Deserts form a belt that spans more than 3500 km from the border of Ecuador and Peru (5°00' S) to La Serena in North-central Chile (29°55' S) and make up two of the driest and least productive terrestrial ecosystems in the world (Rundel *et al.* 1991). The Peru–Chile current system washes the coast of this desert and is one of the most productive marine ecosystems in the world (Ahumada, Pinto & Camus 2000). Near the coast of this region, where the unproductive terrestrial system meets the productive marine ecosystem, it is possible to find many terrestrial vertebrates consuming marine prey, such as the lizards of the genus *Microlophus* (Fariña *et al.* 2003).

The genus *Microlophus* is composed of 20 lizard species distributed from the Galapagos to North-central Chile. It has

been divided into two main groups (Dixon & Wright 1975): *Occipitalis*, composed of 10 species living in the Galapagos and northern Peru, and *Peruvianus*, also composed of 10 species ranging from southern Peru to northern Chile. Within the Peruvian group two different subgroups can be recognized. The inland group, composed of eight species living in the desert mountains and valleys, and the coastal group, composed of two species: *M. quadrivittatus* and *M. atacamensis*. The geographical range of *M. quadrivittatus* (from Arica 18°00' S to Antofagasta 20°32' S) falls into an area where the extreme desert reaches the coast and there is practically no annual precipitation (maximum recorded = 2 mm year⁻¹, Di Castri & Hajek 1976), whereas the geographical range of *M. atacamensis*, the subject of this study and southernmost species of the genus, runs 500 km into the so-called Desert Coastal area which presents a gradient of precipitation from 2 mm year⁻¹ in the North (at Antofagasta) to almost 100 mm year⁻¹ in the South (La Serena).

Within this gradient environmental temperature decrease from the North to the South and the intertidal zone is an unfavourable thermal environment because lizards lose heat quickly by conduction, convection or evaporation when feeding on a wet rock substrate (Catenazzi *et al.* 2005; Sepúlveda *et al.* 2007). For this reason, lizards may face a trade-off between feeding and thermoregulation.

In concordance with the generalizations mentioned previously, we tested the hypothesis that dependent on the biological characteristics of *M. atacamensis*, the use of intertidal areas and maritime food should change within the geographical range of this lizard: in the North where terrestrial productivity is almost null but environmental temperatures are high, dependence on intertidal food should be high and it should decrease towards the South (where terrestrial productivity is high and the environmental temperature is low). The objective of the present study was to evaluate the changes in abundance, habitat utilization and diet of *M. atacamensis* along its geographical range, with special emphasis on the use of intertidal vs. terrestrial areas.

Methods

STUDY AREA

The study was conducted from November 2004 to November 2006 along the entire geographical range (~500 km) of *M. atacamensis* on the Atacama Desert Coast (Victoriano *et al.* 2003; Fig. 1). Within this range, rocky shores and exposed bays with few sand areas characterize the coast. Boulders and small (flat) benches compose most of the intertidal rocky shores, whereas sand patches occurring between high rocks dominate the ~500 m of the adjacent terrestrial area (referred to hereafter as 'terrestrial' habitat). Three sites similar in their exposure to waves (exposed), intertidal morphology (boulders and flat rocky benches) and terrestrial morphology (sand patches alternating with large rocks) were chosen from the geographical range of *M. atacamensis* (Fig. 1): (1) Taltal (24°37'09.8' S, 70°33'25.1' W) at the northern extreme, (2) Zenteno (26°51'40.8' S, 70°47'39.7' W) at the centre and (3) Huasco (28°07'46.3' S, 70°09'40.4' W) at the southern extreme. Di

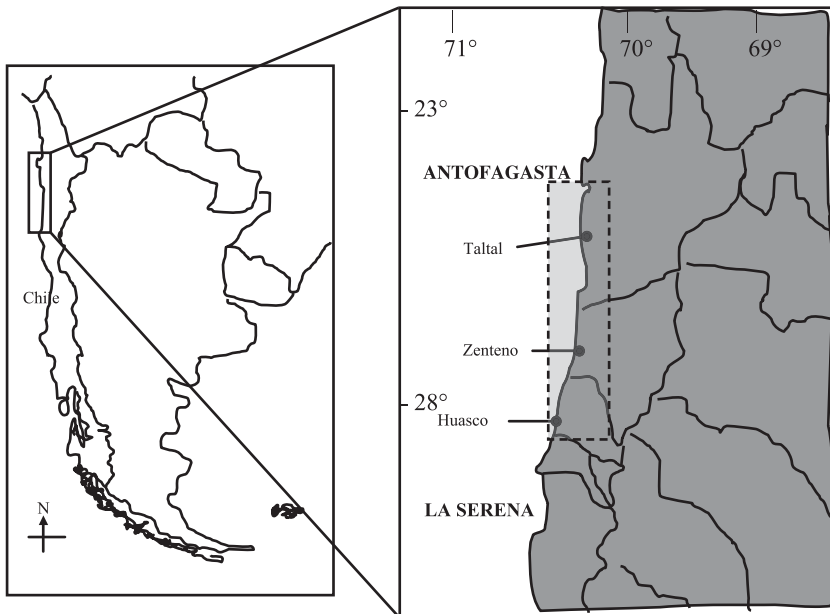


Fig. 1. Map of the study area and sites showing (dark box) the geographical distribution of *Microlophus atacamensis* along the Atacama Desert coast.

