

MORPHOMETRIC AND PARASITOLOGICAL EVIDENCE FOR ONTOGENETIC AND GEOGRAPHICAL DIETARY SHIFTS IN INTERTIDAL FISHES

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ABSTRACT

Studies on the feeding ecology of intertidal fish assemblages have indicated the existence of three trophic groups: herbivores, omnivores and carnivores. This classification has enabled researchers to establish some ecological relationships among their components. However, temporal and spatial variations in the use of food resources have rarely been addressed. In this study, ontogenetic and geographical variations in the diet of two intertidal fish species: *Girella laevis* and *Graus nigra* were evaluated through an integrative analysis of their diet, relation between intestinal length/body length, and their parasite fauna. Results of this combined analysis suggest ontogenetic and geographical variations in the diet of *G. laevis*. In *G. nigra*, no evidence of ontogenetic dietary shifts was found, but marked differences in diet were detected among localities. However, parasitological evidence does not reflect the geographical differences in its diet. Omnivory of *G. nigra* at two localities (viz Caleta Errázuriz and El Tabo) may be indicative of the opportunistic nature of this species related to the greater availability of macroalgae at these localities. The assessment of intestinal length of *G. nigra* highlights the importance of considering macroalgal species composition, and not only their abundance as a group, when estimating the quality of the diet of a given fish species. In general, the geographical differences in diet, length of the intestine and parasitofauna of *G. laevis* and *G. nigra* together suggest that a species' diet is a dynamic feature that may be related to variations in the availability of food resources in the environment.

The study of the biology and ecology of intertidal fish assemblages has been usually centered around the question of the degree of their persistence and spatio-temporal stability (Grossman, 1982; Collette, 1986; Grossman, 1986a), movement patterns (Gibson, 1967; Ralston and Horn, 1986) and trophic ecology and food resource partitioning (Bennett et al., 1983; Grossman, 1986b). Along the Chilean coast, recent studies that have dealt with ecological aspects of entire assemblages, have determined the presence of functional groups of species according to their feeding habits (i.e, guilds) (Varas and Ojeda, 1990; Stepien, 1990; Muñoz and Ojeda, 1997, 1998). These studies have shown that the assemblage can be divided into herbivorous, omnivorous, microcarnivorous and carnivorous species with different degrees of trophic specialization (e.g., Muñoz and Ojeda, 1997).

The identification and analysis of the guild structure of associations or communities has played a fundamental role for understanding the mechanisms responsible for their organization (Pianka, 1980; Jaksic and Medel, 1990; Simberloff and Dayan, 1991; Jaksic et al., 1993; Putman, 1994; Muñoz and Ojeda, 1997). Notwithstanding, spatial and temporal changes in the use of resources have rarely been evaluated. Ontogenetic or geographic changes in the use of resources by a species can result in it belonging to different guilds at different developmental stages or at different localities, respectively (Muñoz and Ojeda, 1998). Ontogenetic shifts in the use of food resources have been reported in different intertidal fish species along the Chilean coast, such as the carnivores *Graus*

nigra, *Tripterygion cunninghami*, *Bovichthys chilensis*, *Auchenionchus microcirrhis* and *Myxodes viridis* (Johnson and Fritzsche, 1989; Stepien, 1990; Muñoz and Ojeda, 1998), the herbivore *Scartichthys viridis* (Ojeda and Muñoz, 1999; Muñoz and Ojeda, 2000) and the omnivore *Sicyases sanguineus* (Cancino and Castilla, 1988). Geographic variations in diet have been reported in subtidal fishes such as the carnivorous fish *Sebastes capensis*, which have been ascribed to differences in the availability of prey taxa in the environment (Moreno et al., 1979).

Among fishes, variations in the use of resources can have important consequences on intra and interspecific interactions because some species would share resources with different members of the assemblage at different stages of their lives or at different localities. Thus, for example, competitive hierarchies between two or more species could potentially be reversed at different stages of their lives (e.g., Werner and Gilliam, 1984; Mittelbach, 1986; Olson, 1996; Muñoz and Ojeda, 1998).

The most direct and commonly used evidence for determining variations in feeding habits of a fish species is a direct analysis of its gut contents (e.g., Yoshiyama, 1980; Stoner and Livingston, 1984; Clements and Choat, 1993; Gerking, 1994; Ojeda and Muñoz, 1999). Nevertheless, it has been reported that a tight relationship exists between the composition of an animal's diet and its digestive mechanisms (Sibly and Calow, 1986; Horn, 1989). Thus, the relationship between intestinal length and body size may also be used to characterize the diet of a species. For example, a characteristic shared among many herbivorous species is the greater length of their intestine in comparison to omnivorous and carnivorous species (Montgomery, 1977; Horn, 1989; Benavides et al., 1994). It has been suggested that an increase in length of the intestine is associated with a greater capacity of the digestive tract of animals that have poor quality diets (Horn and Ojeda, 1999). This way, herbivorous animals would maximize the acquisition of energy by increasing the volume of digesta or the transit time of the food through the digestive tract (Sibly and Calow, 1986).

On the other hand, because many parasites are trophically transmitted to their hosts, these parasites may be taken as indicators of the foraging habits of hosts (Moore, 1987). Because a host's diet can determine the extent of parasite transmission through the food chain, information on the parasites could reveal new insights regarding how an intertidal assemblage is organized as well as the possible interaction pathways among its components. For example, in deepwater fishes, ontogenetic dietary shifts and habitat differences have been shown to affect the parasitic fauna and community diversity of these fishes (Campbell et al., 1980).

In this context, the aim of the present study is to determine whether ontogenetic and geographic variations in diet occur in two intertidal fishes that inhabit the coast of Chile: *Girella laevisfrons* and *Graus nigra*, through an integrative analysis of the relation between intestine length/body length, diet and their parasite fauna.

We hypothesize that herbivorous individuals will possess longer intestines and a low abundance and prevalence of parasites that are trophically transmitted. Furthermore, carnivorous individuals will have shorter intestines and a high level of infection of trophically transmitted parasites. For those fishes that show ontogenetic dietary shifts, the ontogenetic stage in which they would be infected by trophically transmitted parasites would be the carnivorous one.

