

Reproductive biology of the threatened golden galaxias *Galaxias auratus* Johnston and the influence of lake hydrology

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Golden galaxias *Galaxias auratus* (31–235 mm fork length, L_F) were collected monthly from littoral habitats in Lakes Crescent and Sorell, Tasmania, Australia, between July 2000 and December 2002. Spawning habitats were identified and monitored in both lakes, and surveyed in Lake Crescent. Trends in gonado-somatic indices and reproductive stages of development indicated that gonad development in both sexes begins in midsummer and peaks in late autumn to early winter. Males mature at smaller sizes (50% at 52 mm L_F) than females (50% at 76 mm L_F), larger individuals are predominately females (95% of fish ≥ 138 mm L_F), and overall male to female ratios are female biased (c. 1:2). Spawning occurs late autumn to early spring (water temperatures = 1.4–9.7° C) with peaks in spawning activity in winter (mean water temperatures <5° C). Demersal adhesive eggs (c. 1.5 mm diameter) were found on cobble substrata (c. 20–250 mm diameter) in littoral areas (c. 0.2–0.6 m deep) and fecundity of fish 71–181 mm L_F ranged from 619 to 14 478 eggs. The rate of change in water level over the 20 days prior to monthly sampling was important in explaining the occurrence of spent fish and this accounted for temporal differences in spawning between the populations. Lake hydrology influences the reproductive cycle of *G. auratus* by possibly providing a stimulus for spawning and it controls the availability of spawning habitat in Lake Crescent. Seasonal hydrological cycles (*i.e.* rises during late autumn to winter) and a minimum water level of 802.20 m Australian Height Datum in Lake Crescent during autumn (above which littoral areas of cobble substratum are inundated) are critical to *G. auratus* populations.

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INTRODUCTION

Identifying vulnerable aspects of the life histories of threatened freshwater fishes is important to their conservation (Angermeier, 1995), and knowledge of the reproductive biology of these species is a critical component of their management. There is also the need to determine the ecological requirements of fishes,

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including how they use specific habitats. Effective management strategies recognize that species not only depend on the existence of suitable habitat but also on its availability in the right time and place (Naiman & Latterell, 2005).

Water level fluctuations can influence the abundance, distribution and life cycles of lacustrine fishes (Gasith & Gafny, 1990; Winfield, 2004). The reproductive success of some littoral spawning species is positively correlated with water level increases prior to, and during spawning (Maceina & Stimpert, 1998; Sammons *et al.*, 1999, 2001; Ozen & Noble, 2005). Whilst the causes of these relationships are often not understood, in some systems greater reproductive success has been linked to the inundation of suitable spawning habitats (Beam, 1983; Miranda *et al.*, 1984; Gafny *et al.*, 1992; Rowe *et al.*, 2002a). These results suggest variation in the availability of spawning habitats in lentic waters can strongly influence fish production.

Fishes in the Galaxiidae are found on several land masses in the Southern Hemisphere, where they generally occur in cool temperate regions (McDowall & Fulton, 1996). Galaxiids dominate the native freshwater fish fauna of the Tasmanian Central Plateau (TCP), southern Australia, due to the occurrence of seven endemic lacustrine species (Hardie *et al.*, 2006). Whilst the family exhibits two life-history strategies (diadromous and non-diadromous), all endemic species of the TCP are non-diadromous (McDowall & Fulton, 1996). Knowledge of their life cycles, however, is limited and all seven species are currently considered threatened due to their highly restricted distributions (five species have two or fewer natural populations), impacts from introduced fishes and alterations to water level regimes (Hardie *et al.*, 2006).

The golden galaxias *Galaxias auratus* Johnston is the largest of the endemic TCP species growing to *c.* 280 mm in fork length (L_F) (Johnston, 1883). Only four populations of *G. auratus* exist: two natural populations in the interconnected Lakes Crescent and Sorell and two translocated populations in small off-stream agricultural water storages in the Clyde River catchment (Hardie, 2003; Hardie *et al.*, 2004). The reproductive biology of *G. auratus* has not previously been studied in detail. It has been suggested that spawning occurs during spring on rocky shores (Fulton, 1990; McDowall & Fulton, 1996; Allen *et al.*, 2002). The occurrence of fertilized eggs on fyke nets between May and October (Hardie *et al.*, 2005), however, suggests a longer and more winter-based spawning period.