Castri & Hajek 1976) give a good description of the climate in the study areas: at Taltal the climate corresponds with the hyperarid desert with less than 2 mm of rainfall per year and mean temperatures between 21 °C in summer and 14 °C in winter. Zenteno receives ~ 25 mm of rain per year, with mean temperatures of 22 °C and 17 °C in summer and winter, respectively. Huasco is on the border of the area known as coastal desert, receiving 128 mm of rain per year with mean temperatures of 21 °C in summer and 16 °C in winter.

CHARACTERIZATION OF INTERTIDAL AND TERRESTRIAL HABITAT

Intertidal rocky shores in our study area have been described as being dominated by ephemeral green and seasonal red algae (mainly *Ulva* sp. and *Porphyra columbina*; Broitman *et al.* 2001) with high levels of productivity (around 300 g m⁻² year⁻¹, Fariña *et al.* 2003). Because the study area falls into the same marine biogeographical region, no important spatial variations in intertidal species composition, abundance and productivity have been found along it (Santelices 1991; Camus 2001). Fariña & Castilla (2001) confirmed this observation. For terrestrial habitats there have been no specific studies, but rather general descriptions that characterize the coastal area of Taltal (Hyperarid desert) as vegetation-less (Rauh 1985; Rundel *et al.* 1991; Marquet *et al.* 1998). The area of Huasco presents several plant species such as *Nolana divaricata*, *Heliotropum* sp., *Oxalis gigantea*, *Tetragonia maritime*, *Trichocereus coquimbamus* and *Eulychnia acida*, whereas at Zenteno the vegetation is restricted to the lower reaches of ravine and on the coast it is occasionally possible to find some individuals of *Nolana* sp. Despite the lack of descriptions for productivity levels at terrestrial habitats within our study area, following previous works on desert systems (Polis & Hurd 1996; Catenazzi & Donnelly 2006), an estimation using a model of primary productivity as a function of precipitation (Lieth 1978) gives a range from 4.4 to 242.9 g m⁻² year⁻¹, from Taltal to Huasco.

At the intertidal habitat of each site the diversity, abundance and composition of the species living on rocky substrates were assessed. Every 4 months, a series of 20 plots of 0.25 × 0.25 m were placed

randomly parallel to the shoreline at both high and mid-intertidal levels. Each plot was divided into a grid of 100 equally spaced intersection points. Intertidal levels were determined a priori using the high- and low-water marks predicted by tide tables, during days of similar tidal and sea conditions. Sessile algae or invertebrate species occurring underneath each point were identified to the lowest possible taxonomic level. The total cover of each species in the plot was obtained directly by the sum of their intersection points (Castilla 1988).

The diversity, cover and composition of plant species living at terrestrial habitats of each site were assessed. At each site, and every 4 months, a 100 m line was placed parallel to the shoreline. Every 10 m along the line, 5 × 5-m plots were placed giving a total of 10 plots per site. Plant species occurring in each of the plots were identified to the lowest possible taxonomic resolution, and their cover was estimated by dividing each plot into 100 equally sized squares (Steubing, Godoy & Alberdi 2001).

For both intertidal (algae) and terrestrial (plant) primary producer species with highest covers, an area corresponding to 10% of the cover was tilled on each sampling date to estimate biomass from cover data. With the aim of comparing the situation of primary producers geographically (i.e. between sites) at intertidal and terrestrial areas, the information on primary producers at both habitats recorded on each sampling date was pooled.

LIZARD ABUNDANCE PATTERNS

The abundance of *M. atacamensis* at intertidal and terrestrial areas was assessed by visual censuses. Every 4 months different observers walking parallel to the shoreline and covering both intertidal and terrestrial habitats recorded the number of individuals occurring at each site. Observers conducted their censuses at 900, 1100, 1300, 1500 and 1700 h, walking for 1 h on each occasion. Within this hour, the total number of individuals observed was recorded every 10 min. Each census covered the same distance (approximately 1 km of coast). According to previous studies, the ectothermic nature of *M. atacamensis* restricts their activity to daytime hours with substrate temperatures above 22 °C (Fariña *et al.* 2003). Considering this,

the abundance patterns were characterized excluding the data when substrate temperatures were below 22 °C because no individuals were found there.

LIZARD DIET

Individuals of *M. atacamensis* were caught using air-compressed guns [hunting permit no. 98 from the Chilean Agricultural and Livestock Service (SAG)]. The captured individuals were sexed, weighed (TW = total weight of the individual in grams) and measured (SVL = snout–vent length in centimetres), and their digestive tracts were extracted.

GUT CONTENT

In order to characterize the dietary composition, we analysed the contents of the digestive tract identifying prey taxa to the lowest possible taxonomic unit. The minimum number of digestive tracts needed for a reliable analysis was calculated using the rarefaction curve of the taxa occurring in each tract analysed. The curve was drawn following the agglomeration of taxa generated by resampling randomly the original data matrix 1000 times (using EstimateS, Colwell & Coddington 1994). This analysis showed that the minimum number of tracts were 19, 15 and 12 for Taltal, Zenteno and Huasco, respectively. Considering these data, it was necessary to pool all the individuals captured during the entire study period at each site.

STABLE ISOTOPE ANALYSIS

To analyse the relative contribution of marine and terrestrial prey, we analysed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes contents of *M. atacamensis* from each site. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are higher for marine organisms and/or for terrestrial plants and consumers of localities with high marine inputs of marine-derived energy and nutrients than for terrestrial producers and consumers without marine input (Crisholm *et al.* 1982; Mizutani & Wada 1988; Catenazzi & Donnelly 2006).

