

Feeding selectivity of the herbivorous fish *Scartichthys viridis*: effects on macroalgal community structure in a temperate rocky intertidal coastal zone

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ABSTRACT: The ecological importance of fish herbivory was examined in a temperate rocky intertidal zone along the central Chilean coast. In this system, the blenny *Scartichthys viridis* is the most abundant and only herbivorous fish. We describe its diet, determine its field food selectivity (gut contents vs macroalgal field availability comparison), and report on its laboratory dietary preferences in a multiple-choice feeding experiment. Finally, we evaluate the relative effects of fish herbivory and grazing invertebrates on macroalgal abundance, distribution and diversity patterns in the field, using replicated exclusion cages to manipulate grazing intensity. *S. viridis* was found to be a selective grazer; its diet was dominated by 2 macroalgae: the green *Ulva* and the red *Gelidium*, representing 32.6 and 41.4% of its total gut content biomass, respectively. *Ulva* was consumed much above its field availability while *Gelidium* was selected only during fall-winter. In the laboratory, *S. viridis* selected the green macroalgae *Ulva rigida* and *Codium dimorphum* and avoided *Gelidium chilense*. We suggest that *Gelidium* may be included in its diet due to the limited availability of *Ulva* in the field. Experimental exclusion of this fish from rocky surfaces resulted in increased abundance of green foliose macroalgae (*U. rigida* and *Enteromorpha linza*), and, to a much lesser extent, of the red foliose macroalgae *G. chilense*, *Porphyra columbina*, and *Mazzaella laminarioides*, and of the brown macroalgae *Colpomenia phaeodactyla* and *Petalonia fascia*, as well as an extension of the distribution of *P. columbina* from the high intertidal to the mid intertidal zone, where it normally does not occur. Exclusion of grazing invertebrates resulted in a decrease in foliose macroalgal species richness, but had no effect on biomass. To our knowledge, this is the first experimental demonstration of the effect of an herbivorous fish on macroalgal community structure in a temperate rocky intertidal area. The selective feeding displayed by *S. viridis*, its high numerical abundance, and the results of the herbivore exclusion experiment suggest its importance in maintaining the low abundance of foliose macroalgae and the high relative cover of brown and red crustose macroalgae, characteristic of many low to mid rocky intertidal areas along the coast of central Chile.

KEY WORDS: Herbivorous fish · Temperate waters · Rocky intertidal · Macroalgae community structure · Feeding selectivity · Fish grazing

INTRODUCTION

The importance of herbivorous fishes in tropical marine waters has been extensively documented in the last 40 yr (Horn 1989, Choat 1991). In these environ-

ments, this group has been shown to play a major role in shaping the abundance, distribution and diversity patterns of macroalgal assemblages (e.g. Randall 1961, John & Pople 1973, Ogden & Lobel 1978, Lubchenco & Gaines 1981, Lewis 1986, Hixon & Brostoff 1996, Ferreira et al. 1998, Miller & Hay 1998).

In contrast, and based on ecophysiological and biogeographical considerations, it has been proposed that herbivorous fishes are rare in temperate waters, and consequently of minor ecological importance in deter-

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mining macroalgal community structure (Quast 1968, Lubchenco & Gaines 1981, Choat 1982, Horn 1989, Ebeling & Hixon 1991). The effects of herbivory on macroalgal abundance, distribution and diversity patterns in temperate rocky subtidal and intertidal areas have almost always been ascribed to grazing invertebrates such as gastropods and sea urchins (e.g. Paine & Vadas 1969, Lubchenco 1978, Underwood & Jernakoff 1984, Contreras & Castilla 1987, Metaxas & Scheibling 1993).

Recent studies, however, indicate that herbivorous fishes are important components of littoral fish assemblages in temperate waters (Choat & Clements 1992, Barry & Ehret 1993, Cáceres et al. 1994, Horn & Ojeda 1999), which in turn suggests that their ecological role may have been underestimated. Further, the effects of herbivorous fishes on macroalgae have been shown in the few instances and places where they have been investigated in temperate subtidal waters (Foster 1975, Harris et al. 1984, Andrew & Jones 1990, Sala & Boudouresque 1997, but see Jones 1992). Nevertheless, similar studies have not been undertaken in temperate intertidal areas.

The paucity of studies investigating the effects of herbivorous fishes in temperate waters is striking if one considers that many of them have been shown to be highly selective in their feeding habits (e.g. Horn et al. 1982, 1990, Barry & Ehret 1993, Cáceres et al. 1994, Horn & Ojeda 1999), with most preferring green and red foliose macroalgae over brown, encrusting and calcareous macroalgae. It follows that, if their numerical abundance in these habitats were also found to be high, their marked feeding selectivity could be an indication of them having a major role in determining macroalgal community structural patterns. Therefore, there is an essential need to investigate concurrently feeding habits, diet selectivity and effects of herbivorous fishes on macroalgal abundance, distribution, and diversity patterns in temperate marine habitats, and especially rocky intertidal areas.

Preference for different macroalgal species by temperate marine herbivorous fishes has been explained by a number of factors, including: temporal and spatial variation in food availability (Horn et al. 1986, Cáceres et al. 1994), food quality in terms of energy and nutrient contents (Montgomery & Gerking 1980, Horn et al. 1982, 1986, 1990), and presence of chemical deterrent compounds and toughness (Littler & Littler 1980, Hay et al. 1988, Hay & Fenical 1992). Based on an analysis of ash, energy, and nutrient content, as well as digestibility, Montgomery & Gerking (1980) concluded that green macroalgae were better food than red macroalgae, and red were better than brown macroalgae.

