

# Potential for omnivory and apparent intraguild predation in rocky intertidal herbivore assemblages from northern Chile

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**ABSTRACT:** We assessed the ingestion of animal items by 29 herbivore species of the most common invertebrates on rocky intertidal shores of northern Chile (21 to 30° S). Data were obtained from 4 communities sampled seasonally from winter 2004 to spring 2005. Gastric contents of 2671 individuals were categorized into 143 food items, 42.7 % of them corresponding to animal prey. All herbivores were polyphagous generalists, showing a moderate to high dietary overlap and suggesting the potential for exploitation competition. Diet width and the proportion of animal items ingested per species were positively related with body mass, revealing a high potential for true omnivory among larger herbivores. Barnacles were the dominant prey item, followed by a suite of common intertidal animals, including herbivore species. The consumption of herbivores was defined as apparent intraguild (IG) predation, a framework that we used by analogy to describe pairwise interactions at a regional and community level. We recorded 29 IG predator–IG prey interactions, all of them asymmetrical (no reciprocal predation), and directed exclusively towards heterospecific IG prey, which in most cases were juvenile individuals that were taxonomically unrelated. All IG predators were large herbivore species, and they appeared to avoid consuming conspecifics. The high incidence of polyphagy and apparent IG predation may not be simply an epiphenomenon of grazing, nor a response to limited algal resources, and we discuss the nature of herbivores as consumers and the implications of potential omnivory for the connectedness, looping, and chain length of intertidal food webs.

**KEY WORDS:** Herbivory · Diet · Niche breadth · Polyphagy · Connectivity · Food web

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## INTRODUCTION

Herbivorous invertebrates and their food preferences are long recognized to play a key role in the functioning of rocky intertidal systems (Lubchenco 1978, Lubchenco & Gaines 1981). However, herbivores continue to be less studied than carnivores with regard to their nature as consumers and their trophic status within community food webs. Nearly 3 decades ago, Lubchenco (1979) proposed that both herbivorous and carnivorous consumers should be termed predators, because they played an equivalent functional role in terms of predator–prey dynamics. Although this issue

has not received much attention in the marine literature, there are several reasons why it deserves further examination. Many species traditionally considered to be herbivores regularly ingest invertebrate animals in direct or indirect ways (e.g. Santelices & Correa 1985, Wootton 1993, Hughes et al. 2005), raising the question whether they are true herbivores or are actually omnivores. However, proper assessments of the assimilation of ingested food items are rather infrequent in dietary and food web analyses, and the determinations of energy flows and even the trophic level of species are not always clear (Williams & Martinez 2004). Thus, the importance of non-algal food resources to herbivores

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remains poorly understood (Briscoe & Sebens 1988), as is the trophic status of these consumers. Such herbivores could be treated as omnivores in a wide sense (eating plants and animals), but they may also fit particular definitions of omnivory (some not too suitable for herbivores), such as feeding on more than one trophic level (Pimm & Lawton 1978), being linked to a basal species at more than one link in a trophic chain (Yodzis 1984), or eating basal (plant) and intermediate (animal) species (Arim & Marquet 2004). The latter two may apply to the special case of herbivores that eat other herbivores, which are the focus of the present work, and represents a 3-level food chain with a 'predator' herbivore consuming a 'prey' herbivore feeding on basal species, i.e. an omnivore link (*sensu* Yodzis 1984). In addition, if 'predator' and 'prey' herbivores share and potentially compete for algal prey, the omnivore link turns into a closed omnivore loop (*sensu* Sprules & Bowerman 1988), placing their interaction into the domain of intraguild predation (Polis et al. 1989, Polis & Holt 1992). Thus, intraguild predation among rocky intertidal invertebrate herbivores appears to be an intriguing possibility, which partly turns back to Lubchenco's (1979) suggestion about the functional similarity of herbivores and carnivores acting as predators. Analysis of intraguild predation in rocky or estuarine intertidal systems (e.g. Navarrete et al. 2000, Omori et al. 2006) certainly deals with carnivorous or omnivorous predators, but we suggest that an analogous approach for herbivorous consumers may provide some useful insights. On rocky shores, the incidental consumption of herbivores by herbivores is a real phenomenon that, at first instance, we might term 'apparent' intraguild predation. It has a direct negative effect on 'prey' abundance, and even if the 'predator' does not feed on the prey (i.e. receives no direct gain of energy or nutrients), both herbivores may indirectly benefit from a potential reduction of exploitative competition, an outcome similar to that expected from true intraguild predation (Polis et al. 1989).

In this context, we present a first assessment of the consumption of animal items and apparent intraguild predation in invertebrate herbivore assemblages from northern Chile, integrating dietary information from seasonal samplings conducted over one and a half years in 4 rocky intertidal communities. In this regard, we treat herbivore 'prey' and 'predators' in analogous terms to those proposed by Polis et al. (1989) for intraguild predation. All herbivore species in the present study included some fraction of animal items in their diet, thus being polyphagous and potential omnivores in a wide sense or under Pimm & Lawton's (1978) definition. However, at least a third of these species included other herbivores in their animal diet and

shared algal prey to various extents, thus also being potential competitors engaged in closed omnivore loops. Thus, our herbivore food web differentiates organisms into herbivores eating non-herbivorous animals, which may be intraguild prey but not intraguild predators, and those eating other herbivores, which may be either intraguild predators or intraguild prey (if they are in turn consumed by another intraguild predator). Therefore, 'prey' herbivores are treated as species of intermediate trophic position between basal species and 'predator' herbivores, while these latter are treated as omnivores following Yodzis (1984) and Arim & Marquet (2004).