If this species is a winter spawner, it would be unusual amongst lacustrine galaxiids, with the exception of common galaxias *Galaxias maculatus* (Jenyns) in south-western Australia (Chapman *et al.*, 2006). To date, lacustrine populations of galaxiids in Patagonian Argentina (Barriga *et al.*, 2002), New Zealand (Rowe & Chisnall, 1996; Rowe *et al.*, 2002b) and south-eastern Australia (Pollard, 1971; Fulton, 1982; Humphries, 1989) have been found to spawn in spring and summer. Spawning habitats include submerged vegetation in littoral areas (Humphries, 1989) or inflowing tributaries (Pollard, 1971) and rocky shores (Fulton, 1982). Hydrologic conditions such as high flows in inflowing streams (Pollard, 1971) and also increases in water temperature (Humphries, 1989) are thought to be important spawning cues for some lacustrine species. Currently, comprehensive accounts of galaxiid reproduction in Australia are mostly for riverine species (Humphries, 1986; O'Connor & Koehn, 1991,

1998; Pen & Potter, 1991a; Pen *et al.*, 1991, 1993; Shirley & Raadik, 1997; Morgan, 2003) with limited data for lacustrine populations (Pollard, 1971, 1972; Fulton, 1982; Humphries, 1989; Chapman *et al.*, 2006).

The unique TCP galaxiid fauna is currently exposed to impacts from altered hydrology caused by hydroelectric power schemes and agricultural and municipal water allocations. These impacts are likely to be further exacerbated by the effects of climatic change [*e.g.* more frequent and intense El Niño-induced droughts (Kershaw *et al.*, 2003)] in the future. Therefore, links between the reproductive cycles of threatened lacustrine galaxiids, such as *G. auratus*, and lake hydrology need to be documented so that water management strategies for the region can incorporate the species' requirements. This study examined the reproductive biology of *G. auratus* in Lakes Crescent and Sorell on the TCP and investigated the influence of lake hydrology on the reproductive cycle of this species. The aims were to: (1) examine the sex ratio and size of maturation for males and females in both populations, (2) describe gonadal cycles by examining the gonado-somatic index (I_G) and development of gonads over a 30 month period and quantify fecundity, (3) locate and survey spawning habitats and monitor spawning activity and (4) define spawning periods and investigate the timing of spawning events in relation to temperature and water level fluctuations.

MATERIALS AND METHODS

STUDY SITE

The interconnected Lake Crescent (42°18' S; 147°16' E) and Lake Sorell (42°11' S; 147°17' E) lie 1 km apart and are situated at c. 800 m a.s.l. at the head of the Clyde River catchment in the south-east of the TCP (Fig. 1). In comparison to most Tasmanian lakes, both lakes are quite large (surface areas of 23 and 52 km², respectively) and relatively shallow (mean depths of 2.3 and 3.1 m at full supply, respectively). Both originate from natural lakes that have had their levels raised on several occasions since the 1830s for water storage purposes. The Crescent–Sorell system has six ephemeral tributaries, the largest being Mountain Creek [mean annual discharge = 11 767 MI; Uytendaal (2003)] which flows in at the northern end of Lake Sorell, and a single outflow, the Clyde River, which flows out of Lake Crescent to the south-west. The hydrology of the system is largely controlled by relatively low rainfall (annual mean = 699 mm), small catchment area (206 km²) and high evaporation rates during summer (mean = 4.5 mm day⁻¹). Water releases for downstream users (annual mean = 10 000 MI), which are managed by sluice gates in the Interlaken Canal and at the Clyde River outflow, also alter water level fluctuations (DPIWE, 2004). Historically, fluctuations have been seasonal (minimums occur March to April and maximums in October to November) and typically range from c. 0.2 to 0.9 m in both lakes (Inland Fisheries Service, unpubl. data).

Extensive littoral wetlands (Fig. 1), accounting for 17% of the surface area of Lake Crescent and 8% of Lake Sorell at full supply levels (Heffer, 2003), connect to the main bodies of the lakes at high water levels. During this study, these wetlands were not inundated and littoral habitats consisted of defined regions of three substratum types (fine sediment, rock and sand) and in-lake habitats by either fine sediment or rock. Historically, both lakes have also contained in-lake macrophyte beds, but none were present during this study because of low water levels and consequent increased exposure of bed sediments to wave action and elevated turbidity (Uytendaal, 2003).

The fish assemblage in both lakes consists of two native species, the endemic *G. auratus* and indigenous short-finned eel *Anguilla australis* Richardson, and three exotic species,