MATERIALS AND METHODS

G. laevisfrons and *G. nigra* fish individuals were captured between July 1996 and January 1997 in intertidal rockpools at two localities in northern Chile: Caleta Errázuriz CE (23°20'S, 70°38'W) and Carrizal Bajo CB (28°04'S, 71°08'W), and at one locality in central Chile: El Tabo ET (33°27'S, 71°37'W). These localities were selected in consideration of their differences in the abundance and diversity of the most important trophic groups, and in general at the level of the entire community (Vásquez et al., 1998; Camus and Andrade, 1999). All fishes were captured during low tides with the use of the ichthyocide Rotenone and hand nets. All parts of the each tidepool were carefully inspected with the aim of collecting the total number of individuals that it contained. Once collected, fishes were deposited in plastic bags and labeled with the date and locality of capture. In the laboratory, each specimen was measured and weighed with 0.1 cm and 0.1 g precision, respectively. The entire digestive tract was extracted, measured and dissected. Dietary items were analyzed under a stereomicroscope, and then sorted and identified to the lowest possible taxonomic level.

In order to evaluate possible ontogenetic and geographic variations in *G. laevisfrons* and *G. nigra*, the diet, length of the intestine and parasite fauna of these fishes were analyzed. In *G. laevisfrons* the geographic variations between the two localities in northern Chile were considered, while for *G. nigra*, all three localities sampled were analyzed. A total of 129 *G. laevisfrons* specimens captured at CE and 179 at CB were used in the dietary and parasite contents analyses, while 30 individuals collected at each locality were used for assessing relative intestinal length. The gut contents of a total of 22 *G. nigra* specimens from CE, 51 from CB and 12 from ET were analyzed, the relative intestinal length was determined from 51 individuals collected at CE, 28 from CB and 51 from ET, and the parasite fauna from 73 individuals collected at CE, 79 from CB, and 51 from ET.

Regarding gut contents analyses, data on dietary items were expressed as percentage frequency of occurrence (% FO) and as percentage of the total food biomass found (%W) in the sample at each locality. In those individuals that contained food contents, we also recorded the number of species, absolute biomass (g) and relative biomass (%) of macroalgae and invertebrates. Results are presented as percentage of macroalgal biomass. Length of the intestine was standardized by correcting for variations in the body length of specimens so that the relative length of the intestine (intestine length (cm) / body length (cm) × 100) was evaluated. Cumulative trophic diversity plots were used to assess sample adequacy as in Grossman (1986b) and Kotschal and Thompson (1986). Adequate sample size was 30 specimens for *G. laevisfrons*, and 20 for *G. nigra*. The parasite fauna was evaluated in terms of the prevalence and abundance of the parasite taxa encountered. Prevalence and abundance were calculated according to Margolis et al. (1982).

Statistical significance of ontogenetic variations in diet of fish was assessed through Spearman's correlation between the recorded variables and body size. The body size range (TL) of the specimens analyzed in this study were 28 to 191 mm for *G. laevisfrons* and 58 to 175 for *G. nigra*, which are within the size range reported for these species in the intertidal zone (Muñoz and Ojeda, 1997). The differences in relative biomass of algal food in three size classes were analyzed by using one-way ANOVA. In *G. laevisfrons*, the three size classes were <7.2 cm, 7.2 to 11.6 cm, and >11.6 cm individuals. The relative biomass of algal food among size classes in *G. nigra* were compared at CB only because the widest size range of individuals of this species was found at this locality. *G. nigra* size classes were <10 cm, 10 to 14 cm, and >14 cm individuals. Geographic differences were assessed through one-way ANOVA of the independent variables among localities (Zar, 1984).

RESULTS

In 308 *G. laevisfrons* specimens analyzed, 27 prey taxa were found: 14 macroalgal taxa and 13 invertebrate taxa (Table 1). The diet of *G. laevisfrons* captured in CE consisted primarily of macroalgae, representing more than 85% of the total biomass of the gut

Table 1. Dietary composition of *Girella laevis* collected at Caleta Errázuriz (CE) and Carrizal Bajo (CB). The importance of each prey item is expressed as percentage of total weight W (%) and percentage of frequency of occurrence FO (%).

	CE		CB	
	W (%)	FO (%)	W (%)	FO (%)
MACROALGAE	88.78	89.76	45.17	90.23
CHLOROPHYTA				
<i>Ulva</i> sp.	53.83	85.68	40.06	68.96
<i>Enteromorpha</i> sp.	10.66	55.12	19.86	40.70
<i>Chaetomorpha</i> sp.	1.10	18.90	6.69	31.03
<i>Cladophoropsis</i> sp.	14.58	33.86	1.51	21.84
RHODOPHYTA				
<i>Gelidium</i> sp.	5.06	21.26	3.15	38.91
<i>Heterosiphonia</i> sp.	0.62	31.50	6.59	23.56
<i>Porphyra</i> sp.	0.52	9.45	0.72	10.34
<i>Gymnogongrus</i> sp.	<0.01	0.79	0	0
<i>Hypnea</i> sp.	0.13	7.87	0.92	17.82
<i>Callophyllis</i> sp.	<0.01	0.79	0	0
Ceramiales	0.27	19.68	0.30	31.61
Rodhymeniales	0.49	11.81	0.31	1.15
PHAEOPHYTA				
<i>Glossophora</i> sp.	0.06	3.15	1.12	13.79
<i>Colpomenia</i> sp.	0.04	7.87	0.04	14.37
OTHERS	1.41	21.26	1.09	24.14
INVERTEBRATES	11.22	94.49	54.83	94.25
CRUSTACEA				
Copepoda	0.20	44.88	2.31	45.4
Reptantia	3.95	15.75	1.62	6.9
Natantia	0.09	9.45	0.56	6.32
Amphipoda	3.15	56.69	0.72	37.93
Isopoda	0.78	10.24	3.8	13.22
Cirripedia	0.16	13.38	<0.01	1.72
MOLLUSCA				
Gastropoda				
<i>Fissurella</i> sp.	0.92	2.36	0	0
<i>Colisella</i> sp.	0.10	0.79	<0.01	1.15
<i>Prisogaster</i> sp.	0.01	3.15	0.05	1.72
Bivalvia	0	0	0.28	10.34
Polyplacophora				
<i>Chiton</i> sp.	<0.01	0.79	0	0
INSECTA	1.26	56.69	1.85	55.75
ANNELIDA				
Polychaeta	0.02	3.15	5.45	13.79
OTHERS	0.57	15.75	0.95	11.49
Total content (g)	8.55		18.32	
Total number of stomachs with food content		127		174

Table 2. Results of Spearman's correlation analyses of dietary and morphometric variables in relation to body size in *Girella laevis* collected at Caleta Errázuriz (CE) and Carrizal Bajo (CB). Sample sizes (n), the correlation coefficients (rs) and the probability values (P) are shown for each locality. Asterisks indicate significant differences.