In this study, we concurrently determined the feeding habits and field and laboratory food selectivity of

the Chilean comb-tooth blenny *Scartichthys viridis* and evaluated its effects on macroalgal abundance, distribution and diversity patterns in a rocky intertidal site on the temperate coast of central Chile. This species is the most abundant and only herbivorous fish species inhabiting rocky intertidal areas along the Chilean central coast (Muñoz & Ojeda 1997), representing over 18% of the total number of fish individuals in 18 species collected in the last 8 yr (Ojeda unpubl. data). *S. viridis* has been reported to be a grazer (Stepien 1990, Muñoz & Ojeda 1997), consuming both green and red macroalgae. Nevertheless, nothing is known about its dietary preferences when offered a choice of different macroalgae or how its diet relates to the field availability of different algae.

Our aims were to: (1) describe the diet of *Scartichthys viridis* in detail; (2) determine its food selectivity in the field by comparing gut contents with field availability of macroalgae; (3) report on its laboratory dietary preferences in a multiple-choice feeding experiment; and (4) evaluate and compare the relative effects of this fish and grazing invertebrates on macroalgal abundance, distribution and diversity patterns, using replicated exclusion cages, in a rocky intertidal site in central Chile.

We hypothesized that *Scartichthys viridis* would select green foliose macroalgae over red and brown foliose species in the field and laboratory due to their reported greater energy and nutrient content. Secondly, due to the high abundance of this fish herbivore in the studied system, if green macroalgae were preferred over others, we hypothesized that the exclusion of herbivorous fish would result in a significant increase over time in the abundance of these macroalgae and not of non-selected algal species. Finally, we predicted a significantly greater growth of green foliose species in the fish exclusion cages in comparison to the control (no exclusion).

METHODS

Fish collections. We collected fish in rocky intertidal areas at 3 localities along the central Chilean coast: Las Cruces (33° 30' S, 71° 38' W), El Tabo (33° 27' S, 71° 37' W), and Los Molles (32° 14' S, 71° 32' W), either by hook and line fishing, or with hand nets and snorkels aided by a Benzocaine-96° alcohol solution or Rotenone (75 to 100 ml m⁻³) from March 1994 to April 1995. We captured fish from both tidepools and intertidal channels. We placed all captured fish in labeled plastic bags and transported them frozen to the laboratory, where they were stored at -18°C. In the laboratory, each specimen was thawed, measured to the nearest mm (total length = TL), and weighed to the nearest 0.01 g.

Dietary analyses and field feeding preferences.

Stomachs and intestines were cut open and gut contents removed. The gut contents were then subjected to a quick wash with tap water and were sorted; food items were identified to genus level. Identification to species level was not possible in some cases because the food items were partially digested. Each item was damp-dried on paper towel and wet weighed with 1 mg accuracy. The relative importance of each item in the diet was expressed as percentage frequency of occurrence (%FO), and percentage of the total biomass of food (%W). We used plots of cumulative Shannon (H') gut content diversity (which were calculated from values of %W), to determine adequate sample size as in Muñoz & Ojeda (1998). Cumulative diversity values were calculated by combining groups of samples (digestive tracts) ranging from 1 to all guts examined, and plotted against the number of guts combined. We considered sample size to be adequate when gut content diversity stabilized. Adequate sample size was found to be between 25 and 30 specimens. We evaluated seasonal dietary changes using Kendall's Rank Correlation test (Siegel & Castellan 1988). In this study, macroalgae are defined as kelp, small and turfing foliose species, and crustose forms (Hoffmann & Santelices 1997).

We determined field diet selectivity of *Scartichthys viridis* twice, fall-winter 1994 and spring-summer 1994-95, at Las Cruces by comparing gut contents of individuals caught at Las Cruces with the abundance of macroalgae found in the area of the intertidal zone where fish were collected. This was done by sampling all macroalgae found within fifteen 20 × 20 cm quadrats placed along a transect on one of the walls of an intertidal channel, which was perpendicular to the shore line. We stationed quadrats 1 m apart, and just above the water level at low tide. The channel was approximately 30 m long and 2 to 3 m wide.

In the laboratory, we analyzed the samples in the same manner as the gut contents. The relative importance of each macroalgal genus was expressed as the percentage of total available macroalgal biomass (%W). Adequate sample size was found to be between 8 and 12 quadrats.

We used the Linear Resource Selection Index (L in Strauss 1979) to assess preferences of *Scartichthys viridis* for the different macroalgae found in the field. This index is based on the relationship $L = r_i - p_i$, where L is the measure of preference, i = macroalgal taxon, r = relative utilization of different macroalgae (as found in the gut contents), and p = overall field proportional availability of that food type, with r and p each expressed as %W. Index values range from -1 to +1, with negative values indicating non-preference (avoidance) and positive values indicating preference.

Laboratory prey choice experiments. Preference for different macroalgal species was evaluated through multiple-choice feeding experiments, which were carried out at the Coastal Marine Research Station (ECIM) of the P. Universidad Católica de Chile at Las Cruces during July-August 1995 (winter). We collected live specimens from tidepools using the anesthetic BZ 20 (Veterquímica, Chile).

To test the null hypothesis that *Scartichthys viridis* preys equally on different macroalgal species, we used 8 groups of fish (7 to 21 cm TL), each consisting of 3 similarly sized individuals. Groups of 3 individuals were used because, in preliminary experiments, we found that isolated fish seldom fed. Each group of 3 fish was considered 1 replicate. Fish were acclimated, without food, for 1 wk in 180 l aquarium tanks (1 group aquarium⁻¹), with circulating sea water at 8 to 10°C (winter mean sea water temperature) and constant aeration, before we initiated the experiments. Protective refuges were provided by PVC tubing.

