Aquatic Sciences 55/1, 1993

1015–1621/93/010065–11 $ 1.50 + 0.20/0

Effect of the selective feeding of *Galaxias maculatus* (Salmoniformes, Galaxiidae) on zooplankton of a South Andes lake

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Key words: Fish predation, zooplankton, selective feeding, cladocerans, copepods.

ABSTRACT

The effect of larval and juvenile predation of *Galaxias maculatus* on a natural small-sized zooplankton was studied in a South Andes lake. Field data of zooplankton density and composition were combined with fish gut content analysis during a spring-summer season. Results showed that *Galaxias* early stages ingested mostly planktonic preys. A shift was observed in prey electivity: larvae preferred copepod nauplii whereas juveniles preferred cladocerans. Larval predation provokes the failure of the summer cohort of the calanoid copepod *Boeckella gracilipes*. The effect of juveniles is more undefined, but seems to prevent the reappearance of *Ceriodaphnia* in the summer plankton.

Introduction

Planktivorous fish predation plays a major role in changing the zooplankton structure. Such changes are produced by the selective removal of prey by fishes (Kerfoot and Sih, 1987). According to the Size Efficiency Hypothesis (Brooks and Dodson, 1965; Hall et al., 1976) the size-selective predation upon the largest prey results in an inverse relationship between zooplankton size and fish density. This response is clear in large-species zooplankton communities. But, within a small-species community, fish predation may not greatly reduce one species over another (Vanni, 1987).

The temperate lakes of South Andes (south of 39 °S) have a particular small-sized zooplankton (Thomasson, 1959, 1963). Recent studies (Balseiro and Modenutti, 1990; Balseiro et al., 1991; Modenutti and Balseiro, 1991) had shown a very simple composition and a small-sized zooplankton in the araucanian lakes of Argentina (to the east of the Andes). The autochthonous fish *Galaxias maculatus* (Jenyns) (Salmoniformes, Galaxiidae) has a very broad distribution in the area and important lacustrine populations in the Nahuel Huapi system (Mc Dowall, 1971). Adult stages of this fish had been reported as carnivorous euriphagic (Ferriz, 1984). However, early stage diet is fragmentarily known (Cervellini et al., 1991) and the effects on prey populations are unknown.

During our zooplankton studies we had observed schools of juveniles in the limnetic zone of lakes, and larvae had appeared in zooplankton samples. Due to our observations, and since *Galaxias* adults are non-planktivorous (Pollard, 1973; Ferriz, 1984) we propose that the *Galaxias*-zooplankton interaction is mainly restricted to early stages (larvae and juveniles) of the fish. This study focuses on the fish selectivity of fish predation and its effects on prey populations. We explored the effect of *Galaxias*' early stage predation on a natural small-sized zooplankton of a South Andes lake by combining field data of zooplankton density and composition with fish gut content analysis.

Study site

The study was carried out at Laguna Ezquerra (758 m a.s.l.), a shallow lake of the Araucana region. The lake belongs to the Nahuel Huapi system (41°03'S and 71°30'W). Its surface area is 6 ha and its maximum depth 3 m. Because of its shallowness and exposure to the wind, Laguna Ezquerra is not thermally stratified during spring and summer. In winter the surface often freezes. The lake has a very narrow littoral area with scarce macrophytes, *Schoenoplectus californicus* Meyer Steud, all around, and *Potamogeton linquatus* Hangström only in the eastern sector. Mean temperature recorded over two years was 13.5 °C in spring (October–December) and 17 °C in summer (January–March).

Materials and methods

Samples were taken every 3–7 days for six months (October 3, 1988 – March 20, 1989). Zooplankton was captured at 1–1.5 m and 2–2.5 m depth, using a Schindler-Patalas trap with a 35 µm mesh net. It was fixed with a sugar-formalin solution. Two samples of each depth were combined in a 50 l sample and two replicates of the whole sample were taken. This procedure was carried out to reduce the effect of zooplankton clumping. Crustacean zooplankton was counted in a 5 ml Bogorov chamber under a dissecting microscope. Juveniles, non-ovigerous females, ovigerous females and the number of eggs were counted separately for cladocerans. Nauplii and copepodite instars of *Boeckella gracilipes* Daday were separated according to Chapman and Burns (1976). Rotifer species were quantified in a 1 ml Sedgwick-Rafter chamber under a microscope.