	CE			CB		
	n	rs	P	n	rs	P
Nº of species of macroalgae	126	-0.208	0.019*	141	0.359	0.000013*
Nº of species of invertebrates	126	-0.209	0.019*	141	0.0091	0.914
Biomass of macroalgae (g)	126	0.279	0.0016*	141	0.373	0.000005*
Biomass of invertebrates (g)	126	0.166	0.062	141	0.1	0.237
Percentage biomass of macroalgae (%)	126	0.07	0.433	141	0.238	0.0045*
Relative intestinal length (%)	30	0.792	< 0.0001*	30	0.017	0.927

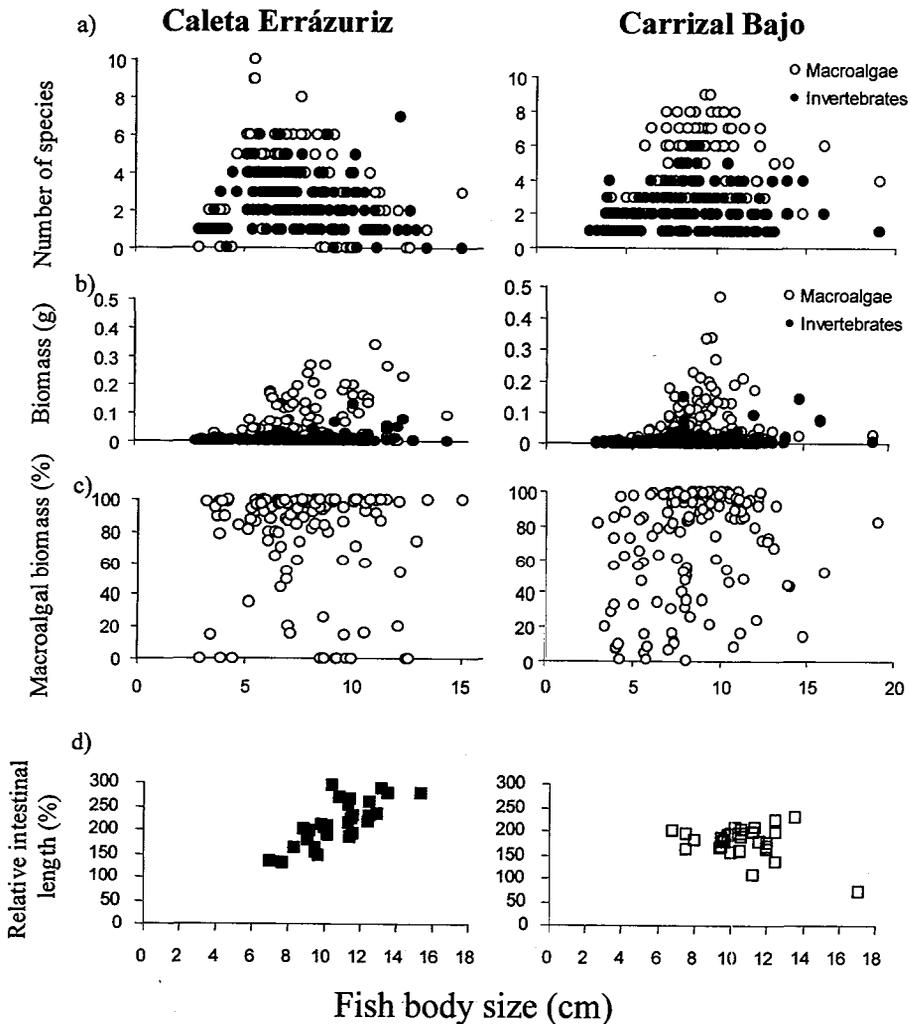


Figure 1. Relation between body size and A) the number of species, B) absolute biomass, C) relative biomass of macroalgae and invertebrates present in the diet and D) the relative length of the intestine of *Girella laevis* collected at Caleta Errázuriz and Carrizal Bajo (both in northern Chile).

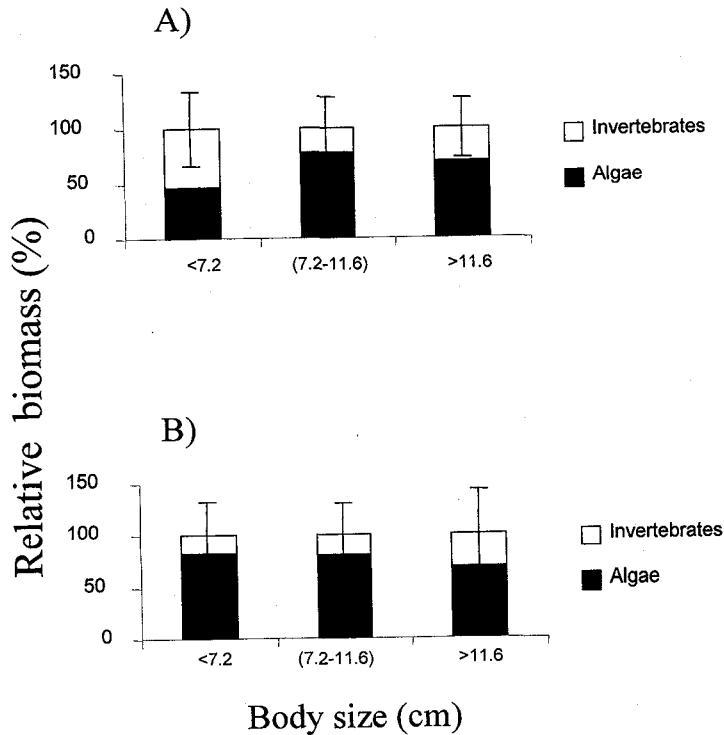


Figure 2. Relation between fish body size and relative abundance of invertebrates and algae in *Girella laevisfrons* collected at (A) Carrizal Bajo (B) Caleta Errázuriz.

contents and being found in 90% of guts analyzed (Table 1). In contrast, the biomass of macroalgae in its diet at CB did not reach 46% of the total gut contents, although they were found in 90% of guts analyzed (Table 1). At both localities, Chlorophytes, principally *Ulva* sp. and *Enteromorpha* sp. were the most abundant prey items in terms of frequency and biomass.

