



## Predator associated morphology in *Galaxias platei* in Patagonian lakes

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Among 158 *Galaxias platei* individuals, collected from nine deep Andean lakes and from one shallow lake on the Patagonian steppe, morphological characters associated with caudal fin length were negatively correlated with predation intensity as measured by the incidence of piscivory. Fish from lakes with high rates of piscivory had relatively short caudal fins and those from lakes with low piscivory had long caudal fins. It is hypothesized that in this species caudal fin length affects swimming ability and thus, ability to escape from predators. The population of *G. platei* from Lake Espejo with an intermediate level of piscivory contained individuals with both long and short caudal fins. Morphological variation within this lake was related to the exploitation of food resources and habitat; individuals with shorter tails ate more amphipods and inhabited shallower habitats. The results indicated that while the among-lakes morphological variation in *G. platei* was influenced largely by differences in predation intensity, within-lake morphological variation, where predation was intermediate, appeared to be affected by both predation and differences in the exploitation of food resources.

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### INTRODUCTION

Intraspecific morphological variability in fishes often results from competition for resources in heterogeneous environments (Robinson & Wilson, 1994; Bell & Andrews, 1997; Skúlason *et al.*, 1999) or from spatial or temporal heterogeneity in predation intensity (Brönmark & Miner, 1992; Swain, 1992; Hori, 1993). Trophic polymorphisms are relatively frequent in oligotrophic, post-glacial, temperate lakes with low species diversity, and have been reported for fishes in both the northern hemisphere [e.g. sticklebacks, *Gasterosteus* sp., Taylor & McPhail, 1999; Arctic charr *Salvelinus alpinus* (L.), Skúlason *et al.*, 1999; Gíslason *et al.*, 1999; whitefishes, *Coregonus* sp., Bernatchez *et al.*, 1999, Taylor, 1999], and the southern hemisphere (Ruzzante *et al.*, 1998; Logan *et al.*, 2000).

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The family Galaxiidae inhabits marine and fresh waters of Australia, New Zealand, South Africa and South America (McDowall, 1971; Campos, 1979). Generally the family exhibits a marked tendency to morphological variation, particularly in trophic related characters and in characters associated with the caudal skeleton (McDowall, 1998, 1999). In a comprehensive recent analysis, McDowall (1998) documented ecomorphological divergence within *Paragalaxias*, a genus comprising four species, two of which live sympatrically. Also genetic and morphological differences have been documented in *Galaxias occidentalis* Ogilby between and within river populations from south-western Australia (Watts *et al.*, 1995).

In southern South America there are 15 native and 10 introduced fish species (Ringuelet *et al.*, 1967; López *et al.*, 1987; Navas, 1987; Ortubay *et al.*, 1994). Three of the native species belong to the genus *Galaxias*: *Galaxias globiceps* Eigenmann is restricted to the western side of the Andes and *Galaxias platei* Steindachner, and *Galaxias maculatus* Jenyns, are found on both sides of the Andes (McDowall, 1971; Ringuelet, 1975; Campos, 1979; Arratia *et al.*, 1983; Milano & Vigliano, 1997). *Galaxias platei* exhibits considerable morphometric variation throughout its distributional range from northern Patagonia to Tierra del Fuego, and this variation has been attributed to thermal causes (McDowall, 1971). The species has an extended larval period (Barriga *et al.*, 2002) and adults appear to be adapted both morphologically and physiologically to benthic life: gills open laterally and fins are also placed laterally, eyes are located rather dorsally, and upper and lower mouth lips are thickened (Matthews, 1998). Retinal cones of *G. platei* exhibit high mitochondrial complexity (Schoebitz *et al.*, 1973; Randall *et al.*, 1997) suggesting adaptation to the high energy requirements for vision in darkness (Ali *et al.*, 1990; Jobling, 1995) and the species also exhibits a high endurance to anoxia (Barriga *et al.*, 1999).

Competition with introduced salmonids and other species affects the spatial distribution of some galaxiids (McIntosh, 2000) and is known to have caused their local extirpation in some stream areas (Tilzey, 1976). Predation may also have an influence on the spatial distribution of *G. platei* (Macchi *et al.*, 1999). No data are available on the abundance and distribution of the native fish species before the introduction of salmonids during the first half of the last century. It cannot be stated, therefore, to what degree this introduction affected the abundance and distribution of the native fish fauna or whether different species have been affected differentially. It is known, however, that the abundant and widely distributed native Patagonian fishes *G. maculatus*, *Odontesthes hatcheri* (Eigenmann) and the various *Percichthys* species are exposed to predation by native fishes and by salmonids as they regularly appear in littoral gillnet and seine collections and in stomach content analyses (Macchi *et al.*, 1999). This is not the case with *G. platei*, which is mostly absent from the littoral zone and occurs almost exclusively in collections associated with benthic habitat at  $\geq 30$  m depth (Milano & Vigliano, 1997), below the thermocline and the euphotic zone (D. Milano pers. obs.). The absence of *G. platei* in the upper littoral zone is probably associated with the relatively high predation in this area possibly by the native piscivorous *Percichthys trucha* (Cuvier & Valenciennes) and by introduced salmonids (Arenas, 1978; Campos, 1985; Macchi *et al.*, 1999).

In this study morphological variation is examined in adult *G. platei* from nine deep glacial Andean lakes and one shallow lake on the Patagonian steppe. The variation is compared with the incidence of piscivory and with trophic characteristics of the fish.

## MATERIALS AND METHODS

### STUDY SITES

The variation in morphology and diet was examined among *G. platei* individuals collected from nine oligotrophic glacial lakes in the Andean temperate rainforest of south-western Argentina (from north to south: Espejo, Moreno, Gutiérrez, Mascardi, Los Moscos, Fonck, Steffen, Martin and Rivadavia) and from one pond (Coyte) in the Patagonian steppe east of the Andes (Fig. 1). The lakes belong to different basins and exhibit some important physical and chemical differences (Table I). Lakes Espejo, Moreno and Gutiérrez drain into the Lake Nahuel Huapi, from which the Limay River originates. The Limay River drains into the Atlantic Ocean. Coyte Pond also drains into the Atlantic Ocean as one small headwater of the Chubut basin and *G. platei* was the only fish caught in this pond. The remaining Andean lakes, all drain into the Pacific Ocean: Lakes Mascardi, Los Moscos, Fonck, Steffen and Martin through the Manso River and Lake Rivadavia through the Futaleufú River. Due to the low samples sizes, fish from the Manso River basin were treated as coming from a single lake.