At the start of the experiments, we offered each group similar amounts (approximate biomass) of the 7 most abundant species of macroalgae present at Las Cruces (the green *Ulva rigida*, *Enteromorpha linza*, and *Codium dimorphum*; the brown *Colpomenia phaeodactyla*; and the red *Corallina officinalis*, *Gelidium chilense* and *Mazzaella laminarioides*) (Hoffmann & Santelices 1997, Muñoz pers. obs.). With the exception of *M. laminarioides*, all these species were found, to a greater or lesser extent, in the gut contents of *Scartichthys viridis*. Each macroalgal species was offered attached to its original rock piece because preliminary experiments showed that *S. viridis* did not eat artificially attached macroalgae (e.g. attached to plastic rods via rubber bands) due to the nature of its feeding mechanism, i.e. grazing. The 7 rock pieces, each with 1 macroalgal species attached, were randomly placed, forming a circle at the center of the aquarium, each piece separated from the next by approx. 5 cm. We recorded the feeding activities of each group for 1 h, using a Canon L1 8 mm video camera placed on a tripod. We later counted the number of bites on each macroalgal species and analyzed the results for significant differences.

Preference rankings (order of choice) among groups of fish for the different macroalgal species offered were calculated and statistically compared through Kendall's coefficient of concordance (W) to test for homogeneity of choice (Siegel & Castellan 1988). We did not detect statistical differences among the 8 groups of fish with regards to the order (rankings) of their preferences ($W = 0.82$, $p < 0.01$). Having established that the among-group selectivities did not differ, we tested the null hypothesis of equal preference for the different macroalgae using Friedman's test (Zar

1996), which may be used when samples are not independent (Conover 1981), thus taking into account the recommendations made by Peterson & Renaud (1989) and Roa (1992) for prey selectivity experiments, and where the normality requirement is not met.

For the null hypothesis to be rejected at the level of $\alpha = 0.05$, the Friedman test statistic, T_2 has to exceed the F distribution value with $k_1 = k - 1$ and $k_2 = (b - 1)$ ($k - 1$) degrees of freedom, where k = number of species of macroalgae offered (7) and b = number of groups of fish tested (8). *A posteriori* multiple comparisons were made if equal preference was rejected (Conover 1981, p. 300).

Fish and invertebrate herbivore exclusion cage experiment. We conducted an herbivore exclusion experiment in a large (0.5 ha) area in a rocky mid-intertidal zone at Las Cruces from December 1995 to May 1996 in which we selectively excluded fish from some

rocky surfaces and invertebrates from others, in order to examine separately the impact of fish and invertebrates on macroalgal abundance, diversity and distribution. This area consisted of channels, formed by heterogeneous, broken rocky outcrops and large stable boulders, which were completely covered by water during high tides and isolated from the sea at low tides. These channels are very common in rocky intertidal areas along the central Chilean coast. The rocky surfaces of vertical walls, large and small boulders, as well as platforms at this study site were largely bare of foliose macroalgae such as *Ulva rigida*, *Gelidium chilense*, *Ceramium* spp., *Colpomenia phaeodactyla*, *Mazzaella laminarioides*, *Porphyra columbina* and *Enteromorpha linza*. Instead, the rocky surfaces were mostly covered by crustose red and brown macroalgae (e.g. *Hildenbrandia lecanellieri* and *Ralfsia confusa*).

Table 1 *Scartichthys viridis*. Gut contents of 115 specimens collected in rocky intertidal areas on the central Chilean coast, 1994–95. The importance of each item is expressed as: frequency of occurrence in the digestive tracts (FO), percentage of FO (%FO), total biomass (W) in g, and percentage of total food biomass (%W)

Food item	FO	%FO	W (g)	%W
Macroalgae				
Chlorophyta				
<i>Chaetomorpha</i>	16	13.9	0.059	0.1
<i>Cladophora</i>	6	5.2	0.009	<0.1
<i>Codium</i>	10	8.7	0.269	0.6
<i>Enteromorpha</i>	86	74.8	1.527	3.6
<i>Rhizoclonium</i>	1	0.9	0.001	<0.1
<i>Ulva</i>	93	80.9	13.977	32.6
Phaeophyta				
<i>Colpomenia</i>	15	13.0	0.404	0.9
<i>Ectocarpus</i>	4	3.5	0.004	<0.1
<i>Giffordia</i>	4	3.5	0.011	<0.1
<i>Glossophora</i>	1	0.9	0.003	<0.1
<i>Halopteris</i>	18	15.7	0.067	0.2
<i>Petalonia</i>	3	2.6	0.051	0.1
<i>Pilayella</i>	2	1.7	0.002	<0.1
<i>Ralfsia</i>	17	14.8	0.837	2.0
Rhodophyta				
<i>Acrochaetium</i>	2	1.7	0.022	<0.1
<i>Ahnfeltia</i>	6	5.2	0.041	<0.1
<i>Ceramiales</i> ^a	68	59.1	3.031	7.1
<i>Corallina</i>	19	16.5	0.678	1.6
<i>Dendrymenia</i>	1	0.9	0.068	0.2
<i>Gastroclonium</i>	18	15.7	0.251	0.6
<i>Gelidium</i>	56	48.7	17.737	41.4
<i>Plocamium</i>	2	1.7	0.002	<0.1
<i>Rhodomenia</i>	3	2.6	0.181	0.4
<i>Schottera</i>	9	7.8	0.153	0.4
Unidentified macroalgae	31	27.0	0.380	0.9
Total macroalgae	100	87.0	39.675	92.8
Invertebrates	68	59.1	3.063	7.2