## MATERIALS AND METHODS

**Sampling and diet evaluation.** From winter 2004 to spring 2005, we sampled 4 rocky intertidal communities distributed over ~1000 km of coast in northern Chile (Fig. 1): Río Seco (hereafter, RIO; 21°00'05" S, 70°09'54" W), Caleta Constitución (CCO; 23°25'23" S, 70°35'26" W), Caleta Angosta (CAN; 28°15'38" S, 71°10'23" W), and Lagunillas (LAG; 30°06'14" S, 71°22'57" W). The 4 sites differ in their local upwelling regimes, as CCO and LAG are known to be influenced by important upwelling centers throughout the year (Vásquez et al. 1998, Thiel et al. 2007). In the present paper we include samplings from 6 austral seasons: winter 2004 (August 15 to 27), spring 2004 (November 8 to 16), summer 2005 (January 20 to 27), autumn 2005 (May 22 to June 1), winter 2005 (August 18 to 25), and spring 2005 (November 8 to 16). The presence and



Fig. 1. Location of rocky intertidal sites sampled along the coast of northern Chile

abundance of herbivores were recorded in 45 quadrats ( $0.25 \text{ m}^2$ ) assigned to 15 transects distributed into 5 permanent sampling blocks, and stratified by intertidal zone (high, mid, low), covering ca. 130 m of coastline. As herbivores differ in vertical distribution, density was calculated from those quadrats where each species occurred (mean  $\pm$  SE sample size =  $125.6 \pm 4.6$ ). At each site and season, herbivorous individuals were collected at different tidal heights from the 5 sampling blocks, in order to incorporate the environmental patchiness of their food resources. Based on previous estimations, we planned to collect 10 individuals per season of each of the most conspicuous herbivorous species at each site, representing 85 to 100% of the food items locally consumed through all seasons by nearly 90% of the studied species, which is similar to reports by other authors (e.g. Winemiller et al. 2001). Actual sample sizes varied depending on the natural occurrence of species, and the average ( $\pm$ SE) number of individuals collected per species, community, and season were  $8.9 \pm 0.9$  (RIO),  $9.7 \pm 0.7$  (CCO),  $8.8 \pm 0.8$  (CAN), and  $8.5 \pm 1.1$  (LAG).

Maximum body length and dry biomass (oven dried to constant weight at  $70^\circ\text{C}$ ) were recorded for each sampled individual, and its intestinal content was analyzed under a stereoscopic microscope to determine the identity of dietary items to the lowest possible taxonomic level. While some identification problems were inevitable, our estimations have, to our best knowledge, the highest taxonomic resolution among dietary studies so far conducted in Chilean intertidal communities. Because most herbivores rasp or scrape their food, their intestinal contents were composed mainly of body parts or tissue fragments, preventing abundance counts and estimations of prey body size. We therefore treated food as a niche dimension of discrete resource states involving the type, number, and frequency of occurrence of consumed food items (note that these values may not indicate gravimetric or numeric importance, and they are not intended to reflect interaction strength in terms of per capita effects). As a complementary estimation, for each of 18 of the most important herbivore species, we measured the total biomass of algal and animal contents in the entire gastric system of 3 individuals per species, calculating their respective proportions (%). On this basis, we also provide a simple estimation of the biomass per algal and animal item per species as the quotient between (algal and animal) biomass, and the average number of (algal and animal) dietary items recorded for all individuals of each species (note that this approximation may vary in field individuals depending on their degree of gastric fullness).

**Trophic relationships.** Across the 4 communities, we calculated: (1) the mean niche breadth of each herbi-

vore species (after Levins 1968), measured by an index integrating both the number and the relative frequency of resource states (trophic items) used by the species (Feinsinger et al. 1981), and expressed as the average of breadth values recorded in the 4 localities, and (2) the mean niche overlap (after Pianka 1973) of each herbivore species with the remaining herbivores, measured by an index providing a pairwise estimation of the extent to which trophic items were shared between 2 herbivore species, and expressed as the average of overlap values obtained for a given herbivore. We then identified all herbivorous individuals that consumed another herbivorous individual, in order to establish the potential pairwise interactions among species and their relative importance in quantitative terms. Due to the low occurrence of herbivorous individuals among non-algal dietary items, we pooled data to assess intraguild predation (IGP) in 2 different ways. At the community level, we combined seasonal data to calculate the occurrence frequency of 'prey' herbivore species within each pairwise interaction, i.e. the proportion of the total number of individuals of each 'predator' herbivore that consumed a given 'prey' herbivore. For simplicity, we hereafter refer to these as IG predator and IG prey, respectively. For each community, the observed predator-prey links were represented as simple web diagrams showing the relative trophic position of the species. Although we lacked quantitative data on the abundance and body size of IG prey in intestinal contents, we kept qualitative records of their size to provide information about ontogenetic stage (juvenile vs. adult). At a regional level, we combined all available data to summarize the observed pairwise interactions. For each interaction, we provide: (1) the mean dietary overlap between IG predator and IG prey at the adult stage, to indicate the potential for exploitation competition; (2) two separate estimates of their body size ratio (IG predator/IG prey), based on the mean maximum length and mean dry biomass of all individuals sampled per species, to describe the symmetry of their adult sizes (i.e. not considering the size of consumed IG prey); (3) the mean dietary breadth of IG predators; (4) the total number of sampled IG predator individuals; and (5) the overall frequency of occurrence of IG prey.

