Reproductive aspects of *Galaxias platei* (Pisces, Galaxiidae) in a deep lake in North Patagonia

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Abstract.   Reproductive characteristics of the native fish *Galaxias platei* were studied in Lake Moreno, an ultra-oligotrophic deep lake in North Patagonia. According to histological analysis of ovaries, *G. platei* presents synchronous oocyte development typical of a group-synchronous spawner. Mature oocyte diameter ranged from 1031 to 1419 μm. Based on the gonadosomatic index, annual spawning occurs between April and June (austral autumn) and is directly related to the water temperature of deeper strata (below 30 m) where this species lives, but not with photoperiod. Female *G. platei* acquire sexual maturity at a length of 105 mm, whereas males acquire sexual maturity at a length of 177 mm. Delaying maturity to obtain higher fecundity, as well as maximum body size and longevity, indicates that *G. platei* is more specialised than the other South American *Galaxias*, *G. maculatus*, in terms of lifestyle. These specialised features are related to the stable environment *G. platei* lives in and indicate that it could eventually become a vulnerable species in unstable environments, such as the Patagonian lakes dominated by salmonids.

Introduction

Reproductive strategies in fish are extraordinarily diverse (Balon 1981). The reproductive success of a species depends primarily on a strategy that maximises the contribution of offspring to the next generation (Wootton 1990). A reproductive strategy is a suite of traits, such as size and age at first reproduction, spawning seasonality and frequency and size- or age-specific fecundity, correlated with and presumably optimised by natural selection (Wootton and Smith 2002). Thereby, reproductive success is determined by multiple ontogenetic and reproductive traits that set up a life history strategy (Stearns 2000). Thus, 'life history' deals with constraints and traits associated with reproduction and the manner in which these constraints or trade-offs form strategies to deal with different environmental factors (Stearns 2000; Hutchings 2008).

Galaxiids exhibit a considerable variety of life history styles (Cussac *et al.* 2004; McDowall 2008). They have indirect ontogeny, characterised by the presence of a larval period (McDowall 2008). Free embryos hatch and move to the breeding area, where they grow for several months before returning as juveniles to adult habitats (McDowall 1998). In South America, examples of this diversity are found in *Galaxias maculatus* and *Aplochiton* sp., which are present as diadromous and landlocked populations (McDowall 1971; Cussac *et al.* 2004). Their migratory movements occur between salt and fresh water (Campos 1969; Boy *et al.* 2007, 2009; Carrea *et al.* 2013), as well as

between freshwater habitats (e.g. intralacustrine movements, or from lentic to lotic environments; Cussac *et al.* 1992; Barriga *et al.* 2002, 2007; Lattuca *et al.* 2008). In *G. platei* and *Brachigalaxias bullocki*, only landlocked populations have been recorded (McDowall 1971; Cussac *et al.* 2004). Another plastic trait in galaxiids is spawning season phenology (McDowall 1971). *G. maculatus* has a spring–summer spawning season in Argentina (Cussac *et al.* 1992; Barriga *et al.* 2002, 2007; Boy *et al.* 2007), but in Chile populations spawn in late winter (Campos 1970). Other galaxiids, such as *Aplochiton zebra*, spawn in winter (Lattuca *et al.* 2008), whereas *Aplochiton taeniatus* spawns from late autumn to mid-winter (Campos 1969) and *B. bullocki* spawns during summer (McDowall 1971).

Galaxias platei is an endemic freshwater fish from the Patagonian and Chilean ichthyogeographic provinces (Ringuelet 1975) of southern South America. Southern Andean orogeny and Pleistocene glacial cycles appear to have played important roles in shaping the current distribution and intraspecific genetic diversity of *G. platei* (Ruzzante *et al.* 2008; Zemlak *et al.* 2008). *G. platei* is the most widely distributed native species in Patagonia and inhabits a variety of habitats in lotic and lentic environments (Cussac *et al.* 2004; Habit *et al.* 2010, 2012). Nevertheless, its distribution has been strongly affected by exotic salmonids (Milano *et al.* 2002, 2006; Habit *et al.* 2010, 2012) because its abundance is inversely proportional to that of salmonids (Habit *et al.* 2010; Correa and Hendry 2012). In this

context, predation and competition for habitat could induce displacement of *G. platei* from optimal habitats (Sobenes *et al.* 2013). Microhabitats with shelter are often used by *G. platei*, where density-dependent selection, such as the tendency for gregariousness, suggests antipredatory behaviour (Sobenes *et al.* 2013). In addition, in deep lakes in which salmonids are present, juvenile and adult *G. platei* are very uncommon in the littoral zone and occur almost exclusively in deeper benthic habitats (i.e. at depths below 30 m; Milano and Vigliano 1997; Milano *et al.* 2002).

Galaxias platei shows physiological and morphological traits that could be associated with a life spent in the deep benthos, such as high endurance to anoxia, low metabolic rate and high thermal tolerance to extreme conditions (Milano 2003; Barrantes *et al.* 2017). In addition, it has a cephalic lateral line, a protective structure to reduce abrasion in gills (Milano 2003), and retinal cones with high mitochondrial complexity (Schoebitz *et al.* 1973), suggesting adaptation to high-energy requirements for vision in the dark (Ali *et al.* 1990; Jobling 1995). Conversely, *G. platei* exhibits considerable morphometric variation throughout its distribution range, explained, in part, by variations in predation intensity (Milano *et al.* 2006) and food resource use among lakes (Milano *et al.* 2002). The morphology of *G. platei* is also related to its vertebral variation with latitude and altitude (Barriga *et al.* 2013).

Recent studies have contributed to the understanding of the ecology and natural history of *G. platei* as it occurs now, in systems with other native and non-native fish species (Cussac *et al.* 2004; McDowall 2006; Habit *et al.* 2010), but the ecology and biology of *G. platei* are poorly documented (Milano 2003; Sobenes *et al.* 2013; Belk *et al.* 2014). The scarcity of data available on *G. platei* ecology prompted an investigation into its life history, including reproductive parameters. The main aim of the present study was to analyse different aspects of the reproductive biology of *G. platei* in order to identify its reproductive strategy. To this end, we described gonad development based on microscopic and macroscopic examination, estimated the gonadosomatic index (GSI) to determine spawning season and its relationship with temperature and photoperiod, and established size at first maturity, sex ratio and the length–weight relationship.

Materials and methods

Study site and fish collection

Fish were collected from Moreno Lake (41°80′50″S, 71°83′20″W), a large (area 10.6 km^2, perimeter 14.6 km), deep ($Z_{Max} = 106$ m, $Z_{Med} = 51$ m) glacial lake located in the Andean temperate rainforest within Nahuel Huapi National Park. Moreno Lake has a warm monomictic thermal regime (Modenutti *et al.* 2000) with thermal stratification during late spring and summer (Pérez *et al.* 2002). The conditions at Moreno Lake are ultra-oligotrophic with highly transparent waters (average Secchi disc = 16 m and diffuse attenuation coefficient of photosynthetically active radiation $K_{dPAR} = 0.16$ m^{-1}, Morris *et al.* 1995) and a euphotic zone that extends to a depth of 36.4 m (Pérez *et al.* 2002).

The fish assemblage in Moreno Lake is composed mostly of exotic salmonids: *Oncorhynchus mykiss* (38%), *Salvelinus*

fontinalis (12%) and *Salmo trutta* (1.2%). The most abundant native fish is *Percichthys trucha* (43%). In contrast, *G. platei* (4%), *Odontesthes hatcheri* (1.2%) and *Olivaichthys viedmensis* (0.2%) are rare in gill net captures (Vigliano *et al.* 2009). Another abundant native fish is *G. maculatus*, which, due to its small size (~7 cm), is captured only when using seine or fyke nets or baited traps.