^aCeramiales genera in decreasing order of abundance: *Herposiphonia*, *Ceramium*, *Centroceras*, *Pterosiphonia*, *Heterosiphonia*, *Polysiphonia*, and *Antithamnion*

Visual observations at the study site showed that the abundance of *Scartichthys viridis* was fairly high, with an estimated density of 1 individual per 4 m². Omnivorous fishes, such as the browser *Girella laevis*, are largely absent, being found only in high intertidal rockpools. The herbivorous sea urchins *Tetrapygus niger* and *Loxechinus albus* are rare in this area, with only a few individuals occurring in nearby tidepools. Grazing limpet gastropods (e.g. *Fissurella crassa* and *Collisella cecilians*), measuring 20 to 40 mm in shell length, were found at densities ranging from 5 to 10 ind. m². Tiny littorinid *Littorina araucana* individuals (1 to 3 mm) occurred as aggregates inside crevices. A few chitons *Chiton granosus* were present at a density of about 1 individual per 10 m² and measuring 8 to 10 cm in length. Barnacles *Jehlius cirratus* and *Chthamalus scabrosus* occurred in small patches covering not more than 5 % of the rocky surfaces.

We applied 4 experimental treatments, which were each replicated 10 times. These treatments consisted of (1) fish exclusion, (2) invertebrate exclusion, (3) 'cage-roof' control, and (4) control (no exclusion). The 2 exclusion and the cage-roof control treatments used replicated cages that had 25 × 25 × 20 cm stainless steel frames totally or partially (depending on treatment, see below) covered with 8 mm galvanized chicken wire mesh, and treated with anti-fouling and anti-oxidant paints. We fixed each cage on approximately flat 25 × 25 cm rocky surfaces with 8 cm screws at each cage corner. The fish exclusion treatment cages allowed access to limpet gastropods and other small invertebrates through 2 cm high spaces in the mesh at the bottom of the sides, while preventing the entry of fish. Therefore, only the effect of excluding fish was evaluated through these cages. The sides of the invertebrate exclusion cages were completely covered with wire mesh, but no roof was added; thus herbivorous invertebrates were prevented from entering and fish were allowed access from above (height 20 cm). Therefore, only the effect of excluding herbivorous invertebrates was evaluated through these cages. A cage-roof control treatment evaluated potential caging artefacts, such as light reduction and water retention effects. The cages used in this treatment consisted of the same stainless steel frames, with the roof but not the sides covered with galvanized chicken wire, thus allowing access to both fish and invertebrates. Ten fairly flat control rocky substrata were also randomly chosen; these were demarcated with screws at each corner. Percentage cover of foliose macroalgae initially did not exceed 5 % and canopy height was 3 to 5 mm (volume < 15 cm³ surface⁻¹); these were similar for all experimental and control substrata. As mentioned above, cover consisted mostly of brown and red crustose macroalgae.

We monitored each cage and control every 2 wk for 150 d. Foliose macroalgal cover and canopy height were measured by using the point-intercept method (100 points) and a vertical ruler randomly placed at 10 points inside the quadrat, respectively. Percentage cover was transformed into area (cm²) and multiplied by mean canopy height, resulting in an estimate of macroalgal volume (cm³). We used macroalgal volume in the analyses because it is more representative of the abundance of foliose macroalgae than percentage cover alone. We analyzed temporal changes in macroalgal abundance among treatments using a 1-way repeated measures ANOVA, after testing for normality using the Shapiro-Wilks test (Zar 1996). Foliose macroalgal diversity also was recorded during each monitoring event, estimated as the number of species present.

RESULTS

Diet

A total of 115 *Scartichthys viridis* specimens, ranging in size from 40 to 302 mm TL, with a mean ± 1 SD = 147 ± 69 mm, were analyzed. Mean biomass of these fish was 75.67 ± 97.44 (1 SD) g, ranging from 0.50 to 394.05 g.

Macroalgae represented almost 93 % of the total food biomass found in the gut contents of *Scartichthys viridis* (Table 1). Only 8 of the 115 fish had empty guts, and 100 (87 %) contained macroalgae. Thirty macroalgal genera were identified, including 6 Chlorophyta, 8 Phaeophyta and 16 Rhodophyta. Two genera formed the bulk of the total gut contents. In terms of percentage biomass, these were the turf-forming red macroalga *Gelidium* (41.4 %) and the green sea lettuce *Ulva* (32.6 %). In terms of percentage frequency of occurrence, the most common items were *Ulva* (found in 80.9 % of guts examined), the green *Enteromorpha* (74.8 %), various red macroalgae belonging to the order Ceramiales (which lumped together were found in 59.1 % of guts), and *Gelidium* (48.7 %). Brown macroalgae, in comparison to the red and green macroalgae, were unimportant in terms of percentage biomass and frequency of occurrence (Table 1).

Animal gut contents represented only 7.2 % of the total biomass and consisted of tiny amphipods, gastropods and bivalves, which live associated with the macroalgal turf. Almost all guts analyzed contained inorganic sediment, representing about 2 to 5 % of the volume of the gut contents. Diatoms and detritus also contributed, to a small degree, towards this fish's diet, together forming approximately 5 to 10 % of the volume of the gut contents. Nevertheless, the importance

of these items is difficult to quantify gravimetrically as they were always mixed with partially digested macroalgal food items. No seasonal dietary differences were found at Las Cruces (Kendall's Rank Correlation test, $T = 0.75$, $p < 0.05$) or at Los Molles ($T = 0.8$, $p < 0.05$). At El Tabo, fish were collected during spring-summer only.

