LIMNETIC FEEDING IN *Eleginops maclovinus* (VALENCIENNES, 1830) IN THE VALDIVIA RIVER, CHILE

HÉCTOR PAVÉS, GERMÁN PEQUEÑO, CARLOS BERTRÁN and LUIS VARGAS

Eleginops maclovinus, Valenciennes, 1830 is a monotypic species of the family Eleginopidae (Osteichthyes), suborder Notothenioidei. The species is thought to be of Antarctic evolutionary origin, and is one of the most eurythermic, euryhaline and stenobathic representative of the suborder (Pequeño, 1989). This species is endemic to southern Chile, southern Argentina and the Malvinas Islands, where it occurs near oceanic beaches, and in large and small estuaries. In Chile it is found south of the Aconcagua River (33ºS) and has been caught in rivers of southern Chile, several kilometers offshore of the river mouths (eg. Valdivia River, this study), and over 20km upstream in low salinity (limnetic) waters.

Previous observations of the trophic relations of *E. maclovinus* had been made on specimens obtained in marine and estuarine habitats. Although this species has been generally considered as an omnivorous predator, the literature reflects two contrasting variations on this point, the first by Guzmán and Campodónico (1973) and Gosztonyi (1979), who postulated an ontogenetic change from carnivorous behavior in early juvenile stages to a herbivorous one in adults. The second opinion, held by Pequeño (1979) and Turner (1988) is that the species tended toward a carnivorous behavior throughout its entire ontogenetic development.

In the present study the trophic relations between juveniles and adults of *E. maclovinus* within a limnetic habitat, namely the upper Valdivia River estuary, are compared. It was also tested whether *E. maclovinus*, the notothenioid species that most commonly inhabits fresh waters, preys upon typical freshwater species during its residence in this habitat, and remains carnivorous as observed in specimens studied from brackish and marine waters. Parasitological evidence obtained from the stomachs of the fish is also used to evaluate the hypothesis of carnivorous tendency in both juveniles and adults of this species.

Materials and Methods

Sample collection

Samples of *E. maclovinus* included 114 individuals obtained using a 1.75×30m gillnet with 32mm openings. Catches were made from 17 to 20 March 2002, at Las Mulatas (39º50'S, 73º15'W), at a distance of about 16km upstream from the Pacific Ocean, in the Valdivia River estuary (Figure 1). Tidal movement in this estuary takes place to about 20km inland of the river's mouth, and limits of salt water (salinity= 0.1‰) reach about 14km inland. All the specimens were measured for total length (TL, live) and standard length (SL) using a ruler graduated in millimeters. Weights were obtained using a field balance graduated to 0.1g. At the laboratory, the fishes were initially fixed in 10% river water formalin for 48h and stored in 70% ETOH. The stomachs were removed from each specimen and stored separately for subsequent contents analysis.

Collection of bottom samples

Sampling of the bottom fauna of the Valdivia River was carried out at two stations, including Las Mulatas and Los Pelúes (Figure 1). At each station samples were obtained both near the shore and at its deepest point, using corers hand-held by divers. Four replicate samples were obtained at each sampling point. These samples were collected on the same dates as the fishes were.

Macrofauna were initially separated from the sediments using a 0.5mm screen, fixed in 10% formalin, and stored in 70% ETOH. These specimens were subsequently separated under a stereomicroscope and identified to the closest possible taxonomic species level using specialized keys. The species richness and relative abundance were determined on each of the samples (Morin, 1999). The samples were finally dried at 60ºC for 48h and weighed to determine

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Héctor Pavés. **Marine Biologist and Doctoral Student, Universidad Austral de Chile (UACh).**
Germán Pequeño. **Ph.D., Oregon State University, USA. Professor, Instituto de Zoología “Ernst F. Kilian”, Universidad Austral de Chile. Address: Casilla 567, Valdivia, Chile. e-mail: gpequeno@uach.cl**
Carlos Bertrán. **M.Sc., UACh. Doctor, Universidad de Concepción, Chile. Professor, UACh.**
Luis Vargas. **Marine Biologist, UACh. Doctoral Student, Universidad de Cadiz, Spain.**

the approximate biomass per species in each sample.

