

# Latitudinal and ecological correlates of morphological variation in *Galaxias platei* (Pisces, Galaxiidae) in Patagonia

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We examined the morphological variability (23 morphometric traits) among individual *Galaxias platei* ( $N = 380$ ) collected from 20 postglacial lakes in the southern Andes. The lakes were chosen to cover the latitudinal range of the species in Patagonia. Diet examined for a subset of these fish ( $N = 261$ ) collected during the summer months (January through March), differed among river basins but there were no clear latitudinal trends in the consumption of any prey type. Diet may, however, have partially shaped morphology, as pelvic measures were negatively correlated with consumption of amphipods. Substantial differentiation among populations was observed, primarily in the shape and dimensions of the head, in caudal morphology and in fin length. Our results indicate that the morphology of *G. platei* varies with latitude, and may be related to risk of predation and diet. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 87, 69–82.

**ADDITIONAL KEYWORDS:** allopatry – benthic fish – ecomorphology – lakes – landlocked – morphs – predation risk – sympatry.

## INTRODUCTION

A fundamental problem in evolutionary biology is to understand the processes that are responsible for the phenotypic and genetic variability observed in nature at various hierarchical levels: among species, among populations belonging to one species, and within populations. Historical contingency (shared ancestry and/or shared ancient environment), stochastic processes (genetic drift) and natural selection are generally thought of as the main factors influencing evolutionary trajectories. The independent actions of historical

contingency (e.g. ancestral secondary contact through shifting drainage connections) and natural selection have been invoked in studies on several northern hemisphere postglacial fish systems, including whitefish (*Coregonus clupeaformis*) and Arctic char (*Salvelinus alpinus*) (Bernatchez, Chouinard & Lu, 1999; Gíslason *et al.*, 1999; Skúlason, Snorrason & Jónsson, 1999). Probably the most complete understanding of the role that the various factors have played in promoting evolutionary novelty has been achieved for the North American three-spine stickleback, *Gasterosteus aculeatus*, where shared histories (repeated marine invasions) have been shown to have interacted with natural selection to cause divergence within populations (Taylor & McPhail, 2000).

The relative simplicity of southern and northern hemisphere post-Pleistocene lake ecosystems presents

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an opportunity to examine the roles of historical contingency and natural selection in effecting evolutionary novelty in fish populations through adaptive radiation and speciation. Glaciers covered much of southern Patagonia during the Pleistocene, extending northward along the Andean mountain chain. Terrestrial plants and animals were probably present in multiple refuges surrounded by ice or an otherwise adverse climate (Haffer, 1979; Simpson, 1979; Cei, 1982; Premoli, Kitzberger & Veblen, 2000). In the late Pleistocene, a number of large glacial and pluvial palaeolakes existed in the Patagonian Andes (Aschero *et al.*, 1998; Tatur *et al.*, 2002). As the climate warmed and glaciers receded, ice barriers broke down and the large lakes drained. The deeper basins became today's lakes, and a number of drainage systems shifted from the Atlantic to the Pacific (González, 1992). These lakes were colonized by fish that had persisted in the unglaciated lowland rivers or as oceanic forms. Some colonization events likely occurred during the palaeolake period; others may have occurred later, or multiple times. The major groups present today include the Siluriformes and Galaxiidae, which have a Gondwanan distribution, and Percichthyidae and Atherinopsidae, which are of marine origin (McDowall, 1971; Nelson, 1994; Dyer, 1998).

The Galaxiidae are a pan-Austral Gondwanan family, whose present circumpolar distribution appears to result from both vicariant (Croizat, Nelson & Rosen, 1974; Rosen, 1974, 1978), and post-Mesozoic dispersal events (McDowall, 1970, 1980; Berra *et al.*, 1996; Waters & Burridge, 1999). Galaxiid species currently inhabit both marine and freshwaters in New Zealand, Australia, South Africa, and South America. Three genera (*Aplochiton*, *Brachigalaxias*, and *Galaxias*), and a total of eight species, have been described for southern South America (Cussac *et al.*, 2004), with three species belonging to *Galaxias*. *Galaxias maculatus* (Jenyns) is a small and widely distributed species, found on both sides of the Andes. A few populations are diadromous, but most are landlocked. *Galaxias globiceps* (Eigenmann) is a rare species, apparently restricted to one river system in Chile (Berra & Barbour, 1998; Murillo & Ruíz, 2002; Cussac *et al.*, 2004). *Galaxias platei* (Steindachner), the focus of this study, is a relatively large fish (up to 365 mm SL), widely distributed throughout Patagonia, and found on both sides of the Andes (Ringuelet, Aramburu & Alonso, 1967; McDowall, 1971; Ringuelet, 1975; Campos, 1979; Arratia, Peñafort & Menu-Marque, 1983; Dyer, 2000; Cussac *et al.*, 2004).

*Galaxias platei* usually inhabits the deep waters (below the thermocline and euphotic zone) of postglacial lakes (Milano *et al.*, 2002), though it can also be found in shallow glacial ponds where the water is murky due to suspended glacial sediments (this

study). The species exhibits considerable morphological variation, which has been attributed to variation in thermal regime (McDowall, 1971) and to variation in the intensity of piscivory (Milano *et al.*, 2002). In the present study we extend these results by examining the morphological variability among populations of *G. platei* from 20 postglacial lakes in southern South America. The lakes cover the north–south distributional range of *G. platei*, from north-western Patagonia to Tierra del Fuego. We examine variability in 23 morphometric traits and relate the variation to factors likely associated with colonization history (geography, direction of drainage, river basin, latitude) and current selection (ecological) pressures (predation and diet).