Field feeding preferences

The different species of macroalgae making up most of the biomass at the study site were not consumed in proportion to their relative percentage availability in the field in either of the 2 seasons (Table 2). *Ulva* was selected during both fall-winter and spring-summer ($L = 0.10$ and 0.16 , respectively). *Gelidium* also was consumed preferentially during fall-winter ($L = 0.20$), and during spring-summer it was taken in proportion to its field availability (Table 2). On the other hand, *Codium*, *Gastroclonium*, and *Corallina* were rejected, whereas the rest of the genera were consumed in similar proportion to their field availability (e.g. order Ceramiales). The only species of *Ulva* and *Codium* present in our study site were *U. rigida* and *C. dimorphum*; more than 80% of *Gelidium* corresponded to *G. chilense*, the rest being *G. linguatum*.

Table 2. *Scartichthys viridis*. Field food selectivity in a rocky intertidal area at Las Cruces, central Chile, estimated using the Linear Resource Selection Index (L in Strauss 1979), based on percentage field availability and percent contribution to its diet, of the 7 most abundant macroalgal genera in its gut contents during fall-winter 1994 and spring-summer 1994-95. Values range from +1 to -1, indicating maximal to minimal preference, respectively. C = Chlorophyta, P = Phaeophyta, R = Rhodophyta

Macroalgae	Contribution to diet (% wet biomass)	Field availability (% wet biomass)	Selectivity (L)
Fall-winter 1994			
<i>Gelidium</i> (R)	51.6	31.2	0.20
<i>Ulva</i> (C)	31.9	21.7	0.10
Ceramiales (order, R)	6.6	12.5	-0.06
<i>Ralfsia</i> (P)	2.6	0.1	0.03
<i>Corallina</i> (R)	1.9	11.5	-0.10
<i>Colpomenia</i> (P)	1.2	0.1	0.01
<i>Codium</i> (C)	0.8	22.4	-0.22
Spring-summer 1994-95			
<i>Gelidium</i> (R)	46.8	43.5	0.03
<i>Ulva</i> (C)	36.8	20.0	0.16
Ceramiales (order, R)	7.7	4.8	0.03
<i>Enteromorpha</i> (C)	2.4	0.1	0.02
<i>Corallina</i> (R)	2.3	15.9	-0.14
<i>Gastroclonium</i> (R)	0.8	11.1	-0.10
<i>Halopteris</i> (P)	0.6	0.4	<0.01

Table 3. *Scartichthys viridis*. Mean feeding rate (number of bites per hour) of 8 replicate groups (each consisting of 3 individuals) on 7 macroalgal species offered during multiple-choice trials, each 1 h long. Preferences for macroalgal species sharing a common letter were not significantly different (Friedman's test)

Macroalgal species	Division	Feeding rate (mean \pm 1 SE)	p < 0.05
<i>Ulva rigida</i>	Chlorophyta	167 \pm 28	a
<i>Codium dimorphum</i>	Chlorophyta	80 \pm 27	b
<i>Enteromorpha linza</i>	Chlorophyta	20 \pm 4	b c
<i>Colpomenia phaeodactyla</i>	Phaeophyta	10 \pm 2	c d
<i>Corallina officinalis</i>	Rhodophyta	7 \pm 1	d e
<i>Gelidium chilense</i>	Rhodophyta	6 \pm 2	e f
<i>Mazzaella laminarioides</i>	Rhodophyta	2 \pm 1	f

Laboratory prey choice experiments

Scartichthys viridis individuals strongly preferred (or avoided) certain macroalgal species in the multiple-choice feeding experiments, rejecting the null hypothesis of equal preference (Friedman test, $T_2 = 29.79$, $p < 0.05$; Table 3). All groups tested preferred green over red or brown macroalgae. Mean feeding rate (number of bites per hour) on the green macroalga *Ulva rigida* (167 \pm 28, 1 SE) was significantly greater than that on the other 6 species offered (Table 3). The green macroalgae *Codium dimorphum* and *Enteromorpha linza* were the next most preferred items, while all other species offered (both red and brown macroalgae) were noticeably avoided. Interestingly, the red macroalga *Gelidium chilense* was one of the least preferred species (6 \pm 2 bites h⁻¹, Table 3).

Fish and invertebrate herbivore exclusion cage experiment

The cages were effective in excluding either fish or invertebrates. Field observations during high tide from platforms next to the channels and at different times during the running of the experiment showed that *Scartichthys viridis* swimming in the vicinity did not enter the fish exclusion cages. On only 2 occasions were individual limpets found in the invertebrate exclusion cages (1 limpet in 2 different replicate cages, at Days 90 and 105); they were removed when found. As expected, limpets were found inside the fish exclusion cages, and *S. viridis* inside the invertebrate exclusion cages.

Fish exclusion produced significant changes in foliose macroalgal abundance, which rapidly increased on the surfaces, reaching a maximum (mean = 7300 cm³; Fig. 1a) at 75 d. Significant differences in the amount (volume) of foliose macroalgae among treatment and through time were detected (1-way repeated measures ANOVA: effect of treatment, $F_{3,37} = 12.883$, $p < 0.01$; effect of time, $F_{10,370} = 4.235$, $p < 0.01$). Macroalgal volume within fish exclusions differed significantly from that which developed under the other 3 treatments (invertebrate exclusion, cage-roof control and control), (*a posteriori* Tukey test: $p < 0.01$), which, in turn, did not differ from each other ($p > 0.05$). The fact that total macroalgal growth did not differ between the control and the cage-roof control suggests that caging artifacts were unlikely to have been present.