## RESULTS

### Consumption of animal food items

We analyzed 2671 herbivorous individuals belonging to 29 species of Mollusca, Echinodermata, and Crustacea, with field densities ranging from 4.5 to 313 individuals  $\text{m}^{-2}$  (Table 1). These species showed

Table 1. Herbivorous species collected during 6 seasonal samplings (winter 2004 to spring 2005) in 4 rocky intertidal communities from northern Chile. Family and abbreviated class (P: Polyplacophora; G: Gastropoda; C: Crustacea; E: Echinoidea). NC: number of communities where the species occurred; PS: percentage of samples where the species was present (total = 24 community × season samples); TN: total number of algal + animal items; NA: number and proportion (P, in %) of animal items; D: density (mean ± SE; individuals m<sup>-2</sup>); na: data not available

Species	Family, class	NC	PS	TN	NA (P)	D
<i>Acanthopleura echinata</i> (Barnes)	Chitonide, P	4	70.8	89	33 (37.1)	6.83 ± 0.46
<i>Chiton cumingii</i> Frembly	Chitonide, P	1	4.2	21	6 (28.6)	10.46 ± 5.81
<i>Chiton granosus</i> Frembly	Chitonide, P	4	75	62	19 (30.6)	7.36 ± 0.52
<i>Chiton magnificus</i> Deshayes	Chitonide, P	1	4.2	37	8 (21.6)	6.80 ± 2.07
<i>Enoplochiton niger</i> (Barnes)	Chitonide, P	4	100	94	35 (37.2)	10.20 ± 0.69
<i>Tonicia elegans</i> Frembly	Chitonide, P	3	12.5	25	4 (16.0)	4.50 ± 0.50
<i>Fissurella costata</i> Lesson	Fissurellidae, G	2	16.7	33	5 (15.2)	na
<i>Fissurella crassa</i> Lamarck	Fissurellidae, G	4	87.5	87	28 (32.2)	5.63 ± 0.29
<i>Fissurella limbata</i> Sowerby	Fissurellidae, G	4	33.3	87	32 (36.8)	5.55 ± 0.37
<i>Fissurella maxima</i> Sowerby	Fissurellidae, G	4	62.5	83	30 (36.1)	5.74 ± 0.33
<i>Fissurella nigra</i> Lesson	Fissurellidae, G	2	8.3	42	8 (19.0)	6.00 ± 2.00
<i>Fissurella picta</i> (Gmelin)	Fissurellidae, G	4	41.7	67	20 (29.9)	5.52 ± 0.42
<i>Lottia orbigny</i> Dall	Lottiidae, G	1	4.2	11	1 (9.1)	10.29 ± 2.04
<i>Scurria araucana</i> (Orbigny)	Lottiidae, G	4	75	49	10 (20.4)	11.39 ± 0.66
<i>Scurria cecilians</i> (Orbigny)	Lottiidae, G	3	29.2	31	8 (25.8)	36.97 ± 3.88
<i>Scurria plana</i> (Philippi)	Lottiidae, G	1	4.2	29	7 (24.1)	7.08 ± 0.97
<i>Scurria scurra</i> (Lesson)	Lottiidae, G	1	4.2	7	1 (14.3)	na
<i>Scurria variabilis</i> (Sowerby)	Lottiidae, G	4	16.7	30	4 (13.3)	7.10 ± 0.53
<i>Scurria viridula</i> (Lamarck)	Lottiidae, G	4	83.3	55	16 (29.1)	7.32 ± 0.58
<i>Scurria zebrina</i> (Lesson)	Lottiidae, G	3	12.5	25	7 (28.0)	8.69 ± 0.96
<i>Onchidella marginata</i> (Gould)	Onchidiidae, G	1	4.2	15	2 (13.3)	10.86 ± 6.22
<i>Siphonaria lessoni</i> (Blainville)	Siphonariidae, G	3	66.7	44	10 (22.7)	15.88 ± 1.18
<i>Diloma nigerrima</i> (Gmelin)	Trochidae, G	2	8.3	10	3 (30.0)	5.14 ± 0.74
<i>Tegula atra</i> (Lesson)	Trochidae, G	4	91.7	63	17 (27.0)	241.78 ± 28.18
<i>Tegula tridentata</i> (Potiez & Michaud)	Trochidae, G	3	12.5	23	6 (26.1)	6.35 ± 0.70
<i>Prisogaster niger</i> (Wood)	Turbinidae, G	3	50	33	9 (27.3)	313.64 ± 41.73
<i>Taliepus dentatus</i> (Milne Edwards)	Majidae, C	1	4.2	30	7 (23.3)	7.00 ± 1.96
<i>Loxechinus albus</i> Molina	Echinidae, E	4	16.7	86	29 (33.7)	11.62 ± 1.18
<i>Tetrapygyus niger</i> Molina	Arbaciidae, E	4	100	99	34 (34.3)	20.87 ± 1.72

an average occurrence of ca. 70% in the study communities and ca. 40% in the 24 samples of communities by seasons, and the assemblage was composed mainly of patellogastropod limpets (Lottiidae), keyhole limpets (Fissurellidae), and chitons (Chitonidae) (Table 1). The herbivore assemblage consumed a total number of 143 dietary items, from which 82 corresponded to algae determined to different taxonomic levels (46 species, 32 genus, 1 family, and 3 groupings). On the whole, the 2671 individuals ingested a total number of 2893 animal prey (sessile and mobile invertebrates), categorized into 61 items, representing >40% of the total number of dietary items. At the species level, the total number of consumed items ranged from 7 to 99, with an average (±SE) of 48.2 ± 5.1 items species<sup>-1</sup>, while the proportion of animal items ranged from 9.1 to 37.2%, with an average (±SE) of 26.2 ± 1.4% species<sup>-1</sup>. In addition, body size (mean dry biomass) of herbivore species was positively related with the total number of dietary items (Pearson's  $r = 0.66$ ,  $p < 0.001$ ,  $n = 29$ ) and the proportion of animal items (Pearson's  $r = 0.50$ ,  $p = 0.006$ ,  $n = 29$ ). We also note that, in particular seasons,

the proportion of animals ingested by larger herbivores could be higher than the overall estimates in Table 1, for example, up to 82% in *Fissurella limbata*, 66% in *F. maxima*, 60% in *Acanthopleura echinata*, 49% in *Enoplochiton niger*, 44% in *Tetrapygyus niger*, and 41% in *F. crassa*.