In the present study, *G. platei* were captured using gill-nets placed (on the lake bottom) at depths of 10, 20, 30, 50 and 100 m. The nets were 60 m in length and 2 m in height and made up of panels that were 10 m in length, each with a different bar mesh size (15, 20, 30, 50, 60 and 70 mm; Vigliano *et al.* 1999). These nets were left for ~12 h overnight. Sampling was performed during 1999 and 2000. Individual fish caught in the nets were killed using an overdose of benzocaine and fixed in 4% formaldehyde.

Lake temperature profiles were generated using a digital thermometer with a 100-m wire. During the sampling period, water temperature was registered monthly for each depth stratum. Daylight data for the sampling period were downloaded from an automated weather monitor (Davis Vantage Pro, Hayward, CA, USA) from the meteorological station located at Laboratorio de Fotobiología (Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional del Comahue) close to Moreno Lake.

Laboratory analyses

In the laboratory, standard length (SL) and total weight (TW) were measured for all fish. Sex was determined, and the gonads were then removed, weighed fresh (GW) to the nearest 0.0001 g and then fixed in Bouin solution (Martoja and Martoja-Pierson 1970) before being preserved in 70% ethanol. Ovaries were then stained with Masson's trichrome using conventional histological techniques (Martoja and Martoja-Pierson 1970). Histological characterisation of the ovarian cycle was based on the affinity of the dye for the cytoplasm and nucleus, and by the presence or absence of different cell structures. The diameter of each oocyte type was measured on digital images of the histological preparations at magnifications of 10× and 20×. Photographs were taken using a Sony SSC-DC50A (Park Ridge, NJ, USA) digital interface camera attached to an Olympus BX40 (Tokyo, Japan) optical microscope, and oocyte diameters were measured using Image-Pro Plus version 4.0 for Windows (Media Cybernetics, Inc., Silver Spring, MD, USA).

Reproductive parameters

The sex ratio was assessed seasonally using mature individuals and then contrasted with the hypothetical 1 : 1 proportion using Chi-Square distribution. The GSI was calculated as follows:

$$GSI = GW \div TW \times 100$$

The GSI was analysed monthly to determine the exact period and amplitude of the spawning season. Relationships between GSI and water temperature at capture depth (as a proxy of temperature at which fish live), depth stratum and daylight time (i.e., photoperiod) were evaluated with Spearman correlation

tests. In addition, relationships between mean GSI and mean water temperature from depths below 30 m (where fish live) and mean water temperature from depths above 30 m (where fish do not live) were evaluated with Spearman correlation tests. The relationship between TW and SL was assessed separately for males and females, as well as in adults and juveniles, using the following equation:

$$TW = a \times SL^b$$

where *a* and *b* are the intercept and the slope of the function respectively. Linear regression analysis was performed with $\log_{10}$-transformed data. The significance of each regression coefficient was tested using an analysis of variance (ANOVA). Slope equality between sexes and between adults and juveniles was then tested using one-way analysis of covariance (ANCOVA) where TW was the dependent variable, sex or juvenile or adult were the factors and SL was the covariable. This equality was tested by verifying non-interaction between the factors and covariable. Size at first maturation was estimated using a binary logistic regression model (Norusis 1986). In this model, sexual maturity was the dependent variable with binary values (0, immature; 1, mature individuals). Fish size (SL) was used as the independent variable. The logistic equation was used as follows:

$$P = (1 + e^{-(a + b\,SL)})^{-1}$$

where *P* is the proportion of mature individuals and *a* and *b* are parameters estimated by the model. The point where $P = 0.5$ represents the transition size where 50% of individuals reach sexual maturity.

Results

Gonad description

The sexual organs of *G. platei* are paired structures of saccular form, lying dorsal to the digestive tract. As they develop, they occupy a large part of the abdominal cavity. In the case of female structures, the ovary lamellae are open to the abdominal cavity (Fig. 1*a*). Macroscopic descriptions of testes and ovaries are given in Table 1.

Four oocyte stages were determined, based on microscopic observations of the ovaries. The oocyte, at the beginning of its primary growth phase (Stage I), consists of scant cytoplasm and a centrally located nucleus containing a single, large basophilic nucleolus. This oocyte period is called the 'chromatin nucleolus stage'. The oocyte itself is entirely surrounded by a few squamous follicle cells. Concurrent with oocyte growth, the nucleus (or germinal vesicle (GV)) increases in size and multiple nucleoli appear ('perinucleolus stage'; Fig. 1*b*). These nucleoli are arranged at the periphery of the GV and their presence throughout oocyte growth becomes ubiquitous. The cytoplasm is strongly basophilic at this stage. In *G. platei*, the oocyte during this phase has a diameter ranging from 37 to 150 μm. Two thin layers surround the oocyte: a layer of follicular cells (granulosa cell layer) and another layer of thecal cells (thecal layer) constitute the follicle. The first structures to then appear within the oocyte cytoplasm during its growth are the 'yolk vesicles'

(Stage II). During this period the nuclear membrane appears to be folded and the cytoplasm has a foamy appearance as a result of the chromophobe vesicles (Fig. 1*c*). Oocytes have diameters ranging between 113 and 223 μm (Fig. 1*c*). The granulose layer is formed by a single row of evident cuboidal cells. Outside this structure, a layer of flat cells constitutes the thecal layer. At this point the process of vitellogenesis begins, characterised by the uptake and packaging of vitellogenin stored inside the oocyte as yolk protein. The beginning of vitellogenesis is called 'early vitellogenesis' (Stage III) and is characterised by small orange granules that occupy the entire cytoplasm. Chromophobe vesicles are displaced towards the periphery of the cytoplasm (Fig. 1*d*). The vitelline membrane appears well defined and its thickness increases throughout oocyte growth. The granulose cell layer (follicular cells) becomes columnar, whereas the thecal layer remains unchanged (Fig. 1*e*). Oocyte diameters range from 208 to 449 μm. At this moment, ovaries are macroscopically cylindrical, slightly flattened and yellowish. The oocytes are visible to the naked eye, being easier to identify as vitellogenesis progresses. In accordance with the process of vitellogenesis, ovaries become larger, occupying much of the abdominal cavity and changing from pale yellow to bright yellow. As vitellogenesis progresses, the yolk granules gradually form a homogeneous mass, occupying almost all the oocyte cytoplasm ('advanced vitellogenesis' or Stage IV). Cortical vesicles are located on the periphery, and the nucleus migrates to the oocyte periphery. Oocytes have diameters ranging between 1031 and 1419 μm. The ovaries at this point have abundant oocytes in Stage IV, which are released (i.e. ovulated) into the abdominal cavity to be released through the oviduct during spawning. At this time, oocytes can be released with slight abdominal pressure. The ovaries are bright yellow, cylindrical and turgid, occupying almost the entire abdominal cavity. After the spawning event, ovaries enter a resting phase (Stage V). Oocytes that are mainly in the perinucleolus and chromatin nucleolus stages are frequently observed, with a low number of cortical alveoli and postovulatory follicles (POFs), as well as atretic oocytes that failed to spawn. POFs are recognisable because they have only a retracted layer of granulose cells, because the oocyte has been released into the lumen of the ovary. In atretic oocytes, the cytoplasm is invaded by granulose cells that have digested the yolk. Macroscopically, ovaries become small and reddish in colour (haemorrhagic appearance).

