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## RESEARCH ARTICLE

## Plasticity in feeding selectivity and trophic structure of kelp forest associated fishes from northern Chile

### Plasticidad en la selección de alimento y estructura trófica de los peces asociados a bosques de macroalgas pardas del norte de Chile

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#### ABSTRACT

One of the primary ways in which species interact with their environment is through foraging; thereby directly consuming some fraction of their surrounding habitat. The habitat itself, in turn, may dictate the types of foraging opportunities that are available to the inhabitants. To investigate the relationship between habitat availability and diet composition of habitat-associated fishes, we estimated the relative abundance of the potential sessile and mobile prey items and the diet of the fish species assemblage associated to kelp forest. Specifically, diet and feeding selectivity of the kelp-forest associated fish assemblage were determined by calculating Manly's alpha selectivity index. We determined the diet of kelp forest associated fishes and their foraging behavior by comparing prey availability with those items present in the stomachs of fishes captured by gill net and spear gun. We calculated the degree of dietary overlap among fishes from four locations along the northern coast of Chile. Results indicate that utilization of prey by predators is predominantly affected by potential prey availability. With the exception of the two carnivorous species such as *Pinguipes chilensis* (Valenciennes, 1883) and *Paralabrax humeralis* (Cuvier & Valenciennes, 1828), whose diet did not change among sites, all other kelp-associated fishes changed their dietary habits to consistent with the availability of local resources. Benthic resources changed among the different study sites, which led to differing diets even in the same species from different locations. Eleven of the 12 kelp forest fishes also showed some selectivity for benthic prey. We conclude that the ability of fishes to be plastic in their feeding preference and, therefore, partition the benthic resources may set adaptations to co-exist in a dynamic environment such as kelp forest.

**Key words:** Chile, Manly  $\alpha$ , predation, trophic guilds, understory.

#### RESUMEN

Una de las principales formas en que las especies interactúan con su medio ambiente es a través de la alimentación, consumiendo directamente una fracción de los componentes del hábitat circundante. El propio hábitat, a su vez, puede determinar la conducta de forrajeo y los tipos de alimentación de sus depredadores. Para investigar la relación entre la disponibilidad de alimento y la composición de la dieta de los peces asociados a hábitat dominados por macroalgas pardas, se estimó la abundancia de las presas potenciales tanto especies sésiles como móviles y se comparó con la dieta de las especies de los peces en cuatro diferentes sitios de la costa del norte de Chile. Se determinó la dieta de los peces y su plasticidad alimentaria mediante la comparación entre la disponibilidad de presas con los ítemes presentes en los estómagos de los peces que fueron capturados por de red de enmalle y arpón de mano. Además se calculó el índice de selectividad alfa de Manly y el grado de sobreposición de la dieta de los peces costeros. Los resultados muestran que la utilización de las presas por los depredadores es afectada principalmente por la disponibilidad de presas potenciales. La mayoría de los peces asociados a las macroalgas difieren en su dieta en consonancia con la disponibilidad de los recursos a escalas locales, con la excepción de dos especies carnívoras tales como *Pinguipes chilensis* (Valenciennes, 1883) y *Paralabrax humeralis* (Cuvier & Valenciennes, 1828), cuya dieta no cambió entre los sitios estudiados. Las diferencias en la dieta de las especies son explicadas por los cambios en los recursos bentónicos que varían entre los sitios de estudio. Once de las 12 especies de peces asociados a los bosques de macroalgas pardas mostraron algún grado de selectividad de presas de origen bentónico. Se concluye que la habilidad de los peces de cambiar sus preferencias de alimentación y, por tanto, la partición de los recursos bentónicos puede obedecer a las adaptaciones para coexistir en un ambiente dinámico como aquel dominado por bosques de macroalgas pardas.

**Palabras clave:** Chile, depredación, gremios tróficos, Manly  $\alpha$ , sub-dosel.

## INTRODUCTION

Trophic resource partitioning plays an important role in the diversification of natural species assemblages (Streelman & Danley 2003), influencing the ability of species to co-exist (Schoener 1974, Schmitt & Coyer 1982). Differential use of resources is one way in which natural assemblages achieve structure (reviewed by Ross 1986). Resource partitioning has been documented among fish assemblages at both tropical (Platell & Potter 1999, Zekeria et al. 2002) and temperate regions (Hixon 1980, Angel & Ojeda 2001). In temperate regions, for example, fish assemblages partition their resources depending almost exclusively on the type of the habitat element were they co-exists (i.e. vegetative structure, boulders or sand substratum, see Angel & Ojeda 2001, Wennhage & Pihl 2002). Few studies, however, have tested the degree of trophic plasticity and how their partition available resources among fish assemblages under similar environmental conditions (but see Feary et al. 2009).

Quantifying non-random predation is critical for the understanding of species diets and the role of a species within the community (Paine 1966). Selective predation involves dynamic ecological processes constrained by the physiology and behavior of predators in exploiting either seasonally or locally abundant sources of food (Barry & Ehret 1993, Schlacher & Wooldridge 1996, Ojeda & Muñoz 1999). Selective predation can explain how resources are partitioned by members of a community (Hughes & Grabowski 2006). Because food is the most important source of energy needed for all biological functions of individuals, by feeding selectively on a high energy (i.e., abundant) resource, organism may enhance their fitness (Manly et al. 2002). Feeding selectivity may be responsible for maintaining suitable habitat for other species (see Jones et al. 2006).

The shallow temperate habitats are known to sustain high numbers of fishes via provision of shelter and prey items (Holbrook et al. 1990, Taylor 1998, Anderson & Millar 2004). The presence of kelp beds may play an important role in regulating prey resources for fishes (Jones 1988, Taylor 1998). Prey resources vary depending on the identity of the large brown macroalgae (e.g., *Macrocystis pyrifera* Linnaeus [C. Agardh 1820], *Lessonia trabeculata* Villouta

& Santelices 1986) (Villegas et al. 2008) and also to the understory habitat-forming species that live in the kelp forest such as foliose algal or fauna (e.g., mytilids) assemblages (Schiel & Foster 1986, Melville & Connell 2001). Trophic structure of nearshore fish assemblages may be strongly affected by the presence of kelp beds; a structurally complex habitat-forming species (Angel & Ojeda 2001, Graham 2004). Similarly, assemblages that occur sympatrically with kelp, such as mussel beds and sponge gardens, can all be considered as biological feeding substrata for numerous fish predators (Jones 1988, Palma & Ojeda 2002). Small-scale changes in distribution and abundance in subtidal habitat may affect the foraging behavior of the entire fish assemblages.

Along the northern coast of Chile, the kelps *Lessonia trabeculata* and *Macrocystis pyrifera* are the most conspicuous canopy-forming algae in subtidal hard-bottoms off northern Chile (Vásquez et al. 1998, Vega et al. 2005). There are differences in the abundance and distribution of each of these kelps as well as in associated understory microhabitats. Pérez-Matus et al. (2007) quantified the abundance and diversity of fish species as a response of the variation in density of kelp beds, cover of associated understory algae and sessile assemblages at the same study sites of the present study. This study revealed that differences in the composition and density of kelp beds (e.g., *L. trabeculata* dominated three of study sites and *Macrocystis pyrifera* only one of the sites) were further translated into differences in the abundance and diversity of fish species. Further, composition and benthic resources depended also on the variation in kelp density and other abiotic factors (i.e., depth, temperature) as such that algae understory was high in richness and abundant at sites where kelp was dense whereas crustose algae and faunal assemblages dominate under less dense or mono-specific kelp bed stands (see Pérez-Matus et al. 2007).