Table 2 shows the animal items ingested by the herbivore assemblage, and their frequency of occurrence with respect to the number of herbivorous individuals analyzed both for northern Chile on the whole and for each community. The occurrence of the main items (frequency ≥1%) was highly consistent and did not show significant differences among the 4 study communities ( $\chi^2 = 58.81$ ,  $p = 0.081$ ,  $df = 45$ ). From the 29 herbivore species, 13 occurred as IG prey and were consumed by 1.77% of the sampled individuals (see Table 4 for a separate analysis of IG prey). In contrast, barnacles were by far the most important animal items, and overall they were consumed by 54.8% of the herbivorous individuals. Barnacle items included larvae and undetermined remains (plates and body parts), plus 5 identified species (Table 2), which, in some

Table 2. Occurrence frequency (%) of animal items ingested by individuals of species listed in Table 1, calculated for northern Chile (Regional) and for each community (RIO: Río Seco; CCO: Caleta Constitución; CAN: Caleta Angosta; LAG: Lagunillas). Higher taxa abbreviated as A: Aracnida; AM: Amphipoda; AN: Anthozoa; B: Bivalvia; CI: Cirripedia; CR: Crustacea; D: Decapoda; G: Gastropoda; I: Insecta; P: Polychaeta; ni: not identified to species or genus level

Animal item	Regional (n = 2671)	RIO (n = 697)	CCO (n = 651)	CAN (n = 654)	LAG (n = 669)
Barnacle remains, CI	42.33	53.66	45.01	33.03	38.42
Foraminifera	5.94	9.90	2.46	4.89	6.43
<i>Notochthamalus scabrosus</i> (Darwin), CI	5.57	7.32	1.84	2.60	10.46
<i>Hyale</i> sp., CR	5.46	8.18	6.30	2.60	4.78
<i>Jehlius cirratus</i> (Darwin), CI	5.27	9.61	4.15	1.53	5.68
Bryozoa, ni	5.09	6.60	2.92	5.50	5.38
Hydrozoa, ni	4.12	3.01	5.53	1.53	6.58
<i>Liopetrolisthes mitra</i> (Dana), D	4.05	3.87	3.99	3.21	5.23
<i>Semimytilus algosus</i> (Gould), B	3.94	9.90	1.08	2.14	2.39
Nematoda, ni	3.90	3.30	3.69	5.20	3.59
<i>Austrolittorina araucana</i> (Orbigny), G	3.86	9.04	1.54	3.52	1.20
<i>Perumytilus purpuratus</i> (Lamarck), G	3.19	7.46	0.92	1.83	2.39
Herbivore IG prey (13 species; see Table 4)	1.77	3.4	1.05	0.9	1.65
Ostracoda, ni	1.37	0.00	0.00	0.15	5.38
Spirorbidae, ni – P	1.23	0.57	0.31	1.99	2.09
Dipteran larvae, ni – I	1.19	0.72	0.92	1.68	1.49
Acari, ni – A	1.19	0.57	1.23	1.07	1.94
Polychaeta, ni	1.00	1.43	0.77	0.92	0.90
Tardigrada, ni	0.97	1.58	0.92	0.92	0.45
Isopoda, ni	0.71	1.00	0.46	0.76	0.60
<i>Notobalanus flosculus</i> (Darwin), CI	0.67	1.29	0.15	0.31	0.90
Cypris larvae, CI	0.63	0.43	0.15	0.76	1.20
Sipunculida, ni	0.48	1.87	0.00	0.00	0.00
Radiolaria, ni	0.48	0.86	0.61	0.15	0.30
<i>Petrolisthes megalopa</i> , ni – D	0.37	0.72	0.77	0.00	0.00
<i>Echinolittorina peruviana</i> (Lamarck), G	0.30	0.57	0.00	0.15	0.45
<i>Brachidontes granulata</i> (Hanley), B	0.30	0.00	0.15	0.61	0.45
<i>Eurhomalea</i> sp., B	0.26	0.57	0.15	0.15	0.15
<i>Phragmatopoma moerchi</i> Kinberg, P	0.26	0.00	0.15	0.76	0.15
<i>Balanus laevis</i> (Bruguère), CI	0.22	0.14	0.15	0.15	0.45
Chironomidae, ni – I	0.19	0.00	0.00	0.00	0.75
Egg capsules of <i>Concholepas concholepas</i> (Bruguère), G	0.15	0.57	0.00	0.00	0.00
Other items <sup>a</sup> (regional frequency < 0.15)	0.98	1.14	0.61	1.07	0.74

<sup>a</sup>Zoea larvae, Copepoda, amphipod larvae, Amphipoda ni, *Austromegabalanus psittacus* (Molina)–CI, Trocophora larvae–G, *Crassilabrum crassilabrum* (Sowerby)–G, *Crepidatella dilatata* (Lamarck)–G, *Ameghinomya antiqua* (King)–B, Nudibranchia ni, *Eatoniella latina* (Marincovich)–D, *Anthothoe chilensis* (Lesson)–AN, Caprellidae ni–AM, *Anemonia alicemartinae* (Sebens & Paine)–AN, *Acanthocyclus gayi* (Milne Edwards & Lucas)–D, copepod larva, nauplius larvae–CI

cases, occurred as entire individuals, juveniles, or adults in the intestine of larger herbivores (urchins, keyhole limpets, and chitons). All of the remaining animal items (Table 2) appeared in lower frequencies, and the most important were mussels, bryozoans, hydrozoans, amphipods, decapods, snails, foraminifera, and nematodes, which, considered as adult and larval stages, presented a summed occurrence of 40.3%.