Stomach contents analysis

The determination of stomach contents was made using a stereomicroscope, aided by specialized taxonomic identification keys (Stuardo, 1961; Yamaguti, 1961; Menzies, 1962; Retamal, 1981), as well as with the aid from the specialists from the Institutes of Zoology and Botany at the Universidad Austral de Chile. The individuals from the identified taxa were counted to obtain the frequency distributions of species and proportions of individual taxa in each analyzed stomach (F: frequency of occurrence per number of stomachs; F%: frequency of occurrence expressed in proportions of stomachs). The abundance of prey items found indicated the number of individuals of a given taxon registered in all the samples analyzed (N: abundance expressed per number of individuals; N%: abundance expressed in percentage of individuals).

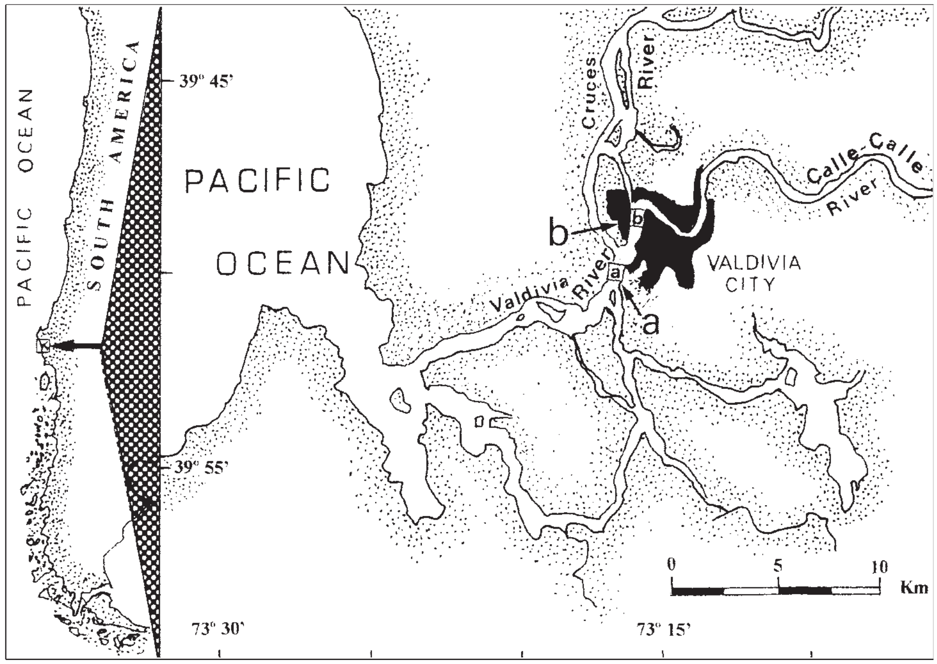

Figure 1. Geographic location of sampling stations, within the estuarine system of the Valdivia River, Chile. a: Las Mulatas, b: Los Pelúes.

Results

A total of 114 specimens of *E. maclovinus* were obtained in the samplings. These had a mean total length (live) of 26.7cm (18-42cm, sd= 4.6cm) and a mean weight (live) of 224.9g (75-800g, sd= 146.7g). Most specimens were immature males of 2-4 years of age (Gosztonyi, 1974; Calvo, *et al*., 1992). The by-catch obtained in sampling for *E. maclovinus* included the salmoniformes *Oncorhynchus mykiss* (exotic, introduced), *Galaxias maculatus* and *G. platei*, the smelts *Austromenidia laticlava* and *Basilichthys australis* (Atherinopsidae), and the cosmopolitan mullet *Mugil cephalus* (Mugilidae).