Fish catch and sex ratio

In Moreno Lake, all *G. platei* individuals were caught at or below a depth of 30 m, with a slight tendency for abundance to increase with depth (Fig. 2). In all, 78 *G. platei* individuals were caught: 46 females (61.4–285.0 mm SL; 3.3–285.0 g), 25 males (60.6–265.0 mm SL; 2.4–245.0 g) and 7 immature specimens (31.3–103.7 mm SL; 0.2–12.9 g) whose sex was not determined. Of the total capture, 59 individuals were mature: 42 females (105–285 mm SL; 15–285 g) and 17 males (180–265 mm SL; 75–245 g). The overall female : male sex ratio was 1 : 0.29, which deviated from the hypothetical distribution of 1 : 1 (χ^2, $z = 6.83$, $P = 0.009$). Given the low number of individuals in some months, the sex ratio was analysed by season and was found to deviate from 1 : 1 in summer (1 : 0.20; χ^2, $z = 6.06$; $P = 0.007$) and autumn (1 : 0.25; χ^2, $z = 3.46$; $P = 0.046$), but
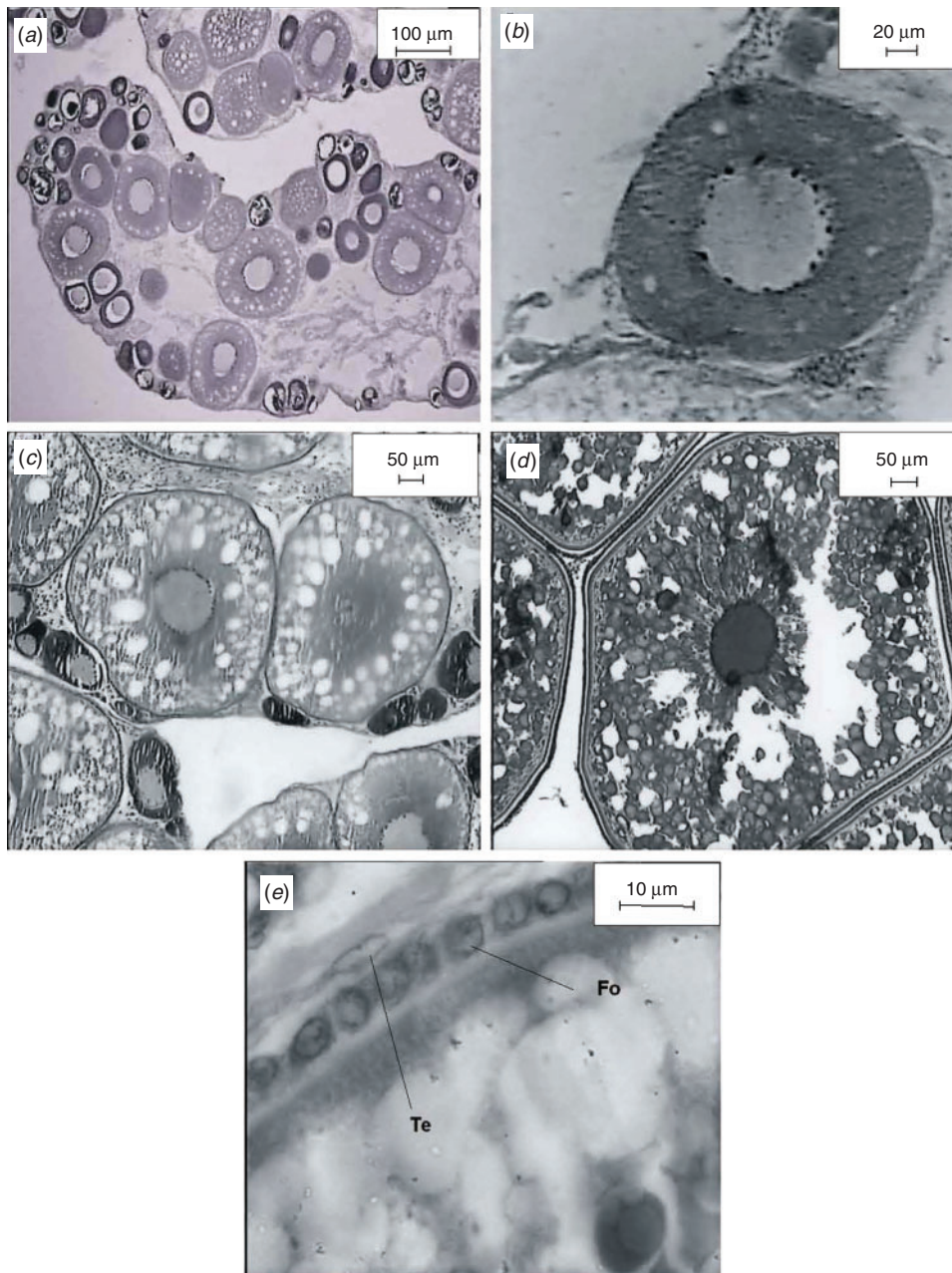
Fig. 1. Ovary of *Galaxias platei*. (*a*) General aspect of the ovarian lamellae, (*b*) oocyte in the perinucleolus stage (Stage I), (*c*) 'yolk vesicles' in the oocyte (Stage II), (*d*) vitellogenic oocyte (Stage III) and (*e*) detail of the follicle. Te, thecal cells; Fo, follicular cells.

not during winter (1 : 0.33; χ^2, $z = 0.92$, $P = 0.317$) or spring (1 : 0.43; χ^2, $z = 0.25$; $P = 0.593$).

Spawning season

Through monthly GSI analysis, it was observed that the gonadal size of *G. platei* increased from March and decreased in June. The lowest gonadal size was detected between August and December. The GSI distribution throughout the year showed a similar pattern in both sexes. The highest GSI values were in April and June for females and in June for males (Fig. 3). In addition, gonadal stage distribution allowed the spawning season to be defined, and it was found to be more clearly demarcated in females than males. Between March and June, the high proportion of individuals observed in transition from Stage III to Stage IV denotes the spawning event. After this period, the large number of individuals in Stage V shows that spawning had ended, and individuals in Stage II indicate the beginning of the next reproductive cycle (Fig. 4). Both approaches enabled the reproductive season for *G. platei* in Lake Moreno to be established as being between April and June (austral autumn).

Table 1.   Macroscopic descriptions of testes and ovary stages, with detailed microscopic descriptions of the ovaries, diameter of oocyte-dominant cohort, and their seasonal occurrence in *Galaxias platei*

AT, atretic oocytes; AV, advanced vitellogenesis; CA, cortical alveoli; CN, chromatin nucleolus; EV, early vitellogenesis; PN, perinucleolus; POF, postovulatory follicles

Gonad stage	Testes macroscopic description	Ovaries		Oocyte diameter (μm)	Season
		Macroscopic description	Microscopic description		
I: immature	Translucent of small size; no apparent irrigation	Small, cylindrical and translucent no apparent irrigation	Oocytes mostly in CN stage, but some in PN stage	37–150	All year
II: maturing	Medium sized and whitish with apparent irrigation	Medium sized, cylindrical, whitish–yellow colour with evident irrigation; oocytes may be visible	Oocytes in CN, PN and CA stages; follicular cells begin to differentiate during CA	113–223	Summer
III: mature	Medium, cylindrical, whitish colour; very apparent irrigation	Large, pale yellow with very evident irrigation; oocytes very visible	Oocytes in CN and EV stages; follicular cells well developed	208–449	Summer to early autumn
IV: spawning	Largest size and very turgid; very evident irrigation	Flaccid, bright yellow; very evident irrigation; yellow and hyaline oocytes	Oocyte in CN and AV; follicular cells well developed	1031–1419	Autumn to early winter
V: resting	Small to medium sized, flaccid and bloody with very evident irrigation	Small ovaries; reddish colour due to evident irrigation	Oocytes mainly in CN stage, POFs and low number of AT		Spring
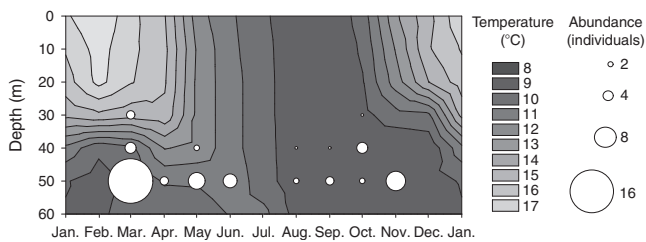
Fig. 2. *Galaxias platei* abundance according to depth stratum and thermal profile of Lake Moreno throughout the year.