The number of species of macroalgae and invertebrates present in the diet of *G. laevisfrons* at CE decreased with increase in body size, while at CB the number of species of macroalgae increased and that of invertebrates did not show any relation with body size (Table 2, Fig. 1A). At both localities, the absolute biomass of macroalgae increased with body size, while the biomass of invertebrates remained constant (Table 2, Fig. 1B). In terms of relative percentages, only at CB there was a positive correlation between biomass of macroalgae and fish body size (Table 2; Fig. 1C). The analysis of relative macroalgal biomass among the three body size classes showed that at CB, the proportion of macroalgae in the diet of *G. laevisfrons* of intermediate body size was greater than that of small individuals (ANOVA $F_{(2,138)} = 11.75$; $P < 0.0001$) (Figs. 1C,2A). At CE, the degree of herbivory tended to decrease with increase in body size, although this was not statistically significant (ANOVA $F_{(2,123)} = 0.69$; $P = 0.504$) (Figs. 1C,2B). Further, small individuals at CB consumed proportionately less algae than those of similar size at CE (ANOVA $F_{(1,67)} = 18.44$; $P = 0.0001$, Fig. 2A,B), while no differences between the two localities in the relative biomass of algae consumed by medium sized and large fish were detected (medium-sized individuals: ANOVA $F_{(1,189)} = 0.20$, $P = 0.65$; large individuals $F_{(1,46)} = 0.22$, $P =$

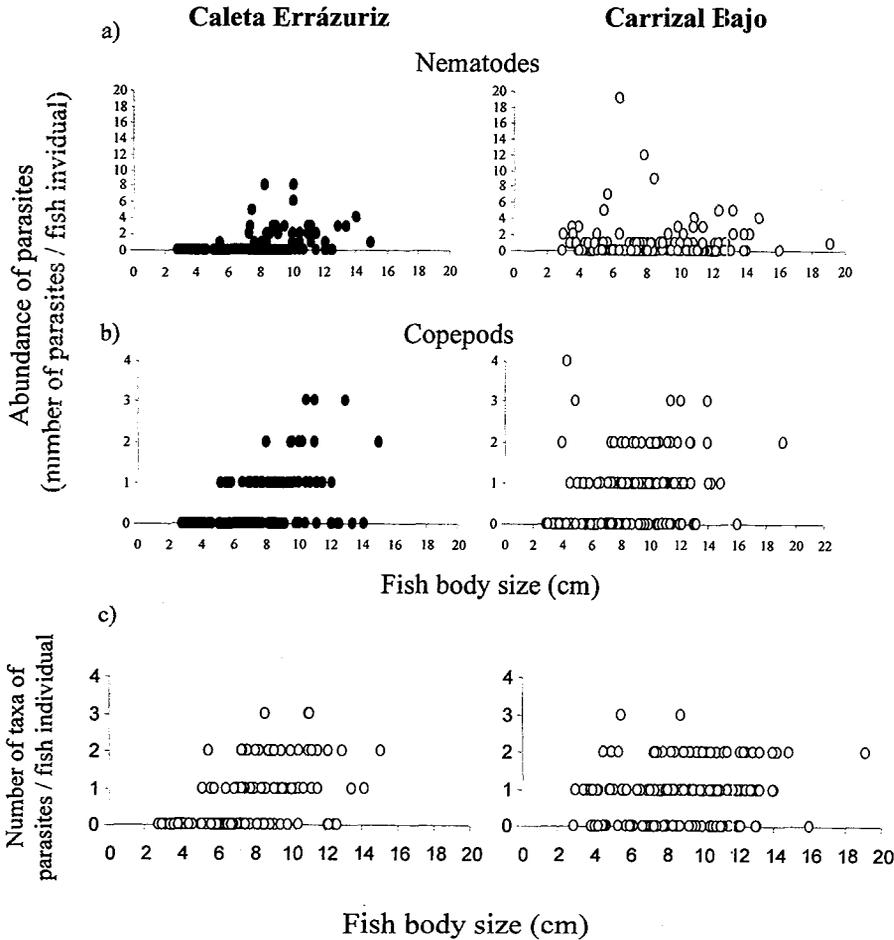


Figure 3. Relation between body size and A) the abundance of nematodes, B) copepods and C) parasitic species richness in *Girella laevisfrons* collected at Caleta Errázuriz and Carrizal Bajo.

0.63; Fig. 2A,B). Correspondingly, the relative length of the intestine was greater in fish collected at CE than those at CB, even though these two groups of fish did not differ in body size (ANOVA Relative length of the intestine: $F_{(1,58)} = 8.69$; $P < 0.005$. Body size: $F_{(1,58)} = 0.01$; $P < 0.942$) (Fig. 1D). Furthermore, at CE, relative intestinal length increased with increase in body size, while at CB it did not show this variation (Table 2, Fig. 1D).

Parasites found in *G. laevisfrons* included copepod ectoparasites as well as the trophically transmitted taxa: nematodes, digeneans and acanthocephalans. The abundance of nematodes increased with body size in fish collected at CE, while those collected at CB did not show any variation (Spearman's correlation; CE: $r_s = 0.518$; $n = 129$, $P < 0.0001$; CB: $r_s = -0.021$, $n = 179$, $P = 0.777$) (Fig. 3A). In contrast, the abundance of copepods increased with fish body size at both localities (Spearman's correlation; CE: $r_s = 0.447$, $n = 129$, $P < 0.0001$; CB: $r_s = 0.302$, $n = 179$, $P < 0.0001$) (Fig. 3B). The low abundance of digeneans and acanthocephalans prohibited a rigorous analysis of the abundance of these taxa with increase in body size in *G. laevisfrons* (Table 3).

Table 3. Prevalence (percentage of infected host) and abundance (number of parasites individuals per host examined) (SD = 1 standard deviation), of parasitic taxa found in *Girella laeivfrons* collected at Caleta Errázuriz (CE) and Carrizal Bajo (CB).

		CE	CB	
	Number of host fish	129	179	
Prevalence	Nematodes	25.58	31.28	
	Digeneans	3.88	2.23	
	Acanthocephalans	0	2.23	
	Copepods	34.88	55.31	
Abundance	Nematodes	mean	0.66	0.76
		S.D.	1.46	2.05
	Digeneans	mean	0.046	0.022
		S.D.	0.24	0.14
	Acanthocephalans	mean	0	0.039
		S.D.	0	0.287
	Copepods	mean	0.46	0.743
		S.D.	0.74	0.807

Although there were no significant differences in body size distribution between CE and CB (Kolmogorov-Smirnov; $D_{max} = 0.33$, $P = 0.1$; Table 4), fish infected with nematodes, digeneans and trophically transmitted parasites in general were smaller at CB compared to CE, and non-infected individuals were larger at CB. Finally, small sized individuals showed a higher species richness of parasites at CB compared to those collected at CE (ANOVA; $F_{(1,67)} = 16.53$, $P < 0.0001$) (Fig. 3C).