## MATERIAL AND METHODS

### STUDY SITES

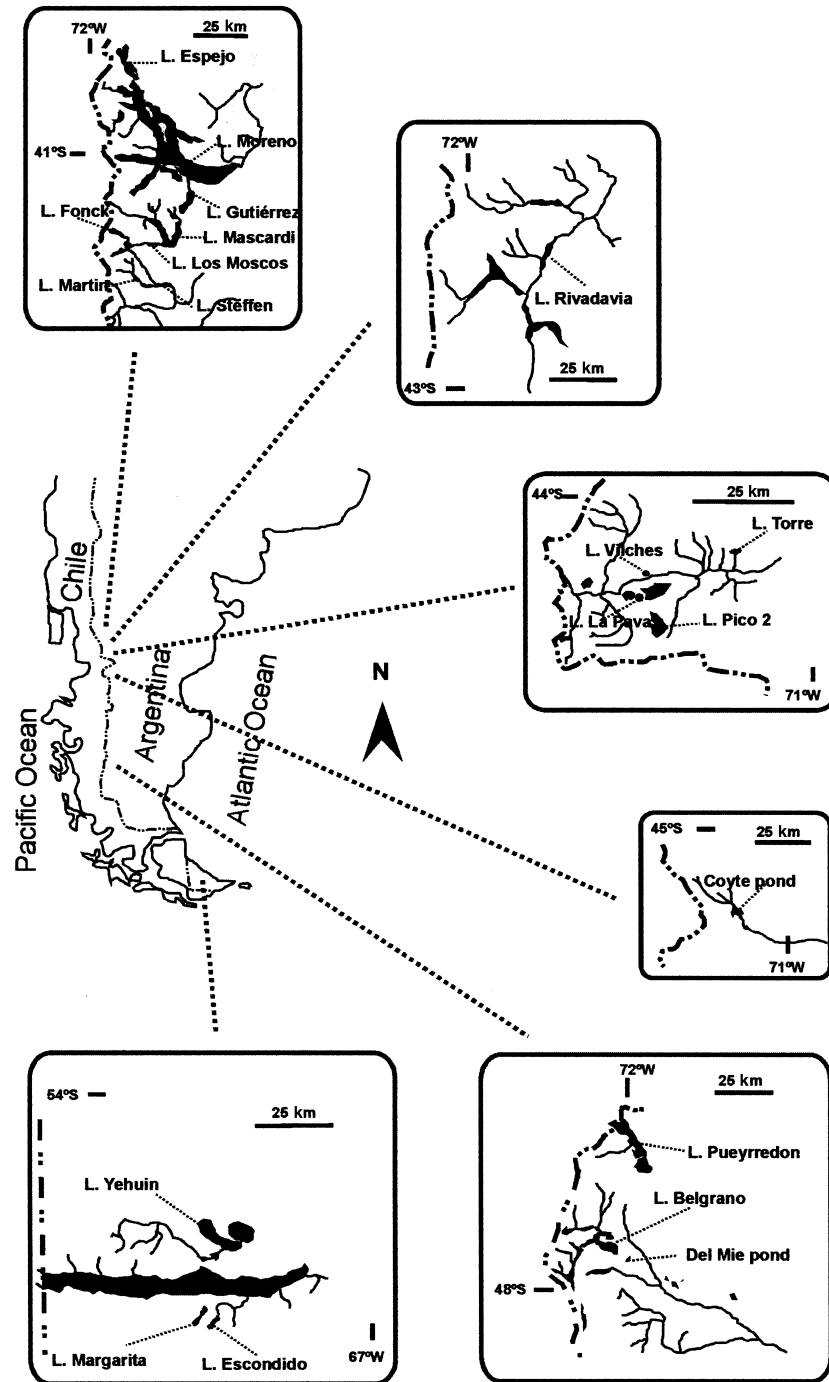
Fish were collected over a period of 6 years (1995–2001) from 20 postglacial lakes in the southern Andes. The lakes sampled span the latitudinal range of *G. platei* in Patagonia (Fig. 1). The northernmost and southernmost lakes sampled are, respectively, Lake Espejo (40°41'S) and Lake Escondido on the island of Tierra del Fuego (54°S). Five of the lakes drain east toward the Atlantic, while the remaining 15 lakes drain west to the Pacific (Table 1). The lakes in the Atlantic watershed are distributed among three river basins, while the 15 Pacific-draining lakes are distributed among six river basins (Table 1).

### FISH COLLECTIONS

Fish were collected from most lakes and ponds using gillnets (15, 20, 30, 50, 60 and 70 mm bar mesh size, each 10 m long and 2 m high) placed at 2, 10, 20, 30, 50, and (occasionally) 100 m depth on the bottom. Gillnets were set parallel to the coast and left in place overnight. Coyte pond was sampled in March of 1996. Lakes Espejo and Rivadavia and the lakes in the Manso river basin were sampled in the summer of 1998. Lakes Gutiérrez and Moreno were sampled seasonally; the former eight times from 1995 to 1997, and the latter four times during 1999. The lakes in the Pico river basin were sampled during February 2000. In these lakes, gillnets (20, 25, 30, 35, 40, 50; 60 and 70 mm mesh bar) were placed at 2 m depth. Lakes Pueyrredón, Belgrano, Yehuin, Escondido, Margarita and Del Mie Pond were sampled in the summer of 2001. In the relatively shallow Del Mie Pond, fish were collected with a seine net (25 m long, 1.5 m high and 5 mm mesh size). All native fish species, including *G. platei*, were identified following Ringuelet *et al.* (1967), and McDowall (1971). Fish were fixed in the field with 4% formaldehyde.