Considering the potential effects of the variation in kelp beds and composition on abundance of associated understory and fish communities, we expect to find differences in the diet that ultimately determine the trophic structure of the associated reef fish community. Here, we aim to determine how the diets of fishes vary between and within sites relative to the differences in the habitat and microhabitat

characteristics. We secondarily aim to identify relationships between the diets of fishes and the potential prey available by determining the abundance of edible habitat-forming species and of mobile invertebrates. By integrating the information on the diet and accessible prey, we quantify use and selectivity of available benthic resources and whether this selectivity varies among fish consumers among different sites. Finally, we identify possible trophic guild structure of fishes associated to different kelp beds.

## METHODS

### Study sites

Sampling was conducted at four sites on the northern Chilean coast spanning almost 10° latitude: Caleta Río Seco (21°00' S), Caleta Constitución (23°15' S), Caleta Angosta (28°15' S), and Lagunillas (30°05' S). Hereafter, these are referred as to RS, CC, CA, and LA respectively. All of the study sites are exposed rocky coast with the exception of CC which is semi protected by southerly winds by the Santa Maria Island. The sampled areas at each site encompassed an area extending from the shoreline to 200 m offshore.

### Potential prey availability

Since some fish species tended to harvest prey only from certain microhabitats, such as benthic understory algae (*Halopteris* spp.) and benthic understory mussel (*Aulacomya atra* (Molina, 1782), *Semimytilus algosus* (Gould, 1850), or *Brachidontes granulata* (Hanley, 1843) or polychaete beds (*Phragmatopoma* spp.) (APM personal observations). We quantify the abundance of benthic understory algae and faunal resources as potential prey by performing random point contact (RPC) using 0.25 m<sup>2</sup> quadrats.

Abundance of motile benthic invertebrate species, as potential prey, was determined seasonally (every three months) from August 2004 to September 2005 using a randomly placed 0.25 m<sup>2</sup> quadrat deployed in two ways. The first consisted of visually counting all motile species in the quadrat. The other method was by removing all sessile and motile species that live associated to benthic algae (i.e., gammarid amphipods, isopods) using scraping knives. Five replicates of visual scans and three of destructive methods were applied within same observed microhabitat at a site. Unidentified species located in visual scans were removed along with destructive samples. All samples were labeled and stored in plastic containers with 10 % buffered formalin, or kept frozen, and transported to the laboratory. Species were identified to the lowest taxonomic level possible.

### Fish sampling

As above with the potential prey availability, fish were seasonally sampled (every three months) from August 2004 to September 2005 using a 3 x 50 m long (graded in mesh size 3.5 cm) gill net. The gill net was randomly set at dawn, perpendicular to the coast along the kelp beds, for five to six hours. Adult individuals were targeted

by this mesh size and the ontogenetic component is, therefore, not incorporated in this study. Captured specimens were identified, total length (TL) measured to the nearest 0.01 cm, and weighed to the nearest 0.1 g. Stomach and intestines were then removed and kept in 10 % buffered formalin prior to analysis. Abundance, based on CPUE (catch per unit of effort), was calculated as the total number of fish divided by the total number of sampling hours. Additionally, by means of SCUBA, a spear gun was used to capture conspicuous species that were not captured by the gill net, or those were present in low numbers in the gill net samples. This sampling could only be conducted haphazardly, however.

### Fish trophic analysis

In the laboratory, prey items from the stomach, or 1/3 of the intestines for those species that lack true stomach such as *Aplodactylus punctatus* (Valenciennes, 1832) and *Semicossyphus darwini* (Jenyns, 1842), were identified to the lowest taxonomic level possible, damp-dried on paper towel and weighed. All stomachs were pooled for each fish species in within each site and the composition of their diets was presented as percentage of total food weight (% W), which is the weight of any given prey item divided by the weight of all prey items. The minimum number of stomachs needed to accurately describe diet for any given site was determined by cumulative prey curves. Curves were generated from the number of new prey items from each fish species at the respective site and plotted against the number of guts examined (Ferry & Cailliet 1996). For subsequent analyses, prey species were grouped into higher taxonomic groups facilitating comparisons among species and sites. Since relative prey available did not fluctuate seasonally (see Pérez-Matus et al. 2007), dietary data were pooled across sampled dates; this facilitated the comparison among species and sites.

### Data analysis

In order to test for differences in the total abundance of fishes among sites, expressed as CPUE, a non-parametric Kruskal-Wallis test was used. For those species for which a sufficient number of specimens had been collected, changes in dietary composition across seasons were examined with the non-parametric Kendall Coefficient of Concordance (W; alpha = 0.20). Following Angel & Ojeda (2001) each fish species was classified as herbivore if their algal consumption was more than 80 % of the total biomass consumed, as omnivores if consumption of algae ranged between 20 and 80 % of the biomass and as carnivore if consumption of algae represented less than 20 % of the of the total biomass in the diet.

Feeding selectivity was determined using the Manly's alpha selectivity index (Chesson 1983, Manly et al. 2002). The diets were pooled for all individuals at each of the study sites. We used Manly's alpha index utilizing the prey resources considered as food by every fish species. At a particular site, there are S fish species and T types of food (prey resources that occurred in the species' diet only). For species j (j = 1, ..., S), the Manly's alpha values for food types t (t = 1, 2, ..., T) are

$$\alpha_{jt} = \frac{f_{jt} / g_t}{\sum_{i=1}^T f_{ji} / g_i} \quad (1)$$

where,  $f_{jt}$  is the usage of prey items by fish species  $j$  of food type  $t$ ,  $g_t$  is the availability of food type  $t$  at that site. A value of  $\alpha_{jt} = 1$  indicates exclusively feeding on food type  $t$ .

To determine if a food item was selected or if a food choice was driven by the availability, we used a randomization test by comparing observed and expected consumption of prey items. The Bray-Curtis distance (BCD) between observed and expected food consumption was chosen as a test statistic. Randomizations generated pseudo-values of BCD, which form the null distribution of BCD. We calculated P-values by estimating the proportion of BCD pseudo-values above the data value. The Bray-Curtis distance (BCD) for the discrepancy between observed and expected usages is:

$$BCD = \frac{\sum_{t=1}^T |f_t - E(f_t)|}{\sum_{t=1}^T (f_t + E(f_t))} \quad (2)$$

where, one fish species at one site consumed ( $f_1, f_2, \dots, f_i$ ), total weights of each prey type in the guts analyzed,

with total weight of  $F = \sum_{t=1}^T f_t$ . The availabilities are

relative proportions ( $g_1, g_2, \dots, g_T$ ), with  $\sum_{t=1}^T g_t = 1$  under

null hypothesis of all manly's alpha index  $\alpha_t = 1/T$ , the expected food consumptions are proportional to relative resource availability,  $E(f_t) = g_t F$ .