In 85 *G. nigra* specimens analyzed, a total of 21 prey taxa were found: 9 macroalgal and 12 invertebrate taxa (Table 5). At CB, the diet of *G. nigra* consisted chiefly of inver-

Table 4. Body size of *Girella laeivfrons* individuals infected and not infected with nematodes, digeneans, trophically transmitted parasites in general and copepods, The number of specimens analyzed (N), mean body size and standard deviation (S.D.) of fish collected at Caleta Errázuriz (CE) and Carrizal Bajo (CB) are indicated. Asterisks indicate significant differences.

		Infected		Not infected	
		CE	CB	CE	CB
Nematodes	N	33	56	96	123
	mean	9.96	8.54	6.98	8.63
	S.D.	2.09	3.5	2.22	2.61
Digeneans	N	5	4	124	175
	mean	9.05	10.75	7.69	8.55
	S.D.	1.90	3.62	2.56	2.88
Trophically transmitted parasites	N	42	65	95	119
	mean	9.95	8.71	6.97	8.55
	S.D.	2.21	3.36	2.23	2.59
Copepods	N	45	99	84	80
	mean	9.07	9.32	7.02	7.70
	S.D.	2.08	2.57	2.49	3.06

Table 5.- Dietary composition of *Graus nigra* collected at Caleta Errázuriz (CE), Carrizal Bajo (CB) and El Tabo (ET). The importance of each prey item has been expressed as percentage of total biomass W (%), and percentage of frequency of occurrence FO (%).

	CE		CB		ET	
	W (%)	FO (%)	W (%)	FO (%)	W (%)	FO (%)
MACROALGAE	36.21	71.42	8.36	50	43.0	81.82
CHLOROPHYTA						
<i>Ulva</i> sp.	31.88	61.9	6	28	18.29	54.54
<i>Enteromorpha</i> sp.	3.88	23.81	0.01	4	1.07	18.18
<i>Chaetomorpha</i> sp.	0	0	0.17	4	0	0
RHODOPHYTA						
<i>Gelidium</i> sp.	0	0	0.02	6	0	0
<i>Porphyra</i> sp.	0	0	0.20	2	11.58	45.45
<i>Hypnea</i> sp.	0	0	0.01	4	0	0
Ceramiales	0	0	1.06	12	0.3	9.1
Rhodymeniales	0	0	0.01	4	11.8	27.27
PHAEOPHYTA						
<i>Colpomenia</i> sp.	0	0	0.03	16	0	0
OTHERS	0.44	9.52	0.86	12	0	0
INVERTEBRATES	63.79	100	91.64	100	57	100
CRUSTACEA						
Copepoda	0.23	9.52	0.05	32	0	0
Reptantia	6.32	33.33	59.35	68	50.32	63.64
Natantia	0	0	9.16	20	0	0
Amphipoda	15.51	80.95	11.90	82	0	0
Isopoda	0.10	4.76	7.06	24	4.9	36.36
MOLLUSCA						
Gastropoda						
<i>Fissurella</i> sp.	1.56	19.05	1.63	4	0	0
<i>Colisella</i> sp.	0	0	0.61	4	1.39	27.27
<i>Prisogaster</i> sp.	5.93	52.38	0.14	6	0.39	9.10
Bivalvia	0.03	14.28	0.54	8	0	0
Polyplacophora						
<i>Chiton</i> sp.	0	0	0.37	2	0	0
INSECTA	0.13	19.05	0.33	18	0	0
ANNELIDA						
Polychaeta	0.51	9.52	0.05	4	0	0
OTHERS	33.48	38.10	0.46	6	0	0
Total content (g)	1.55		6.12		1.68	
Total number of stomachs with food contents		21		50		11

tebrates, which together constituted more than 90% of the total food biomass consumed and were found in 100% of guts analyzed (Table 5). In contrast, the percentage biomass and percentage frequency of occurrence of macroalgal items in *G. nigra* was fairly high at CE (36 and 72%, respectively) and at ET (43 and 82%, respectively) (Table 5). At all three localities, crustaceans followed by gastropods were the most abundant prey items, although at CB, the diet of *G. nigra* was more diverse, showing an increase in the importance of other prey items such as polychaetes, chitons and insects (Table 5). Green

macroalgae (principally *Ulva* sp.) were the most important group of algae consumed in terms of biomass and frequency of occurrence, although there was an increase in the biomass and frequency of occurrence of Rhodophyta and Phaeophyta at ET and CB (Table 5).

The number of macroalgal or invertebrate species present in the diet of *G. nigra* did not change with increase in fish body size at any of the localities (Table 6, Fig. 4A). Absolute biomass of invertebrates increased with body size at CB only (Table 6, Fig. 4B,C). Relative macroalgal biomass consumed by fish of the same body size was less at CB than at CE and ET (ANOVA $F_{(2,63)} = 7.4$; $P = 0.0013$, (Figs. 4C,5A). However, no evidence of ontogenetic dietary shifts was found in *G. nigra* (Figs. 4C,5B). Relative intestinal length of *G. nigra* individuals collected at ET was greater than that of those collected at CB and CE, even though no differences in fish body size among localities were detected (ANOVA, Relative intestinal length; $F_{(2,127)} = 24.71$, $P < 0.0001$; body size: $F_{(2,127)} = 0.25$, $P < 0.776$, Fig. 4D). In addition, relative intestinal length increased with body size increase at ET, while at the other two localities, it did not change (Table 6, Fig. 4D).