Table 3 shows the biomass in gastric contents for a small sample of individuals per species, which, on average, ingested 87.1% (range: 55.0 to 97.8%) of algae and 12.9% (range: 2.2 to 45%) of animals. Notably, some small-sized species such as *Scurria viridula*, *S. ceciliana*, *Siphonaria lessoni*, and *Lottia orbigny* had a much higher proportion of animal bio-

mass than larger species, although quantitatively smaller in absolute terms. In fact, the dry weight of herbivore individuals was positively correlated with the ingested biomass of algae (Spearman's  $r = 0.87$ ,  $p < 0.00001$ ,  $n = 18$ ) and animals (Spearman's  $r = 0.70$ ,  $p = 0.0013$ ,  $n = 18$ ), i.e. larger herbivores eat more and the quantitative importance of animal consumption increases with herbivore size. On the other hand, herbivore weight was highly correlated with the ingested biomass per algal item (Spearman's  $r = 0.86$ ,  $p < 0.00001$ ,  $n = 18$ ), but not per animal item (Spearman's  $r = 0.31$ ,  $p = 0.205$ ,  $n = 18$ ), and this latter value was very high in more than a third of the species irrespective of their size. A 2-way Friedman test did not show significant differences between species ( $Fr = 26.08$ ,  $p =$

Table 3. Biomass of algal and animal items in the gastric content of herbivore individuals, expressed as mg wet weight and percentage of total biomass. BPI: estimation of biomass per algal and animal item (see 'Materials and methods' for calculation details)

Species	Algae		Animals	
	Mean $\pm$ SE (%)	BPI	Mean $\pm$ SE (%)	BPI
<i>Acanthopleura echinata</i>	1812 $\pm$ 390 (95.8)	226.8	79 $\pm$ 47 (4.2)	39.5
<i>Chiton cumingii</i>	30 $\pm$ 13 (80.5)	10.0	7 $\pm$ 5 (19.5)	8.6
<i>Chiton granosus</i>	96 $\pm$ 21 (90.3)	23.1	10 $\pm$ 3 (9.7)	8.9
<i>Enoplochiton niger</i>	1192 $\pm$ 171 (95.9)	174.6	51 $\pm$ 20 (4.1)	34.4
<i>Fissurella costata</i>	228 $\pm$ 164 (97.8)	39.0	5 $\pm$ 4 (2.2)	10.8
<i>Fissurella crassa</i>	338 $\pm$ 131 (87.2)	47.0	50 $\pm$ 27 (12.8)	33.2
<i>Fissurella limbata</i>	130 $\pm$ 28 (94.9)	17.0	7 $\pm$ 2 (5.1)	3.9
<i>Fissurella maxima</i>	1378 $\pm$ 219 (95.8)	203.1	60 $\pm$ 14 (4.2)	38.4
<i>Fissurella picta</i>	1565 $\pm$ 324 (97.1)	200.2	47 $\pm$ 18 (2.9)	24.0
<i>Lottia orbigny</i>	19 $\pm$ 5 (74.7)	4.9	6 $\pm$ 2 (25.3)	5.4
<i>Loxechinus albus</i>	7948 $\pm$ 2758 (97.2)	696.6	225 $\pm$ 27 (2.8)	62.2
<i>Scurria ceciliana</i>	20 $\pm$ 13 (57.6)	6.6	15 $\pm$ 6 (42.4)	38.8
<i>Scurria variabilis</i>	15 $\pm$ 1 (91.7)	3.2	1 $\pm$ 0.3 (8.3)	3.9
<i>Scurria viridula</i>	37 $\pm$ 14 (55.0)	9.6	30 $\pm$ 14 (45.0)	54.6
<i>Siphonaria lessoni</i>	39 $\pm$ 18 (74.4)	9.5	13 $\pm$ 12 (25.6)	43.7
<i>Taliepus dentatus</i>	149 $\pm$ 2 (94.0)	23.3	10 $\pm$ 3 (6.0)	5.6
<i>Tegula atra</i>	394 $\pm$ 131 (91.0)	86.2	39 $\pm$ 12 (9.0)	57.1
<i>Tetrapygyus niger</i>	3278 $\pm$ 1277 (97.6)	415.3	80 $\pm$ 48 (2.4)	2.4

Table 4. Quantitative descriptors characterizing apparent IG predator–IG prey pairwise interactions among herbivores of northern Chile (for full binomial names see Table 1). Some values involving *Scurria* sp. were omitted due to its unresolved specific status. Ov: mean ( $\pm$ SE) diet overlap; BR: body size ratio IG predator/IG prey calculated from mean dry biomass (BRb) and mean maximum length (BRI); BPr: mean ( $\pm$ SE) niche breadth of IG predator; NPr: total number of IG predator individuals; OFPy: occurrence frequency (%) of IG prey