Unlike the Pearson's or G-likelihood ratio  $\chi^2$  statistics, which require count data and high expected values, the BCD as test statistics is sensible with low numbers of expected values. The unit of randomization must represent an independent choice of prey. Assuming independence among different fish species, the unit is taken to be a morsel or a fragment, defined as the total amount of prey type  $t$  in the stomach (e.g., a fish gut with three prey types has three fragments, representing at least three independent choices, and each morsel has an associated weight). To generate the null distribution of BCD, at each randomization the original amount of independent choice must be available ( $n$  number of food fragments), but the prey types must be adjusted to make the expected usage of each prey type proportional to the relative resource availability. This is achieved by conceptualizing a large pool of prey types all of the same weight,  $\bar{w} = F/n$ , the average weight of the observed data prey types, with the proportions of prey types set at the relative availability proportions ( $g_1, g_2, \dots, g_T$ ). A sample of  $n$  prey types has a multinomial distribution of prey types sampled. The counts are multiplied by  $\bar{w}$  to give the pseudo-usages of food types by weight, i.e. at each randomization the count vector  $X$  is sampled from the multinomial ( $n; g_1, g_2, \dots, g_T$ ) distribution, and the pseudo-usage vector is  $Y = \bar{w}X$ . This method ensured that the right numbers of independent choices were made, and the expected usages (utilization of prey items) are proportional to relative resource availabilities. The BCD is calculated between this pseudo-usage vector and the previously found expected use of food items  $E(f)$ . To find which resources were significantly over- or under-selected, each prey type  $t$  has its deviation from

expected,  $f_t - E(f_t)$ , recorded during the randomizations. The location of the data-based deviation within the distribution of pseudo-deviations is used to test the null hypothesis of no selection of prey type  $t$ . The P-value for over-selection is the proportion of pseudo-deviations higher than the observed deviation, and the P-value for under-selection is the proportion lower than the observed. A sequential Bonferroni correction is applied to allow for multiple testing over the  $T$  different prey types among sites.

### Trophic groups

To examine trophic guild formation among fish species within a site, Pianka's niche dietary overlap index was performed using percent weight of food items, which allows comparisons among herbivores, omnivores and carnivores. The values ranges from 0, no overlap, to 1, complete similarity of diets between species. With Pianka's niche overlap values a similarity matrix was introduced into cluster analysis generated by UPGMA (unweighted pair-group method using arithmetic averages). Four phenograms were generated, one for each study site. Guild formation at each site was determined according to Muñoz & Ojeda (1997); a frequency distribution of overlap values was randomly generated by bootstrapping techniques, using 10000 random reshuffles of the Pianka similarity matrix data (Jaksic & Medel 1990). The frequency distribution was compared with the observed overlap similarly as in Jaksic & Medel (1990). All analyses were conducted using the R environment (R Development Core Team 2010).

## RESULTS

### Fish composition

*Aplodactylus punctatus* was the abundant species at RS and CA in low numbers at CC and LA with 9 and 16 individuals respectively. At CA, this species was the most abundant of all fishes. *Cheilodactylus variegatus* (Valenciennes, 1833) was abundant at all study sites with more than 10 individuals but highest at RS. *Girella laevifrons* (Tschudi, 1846) was important numerically at RS, CC, and CA only, and was completely absent at LA. At RS, important species in terms of numerical abundance were *Anisotremus scapularis* (Tschudi, 1846) and *Seriolella violacea* (Guichenot, 1848). At CC *Isacia conceptionis* (Cuvier, 1830) and *Sciaena deliciosa* (Tschudi, 1846) were abundant, while *Pinguipes chilensis* and *Semicossyphus darwini* were abundant at CA. There were no differences detected in the total CPUE (all species) among sites (Kruskal-Wallis;  $H = 16$ ,  $P = 0.453$ ). We exclude *Mugil cephalus* (Linnaeus, 1758) at CC, from this study due to the detritivorous nature of this species and our

subsequent inability to quantify prey items from the stomachs (Table 1).

#### Potential prey availability

Brown macroalgae was abundant at RS, CC and CA and nearly absent at LA. Red algae was abundant the benthic resource at all study sites but highly important at LA (mainly *Asparagopsis armata* (Harvey, 1855)). Green algae (mainly *Ulva* spp.) were more abundant at RS and CC than at CA or LA. In terms of fauna, gastropods were abundant, making them the most potentially

available prey, with total relative abundances of 80, 60, 45 and 25 % at CC, CA, LA, and RS respectively. Bivalves constituted an important source of prey for reef fishes at RS only. Decapod crustaceans (e.g., *Pagurus edwardsii* [Fabricius, 1775] and *Pilumnoides perlatus* [Poëppig, 1836]) were an important source of prey items but only at CA and LA. Rock shrimps (*Rynchocinetes typus* [H. Milne Edwards, 1837]) increased in the southern sites and represent nearly 10 % of the sampled invertebrates. Another important group were amphipods, which were abundant at RS, CC, and CA (Fig. 1).

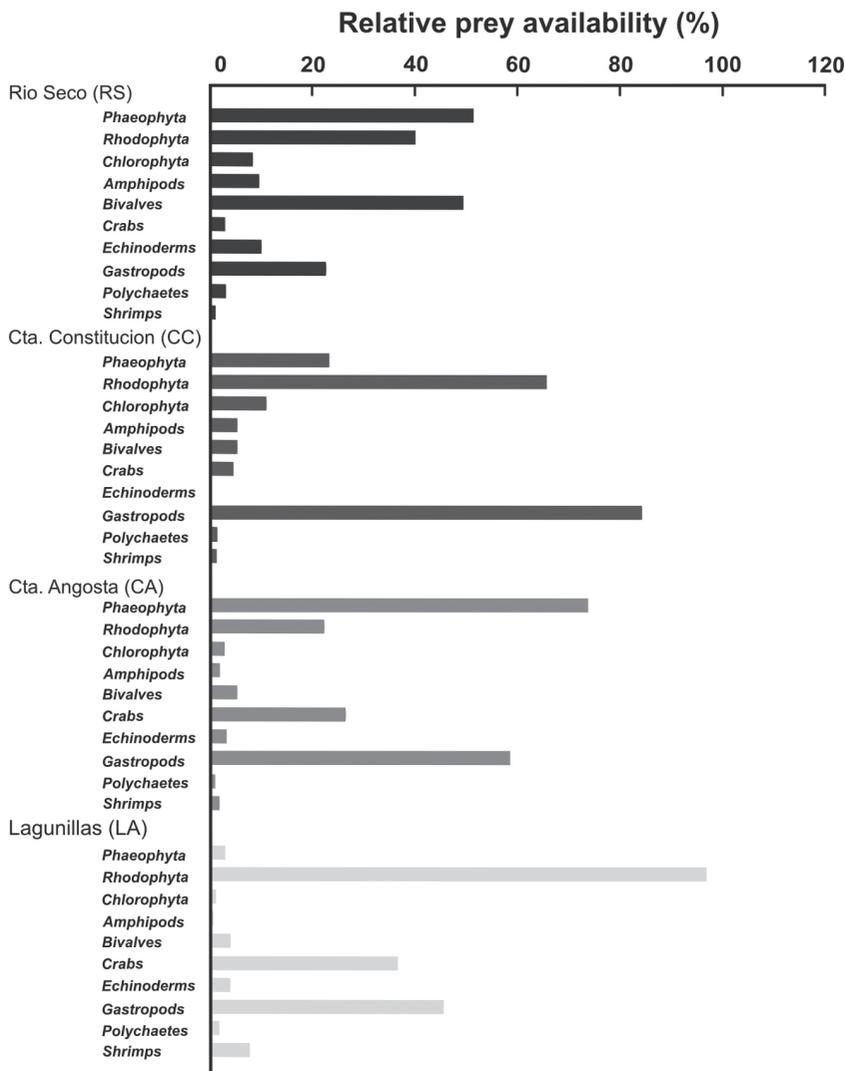


Fig. 1: Relative prey availability (%) at the different sampled sites.

Disponibilidad relativa de presas (%) en los diferentes sitios de muestreo.