Parasites encountered in *G. nigra* included only trophically transmitted taxa: nematodes, digeneans and acanthocephalans. At CE, the abundance of nematodes increased with fish body size, while at CB and ET their abundance was not related to body size (Spearman's correlation; CE: $r_s = 0.357$; $n = 73$, $P = 0.002$; CB: $r_s = 0.025$; $n = 79$; $P = 0.826$. ET: $r_s = 0.213$, $n = 51$, $P = 0.133$) (Fig. 6A). As in *G. laeivfrons*, the low prevalence of digeneans and acanthocephalans did not allow for a rigorous analysis of the relation between the abundance of these taxa and the body size of *G. nigra* (Table 7). The abundance of nematodes and digeneans did not differ among localities, while the differences in the abundance of acanthocephalans are probably due to their absence in fish collected at CB (ANOVA; Nematodes: $F_{(2,200)} = 1.65$, $P < 0.195$; Digeneans: $F_{(2,200)} = 0.85$, $P < 0.429$. Acanthocephalans: $F_{(2,200)} = 3.29$, $P < 0.039$) (Table 7).

DISCUSSION

G. laeivfrons and *G. nigra* are the dominant fish species inhabiting tidepools in high intertidal areas on the northern and central Chilean coast, although their presence is only temporary, occupying these tidepools at the juvenile stage only (Stepien, 1990; Varas and Ojeda, 1990; Muñoz and Ojeda, 1998; Pulgar et al., 1999). The results of this study suggest that, during this stage, *G. laeivfrons* shows ontogenetic and geographical variations in diet. At CB, *G. laeivfrons* changes its diet from carnivory to herbivory as it grows, while at CE, this species maintains a herbivorous diet but with a slight trend involving a decrease in the degree of herbivory with increase in body size (>10 cm TL) (Figs. 1,2, Table 2). Changes in the proportions of macroalgae and invertebrates present in the diet of subtidal and intertidal fishes have previously been reported both within and among species in the genus *Girella* (e.g., Bell et al., 1980 cited in Johnson and Fritzsche, 1989; Barry and Ehret, 1993; Clements and Choat, 1997).

Differences in diet of this fish between the two localities could perhaps be explained by the environmental availability of macroalgae and invertebrates. Recently, it has been reported that cover and biomass of those macroalgal species mostly consumed by *G. laeivfrons* (Ulvoid species such as *Ulva*, *Enteromorpha* and *Chaetomorpha*, Table 1) is greater at CE (Vásquez et al., 1998; Camus and Andrade, 1999), where this fish is mainly herbivorous (Fig. 1C,2B). Furthermore, species richness of invertebrates in rocky inter-

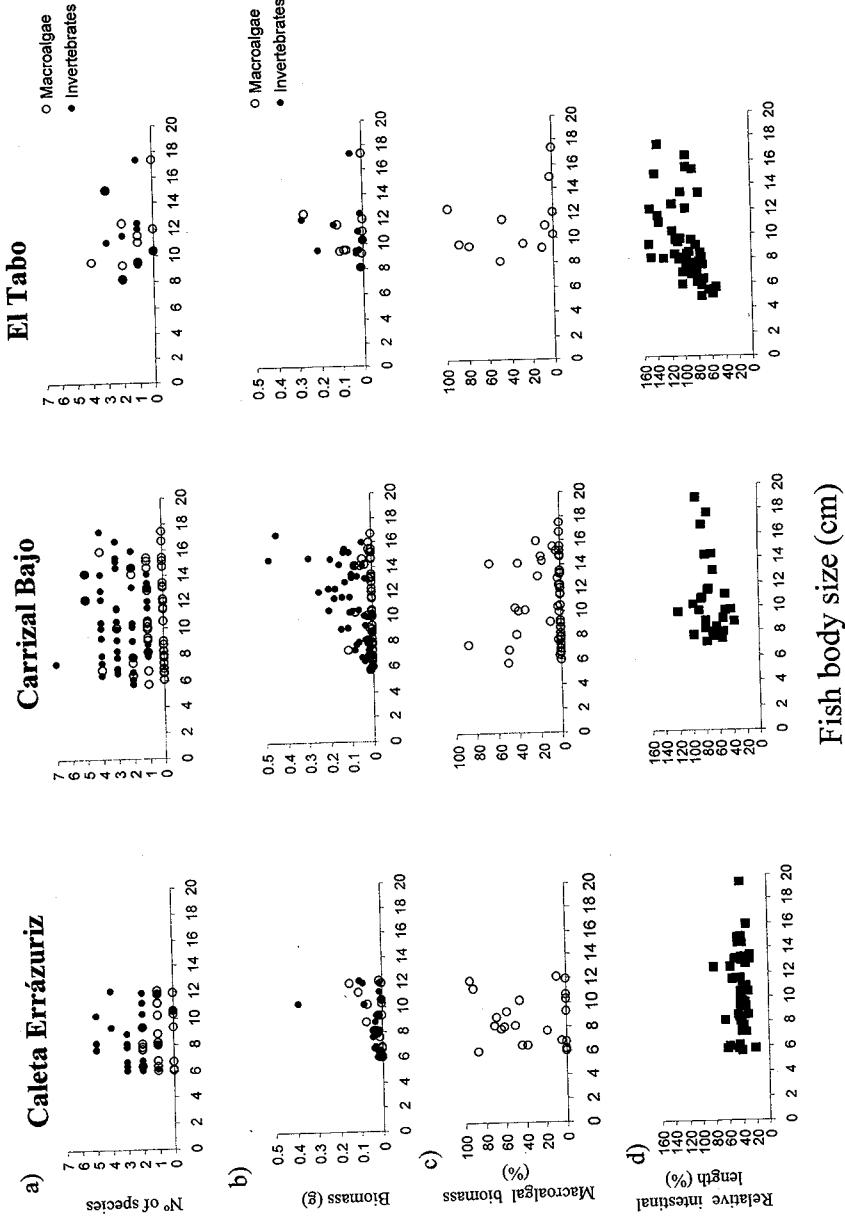


Figure 4. Relation between body size and A) number of species, B) absolute biomass, C) relative biomass of macroalgae and invertebrates present in the diet and D) the relative length of the intestine of *Graus nigra* collected at Caleta Errázuriz, Carrizal Bajo (both in northern Chile) and El Tabo (central Chile).

Table 7. Prevalence (percentage of infected host) (%) and abundance (number of parasites individuals per host examined. SD = 1 standard deviation), of parasitic taxa found in *G. nigra* collected at Caleta Errázuriz (CE), Carrizal Bajo (CB) and El Tabo (ET).