### DATA COLLECTION

Fish were collected with gillnets (15, 20, 30, 50, 60 and 70 mm bar mesh sizes, each 10 m long and 2 m high) placed at 10, 20, 30, 50 and (occasionally) 100 m depth on the bottom following Vigliano *et al.* (1999). Gillnets were set parallel to the shore and left in place overnight. The majority of the lakes were sampled in the summer of 1998. In addition, Lakes Gutiérrez and Moreno were sampled seasonally, Gutiérrez, eight times from 1995 to 1997 and Moreno, four times during 1999. Coyte Pond was sampled in March of 1996. All the fish were fixed with 4% formaldehyde, in the field. All native species were identified, including *G. platei*, following Ringuélet *et al.* (1967), McDowall (1971) and Berra & Ruiz (1994).

### MORPHOLOGICAL MEASUREMENTS

Using a digital calliper 27 morphological characters in 158 adult specimens, >103.7 mm in standard length,  $L_S$ , were measured in the laboratory. These characters largely coincide with those considered by McDowall (1971) and Berra & Ruiz (1994). The 27 characters were:  $L_S$ , caudal fin length (CFL), depth of the caudal peduncle (DCP), caudal peduncle length (CPL), pre-dorsal length (PDL), pre-anal length (PAL), length of the dorsal fin base (LDB), maximum dorsal fin length (MDL), length of the anal fin base (LAB), maximum anal fin length (MAL), pre-pelvic length (PVL), pectoral-pelvic distance (PVD), maximum pectoral fin length (MPL), pelvic-anal distance (VAD), maximum pelvic fin length (MVL), head length (HEL), head depth (HED), head width (HEW), snout length (SNL), inter-orbital width (IOW), eye diameter (EYD), length of the upper jaw (LUJ), length of the lower jaw (LLJ) and mouth width (MOW) (Fig. 2).

There were significant differences in body size of *G. platei* among lakes (Kruskal-Wallis test,  $n=158$ ,  $P<0.001$ , Table II). To eliminate both inter and intra-lake size dependent differences all measurements were adjusted to a mean  $L_S$  using the relationship:  $AM_i = \log(OM_i) - b[\log(L_{Si}) - \text{mean}(\log(L_S))]$  where  $AM_i$  and  $OM_i$  are the adjusted and original measures for the character in the individual  $i$ ,  $L_{Si}$  is the individual standard length, and  $b$  is the regression coefficient of the logarithm of OM and the logarithm of  $L_S$  (Cussac *et al.*, 1998; Ruzzante *et al.*, 1998). The constancy of  $b$  over the size range was assessed through double logarithmic scatter plots of AM v.  $L_S$ , following Battini (1997). Measurements were adjusted using lake-specific regression coefficients ( $b$ ) and a common overall  $L_S$  mean. There were no differences between sexes for any of the

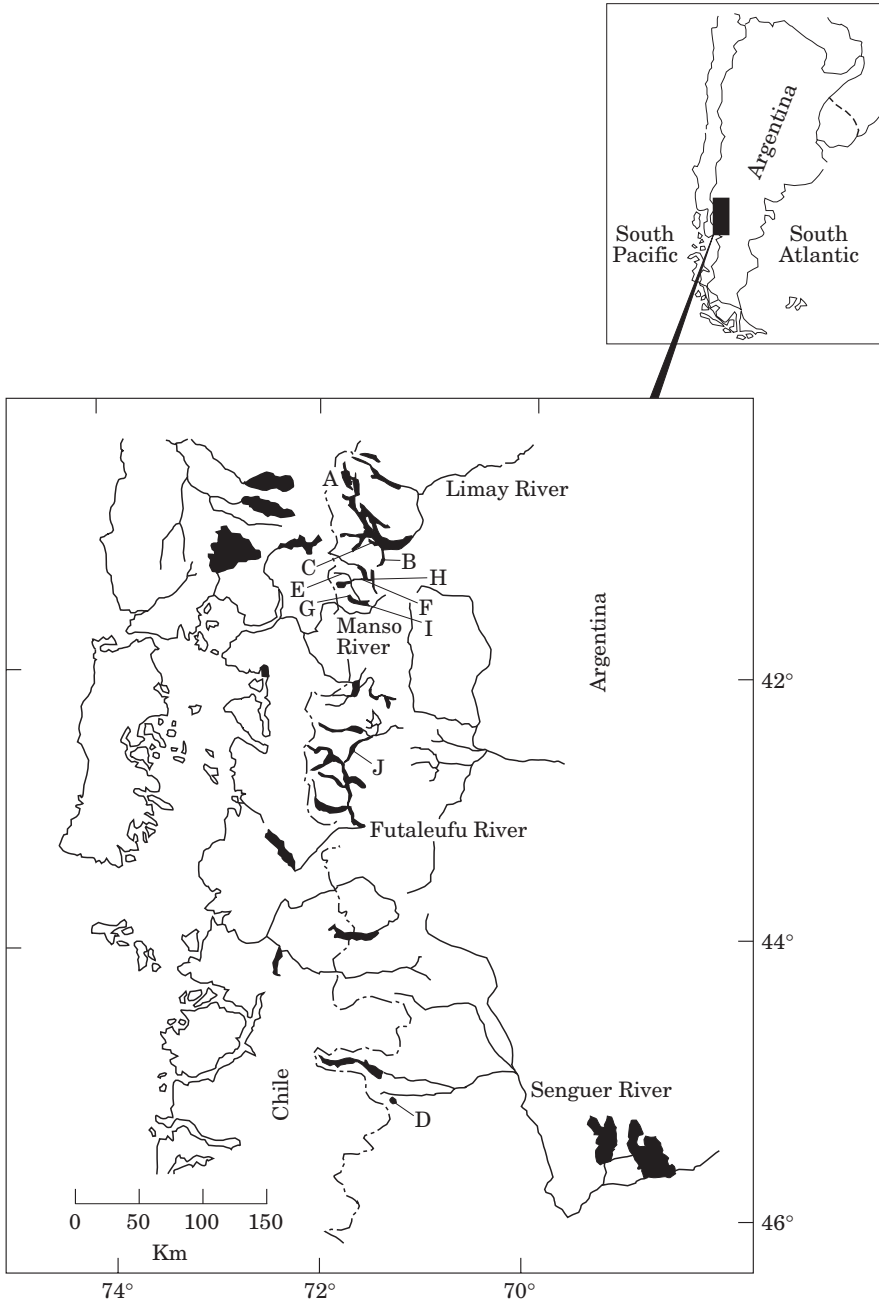


FIG. 1. Geographic location of lakes. All lakes are situated within Neuquén, Río Negro and Chubut Provinces, Argentina. Limay River basin: A, Espejo; B, Gutiérrez; C, Moreno. Chubut River basin: D, Coyte. Manso River basin: E, Fonck; F, Los Moscos; G, Martín; H, Mascardi; I, Steffen. Futaleufu River basin: J, Rivadavia. Some major lakes in the area were not sampled.