TABLE 1. Continuation

<i>Acanthistius pictus</i>	5	36.6-38.5			2*	2*	27.0-41.6											
Labridae																		
<i>Semicossyphus darwini</i>					7*	6* 3* 1*	33.3-65.5											
Centrolophidae																		
<i>Seriola violacea</i>	6	29.8-39.0	1				33.0											
Mugilidae																		
<i>Mugil cephalus</i>				3	5	1	32.5-41.6											
Labrisomidae																		
<i>Labrisomus philippii</i>	1	27.0-29.3	1	1			23.7-30.3											
Pomacentridae																		
<i>Nexilosus latifrons</i>	1	20.6		1	2		21.9-23.2											
Scorpaenidae																		
<i>Sebastes oculatus</i>						3	20.0-28.0											
Ophidiidae																		
<i>Genypterus chilensis</i>	2	42.9-48.9																
Carangidae																		
<i>Thyrsites atun</i>																		
Total	37	38	50	37	49	39	50	27	51	43	27	43	14	11	15	0	1	81.5

### Trophic analysis and feeding selectivity

Prey composition differed among the study sites. Seventy-six different items from 22 functional groups were present in the stomach contents of the six species analyzed in RS. At CC, 63 different items from 21 functional groups were present in the guts of seven fish species. Twenty-two functional groups from 81 different items were identified at CA in the stomachs of seven fish species. At LA, 55 items from 17 functional groups were present in the stomachs of the three species analyzed (see Tables A1-A4).

Seasonal variation in the diet of the herbivore, *Aplodactylus punctatus*, was not detected in RS (Kendall  $W = 0.6$ ,  $df = 3$ ,  $P > 0.8$ ), CC (Kendall  $W = 0.2$ ,  $df = 2$ ,  $P > 0.4$ ), CA (Kendall  $W = 0.1$ ,  $df = 2$ ,  $P > 0.4$ ), and at LA (Kendall  $W = 0.4$ ,  $df = 2$ ,  $P > 0.1$ ). This herbivore consumed large brown macroalgae at all sites with the exception of RS, where red algae were utilized. *A. punctatus* at RS and LA consumed red algae in large amounts. Green algae (mainly *Ulva* spp.) were also consumed by this species at CA and LA. Bivalves were present in the guts and in high proportion at RS (Fig. 2A, Table 2). Other animal materials were also consumed by this species but in low proportions and frequencies (see Tables A1-A4, for details). According to our randomization tests, the use and feeding selectivity of *A. punctatus* diets from CC were different from individuals from LA ( $P = 0.04$ ) and between RS and those at LA ( $P < 0.0001$ ).

Omnivores were represented by two species: *Girella laevis* and *Isacia conceptionis*. Seasonal variation was not detected in *G. laevis* from RS (Kendall  $W = 2.2$ ,  $df = 3$ ,  $P > 0.5$ ), CC (Kendall  $W = 2.3$ ,  $df = 2$ ,  $P > 0.3$ ), CA (Kendall  $W = 0.4$ ,  $df = 1$ ,  $P > 0.4$ ) and in *I. conceptionis* at CC (Kendall  $W = 0.2$ ,  $df = 1$ ,  $P > 0.9$ ), CA (Kendall  $W = 0.1$ ,  $df = 2$ ,  $P > 0.4$ ). Differences in diet composition were detected among the study sites in these species. At RS, *G. laevis* consumed large brown macroalgae in high proportions as well as decapod crustaceans. At CC, *G. laevis* consumed green algae and large brown algae. At CA, high proportions of green algae were used by this species as well as gastropod species. At this site, brown macroalgae were also consumed (mostly pneumatocyst of *M.*

*pyrifera*) and some red turfing algae. The other omnivore, *I. conceptionis*, consumed green algae (*Ulva* spp.) at CC and brown macroalgae at CA (Fig. 2C, Table 2). No statistical significance was detected in the use or feeding selectivity among the study sites within these species according to our randomizations test.

Carnivores were represented by eight species among the study sites. Seven of these species selected decapod crustaceans as preferred prey in most of the study locations. Gammarid amphipods, bivalves and nudibranchs were also selected prey by some carnivorous fish species (Table 2). *C. variegatus* did not show differences among seasons at RS (Kendall  $W = 0.7$ ,  $df = 3$ ,  $P > 0.2$ ), CC (Kendall  $W = 0.9$ ,  $df = 3$ ,  $P > 0.4$ ), CA (Kendall  $W = 0.01$ ,  $df = 2$ ,  $P > 0.9$ ), and at LA (Kendall  $W = 0.03$ ,  $df = 2$ ,  $P > 0.7$ ). This species took decapod crustaceans only at RS, where as amphipods at CC and CA.