The volume of green foliose *Ulva rigida* and *Enteromorpha linza* rapidly increased in the fish exclusion cages, reaching a maximum (mean = 2500 cm³; Fig. 1b) at 60 d. The percentage cover of these macroalgae approached 100%, and canopy height was over 8 cm on some surfaces. In contrast, no consistent increase was detected where invertebrates were excluded or under the cage-roof treatment or control (no herbivores excluded) (Fig. 1b). Significant differences in the amount (volume) of green macroalgae present under the different treatments and through time were detected (1-way repeated measures ANOVA: effect of treatment, $F_{3,37} = 20.578$, $p < 0.01$; effect of time, $F_{10,370} = 5.392$, $p < 0.01$). The volume of green macroalgae that developed where fish were excluded differed significantly from that which appeared under the 3 other treatments (*a posteriori* Tukey test: $p < 0.01$), which in turn did not differ from each other ($p > 0.05$).

Although the volume of red and brown foliose macroalgae also increased on some of the fish exclusion surfaces, there was a delay in their growth in comparison to green macroalgae (Fig. 1c). These consisted of the red macroalgae *Gelidium chilense*, *Porphyra columbina*, and *Mazzaella laminarioides* and the brown macroalgae *Colpomenia phaeodactyla* and *Petalonia fascia*. The abundance of these species started to increase in the fish exclusion surfaces after 15 to 30 d, representing a tiny fraction (<1%) of the total foliose macroalgal volume present, and peaked after 75 d with a mean of 700 cm³ (Fig. 1c). A number of *P. columbina* fronds reached >14 cm in height. The brown *C. phaeodactyla* occurred only on the fish exclusion surfaces, and only *Ulva rigida* grew within invertebrate exclusions. No significant differences were detected in the volume of brown and red foliose macroalgae among the fish exclusion, cage-roof control and control treatments (1-way repeated measures ANOVA: effect of treatment, $F_{2,27} = 1.073$, $p = 0.35$;

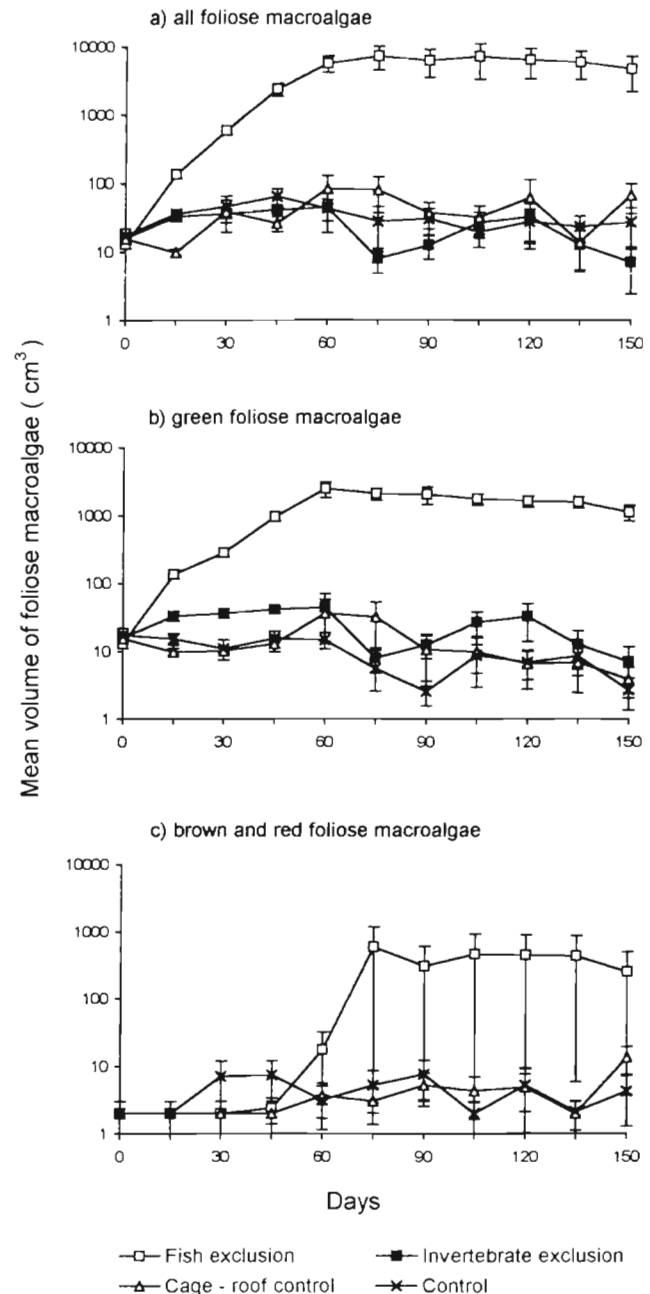


Fig. 1. Abundance (volume) of foliose macroalgae (mean \pm 1 SE) through time on rocky surfaces in a mid intertidal area in central Chile, under 4 different experimental treatments: fish exclusion, invertebrate exclusion, cage-roof control, and control (no exclusion). Each treatment has 10 replicates. (a) All foliose macroalgae, (b) green foliose macroalgae, (c) brown and red foliose macroalgae. Note logarithmic ordinate

effect of time, $F_{10,270} = 1.135$, $p = 0.33$). The invertebrate exclusion treatment was excluded from this analysis because no brown and red algae developed on these surfaces. The absence of significant differ-

ences is due to high within-treatment variability in the amount of brown and red foliose macroalgae on the fish exclusion substrata, indicated by the large standard error values (Fig. 1c). Small amounts of sediment were observed in a few cages, usually not covering more than 3 to 5 % of the surfaces.