**Table 1.** Physical characteristics of lakes studied. *Abbreviation* P × A, Perimeter × Area

Water-sheds	Basin	Lakes	Location	Altitude m.a.s.l.	Area km <sup>2</sup>	P × A <sup>-1</sup> km <sup>-1</sup>	Volume hm <sup>3</sup>	Max. depth m	Mean depth m	Secchi disk m	Conductivity µS cm <sup>-1</sup>	
Atlantic	Limay	Espejo	40°41'S-71°40'W	772	38.2	1.7	—	245	—	16	29.6	
		Gutiérrez	41°05'S-71°25'W	750	16.4	1.5	1307	111	79.7	18	58.1	
		Moreno	41°05'S-71°32'W	758	10.6	3.2	666	112	63	19.5	37.1	
Chubut	Chico	Coyte	45°25'S-71°22'W	795	7.3	1.8	—	6	—	<0.2	304	
		Del Mie	47°54'S-71°59'W	800	—	—	—	2	—	0.01	610	
Pacific	Manso	Mascardi	41°17'S-71°38'W	796	39.2	1.4	4351.2	218	111	12	44.9	
		Los Moscos	41°21'S-71°36'W	—	2.3	2.6	67.9	50	29.6	12	—	
	Futaleufú	Fonck	41°19'S-71°45'W	775	3.7	3.9	148.6	85	40	9.5	29.8	
		Steffen	41°31'S-71°33'W	509	6.3	2.6	294	76.8	46.7	13	40	
		Martin	41°30'S-71°40'W	510	1.78	5.4	76.6	68	43	11	—	
	Pico	Rivadavia	42°30'S-71°45'W	527	21.7	1.5	2250	147.2	103.7	20.5	56	
		Vilches	44°07'S-71°34'W	—	2	—	—	5.6	3.7	3.7	49	
	Baker	Nansen	Torres	44°07'S-71°06'W	—	—	—	—	9.4	3.6	5	140
			La Pava	44°10'S-71°30'W	—	—	—	—	13.4	7.7	10	40
			Pico 2	44°18'S-71°30'W	—	—	—	—	24.4	11.1	7	60
Azopardo	Margarita	Pueyrredon	47°18'S-71°55'W	—	—	—	—	—	—	11	159	
		Belgrano	47°55'S-72°09'W	780	47	—	—	—	—	0.5-1	70.5	
Escondido	Escondido	Yehuín	54°24'S-67°44'W	241	43.5	—	1857.45	—	42.7	17	208	
		Escondido	54°38'S-67°48'W	142	7	—	266	—	38	4	140	

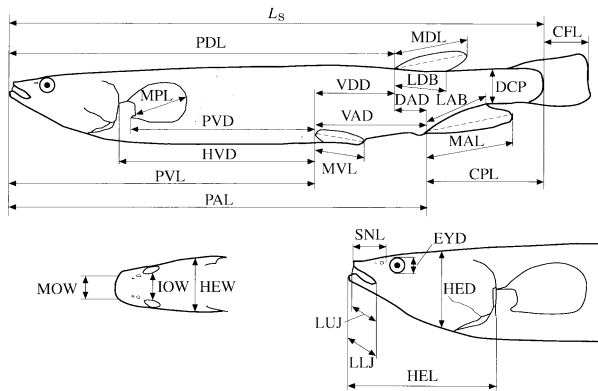


**Figure 1.** Location of study lakes. Limay River basin: Espejo; Gutiérrez; Moreno. Chubut River basin: Coyte Pond. Chico River basin: Del Mie Pond. Manso River basin: Mascardi; Los Moscos; Fonck; Steffen; Martin. Futaleufú River basin: Rivadavia. Pico River basin: Vilches, Torres, Pico 2, La Pava. Baker River basin: Pueyrredón. Nansen River basin: Belgrano. Azopardo River basin: Yehuín; Margarita; Escondido.

MORPHOMETRIC TRAIT MEASUREMENT  
IN *GALAXIAS PLATEI*

In total, 23 morphological characters were measured in all adult (> 103.7 mm, Milano *et al.*, 2002) speci-

mens ( $N = 380$ ), using a digital calliper and following McDowall (1971), Milano & Vigliano (1997) and Milano *et al.* (2002). Measurements taken were: standard length (STL), caudal fin length (CFL), depth of the caudal peduncle (DCP), caudal peduncle length (CPL),



**Figure 2.** Dimensions measured in the morphological analysis of *Galaxias platei*. Abbreviations: STL, Standard length; CFL, caudal fin length; DCP, depth of the caudal peduncle; CPL, caudal peduncle length; LDB, length dorsal fin base; MDL, maximum dorsal fin length; LAB, length anal fin base; MAL, maximum anal fin length; PDL, predorsal length; PAL, preanal length; PVL, prepelvic length; PVD, pectoral–pelvic distance; MPL, maximum pectoral fin length; VAD, pelvic–anal distance; MVL, maximum pelvic fin length; HEL, head length; HED, head depth; hHEW, head width; SNL, snout length; IOW, interorbital width; EYD, eye diameter; LUJ, length of the upper jaw; LLJ, length of the lower jaw; MOW, mouth width.

length dorsal fin base (LDB), maximum dorsal fin length (MDL), length anal fin base (LAB), maximum anal fin length (MAL), predorsal length (PDL), preanal length (PAL), prepelvic 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), interorbital width (IOW), eye diameter (EYD), length of the upper jaw (LUJ), length of the lower jaw (LLJ), and mouth width (MOW) (Fig. 2).

#### DIET ANALYSIS

The stomach contents of 261 individual *G. platei* collected during summer months (January through March) were examined. Percent of total prey volume was estimated for each prey category (i.e. family, genus, or species) present in the stomach content of individual fish.

#### STATISTICAL ANALYSIS

Morphometric measures were log-transformed prior to analysis. All measures of morphometric traits were first standardized to a common fish size by regressing the measure against standard length of the fish. The standardized values (regression residuals) were then

used in a principal component analysis (PCA). Diet composition was examined using discriminant analysis (DA). For each lake, incidence of piscivory was estimated as the percentage of fish (over all species including introduced salmonids) with fish in their guts. We correlated morphological variables with incidence of piscivory and latitude using the Spearman's rho coefficient and using partial correlations between morphological variables and piscivory while controlling for latitude. Also, we analysed river basin- and watershed- (Atlantic vs. Pacific) dependent differences using Kruskal–Wallis (K-W) and Mann–Whitney (M-W) tests, respectively. Differences in body size of *G. platei* among lakes were examined by K-W tests. All the statistical analyses were conducted using SPSS (Norusis, 1986; Zar, 1999).

## RESULTS

### PHYSICAL CHARACTERISTICS AND SPECIES

#### COMPOSITION OF LAKES

The lakes and ponds examined in this study exhibit a range of physical and chemical characteristics; in general, they are characterized by low productivity, as indicated by Secchi disk depths and conductivity measurements (Table 1). The lakes differ in fish species assemblages (Table 2). In four cases (Coyte, Del Mie, La Pava, Belgrano), *G. platei* was the only species collected, and presumably the only one present. In the other lakes, several native species and 1–3 species of introduced salmonids were present. Rainbow trout (*O. mykiss*) was found in more lakes than the other salmonids, but when found together, the relative abundance of the two to three salmonids varied from lake to lake. *Galaxias maculatus* (Galaxiidae) was found in the littoral zone of most of the northern lakes and *Aplochiton zebra* (Galaxiidae) was found in only one lake. Other native species included *Percichthys trucha* (Percichthyidae), *Diplomystes vielmensis* (Diplomystidae), and *Odonthestes hatcheri* (Atherinopsidae).