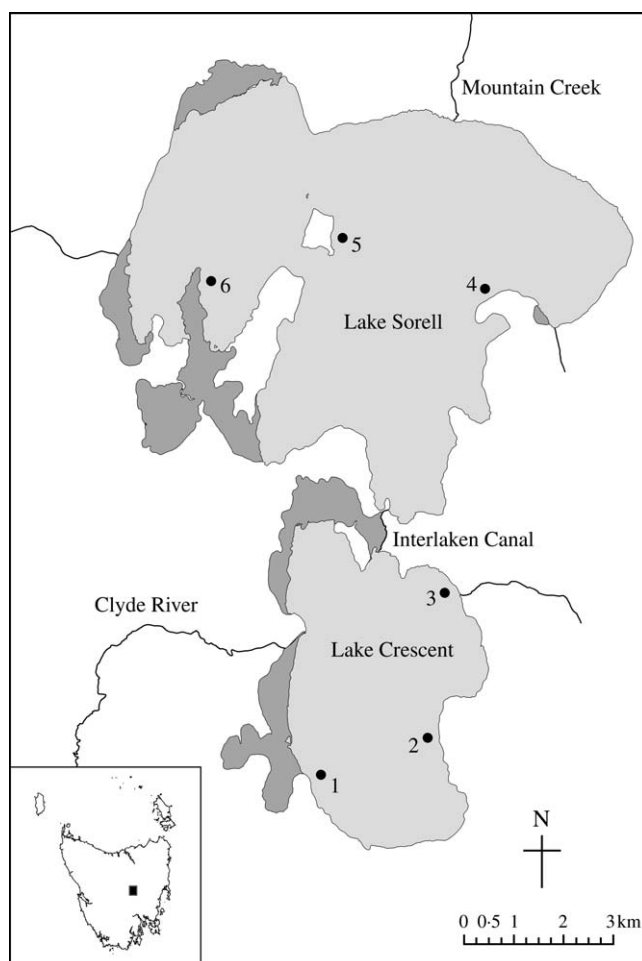


FIG. 1. Location of sampling sites (●) for *Galaxias auratus* in Lakes Crescent and Sorell, Tasmania, Australia. Lake perimeters are at full supply levels. Wetland areas are depicted by dark shading.

brown trout *Salmo trutta* L., rainbow trout *Oncorhynchus mykiss* (Walbaum) and common carp *Cyprinus carpio* L. *Galaxias auratus* are *c.* eight times more abundant in Lake Crescent than in Lake Sorell, possibly due to differences in salmonid predation rates and lake productivity (Hardie *et al.*, 2005).

ENVIRONMENTAL VARIABLES

Mean daily in-lake water temperatures between January 2000 and December 2002 were measured (depth 0.5 m) using Optic StowAway Temperature loggers (Model WTA; Onset Computer Corp., Bourne, MA, U.S.A.). Mean daily water temperature in both lakes during this period was also modelled with the Dynamic Reservoir Simulation Model (DYRESM) (Antenucci, 2001) using meteorological data supplied by Hydro Tasmania, Tasmanian Bureau of Meteorology and the Tasmanian Inland Fisheries Service. Modelled temperatures closely approximated observed values ($r^2 \geq 0.95$) and were used to fill in occasional gaps in observed data caused by equipment failure.

Daily water level data for both lakes during the study was supplied by the Tasmanian Inland Fisheries Service and photoperiod data by Geoscience Australia (2006).

FISH SAMPLING AND BIOLOGICAL ANALYSIS

Galaxias auratus were sampled monthly from littoral habitats in Lakes Crescent and Sorell between July 2000 and December 2002. On each sampling occasion, fish were collected at three sites in each lake (Fig. 1) which each represented one of the dominant littoral habitats (fine sediment, sand and rock substrata) in both lakes. On the first three sampling occasions, fish were sampled by electrofishing 100 m of shoreline at each site with a backpack electro-fisher (12-B POW; Smith and Root Inc., Seattle, WA, U.S.A.). On the remaining sampling occasions, fish were sampled using four tandem-set fyke nets (2 mm stretched mesh) at each site (*i.e.* 12 nets per lake). All nets had an 84 × 70 mm aluminium screen in the entrance to avoid the capture of platypus *Ornithorhynchus anatinus*, water birds and larger fish species (*e.g.* salmonids). Nets were set overnight (mean soak time = 18 h) in shallow margins (depths ≤ 1.2 m). A monthly sub-sample of *G. auratus* from each lake (Lake Crescent: $n = 43\text{--}77$; Lake Sorell: $n = 10\text{--}70$) was euthanized in a lethal anaesthetic solution (Aqui-s™) and preserved in 70% ethanol for further analysis. The remaining captured fish were allowed to recover from anaesthesia and released at the site of capture.

Each *G. auratus* (Lake Crescent: $n = 1624$, Lake Sorell: $n = 1354$) was measured (L_F , mm) and weighed (M , g). Gonads were removed and weighed (M_g , mg) and the gonadosomatic index (I_G , %) was calculated from: $I_G = 100M_g M^{-1}$. Sex was determined by macroscopic and microscopic examination of gonads and gonadal stages of development of ovaries and testes (Table 1) were recorded. The fecundity (F) of stage IV female fish in the June and July 2001 samples from both lakes ($n = 87$) was examined. The number of eggs in 200 mg sub-samples of ovary from each fish was counted microscopically and the total number present in ovaries was extrapolated. The mean ± s.e. sub-sample proportion of M_g was $10.9 \pm 0.8\%$. For eight fish, F analysis was replicated ($n = 5$) to determine the consistency of the ovaries and, hence, the precision of the technique (s.e. of each replication was <16 eggs).