Of all the *E. maclovinus* stomach samples, 103 (90%) could be analyzed, while the remainder (11) were in a degraded condition. The analyzed specimens had mean total length (fixed) of 25.0cm (18-40.1cm, sd= 3.3cm) and their mean standard length was 22.0 cm (15.5-30.2cm, sd= 2.8cm).

Almost all the samples from which the complete digestive tract could be extracted (93%, n=96) had stomach contents present. In these it was possible to identify species or high taxonomic levels of plant and animal remains. Only 7 (7%) of the stomachs were empty. A total of 55 (53%) stomachs analyzed contained nematode parasites.

The analysis of the stomach contents revealed a broad range of food items, accompanied by appreciable amounts of detritus such as sand and rock grains (*eg*. schist, mica). Items observed included algae, plant material, gastropods, crustaceans, insects, and fishes, mostly of estuarine or lacustrine origin. Of the analyzed stomachs, 96 (93%) contained animal remains, and 89 (84%) contained plant remains (Table I). The highest frequency group on the

TABLE I
FREQUENCY OF OCCURRENCE IN RELATION TO TOTAL NUMBER OF STOMACHS ANALYZED (F, F%) AND NUMBER OF ITEMS (N, N%) IN THE STOMACH CONTENTS OF *Eleginops maclovinus* IN THE VALDIVIA RIVER

Taxa	N	N%	F	F%
Crustacea			96	93.20
Corophiidae (Amphipoda)	59246	97.148	96	93.20
Tanaidacea (Malacostraca)	104	0.171	14	13.59
Ciprinidae (Ostracoda)	20	0.033	10	9.71
Hemigrapsus crenulatum	5	0.008	5	4.85
Idotheinae (Valvifera)	3	0.005	3	2.91
Zoea larvae	1	0.002	1	0.97
Gastropoda			20	19.42
Littoridina comingii	20	0.033	19	18.45
Bivalvia larvae	1	0.002	1	0.97
Insecta			72	69.90
Chironominae (Diptera:Chironomidae)	918	1.505	70	67.96
Hygrobatidae (Acarii)	2	0.003	2	1.94
Trichoptera (Tubo)	2	0.003	2	1.94
Inderminate	4	0.007	3	2.91
Teleostei			1	0.97
Inderminate	1	0.002	1	0.97
Bryozoa			81	78.64
Indet. ovoid structures	519	0.851	57	55.34
Filaments			44	42.72
Plants			48	46.60
Scirpus californicus (Cyperaceae)*	139	0.228	29	28.16
Inderminate			46	44.66
TOTAL	60985		103	

* Seeds

stomachs (F%) were the crustaceans (93.2%), followed by ramose bryozoans (78.64%), insects (69.9%), lake plants (46.6%), gastropods (19.42%) and, finally, a bony fish (0.97%, Table I). In relation to the number of individuals per group (N%) the class Crustacea represented 97%, followed by Insecta (1.5%) and bryozoans, lake plants, gastropods and Teleostei, each at proportions below 1% (Table I). A grand total of 98.9% (N, N%) of the items recorded in the stomachs were of animal origin, with less than 1.1% of plant origin.

Taxonomic analysis of the stomach contents by systematic group

Statistically significant differences were observed among the abundances (N) of the different food items analyzed (Kruskal-Wallis test: H(15, N=1599)= 949.94 p<0.01).

The taxa showing the statistically greatest abundances were 1) the corophiid amphipods (mostly *Paracorophium hartmannorum*), 2) Diptera: Chironomidae, 3) bryozoans, and 4) lake plants (Multiple Comparison Kruskal-Wallis test, p<0.01). Each of the preceding groups demonstrated absolute, elevated abundances, and distinct tendencies among themselves (Table I).