Mean number of foliose macroalgal species per treatment did not vary throughout the experiment, averaging 2 species per treatment. Total number of species per treatment varied through time (2 to 6 species), apparently stochastically, except for the invertebrate exclusion cages, where only *Ulva rigida* was found.

Cages were removed after 150 d and most macroalgal biomass disappeared, with only a few small patches remaining in some areas. *Scartichthys viridis* scrape marks were clearly visible on many of the rock surfaces.

DISCUSSION

In this study, we have demonstrated that *Scartichthys viridis* has an herbivorous diet, primarily consuming the foliose macroalga *Gelidium* (Rhodophyta) and *Ulva* (Chlorophyta). Diets of other rocky intertidal herbivorous fishes are also dominated by green and red macroalgae (e.g. Bennett et al. 1983, Barry & Ehret 1993, Horn & Ojeda 1999). Selectivity for these macroalgae has been explained in terms of their greater protein, caloric and digestibility values in comparison to brown macroalgae (Montgomery & Gerking 1980, Benavides et al. 1986, Cáceres et al. 1994, Horn & Ojeda 1999, Cáceres & Ojeda in press).

Field and laboratory diet selectivity

In the multiple-choice feeding experiments, *Scartichthys viridis* selected the green macroalgae *Ulva rigida*, *Enteromorpha linza* and *Codium dimorphum*, while the red macroalga *Gelidium chilense* was rejected. Horn et al. (1982) found that 2 stichaeid fishes, *Cebidichthys violaceus* and *Xiphister mucosus*, occurring in rocky intertidal habitats in California, also selected *Ulva* in multiple-choice experiments, while Barry & Ehret (1993) showed similar results for the kyphosid *Girella nigricans*. Green macroalgae have traditionally been considered better food items than red macroalgae, based on energetic and nutrient content, as well as greater digestibility (Paine & Vadas 1969, Montgomery & Gerking 1980, Horn 1989). Nevertheless, this statement has been questioned. For example, Paine & Vadas (1969) reported very similar energetic contents for *Enteromorpha* sp., *U. rigida*, and *Gelidium cartilagineum* from the Washington coast.

Recently, Cáceres & Ojeda (in press) found percentage protein, carbohydrates, and ash to be similar among *U. rigida*, *E. linza* and *G. chilense* in central Chile, while assimilation efficiency for these macroalgae by *S. viridis* did not differ significantly. Further, energetic content did not differ substantially between *U. rigida* and *G. chilense* (Ojeda unpubl. data).

Then, why did this species reject *Gelidium chilense* in laboratory multiple-choice experiments, considering that this red macroalga forms an important part of its diet? We hypothesize that although *Ulva rigida*, *Enteromorpha linza* and *G. chilense* are equivalent, *Scartichthys viridis* actively selects the green macroalgae because they are more easily dislodged from rock substrata and are not as tough. The mechanical force necessary for dislodging *Gelidium* is probably greater than for *Ulva* or *Enteromorpha*. Further, *Gelidium* is attached by creeping axes with many stolons, and is quite tough, consisting of profusely branched thalli containing several layers of cells, including cortex and medulla (Hoffmann & Santelices 1997). In contrast, *Ulva* and *Enteromorpha* consist of soft and very thin sheet-like, 2-cell layered thalli (Hoffmann & Santelices 1997).

Why does *Scartichthys viridis* consume *Gelidium* in the field? Although *Ulva* is preferred, there may not be enough available biomass to sustain the large population sizes of this blenny along the central Chilean coast (Cáceres & Ojeda in press). Therefore, the inclusion of a lower quality (due to its toughness and structure) but more abundant food item such as *Gelidium* may be necessary under these circumstances. This leads to the prediction that *Gelidium* should be selected only when the amount of *Ulva* available is low. Some evidence supports this hypothesis, since *Gelidium* was selected in the field only during fall-winter (Table 2; $L = 0.20$), when the field biomass of *Ulva* was only 19.0 g m^{-2} . In contrast, *Gelidium* was taken only in proportion to its field availability in spring-summer ($L = 0.03$), when the amount of *Ulva* in the field had more than doubled (42.2 g m^{-2}).

The selection of *Codium dimorphum* in our laboratory experiments is puzzling and contrasts with their field selectivity and gut contents. *Codium* is perhaps consumed by *Scartichthys viridis* in the field, but disintegrates, as its thalli consist of profusely branched tubular coenocytic cells (Hoffmann & Santelices 1997). Also, the digestion rate may be faster due to its structure.

Feeding mechanism and food selectivity in temperate waters

Herbivorous fishes are classified as either grazers or browsers (Horn 1989). Jones (1968) suggested that

grazers pick up inorganic sediment while feeding by scraping or sucking, whereas browsers bite or tear more upright macroalgae and rarely ingest any inorganic material. The type of macroalgae that *Scartichthys viridis* consumes, together with the finding of inorganic sediment in its gut contents and feeding observations, demonstrates that this species is a grazer.