SPAWNING SITE SURVEY AND ROCKY SUBSTRATUM MAPPING

Regular searches for spawning sites were performed in Lakes Crescent and Sorell during the 2000 and 2001 spawning periods (winter to early spring). Littoral areas were searched by visual examination of submerged habitat such as rocks and woody debris, and kick-net sweeps using hand nets (250 µm mesh) were performed over different substratum types. Where eggs were found, water depth was measured and the composition of the habitat was recorded. Subsequently, spawning activity was monitored *c.* 14 days at known spawning sites in each lake (sites 2 and 4; Fig. 1) during the 2001 and 2002 spawning periods (late April to late September). The relative abundance of eggs at each site (eggs per sweep) was assessed by 30 kick-net sweeps (hand net, 250 µm mesh) of 30 s duration. These results estimated the density of eggs incubating at the site and, hence, indicated recent spawning activity.

Littoral areas of rocky substratum in Lake Crescent were surveyed during March 2002, when the water level was near an historical low [*c.* 802–445 m Australian Height Datum (AHD)], and significant proportions of these areas were dewatered. The extent of the regions of rocky substratum was recorded along transects (intervals of 100 m) at 90° to the shore using a global positioning system (GPS). Water depth (±10 mm) at the rock–sediment interface was recorded and daily water levels were used as reference levels for submerged sites. These survey data were used to construct a map of the rocky shore habitat in Lake Crescent (using MapInfo®, Troy, NY, U.S.A.) and determine the influence of lake levels on its availability.

TABLE I. Volume and appearance of *Galaxias auratus* ovaries and testes at five stages of development*

Stage	Volume† (%)	Macroscopic/microscopic‡ appearance
I. Immature/resting mature	<25	Lobes of testes and ovaries thin and transparent and not meeting each other at the ventral end of visceral cavity. Oocytes only visible upon rapture of <i>Tunica albuginea</i> . Oocytes transparent and small to indistinct
II. Immature developing/mature re-developing (early)	26–50	Lobes of testes and ovaries close to meeting each other at the ventral end of visceral cavity. Testes white in colour with vermicular appearance. Oocytes distinct, and variable in size, some white, some yellow
III. Immature developing/mature re-developing (late)	51–75	Lobes of testes and ovaries meeting each other at the ventral end of visceral cavity. Testes white in colour with vermicular appearance. All oocytes yellow-orange in colour but small in size
IV. Ripe	>76	Body wall slightly, very distended with testes and ovaries filling the visceral cavity. Testes white in colour. Oocytes uniform in size and yellow-orange in colour. Sexes may be determined externally with smooth v. nodular patterns visible on the body wall of males and females, respectively
V. Spent	Variable	Lobes of testes have slack appearance with flaccid <i>Tunica albuginea</i> . Testes may have grey colour. An obvious decrease in the amount of ripe oocytes present in visceral cavity. Remaining oocytes may be disfigured and more pale in colour than viable oocytes. This stage also includes fish with very small, newly formed, resting-stage gonads with residual oocytes and testes still present

*Stages of development are modified from Fulton (1982).

†Estimated volume of visceral cavity occupied by gonads.

‡Viewed at ×25 magnification.

STATISTICAL ANALYSES

Sizes at which the proportion of females accounted for 50% (P_{50}) and 95% (P_{95}) of sampled fish, and at which 50% (L_{F50}) and 95% (L_{F95}) of both males and females reached sexual maturity were estimated using binary logistic regression (Roa *et al.*, 1999). For maturity analyses, fish with gonads at stages 3–5 were considered sexually mature and only fish collected during the 2001 and 2002 spawning seasons (April to July) were included. Additionally, unsexed fish <80 mm L_F were regarded as immature and used to construct regression curves for both sexes. The significance level for hypothesis tests was $P = 0.05$.

To investigate the roles of the environmental variables in spawning during the 2000, 2001 and 2002 breeding seasons, multi-model procedures as described by Burnham & Anderson (2002) were used on a set of carefully considered *a priori* regression models. The response variable was the percentage of fish in a sample that was spent [*spent* (%)], and all models included the mean I_G of females in the previous sample [I_{Gf} (%)] as an explanatory variable since spawning can only occur if large numbers of females in the population have substantial ovarian mass.