1) Class Crustacea: In this group the main taxon in numerical abundance (N%) as well as in frequency of occurrence in stomachs (F%) was shown by the lacustrine amphipod *Paracorophium hartmannorum*, which represented 97% of the individual prey species, and was found in 93.2% of the stomachs analyzed (Table I). Other crustacean items included Tanaidacea (Malacostraca), Ciprinidae (Ostracoda), *Hemigrapsus crenulatus* (Decapoda), and Idotheinae (Isopoda, Valvifera) which as a group represented less than 1% of the total individuals counted. The tanaids, ciprinids, and *H. crenulatus* gave frequencies of occurrence of between 2.9 and 13.5%. Finally, a brachyuran zoea larva was encountered, representing less than 1% both in abundance and frequency.

2) Class Mollusca: Only one species of gastropod, *Littorina cumingii*, was recorded, which had a frequency of occurrence of near 18.4%, and an abundance of less than 1%. A few bivalve veliger larvae were also observed.

3) Class Insecta: The most important taxon of this group were Diptera of the family Chironomidae, with an abundance of 1.5%, and a frequency of occurrence of 67.9%, making it the second most common item eaten by the fish. Also identified were trichopteran tubes and a hygrobatid mite, representing less than 1% in abundance and 1.9% in frequency of occurrence.

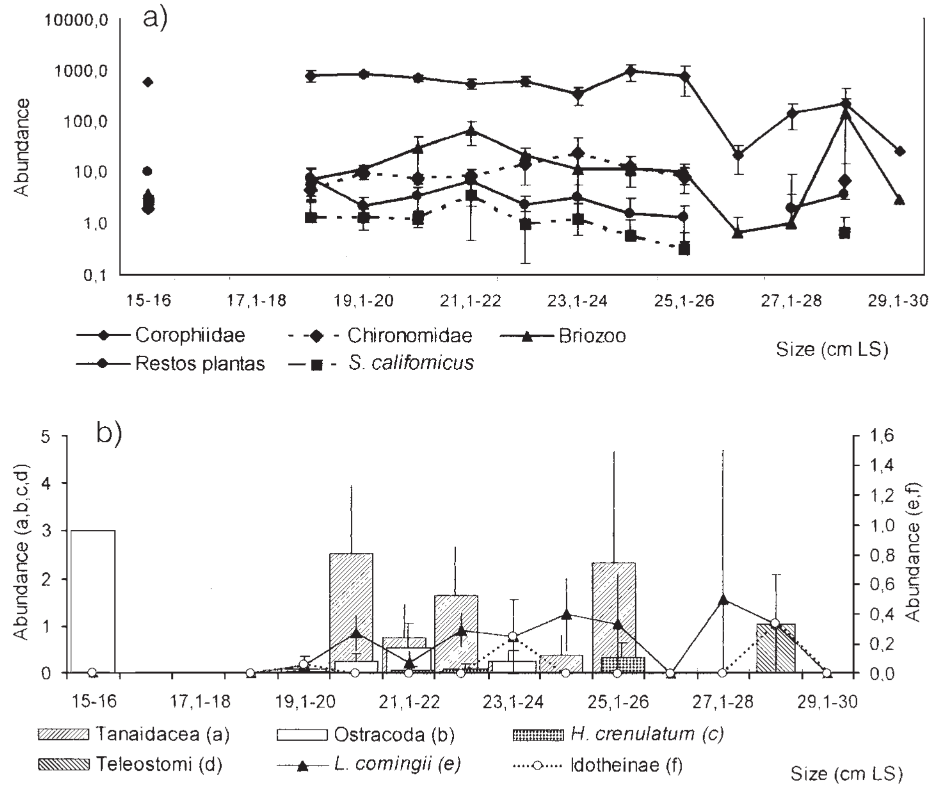

Figure 2. Variation in the stomach contents of *Eleginops maclovinus*. a: common items, b: less common items (lower occurrence and presence).