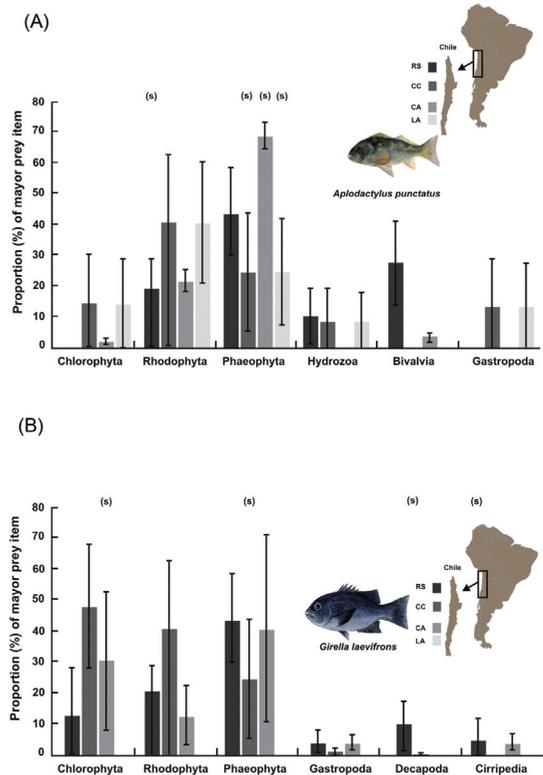
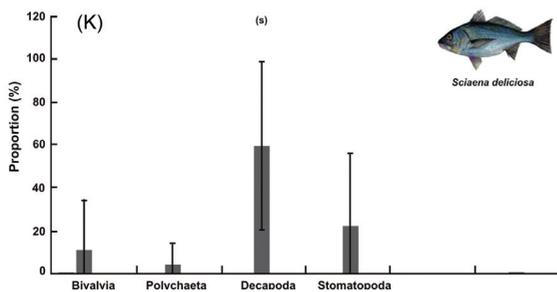
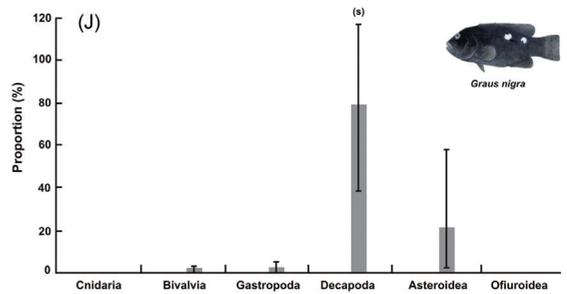
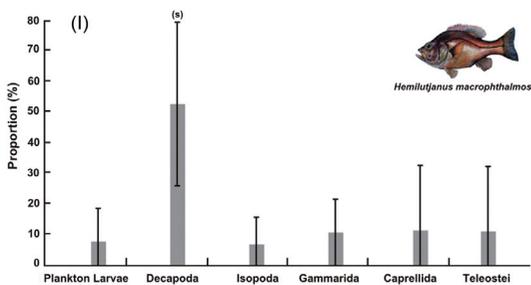
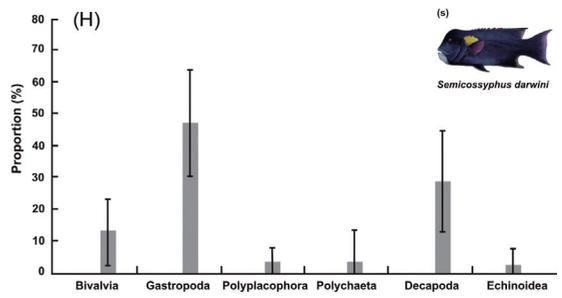
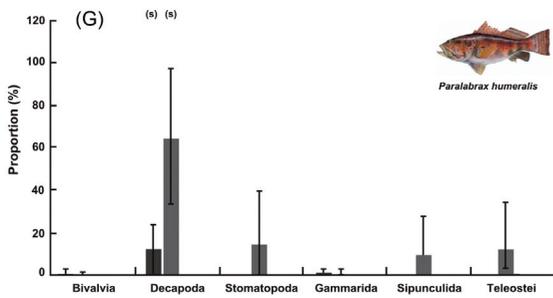
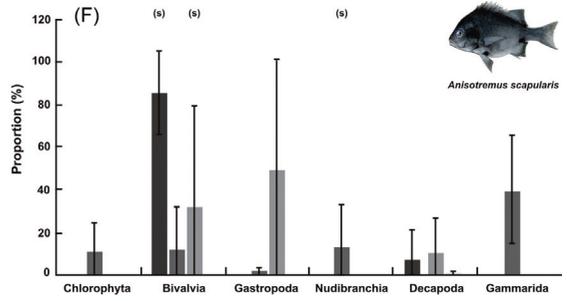
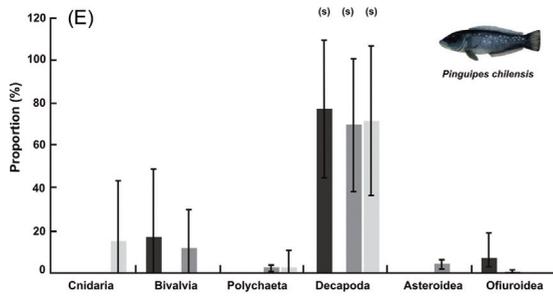
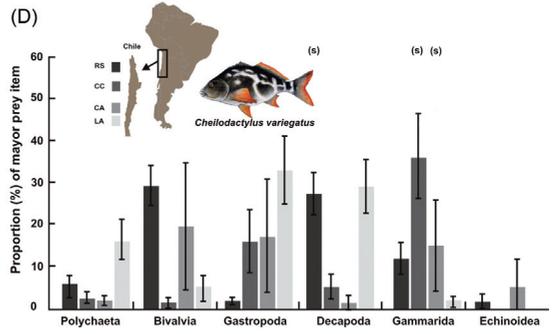
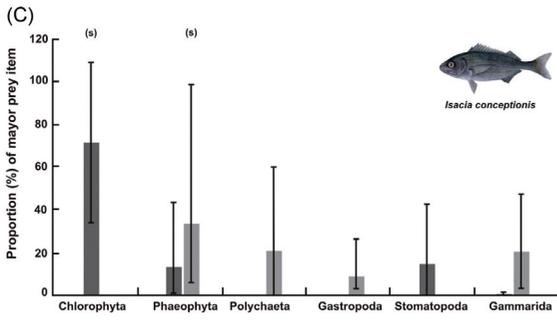


Fig. 2: Mean ( $\pm 2SE$ ) weight in proportion (%) and feeding selectivity (s) of mayor prey items categories for (A) herbivores (1 species), (B-C) omnivores (2 species), and (D-K) Carnivores (8 species).

Promedio ( $\pm 2EE$ ) de la proporción (%) en peso e ítem presa seleccionado (s) para (A) herbívoros (1 especie), (B-C) omnívoros (2 especies), y (D-K) carnívoros (8 especies).





This difference was significant as determined by our randomization tests ( $P = 0.01$ ). At LA, gastropods such as *Fissurella* spp., *Calyptrea trochiformis* (Born, 1778), and *Prisogaster niger* (Wood, 1828), were the most conspicuous food item, but this predator species did not show a statistically significant preference for any of them. Bivalves were also important food items at RS and LA for *C. variegatus*. The diet of *P. chilensis* did not vary among seasons at RS (Kendall  $W = 0.01$ ,  $df = 1$ ,  $P > 0.9$ ). Decapod crustaceans, principally *Pilumnoides perlatus* and porcelain decapod crustaceans from the genus *Petrolisthes*, were important in the diets of *P. chilensis* at RS and LA. At CA, bivalves contributed to more than 10 % of the diet of *P. chilensis*. At RS, CA, and LA, *P. chilensis* consumed red rock shrimp (*Rhynchocinetes typus*). Individuals of *P. humeralis* at RS and CC also consumed this prey species and by *Sciaena deliciosa* at CC. The diet of *Anisotremus scapularis* did not show differences among seasons at RS (Kendall  $W = 7.5$ ,  $df = 3$ ,  $P > 0.06$ ) ad at CC (Kendall  $W = 0.01$ ,  $df = 2$ ,  $P > 0.9$ ). This species consumed bivalves at RS and CA where as nudibranchs at CC. At CA, gastropods were present in high proportions within individuals of *Semicossyphus darwini*, but decapods crustaceans were actively selected. Diet of *S. darwini* did not show seasonal variation herein (Kendall  $W = 0.5$ ,  $df = 2$ ,  $P > 0.9$ ). This species also consumed bivalves in high proportions. Decapod crustaceans were also selected by *Graus nigra* (Philippi, 1887), which did not show variation among seasons (Kendall  $W = 0.5$ ,  $df = 2$ ,  $P > 0.7$ ) and *Hemilutjanus macrophthalmos* (Tschudi, 1846) at CA. The serranid, *H. macrophthalmos*, consumed teleost fishes (mainly blennoid fishes) (Fig. 2E, Table 2). *Seriotelella violacea* consumed pelagic crustaceans at RS (Table A1).

Using the complete dietary dataset, there was no objective guild formation among the fishes analyzed from all of the study sites. However, significant clustering emerged when we pooled the data into higher prey categories. The diet similarity cluster showed that there were as many as five different groups present at RS. One group includes *A. scapularis* and *C. variegatus* (Fig. 3A), who have a high degree of feeding overlap and feed mostly on bivalves (85%). *Aplodactylus punctatus* is the next closest species (Fig. 3A), which is explained by the

presence of bivalves in the stomach. Another group was composed by *G. laevifrons*, then *P. chilensis*. These are below the 60 % similarity cut-off established by the UPGMA grouping and therefore would not be considered members of the *A. scapularis* and *C. variegatus* guild. Brown and green algae are conspicuous items in the diet of *A. scapularis* and benthic crustaceans in that of *C. variegatus*. The most distant species is *S. violacea* (Fig. 3A), which had no trophic similarity to the other species due to the prevalence of pelagic amphipods from the order Hyperiidia (see Table A1).