#### MORPHOLOGICAL DIVERSITY

The PCA was based on the 23 morphological variables obtained for 370 individuals (10 individuals eliminated because of missing values). The first five PCs explained 72% of the total variance (Table 3). Morphological traits segregated quite cleanly onto the first three PCs. Variables with high loading on PC1 (36% of total variance) included most of the head characters (head length, depth, and width, mouth width, jaw and snout lengths, and interorbital width), as well as two tail characters (depth of the caudal peduncle and length of the anal fin base) (Table 3). All variables with high loading on PC2 were measures of fin length

**Table 2.** Composition of fish assemblages by lake. Numbers indicate catch by unit of effort [number of fishes  $\times$  (100 m<sup>2</sup> mesh  $\times$  15 h)<sup>-1</sup>] and numbers of individuals captured within parentheses, in summer. In Pico basin, number indicate percentage of capture by each lake. \*Captures with seine net or baited traps. #Introduced species. Standard length range, mean and number of *G. platei* by basins. Abbreviations: *S.t.*, *S. trutta*; *S.f.*, *S. fontinalis*; *O.m.*, *O. mykiss*; *G.m.*, *G. maculatus*; *A.z.*, *A. zebra*; *D.v.*, *D. viedmensis*; *O.h.*, *O. hatcheri*; *P.t.*, *P. trucha*; *G.p.*, *G. platei*

Water-shed	Basin	Lakes	<i>S. t</i> #	<i>S. f</i> #	<i>O. m.</i> #	<i>G. m.</i>	<i>A. z.</i>	<i>D. v</i>	<i>O. h.</i>	<i>P. t.</i>	<i>G. p.</i>	Lst Range	Mean	
Atlantic	Limay	Espejo	0.7 (6)	2.8 (35)	3.0 (29)	*	–	0.1 (1)	–	5.8 (59)	3.4 (37)	130–275	190	
		Gutiérrez	0.19 (10)	0.37 (19)	1.0 (53)	*	–	0.04 (2)	–	–	0.1 (4)	155–200	181.5	
		Moreno	0.2 (2)	2.2 (21)	4.0 (37)	*	–	0.1 (1)	0.1 (1)	7.8 (73)	1.2 (11)	161–270	238.7	
	Chubut	Coyte	–	–	–	–	–	–	–	–	*	175–305	217	
		Chico	Del Mie	–	–	–	–	–	–	–	*	105–134	108	
Pacific	Manso	Mascardi	1.4 (58)	1.0 (40)	1.0 (39)	*	–	–	–	–	0.4 (15)	110–255	172	
		Los Moscos	0.8 (7)	0.8 (7)	1.2 (12)	*	–	–	–	–	0.3 (3)	126–180	154	
		Fonck	0.4 (10)	4.2 (30)	1.9 (15)	*	–	–	–	–	1.1 (12)	115–190	139	
		Steffen	15.1 (71)	0.7 (2)	2.9 (18)	*	–	–	–	–	0.5 (3)	117–155	132	
		Martin	7.3 (56)	1.8 (15)	5.1 (31)	*	–	–	–	–	*	110	110	
	Futaleufú	Rivadavia	0.1 (1)	2.1 (20)	11.1 (97)	–	*	–	6.4 (34)	10.2 (68)	1.5 (16)	130–290	192	
	Pico	Vilches	–	–	36.4 (4)	–	–	–	–	–	–	63.6 (7)	240–260	249
		Torres	–	–	60.4 (32)	–	–	–	–	–	–	39.6 (21)	155–300	209.9
		Pico 2	–	–	4.8 (3)	–	–	–	–	–	–	95.2 (59)	142–275	190.2
		La Pava	–	–	–	–	–	–	–	–	–	100 (7)	155–197	179.2
	Baker	Pueyrredón	–	–	1.6 (20)	–	–	–	1.1 (19)	4.3 (54)	1.3 (18)	175–348	325	
	Nansen	Belgrano	–	–	–	–	–	–	–	–	–	10.4 (132)	103–266	205
	Azopardo	Yehuín	0.3 (3)	–	–	–	–	–	–	–	–	0.6 (7)	335–365	349.3
Margarita		1.3 (7)	3.0 (16)	1.9 (10)	–	–	–	–	–	–	0.4 (2)	107–154	130.5	
Escondido		1.1 (15)	0.7 (9)	0.3 (4)	–	–	–	–	–	–	0.9 (10)	105–135	120.2	

and those loading onto PC3 were pelvic and anal distance measures (Table 3).

A plot of PC1 vs. PC2 for the river basins shows three main clusters (Fig. 3). The Pico, Baker, Chico, Nansen and Tierra del Fuego (two of the lakes) river basins separate from the rest along the PC1 axis, with larger heads and thicker caudal peduncles. The Chubut and

Manso river drainages separate from the others along the PC2 axis, containing fish with longer fins.

#### GEOGRAPHICAL FACTORS

There was significant variation in morphology among the different river basins; all 23 morphometric traits

**Table 3.** Shape differences among *Galaxias platei*. Loading for the morphometric variables onto PC1 to PC5 and the variance explained. In bold, the highest contribution of each morphological variable to five principal components