4) Subdivision Teleostei: Only one individual was recorded, and this was in an advanced stage of digestion, remaining unidentified. This represented less than 1% in frequency of occurrence and abundance among the items analyzed.

5) Ramose invertebrates: Due to their advanced state of digestion, specific identification of this material was impossible, although its tubular structure, dichotomous ramification and presence of ovoidal structures in the external walls suggested it to be assigned to “bryozoa”. These remains were found in 78.64% of the stomachs, but with an abundance near 1%. Quantification of this material was difficult due to clumping, but undoubtedly represented a frequent item in the stomachs of *E. maclovinus*.

6) Lacustrine plants: 46.6% of the stomachs contained remains of lake plants, including both vegetal portions and seeds: the latter were determined to be seeds of *Scirpus californicus* (Cyperaceae) and had a frequency of occurrence of 28.1% and an abundance of less than 1% (Table I; Ramírez *et al.*, 1976).

7) Nematode parasites (Table II): The main nematode parasite in the stomachs of the fish was *Ascarophis* sp. (Cystidocolidae), with both mature males and females present. This nematode had a frequency of 44.6% and an abundance of 75.7% (n= 87), and was the most numerous of the helminths identified. Also identified from the stomachs were ma-

TABLE II
FREQUENCY OF OCURRENCE (F, F%) AND NUMBER OF PARASITE NEMATODS (N, N%) IDENTIFIED WITHIN THE STOMACH CONTENTS OF *Eleginops maclovinus* IN THE VALDIVIA RIVER

Parasites	N	N(%)	F	F (%)
Ascarophis spp. (Cystidicolidae)	87	75.7	46	68.7
Anisakids	28	24.3	21	31.3
Total	115	100	67	100

ture anisakids, at a frequency of 20.3%. This group included 15 larvae and 13 adults.

Analysis by size of fish

When the fish samples were separated into size ranges of 1cm, to give 13 ranges between 15 and 30cm TL, no statistically significant differences were observed in total species abundance in stomachs from the different size groups (Kruskal-Wallis test H(12, N= 1599)= 19.21559, p>0.05). However, a decrease in abundance of the Corophiidae, lacustrine plants (*S. californicus*), bryozoan remains, Chironomidae, and Ostracoda was observed as total length of the fishes increased (Figures 2a, b). In contrast, the Idotheidae, *H. crenulatus*, one teleost, and *L. cumingii* were recorded in specimens over 19cm SL, and increasing in the larger *E. maclovinus* (Figure 2b).

With the nematode parasites, greater numbers of anisakids were found in the smaller fish specimens, contrary to the numbers of ascarophites which were more common in the larger fishes.

Comparison of the fish stomach contents and river fauna

Items found in the *E. maclovinus* stomachs were common at both stations sampled in the Valdivia River, including *P. hartmannorum*, Chironomidae, and Trichoptera. (Tables II, III). There was, however, variation in abundance and diversity of the four taxa in relation to the sampling depth in the river (shore *vs*. depth). Amphipods were more abundant in shore samples at Las Mulatas. In mid-river, the polychaetes *Prionospio* sp. and *P. gualpensis* were more abundant, although they were not recovered from the stomach contents of the fish. Lower abundance and biomass were found at Los Pelúes than at Las Mulatas, where the oligochaete *Tubifex* sp. inhabited anoxic bottoms rich in organic matter. This species was not recovered from fish stomachs. Thus, some of the potential preys are not used by the fishes.