Following standard procedures (Catenazzi & Donnelly 2006; Sabat *et al.* 2006), tissue samples were collected from the captured individuals at each site and lipids were extracted; the remaining tissue was dried and ground into a powder. Treated samples were then submitted to the University of Arkansas Stable Isotope Laboratory for analysis.

DIET

Trophic level (TL) of *M. atacamensis* from each site was calculated using the formulae (Post 2002) for one-source (for Zenteno and Huasco) or two-source food webs (for Taltal).

$$\text{One source: TL} = \lambda + (\delta^{15}\text{N}_{\text{lizard}} - \delta^{15}\text{N}_{\text{source 1}} \times \text{frec}_{\text{source 1}}) / \Delta_n$$

$$\text{TL} = \lambda + (\delta^{15}\text{N}_{\text{lizard}} - [\delta^{15}\text{N}_{\text{Ulva}} \times \text{frec}_{\text{Ulva}} + \delta^{15}\text{N}_{\text{Porphyra}} \times (1 - \text{frec}_{\text{Ulva}})]) / \Delta_n$$

where λ is the trophic level of the basal resource (= 1 for *Ulva* and *Porphyra*) and Δ_n (= 3.4) is the mean trophic fractionation of $\delta^{15}\text{N}$ for each trophic level (Post 2002).

Considering their importance in diet, both by weight and frequency (Table 3), we assumed that main primary producer sources were: *Ulva* sp. and *P. columbina* in Taltal (a two-source model), *P. columbina* in Zenteno and *Ulva* sp. in Huasco (a one-source model

in each case). In every case the equations were calculated using the sources' $\delta^{15}\text{N}$ values and the lizards for each particular site.

For each site, contribution of each prey item to *M. atacamensis* was evaluated by using a linear mixing model (IsoSource; Phillips & Gregg 2003), considering three sources in every case (i.e. the signatures of the three most important prey from each site) and two isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). In these models, all possible combinations of each source (i.e. prey) contribution (in proportions from 0 to 1) are examined in small increments (0.1 in our case) and the combinations that make up the observed mixture (i.e. consumer isotopic signature) within a small tolerance (± 0.01 in our case) are considered to be feasible solutions. The frequency and range of potential source contributions are reported as the distribution of feasible solutions for each source (prey). The breadth of the isotopically determined ranges depends upon the geometry of the mixing space and the similarity of source and mixture isotopic signatures. In this analysis, the model was run with the mixture (*M. atacamensis* isotopic signature) adjusted for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic fractionation (+0.4 and +3.4 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ /trophic level, respectively, *sensu* Post 2002) in accordance with its calculated trophic level (see above).

STATISTICAL ANALYSIS

Total cover of plants occurring at terrestrial habitats, abundance patterns of *M. atacamensis* and the proportion of *M. atacamensis* recorded at intertidal and terrestrial habitat were compared between sites using one-way analysis of variance (ANOVA) models (Winer 1971). In these cases, site was considered a unique and random factor because no a priori hypothesis about it was stated and because its levels represented one of the several potential combinations over which the study could be done (Underwood 1997). In the case of algal cover at high and mid-intertidal zones, the results were compared between sites using two-way ANOVA models. Site and intertidal levels were considered as random factors, with three and two levels, respectively. After this was performed, a Tukey honestly significant difference (HSD) multiple-comparison test was performed to determine which means were significantly different (Day & Quinn 1989). Normality of the data was checked by graphical procedures and, when appropriate (i.e. for cover and abundance), the data were transformed (i.e. arcsine square root and $\log(x + 1)$ for cover and abundance, respectively). Results are reported using the original (i.e. non-transformed) variables. Homogeneity of variances and independence of the data were verified using Levene's and Durbin–Watson tests, respectively (Wilkinson, Blank & Gruber 1996).

The Bray–Curtis similarity index (Wolda 1981) was used to analyse the similarity in the species composition observed at the intertidal habitats of each site. Patterns of species composition similarities were contrasted using a cluster diagram of the Bray–Curtis index calculated for each site and intertidal level (high or mid). The cluster was drawn using unweighted average linkage methods (Wilkinson *et al.* 1996) and significant level of similarity was estimated using the distribution of the Bray–Curtis index, calculated after bootstrapping the species abundances matrix (Clarke 1993) 1000 times.

Dietary compositions of *M. atacamensis* from each site were compared applying the Kendall non-parametric coefficient of concordance (*W*) on prey percentage of total biomass (Table 3). This coefficient indicates the level of association between the rankings of two or more variables, with a null hypothesis of no association (Siegel & Castellan 1988).

Results

CHARACTERIZATION OF INTERTIDAL AND TERRESTRIAL HABITAT

A total of 14 algae and two invertebrate species were recognized at the high and mid-rocky intertidal zones of each site (Table 1). No significant differences were detected in algal cover among sites ($F_{2,293} = 2.01$, $P = 0.13$). Although algae cover was generally higher at mid- than at high intertidal levels ($F_{1,293} = 157.03$, $P < 0.001$), within each site this difference was not statistically significant. At the three sites, high intertidal zones were dominated by the rodophyta *P. columbina*, whereas mid-intertidal zones showed higher covers of the chlorophyta *Ulva* sp. and of the rodophyta *Gelidium chilense*. It is worth noting that this last species occurred as small turf, whereas both *Ulva* sp. and *Porphyra* occurred as fleshy algae. Transformation of algal cover into biomass gives an estimate of 29.1, 22.1 and 24.5 g m² for *P. columbina* at high intertidal levels of Taltal, Zenteno and Huasco, respectively. For *Ulva* sp., the estimated biomass corresponded to 19.0, 19.3 and 19.1 g m² for the mid-intertidal levels of these three sites, respectively.