	PC1	PC2	PC3	PC4	PC5
Head length	<b>0.912</b>	0.043	0.074	-0.071	-0.046
Mouth width	<b>0.891</b>	0.178	-0.052	0.146	-0.025
Head width	<b>0.879</b>	0.164	-0.036	0.104	-0.052
Length of the upper jaw	<b>0.841</b>	-0.112	0.150	-0.224	0.053
Head depth	<b>0.815</b>	0.192	-0.015	0.123	-0.085
Depth of the caudal peduncle	<b>0.811</b>	0.311	-0.110	0.243	-0.079
Snout length	<b>0.806</b>	0.001	0.035	-0.121	-0.013
Length of the lower jaw	<b>0.775</b>	-0.229	0.208	-0.295	0.055
Inter-orbital width	<b>0.653</b>	0.088	-0.094	-0.117	0.108
Length anal fin base	<b>0.597</b>	0.426	-0.032	0.388	-0.355
Maximum pectoral fin length	0.264	<b>0.736</b>	0.097	-0.082	0.188
Maximum pelvic fin length	0.468	<b>0.707</b>	-0.005	0.050	0.161
Maximum dorsal fin length	0.554	<b>0.700</b>	0.077	-0.011	-0.014
Length dorsal fin base	0.358	<b>0.662</b>	0.046	-0.109	-0.124
Maximum anal fin length	0.555	<b>0.616</b>	-0.014	0.331	-0.200
Caudal fin length	-0.427	<b>0.511</b>	0.019	-0.158	0.217
Pre-pelvic length	0.117	-0.040	<b>0.881</b>	-0.150	-0.160
Pre-anal length	0.335	0.167	<b>0.781</b>	0.199	0.317
Pectoral–pelvic distance	-0.458	0.188	<b>0.650</b>	-0.016	-0.064
Eye diameter	0.127	0.100	0.124	<b>-0.686</b>	0.028
Pre-dorsal length	0.397	-0.004	0.309	<b>0.545</b>	0.199
Pelvic–anal distance	-0.069	0.346	0.077	0.252	<b>0.728</b>
Caudal peduncle length	0.260	0.074	0.143	0.401	<b>-0.618</b>
Variance explained (%)	35.90	14.17	8.97	7.13	6.12
Total variance explained (%)	35.90	50.07	59.04	66.16	72.28

differed significantly between at least some basins (K-W,  $N = 9$ ,  $P \leq 0.001$ ). Average adult body size also varied among river basins (pairwise comparisons, K-W,  $P < 0.05$ ). For example, individuals tended to be small in the Manso basin, but reach a large maximum size in some of the lakes in the southern basins (Pico, Baker, Nansen, Azopardo) (Table 2).

The variation in morphology was not obviously related to Atlantic vs. Pacific drainage. One of the eastern-draining basins fell into each of the three main clusters (Fig. 3).

Some of the morphological variation could be related to latitude (Fig. 4). Latitude correlated significantly and positively with PC1 (Spearman's  $\rho = 0.653$ ,  $N = 20$ ,  $P < 0.002$ ) and significantly and negatively with PC3 (Spearman's  $\rho = -0.503$ ,  $N = 20$ ,  $P < 0.024$ ). Fish from the more southern lakes tended to have larger heads, thicker caudal peduncles and shorter pelvic distances.

#### ECOLOGICAL FACTORS

##### *Predation risk*

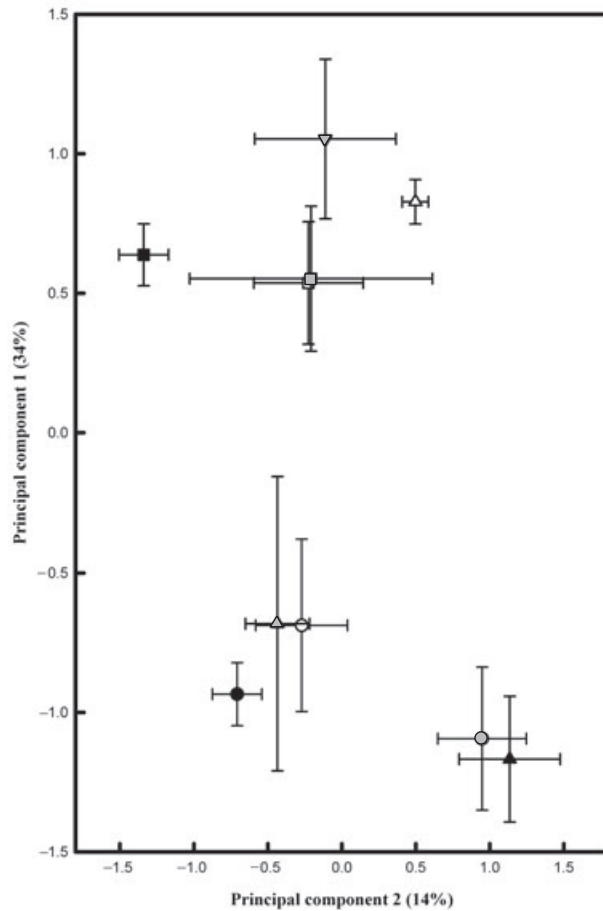
Predation risk, measured as incidence of piscivory, varied greatly among lakes, from a low of zero in many

lakes, particularly those in the south, to a high of 44% in one of the northern lakes (Moreno) (Table 4). Incidence of piscivory was the proportion of fish of all species (including native and introduced species) that had fish in their stomachs.

Incidence of piscivory was negatively correlated with latitude (Spearman's  $\rho = -0.674$ ,  $N = 20$ ,  $P < 0.001$ ); southern lakes had negligible levels of piscivory. Fish community composition also varied with latitude, for example, the small *G. maculatus* and *A. zebra* were only found in the northern lakes in this study (Table 2).

Incidence of piscivory correlated negatively with PC1 (Fig. 5) (Spearman's  $\rho = -0.574$ ,  $N = 20$ ,  $P < 0.008$ ). *G. platei* in basins with high levels of piscivory thus had smaller heads and thinner caudal peduncles. PC5 was positively correlated with piscivory (Spearman's  $\rho = 0.578$ ,  $N = 20$ ,  $P < 0.008$ ), indicating that in basins with piscivory, pelvic–anal distances were longer, but caudal peduncles were shorter.