Two groups can be identified in fish assemblages from CC. One is composed of *S. deliciosa* and *C. variegatus* (Fig. 3B), which are more than 65 % similar due mainly to decapoda items in their diet. It is important to note, however, that 100 % of the decapods consumed by *S. deliciosa* are brachyuran from the genus *Pinnixa* that inhabits soft bottom habitats while *C. variegatus* feed more on brachyurans of the genus *Cancer* and porcelain decapod crustaceans. Outside of this group is *P. humeralis* and *A. scapularis*, which feed on sipunculans and bivalves and amphipods respectively. These four species form a group of carnivores, although *A. scapularis* is technically too dissimilar to be included in this guild. The second group includes the herbivore, *A. punctatus* and two omnivores, *G. laevifrons* and *I. conceptionis* (Fig. 3B). The first two species consumed mainly *Lessonia* spp. and *Macrocystis* sp. recruits and blades as well as pneumatocyst, while the more pelagic species (*I. conceptionis*) consumed mainly ephemeral algae such as *Ulva* spp. No pelagic invertebrates were consumed by these species at this site.

At CA two main groups can be visualize one composed by four species and the other by two species. Fishes (*G. nigra* and *P. chilensis*) from the first group share more similarities in their diets consumed decapod crustaceans in high proportions. Close to this cluster is *S. darwini*, then *C. variegatus* (Fig. 3C). *Semicossyphus darwini* is separated from the other carnivores mainly due to the consumption of gastropods (particularly *Nassarius* sp. and *Turritella cingulata* (Sowerby, 1825)) and hermit decapod crustaceans, while *C. variegatus* feed primarily on bivalves and decapod crustaceans. The following group is a group composed by an herbivore (*A. punctatus*) and one omnivore

(*Girella laevis*) group (Fig. 3C). These two species only overlap in diet by 42 % due primarily to abundance of brown algae found in *A. punctatus*, which represents 78 % of its diet (it feeds principally on *L. trabeculata* and *M. pyrifera* fronds). In contrast, *G. laevis* feeds mainly on *Ulva* sp., turfing algae, and then pneumatocyst of *M. pyrifera*. *H. macrophthalmos* differs from the other groups due to the dominance of teleosts in the diet (see Tables A 2,3).

Since only a few species were analyzed at LA, the dietary overlap showed little similarity. *Pinguipes chilensis* and *C. variegatus* showed some degree of overlap principally due to high number of decapod crustaceans in their stomach contents. *A. punctatus* showed no overlap due to the high proportion of brown macroalgae (*L. trabeculata*) consumed and selected by this species at this site (Fig. 3D).

#### DISCUSSION

Our study indicated that (a) 12 of 13 kelp forest reef fishes analyzed, utilized benthic resources for feeding, (b) four of six fishes that occurred in more than one study site were plastic, exhibiting adaptability to change in their foraging habits, (c) five of six fishes showed feeding selectivity to a prey item, (d) differences in benthic resources among different kelp-forests sites provided evidence of the observed variation in the diet preference and, importantly, (e) the overall trophic structure of kelp forest reef fishes.

The composition of the diets was related to the available resources. Kelp forest fishes consumed prey items that were associated with some kind of biological substrata (i.e., mussel beds, amphipod reefs, understory algae). This finding is congruent to results obtained in other kelp forest sites such as those presented by Love & Ebeling (1978) and more recently by Angel & Ojeda (2001). Kelp forests provide suitable habitat for benthic prey items through the understory community. We suggest that understory habitats directly affect the diets of the fishes (Palma & Ojeda 2002).

The diets of carnivorous species were composed of benthic invertebrates such as decapod crustaceans, gammarid amphipods, and bivalves. Such prey items are abundant in macroalgal-beds (Taylor 1998, Vásquez et al.

1998, Villegas et al. 2008). Kelps and bivalves provide suitable habitat for several crustacean species (at RS for instance), and foliose algae, which harbors shrimps and amphipods (at CC, CA and LA). Despite of plasticity in feeding habits, fishes consumed benthic prey items. One example of this from our study is the bilagay, *Cheilodactylus variegatus*, the most conspicuous predator among kelp beds of northern Chile. Decapod crustaceans were consumed in high proportions at RS and LA where as gammarid amphipods at CC and CA. Gammarid amphipods are important prey of this species throughout its ontogeny (Díaz, F. personal communication), a pattern consistent by its congener in other temperate waters (McCormick 1998). However, large individuals tended to consume more decapods crustaceans as well polychaetes (McCormick 1998, Palma & Ojeda 2002, Medina et al. 2004). Omnivores such as the baunco, *Girella laevis*, also consumed benthic resources such as green and red algae. At CC, most of the algal blades on which *G. laevis* fed were epiphytized by filamentous reds, which may have been incidentally consumed. Animal material is far more common in the diet of *G. laevis* (Vial & Ojeda 1990). In two sites, this species selected animal protein but was consumed in very low proportions. Studies on *G. nigricans*, a temperate reef species, indicated that this consumes energy-rich algae when available, shifting to an animal diet only when algae are in short supply (e.g., at RS) (Clements & Choat 1997). We note that morphological features associated with herbivory are likely not prohibitive for manipulating and processing other materials such as animal structures (Choat 1982, Ojeda & Cáceres 1995, Clements & Choat 1997, Choat et al. 2002). The other omnivore such as the cabinza, *Isacia conceptionis*, was abundant at CC only where consumed and select green algae from bottom substrata. This finding is congruent with Angel & Ojeda (2001) of individuals from kelp forest sites. However, at CA this species consumed more brown macroalgae and associated gammarid amphipods.

Herbivores were abundant in the study sites. We suggest that a high turnover exists in terms of utilization of macroalgae reflecting the diversity of available prey items. Brown macroalgae were consumed

most frequently followed by benthic red algae and green ephemeral. The jerguilla, *Aplodactylus punctatus*, foraged and selected brown macroalgae, specifically on *L. trabeculata* (blades and recruits), *Halopteris* spp, and turfing algae at CC, CA, and LA. Cáceres et al. (1994) suggested that when green algae are present in low abundance, this species forages on brown algae. This pattern was upheld at CC, CA, and LA. The understory algae are scarce at RS, amphipods reefs monopolize the substratum at this site, and benthic animal material was found in the guts of *A. punctatus*.

It has been suggested that benthic resources associated with kelp forests influence the abundance, distribution, and diversity of

the associated fauna (Coull & Wells 1983, Hay 1984, Kelaher & Castilla 2005). In general, these understory assemblages vary greatly, as when kelp structures are densely or patchily distributed (Fowler-Walker & Connell 2002), or if they are composed by mono-specific or mixed stands (Schiel & Foster 1986, Irving & Connell 2006). Different understory assemblages offer different associated prey for fishes and the accessibility of food items is one of the most important factors that influence on the diets of fish species (Cowen 1986, Gillanders 1995). We found high trophic plasticity of similar species under different kelp forests. We suggest that this is an adaptation mediated by behavioral flexibility in prey selection. This increases