TABLE I. Physical characteristics of the lakes studied

Lake	Maximum depth (m)	Mean depth (m)	Volume ( $\times 10^6 \text{ m}^3$ )	Area ( $\text{km}^2$ )	[Perimeter (km)] [Area ( $\text{km}^2$ )] <sup>-1</sup>	Secchi disk (m)	Conductivity ( $\mu\text{S cm}^{-1}$ )
Espejo	245	—	—	38.2	1.7	16.0	33.7
Gutiérrez	111	80	1307	16.4	1.5	18.0	58.1
Moreno	112	63	666	10.6	3.2	19.5	37.1
Coyte	6	—	—	7.3	1.8	0.3	304.0
Fonck	85	40	148.6	3.7	3.9	9.5	29.8
Los Moscos	50	29.55	67.9	2.3	2.6	12	—
Martin	68	43	76.6	1.78	5.4	11	—
Mascardi	218	111	4351.2	39.2	1.4	12	44.9
Steffen	76.8	46.7	294	6.3	2.6	13	—
Rivadavia	147	104	2250	21.7	1.5	20.5	56.0

traits measured, with the exceptions of eye diameter (Mann–Whitney  $U$  test,  $n=158$ ,  $P<0.002$ ), the length of the upper jaw (Mann–Whitney  $U$  test,  $n=158$ ,  $P<0.011$ ) and the length of the lower jaw (Mann–Whitney  $U$  test,  $n=158$ ,  $P<0.002$ ). These three variables were adjusted using sex specific slopes. Adjusted variables were used to assess the existence of morphological types.

Principal component analysis (PCA) and discriminant analysis were conducted. The Pearson coefficient was applied to correlation analysis while the Spearman coefficient was used when assumptions regarding normality were not validated. All statistical analyses were conducted with SPSS (Norusis, 1986).

## DIET

Gut contents were examined of all individuals of *G. platei* and of the other fish species collected (Tables III and IV). For each prey category (i) the relative volume ( $V_i$ ) contributed to the total volume of food in each stomach was calculated. The specimens considered were caught at different times during the calendar year. For comparisons among lakes individuals caught in the summer ( $n=135$  for *G. platei*) were used.

Diet differences among lakes were tested using PCA and discriminant analysis. As with the morphological data, correlations were estimated using the Pearson or Spearman coefficients.

For each lake, piscivory was estimated as the percentage over all species, of fish with fish in their guts. Kruskal–Wallis was used to test for mean differences when normality assumptions were not validated. All statistical analyses were conducted with SPSS (Norusis, 1986).

## RESULTS

### STUDY SITES

There are important differences in the physical characteristics of Coyte Pond and the Andean lakes as well as among the glacial, strongly oligotrophic lakes possessing a dissimilar degree of shoreline development (Table I). The fish species composition also differed among lakes (Table III). Most notably *P. trucha* and *O. hatcheri* were both absent from Lake Gutiérrez and from all lakes in the Manso Basin. The small, littoral fish, *G. maculatus* was absent from Lake Rivadavia where *Aplochiton zebra* Jenyns, a small littoral species absent

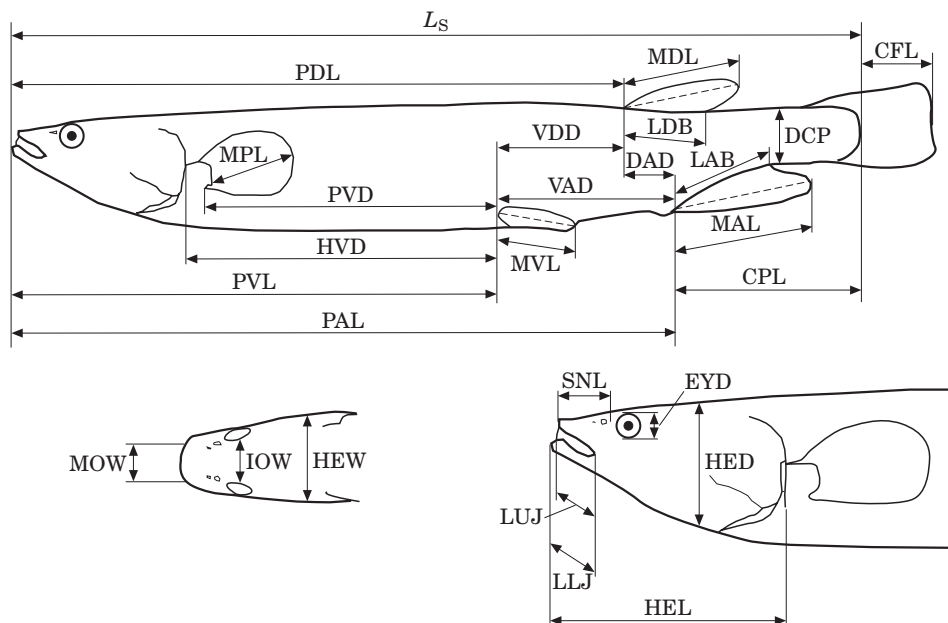


FIG. 2. Dimensions measured in the morphological analysis of *Galaxias platei*. Standard length,  $L_s$ ; caudal fin length, CFL; depth of the caudal peduncle, DCP; caudal peduncle length, CPL; pre-dorsal length, PDL; pre-anal length, PAL; length of the dorsal fin base, LDB; maximum dorsal fin length, MDL; length of the anal fin base, LAB; maximum anal fin length, MAL; pre-pelvic length, PVL; pectoral-pelvic distance, PVD; maximum pectoral fin length, MPL; pelvic-anal distance, VAD; maximum pelvic fin length, MVL; pelvic-dorsal fins distance, VDD; dorsal-anal fins distance, DAD; head-pelvic distance, HVD; head length, HEL; head depth, HED; head width, HEW; snout length, SNL; inter-orbital width, IOW; eye diameter, EYD; length of the upper jaw, LUJ; length of the lower jaw, LLJ; mouth width, MOW. MOW was measured ventrally as an intercomisural width.

elsewhere, was found. Lake Rivadavia exhibited the highest overall fish abundance, which was due in particular to high abundance of *Oncorhynchus mykiss* (Walbaum), *P. trucha* and *O. hatcheri*. *Salmo trutta* L. and *Salvelinus fontinalis* (Mitchill) were instead less abundant in Lake Rivadavia than elsewhere.