The GSI was positively correlated with water temperature at capture depth (Spearman, $\rho = 0.361$, $n = 63$, $P = 0.04$), but no correlation was found between GSI and daylight time (i.e. photoperiod) or between GSI and depth (Spearman, $P > 0.05$; Fig. 3). Moreover, mean GSI was positively correlated with mean water temperature at depths below 30 m, where these fish live (Spearman, $\rho = 0.880$, $n = 8$, $P = 0.004$). However, no correlation was found between mean GSI and mean water temperatures at depths above 30 m (Spearman, $\rho = 0.619$, $n = 8$, $P = 0.102$; Fig. 2).

Length–weight relationship

The length–weight relationship for females was $TW = 0.009 \times SL^{2.90}$ (ANOVA, $R^2 = 0.99$, $F_{1,43} = 3622.40$, $P < 0.001$), whereas for males it was $TW = 0.005 \times SL^{3.17}$ (ANOVA, $R^2 = 0.98$, $F_{1,24} = 1247.40$, $P < 0.001$). There was no significant difference between females and males regarding slopes, (i.e., *b* values; ANCOVA, $F_{1,55} = 0.08$, $P = 0.782$). Both models proved to be isometric, with *b* values of 2.90 (95%
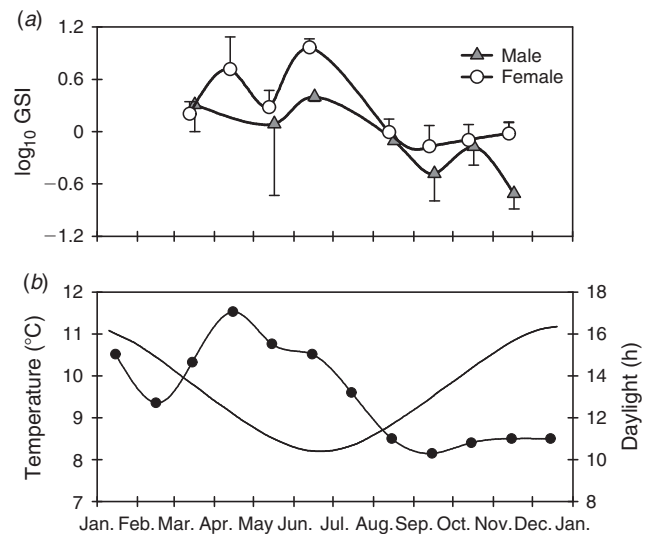
Fig. 3. (*a*) Variations in the gonadosomatic index (GSI) in *Galaxias platei* over 1 year in Lake Moreno. (*b*) Mean water temperature (dotted line) at depths between 30 and 60 m and daylight variation (solid line) throughout the year.

confidence interval (CI) 2.81–3.00) for females and 3.17 (95% CI 2.98–3.36) for males. Thus, a common relationship could be estimated including both sexes, namely $TW = 0.007 \times SL^{3.02}$ ($R^2 = 0.99$, $F_{1,75} = 6346.30$, $P < 0.001$) with a *b* value of 3.02 (95% CI 2.92–3.11). For juveniles the length–weight relationship was $TW = 0.003 \times SL^{3.45}$ ($R^2 = 0.95$, $F_{1,13} = 259.80$, $P < 0.001$; Fig. 5). Differences were found in the slope of the relationship between adults and juveniles (ANCOVA, $F_{1,74} = 88.63$; $P < 0.001$).

Size at first maturity

Size at first maturity was higher for males than females. The size at which 50% of males are mature was 177.5 mm SL, compared

with 105.6 mm SL for females (Fig. 6). The equations for females and males were respectively:

$$P = (1 + e^{(-13.05+124\ SL)})^{-1}$$

and

$$P = (1 + e^{(-52.66+297\ SL)})^{-1}$$

Discussion

Ovaries of *G. platei* are paired structures, saccular in form, like those of most teleosts (Nagahama 1983). They lie dorsal to the digestive tract and can occupy the entire abdominal cavity. Ovarian lamellae are open to the abdominal cavity, being of the gymnovarian type (*sensu* Nagahama 1983), where oocytes are ovulated into the coelomic cavity and then released through the oviduct to the environment. Histological observation indicates that two populations of oocytes can be recognised in ovaries of *G. platei*: a synchronous population of larger oocytes and a more heterogeneous population of smaller oocytes. Specifically, the cohort of most developed oocytes is spawned first, during the next spawning season, whereas the cohort of less developed oocytes is retained and spawned in future spawning seasons. The former group developed, matured and ovulated in unison; this condition defines *G. platei* as a group-synchronous spawner (*sensu* Murua and Saborido-Rey 2003). This type of ovary occurs in those species that generally spawn once per year, have a relatively short spawning season (Wootton 1990) and spawn several times during their lifespan (i.e. iteroparous species; Murua and Saborido-Rey 2003). A single annual spawning is typical of species living at high latitudes, where there are wide annual variations in temperatures and photoperiod (Matthews 1998).
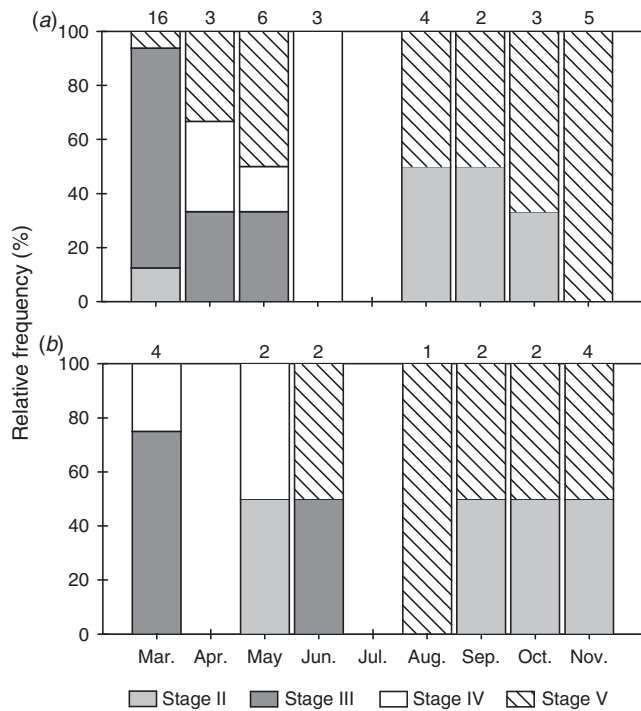