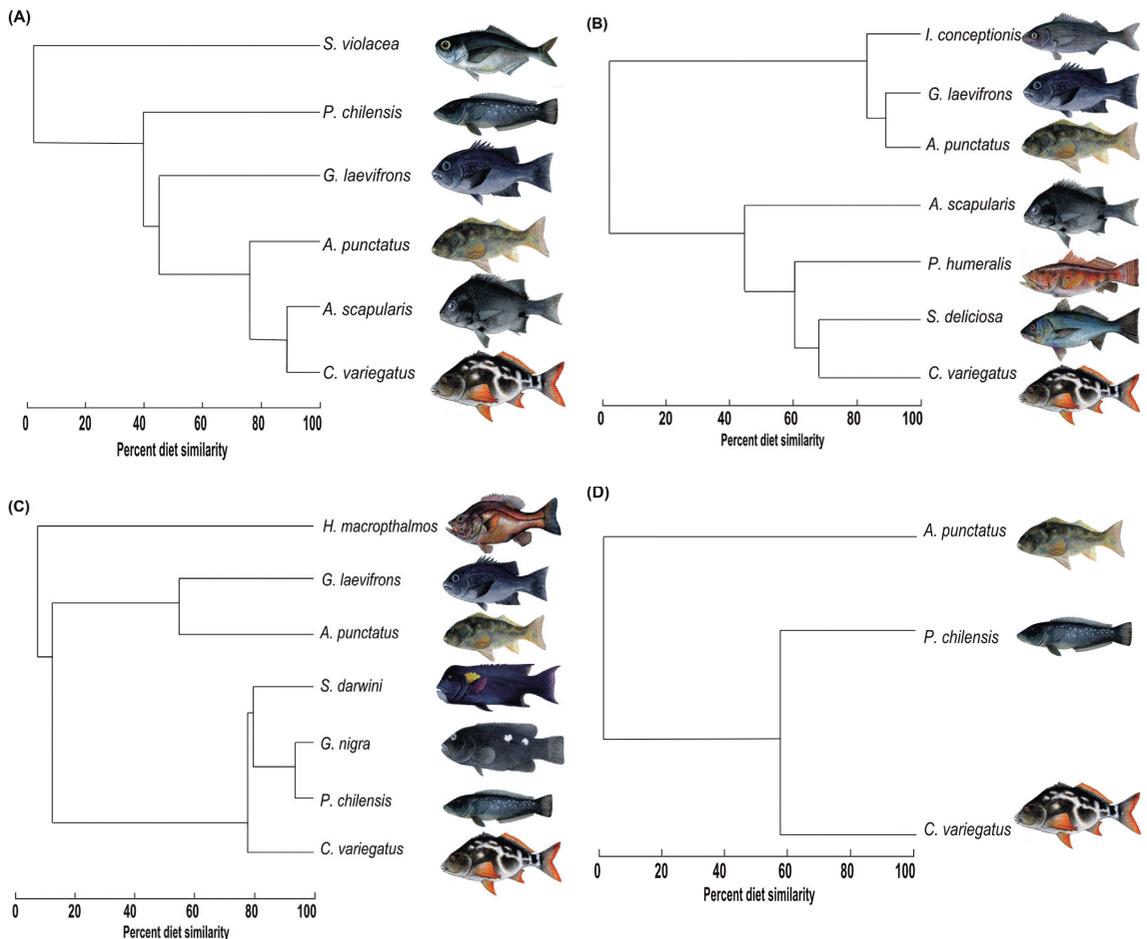


Fig. 3: Diet similarity phenograms (UPGMA) from the sampled sites: (A) Río Seco (RS), (B) Caleta Constitución (CC), (C) Caleta Angosta (CA), (D) Lagunillas (LA).

Diagramas de similitud dietaria (UPGMA) de los sitios de muestreo: (A) Río Seco (RS), (B) Caleta Constitución (CC), (C) Caleta Angosta (CA), (D) Lagunillas (LA).

feeding opportunities, under similar habitat (i.e., kelp beds) but confronted to a different configuration of the substratum which allow species to success in searching and handling prey (Glasby & Kingsford 1994). With few exceptions, such as the rollizo, *Pinguipes chilensis* (which fed mostly on rock shrimps (*R. typus*) at all study site) and cabrilla, *Paralabrax humeralis*, resource utilization and selectivity varied among all species and sites. Quite a few studies have reported changes in the diet of fish populations. For example, *Semicossyphus pulcher* in California (Cowen 1986), *S. darwini* in Chile (Fuentes 1981), *Notolabrus fucicola* in New Zealand (Denny & Schiel 2001), *Sebastes capensis* along South American coast (Barrientos et al. 2006) as well as changes in the diet of entire fish assemblages, in northern Chile (Angel & Ojeda 2001, Medina et al. 2004) and California (Graham 2004). Most of these studies explain these changes as a reflection of the habitat's availability, which in turn modifies the available prey and stabilize predator-prey interactions by the increasing refuges of prey when facing a predator (Hughes & Grabowski 2006). This can be linked to the optimal foraging theory (OFT), which principally states that predators should prefer prey that yield more energy per unit of handling time (Sih & Christensen 2001). We link this back, again, to the changes in composition of kelp-beds community at each of the sites, and therefore changes in foraging opportunities even for members of the same species; thus the OFT predicts that when prey abundances of higher energetic value increases, the lower value items should be dropped from the species' diets (Sih & Christensen 2001).

The presence of foraging opportunities is important, as are the interactions between species that potentially modify and maintain those opportunities. An example of this phenomenon may be found among patterns of trophic group formation and dietary overlap. Dietary overlap was higher at sites where understory microhabitat was diverse such as in CC and CA especially in the micro-carnivore group; this might leads to substitutable effects of predators over prey items as prey face several microhabitats, hence different predators decrease in interspecific interactions. However, only one foraging guild was generated at RS. A reduced overlap at RS may be a direct reflection

of the reduced number of microhabitats. Bivalves may be so abundant that their levels cannot effectively be reduced by the foraging species that are present at RS, therefore a greater diversity of microhabitats has not been able to establish itself. These interactions, and the potential outcomes, are difficult to measure without accurate field observations or exclusion experiments. Alternatively, the abundance of bivalves as prey may ameliorate the negative effect of horizontal interactions (i.e. competition) for the three important predators, thereby allowing them to co-exist (Griffen & Byers 2006, Huxel 2007). This helps us to visualize the importance of resource selection, which may help us to interpreting how habitats are identified by predators in encountering prey and how we can predict from the habitats the level of interactions between the species in the community (Boyce 2006).

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## APPENDIX

TABLE A1

Dietary composition expressed as percent of total food weight and frequency of occurrence of prey items (in parenthesis) for six fish species analyzed in subtidal habitat at Río Seco (RS).

Composición dietaria expresada en porcentaje de ocurrencia (en paréntesis) de cada ítem presa para seis especies estudiadas en el hábitat submareal de Río Seco (RS)

Prey Category	<i>A. scapularis</i>	<i>A. punctatus</i>	<i>C. variegatus</i>	<i>G. laevisfrons</i>	<i>P. chilensis</i>	<i>S. violacea</i>
Chlorophyta	0	0.04		11.6 (42.8)	0	0
Rhodophyta	0	34.2 (83.3)		15.3 (7.1)	0	0
Phaeophyta	0.1 (7.6)	17.8 (50.0)	0.26 (4.0)	36.7 (50.0)	0	0
Unidentified algae	0	4.9 (8.3)		1.1 (14.3)	0	0
Porifera	0	0		1.1 (7.1)	0	0
Hydrozoa	0	5.5 (16.7)		23.4 (7.1)	0	0
Anthozoa	0	0	2.9 (7.0)	0	0	0
Polychaeta	0.3 (15.3)	0	4.2 (25.0)	0.2 (14.3)	0	0
Gastropoda	0	0	1.1(14.3)	0.5 (28.5)	0	0
Bivalvia	99.2 (92)	37.0 (83.3)	48.22 (57.1)	2.2 (50.0)	0	0
Nudibranchia	0	0	0.2 (3.6)	0	0	0
Gammarida	0	0	1.77 (42.9)	0.1 (78.1)	0	0
Isopoda	0	0		0	0	100 (100)
Tanaidacea	0	0	0.05 (10.7)	0	0	0
Decapoda	0.2 (7.6)	0	30.5 (50.0)	7.2 (50.0)	96.81(83.3)	0
Cirripedia	0	0		0.6 (7.1)	0	0
Sipunculida	0.2 (7.6)	0	2.6(10.7)	0	0	0
Echinoidea	0.03	0	0.9 (42.9)	0	0	0
Ophiuroidea	0	0	7.2 (10.7)	0	3.19 (33.3)	0
Planktonic larvae	0.01 (15.3)	0	0.1 (10.7)	0	0	0

TABLE A2

Dietary composition expressed as percent of total food weight and frequency of occurrence of prey items (in parenthesis) for seven fish species analyzed in subtidal habitat at Caleta Constitución (CC).