#### INTERSPECIFIC DIET DIFFERENCES AND INCIDENCE OF PISCIVORY

There were major interlake differences in the diet of the various species. Stomach content analysis revealed the general absence or near absence of planktonic food items in all lakes except Lake Rivadavia. *Galaxias platei* exhibited a piscivorous (cannibalistic) habit in Coyte Pond but not elsewhere. The relative importance of benthos, fishes and terrestrial insects in the diet of salmonids differed among lakes (Fig. 3).

Piscivory (% of fish with fishes in their guts) was lowest in Lake Rivadavia (1.2%) and in the lakes from the Manso Basin (8.5%) and it was highest in Gutiérrez and Moreno Lakes (35.6% and 44.2%, respectively). Piscivory was intermediate in Lake Espejo and Coyte Pond (14.5% and 24.0%, respectively). *Galaxias platei* was the only fish species present in Coyte pond (Table III), thus, piscivory in this pond was due entirely to cannibalism (Table IV).

TABLE II. Standard length (mean, median and range) and number of *G. platei* captured by sex, for each lake

Lake	$L_S$ (mm)			Females	Males
	Mean	Median	Range		
Espejo	190	195	130–275	17	20
Gutiérrez	190	189	140–260	14	11
Moreno	229	250	104–276	14	4
Coyte	217	195	175–305	11	16
Fonck	139	130	115–190	10	1
Los Moscos	154	155	126–180	3	0
Martin	110	110	110	1	0
Mascardi	172	175	110–255	10	5
Steffen	132	125	117–155	3	0
Rivadavia	192	188	130–290	10	8

MORPHOLOGICAL MEASUREMENTS IN *G. PLATEI* AND PISCIVORY

To examine potential interlake shape differences among *G. platei* PCA was performed using all 26 size-adjusted morphometric variables on 149 fish (nine individuals were rejected because of missing values). Six principal components explained 68% of the total variance (Table V). Discriminant analysis was then conducted for *G. platei* grouped by lake and five significant ( $P < 0.001$ ) discriminant functions were obtained. Together, these five functions classified correctly to their lake of origin 96% of the 149 individuals. The five functions explained a major proportion of the total variability (Table VI). Incidence of piscivory was then correlated with the six principal components and with the five discriminant functions. In spite of the low number of lakes, PC4 (11% of total variance) correlated significantly with the incidence of piscivory (Pearson coefficient  $r = -0.95$ ,  $n = 6$ ,  $P < 0.003$ ). The variables with the highest load on PC4 were head width, mouth width, height of the caudal peduncle, caudal fin length, snout length and head depth.

A plot of caudal fin length and  $L_S$  (Fig. 4) indicated that *G. platei* inhabiting lakes with a relatively high incidence of piscivory (Lakes Gutierrez and Moreno, Table IV) were characterized by relatively short caudal fins (Fig. 4). Conversely, *G. platei* inhabiting lakes with low piscivory (Lake Rivadavia and the lakes from the Manso Basin, Table IV) exhibited relatively long caudal fins (Fig. 4). Espejo was the only lake with intermediate body shape. Caudal fin length was also the variable with greatest difference between lakes with relatively high (Gutiérrez and Moreno) and low (Rivadavia and lakes in the Manso Basin) piscivory, with adjusted mean values differing by up to 13.8% of the total mean.

DIET ANALYSIS OF *G. PLATEI*

There were differences among lakes in the diet of *G. platei* (Fig. 5). *Galaxias platei* from Lake Rivadavia had more detritus, molluscs and terrestrial insects in their guts than *G. platei* caught elsewhere. Conversely, *G. platei* from Lake Rivadavia did not feed on Amphipoda, present in the stomach content of *G. platei* caught elsewhere (Fig. 5). Large and mobile prey dominated the stomach

TABLE III. Composition of the fish assemblages by lake. Numbers indicate catch by unit of effort [number of fishes (100 m<sup>2</sup> mesh for 15 h)<sup>-1</sup>] in summer. \*Littoral captures with seine or bottom trap; †introduced species

Drainage: River basin: Lake:	Atlantic					Pacific				
	Limay Espejo	Gutiérrez	Moreno	Chubut Coyte	Manso Fonck	Los Moscos	Martin	Mascardi	Steffen	Futaleufu Rivadavia
<i>S. trutta</i> †	0.66	0.97	0.23		0.38	0.74	7.32	1.43	15.07	0.09
<i>S. fontinalis</i> †	2.83	2.23	1.71		4.21	0.74	1.77	1.04	0.73	2.09
<i>O. mykiss</i> †	2.98	7.39	1.89		1.88	1.27	5.05	0.96	2.93	11.17
<i>G. maculatus</i>	*	*	*		*	*	*	*	*	*
<i>G. plabei</i>	3.38	0.39	0.59	*	1.12	0.31	*	0.39	0.54	1.50
<i>A. zebra</i>										*
<i>D. vieidmensis</i>	0.09	0.39	0.12							6.41
<i>O. hatcheri</i>			0.12							10.20
<i>P. trucha</i>	5.77	5.97	5.97							31.46
Total	15.71	11.37	10.63		7.59	3.07	14.15	3.82	19.27	