IG predator–IG prey	Ov	BRb	BRI	BPr	NPr	OFPy
<i>A. echinata</i> – <i>T. atra</i>	0.61	3.10	4.99	12.30 $\pm$ 1.52	166	1.20
<i>A. echinata</i> – <i>S. araucana</i>	0.44	62.27	8.50	"	"	0.60
<i>E. niger</i> – <i>L. orbigny</i>	0.11	57.82	7.05	11.55 $\pm$ 0.98	268	0.37
<i>E. niger</i> – <i>Scurria</i> sp.	–	–	–	"	"	0.75
<i>E. niger</i> – <i>T. niger</i>	0.54	1.40	2.31	"	"	0.37
<i>E. niger</i> – <i>T. atra</i>	0.54	3.09	4.54	"	"	0.75
<i>E. niger</i> – <i>S. ceciliana</i>	0.48	227.14	15.12	"	"	0.75
<i>E. niger</i> – <i>S. variabilis</i>	0.56	138.26	8.90	"	"	0.37
<i>F. crassa</i> – <i>F. limbata</i>	0.79	0.75	0.97	10.07 $\pm$ 2.20	194	1.55
<i>F. crassa</i> – <i>F. maxima</i>	0.74	0.59	0.88	"	"	1.03
<i>F. crassa</i> – <i>O. marginata</i>	0.51	411.15	4.61	"	"	0.52
<i>F. crassa</i> – <i>T. atra</i>	0.41	0.91	1.70	"	"	0.52
<i>F. limbata</i> – <i>S. ceciliana</i>	0.47	94.57	5.81	12.89 $\pm$ 1.54	142	0.70
<i>F. limbata</i> – <i>D. nigerrima</i>	0.48	57.56	4.77	"	"	1.41
<i>F. limbata</i> – <i>T. atra</i>	0.60	1.21	1.75	"	"	1.41
<i>F. limbata</i> – <i>Scurria</i> sp.	–	–	–	"	"	0.70
<i>F. limbata</i> – <i>O. marginata</i>	0.58	547.1	4.73	"	"	0.70
<i>F. maxima</i> – <i>P. niger</i>	0.46	42.69	6.04	11.86 $\pm$ 1.28	181	1.10
<i>F. maxima</i> – <i>C. cumingii</i>	0.67	11.02	1.43	"	"	0.55
<i>L. albus</i> – <i>S. variabilis</i>	0.39	119.56	4.06	17.53 $\pm$ 1.77	39	2.56
<i>L. albus</i> – <i>S. ceciliana</i>	0.26	190.97	6.90	"	"	2.56
<i>L. albus</i> – <i>T. atra</i>	0.47	2.52	2.06	"	"	7.69
<i>L. albus</i> – <i>T. niger</i>	0.63	1.21	1.05	"	"	2.56
<i>T. dentatus</i> – <i>T. atra</i>	0.44	0.22	1.34	9.72	10	10.00
<i>T. niger</i> – <i>T. atra</i>	0.43	2.08	1.95	12.81 $\pm$ 0.04	251	1.59
<i>T. niger</i> – <i>Scurria</i> sp.	–	–	–	"	"	0.40
<i>T. niger</i> – <i>S. ceciliana</i>	0.31	157.15	6.53	"	"	1.20
<i>T. niger</i> – <i>D. nigerrima</i>	0.41	98.39	5.36	"	"	0.40
<i>T. niger</i> – <i>P. niger</i>	0.33	58.02	6.15	"	"	0.40

0.0731,  $df = 17$ ) or between algal and animal biomass per item ( $Fr = 3.56$ ,  $p = 0.0593$ ,  $df = 1$ ), but we note that probability values are marginal and ranking procedures diminish the differences among values. Thus, the above results should be considered preliminary and need support from a larger sample. Notwithstanding, Table 3 confirms the consistency of animal consumption by herbivores, and clearly shows that some species may consume animal items with similar or greater intensity than algal items.

### Apparent intraguild predation

Herbivore consumers ingested almost exclusively heterospecific herbivore prey, as the consumption of conspecifics occurred only once in 2671 cases (0.03%; a juvenile black urchin *Tetrapygyus niger*); this behavior was excluded from subsequent analyses due to its extremely low occurrence. Thus, we identified a total of 29 pairs of interspecific herbivore–herbivore interactions (Table 4) involving 19 species, 8 of them appearing as IG predators and 11 as IG prey, although 3 species were recorded in both categories (*Fissurella limbata*, *F. maxima*, *T. niger*). Among IG prey, *Scurria* sp. could not be identified with the available diagnostic characters (Espoz et al. 2004), which forced us to omit some descriptors for this IG prey in Table 4 (we provisionally treated this species as different from those listed in Table 1). The 29 IG predator–IG prey pairs shared food resources to different extents, with mean dietary overlaps ranging from 0.11 to 0.79, and an average ( $\pm SE$ ) dietary overlap of  $0.49 \pm 0.03$  for all

pairs (Table 4). Six IG predator–IG prey pairs had a mean dietary overlap  $\geq 0.6$ , and 4 of these cases involved keyhole limpets (*F. crassa*, *F. limbata*, or *F. maxima*). Notably, the 29 interactions were all taxonomically asymmetrical (no reciprocal predation), and only 3 (10.3%) occurred among taxonomically related species (keyhole limpets: *F. crassa* on *F. limbata* and *F. maxima*; sea urchins: *Loxechinus albus* on *T. niger*). All IG predators (Table 4) were generalist consumers with a large dietary breadth (considering their whole resource spectrum), and only 5 of them (*Enoplochiton niger*, *F. crassa*, *F. limbata*, *L. albus*, and *T. niger*) gave origin to 24 (>80%) of the pairwise interactions.

Adult body size ratios (IG predator/IG prey) were largely asymmetrical both in biomass and length (Table 4), favoring IG predators, with a few exceptions (mainly involving *Fissurella crassa*). Length ratio was a better descriptor of size asymmetry, as biomass ratio produced extremely high values for large IG predators with shells or skeletons (e.g. fissurellids, urchins) eating small IG prey such as the limpets *Scurria* spp. and the shell-less sea slug *Onchidella marginata*. On the other hand, IG prey showed relatively low occurrence frequencies, and the 2 interactions with the highest prey frequencies (*Taliepus dentatus* on *Tegula atra*, *Loxechinus albus* on *T. atra*) involved the 2 IG predators with the smallest sample size, suggesting that their importance may be overestimated.

The above data were separated to represent IGP webs (omnivore links) by community (seasonal data pooled), with the respective occurrence frequencies of IG prey (Fig. 2; links to basal algal species were omitted for clarity). Among all IG predators, only 2 (the chi-