Fig. 4. Monthly variations in the relative frequency of different gonadal stages in adult (*a*) female and (*b*) male *Galaxias platei* (for descriptions of the different stages, see Table 1) throughout the year in Lake Moreno. Numbers above the columns indicate the number of samples.
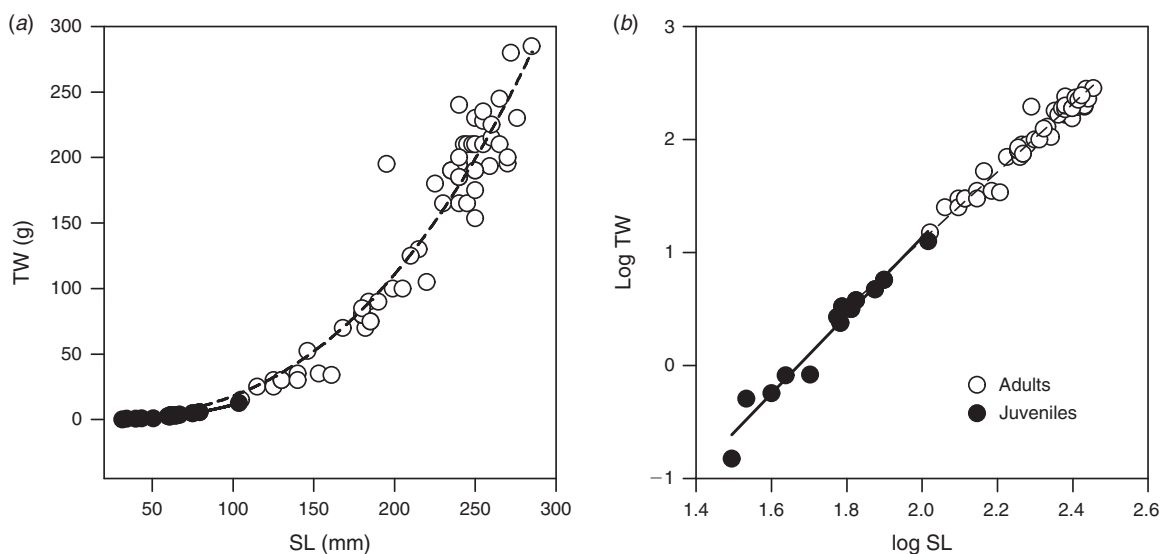

Fig. 5. (*a*) Weight–length relationships and (*b*) double-logarithmic plot for adult and juvenile *Galaxias platei*. Fitted curves are shown for adults (dashed lines) and juveniles (solid lines). SL, standard length; TW, total weight.
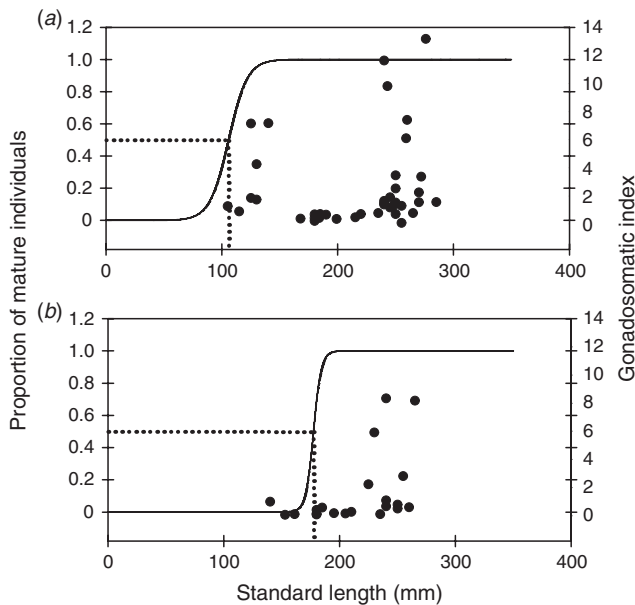
Fig. 6. Proportion of mature individuals and gonadosomatic index in relation to the size of (*a*) female and (*b*) male *Galaxias platei* in Lake Moreno. The solid lines show the binary logistic regression model curve; the dotted lines show the length at which 50% of individuals are mature.

The GSI of *G. platei* in Lake Moreno starts to increase in summer and reaches a maximum during autumn, when spawning occurs, indicating that this species has an annual spawning period. This spawning season coincides with the findings from Lake Rosario (43°23′S; Ortubay and Wegrzyn 1991) and Lake Gutiérrez (41°11′S; Barriga *et al.* 2002). However, Zama (1986) suggested that spawning of *G. platei* occurs in summer in Lake Poli (46°15′S), as with some other southern Patagonian lakes, such as Pueyrredón (47°18′S), Belgrano (47°50′S) and Yehuin (54°19′S) lakes, where specimens in spawning or post-spawning stages were collected in summer (D. Milano, pers. comm.). This information about the reproductive season of *G. platei* is scarce, but suggests that the spawning season in this species is very variable (Zama 1986; Ortubay and Wegrzyn 1991; Barriga *et al.* 2002).

The timing of gametogenesis and spawning events during an annual cycle (i.e. reproductive phenology) is mediated by environmental cues. In cool temperate freshwater fish, the main cues are changes in photoperiod and water temperature (Pankhurst and Porter 2003). These factors may act synergistically or independently to stimulate the reproductive cycle (Acharjee *et al.* 2017). For this reason, the habitat used by each species, and specifically the thermal habitat, becomes fundamental in reproductive phenology. Most Patagonian native species spawn between spring and early summer, when photoperiod and water temperature change with a similar pattern. Photoperiod and temperature reach their maximum in summer and their minimum in winter. This spawning pattern is found in those species whose thermal habitat variations are very similar to the seasonal air temperature variation throughout the year, namely species that mostly live in the upper strata of lakes or rivers. For example, the spawning substrate of several species consists of macrophyte patches in shallow zones. Examples of these spawners are landlocked *G. maculatus* (Barriga *et al.* 2002, 2007), *P. trucha* (Buria *et al.* 2007), *O. hatcheri* (Dománico and Lauce Freyre 2008) and *Hatcheria macraei* (Chiarello-Sosa *et al.* 2016).

In the case of *G. platei* in Moreno Lake, reproductive phenology is related to water temperature but not to photoperiod. The temperature that guides reproductive events is that of the deeper strata, at depths below 30 m, where *G. platei* mostly lives in deep lakes (Milano and Vigliano 1997). Surprisingly, temperature variation in these deeper habitats is not as similar to air temperature variation as it seems to be in the upper strata of the lake. Temperate monomictic lakes are characterised by summer stratification, where a warm surface layer is isolated from the colder deep waters by a marked thermal discontinuity, the thermocline. After this period, due to wind and rains, the thermocline becomes deeper, and finally the mixing process homogenises the water column (Wetzel 2001). The consequence of this event is the warming of deeper water strata in the April–June period (see Fig. 3). Our results show that spawning of *G. platei* begins in April (the austral autumn), towards the end of the lake stratification period, when the water temperature in deep strata reaches its maximum values, between 14.7°C at 30 m and 10°C at 60 m, due to the mixing process (see Fig. 2).

Galaxias platei seems to have found refuge in benthic deep areas as a response to predation or competition with salmonids (Milano *et al.* 2002, 2006; Correa and Hendry 2012; Correa *et al.* 2012). In addition, *G. platei* shows several physiological and morphological characteristics that enable it to live in the deep stratum, such as a broad thermal tolerance range (eurythermic, 0–30°C), and particularly good acclimatisation and metabolic abilities at low temperatures (Milano 2003; Barrantes *et al.* 2017). Furthermore, vision in the dark (Schoebitz *et al.* 1973; Ali *et al.* 1990) and a well-developed cephalic lateral line (Milano 2003) permit the perception of prey and predators when visual conditions are poor, such as in the low light intensity of the deep-water strata (Pitcher 1993). Given the extent of its adaptations (Shuter *et al.* 2012), this species may be able to respond sufficiently to cold-water environments, even to face a spawning season in autumn in the deep strata of Patagonian lakes.