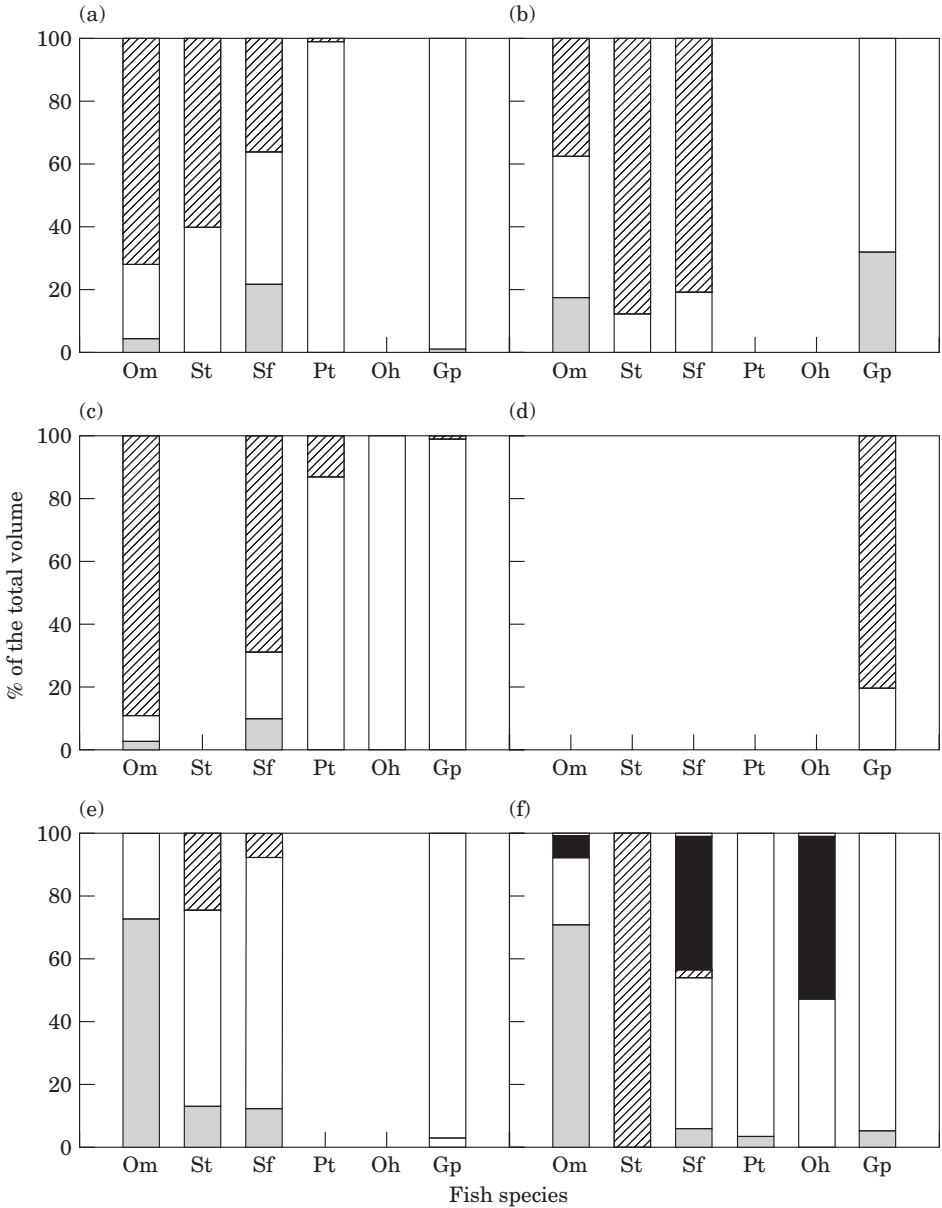


FIG. 3. Diet composition, terrestrial insects (▨), benthos (□), fishes (▤) and plankton (■) (relative volume contributed to the total volume of food in each stomach) of *O. mykiss* (Om), *S. trutta* (St), *S. fontinalis* (Sf), *P. trucha* (Pt), *O. hatcheri* (Oh) and *G. platei* (Gp) in (a) Lake Espejo, (b) Lake Gutiérrez, (c) Lake Moreno, (d) Coyte Pond, (e) Manso Basin and (f) Lake Rivadavia.

content of *G. platei* in Lake Moreno, while Amphipoda, Diptera larvae and pupae, and detritus dominated the stomach content of *G. platei* in the Manso Basin.

A principal component analysis for the diet of *G. platei* demonstrated significant differences among lakes (Kruskal–Wallis test,  $n = 135$ ,  $P < 0.05$ ) for the

TABLE IV. Number of fish analysed and percentage of individuals with fish in their guts within parentheses

	Espejo	Gutiérrez	Moreno	Coyte	Manso Basin	Rivadavia	Total
<i>S. trutta</i>	6 (50)	12 (67)	0 (0)	—	170 (11)	1 (100)	189
<i>S. fontinalis</i>	30 (20)	19 (53)	18 (72)	—	89 (6)	20 (5)	176
<i>O. mykiss</i>	25 (24)	53 (25)	28 (50)	—	110 (9)	80 (0)	296
<i>G. platei</i>	23 (4)	3 (0)	8 (25)	21 (24)	32 (0)	13 (0)	100
<i>O. hatcheri</i>	—	—	—	—	0 (0)	8 (0)	8
<i>P. trucha</i>	54 (8)	—	32 (28)	—	0 (0)	45 (0)	131
Total	138 (15)	87 (36)	86 (44)	21 (24)	401 (9)	167 (1)	900

first nine PCs. Discriminant analysis among lakes based on detritus, Mollusca, Decapoda, Diptera larvae and pupae provided three significant ( $P < 0.007$ ) discriminant functions (Table VII). DF1 for diet (Table VII) correlated negatively (Pearson  $r = -0.91$ ,  $n = 6$ ,  $P < 0.012$ ) with DF2 for morphology (Table VI), where the main variables for DF2 were maximum pelvic fin length, length of the lower jaw, pelvic-anal fins distance and maximum pectoral fin length.

#### MORPHOLOGICAL VARIATION V. DIET WITHIN LAKE ESPEJO

The morphological variation was examined among *G. platei* within Lake Espejo, a lake with an intermediate incidence of piscivory and a large variance in morphology. Using only individuals from Lake Espejo, PCA was conducted on morphology and independently on stomach content. The correlation between these two sets of principal components was then investigated.

Within Lake Espejo, the PC3 for morphology correlated significantly (Spearman coefficient,  $n = 36$ , one individual rejected because of empty gut) with four principal components for diet, PC2 ( $P < 0.005$ ), PC4 ( $P < 0.014$ ), PC5 ( $P < 0.017$ ) and PC7 ( $P < 0.007$ ). These significance values were only indicative of a tendency, due to the large number of tests performed. The main variables involved in PC3 (for morphology) were the pre-dorsal length, pre-anal length and pre-pelvic length. Adjusted pre-anal length was positively correlated (Spearman's  $\rho = 0.41$ ,  $n = 36$ ,  $P < 0.013$ ) with the percentage in volume of Amphipoda in gut content. These results are consistent with the hypothesis that morphological variation in *G. platei* from Lake Espejo is related to differences in the exploitation of food resources (Fig. 6).

There was no significant correlation of diet with depth of collection (Fig. 7). Some aspects of morphology, however, did appear to correlate with depth (PC5, Spearman's  $\rho = -0.46$ ,  $n = 36$ ,  $P < 0.004$ ). Length and depth of the caudal peduncle correlated positively (Spearman's  $\rho = 0.33$ ,  $n = 36$ ,  $P < 0.049$ ) and negatively (Spearman's  $\rho = 0.34$ ,  $n = 36$ ,  $P < 0.049$ ), respectively with depth of capture. Individuals caught in relatively shallow waters appeared to be characterized by relatively short tails, deeper and shorter caudal peduncles and a high volume of amphipods in their guts. Conversely, individuals caught in deeper waters appeared to exhibit relatively long tails, shallower and longer caudal peduncles and a relatively high volume of detritus in their guts.