The full list of candidate models (M_1 – M_6) is presented in Table II, and their rationale is as follows. Temperature is often cited as a cue for spawning of teleosts (Jobling, 1995). Changes in lake level were potentially important since sustained, rapid rises in water level would probably inundate spawning habitat (rocky littoral areas) and keep it clear of fine sediments, whereas modest rises resulted in slow inundation of spawning habitat, which was usually accompanied by significant sedimentation of otherwise suitable spawning substrata; falls in lake level usually resulted in deposition of sediments or dewatering of spawning habitat. For both temperature [*temp20* (° C)] and lake level [*level20* (mm)], the rate of change over the 20 days prior to fish sampling (estimated from linear regression over time; 21 days was the shortest interval between sample dates) was used because rises in water levels are gradual in these lakes and, therefore, fish would more likely respond to a trend in these variables integrated over time rather than to a short-term event. There may be other habitat features in each lake that could generate differences between the lakes in the time of spawning, so the lake effect (*lake*) was included as a factor. Finally, the bathymetry and habitat maps of the two lakes suggested that the availability of spawning habitat would be more sensitive to water level in Lake Crescent than in Lake Sorell. Therefore, the most complicated model (M_6) that could be justified for this sized data set [termed the 'global model' by Burnham & Anderson (2002)] also included the lake \times water level interaction

TABLE II. Multiple linear regression results of models of environmental conditions used to predict the timing of *Galaxias auratus* spawning in Lakes Crescent and Sorell during 2000–2002 based on the occurrence of spent fish. Models are ranked in order of best fit according to Akaike Information Criterion (AICc), $\Delta_i c$ is the difference in AICc and w_i is the AICc weight

Rank	Model	Model*	AICc	$\Delta_i c$	w_i
1	M_3	$spent \sim I_{Gf} + level20$	–30.53	0.000	0.349
2	M_5	$spent \sim I_{Gf} + level20 + temp20 + lake$	–30.17	0.362	0.292
3	M_4	$spent \sim I_{Gf} + level20 + temp20$	–29.17	1.360	0.177
4	M_6	$spent \sim I_{Gf} + level20 + temp20 + lake + lake:level20$	–29.04	1.489	0.166
5	M_2	$spent \sim I_{Gf} + temp20$	–23.23	7.300	0.009
6	M_1	$spent \sim I_{Gf}$	–22.61	7.923	0.007

*Modelling variables include the occurrence of spent fish [*spent* (%)], mean I_G of females in previous sample [I_{Gf} (%)], change in daily water level over the previous 20 days [*level20* (mm)], change in mean daily water temperature over the previous 20 days [*temp20* (° C)], differences between lakes (*lake*) and the lake \times water level interaction (*lake:level20*).

(lake:level20). None of the explanatory variables were strongly correlated with any of the others (all $|r| < 0.43$) and inspection of the diagnostic plots of M_6 suggested an arcsine-square-root transformation of the response variable was needed to improve the normality of residuals. Several other explanatory variables were considered (e.g. photoperiod and lake \times temperature interaction) but were not included in the model set because they did not vary from year to year or between the lakes.

To rank the models, a variant of the Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) was used (Burnham & Anderson, 2002). To judge the relative importance of lake level and temperature, the Akaike weights (w_i) were summed across all models (w_+) that contained each of these two variables (Burnham & Anderson, 2002). The values of the individual parameter estimates for each explanatory variable were averaged across the entire model set for reporting, although the different units of these variables imply that most interest is in their signs rather than relative magnitudes. All statistical analyses were carried out in R v.2.2.0 (R Development Core Team, 2005).

RESULTS

ENVIRONMENTAL VARIABLES

Abnormal climatic conditions just prior to, and early in the study, with an extended El Niño-induced drought between 1997 and 2001, caused below average and unseasonal rainfall in the catchment. As a result, Lakes Crescent and Sorell experienced low levels (maxima <0.6 m below full supply levels) during this study, including record minima in 2000 in Sorell (802.62 m AHD) and in 2001 in Crescent (801.77 m AHD). Water level fluctuations followed similar trends in both lakes and there was considerable interannual variation with seasonal rises ranging from 0.20 to 0.97 m and falls from 0.28 to 0.64 m. Minimum and maximum levels in both lakes occurred during March to May and October to December, respectively. Whilst fluctuations in both lakes were similar, levels in Lake Sorell usually began to rise slightly earlier than those in Lake Crescent in response to late autumn and winter rainfall due to direct seasonal input from the primary tributary, Mountain Creek. Fluctuations in Lake Sorell were also typically more rapid because of this input, and regulation of flows between the lakes and discharge from Lake Crescent.

Water temperatures in both lakes were similar between 2000 and 2002 with only a marginally significant difference between the monthly means of each lake (paired t -test, d.f. = 35, $P < 0.05$). The mean difference in the average monthly temperatures of the lakes, however, was small ($<0.2^\circ\text{C}$) and not biologically meaningful. Temperature cycles had strong seasonal fluctuations with mean \pm s.d. monthly temperatures being $<5^\circ\text{C}$ during winter (minimum = $4.2 \pm 0.9^\circ\text{C}$ during June) and $>14^\circ\text{C}$ during summer (maximum = $16.4 \pm 1.7^\circ\text{C}$ during February). Daylength in the study region varied from 9.08 to 15.27 h in June and December, respectively.