TABLE III
ABUNDANCE AND BIOMASS OF MACROBENTHOS SPECIES IN SECTORS* OF LOS PELÚES AND LAS MULATAS AT THE VALDIVIA RIVER

Taxa	Los Pelúes margin		Los Pelúes center	
	Abundance / m^2	Biomass (gr/m^2)	Abundance / m^2	Biomass (gr/m^2)
Prionospio sp.	63.14	0.006	357.77	0.08
Perinereis gualpensis	168.36	0.59	631.36	1.30
Paracorophium hartmanorum	841.81	0.07	2209.75	0.27
Tubifex sp.	168.36	0.010	21.04	0.002
	Las Mulatas margin		Las Mulatas center	
Prionospio sp.	105.23	0.019	3556.65	0.85
Perinereis gualpensis	526.13	0.73	1452.12	1.85
Paracorophium hartmanorum	2336.02	0.24	589.27	0.06
Trichoptera	21.04	0.09	0	0
Chironomidae	21.04	0.006	0	0

* The sectors are differentiated according to sampling locations, margin or center.

Discussion

Among the large variety of food items present in the stomach contents of *E. maclovinus* we found remains of algae, land plants, crustaceans, insects, mollusks and fishes.

The item with the highest frequency of occurrence was *Paracorophium hartmannorum*, somewhat similar to that recorded by Pequeño (1979). It should be noted that Pequeño (1979) considered specimens between 280 and 880mm TL, to be inhabitants of marine or mixohaline habitats. In the present study samples obtained were between 180 and 400mm TL, and distributed in areas of strong limnetic affinity and low salinity (Valdivia River surface salinity= 0‰, bottom salinity= 5‰; Wladimir Steffen, personal communication).

The Las Mulatas station is at the limit of effect of the estuarine salt wedge in the Valdivia River estuary, with freshwater occurring to the head of the estuary, and tidal motion noted up to 20km inland from the mouth of the estuary (Pers. Comm. Wladimir Steffen). The majority of samples of *E. maclovinus* having stomach contents (93%), the low degree of digestion of the prey, and the similarities between species ingested and those recorded from the environment, allow the assumption that Las Mulatas is a feeding area used by the fishes to exploit resources located near the rivers edge (Table I, III).

Various species of polychaetes, including *Perinereis gualpensis* and *Prionospio* sp. were found in the sediment, but not among the stomach contents although other investigators recorded the presence of polychaete remains as well as remains of the oligochaete *Tubifex* sp. (Ruiz, 1993). This situation may be explained by the life style of these annelids (buried, as endofauna), and with soft body structures which are easily digested, impeding their identification in the stomachs. Another possibility is that they may be negatively selected by the fish, based on its feeding behavior which includes grazing over sand or gravel, not appearing to consume species which are in lime-clay sediments containing decomposing organic material as typical of *Prionospio* sp. and *P. gualpensis*. This situation would reflect a selective behavior toward species which inhabit gravel and sandy areas, or in association with small filamentous algae where benthic grazing behavior is possible (*eg*. Trichoptera, Chironomidae, and *P. hartmannorum*). The fish may be an opportunistic predator (Morin, 1999) since it exploits the resource in major abundance in the environment (*eg. P. hartmannorum*).

The remains assigned to bryozoa and lacustrine plants observed in the stomach contents of *E. maclovinus* probably represent items accidentally consumed during feeding on crustaceans and/or insects due to the common behavior arthropods such as the amphipods, isopods and insects in seeking refuge in filamentous microhabitats such as algae and other plants, reducing predator pressure and indirectly increasing the food offering of the substrate (Schneider and Mann 1991a, b; Peñaloza, 1993). Another aspect suggesting the accidental nature of consumption of the bryozoans was the low degree of digestion of this material in the fish stomachs. The same occurred for *Scirpus californicus*, where accidental ingestion of the seeds may be related to sedimentary grazing on animal prey, particularly the chironomids. The accidental consumption of seeds may lead to probable "ichthyochoria" or seed dispersal by fishes as found in the Amazon by Gottsberger (1978). This was also noted by Guzmán and Campodónico

(1973) who reported seeds of graminea in *E. maclovinus* stomach contents.