The prevailing notion is that grazers feed non-selectively because their macroalgal food is small and tightly adhered to the substratum (Choat 1982, but see Horn et al. 1990), whereas most browsers select larger macroalgae (Choat & Clements 1992, Cáceres et al. 1994). Further, grazing fishes are considered to be largely absent from temperate waters, which are dominated instead by browsers (Choat 1991). It has been suggested that grazing fishes, which have high metabolic rates, may be unable to sustain themselves, given the low productivity and turnover of turfing macroalgae (Choat 1991). For this reason, only invertebrate grazers (with lower metabolic rates) should be present in temperate waters. Contrary to the above 2 generalizations, we have shown in the present study that *Scartichthys viridis* is a grazer in a temperate system and displays a high degree of feeding selectivity.

Effect of fish herbivory on macroalgal abundance, diversity and distribution

The exclusion of herbivorous fish resulted in an enormous increase of foliose algae, particularly green macroalgae and, to a much lesser extent, red and brown macroalgae. In contrast, the exclusion of invertebrates did not produce results significantly different from those in control substrata, both remaining almost bare of foliose species. To our knowledge, this is the first experimental study demonstrating significant effects of an herbivorous fish on macroalgal abundance in a temperate rocky intertidal area, although a few studies have been carried out in temperate subtidal reefs (Foster 1975, Harris et al. 1984, Andrew & Jones 1990, Sala & Boudouresque 1997).

Although *Scartichthys viridis* is the only fish species that is strictly herbivorous in rocky intertidal areas along the coast of central Chile (Muñoz & Ojeda 1997), it may be argued that other fishes also consume macroalgae and could have contributed to the effects observed. Candidate species are the clingfish *Sicyases sanguineus*, the kyphosid *Girella laevisfrons*, and the blenny *Hypsoblennius sordidus*, all of them omnivores, which consume invertebrate prey as well as macroalgae (Muñoz & Ojeda 1997). Cancino & Castilla (1988) found that only small individuals of *S. sanguineus* consumed significant amounts of macroalgae, and larger

individuals ate mostly barnacles, snails and limpets. Although only the former could have a direct effect on macroalgal abundance, they are uncommon in these environments (Stepien 1990, Muñoz & Ojeda 1997). On the other hand, although juveniles of *G. laevisfrons* are highly abundant in rocky intertidal areas of central Chile, they are usually restricted to high intertidal tide-pools (Varas & Ojeda 1990), not occurring in low and mid intertidal areas, where the present study was conducted. Finally, the blenny *H. sordidus* is rare (Stepien 1990, Muñoz & Ojeda 1997). Therefore, the fish exclusion effects seen in this study are likely mostly due to *S. viridis*.

Further evidence supporting the role of *Scartichthys viridis* comes from the observation of their comb-like teeth scrape marks, which were observed on numerous rocky surfaces in the area where the experiment was conducted. These marks are very common on intertidal rocks and boulders along the central Chilean coast. They can also easily be observed in aquaria. Paine & Palmer (1978) mistakenly identified these scrape marks as belonging to limpets and to the clingfish *Sicyases sanguineus* (see Fig. 2 in Paine & Palmer 1978), but this species does not possess the comb-like teeth typical of blennies (see Fig. 3 in Horn & Ojeda 1999).

We hypothesized that if green macroalgae were preferred over others in the laboratory, the exclusion of herbivorous fish would result in a significant increase over time in the abundance of these macroalgae and not of non-selected algal species. This was largely upheld because large amounts of green foliose macroalgae (*Ulva rigida* and *Enteromorpha linza*) that were selected in the laboratory experiments grew in the fish exclusion cages. Non-selected macroalgae (e.g. *Gelidium chilense*, *Mazzaella laminarioides* and *Colpomenia phaeodactyla*) were fewer and took much longer to appear. Feeding selectivity by *Scartichthys viridis* thus may be determining which macroalgal species are most abundant on these rocky mid intertidal areas. Fish exclusion resulted in a system largely dominated by green foliose macroalgae, while their presence (control) resulted in a very high cover of crustose brown and red macroalgae. Further, the paucity of sessile invertebrates (e.g. barnacles and mussels) in these channels, characteristic of the central Chilean coast, may well be due to the excavating effect exerted by the grazing action of *S. viridis*, in a similar way to that shown by limpets (Steneck & Watling 1982).

The non-dietary species *Porphyra columbina* grew substantially on surfaces from where fish were excluded. This species was not offered in the multiple-choice feeding tests because it grows only in high intertidal areas (Hoffmann & Santelices 1997), which *Scartichthys viridis* does not reach (Varas & Ojeda

1990). The occurrence of *P. columbina* inside the cages extended its distribution into the mid intertidal zone. Nevertheless, as mentioned, *P. columbina* does not form part of the diet of *S. viridis*. Then, why did it appear in substrata from where fish were excluded? This question remains to be answered.

Decrease in algal diversity within invertebrate exclusions may be due to selective grazing by small limpets, such as *Collisella* spp. Perhaps diversity is enhanced in the rocky intertidal areas by these invertebrates laying fecal pellets containing macroalgal propagules that have passed through their guts (Santelices et al. 1983). Macroalgal propagules surviving in fecal pellets have been shown to resist longer desiccation periods and grow faster than non-ingested propagules (Santelices 1992).

Scartichthys viridis is a species widely distributed along the central coast of Chile, reaching high densities in rocky intertidal areas (Muñoz & Ojeda 1997). The intertidal habitats, where this species occurs, are also characteristically depleted of foliose macroalgae and dominated by crustose macroalgae, and scrape marks are a common feature. These patterns together with the results presented in this study suggest that *S. viridis* plays an important role in determining abundance and distribution patterns of foliose macroalgae on a broad spatial scale along the Chilean coast.

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