SEXUAL DIMORPHISM AND SEX RATIO

A total of 2978 *G. auratus* were examined and fish from both populations covered large size ranges (Lake Crescent = 38–235 mm L_F ; Lake Sorell = 31–179 mm L_F). Sexual composition of pooled lake samples was dominated

by females (60%) followed by males (31%) and unsexed (mostly immature) fish (9%). Female size range differed significantly from that of males in Lake Crescent (Kolmogorov–Smirnov test, $n = 1488$, $P < 0.001$) and Lake Sorell (Kolmogorov–Smirnov test, $n = 1208$, $P < 0.001$) and in both lakes, mean \pm S.D. female L_F (Lake Crescent = 95 ± 21 mm; Lake Sorell = 92 ± 22 mm) was greater than males (Lake Crescent = 80 ± 17 mm; Lake Sorell = 77 ± 14 mm). The largest female measured was 235 mm (L_{Fmax}) and largest male was 179 mm L_{Fmax} .

Overall male to female ratios were female biased and differed significantly from unity in Lake Crescent (1:2.0) (Pearson χ^2 proportions test, d.f. = 1, $n = 1488$, $P < 0.001$) and Lake Sorell (1:1.8) (Pearson χ^2 proportions test, d.f. = 1, $n = 1208$, $P < 0.001$). In pooled population data, the proportion of females increased in progressive L_F classes [Fig. 2(a)], with mean \pm S.E. $P_{50} = 71 \pm 1$ mm L_F and $P_{95} = 138 \pm 3$ mm L_F .

SEXUAL MATURATION

Over the 30 month study period, 47% of fish sampled had gonads at stage III (late phase of development) or beyond. The smallest stage IV (ripe) male measured 51 mm L_F and smallest female 60 mm L_F . The mean \pm S.E. L_{F50} of pooled population data for males was 52 ± 2 mm and females 76 ± 1 mm, while the L_{F95} for males was 75 ± 3 mm and females 87 ± 1 mm [Fig. 2(b)]. Individuals appeared to remain sexually active at large sizes, with the largest stage IV male measuring 171 mm L_F (100% of L_{Fmax}) and largest female 181 mm L_F (77% of L_{Fmax}). The mean \pm S.D. L_F of stage IV fish (males: 78 ± 15 mm; females: 103 ± 19 mm) were $<50\%$ of their respective L_{Fmax} .

GONADAL CYCLE AND FECUNDITY

Annual cyclic patterns in male and female mean monthly I_G values were similar in both populations, although the timing and extent of periods when maximum I_G values were recorded varied (Fig. 3). Mean I_G of males and females were generally <3 between October and December (except females in Lake Sorell during October 2000). In both populations, mean I_G of both sexes increased from January onwards, while water temperatures and photoperiod were decreasing, and males developed earlier than females in both populations. In Lake Crescent [Fig. 3(b)], during 2001, peak I_G values for males (>16) occurred from March to July and from May to July for females (>15). During 2002, the peak periods (>13) for both sexes respectively began in the same months, but extended into August. Conversely, in Lake Sorell [Fig. 3(a)], the periods where peak I_G values occurred were shorter. Males in Lake Sorell maintained I_G values >14 between February and May during 2001 and I_G values >16 between April and July during 2002. Sorell females had I_G values >12 between April and June during 2001 and an abrupt peak I_G of 16.1 during April 2002. The maximum and minimum individual I_G values were 0.06 and 37.8, and 0.09 and 33.2 for males and females, respectively.

Trends in I_G were complemented by synchronous progression of gonadal stages of development in pooled sex data in both populations (Fig. 4). Minimal