In the case of terrestrial areas, 12 plant species from eight families were recognized. *Nolana* (Solanaceae) was the genus with higher species representation (five species). As expected, no plants were recorded during the entire study period on the northernmost site of Taltal. From this site South, the cover of plants increased (from 24.28 ± 2.1 in Zenteno to 33.35 ± 2.5 in Huasco). Mean plant cover transformed into biomass (Table 2) also increased from North to South, with *Nolana*

species dominating at the mid-range and at the southernmost site (*N. incana* in Zenteno and *N. crassulifolia* in Huasco). *T. ovata* was another species with high cover and biomass at both sites.

LIZARD ABUNDANCE PATTERNS

The abundance of *M. atacamensis* was significantly different among sites ($F_{2,1123} = 76.46$, $P < 0.001$, Fig. 2a). The highest values occurred at Zenteno (at the mid-geographical range), followed by Taltal (North) and Huasco (South). In terms of activity, most of the individuals were recorded at terrestrial habitats in each site (Fig. 2b). In spite of this, there were significant differences among sites for this variable ($F_{2,1123} = 87.96$, $P < 0.001$). Taltal and Zenteno showed similar proportions of individuals at both intertidal (near 30% on average) and terrestrial habitats (near 70% on average), but the southernmost site, Huasco, showed the lowest proportion at the intertidal (less than 20% on average) and the highest at the terrestrial (above 80% on average).

LIZARD DIET

A total of 14 prey items were identified (Table 3) in the 66 analysed digestive tracts ($n = 23$, 21 and 22 for Taltal, Zenteno and Huasco, respectively). The dietary composition was significantly different between sites ($W_{2,21} = 0.36$, $P = 0.5$). Of the 13 prey items identified in Taltal, the algae *Ulva* sp. and *P. columbina* were the dominant items in both biomass and frequency. In Zenteno, a lower number of prey (= 6) was recognized and *P. columbina* was the most important item in

Table 1. Mean cover (± 1 SE) of the sessile species occurring at high and mid-intertidal levels of each site. In every case higher values are shown in bold type

	Medano		Zenteno		Huasco	
	High	Mid	High	Mid	High	Mid
Phaeophyta						
<i>Ralfsia</i> sp.	1.84 (0.9)	17.5 (3.3)	0.02 (0.02)	10.7 (2.6)	0.8 (0.8)	4.9 (1.6)
<i>Lessonia nigrescens</i>				0.06 (0.04)		
<i>Halopteris ordacea</i>		0.2 (0.2)				
Chlorophyta						
<i>Ulva</i> sp.	2.34 (0.7)	35.6 (5.4)	8.4 (2.7)	36.1 (5.9)	3.44 (1.3)	35.8 (5.0)
<i>Codium</i> sp.				1.0 (1.0)	0.1 (0.1)	1.4 (0.9)
Rodophyta						
<i>Porphyra columbina</i>	27.62 (4.9)	3.8 (1.4)	21.0 (3.8)	5.3 (1.3)	23.3 (3.7)	3.4 (1.2)
<i>Gelidium chilense</i>		10.4 (2.4)		22.5 (2.8)	0.04 (0.04)	16.0 (2.8)
<i>Corallina officinalis</i>				0.1 (0.1)		1.3 (0.5)
<i>Gimnogongrus</i> sp.						0.02 (0.02)
<i>Trematocarpus</i> sp.						0.9 (0.6)
<i>Ceramium rubrum</i>		0.3 (0.1)		0.6 (0.2)		2.2 (0.9)
Crustosa		0.3 (0.2)		1.4 (0.5)		4.1 (1.5)
<i>Hildenbrandtia lecanellieri</i>					0.4 (0.4)	0.7 (0.4)
<i>Chondrus</i> sp.		0.06 (0.06)				
Crustacea						
<i>Notochtamalus scabrosus</i>	9.4 (2.9)	12.2 (2.5)	8.1 (2.2)	3.9 (1.3)	2.1 (0.6)	5.6 (1.2)
Mollusca						
<i>Perumitlyus purpuratus</i>	0.08 (0.06)				0.3 (0.1)	0.4 (0.4)

Table 2. Mean biomass (± 1 SE) of plant species occurring at the adjacent (~500 m) terrestrial areas of each site. In every case numbers shown in bold type represent the highest values per site

	Taltal	Zenteno	Huasco
Solanaceae			
<i>Nolana crassulifolia</i>	–	–	1260.9 (110.5)
<i>Nolana rupicola</i>	–	20.0 (8.5)	–
<i>Nolana incana</i>	–	400.9 (60.4)	–
<i>Nolana sedifolia</i>	–	19.9 (9.6)	20.8 (10.5)
<i>Nolana salsoloides</i>	–	100.5 (60.5)	–
Aizoaceae			
<i>Tetragonia ovata</i>	–	362.9 (93.8)	600.4 (133.3)
Asteraceae			
<i>Polyachyrus</i> sp.	–	220.0 (35.7)	381.3 (121.1)
Frankeniaceae			
<i>Frankenia chilensis</i>	–	1.2 (1.2)	23.4 (4.5)
Boraginaceae			
<i>Heliotropium pycnophyllum</i>	–	6.2 (6.2)	19.8 (15.4)
Malvaceae			
<i>Cristaria pinnata</i>	–	2.0 (1.0)	20.0 (10.5)
Amaranthaceae			
<i>Chenopodium petiolare</i>	–	–	6.3 (6.3)
Plumbaginaceae			
<i>Limonum plumosum</i>	–	22.8 (18.3)	–