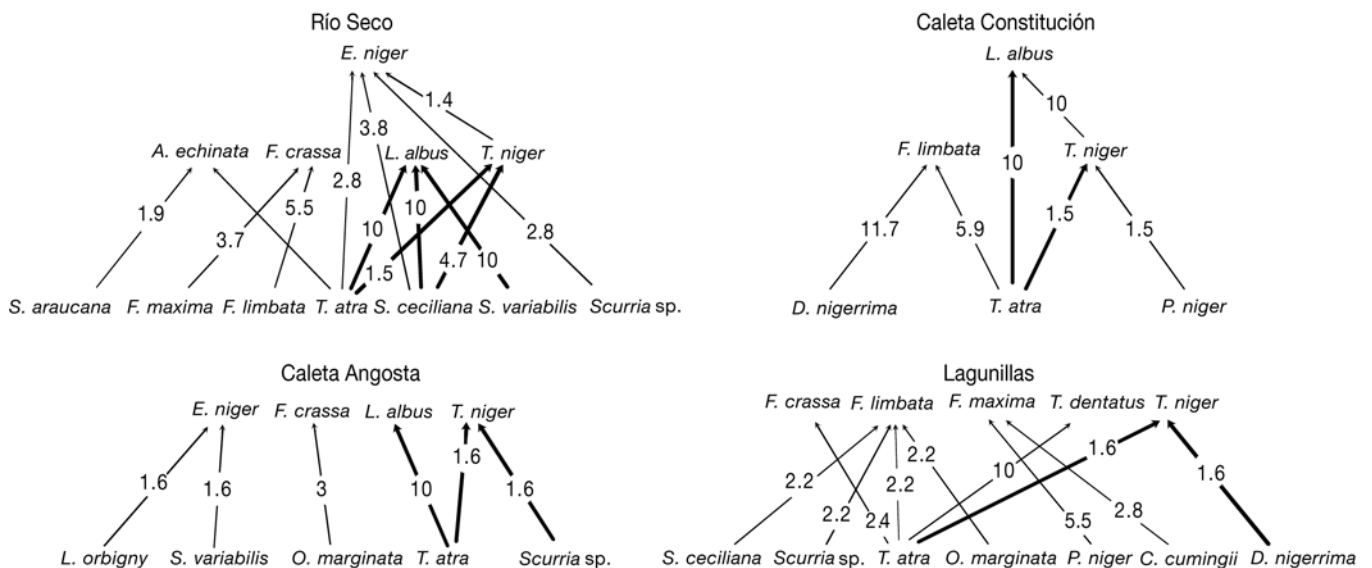


Fig. 2. Intraguild predation subwebs (arrows point to intraguild predators) detected in the 4 study communities: intraguild predation upon juvenile prey only (thin arrows) or both juvenile and adult prey (thick arrows). Numbers on arrows: dietary occurrence frequency (%) of intraguild prey. For full binomial names see Table 1

ton *Enoplochiton niger* in RIO and the urchin *Loxechinus albus* in CCO) appeared at a higher trophic position generating 3-link food chains. In all communities, IG predators were all large-sized species and ate mainly juvenile or small-sized individuals. The proportion of pairwise interactions per community in which IG predators ate only juvenile IG prey was 58.3% in RIO, 66.7% in CCO, 50% in CAN, and 80% in LAG. In addition, from dietary overlap values in Table 4, it follows that each IG predator shared several resources with each of its IG prey, and thus closed loop omnivory was the rule in all food webs represented in Fig. 2.

## DISCUSSION

### Potential for omnivory

The consumption of animals by rocky intertidal herbivores in northern Chile seems a common and widespread phenomenon, and its high frequency justifies a more thorough evaluation of its ecological significance and strength. We highlight the great relative importance of barnacles, particularly the species *Jehlius cirratus* and *Notochthamalus scabrosus*, both of which are common and dominant in northern Chile (Camus & Lagos 1996, Lagos et al. 2005), suggesting that their consumption could be related, in part, to their high abundance and frequency of occurrence on rocky substrata. In contrast, the consumption of a wide variety of items, including planktonic organisms, larval stages, chironomid insects, egg capsules of carnivores, and even some carnivore snails and crabs, was infrequent and diffuse. Likely, the ingestion of such miscellaneous items is a casual phenomenon that would hardly be a source of important indirect effects. In this regard, however, the recurrent consumption of sessile animals, such as mussels and barnacles, has the potential to greatly affect space occupancy patterns, and deserves more attention in future studies. In the same terms, the frequent ingestion of other sessile organisms, such as bryozoans and hydrozoans, could be less important because of their small size, although (as with barnacles and mussels) they cannot be ignored as a potential food source for herbivores. Regardless of interaction strength, nonetheless, the sole existence of true omnivory would be highly significant in autoecological terms.

The potential for omnivory was high and positively related with the body mass of herbivores, as larger species consumed a wider spectrum of food resources and a higher proportion and biomass of animal items. In particular, large chitons, keyhole limpets and urchins appear as strong candidates to display omnivory at least as an opportunistic strategy, and

their joint effect on animal prey may not be negligible. However, smaller species should not be underestimated, as some of them may ingest animals in higher proportion than larger ones, and others may show lower consumption but have very high densities in the field. Thus, the ingestion of animals by the whole herbivore assemblage has the potential to generate community-wide effects involving species' abundances and energy flows, which may be investigated in the same way as for algal prey (e.g. Sala & Graham 2002).

None of the herbivores studied in this work have been assessed with respect to the digestion and assimilation of animal food, probably because they have always been treated as herbivores. Nonetheless, we suggest that our view of intertidal consumers on Chilean rocky shores needs a reappraisal from an energetic and food web perspective, noting that true omnivory and carnivory behaviors have been well documented in urchins (e.g. Hughes et al. 2005), chitons (e.g. Latyshev et al. 2004), and fissurellids (e.g. Grall et al. 2006) from other regions. In particular, the consumption of animals by Chilean fissurellids such as *Fissurella crassa* and *F. maxima* has long been recognized (Santelices & Correa 1985, Santelices et al. 1986, Osorio et al. 1988), and our data confirm that this is a consistent phenomenon. For instance, *F. picta* in southern Chile consumes a nearly constant proportion of 30 to 35% of invertebrates throughout the year (López et al. 2003), very similar to our records in northern Chile (~30%) and to those observed in some true omnivores on other coasts (e.g. Cannicci et al. 2002). In fact, *Fissurella* species are efficient in consuming rough and hard materials (Santelices et al. 1986, Osorio et al. 1988), and exhibit a high capability to discriminate and select food items (Franz 1990a,b), but, in some cases, they cannot digest cellulose and agar (Ward 1966), suggesting some constraints to maintaining a strictly herbivorous diet. In this context, we recently performed physiological assays on 3 of our study species (*F. maxima*, *F. picta*, *Chiton granosus*) fed with mussel tissue, finding proteolytic digestion and assimilation of food to different extents (Camus et al. unpubl. data), although more detailed studies must be conducted for confirmation. Intertidal herbivores may thus be more complex consumers than previously thought, and an active search for true omnivory behavior among these species would help to establish their functional role with accuracy.