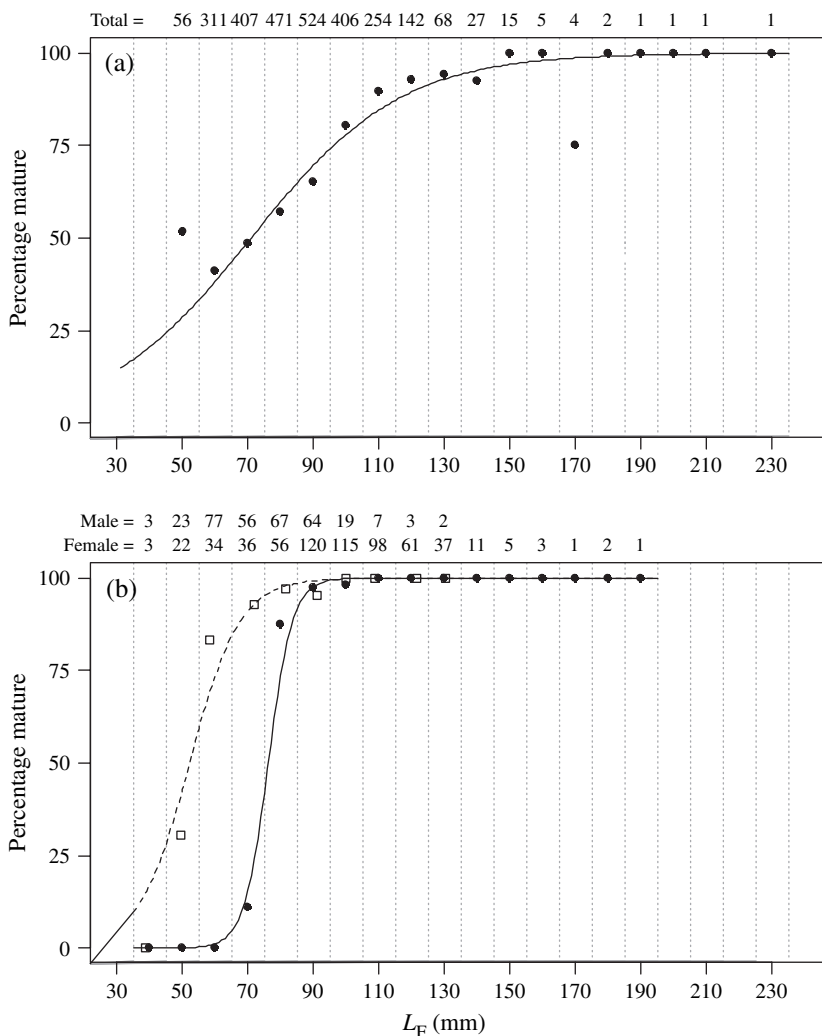


FIG. 2. Percentage of (a) females and (b) mature males (---) and females (—) as a function of fork length (L_F) of *Galaxias auratus*. Maturity analyses are based on fish collected from Lakes Crescent and Sorell between April and July of 2001 and 2002, whilst sexual proportions are from fish collected between July 2000 and December 2002. The percentage of sexually mature fish or females within each sequential 10 mm L_F class is plotted using logistic regression. Samples sizes for L_F increments are shown.

development occurred between October and December, with >85% of fish having stage I (resting) gonads (with the exception of fish in Lake Sorell during October 2000). The prominence (5–47%) of transitional developing stages II and III was brief (January to March) and the majority (49–100%) of fish were stage IV (ripe) in April to June. Stage V (spent) fish appeared as early as April in both lakes but were most common (>22%) during July to September of 2001 and 2002. The F of fish ($n = 87$) ranging in size from 71 to 181 mm

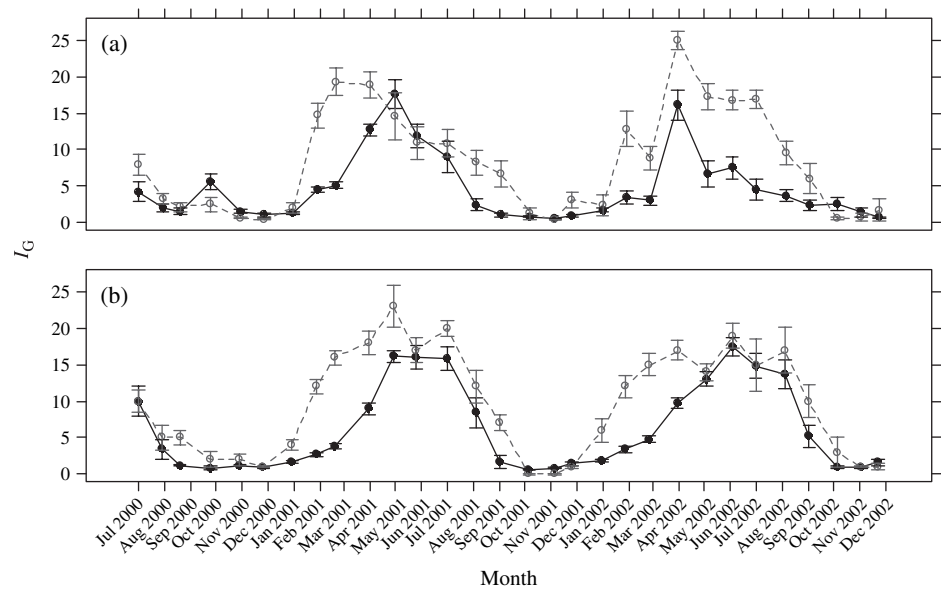


FIG. 3. Mean \pm s.e. monthly gonado-somatic indices (I_G) of male (○) and female (●) *Galaxias auratus* in (a) Lake Sorell and (b) Lake Crescent between July 2000 and December 2002.