TABLE V. Interlake shape differences among *G. platei*. Loading for the morphometric variables onto principal components 1 to 6 (PC1 to PC6) and the variance explained. In bold, the highest contribution of each morphometric variable to the six principal components

	PC1	PC2	PC3	PC4	PC5	PC6
Maximum pelvic fin length	<b>0·843</b>	-0·027	0·080	0·061	0·109	0·117
Maximum pectoral fin length	<b>0·825</b>	0·075	0·120	0·084	-0·069	0·032
Maximum dorsal fin length	<b>0·682</b>	0·019	0·192	0·132	-0·189	0·440
Pelvic-anal fins distance	<b>0·593</b>	-0·134	-0·209	0·098	0·295	-0·318
Caudal peduncle length	<b>0·583</b>	-0·082	0·131	-0·009	0·072	0·376
Dorsal fin base length	<b>0·459</b>	0·073	0·060	0·290	-0·210	0·405
Pre-pelvic length	-0·096	<b>0·893</b>	0·227	0·107	-0·142	0·157
Head-pelvic fin distance	-0·145	<b>0·878</b>	-0·186	-0·067	-0·185	0·124
Pectoral-pelvic fins distance	0·169	<b>0·761</b>	-0·117	0·098	0·025	-0·007
Pre-anal length	0·278	<b>0·719</b>	0·124	0·128	0·341	-0·128
Length of the lower jaw	-0·154	0·047	<b>0·886</b>	0·101	-0·016	0·046
Length of the upper jaw	-0·121	0·027	<b>0·868</b>	0·129	0·090	0·024
Head length	0·082	0·085	<b>0·749</b>	0·315	0·074	0·064
Inter-orbital width	0·234	-0·133	<b>0·568</b>	0·020	-0·035	-0·027
Eye diameter	0·322	0·079	<b>0·404</b>	-0·097	-0·187	-0·098
Head width	-0·013	0·205	0·255	<b>0·742</b>	-0·218	-0·019
Mouth width	-0·026	-0·028	0·346	<b>0·716</b>	0·066	0·058
High of the caudal peduncle	0·318	0·142	-0·129	<b>0·655</b>	0·008	-0·008
Caudal fin length	0·448	-0·088	-0·151	<b>0·643</b>	-0·042	0·086
Snout length	-0·028	-0·245	0·422	<b>0·601</b>	0·103	0·176
Head depth	0·118	0·413	0·179	<b>0·581</b>	-0·158	-0·091
Pelvic-dorsal fins distance	-0·015	-0·299	-0·082	-0·103	<b>0·846</b>	-0·177
Pre-dorsal length	-0·092	0·496	0·123	-0·040	<b>0·815</b>	-0·080
Dorsal-anal fins distance	0·469	0·139	-0·055	0·154	- <b>0·520</b>	-0·037
Anal fin base length	-0·231	0·024	-0·035	0·094	-0·030	<b>0·783</b>
Maximum anal fin length	0·286	0·088	0·037	-0·024	-0·099	<b>0·783</b>
Variance explained (%)	14·54	13·07	12·63	11·34	8·31	7·71
Total variance explained (%)	14·54	27·61	40·24	51·59	59·90	67·61

## DISCUSSION

*Galaxias platei* exhibits a marked morphological variation among lakes. This variation largely involves traits related to caudal fin dimensions and correlates with the intensity of piscivory. Morphology also varies within lakes, most significantly, within Lake Espejo, a lake with an intermediate level of piscivory. Variation in the position of dorsal, anal and pelvic fins among *G. platei* within this lake correlated with the use of some food resources.

Incidence of piscivory, i.e. predation risk, was estimated taking into account simultaneously, the presence, abundance and diet of predators (Table III, IV and Fig. 3). This led to the establishment of three predation risk categories of lakes: high risk (Gutiérrez and Moreno Lakes), mid risk (Lake Espejo and Coyte Pond) and low risk (Lake Rivadavia and Manso Basin lakes). Lakes Gutiérrez and Moreno, both high predation risk lakes, are characterized, respectively, by little or no littoral refuge area and by the presence of the native *P. trucha*. The lakes

TABLE VI. Interlake shape differences among *G. platei*. Standardized canonical discriminant functions 1 to 6 (DF1 to DF6), variance explained, Wilks' Lambda and canonical correlation. In bold, the highest contribution of each morphometric variable to the five discriminant functions

	DF1	DF2	DF3	DF4	DF5
Caudal fin length	<b>1.057</b>	-0.350	0.158	-0.101	-0.128
Snout length	<b>0.527</b>	-0.229	-0.104	0.260	0.344
Head width	- <b>0.395</b>	-0.117	0.638	-0.660	0.335
Dorsal fin base length	<b>0.317</b>	0.224	-0.170	0.189	0.301
Maximum pelvic fin length	0.026	<b>0.593</b>	-0.223	0.097	-0.203
Length of the lower jaw	-0.345	- <b>0.537</b>	-0.168	0.052	-0.222
Pelvic-anal fins distance	0.297	<b>0.525</b>	-0.363	-0.122	-0.123
Maximum pectoral fin length	-0.174	<b>0.505</b>	0.444	-0.380	0.436
Head-pelvic fin distance	-0.034	-0.233	<b>0.458</b>	-0.054	0.077
Inter-orbital width	-0.264	0.358	<b>0.401</b>	-0.113	-0.621
Pre-dorsal length	0.006	-0.077	- <b>0.394</b>	-0.258	0.725
Mouth width	0.273	0.241	- <b>0.338</b>	0.121	-0.211
Maximum anal fin length	-0.158	-0.173	-0.258	<b>0.582</b>	-0.108
Maximum dorsal fin length	-0.205	-0.260	0.300	<b>0.575</b>	0.049
Anal fin base length	-0.045	-0.163	-0.142	- <b>0.495</b>	-0.277
Head depth	-0.168	-0.175	0.193	0.305	- <b>0.332</b>
Eye diameter	-0.081	0.292	0.174	0.295	<b>0.310</b>
Variance explained (%)	53.9	23.8	12.9	6.2	3.2
Total variance explained (%)	53.9	77.7	90.6	96.8	100
Wilks' Lambda	0.002	0.023	0.111	0.337	0.666
Squared canonical correlation	0.895	0.790	0.671	0.494	0.334

perceived as having low predation risk (i.e. Rivadavia and the lakes in the Manso Basin) are characterized by a relatively high abundance of planktonic food (e.g. Rivadavia) or by relatively turbid waters (Manso Basin) which probably provide shelter from visual predators. Salmonids in Lake Rivadavia prey on large zooplankton (Fig. 3), e.g. *Daphnia* sp., frequently absent in many Andean lakes (Modenutti & Balseiro, 1994; Balseiro *et al.*, 1997; Modenutti *et al.*, 1998), but highly abundant in this lake (M. A. Battini, unpubl. data).