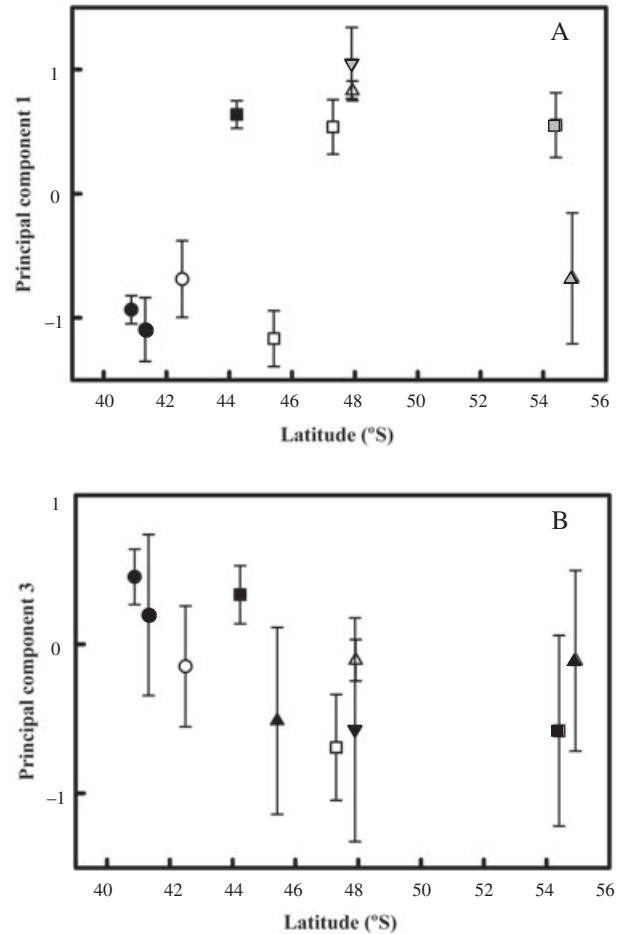
However, when controlled for the correlation with latitude, only caudal fin length (PC2 scores) correlated with incidence of piscivory (Partial Correlation  $r = -0.5525$ ,  $N = 20$ ,  $P < 0.014$ ).



**Figure 3.** Principal component analysis of the morphological variation in *Galaxias platei*. Mean and 95% confidence interval for the PC 1 and 2 by river basin. (●) Limay basin; (○) Manso basin; (○) Futaleufú basin; (■) Pico basin; (▲) Chubut basin; (□) Baker basin; (△) Nansen basin; (▽) Chico basin and Azopardo basin; (△) Lake Escondido lake; (□) Lakes Margarita and Yehuín.

#### Diet

There were marked differences among river basins in the diet of *G. platei* (Table 5). Amphipods made up 25% or more of the diet in six of nine basins. In only one river basin (Chubut) was consumption of fish by *G. platei* greater than 20% of the diet; piscivory in this case equated to cannibalism. The larvae of various aquatic insects, molluscs and annelids made up most of the rest of the diet of *G. platei* (Table 5). We used discriminant analysis to distinguish diet among river basins, including all the food categories for 260 individuals. Five significant ( $N = 260$ ,  $P < 0.002$ ) discriminant functions explained 99.2% of the total variance and correctly classified 60.4% of the fish (Table 5).



**Figure 4.** Morphological variation by latitude in *Galaxias platei*. Mean and 95% confidence interval for the (A) first and (B) third principal components in relation to latitude by river basin. Key per Fig. 3.

There were no clear latitudinal trends in the consumption of any prey type, suggesting that variation in diet did not contribute to the latitudinal variation in morphology. However, diet may have shaped morphology in part, as PC3 (pelvic measures) was negatively correlated with consumption of amphipods (Fig. 6).

#### DISCUSSION

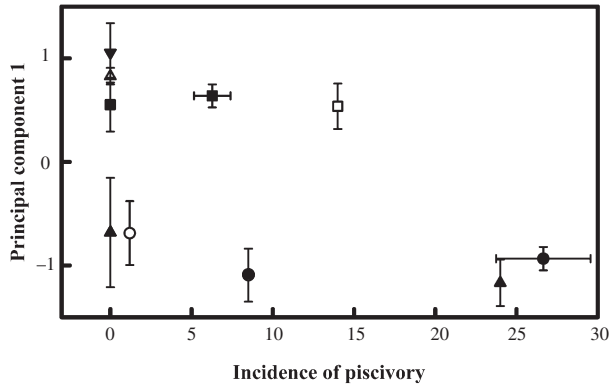
We have shown that *Galaxias platei* exhibits substantial morphological differentiation among populations throughout its distributional range in Patagonia. Populations of *G. platei* differ primarily in the shape and dimensions of the head, in caudal morphology and in fin length. We have also provided evidence that some of this differentiation is associated with geography (river basin and latitude), and some can be related to ecological factors (predation risk and diet). Sorting out

**Table 4.** Number of fish analysed and percentage (per lake and species in the cells and per lake or per species in the totals) of individuals with fish in their guts (within brackets). Abbreviations: *S.t.*, *S. trutta*; *S.f.*, *S. fontinalis*; *O.m.*, *O. mykiss*; *G.p.*, *G. platei*; *O.h.*, *O. hatcheri*; *P.t.*, *P. trucha*

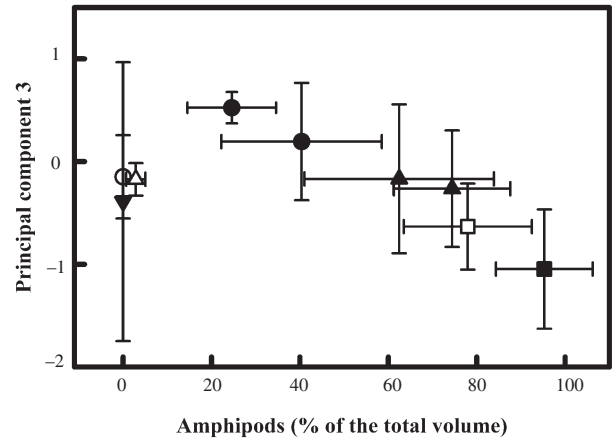
Water-sheds	Basin	Lakes	<i>S.t.</i>	<i>S.f.</i>	<i>O.m.</i>	<i>G.p.</i>	<i>O.h.</i>	<i>P.t.</i>	Total	
Atlantic	Limay	Espejo (January 98)	6 (50)	30 (20)	25 (24)	23 (4.3)	—	54 (7.5)	138 (15)	
		Gutiérrez (March 96 & 97)	12 (66.7)	19 (52.6)	53 (24.5)	3 (0)	—	—	87 (36)	
	Chubut	Moreno (March 99)	0 (0)	18 (72.2)	28 (50)	8 (25)	—	32 (28.1)	86 (44)	
		Coyte (March 96)	—	—	—	21 (24)	—	—	21 (24)	
Pacific	Chico	Del Mie (February 01)	—	—	—	28 (0)	—	—	28 (0)	
	Manso	Manso basin (Jan–March 97 & March 98)	170 (11.2)	89 (5.6)	110 (9.1)	32 (0)	—	—	401 (9)	
		Futaleufú	Rivadavia (February 98)	1 (100)	20 (5)	80 (0)	13 (0)	8 (0)	45 (0)	167 (1)
	Pico	Vilches (January 00)	Torres (January 00)	—	—	4 (25)	7 (0)	—	—	11 (9)
Pico 2 (January 00)			—	—	32 (0)	21 (0)	—	—	53 (0)	
La Pava (January 00)		Pueyrredón (February 01)	—	—	3 (0)	59 (6.78)	—	—	62 (6)	
		Belgrano (February 01)	—	—	—	7 (14.29)	—	—	7 (14)	
Nansen Azopardo	Yehuín (January 01)	Margarita (January 01)	—	16 (0)	18 (22.22)	15 (0)	15 (0)	52 (19.23)	100 (14)	
		Escondido (January 01)	15 (0)	9 (0)	4 (0)	132 (0)	—	—	132 (0)	
	Total			214 (15)	201 (18)	367 (13)	387 (3)	23 (0)	183 (13)	1375