Table 3. Dietary composition of *Microlophus atacamensis* at the study sites. Total weight (W in grams), the frequency of occurrence (FO in guts) and their respective proportions (%) are shown. Numbers in bold type corresponded to the highest values

Dietary items	Taltal		Zenteno		Huasco	
	W (%)	FO (%)	W (%)	FO (%)	W (%)	FO (%)
Algae						
<i>Enteromorpha compressa</i>	13.3 (12.1)	3 (3.4)				
<i>Ulva</i> sp.	49.4 (44.9)	21 (23.6)			13.4 (41.2)	19 (31.2)
<i>Porphyra columbina</i>	41.6 (37.8)	13 (14.6)	22.1 (86.5)	13 (31.9)		
Mollusca						
<i>Prisogaster niger</i>	0.03 (0.03)	1 (1.1)				
<i>Nodilittorina peruviana</i>	0.5 (0.4)	9 (10.1)	0.2 (1.6)	4 (9.8)	0.7 (2.3)	3 (4.9)
Crustacea						
<i>Acanthocycclus hassleri</i>	0.4 (0.4)	2 (2.3)				
<i>Allopetrolisthes punctatus</i>	0.7 (0.6)	2 (2.3)	1.0 (4.1)	4 (9.8)		
<i>Amphipoda-Gammaridae</i>	0.3 (0.3)	9 (10.1)	0.4 (1.7)	4 (9.8)	2.8 (8.6)	12 (19.7)
<i>Leptograpsus variegattus</i>	0.4 (0.4)	3 (3.4)				
Insecta						
Diptera	0.6 (0.5)	14 (15.7)	0.3 (1.2)	8 (19.5)	9.0 (27.7)	17 (27.9)
Diptera larvae	0.8 (0.7)	6 (6.7)				
Coleoptera	1.9 (1.7)	5 (5.6)				
Isopoda			1.3 (4.9)	8 (19.5)	6.6 (20.3)	10 (16.4)
Vertebrata						
<i>Microlophus atacamensis</i>	0.2 (0.2)	1 (1.1)				

terms of both biomass and frequency. It is worth mentioning that at this site the terrestrial prey, Diptera and Isopoda, were found high in frequency but not high in biomass. The lowest number of prey items (= 5) was observed at the southernmost site (Huasco). At this site the marine *Ulva* sp. and the terrestrial Diptera and Isopods were the most important items in terms of biomass and frequency.

Qualitatively, the incidence of marine vs. terrestrial items showed a clear geographical trend (Fig. 3). From North to South, in Taltal more than 90% of the diet was composed of marine items; in Zenteno this representation decreased (close to 80%), and in the southernmost site marine items accounted

for less than 55% of the diet. Interestingly, these geographical changes were related to an increase (from North to South) in the representation of terrestrial-animal and a reduction in marine-floral (algae) items in the diet. In these terms, from North to South, the diet of *M. atacamensis* changed from herbivory to carnivory–omnivory (Fig. 3).

STABLE ISOTOPE ANALYSIS

In accordance with the dietary composition and with the observed changes in the importance of marine vs. terrestrial prey, in the stable isotope analysis (Fig. 4) there were

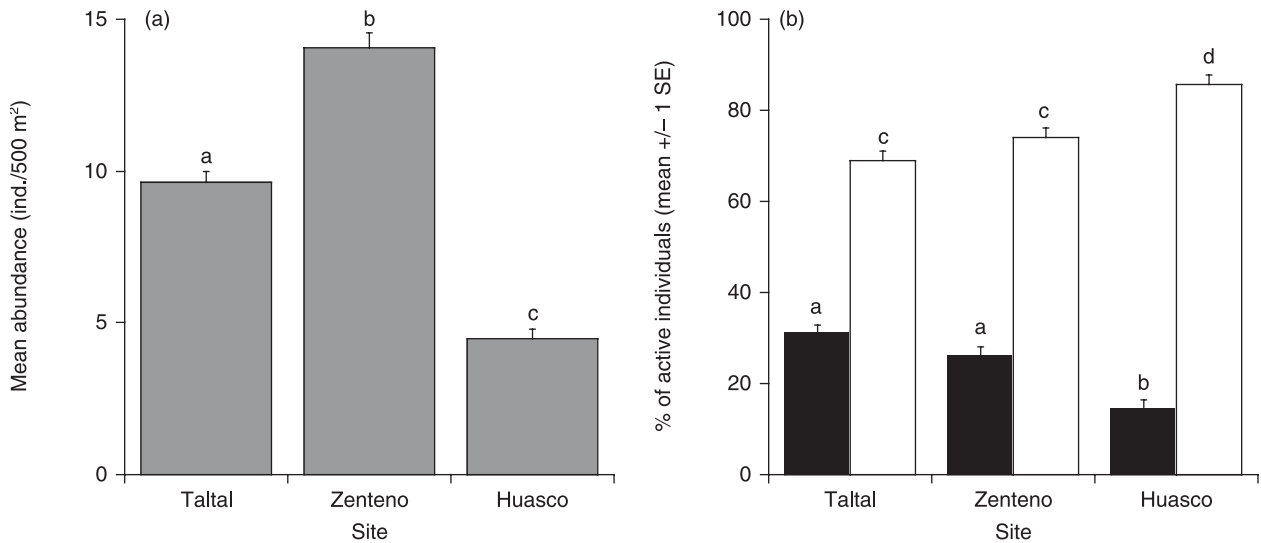


Fig. 2. Geographical variations (from North to South) in the total abundance (a) and in the proportion of active individuals (b) recorded in the intertidal (dark bars) and terrestrial (white bars) habitats of each site.