In general, *G. platei* exhibits a higher degree of piscivory in lakes where *P. trucha* is also present (Espejo and Moreno) than where *P. trucha* is absent. The two exceptions are Lake Rivadavia, which has a clearly different trophic structure and Coyte Pond, where no other fishes are present. It is likely for the shift to piscivory in *G. platei* to be induced by competition for benthic food resources with *P. trucha* (Fig. 3).

Exposure of individuals to predation has been shown to be an important determinant of microhabitat use in both freshwater and marine fishes (Werner & Hall, 1988; McCormick, 1998). Ontogenetic changes in fish diet, habitat use and growth are also likely to be influenced by changes in predation risk (Mittelbach & Chesson, 1987). For example, *S. alpinus* are confined to deep benthic and pelagic areas in sympatry with *S. trutta* whereas they exploit littoral areas in allopatry with this species (L'Abée-Lund *et al.*, 1993). *Lepomis macrochirus* Rafinesque prefers benthos, where food is more plentiful, when predators are

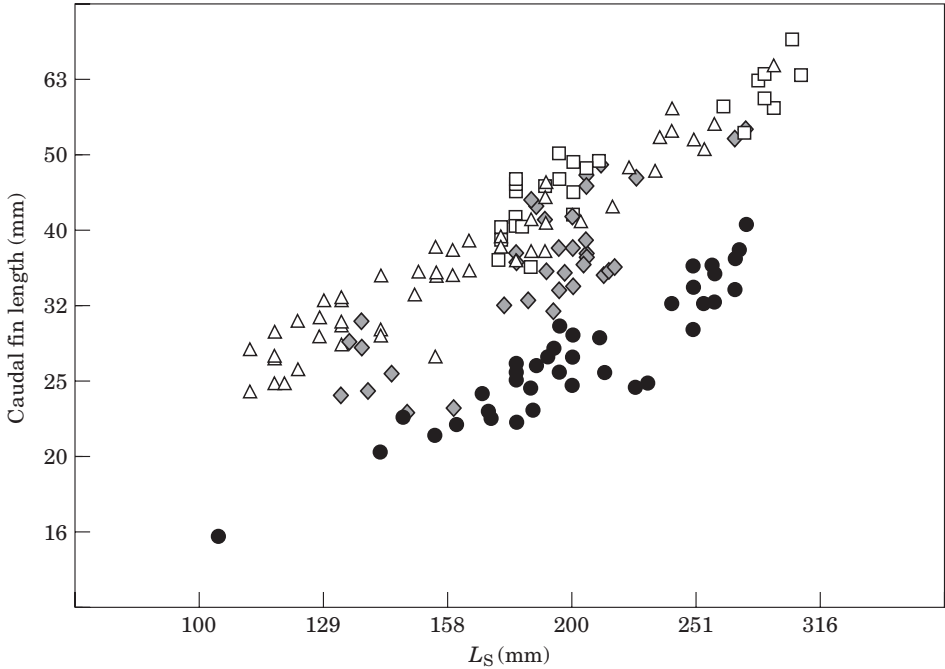


FIG. 4. Scatter plot of caudal fin length and standard length, on a double logarithmic scale. Lakes with relatively high piscivory (●, Lakes Gutiérrez and Moreno) showed *G. platei* with relatively short caudal fins. Conversely in lakes with low piscivory (△, Lake Rivadavia and the Manso Basin) *G. platei* exhibited relatively long caudal fins. Intermediate piscivory [Espejo Lake (◆) and Coyote Pond (□)] lakes were the only lakes with intermediate body shape.

absent. When the predator largemouth bass *Micropterus salmoides* (Lacapède) is present, the smaller individuals of *L. macrochirus* exhibited less preference for the benthos (Milinski, 1993).

Predation has the potential to also influence morphology and life history traits (Swain, 1992). In most cases the life-history shifts include a growth reduction caused by predator-induced feeding depression. Conversely, growth may also increase due to the reduction of population density (Stoks *et al.*, 1999).

Some inducible morphological defences in vertebrates respond to chemical signs from the predator. In the crucian carp *Carassius carassius* (L.) Brönmark & Miner (1992) demonstrated a predation-induced modification of body shape that reduced vulnerability to predation (Swain & Foote, 1999).

A significant relationship was observed between piscivory rate and *G. platei* caudal fin length and depth: *G. platei* inhabiting lakes where piscivory is high exhibit shorter and deeper caudal fins. Increased tail depth should improve caudal fin transient propulsion, resulting in faster starts and powered turns, both of which may help to evade predators once they are detected. For example, while inactivity in tadpoles may reduce detection, improved swimming ability can help tadpoles escape from predators once they are detected (McCollum & Leimberger, 1997). The present results suggest that the morphological variation of *G. platei* (McDowall, 1971) can be interpreted and ascribed, at least in part, to differences in feeding habit and predation risk. The longer caudal fins exhibited by *G. platei* under low predation risk conditions probably result from selection

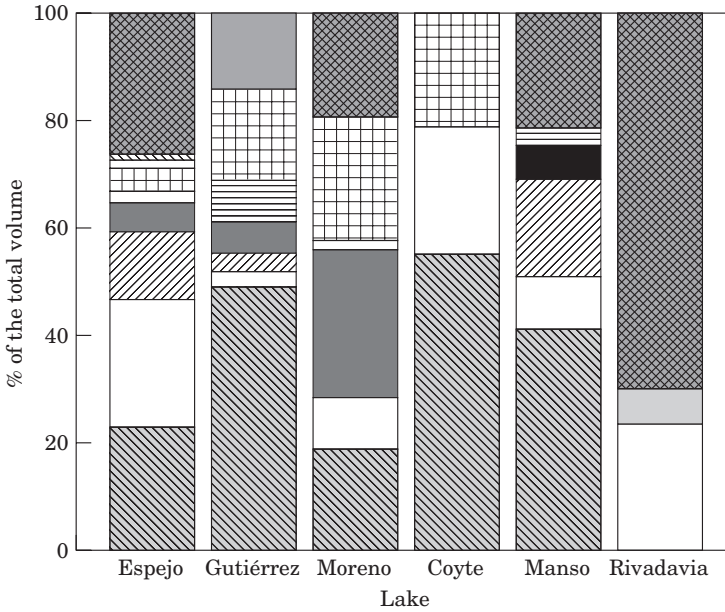


FIG. 5. Diet composition (% of the total gut volume) of *Galaxias platei* by lake. Amphipoda (▨), Mollusca (□), Diptera larvae and pupae (▩), Oligochaetae (■), Decapoda (▧), insect larvae (▧), fishes (▧), terrestrial insects (▧), Hirudinea (▧) and detritus (▧).