the relative contribution of each factor based on observational data is difficult as there is a strong correlation between some of them (e.g. piscivory and latitude). In addition, the colonization history may be complex, as direction of drainage for some of the lakes has changed over the course of the last several thou-

sand years and perhaps more than once. Thus we present these correlations as interesting patterns, but emphasize that they must be interpreted with caution. They do provide, however, a basis for further investi-



**Figure 5.** Morphological variation by incidence of piscivory in *Galaxias platei*. Mean and 95% confidence intervals between first principal component and incidence of piscivory by river basin. Key per Fig. 3.



**Figure 6.** Morphological variation in relation to percentage of amphipods in the diet of *Galaxias platei*. Mean and 95% confidence intervals between third principal component and percentage of the amphipods' volume by river basin. Key per Fig. 3.

**Table 5.** Diet composition (% of the total gut volume) of *Galaxias platei* by river basin

	Limay	Manso	Futaleufúa	Pico	Chubut	Chico	Baker	Nansen	Azopardo
Fishes	7.21		8.41	23.81					
Crustacea									
Decapoda ( <i>Samastacus</i> )	5.09								
Amphidoda ( <i>Hyallela</i> )	24.70	36.59		45.96	59.47	5.22	77.97	3.06	82.77
Harpacticoidea						9.80			
Cladocera						7.62			
Ostracodae						16.58			
Tardigrada						0.03			
Insects									
Tricoptera larvae	5.13			5.62			1.41	32.89	4.91
Odonata larvae		2.95		1.40				0.06	
Plecoptera larvae								3.20	
Coleoptera larvae	0.37			0.42		3.13			
Tipulidae ( <i>Helobia</i> )		2.32	16.06				0.04	0.08	
Chironomidae larvae	12.49	12.40	2.27	6.67		40.91	9.40	22.89	3.48
Chironomidae pupae	0.75	2.69	0.39			3.79	0.10	8.62	0.35
Ceratopogonidae larvae	0.34	8.93							
Tabanidae larvae			4.06			10.45	0.05	0.77	
Terrestrial insects	3.41	0.79	6.73	4.60					0.20
Mollusca									
<i>Chilina</i> sp.	3.52	6.31	7.13	16.51	16.57		6.65	16.26	2.94
<i>Diplodon</i> sp.				0.83					
<i>Uncacylidos piscidium</i>	12.27				0.15		0.20	1.15	0.15
Annelida									
Hirudinea	0.74			9.58		2.46	0.05	3.99	0.55
Oligochaetae		13.52							
Oligochaetae eggs								0.17	
Detritus									
Vegetal remains			1.84				3.23	4.42	0.84
Unidentified	23.97	13.50	61.52				0.91	2.42	3.82

gation into the probable causes of the marked variation in morphology that we have found.

There were significant differences in the morphology of *G. platei* inhabiting the different river basins. Such results are not surprising, and could be the result of different colonization routes and histories and/or different ecological conditions and selection pressures. Lakes in the Limay and the Chubut river basins, currently draining into the Atlantic, may have been colonized by an ancestral diadromous *Galaxias* form invading from the Atlantic Ocean; alternatively, lowland rivers may have constituted a refuge for this species during the periods of glaciation (the diadromy of *G. platei* is not well documented; Cussac *et al.*, 2004).

Most of the sampled lakes currently drain into the Pacific, and one might have expected greater morphological separation of these populations from Atlantic-draining basins. In the Chico river basin, for example, which drains to the east, there are *G. platei* that are morphologically very similar to those from nearby, west-draining lakes (Baker and Nansen basins). While this ostensibly appears to argue for the importance of ecological factors over past colonization history, drainage patterns are known to have shifted over the past 10 000 years in at least some regions. In particular, it has been documented that, historically both the Nansen and Chico basin lakes (and probably also the Baker basin) drained into the Atlantic (González, 1992).

During the late Pleistocene, a number of large proglacial palaeolakes east of the Andes in the Patagonian region drained into the Atlantic, limited by moraines to the east and by the Andes and its glaciers to the west. During the late Pleistocene climate warming, deep valleys across the Andes were emptied of ice. In some cases this opened fluvial channels across the mountains, ultimately causing the catastrophic drainage of the big palaeolakes to the Pacific Ocean. Smaller lakes remained in the deeper parts of the palaeolakes, but the drainage changed to the Pacific (Tatur *et al.*, 2002). One of these palaeolakes was 'Caldenius', which encompassed the Nansen, Chico and probably the Baker basin lakes (González, 1992; Aschero *et al.*, 1998; Tatur *et al.*, 2002). Thus initial colonization of currently Pacific-draining lakes may have been from the east, though subsequent immigration from the west is also probable.

The morphological similarity among these *Galaxias* populations may thus result from a shared colonization history that is not reflected in current drainage patterns, rather than just from similar selective regimes. Changing drainage patterns are probably the rule rather than the exception; they have also, for example, influenced the *G. vulgaris* complex inhabiting some rivers in South Island, New Zealand (Waters

*et al.*, 2001a). However, other cases, such as the large differences in morphology of *G. platei* among lakes in Tierra del Fuego (geographically close and with similar drainages), suggest that ecological conditions can be very important.