Bosmina longirostris (O. F. M.) mortality was estimated as $d = b - r$, where b is the instantaneous birth rate according to Paloheimo's formula (Paloheimo, 1974) and r is the instantaneous rate of increase

$$r = \frac{\ln N_t - \ln N_0}{t} \qquad (1)$$

Egg development time was calculated according to Bottrell et al. (1976) for "all cladocera". Some of our own experiments at summer temperatures (17–19 °C) showed that this population has a temperature dependence of its development that is comparable to Bottrell's "general cladocera" equation.

For the comparison of mortality rates, a Box-Whisker Plot and a nonparametric Kruskal-Wallis analysis were applied.

Fish larvae were sampled with a large (0.5 m diameter) conical net, 250 μm mesh size, with flowmeter. Two replicate fish samples were collected at the limnetic zone. Trawls of 3–6 m^3 were made with a rowing boat. Fishes of the littoral zone were sampled with a dip net. All fish samples were preserved in 10% formalin solution previously treated with carbonate water to avoid food regurgitation. Total length of individuals was measured to the nearest 0.1 millimeter by means of a caliper.

Digestive content analyses were made for all fish collected. The entire digestive tract was removed and dissected under a stereomicroscope in a Sedgwick-Rafter chamber. Preys were enumerated under a microscope for a total of 232 *Galaxias*. Copepods were classified and counted by instars within species, and rotifers and cladocerans were classified and counted by species. Complete counts of preys were made for all gut contents.

Prey species preference was estimated by computing the Ivlev electivity index, which is one of the most common indices

$$I = \frac{r_i - p_i}{r_i + p_i} \tag{2}$$

where r_i and p_i are the proportions of species i in the gut content and in the environment, respectively.

Results

Two zooplankton community structures were recorded during the sampling period. In spring, two cladocerans coexisted in Laguna Ezquerra. *Ceriodaphnia dubia* Richard had a unimodal cycle from October to December with maxima of 80 ind l^{-1} towards the end of November. *Bosmina longirostris* appeared throughout the whole period. A density of about 100 ind l^{-1} of *Bosmina* was recorded from October to December, after which it declined towards the end of December and January and then increased reaching 700 ind l^{-1} in late February. The summer community structure consisted almost of rotifers only. Individual densities and species richness increased from December to March up to 1200 ind l^{-1} and 7 species, respectively. *Bosmina longirostris* was the only cladoceran in the summer season (Fig. 1).

Copepods as a whole were present during all the study period. The calanoid *Boeckella gracilipes* had a temporal variation as a function of its developmental stages. Nauplii were present during spring and summer with two maxima, one in October (the end of winter cohort) and another one in January. Copepodites developed during spring and adults persisted at low densities during summer. Cyclopoids (*Microcyclops anceps* (Richard) and *Tropocyclops prasinus meridionalis* (Kiefer)) were present during spring and summer as nauplii. Copepodites and adults were very scarce in the zooplankton samples (Fig. 2).

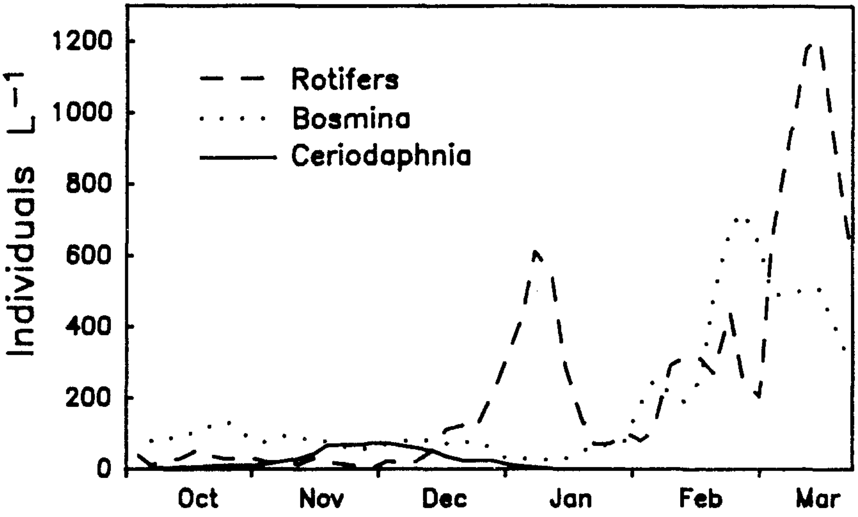

Figure 1. Cladoceran and rotifer density in Laguna Ezquerra during the 1988/89 study period