TABLE VII. Standardized canonical discriminant functions 1 to 3 (DF1 to DF3), variance explained and canonical correlation. In bold, the highest contribution of each morphometric variable to the three discriminant functions

	DF1	DF2	DF3
Detritus	<b>1.095</b>	0.131	0.014
Mollusca	<b>0.642</b>	-0.037	-0.146
Decapoda	0.155	<b>0.916</b>	0.392
Diptera larvae and pupae	0.370	-0.354	<b>0.902</b>
% of variance	62.8	22.0	10.4
Cumulative %	62.8	84.7	95.1
Squared canonical correlation	0.367	0.169	0.088

for sustained locomotor ability. Further studies are necessary to assess whether the variation in tail morphology represents an antipredator inducible defence (Brönmark *et al.*, 1999).

Niche characteristics, other than the incidence of piscivory, are also likely to influence the morphology of *G. platei*. Little information is available on the feeding behaviour of *G. platei*. The relation between caudal morphology and diet within lakes, however, suggests a major role for 'ram' feeding (Wainwright, 1998). Enhanced locomotor abilities (longer tail) may have beneficial effects on the ability to eat detritus, probably due to the forces needed for bottom disturbance.

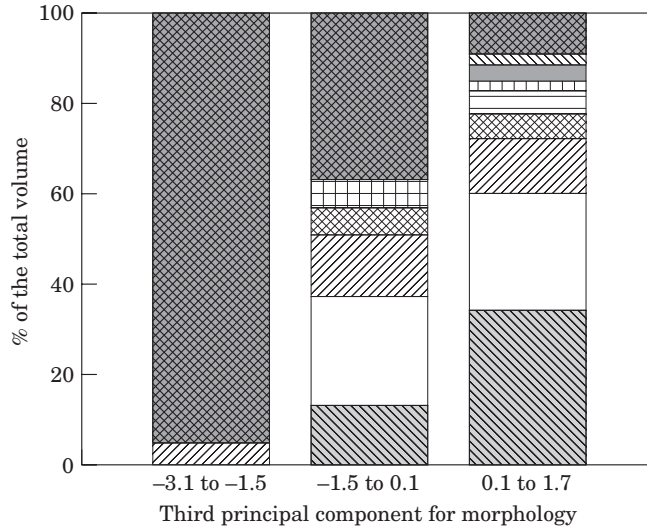


FIG. 6. Diet composition (% of the total and volume) of *Galaxias platei* in Lake Espejo in relation to the third principal component for morphology. Amphipoda (▨), Mollusca (□), Diptera larvae and pupae (▩), Decapoda (▧), insect larvae (▭), fishes (▮), terrestrial insects (▯), Hirudinea (▮) and detritus (▩).

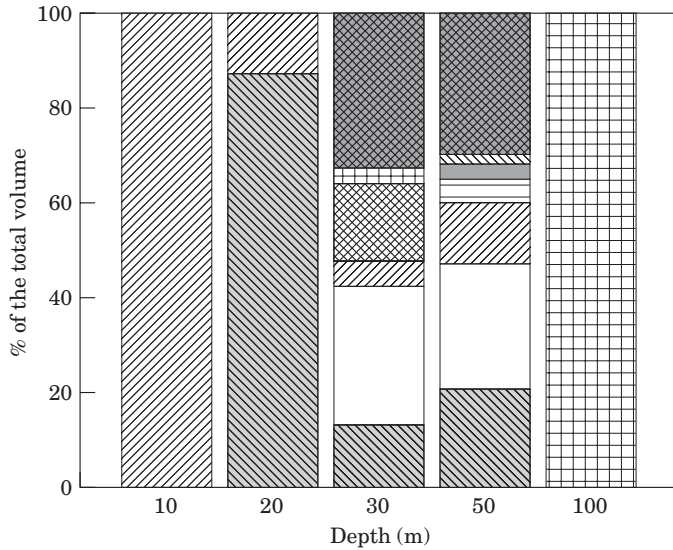


FIG. 7. Diet composition (% of the total gut volume) of *Galaxias platei* in Lake Espejo in relation to capture depth. Amphipoda (▨), Mollusca (□), Diptera larvae and pupae (▩), Decapoda (▧), insect larvae (▭), fishes (▮), terrestrial insects (▯), Hirudinea (▮) and detritus (▩).

The deeper body of crucian carp that coexist with piscivorous fishes results in hydrodynamic disadvantage relative to more shallow bodied conspecifics. The deep-bodied individuals, however, compensate for the increase in drag by having lower standard metabolic rates (Pettersson & Brönmark, 1999). Similarly, the

ensemble of characteristics of *G. platei*, adaptive to the benthic life, i.e. general morphology (McDowall, 1971; Matthews, 1998), mitochondrial complexity in retinal cones (Schoebitz *et al.*, 1973; Ali *et al.*, 1990) and high endurance to anoxia (Barriga *et al.*, 1999), suggest the existence of a complex ensemble of traits and cost-benefit trade-offs. The benthic habit would allow the species to feed and seek refuge in the mud, probably as an antipredatory shelter (Wootton, 1998). At the same time, the high frequency of terrestrial foods in gut of *G. platei* (Macchi *et al.*, 1999) and nocturnal captures in the littoral zone (D. Milano unpubl. data) suggest nocturnal swimming towards littoral subsurface waters (McIntosh *et al.*, 1992). This is in agreement with the considerable evidence that fishes that are most active at night forage with the aid of the lateral line system (Van Snik Gray & Stauffer, 1999).

The present results indicate that *G. platei*, a specialized bottom dweller, exhibits among-lake morphological variability in the caudal region and that this variation is influenced largely by differences in predation intensity. Within a lake where predation is intermediate, morphological variation appears to be affected by both predation and differences in the use of food resources.

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