The crustaceans, insects, and plants observed in the stomach contents in this study, have only been reported from limnetic or estuarine environments (see Stuardo, 1961; Ramírez *et al*., 1976; Pequeño, 1979; Artigas *et al*., 1985; Jaramillo *et al*., 1985; Bertrán, 1989; Ruiz, 1993). This suggested that the fishes sampled had not migrated into brackish (Corral Bay, 9.2‰ surface, 33.7‰ bottom salinity) or marine areas to feed, but rather consumed prey from freshwater, upper reaches of the river (0‰). This capacity for tolerating low salinity and feeding on limnetic species explains catches of these fishes to more than 21km inland from the mouth of the Valdivia River. This aspect is corroborated by the limnetic fish fauna associated with the areas from which present samples were obtained, such as *Austromenidia laticlavia*, *Basilichthys australis*, *Oncorhynchus mykiss*, *Mugil cephalus*, *Galaxias maculatus*, *G. platei*, *Cheirodon* sp. (Ruiz, 1993; Vila *et al.*, 1999). Of these only *M. cephalus* is capable of life both in the sea and in freshwater (Ruiz, 1993).

It has been recognized that freshwater fishes have a diet similar to that of *E. maclovinus* in this study in these habitats. Thus *Oncorhynchus mykiss* and *Cauque mauleanum* feed principally on chironomid larvae and pupae, Littorinidae, Trichopteridae, Acarii, and Amphipoda (Artigas *et al.*, 1985; Klink and Eckmann, 1985).

The data showing that as the fishes grew in size and weight, corophiid crustaceans (*P. hartmannorum*) significantly decreased in the stomach contents, as also found with the ostracods, suggested a succession of species taken by *E. maclovinus* with increase in size, where smaller prey items are progressively replaced by larger ones. In spite of these changes in predation, the fish was observed to be more of a carnivore than herbivore, in agreement with Pequeño (1979), Turner (1988), Acevedo (1994), and Isla and San Román (1995) and differing from the hypothesis of Guzmán and Campodónico (1973). Pequeño (1979) and Acevedo (1994) recorded that in individuals of 240-280mm TL from marine and mixohaline environments 84% of the food items were of animal origin (e.g. crustaceans, chordates) and over 11% of plant origin, increasing in the present study to 98.9% animal, and >1% plant remains. Algal remains cited by Pequeño (1979) and Acevedo (1994) and other studies included *Enteromorpha*, *Porphyra*, and *Ulva* which are species which typically harbor crustaceans and show little sign of digestion in the digestive tract of the fishes, which makes it doubtful that they serve as an energy source (Isla and San Román, 1995). However, it is difficult to say at what point microscopic algae, generally present in the surface of other organisms, may play a role in fish nutrition.

Pequeño (1979), Acevedo (1994), Ruiz (1993) and Isla and San Román (1995) determined that *E. maclovinus* was predominantly feeding on crustaceans, since amphipods, isopods, cumaceans, and decapods were the most abundant prey found in individuals from 61 to 240mm TL and from 180 to 700mm TL.

Although the results of the present study concur with those of Guzmán and Campodónico (1973) in relation to the predominance of carnivorous feeding in *E. maclovinus*, those authors maintained that individuals of this species greater than 160mm SL were basically herbivorous. They mentioned that individuals from 160 to 410mm SL fed predominantly on algae, which had a frequency of occurrence of 94% and occupied approximately 83.4% of the volume of the stomachs.

The present study, although showing a frequency of occurrence of plant material of 86.7%, showed an abundance of significantly less than 1% which was markedly different than that observed by Guzmán and Campodónico (1973). This suggested carnivorous behavior in the size classes studied from the Valdivia River, which may be a tendency maintained over time in accordance with the stability of food resources (Acevedo, 1994).

Gosztonyi (1979), similarly to Guzmán and Campodónico (1973) suggested that the *E. maclovinus* studied was an omnivorous species with clear tendencies towards consumption of plant material in all stages of its development. However, he did not present evidence for digestion of the plant material placing doubts on its value as an energetic input. Gosztonyi's (1979) observations have also been noted by other authors. According to him filamentous structures such as the form of some bryozoans, provide refuge for crustaceans, and as presently suggested there is no evidence that the fish is a primary consumer.