Spawning during autumn could have a strong effect on the survival of the offspring. The size of eggs and free embryos of *G. platei* suggest that larval size may be greater than that of *G. maculatus* (Barriga *et al.* 2002). A robust larva minimises specific metabolic rate and maximises stored energy, conferring resistance during periods of scarce resources (Shuter and Post 1990). Although there are no studies on the thermal tolerance of *G. platei* larvae, embryonic development until hatching occurs in 20 days at 11.5°C and in 28 days at 7.5°C (Ortubay and Wegrzyn 1991), which indicates that larvae undergo the low temperatures of winter. Food availability and quality are other important factors for larvae survival. The occurrence of larvae usually coincides with a peak in the abundance of zooplankton, which maximises larval feeding (Johnson 2000). Although *Boeckella* sp. copepodites and adults are present in autumn and early winter in Lake Moreno (Balseiro *et al.* 2001; Alonso *et al.* 2004), the relationship between prey abundance and its benefits for larvae

Table 2. Comparative data for Southern American Galaxiidae
SL, standard length; L, lake; P, pond; R, river

Species	Egg diameter (mm)	Hatched free embryos (mm)	Size at first maturity (mm SL)	Fecundity (number of eggs per female)	Adult female size (mm)	Spawning season	Location	References
Galaxias platei	1.03–1.41		177.5 (♂), 105.6 (♀)		105–285	Autumn–winter	L. Moreno	Present study
	1.15–1.65	4.7–7.1		85 000–130 000	280–380	Autumn	L. Rosario	Ortubay and Wegrzyn (1991)
	1.7–1.9			20 000	207–286	Summer	L. Poli	Zama (1986)
				1300–30 000	70–170		L. Panguipulli	Campos (1984)
Galaxias maculatus								
Landlocked populations	0.99–1.1	4.2–5.1	31.3 (♂), 32.1 (♀)	400–800	32–80	Early spring to early summer	P. Ezquerra, L. Gutiérrez	Cussac *et al.* (2004), Barriga *et al.* (2002)
				107–2825		Summer	R. Limay	Ferriz (1987)
Diadromous populations	0.9–1.6	5.6–6.9	–	390–7400	48–160	Spring–autumn	R. Valdivia	Campos (1970)
	0.70–1.00		–	470–2097		Spring–summer	R. Ovando	Boy *et al.* (2009)
Aplochiton zebra	1.45–1.80	8.0–12.7	116.4 (♂), 129.8 (♀)	5700	160–240	Spring	L. Lácar, L. Puelo, L. Rivadavia	Lattuca *et al.* (2008)
Aplochiton taeniatus	1.0–1.7	6.2–6.5	–	2500–3000	98–125	Late autumn to mid-winter	L. Llamquihue	Campos (1969)
Brachigalaxias bullocki	2	–	–	61–163	38–60	Summer	Data from 14 lakes	McDowall (1971)

during the winter period is not known. Thus, we do not know whether winter starvation, exposure to low temperatures or both could have negative effects on *G. platei* offspring.

In Moreno Lake, both sexes of G. *platei* showed isometric growth, with an increase in body thickness proportional to size during growth. Even though females reach sexual maturity at smaller sizes than males, maturation occurs between the second and the third year of life (Belk *et al.* 2014), which indicates that *G. platei* delays maturation, prioritising somatic growth. Furthermore, the number of mature females was higher than that of mature males at the beginning of the spawning season (austral autumn), suggesting greater female reproductive investment in terms of egg production during the reproductive season (Kokita and Nakazono 1998). Therefore, the energy allocated to somatic growth to reach larger sizes, at the expense of maturation, indicates reproductive investment to achieve greater future egg biomass (Roff 1984).

Differences in life history traits among South American galaxiid species are evident in terms of egg and free embryo size at hatching (*sensu* Balon 1981). Landlocked *G. maculatus* populations have the smallest eggs and consequently the smallest free embryos, whereas *Aplochiton* spp. and *Brachigalaxias* spp. seem to have the largest eggs and free embryos. *G. platei* lies in an intermediate position among galaxiids (Table 2). Comparing life histories within the *Galaxias* genus, *G. maculatus* expends a large amount of energy on early reproduction in its first year of life (Barriga *et al.* 2002), whereas *G. platei* invests more energy in growth while delaying sexual maturity. Within the context of lifestyles, *G. platei* seems to be more

specialised than *G. maculatus*. In addition, *G. platei* is the largest (Table 2) and longest-lived species of the Patagonian Galaxiidae species, reaching ~350 mm TL and 18 years of age (Belk *et al.* 2014). Both traits are closer to the 'periodic' lifestyle within the space encompassed by the opportunistic–periodic–equilibrium trichotomy (Winemiller and Rose 1992).

In conclusion, reproductive traits found in *G. platei* are related to the stable environment in which it lives, namely the deeper benthos of deep Patagonian lakes. These specialised life history traits (*sensu* Winemiller and Rose 1992; Winemiller 2005) are consistent with the remarkably specialised morphological and physiological features of this species (Schoebitz *et al.* 1973; Milano 2003; Milano *et al.* 2002, 2006; Barrantes *et al.* 2017). Several traits indicate that *G. platei* behaves as a winter specialist (*sensu* Shuter *et al.* 2012), exhibiting adaptations to extended periods of low temperature, light and food levels. In sum, all these specialised features indicate that *G. platei* could eventually become a vulnerable species in unstable environments (Olden *et al.* 2008) such as the Patagonian lakes dominated by salmonids.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

References

Acharjee, A., Chaube, R., and Joy, K. P. (2017). Effects of altered photoperiod and temperature on expression levels of gonadotrophin subunit mRNAs in the female stinging catfish *Heteropneustes fossilis*. *Journal of Fish Biology* **90**, 2289–2311. doi:10.1111/JFB.13305

Ali, M. A., Sakurai, S., and Collin, S. P. (1990). Adaptive radiation of the retina in Galaxiidae (Salmoniformes). *Australian Journal of Zoology* **38**, 173–186. doi:10.1071/ZO9900173

Alonso, C., Rocco, V., Barriga, J. P., Battini, M. A., and Zagarese, H. (2004). Surface avoidance by freshwater zooplankton: field evidence on the role of ultraviolet radiation. *Limnology and Oceanography* **49**, 225–232. doi:10.4319/LO.2004.49.1.0225

Balon, E. K. (1981). Additions and amendments to the classification of reproductive styles in fishes. *Environmental Biology of Fishes* **6**, 377–389. doi:10.1007/BF00005769

Balseiro, E. G., Modenutti, B. E., and Queimaliños, C. (2001). Feeding of *Boeckella gracilipes* (Copepoda, Calanoida) on ciliates and phytoflagellates in an ultraoligotrophic Andean lake. *Journal of Plankton Research* **23**, 849–857. doi:10.1093/PLANKT/23.8.849

Barrantes, M. E., Lattuca, M. E., Vanella, F. A., and Fernández, D. A. (2017). Thermal ecology of *Galaxias platei* (Pisces, Galaxiidae) in South Patagonia: perspectives under a climate change scenario. *Hydrobiologia* **802**(1), 255–267. doi:10.1007/S10750-017-3275-3