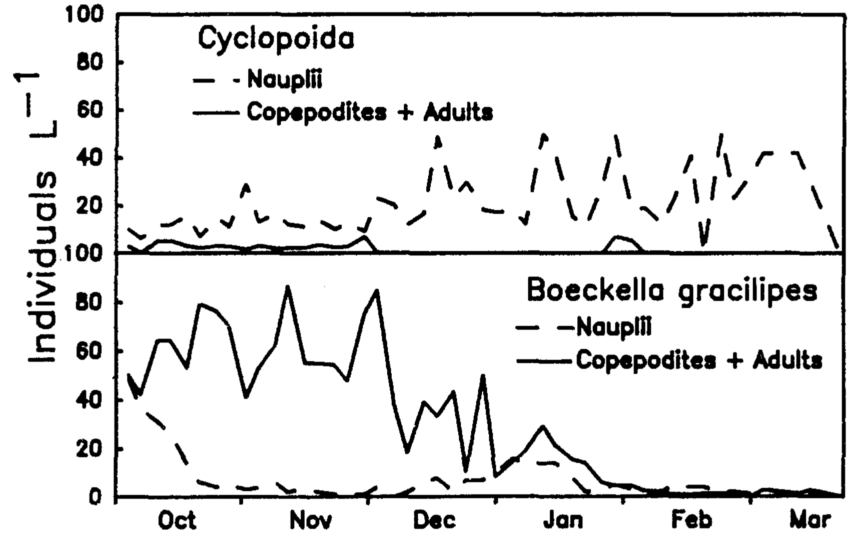

Figure 2. Copepod density in Laguna Ezquerra during the 1988/89 study period. Cyclopoida include *Microcyclops anceps* and *Tropocyclops prasinus meridionalis*

Galaxias early life stages were collected from November 1988 on. Fish were grouped in two sizes corresponding to larvae and juveniles (Fig. 3). Larvae of total length less than 15 mm appeared from November to January and were restricted to the limnetic zone. Juveniles were larger than 20 mm and were present from January to March in both the limnetic and littoral zones. It must be noted that no individuals of size between 15 to 20 mm were collected. This may be due to a deficiency of the

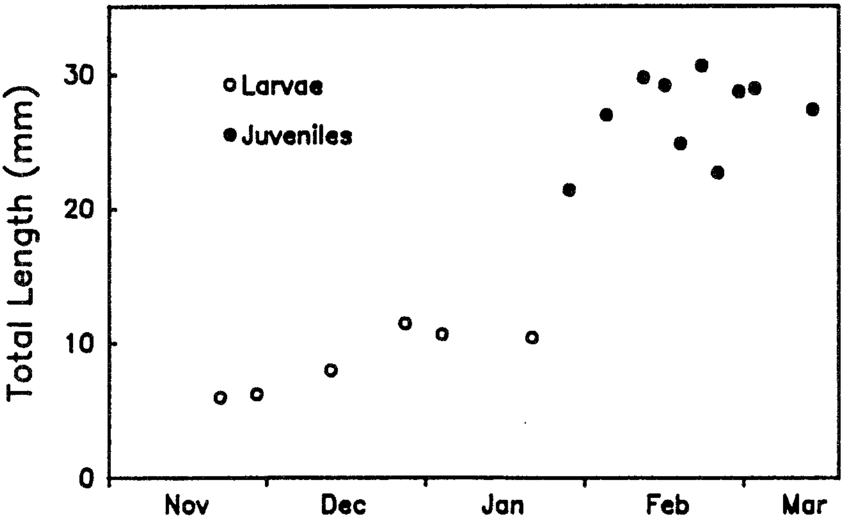

Figure 3. Total length (mm) distribution of early stages of *Galaxias maculatus* in Laguna Ezquerra during the 1988/89 study period. Average for each sampling date

sampling techniques used. According to Cussac et al. 1992, fish density in Laguna Ezquerra was less than 1 ind m^{-3}, estimated by echosounding.