In addition to previous studies concerning the broad scope of feeding of *E. maclovinus* (Pequeño, 1979; Turner, 1988; Acevedo, 1994), the present study shows its capacity to feed in limnetic habitats as part of its capacity for survival in freshwater. The reduced number of species found in the fish stomachs in the limnetic habitat (14 items, present study) is a reflection of the reduced species diversity of the freshwater habitat compared with those of the estuary (Beagle Channel, 24 items; Isla and San Román, 1995) and marine habitats (Mehuín, 35 items; Pequeño, 1979). This aspect is related to the selectivity of the predator and lower diversity of prey in inner beaches of the estuary compared with the mouth of the estuary of the Valdivia River (Low, 1993; García and Ojeda, 1995), together with the general tendency towards lower species diversity in estuaries than in seas or lakes (Kiely, 1999).

It was of interest that mature nematodes of the genus *Ascarophis* occurred in *E. maclovinus*, since this fish had not been considered as a definitive host for this nematode (Muñoz and George-Nascimento, 2002). Our records indicate that infection by these parasites (anisakids and *Ascarophis* sp.) occurred in *E. maclovinus* at sizes less than 150mm SL, both in limnetic and estuarine systems. This point was not mentioned in the review of Marcogliese (2002) although reported by Muñoz and George-Nascimento (2002).

Another parasite, *Cystidicola* sp. (fam. Thelaziidae), was identified from *E. maclovinus* stomachs by Szidat (1950). This parasite is only known from freshwater habitats where it infects intermediate and definitive hosts, in contrast to *Ascarophis* sp. which are found in hosts in both estuarine and limnetic habitats (Ronald, 1986). Identification of *Cystidicola* sp. in this study demonstrates that these fishes were feeding on freshwater crustaceans.

Marcogliese (2002) suggested that the definitive host for this species could be fishes, birds, or mammals, with the intermediate hosts being mainly crustaceans, particularly decapods of the genera *Pagurus* or *Carcinus*. Fagerholm and Butterworth (1988) previously indicated that both larvae and some adult stages of *Ascarophis* sp. were isolated from decapods, isopods, and mainly amphipods of 18-20mm in TL in marine and estuarine environments. The preceding two reports suggest that the intermediate hosts of *Ascarophis* sp. in the Valdivia River may be *Hemigrapsus crenulatus* or *Paracorophium hartmannorum* based on their high frequency of occurrence in the fish stomach contents, which merits future study. The preceding *indirectly* confirms our observations on the occurrence of carnivorous feeding in *Eleginops maclovinus* in the Valdivia River. Marcogliese (2002) suggested that *Ascarophis* sp. (Cystidicolidae) had gadiform fishes as definitive hosts, and this type of result should be tested in *E. maclovinus* because it is a perciform fish (Eleginopsidae: Notothenioidae, this study; Muñoz and George-Nascimento, 2002). The parasitological research needs to be broadened by extending the range of the area considered and using larger sample numbers and a broad range of sizes, as well as extending the parasitological analyses and obtaining more information on the food species availability. All this with the object of better understanding the ontogenetic variation and trophic behavior of *E. maclovinus* within a referential framework which may provide new light on the biological and phylogenetic history of the suborder Nothothenoidei.

The present results support our initial hypothetical idea, stated in the Introduction, that *E. maclovinus* living in fresh waters has to eat freshwater organisms, despite the fact that the species is well known as a marine fish. The present study also opens possibilities to the hypothesis that this species lives in freshwater for extended periods of time, without needing marine salinity for survival. This behavior, to some extent, contributes to the idea that this species is probably one of the oldest living species of notothenioid, which, due to its Antarctic origin, must have been initiated by individuals capable of living in areas with permanent melting of ice, at very low salinities.

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