Composición dietaria expresada en porcentaje de ocurrencia (en paréntesis) de cada ítem presa para siete especies estudiadas en el hábitat submareal de Caleta Constitución (CC).

Prey Category	<i>A. scapularis</i>	<i>A. punctatus</i>	<i>C. variegatus</i>	<i>G. laevisfrons</i>	<i>I. conceptionis</i>	<i>P. humeralis</i>	<i>S. deliciosa</i>
Chlorophyta	10.9 (36.4)	1.1 (37.5)	0.1 (12.5)	18.3 (85.5)	64.2(66.7)	0	0
Rhodophyta	3.0 (9.1)	33.5 (75.0)	0	6.7 (50.0)	0	0	0
Phaeophyta	2.9 (9.1)	62.0 (62.5)	0.8 (6.3)	73.5 (60.0)	35.7(16.6)	0	0 (11.1)
Hydrozoa	0	2.5 (12.5)	0	0.4 (10.0)	0	0	0
Polychaeta	1.5 (27.3)	0.1 (12.5)	4.0 (25.0)	0.4 (5.0)	0	0	2.4 (11.1)
Gastropoda	1.6 (9.1)	0.2 (12.5)	15.5 (50.0)	0.3 (20.0)	0	0	0
Bivalvia	35.9 (27.3)	0	0.5 (6.3)	0	0	0	6.0 (11.1)
Nudibranchia	1.1 (27.3)	0	0	0	0	0	0
Stomatopoda	0	0	0	0	0	8.1 (14.3)	38.1 (22.2)
Ostracoda	0	0	0	0 (5.0)	0	0	0
Gammarida	27.2 (63.6)	0.1 (12.5)	20.9 (56.3)	0.1 (35.0)	0	0.5 (14.3)	0
Isopoda	0	0	0.0	0 (10)	0	0	0
Tanaidacea	0	0	0.2 (31.3)	0	0	0	0
Decapoda	16.0 (27.3)	0.5 (12.5)	42.7 (56.3)	0	0	32.1 (57.1)	53.5 (33.3)
Sipunculida	0	0	0.0	0	0	47.8 (14.3)	0
Echinoidea	0	0	2.1 (18.8)	0 (5.0)	0	0	0
Planktonic larvae	0	0	1.3 (12.5)	0	0	0	0
Urochordata	0	0	11.8 (6.3)	0	0	0	0
Teleostei	0	0	0	0	0	11.4 (14.3)	0

TABLE A3

Dietary composition expressed as percent of total food weight and frequency of occurrence of prey items (in parenthesis) for seven fish species analyzed in subtidal habitat at Caleta Angosta (CA).

Composición dietaria expresada en porcentaje en peso y frecuencia de ocurrencia (en paréntesis) de cada ítem presa para siete especies estudiadas en el hábitat submareal de Caleta Angosta (CA).

Prey Category	<i>A. punctatus</i>	<i>C. varrigatus</i>	<i>G. laevifrons</i>	<i>G. nigra</i>	<i>H. macrophthalmos</i>	<i>P. chilensis</i>	<i>S. darwini</i>
Chlorophyta	1.7 (30.0)	0	45.8 (40.0)	0	0	0	0
Rhodophyta	13.8 (70.0)	0	20.1 (60.0)	0	0	0	0
Phaeophyta	78.7 (100.0)	1.2 (12.5)	18.6 (20.0)	0	0	0	0
Porifera	1.9 (20.0)	0	7.0 (20.0)	0	0	0	0
Hydrozoa	0.2 (13.3)	0	0	0	0	0	0
Polychaeta	0 (3.3)	7.0 (25.0)	0	0	0	0.5 (14.8)	0.1 (10.5)
Gastropoda	0.1 (63.3)	1.4 (37.5)	2.0 (20.0)	1.1 (33.3)	0	0.3 (57.4)	44.2 (63.2)
Bivalvia	2.3 (36.7)	44.2 (37.5)	1.1 (20.0)	0.3 (33.3)	0	14.8 (57.1)	9.8 (47.4)
Polyplacophora	0	0	0	0	0	5.1 (25.5)	3.7 (26.3)
Gammarida	0 (3.3)	8.8 (37.5)	0	0	0.6 (85.7)	0	0
Isopoda	0	0.2 (25.0)	0	0	1.5 (28.6)	0	0
Tanaidacea	0	0	0	0	0.1 (28.6)	0	0
Decapoda	0	34.8 (62.5)	0	90.4 (83.3)	7.0 (85.7)	79.3 (100.0)	40.7 (42.1)
Cirripedia	0 (3.3)	0	5.2 (20.0)	0	0	0	0.7 (26.3)
Echinodea	0	0	0	0	0	0	0.7 (26.3)
Asteroidea	0	0	0	8.3 (33.3)	0	0	0
Planktonic larvae	0	0	0	0	0.4 (42.9)	0	0
Urochordata	1.3 (16.7)	0	0	0	0	0	0
Teleostei	0	2.39	0	0	90.4 (14.3)	0	0

TABLE A4

Dietary composition expressed as percent of total food weight and frequency of occurrence of prey items (in parenthesis) for three fish species analyzed in subtidal habitat at Lagunillas (LA).

Composición dietaria expresada en porcentaje en peso y frecuencia de ocurrencia (en paréntesis) de cada ítem presa para tres especies estudiadas en el hábitat submareal de Lagunillas (LA).

Prey Category	<i>A. punctatus</i>	<i>C. variegatus</i>	<i>P. chilensis</i>
Chlorophyta	1.5 (36.4)	0	0
Rhodophyta	13.8 (81.8)	1.1 (15.4)	0
Phaeophyta	80.5 (81.8)	0	0
Porifera	0.8 (9.1)	0.3 (7.7)	0
Anthozoa	0	0	2.7 (12.5)
Hydrozoa	1.0 (9.1)	0	0
Platyhelminthes	0	0 (7.7)	0
Polychaetes	0 (9.1)	17.9 (76.9)	0.9 (25.0)
Polyplacophora	0	5.5 (15.4)	0
Gastropoda	0 (9.1)	30.8 (84.6)	1.6 (25.0)
Bivalvia	0.2 (18.2)	11.6 (30.8)	0
Gammarida	0	1.7 (53.8)	0
Isopoda	1.4 (18.2)	0 (15.4)	0
Decapoda	0	28.7 (84.6)	94.8 (50.0)
Cirripedia	0.3 (9.1)	0.2 (7.7)	0
Planktonic larvae	0	0.2 (15.4)	0
Echinoidea	0	0 (23.1)	0
Urochordata	0.4 (9.1)	0	0
Teleostei	0	1.8 (7.7)	0