G. maculatus adults are carnivorous euriphagic including in their diet chironomid larvae as a major item (Ferriz, 1984). The shift to this mainly benthonic diet occurs at 40–50 mm total length. The diet of *Galaxias* larvae and juveniles included 13 prey items of which 11 are planktonic (Table 1). This reveals that *Galaxias* larvae have pelagic habits, and although juveniles have intralacustrine movements (Cussac et al., 1992, they feed mainly in the limnetic zone. Electivity analysis showed that there is a noticeable change according to fish size and zooplankton structure. Individuals less than 15 mm had a very high electivity for nauplii of calanoids and cyclopoids (Fig. 4). Nauplii are the only prey positively selected by *Galaxias* larvae. All preys of larval gut contents were smaller than 170 μm. Juveniles switched their electivity to *Bosmina* (Fig. 4). Although *Bosmina* is a very important prey for juveniles, Ivlev's index was higher than 0.5 only in 1% of the fish. In late summer, this cladoceran represents almost the only item of *Galaxias* juveniles diet. Nevertheless, the weak selectivity observed is due to a very high availability of this prey. We also observed a high electivity of juveniles (Ivlev's index = 1) for cyclopoid copepods (copepodites and adults of *Microcyclops anceps* and *Tropocyclops prasinus meridionalis*). Cyclopoids were absent in zooplankton samples causing these extreme Ivlev's values. Cyclopoid limnetic population cycle was made up of nauplii almost exclusively. The densities of the later developmental stages were always very low. This may be due to a diapause as a means of escape from predation during a vulnerable period (Walls et al., 1990), or due to their presence in habitats other than the limnetic zone. Probably, during intralacustrine movements, juveniles fed on these preys. Nevertheless, cyclopoid densities in the gut contents were extremely low in comparison with those of *Bosmina*. Rotifers appeared in juveniles' guts during summer when rotifer densities were very

Table 1. List of prey species of larvae and juveniles of *Galaxias maculatus*

Rotifera		
Keratella cochlearis (Gosse)	+	
Polyarthra vulgaris (Carlin)	+	
Pompholix sulcata (Hudson)	+	
Trichocerca similis (Wierzejski)	+	
Cladocera		
Bosmina longirostris (O.F.M.)	+	
Ceriodaphnia dubia (Richard)	+	*
Chydorus sp	–	
Copepoda		
Boeckella gracilipes (Daday) nauplii	+	
Microcyclops anceps (Richard) nauplii	+	
Microcyclops anceps copepodites + adults	+	*
Tropocyclops prasinus meridionalis (Kiefer) nauplii	+	
Tropocyclops prasinus meridionalis copepodite + adults	+	*
Ostracoda	–	