Locality	n	Prevalence (%)			Abundance			
		Nematoda		Acanthocephala	Digenean		Acanthocephala	
		mean	S.D.	mean	mean	S.D.	mean	S.D.
CE	73	57.53	6.43	2.74	0.18	0.69	0.027	0.16
CB	79	56.96	4.30	0	0.05	0.22	0	—
ET	51	51.00	3.25	4.08	0.20	1.15	0.69	3.24

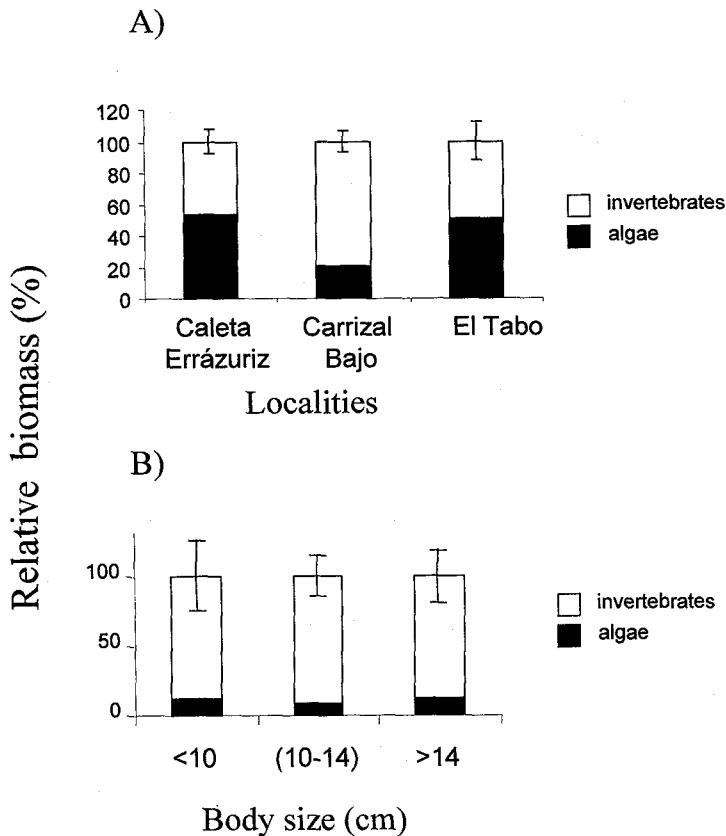


Figure 5. A) Relative abundance of invertebrates and algae in *Graus nigra* collected at Caleta Errázuriz, Carrizal Bajo and El Tabo. B) Relation between fish body size and relative abundance of invertebrates and algae in *Graus nigra* collected at Caleta Errázuriz, Carrizal Bajo and El Tabo.

tidal areas was higher at CB during the period of time when the present study was done (Camus and Andrade, 1999), which was the locality where small *G. laevisfrons* individuals were carnivorous (Fig. 1C,2A). The use of locally abundant food resources is a commonly reported phenomenon among littoral fishes (Wootton, 1991; Gerking, 1994).

On the other hand, the ontogenetic changes in diet reported in *G. laevisfrons* may be related to resource utilization abilities and predation risk experienced by these fish throughout their ontogeny. In this sense, it has been reported that body size can strongly influence an animal's ability to avoid predators or to harvest resources from different habitat types (Werner and Gilliam, 1984). Recruitment of *G. laevisfrons* occurs exclusively in high intertidal pools. As individuals grow older, however, they move towards the subtidal zone. During this migration, individuals encounter different ecological conditions (Mann, 1954). It has been suggested that those species with omnivorous diets exposed to differential regimes in food availability are capable of regulating their phenotypic digestive mechanisms (Diamond and Buddington, 1987). Differences in dietary composition and digestive mechanisms have been observed in fish species belonging to the same family, even though they are phylogenetically closely related and possess intestines with very

similar morphology (Clements and Choat, 1997). In the present study, differences in intestinal morphometry were found among individuals of the same species (*G. laevisfrons*) collected at different sites on the Chilean coast (Fig. 1D, Table 2). The importance of an increase in the length of the intestine in herbivorous fishes seems to lie in a greater capacity of consumption of low quality food, maximizing its digestion and assimilation (Sibly and Calow, 1986; Buddington et al., 1987; Horn, 1989; Benavides et al., 1994; Horn and Ojeda, 1999). Correspondingly, relative gut length of *G. laevisfrons* individuals was greater at the site where it was principally herbivorous (i.e., CE) (Fig. 1D,2B), which also increased as the fish grew (Fig. 1D, Table 2).

The ontogenetic and geographical variations in the diet of *G. laevisfrons* can also be observed in the results of the analyses of its parasites. Fish collected at CB were found to be infected at an earlier stage in their ontogeny (Fig. 3A,C, Table 4). This can be explained by the finding that the smallest fish analyzed at this site were carnivorous, thus exposing them at an earlier age to parasitic larval stages (Figs. 1C,2A,3C). In contrast, this pattern was not observed in fish infected with copepods, which infect fish directly and not indirectly through the fish's diet (Fig. 3B, Table 4). In addition, acanthocephalans were present only in fish captured at CB (Table 3), thus indirectly suggesting that -in this locality- crustaceans are more consumed, which are the prey responsible for the transmission of larval stages of this parasite.

At CE, larger sized *G. laevisfrons* individuals had a greater number of nematodes compared to smaller sized fish (Fig. 3A) although species richness of invertebrates was found to decrease with increasing fish body size (Fig. 1A). Nevertheless, because the absolute biomass of invertebrates did not change throughout its ontogeny (Fig. 1B), it is plausible that larger sized fish specialize on, and consume a greater proportion of, host prey that are intermediate hosts of nematodes, and that these differences show up in nonetheless herbivorous individuals. In contrast, the abundance of nematodes in *G. laevisfrons* did not vary with body size at CB (Fig. 3A), suggesting that these fish are constantly exposed to parasites along their ontogeny, which is probably related to an absence of variation in the species richness and biomass of invertebrates in this fish's diet (Fig. 1A).

No evidence of ontogenetic dietary changes was found in *G. nigra* (Table 6, Figs. 4,5B), but marked differences in diet were detected among fish collected at the three different rocky intertidal sites (Table 5A). Whereas at CB, *G. nigra* was essentially carnivorous, at CE and ET it was omnivorous (Table 5, Figs. 4C,5A). These results contradict previously published information on the diet of *G. nigra* that indicated that this species is strictly carnivorous (Muñoz and Ojeda, 1997, 1998). Our results show that at CB, approximately 80% of its diet consisted of invertebrates while at CE and ET only 50% of its gut contents were invertebrates (Figs. 4C,5A). Again, our results may be related to the availability of food resources in the environment, at least at CE and CB, localities where a greater biomass of algae and invertebrate species richness, respectively, have been indicated (Vásquez et al., 1998; Camus and Andrade, 1999). Unfortunately, data on resource availability at ET are lacking, which would be useful in order to test the above hypothesis.