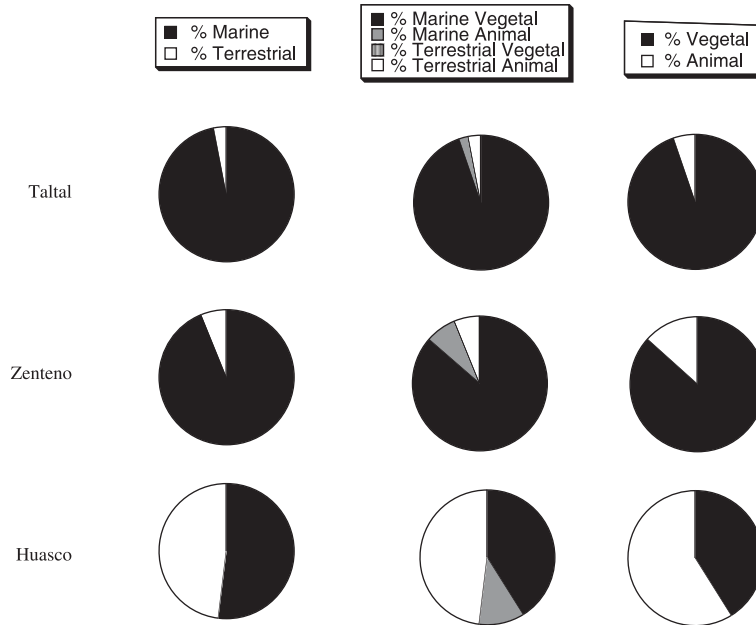


Fig. 3. Geographical variation on some general aspects of *Microlophus atacamensis* trophic ecology based on the proportion of prey in the diet (two-source model).

practically no differences in *M. atacamensis* $\delta^{13}\text{C}$ signatures, a clear geographical trend for $\delta^{15}\text{N}$: significantly higher values (i.e. more enriched) were observed in the individuals from Taltal (northernmost site), followed by Zenteno (mid-range site) and Huasco (southernmost site). The decrease on the position along the $\delta^{15}\text{N}$ axis shows the shift from marine (Taltal) to terrestrial (Huasco) diet.

DIET

Calculated trophic levels of *M. atacamensis* were 2.0 in Taltal, 2.2 in Zenteno and 2.6 in Huasco, corresponding to herbivory (Taltal), omnivory (Zenteno) and to carnivory-omnivory

(Huasco). Analysis of the linear mixing model (Fig. 4) confirmed that the most important items observed in the digestive tract analysis (both in weight and frequency) contributed effectively to *M. atacamensis* nutritional balance (at least for nitrogen and carbon). For every site a 'constrained solution' (*sensu* Phillips & Gregg 2003) was produced indicating that, of the three main sources considered, only two produced feasible solutions. For Taltal, the model produced feasible solutions that included *Ulva* sp. (median = 0.38, range: 0.08–0.65) and *P. columbina* (median = 0.57, range: 0.31–0.86) but practically excluded Diptera (median = 0.05, range: 0–14). The graphical representation of the model for this site (Fig. 4) shows that the

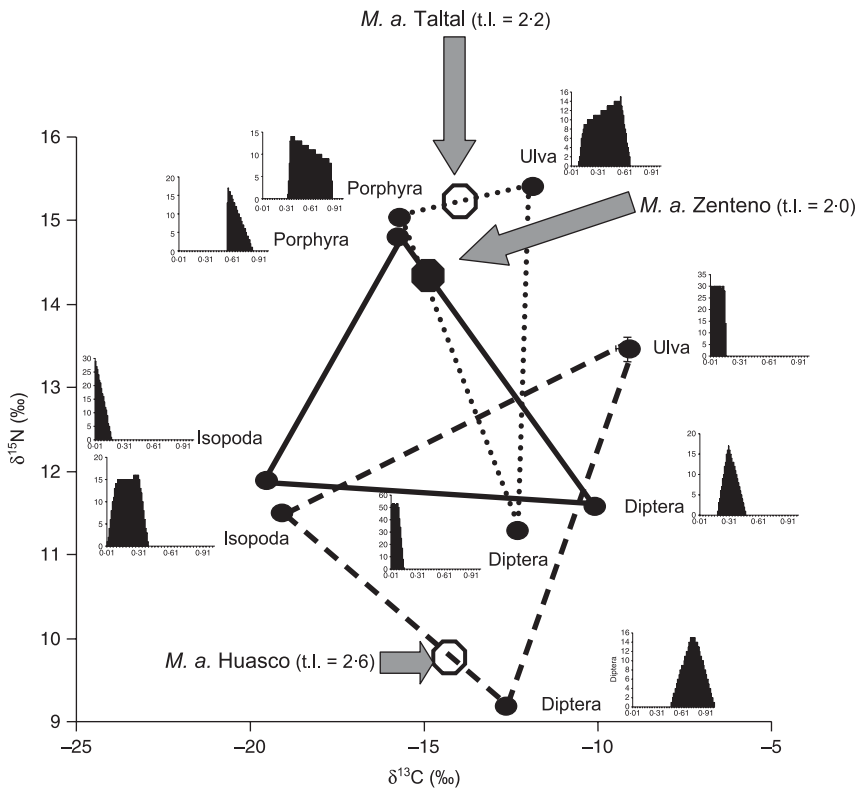


Fig. 4. *Microlophus atacamensis* and its main prey's carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic signatures from the study sites. Lines represents the results of the three-source mixing model and for each prey the diagram of frequency on the possible solutions is included.