References:
+ found in plankton samples
* not recorded in plankton when eaten

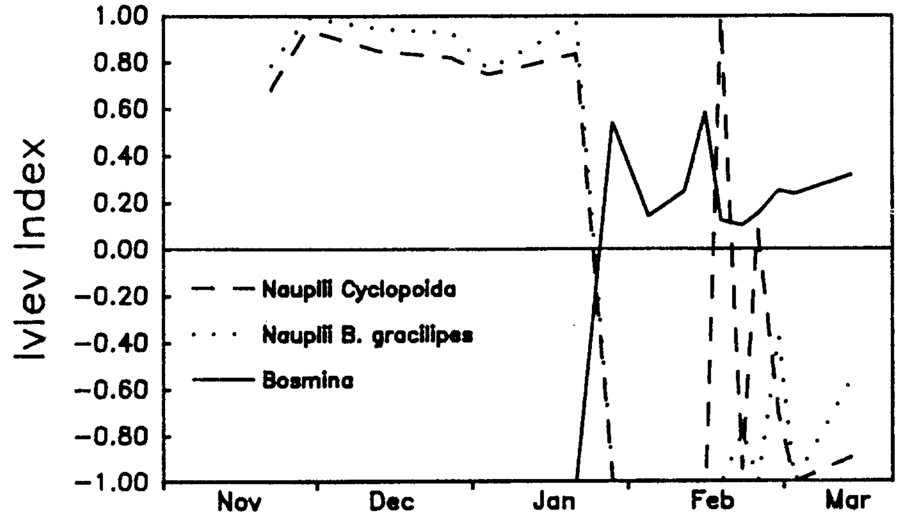

Figure 4. Ivlev index values for the most important preys of the early stages of *Galaxias maculatus*

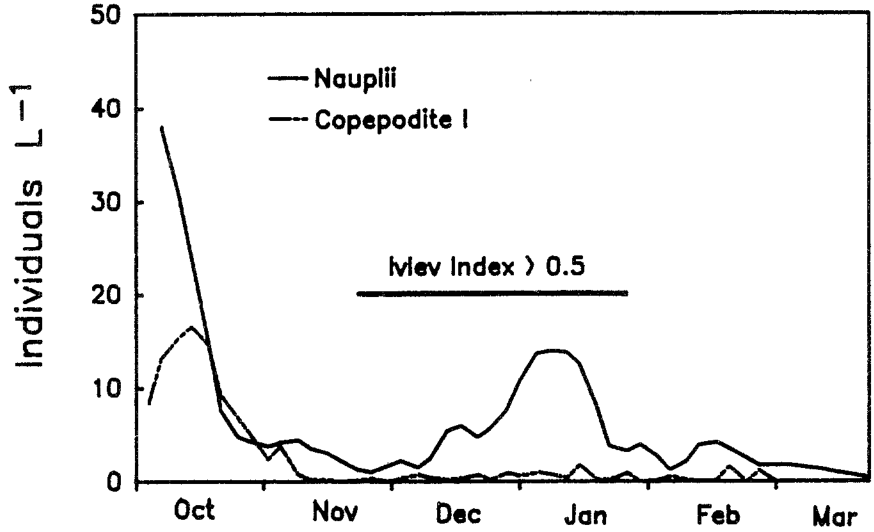

Figure 5. Nauplii and copepodite I density of *Boeckella gracilipes*. The horizontal line shows the period when the Ivlev index was > 0.5 for nauplii

high (Fig. 1). Although rotifers may be an additional food item, it is clear that *Galaxias* does not select these preys.

Ceriodaphnia dubia coexisted with *Bosmina* from October until December, then it disappeared and was absent in plankton samples for the whole summer season (Fig. 1). However, in February individuals of *Ceriodaphnia* were recorded in the guts of *Galaxias* juveniles. *Ceriodaphnia* was never observed in the gut content during its unimodal cycle. These situations caused the extreme electivity values of −1 (November–December) and +1 (February, 16 and 20). Since *Ceriodaphnia* summer density was undetectable it seems probable that *Galaxias* juveniles were able to detect it because of a high visual selection.

Predation has a general effect on prey life-history (Gliwicz and Pijanowska, 1989). The analysis of zooplankton prey populations is necessary for understanding the *Galaxias* predation effects. The calanoid copepod *Boeckella gracilipes* has a marked annual age sequence (Balseiro and Modenutti, 1990; Balseiro, 1991). Nauplii have a maximum in winter and a second one in early summer. In Laguna Ezquerra we observed a recruitment of CI in spring corresponding to the winter cohort (Fig. 5). However, the recruitment of CI from summer nauplii actually failed. We have superimposed Ivlev's values for nauplii higher than 0.5 in Fig. 5 (horizontal line) and have linked the absence of CI recruitment with *Galaxias* larval predation.