One of the strongest relationships was that between latitude and morphology, particularly the morphological variation in head and tail characters. However, rather than a continuous change in morphology from north to south, the lakes tended to sort into clusters: a southern cluster and two northern clusters (with one southern lake as an anomaly). *G. platei* from the northern lakes had smaller heads, as well as thinner caudal peduncles. The clustering (as well as the anomalous Lake Escondido in Tierra del Fuego) suggests that a continuous environmental factor such as temperature is probably not responsible for the variation in morphology. Variation in biotic factors such as predation and food availability or type seems more likely.

Degree of piscivory is one biotic factor that was correlated with latitude and with variation in morphology of *G. platei* across lakes. The strongest relationships were between piscivory and the variables loading heavily onto PC1 (head and tail characters). We measured piscivory as the proportion of all individuals (all species, including *G. platei*) that had fish in their stomachs, and interpreted degree of piscivory as predation risk. The relationship suggests that risk of predation may be partly responsible for the morphological variation among populations of *G. platei* in Patagonia. *G. platei* is a soft-bodied species without protective spines, and small individuals are likely to be very vulnerable to predators, including conspecifics (the cannibalism rate was 24% in Coyte, a pond with no other species of fish). The relatively smaller heads of *G. platei* in lakes with high piscivory suggests that the pattern of increased body width associated with decreased vulnerability to gape-limited predators described elsewhere for crucian carp (*Carassius carassius*) (Brönmark & Miner, 1992) probably does not apply to *G. platei*.

One factor contributing to the relationship between piscivory and latitude might be the presence of the small congener, *G. maculatus*, in the northern lakes. Another contributing factor might be warmer temperatures and associated higher levels of productivity. Change in degree of piscivory is thus one of the factors that could be driving a change in morphology from north to south. These results reinforce and extend a previously reported pattern for this species (Milano *et al.*, 2002), where caudal (but not head) morphology was correlated with predation risk over a much smaller geographical range.

Marked differences in resource use, including differences in diet and their association with differences in trophic morphology are indicative of adaptation

(Schluter, 2000). There were large differences in diet among river basins. In more than half the basins, amphipods were a significant or dominant food item (e.g. more than 80% of the diet in the Tierra del Fuego lakes), but no amphipods were consumed in the Futaleufú river basin. The lack of latitudinal trends in the consumption of any prey type indicates that variation in diet did not contribute uniformly to the latitudinal variation in morphology. However, diet may have nevertheless contributed to variation in morphology, as indicated by the correlation between PC3 (pelvic measures) and use of amphipods.

Previous observations of the Patagonian genus *Percichthys* (Cussac *et al.*, 1998; Ruzzante *et al.*, 1998, 2003; Logan *et al.*, 2000) suggest that ecosystem conditions in the post Pleistocene Andean (i.e. relative simplicity; Báez & Scillato Yané, 1979; Simpson, 1979) may have been conducive to the emergence of morphological variation and differentiation of the few species present in these lakes. Similar conditions in the northern hemisphere led to differentiation within several species of freshwater fish inhabiting north temperate postglacial lakes (Taylor, 1999). Within the Galaxiidae, sympatric morphs (or species) have been described within a related genus (*Paragalaxias*) inhabiting submontane Tasmanian lakes (McDowall, 1998). In our study of *G. platei*, we found no evidence of divergent morphological variation within lakes. Rather, there is a great deal of variation across lakes and river basins, with each lake considered here containing a single form of *G. platei*, which generally inhabits the very deep benthic environments of the lake.

*Galaxias platei* is one of the species that colonized the Andean lakes of Patagonia most extensively after the last glacial retreat (Cussac *et al.*, 2004). This ability seems to have been related to a physiological tolerance of low temperatures, lower oxygen levels and gill epithelial abrasion (Milano, 2003); indeed, it is still the only species found in lakes with suspended glacial sediments, such as Lake Belgrano in this study. *G. platei* shows strong morphological and physiological adaptations to benthic life: eyes are located rather dorsally, upper and lower mouth lips are thickened (Milano, 2003), and retinal cones exhibit high mitochondrial complexity (Schoebitz *et al.*, 1973), related to the high energy requirements for vision in darkness (Ali, Sakurai & Collin, 1990). These adaptations presumably allow *G. platei* to inhabit the deep benthic zone, where few other species can survive. However, they do not preclude the species from occupying shallow zones when other species are absent (e.g. Coyte and Del Mie Ponds).

Numerous species flocks within the Galaxiidae have been described in New Zealand and Tasmania, based on both morphological and genetic differentiation

(Allibone & Wallis, 1993; Allibone *et al.*, 1996; Ling *et al.*, 2001; Waters & Wallis, 2001a, b; Waters *et al.*, 2001b). In Northern Patagonia, parasitological evidence for *G. maculatus* suggests a sedentary habit for lake-inhabiting populations (Trochine, 2000; Revenga, 2003) and gene flow appears to be limited between *G. maculatus* populations from different lakes within a single basin (Zattara & Premoli, 2004). These observations for the northern border of the Pleistocene glacial area of Patagonia (Cussac *et al.*, 2004), agree with those of Wallis *et al.* (2001), who noted greater genetic structuring in nonglacial areas when compared with those where *G. vulgaris* was extirpated by Pleistocene ice.

Morphological differences that have been linked to environmental characteristics appear to exist among river-inhabiting groups of *G. maculatus* (Férriz *et al.*, 2001). The large amount of morphological variation among lakes that we observed in this study, particularly when compared with the interspecific differences between *G. platei* and *G. globiceps* (McDowall, 1971; Berra & Barbour, 1998; Milano, 2003), leads us to suggest whether *G. platei*, like *G. vulgaris* (Wallis *et al.*, 2001), is also a species complex rather than a single species. Efforts are underway to examine the genetics of the *Galaxias* species complex in southern South America in an attempt to resolve this question. However, regardless of whether the morphological variation reflects radiation into distinct species, or variation within a species, the important question remains: how did the morphological variation come about and how is it maintained? We have identified several patterns: morphology varies with latitude, with degree of piscivory and with diet. Experimental work will be required to further describe the role that ecological conditions play in maintaining morphological diversity in this group.

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