mixture (*M. atacamensis* isotopic signature) fails in the line between *Ulva* sp. and *P. columbina* signatures, far from the Diptera position confirming the status of herbivore for the individuals of this site. In the case of Zenteno, feasible solutions included *P. columbina* (median = 0.6, range: 0.54–0.82) and Diptera (median = 0.3, range: 0.18–0.46), but excluded Isopoda (median = 0.05, range: 0–0.16). For this site, *M. atacamensis* signature failed in the line between *P. columbina* and Diptera (Fig. 4), indicating omnivory (with preferences for algae). In Huasco, solutions included Diptera in high proportions (median = 0.74, range: 0.47–1), Isopoda in lower proportions (median = 0.19 range: 0–0.38), and practically excluded *Ulva* sp. (median = 0.07, range: 0–0.15). The graphic representation of these solutions located *M. atacamensis* in the line between Isopoda and Diptera, but closest to the Diptera position, indicating carnivory with preferences towards this last prey.

Discussion

Habitat use and trophic patterns of *M. atacamensis* at the Atacama Desert coast are in agreement with observed changes in primary productivity along its geographical range. Two main features represented these changes. (a) Primary productivity at intertidal zones seems to be equivalent, but terrestrial plant representation increases from North to South. The rocky intertidal habitats along the entire study area showed similar patterns of species composition and biomass and the only difference detected within this assemblage was the change in species dominance at mid- (*Ulva* sp.) and

high (*P. columbina*) intertidal levels. In contrast, terrestrial habitats showed conspicuous geographical changes that corresponded with variations in total precipitation (see Introduction). (b) Primary consumers, especially animal prey of *M. atacamensis*, showed important differences in species composition and abundance among sites. Studies on Deserts of Baja California (Polis & Hurd 1995), Peru (Catenazzi & Donnelly 2006) and Chile (Jerez 2000; Cepeda-Pizarro, Pizarro-Araya & Vásquez 2005) have shown that primary consumers and detritivores track their abundance strongly to the standing-stock of both *in situ* (e.g. plant production) and/or *ex-situ* (e.g. subsidies) primary producers. Considering this, for our study area, we expected an increment in the abundance of the terrestrial associated fauna from North to South. Preliminary data from pitfall traps ($n = 322$) run for a year at the terrestrial area of each study site show that the number of arthropods was the lowest at Taltal (0.11 ± 0.03 ind. trap $^{-1}$) but increased to the South, reaching similar levels in Zenteno (0.70 ± 0.16 ind. trap $^{-1}$) and Huasco (0.57 ± 0.19 ind. trap $^{-1}$). In the case of biomass, similar low levels were detected at Taltal (5.92 ± 2.09 mg trap $^{-1}$) and Huasco (5.89 ± 2.30 mg trap $^{-1}$), while Zenteno presented the highest levels (29.02 ± 8.34 mg trap $^{-1}$). The geographical differences between these abundance and biomass patterns are due to changes in primary consumers' species composition. At Taltal the reduced number of arthropods corresponded to coleoptera and spiders. In Zenteno the abundance of insects was represented mainly by coleoptera and isopods with large body sizes, whereas in Huasco, where the highest species richness was observed, most of the insects corresponded to

hymenoptera (ants), diptera, thysanura and spiders, all with small body sizes. In the case of intertidal areas, preliminary samples of the fauna associated with the algae did not show differences among sites in either number or biomass, but did so between intertidal levels. In the high intertidal zones dominated by *P. columbina*, the most abundant fauna were gastropods (recruits of *Nodolittorina peruviana*) and amphipods (Gamaridae), while in the mid-intertidal zones dominated by *Ulva* sp., the dominant fauna corresponded to amphipods (Gamaridae) and diptera larvae.

It is worth noting that *Ulva* sp. supported a higher abundance of animals than *P. columbina*. For example, in the case of amphipods, for all the sites, mean abundance in *Ulva* sp. was 100–120 ind. cm² while for *P. columbina* it was 9–10 ind. cm². Several studies have noted that changes in the associated fauna depend on algal species' architecture (Hacker & Steneck 1990) and nutritional value (Christie & Kraufvelin 2004), but more importantly on physical factors correlated with algae distribution at intertidal areas (Buschman 1990; Chavanich & Wilson 2000). In our study, because not only amphipods but also most of the associated fauna showed lower abundances in *P. columbina*, differences in physical factors such as humidity, temperature and solar radiation exposure between high and mid-intertidal levels should explain the observed differences in the associated faunal abundances.

Ambient temperature can largely restrict lizard activity (Huey 1974; Huey & Stlakin 1976; Catenazzi, Carrillo & Donnelly 2005) and is a key factor regulating their abundance. For our study, in terrestrial habitats active lizards were observed over the whole range of temperatures, indicating that there were no thermal restrictions to their activity. Regarding the averages of these temperatures, it is worth noting that both Taltal and Huasco showed similar levels (19.41 ± 0.09 °C and 18.75 ± 0.21 °C, for Taltal and Huasco, respectively) while Zenteno showed the highest values (24.6 ± 0.18 °C). In the case of the intertidal habitats, lizards were not active over the whole range of temperatures recorded at each site. In Taltal, with a range of 11.5–48.0 °C, they were active just over 14 °C. In Zenteno, with a range of 11.5–48.0 °C they were active over 12.5 °C and in Huasco with a range 11.5–45.5 °C, they were active over 16 °C. Despite these range differences, there were practically no differences in the mean temperature at which active lizards were recorded at the intertidal habitat of each site (30.24 ± 0.27 °C, 29.37 ± 0.32 °C and 29.88 ± 0.48 °C, for Taltal, Zenteno and Huasco, respectively). Based in this information, it seems that the thermal scenario along the geographical range of *M. atacamensis* does not change in terrestrial habitats from North to South and does not seem to impose restrictions on *M. atacamensis* activity, but shows a peak in the average active temperature at the mid-range site, Zenteno. In the case of intertidal habitats, this scenario decreases smoothly from North to South, possibly restricting lizard activity by lower temperatures.