In the case of *Bosmina* we analysed the mortality rates directly. We divided the whole period in two fractions. One fraction includes the mortality values when *Bosmina* is not eaten by *Galaxias* (October–January), and the second one (January–March) includes those mortalities when we measured positive Ivlev's values (Fig. 6). A Kruskal-Wallis analysis showed on differences in mortality values between these

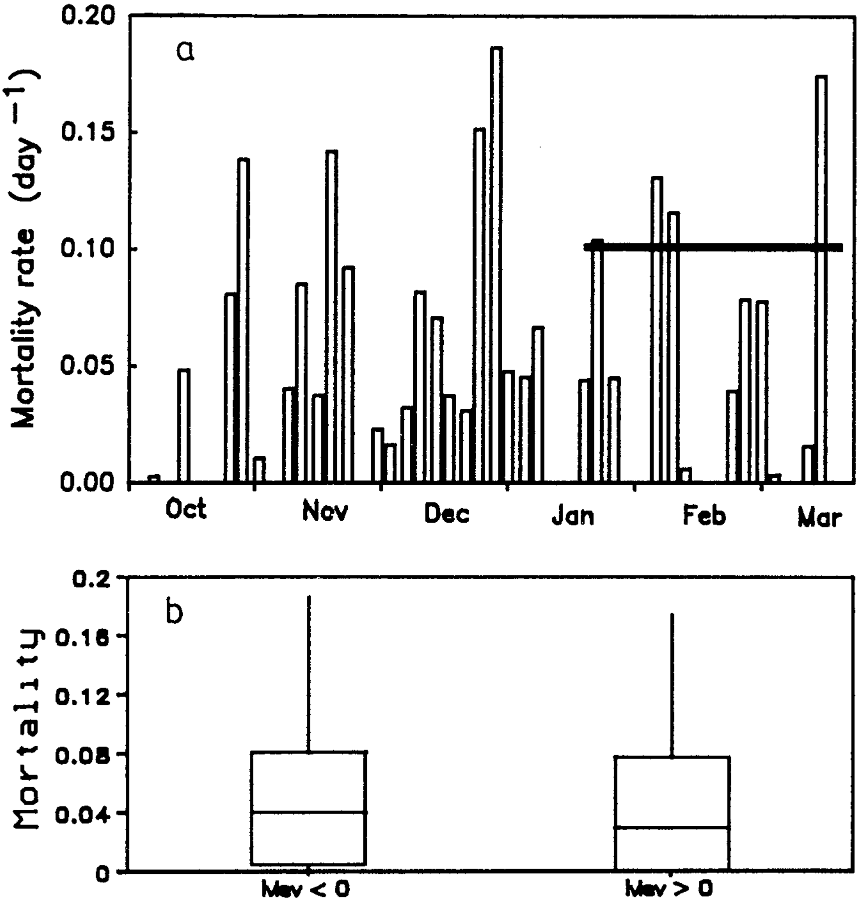

Figure 6. a) Mortality rates of *Bosmina longirostris*. The horizontal line shows the period when the Ivlev index was > 0 for *Bosmina longirostris*. b) Box-Whisker plot of mortality rates comparing the periods with (Ivlev > 0) and without (Ivlev < 0) predation pressure

two fractions (P > 0.5). This result means that *Galaxias* does not increase *Bosmina*'s mortality although *Galaxias* juveniles feed almost exclusively on this prey.

Discussion

Galaxias maculatus larvae and juveniles showed a marked planktophagous diet. Its effect on zooplankton populations is different according to fish size and prey.

During late spring, when larvae appear, the effect of predation seems to be restricted to the naupliar stages of *Boeckella gracilipes* population. In earlier studies (Balseiro and Modenutti, 1990) we had observed the development of copepodite stages during spring, corresponding to the winter nauplius cohort. A second cohort of naupliar stages appears during November–January. In Laguna Ezquerra, the same pattern has been detected during this study. The lack of CI recruitment in summer (Fig. 5) indicates a high naupliar mortality. Based on our results, we assume that *Galaxias* larval predation causes this mortality. As a consequence, the summer *B. gracilipes* cohort fails to develop. This explanation agrees with previous observations that the only successful cohort is the one that begins in winter, and that the summer population is made up of adults and few late stages copepodites (Balseiro and Modenutti, 1990).

Fish larvae also feed on cyclopoid nauplii. However, the predation effect on these populations is unclear, as copepodites and adults may move to other habitats, including bottom and littoral, or enter a diapause to avoid temporal overlap with a predator (Nilssen, 1977; Hairston, 1987). This feature precludes to make a cohort analysis for evaluating the effect of fish predation on naupliar mortality.