Barriga, J. P., Battini, M. A., Macchi, P. J., Milano, D., and Cussac, V. E. (2002). Spatial and temporal distribution of landlocked *Galaxias maculatus* and *Galaxias platei* (Pisces, Galaxiidae) in a lake in the South American Andes. *New Zealand Journal of Marine and Freshwater Research* **36**, 345–359. doi:10.1080/00288330.2002.9517092

Barriga, J. P., Battini, M. A., and Cussac, V. E. (2007). Annual dynamic variation of a landlocked *Galaxias maculatus* (Jenyns 1842) population in a Northern Patagonian river: occurrence of juvenile upstream migration. *Journal of Applied Ichthyology* **23**, 128–135. doi:10.1111/J.1439-0426.2006.00820.X

Barriga, J. P., Milano, D., and Cussac, V. E. (2013). Variation in vertebral number and its morphological implication in the South American galaxiid, *Galaxias platei*. *Journal of Fish Biology* **83**, 1321–1333. doi:10.1111/JFB.12233

Belk, M. C., Habit, E., Ortiz-Sandoval, J. J., Sobenes, C., and Combs, E. A. (2014). Ecology of *Galaxias platei* in a depauperate lake. *Ecology Freshwater Fish* **23**, 615–621. doi:10.1111/EFF.12114

Boy, C. C., Morriconi, E., and Calvo, J. (2007). Reproduccion in puyen, *Galaxias maculatus* (Pisces: Galaxiidae), in the southermost extreme of distribution. *Journal of Applied Ichthyology* **23**, 547–554. doi:10.1111/J.1439-0426.2007.00842.X

Boy, C. C., Pérez, A. F., Lattuca, M. E., Calvo, J., and Morriconi, E. (2009). Reproductive biology of *Galaxias maculatus* (Jenyns 1842) in the Río Ovando, a high-latitude environment in southernmost Patagonia, Argentina. *Journal of Applied Ichthyology* **25**, 661–668. doi:10.1111/J.1439-0426.2009.01309.X

Buria, L., Walde, S. J., Battini, M., Macchi, P. J., Alonso, M., Ruzzante, D. E., and Cussac, V. E. (2007). Movement of a South American perch *Percichthys trucha* in a mountain Patagonian lake during spawning and pre-spawning periods. *Journal of Fish Biology* **70**, 215–230. doi:10.1111/J.1095-8649.2006.01297.X

Campos, H. (1969). Reproducción del *Aplochiton taeniatus* Jenyns. *Boletín del Museo Nacional de Historia Natural* **29**, 207–222.

Campos, H. (1970). *Galaxias maculatus* (Jenyns) en Chile, con especial referencia a su reproducción. *Boletín del Museo Nacional de Historia Natural* **31**, 5–20.

Campos, H. (1984). Gondwana and neotropical galaxioid fish biogeography. In 'Evolutionary Ecology of Neotropical Freshwater Fishes'. (Ed. T. M. Zaret.) pp. 113–125. (Dr Junk Publishers: The Hague, Netherlands.)

Carrea, C., Cussac, V. E., and Ruzzante, D. E. (2013). Genetic and phenotypic variation among *Galaxias maculatus* populations reflects contrasting landscape effects between northern and southern Patagonia. *Freshwater Biology* **58**, 36–49. doi:10.1111/FWB.12036

Chiarello-Sosa, J. M., Battini, M. A., and Barriga, J. P. (2016). Reproductive strategy of the Patagonian catfish *Hatcheria macraei*. *Journal of Fish Biology* **89**, 1810–1827. doi:10.1111/JFB.13093

Correa, C., and Hendry, A. P. (2012). Invasive salmonids and lake order interact in the decline of puye grande *Galaxias platei* in western Patagonia lakes. *Ecological Applications* **22**, 828–842. doi:10.1890/11-1174.1

Correa, C., Bravo, A. P., and Hendry, A. P. (2012). Reciprocal trophic niche shifts in native and invasive fish: salmonids and galaxiids in Patagonian lakes. *Freshwater Biology* **57**, 1769–1781. doi:10.1111/J.1365-2427.2012.02837.X

Cussac, V. E., Cervellini, P. M., and Battini, M. A. (1992). Intralacustrine movements of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae) during their early life history. *Environmental Biology of Fishes* **35**, 141–148. doi:10.1007/BF00002189

Cussac, V. E., Ortubay, S., Iglesias, G., Milano, D., Lattuca, M., Barriga, J. P., Battini, M. A., and Gross, M. (2004). The distribution of South American galaxiid fishes: the role of biological traits and post glacial history. *Journal of Biogeography* **31**, 103–121. doi:10.1046/J.0305-0270.2003.01000.X

Dománico, A. A., and Lauce Freyre, R. (2008). Reproductive aspects of the Patagonian silverside (*Odontesthes hatcheri* Eigenmann, 1909) from the Ezequiel Ramos Mexía reservoir (Argentina). *Revista Mvz Cordoba* **13**, 1446–1455. doi:10.21897/RMVZ.375

Ferriz, R. A. (1987). Biología del puyen *Galaxias maculatus* (Jenyns) (Teleostomi, Galaxiidae) en un embalse norpatagónico. Ciclo de vida, ciclo gonadal y fecundidad. *Revista del Museo Argentino de Ciencias Naturales – B. Rivadavia* **6**, 29–38.

Habit, E., Piedra, P., Ruzzante, D. E., Walde, S. J., Belk, M. C., Cussac, V. E., Gonzalez, J., and Colin, N. (2010). Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects. *Global Ecology and Biogeography* **19**, 697–710. doi:10.1111/J.1466-8238.2010.00541.X

Habit, E., Gonzalez, J., Ruzzante, D. E., and Walde, S. J. (2012). Native and introduced fish species richness in Chilean Patagonian lakes: inferences on invasion mechanisms using salmonid-free lakes. *Diversity & Distributions* **18**, 1153–1165. doi:10.1111/J.1472-4642.2012.00906.X

Hutchings, J. A. (2008). Life histories of fish. In 'Handbook of Fish Biology and Fisheries'. (Eds P. J. B. Hart and J. D. Reynolds.) pp. 149–174. (Blackwell Science: Oxford, UK.)

Jobling, M. (1995). 'Environmental Biology of Fishes', 1st edn. (Chapman and Hall: London, UK).

Johnson, D. L. (2000). Preliminary examination of the match–mismatch hypothesis and recruitment variability of yellowtail flounder, *Limanda ferruginea*. *Fish Bulletin* **98**, 854–863.

Kokita, T., and Nakazono, A. (1998). Plasticity in the mating system of the longnose filefish, *Oxymonacanthus longirostris*, in relation to mate availability. *Journal of Ethology* **16**, 81–89. doi:10.1007/BF02769286

Lattuca, M. E., Brown, D., Castineira, L., Renzi, M., Luizon, C., Urbanski, J., and Cussac, V. (2008). Reproduction of landlocked *Aplochiton zebra* Jenyns (Pisces, Galaxiidae). *Ecology Freshwater Fish* **17**, 394–405. doi:10.1111/J.1600-0633.2008.00292.X

Martoja, R., and Martoja Pierson, M. (1970). 'Técnicas de histología animal', 1st edn. (Editorial Toray-Mason: Barcelona, Spain.)

Matthews, W. J. (1998). 'Patterns in Freshwater Fish Ecology', 2nd edn. (Chapman and Hall: New York, NY, USA.)