Considering both the prey availability scenario (assessed from the analysis of primary producer and consumer species composition and abundance) and the observed thermal conditions, it is possible to understand the pattern of

geographical variations of *M. atacamensis* abundance, habitat use and diet. In terrestrial habitats of Taltal, the northernmost site, practically no producers or prey occurred at low abundance and biomass. Intertidal substrate presents the highest temperatures with a mean close to the average active temperature of the lizards. In relation to this scenario, the diet of *M. atacamensis* is composed mainly of intertidal prey, with a high representation of algae. Regarding habitat use, although lizards spent most of their time in terrestrial habitats (possibly thermoregulating but not feeding) it is highly probable that feeding activities in this site occur mainly in the intertidal zone, where they spend the highest proportion of the time.

In the mid-range site, Zenteno, several primary producer species occurred in terrestrial habitats and fuelled a high abundance and biomass of prey, especially those with big body sizes. In terms of temperature the conditions in intertidal zones are similar to those observed in the northernmost site, but in terrestrial habitats, in spite of the fact that the range of temperatures is similar to other sites, the average is clearly higher. This scenario defines a site with good temperature conditions in intertidal and terrestrial habitat, with high prey availabilities. In accordance with these conditions, *M. atacamensis* effectively uses both habitats for its omnivorous feeding activities.

At the southernmost site, Huasco, in spite of the increase in primary producer cover and biomass, the changes in species composition (with a reduction on *Nolanas*' species richness) are associated possibly with changes in terrestrial prey species composition (with a dominance of small body-sized organisms) and richness (the highest diversity was recorded here). In terms of temperature at this site, the lowest mean substrate temperature registered at intertidal levels could be related to the fact that the highest minimum for active animals at intertidal areas was also recorded here. In these terms, this site seems to be a place where *M. atacamensis* use mainly terrestrial habitats, given that it was here where the lowest abundances, the lowest proportion of lizards at intertidal zones and a diet with a high proportion of terrestrial prey were recorded.

Early studies on the influence of marine subsidies on terrestrial food webs showed that terrestrial animals effectively consumed mainly dead marine materials such as carrion and drift algae driven to shorelines by physical agents in those areas where terrestrial productivity was low, and not enough to maintain these trophic webs (Polis 1995; Polis & Hurd 1995). These terrestrial consumers include isopods, amphipods, beetles and flies (Koepcke & Koepcke 1952; Hayes 1974; Griffiths & Stenton-Dozey 1981), which by reaching astounding densities serve as prey for secondary consumers such as scorpions, reptiles and spiders (Koop & Field 1980; Griffiths & Griffiths 1983). Since then, most of the studies highlight the importance of some physical (i.e. landscape) and biotic components (vector and recipient species) that regulate these cross-ecosystem linkages (Sabo & Power 2002a,b; Catenazzi & Donnelly 2006). Focusing on particular characteristics of physical and biotic components of the cross-ecosystem linkages allowed researchers to recognize that, in cases where

consumers living in one habitat consume prey from another, the process could be highly dynamic in space and/or time and it depended effectively on (Polis *et al.* 1997): (a) the energetic balance of linked habitats, (b) the biological characteristics of prey and consumers and (c) the nutritional quality of each habitat.

Our study confirms that the movement of consumers between habitats depends on the energetic balance of linked habitats (intertidal vs. terrestrial primary and secondary productivity) and on some biological characteristics of consumer species that can facilitate or restrict the process (e.g. thermoregulation). More importantly, it shows that within the geographical range of one species it is possible to find a variation in the use of alternative habitats (intertidal in our case) and important changes in trophic status (from herbivory to carnivory, and in the relative importance of marine vs. terrestrial prey). Within the genus *Microlophus*, *M. atacamensis* is the southernmost species of the *Peruvian* group. Two more species of this group lives at the coast of the extreme Atacama Desert and in the milder Peruvian Desert, which shows a precipitation gradient similar to that of our study area. For the *Occipitalis* group, at least six species live on different islands of the Galapagos archipelago occurring in almost all types of habitat from the high volcanoes to the coast (Stebbins, Lowenstein & Cohen 1967; Carpenter 1970; Schluter 1984; Jordan & Snell 2002). Considering the results of our study, it could be interesting to compare the situation of the diverse group of *Microlophus* species experiencing different habitats, productivity levels and thermal regimes, which none the less are linked phylogenetically. *M. atacamensis* diet and habitat respond to both regional (i.e. gradient of terrestrial productivity) and local (intertidal prey distribution and the thermal regime) processes. Apart from the rich and diverse ecosystem types occurring within the geographical range of coastal and island *Microlophus* species; the region (from Ecuador to central Chile) is severely affected by climatic events (ENSO) that are modulated importantly on local scales. From the perspective of cross-ecosystem linkages, such events are particularly interesting because they reverse the pattern of productivity imbalance between marine and terrestrial ecosystems described in our study, thus providing an outstanding opportunity to explore the temporal and spatial variation of the phenomena (Sears, Holt & Polis 2004).

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