Since *Galaxias* larvae did not eat cladocerans, the coexistence of *Bosmina* and *Ceriodaphnia* during spring is not affected by fish predation. The extinction of *Ceriodaphnia* in December and the prevalence of *Bosmina* is determinated by food limitation and exploitative competition as was demonstrated through laboratory and field studies (Balseiro et al., 1992).

In summer *G. maculatus* juveniles seem to have an important effect on *Ceriodaphnia dubia*. This cladoceran was not recorded in summer plankton samples. However, individuals of *Ceriodaphnia* were observed in the guts of *Galaxias* juveniles. This high selectivity for *Ceriodaphnia* could imply that *Ceriodaphnia* is not able to become abundant in the plankton because its incipient population is strongly depressed by predation. Interannual changes in fish predation pressure may allow *Ceriodaphnia* to reappear in a scarce summer population, as was observed in February–March 1988 (Balseiro, personal observation).

Although *B. longirostris* is the most important prey in the diet of *Galaxias* juveniles, the predation effect seems to be weak. A strong fish predation pressure on cladocerans would result in populations with low density, high fecundity and high mortality (Ghilarov, 1982). However, our data showed very contrasting results. *Bosmina* had very high densities (Fig. 1), and its decline was a consequence of a drop in fecundity due to starvation (Balseiro et al., 1991). On the other hand, the mortality analysis (Fig. 6) showed no differences between the periods with and without predation on this population (K–W $P > 0.5$).

The observed shift in *Galaxias*' diet towards larger prey sizes is related with its own growth. The size of a fish's gape determines the maximum prey size (Wright and O'Brien, 1984; Liem, 1984). Early life stages are effectively gape limited and they increase their prey size when they grow (Gliwicz and Pijanowska, 1989). In fact, Ferriz (1984) reported another shift towards a very broad diet in *Galaxias* from juveniles to adults. Carnivorous feeding habits with a wide variety of aquatic and terrestrial organisms was found in *Galaxias maculatus* adults (Mc Dowall, 1968; Pollard, 1973; Ferriz, 1984). We observed preference of *Galaxias* larvae for naupliar stages of calanoid and cyclopoid copepods less than 170 µm in length. As a consequence of the increase in gape, the growing predators switched to *Bosmina* (up to 350 µm) as dominant item of the diet. The absence of copepodites and adults of *Boeckella* in the diet must be related to the high evasion rates of calanoid copepods (Wright and O'Brien, 1984). Cyclopoids are less evasive and cladocerans are unable to evade the suction attack of planktivorous fishes (Drenner et al., 1978; Kerfoot et al., 1980).

It is clear that in a zooplankton assemblage with large species (*Daphnia*), fish predation pressure may produce dramatic changes in these populations (Brooks and Dodson, 1965). However, within a small-species community, fish predators may not greatly reduce on species over another (Vanni, 1987). In Laguna Ezquerra, predation by *Galaxias* did not produce any shifts in the community structure. With the hatching of larvae in late spring, the *B. gracilipes* population is partially affected through the failure of the summer cohort. Nevertheless, the population remains made up by late stages of copepodites and adults which are not eaten. As *Galaxias* changes towards larger items, *Bosmina* becomes the principal prey, but the predation effect is not related with an increase in mortality. However, we believe that *Galaxias* juveniles may have a greater effect on other cladocerans such as *Ceriodaphnia*, preventing its reappearance. The beginning of summer is the time when predation on zooplankton has the greatest effect in most lakes in the temperate zones (Gliwicz and Pijanowska, 1989). This appears to be the case also in Laguna Ezquerra, when *Galaxias* juveniles attain a large-enough gape size to cover the whole range of prey species. *Ceriodaphnia* seems to be affected by a high predation pressure and unable to compensate for predatory losses.

ACKNOWLEDGEMENTS

To M. A. Battini for the field assistance. This work was supported by a IFS Grant A/1590-1 to E. G. B. and CONICET 5168/89 to B. E. M.

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Received 11 March 1992;
revised manuscript accepted 19 October 1992.