On general grounds, recent assessments of aquatic and terrestrial systems (e.g. Beaudoin et al. 2001, Link 2002, Arim & Marquet 2004, Vadas 2004, Bode et al. 2006, Thompson et al. 2007; but see Williams & Martinez 2004), suggest that omnivory is common in real food webs. In this respect, all members of the herbivore trophic level in this study consumed prey at more than



one trophic level, and trophic omnivory has been shown to be frequent among other intertidal consumers such as fish (e.g. Muñoz & Ojeda 1997), birds (e.g. Hori & Noda 2001), and non-herbivorous invertebrates (e.g. Navarrete et al. 2000). Thus, the prevalence of omnivory could be high across the whole rocky intertidal food web, independent of its significance with regard to food web stability or top-down and bottom-up cascading effects.

### Apparent intraguild predation

Our data suggest that, even in the absence of true omnivory, indirect effects derived from apparent IGP could be potentially important among herbivore populations. However, if some of our study species were true omnivores and/or true IG predators, both their role and trophic position should be entirely reconsidered. A higher incidence of IGP may have several implications for the structure and stability of intertidal food webs (Arim & Marquet 2004), derived from the introduction of longer food chains, new links, and closed omnivore loops. For instance, each of the 8 IG predators were connected with at least 83 food items (including IG prey) of varying trophic positions, and they were in turn consumed by a high number of top and intermediate carnivores, such as gastropods, crabs, seastars, fishes, birds, otters, and rodents (e.g. Soto 1996, Muñoz & Ojeda 1997, 1998, Fariña et al. 2003). Conversely, our ongoing research on the northern Chilean food web shows that keystone predators, such as the carnivorous sunstar *Heliaster helianthus* (Lamarck), consume all our IG predators, except *Taliopus dentatus* (Camus et al. unpubl. data). Thus, the studied IG predators are highly connected species, strongly linked to basal organisms, participating in a high number of closed loops involving other herbivores, and linked to a number of higher level consumers including top and intermediate predators. In addition, IG predators are involved in the interplay between bottom-up and top-down processes, when food web directionality becomes a crucial aspect (Borer et al. 2002). Key herbivores such as *Loxechinus albus* and most *Fissurella* species are heavily collected by coastal food-gatherers (Oliva & Castilla 1986, Fernández & Castilla 2005), and reduction of that pressure might not only increase their connectivity, but also trigger structural changes in the food web (e.g. see Vasas et al. 2007). On the other hand, the high connectivity of the studied species is partially an expected by-product of more intensive samplings and diet analyses (as pointed out by Polis 1991 and Link 2002), but the importance of the contributed links will depend on their nature and strength. Most IG predator–IG prey

interactions showed quantitatively low importance in terms of consumption frequency of IG prey, as compared, for instance, with the consumption of barnacles. However, weak links could promote community stability (McCann et al. 1998, Neutel et al. 2002), and any IG predator–IG prey link would be important if it turns out to be a real pathway for energy and nutrient acquisition. In this context, 2 of our results remain intriguing: the complete taxonomical asymmetry of IG predator–IG prey interactions and the absence of self-consumption. Such a pattern was not expected to arise from purely incidental consumption by herbivores, where at least part of their ingested prey should be incorporated at random, including conspecific juveniles. The above suggests that apparent IGP may not be a side-effect of grazing, and thus leaves the possibility open that some IG predators may discriminate among IG prey, avoiding the consumption of conspecifics, while they clearly do not avoid heterospecifics. (However, we do not suggest that IG predators pursue, attack, or capture their prey as do some true carnivorous predators.)

Additionally, as observed in some lotic systems (Lancaster et al. 2005), it is possible that herbivores are forced to use or even select animal prey during periods of strong resource limitation, increasing the incidence of polyphagy and apparent IGP. In this regard, our study period included the complete development of a weak El Niño event (August 2004 to March 2005; CPC 2007), when algal resources are likely to diminish due to nutrient limitation (Thiel et al. 2007). However, polyphagy and apparent IGP occurred at all study sites, although 2 of them (CCO, LAG) could sustain a higher nutrient loading and algal productivity due to the persistent influence of upwelling, even during El Niño periods (Thiel et al. 2007). Therefore, polyphagy and apparent IGP may be part of the normal feeding behavior of herbivores, rather than a consequence of resource limitation.

For our study communities, we should conclude that the apparent IGP itself is probably weak in terms of per capita effects, but it is relatively common and potentially significant in the face of true omnivory. In such a context, eating at more than one trophic level or ingesting plants and animals appear to be necessary but not sufficient conditions to define omnivory, as they do not clarify the distinction between eating and feeding. We also note that the high connectedness and trophic diversity of the studied assemblage were, as envisaged by Polis (1991), inevitable by-products of improving the resolution of dietary analyses and the intensity of samplings (see also Hall & Raffaelli 1991, Link 2002). Thus, our data show that rocky intertidal food webs may indeed have a high degree of connectivity, long food chains, and a widespread occurrence

of polyphagy and loops, which are not necessarily different or more complex than those of other marine or non-marine systems (see Dunne et al. 2004, Thompson et al. 2007). In addition, the studied herbivores seem far from being equivalent members of a single trophic level, and we would clearly misjudge their role in bottom-up processes by simply considering them primary consumers.

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