In accordance with these results, it might be expected that relative gut length would be shorter at CB compared to CE and ET. Instead, gut length of individuals captured at CE was shorter (Fig. 4D). Differences in gut length may not only be related to differences in the relative abundance of macroalgae as a whole in the diet of fish among localities, but also to differences in species composition of macroalgae eaten. Based on the limited

information on endogenous digestive mechanisms available for fishes, it has been suggested that green macroalgae (Chlorophyta) have greater digestibility than red (Rhodophyta) and brown macroalgae (Phaeophyta) (Clements and Choat, 1997). Thus, the shorter relative gut length of fish collected at CE could be ascribed to the fact that the macroalgae that these fishes consumed at this site consisted almost exclusively of Chlorophytes (Table 5).

The absence of ontogenetic dietary shifts in *G. nigra* found in this study concurs with evidence reported by Muñoz and Ojeda (1998), who showed that, at five rocky intertidal sites in central Chile, this species maintained a carnivorous diet throughout its ontogeny, although the type of invertebrates consumed changed from small prey items such as amphipods in individuals <80 mm TL to larger ones such as decapods in individuals between 80 and 200 mm TL. A shift from smaller sized prey (e.g., copepods and amphipods) to larger ones (e.g., crabs and limpets) has also been found in many other intertidal carnivorous fishes on the Chilean coast (Muñoz and Ojeda, 1998) and elsewhere (e.g., Bennett et al., 1983; Grossman, 1986b; Kotschal and Thomson, 1986; Horn and Gibson, 1988; Norton, 1991). In contrast, Johnson and Fritzsche (1989), also working in central Chile, found that the *G. nigra* individuals they analyzed underwent striking ontogenetic shifts in diet, with all specimens below 80 mm SL being exclusively carnivorous, consuming mostly crustaceans, while specimens above 115 mm SL had eaten mostly macroalgal material, constituting as much as 75% or more of the total gut contents, the remainder comprising crustaceans, molluscs, polychaetes and bryozoans.

Data on the parasites encountered in *G. nigra* does not reflect the geographical differences in its diet found among the three localities (Fig. 6, Table 7). The abundance of nematodes and digeneans did not differ among localities, while acanthocephalans were absent in fish collected at CB, where fish individuals had a carnivorous diet. As most gastrointestinal parasites are acquired by ingestion, host diet is expected to determine, at least partially, the number of parasite species to which a host will be exposed and so the parasite fauna has been amply documented as evidence of fish foraging habits (Scott, 1982; Rohde, 1984; Moore, 1987). However, data obtained from gut contents analysis show what the fish individual consumed shortly before being captured. Variations in the degree of parasitism will probably not be detectable in a fish species that is primarily carnivorous, as has been described in *G. nigra* at CB in the present study, as well as in other studies at various localities along the coast of central Chile (Muñoz and Ojeda, 1997, 1998). The omnivorous diet of *G. nigra* at CE and ET may well be a reflection of the opportunistic habit of this species on a resource that is temporarily variable (Wootton, 1991). If this were the case, the diet of a species would be considered dynamic in nature and could be determined to a great extent by the availability of resources in the field.

In summary, the diet, relation between intestinal length/body length and parasitological evidence together suggest that geographical and ontogenetic variations in diet occur in *G. laevisfrons*. In *G. nigra*, no evidence of ontogenetic dietary shifts was found, but marked differences in diet were detected among localities. Parasitological evidence does not reflect the geographical difference in its diet, which could imply that the omnivorous diet of *G. nigra* at CE and ET may be a reflection of the opportunistic nature of this species associated with a greater abundance of macroalgae at these localities. The evaluation of intestinal length in this species highlights the importance of considering the species composition of macroalgae and not only their abundance, when estimating the quality of a given diet of a species. In general, the geographic differences in diet, intestinal

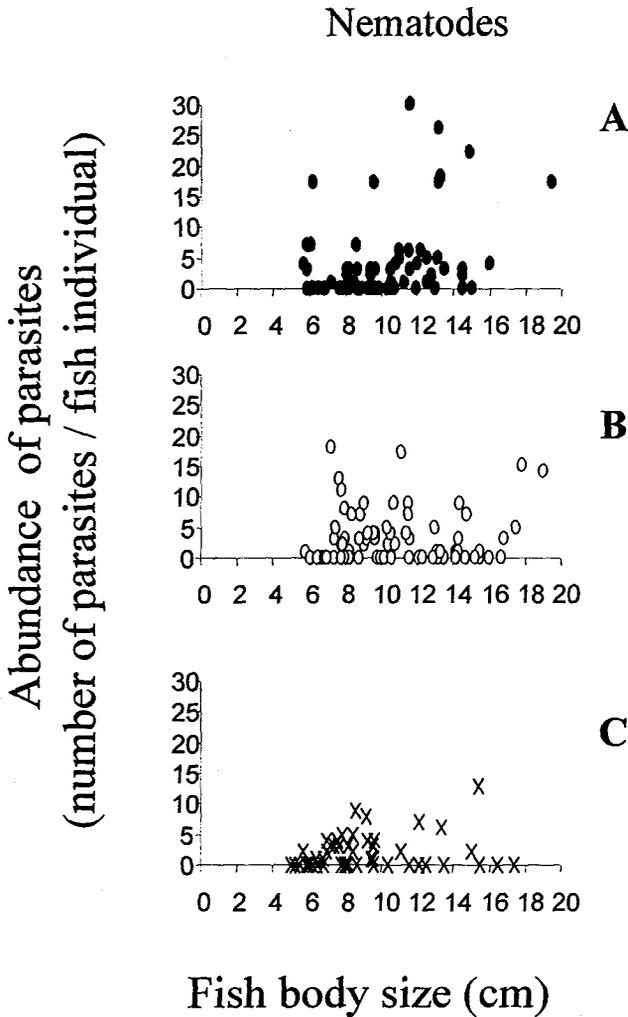


Figure 6. Relation between fish body size and nematode abundance in *Graus nigra* collected at (A) Caleta Errázuriz, (B) Carrizal Bajo and (C) El Tabo.

length and parasitofauna in *G. laevis* and *G. nigra* suggest that the diet of a species should be considered a dynamic element that may be related to variations in the availability of trophic resources in the field.

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