McDowall, R. M. (1971). The galaxiid fishes of South America. *Zoological Journal of the Linnean Society* **50**, 33–73. doi:10.1111/J.1096-3642.1971.TB00751.X

McDowall, R. M. (1998). Phylogenetic relationships and ecomorphological divergence in sympatric and allopatric species of *Paragalaxias* (Teleostei: Galaxiidae) in high elevation Tasmanian lakes. *Environmental Biology of Fishes* **53**, 235–257. doi:10.1023/A:1007421316768

McDowall, R. M. (2006). Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Reviews in Fish Biology and Fisheries* **16**, 233–422. doi:10.1007/S11160-006-9017-7

McDowall, R. M. (2008). Diadromy, history and ecology: a question of scale. *Hydrobiologia* **602**, 5–14. doi:10.1007/S10750-008-9290-7

Milano, D. (2003). Biología de *Galaxias platei* (Pisces, Galaxiidae): especializaciones relativas a su distribución [Biology of *Galaxias platei* (Pisces, Galaxiidae): Specializations relating to their distribution]. Ph.D. Thesis, Universidad Nacional del Comahue, Bariloche, Argentina.

Milano, D., and Vigliano, P. H. (1997). Nuevos registros de *Galaxias platei* Steindachner, 1898 en lagos andinos-patagónicos (Teleostei: Osmeriformes: Galaxiidae). *Neotrópica* **43**, 109–111.

Milano, D., Cussac, V. E., Macchi, P. J., Ruzzante, D. E., Alonso, M. F., Vigliano, P. H., and Denegri, M. A. (2002). Predator associated morphology in *Galaxias platei* in Patagonian lakes. *Journal of Fish Biology* **61**, 138–156. doi:10.1111/J.1095-8649.2002.TB01742.X

Milano, D., Ruzzante, D. E., Cussac, V. E., Macchi, P. J., Ferriz, R. A., Barriga, J. P., Aigo, J. C., Lattuca, M. E., and Walde, S. (2006). Latitudinal and ecological correlates of morphological variation in *Galaxias platei* (Pisces, Galaxiidae) in Patagonia. *Biological Journal of the Linnean Society. Linnean Society of London* **87**, 69–82. doi:10.1111/J.1095-8312.2006.00556.X

Modenutti, B. E., Balseiro, E. G., and Queimaliños, C. P. (2000). Ciliate community structure in two South Andean lakes: the effect of lake water on *Ophrydium naumanni* distribution. *Aquatic Microbial Ecology* **21**, 299–307. doi:10.3354/AME021299

Morris, D. P., Zagarese, H. E., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B., Moeller, R., and Queimaliños, C. (1995). The attenuation of UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography* **40**, 1381–1391. doi:10.4319/LO.1995.40.8.1381

Murua, H., and Saborido-Rey, F. (2003). Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science* **33**, 23–31. doi:10.2960/J.V33.A2

Nagahama, Y. (1983). The functional morphology of teleost gonads. In 'Fish Physiology: Reproduction. Endocrine Tissues and Hormones'. (Eds W. S. Hoar, D. J. Randall, and E. M. Donaldson.) pp. 223–275. (Academic Press: New York, NY, USA.)

Norusis, M. J. (1986). 'SPSS/PC+ Advanced Statistics' (SPSS Inc.: Chicago, IL, USA.)

Olden, J. D., Poff, N. L., and Bestgen, K. R. (2008). Traits synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology* **89**, 847–856. doi:10.1890/06-1864.1

Ortubay, S., and Wegrzyn, D. (1991). Fecundación artificial y desarrollo embrionario de *Galaxias platei* Steindachner (Salmoniformes, Galaxiidae). *Medio Ambiente* **11**, 84–89.

Pankhurst, N. W., and Porter, M. J. R. (2003). Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry* **28**, 385–389. doi:10.1023/B:FISH.0000030602.51939.50

Pérez, G. L., Queimaliños, C. P., and Modenutti, B. E. (2002). Light climate and plankton in the deep chlorophylly maxima in North Patagonian Andean lakes. *Journal of Plankton Research* **24**, 591–599. doi:10.1093/PLANKT/24.6.591

Pitcher, T. J. (1993). 'Behaviour of Teleost Fishes', 2nd edn. (Chapman and Hall: London, UK.)

Ringuelet, R. A. (1975). Zoogeografia y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. *Ecosur* **2**, 1–122.

Roff, D. A. (1984). The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 989–1000. doi:10.1139/F84-114

Ruzzante, D. E., Walde, S. J., Gosse, J. C., Cussac, V. E., Habit, E. M., Zemlak, T. S., and Adams, E. D. M. (2008). Climate control on ancestral population dynamics: insight from Patagonian fish phylogeography. *Molecular Ecology* **17**, 2234–2244. doi:10.1111/J.1365-294X.2008.03738.X

Schoebitz, K., Rodríguez Echandia, E. L., and Campos, H. (1973). Complex mitochondria in the retinal cones of the teleost *Galaxias platei*. *Journal de Microscopie* **18**, 109–114.

Shuter, B. J., and Post, J. R. (1990). Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* **119**, 314–336. doi:10.1577/1548-8659(1990)119<0314:CPVATZ>2.3.CO;2

Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimüller, I., and Hölker, F. (2012). The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences* **74**, 637–657. doi:10.1007/S00027-012-0274-3

Sobenes, C., Link, O., and Habit, E. (2013). Density-dependent microhabitat selection in *Galaxias platei*: an experimental study. *Gayana (Concepción)* **77**, 35–42. doi:10.4067/S0717-65382013000100005

Stearns, C. S. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* **87**, 476–486. doi:10.1007/S001140050763

Vigliano, P., Macchi, P., Alonso, M., Denegri, A., Milano, D., Lippolt, G., and Padilla, G. (1999). Un diseño modificado y procedimiento de calado de redes agalleras para estudios cualicuantitativos de peces por estratos de profundidad en lagos araucanos. *Natura Neotropicalis* **30**, 1–11.

Vigliano, P. H., Beauchamp, D. A., Milano, D., Macchi, P. J., Alonso, M. F., Garcia Asorey, M., Denegri, M. A., Ciancio, J. E., Lippolt, G., Rechencq, M., and Barriga, J. P. (2009). Quantifying predation on galaxiids and other native organisms by introduced rainbow trout in an ultraoligotrophic Lake in Northern Patagonia, Argentina: a bioenergetics modeling approach. *Transactions of the American Fisheries Society* **138**, 1405–1419. doi:10.1577/T08-067.1

Wetzel, R. G. (2001). 'Limmnology. Lake and River Ecosystems', 3rd edn. (Academic Press: San Diego, CA, USA.)

Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 872–885. doi:10.1139/F05-040

Winemiller, K. O., and Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196–2218. doi:10.1139/F92-242

Wootton, R. J. (1990). 'Ecology of Teleost Fishes', 2nd edn. (Kluwer Academic Publications: London, UK.)

Wootton, R. J., and Smith, C. (2002) 'Reproductive Biology of Teleost Fishes', 1st edn. (Wiley: Oxford, UK.)

Zama, A. (1986). Some biological observations on the galaxiid fish, *Galaxias platei*, collected in Southern Chile. *Japanese Journal of Ichthyology* **32**, 450–453. doi:10.11369/JJI1950.32.450

Zemlak, T. S., Habit, E. M., Walde, S. J., Battini, M. A., Adams, E. D. M., and Ruzzante, D. E. (2008). Across the southern Andes on fin: glacial refugia, drainage reversals and a secondary contact zone revealed by the phylogeographical signal of *Galaxias platei* in Patagonia. *Molecular Ecology* **17**, 5049–5061. doi:10.1111/J.1365-294X.2008.03987.X