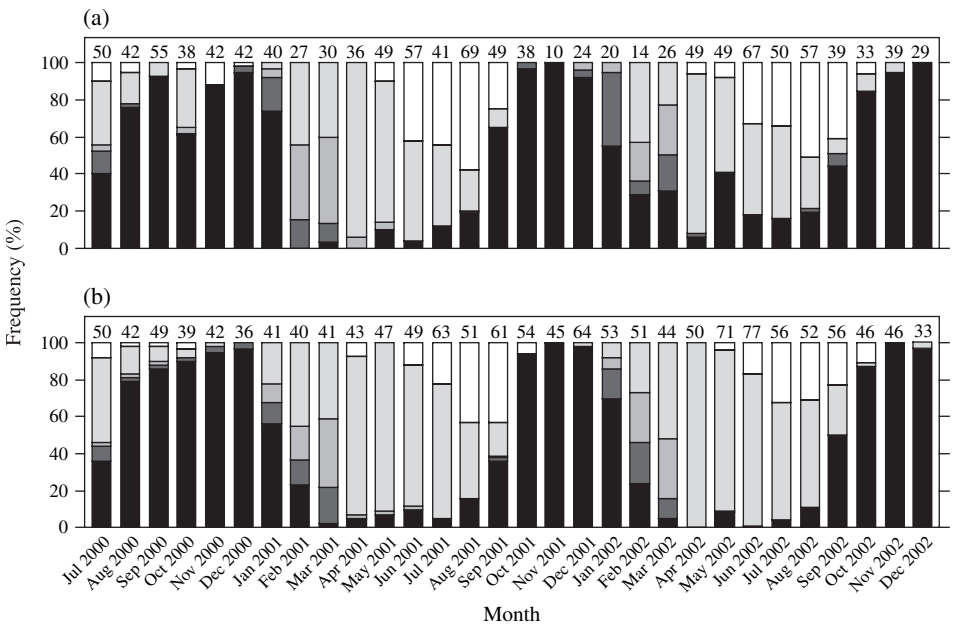


FIG. 4. Frequency of pooled male and female *Galaxias auratus* in (a) Lake Sorell and (b) Lake Crescent at each gonadal stage of development (■, I; ■, II; ■, III; □, IV; □, V; see Table I), July 2000 to December 2002. Sample sizes are shown for each month.

L_F varied from 619 to 14 478. The relationship between F and L_F was: $F = 0.0018L_F^3 (r^2 = 0.72)$.

SPAWNING

Habitat

In both lakes, spawning sites were found in littoral areas (0.2–0.6 m deep and usually <10 m from the shore) of cobble substratum (c. 20–250 mm diameter) mostly during winter to early spring in 2000–2002. No eggs were found in habitats other than those dominated by rocky substrata. On a single occasion, three eggs were found adhered to a single stem of the aquatic macrophyte common water milfoil *Myriophyllum simulans*, which was emerging in an area of rocky substratum.

Fertilized eggs (c. 1.5 mm in diameter) were transparent and adhesive, and developing embryos were clearly visible in advanced eggs. Eggs were scattered on the top and sides of rocks, positioned individually and occasionally in small clusters of two to five. The locations of spawning sites moved progressively further in-shore as water levels rose, so the depth of spawning sites remained reasonably constant and eggs were continually deposited on new areas of substratum. Sedimentation of suitable spawning substratum and some spawning sites was evident following periods of strong winds, particularly in Lake Crescent.

The availability of suitable spawning habitat differed between the lakes. In Lake Crescent, littoral areas of rocky substratum were only found at four defined sites (Fig. 5) and at all locations this habitat was inundated at water levels >802.20 m AHD. Conversely, several regions in Lake Sorell (whilst not quantitatively surveyed) contained vast littoral areas of rocky substratum which generally extended well into the lake's basin.

Timing and environmental conditions

Females appeared to determine the time of spawning, with males developing gonad mass much earlier than females and maintaining it for longer (Fig. 3). Fish in Lake Sorell generally spawned earlier than those in Lake Crescent. During both 2001 and 2002, decreases in mean I_G values (Fig. 3) and increases in proportions of spent fish (Fig. 6) occurred during May to August in Lake Sorell and June to September in Lake Crescent. Maximum densities (range = 20–67 eggs per sweep) of eggs at spawning sites in 2001 and 2002 were observed in late August to early September in Lake Crescent and early July in Lake Sorell. At these times, average daily mean water temperatures were 4.8° C (range = 1.4–9.7° C) and water levels were rising (Fig. 6), and day-length was <11.8 h.

The proportion of spent fish on a sampling occasion was best explained ($w_+ = 0.984$) by models (M_3 , M_4 , M_5 and M_6), which included the rate of change in water levels over the previous 20 days (*level20*) (Table II). The best performing model (M_3) included only *level20*; however, all other models including this variable also had a Δ_{IC} of <2, therefore, their performance was approximately equal (Burnham & Anderson, 2002). The sign of the averaged estimate for this parameter was positive (value of 0.0177) showing that the proportion

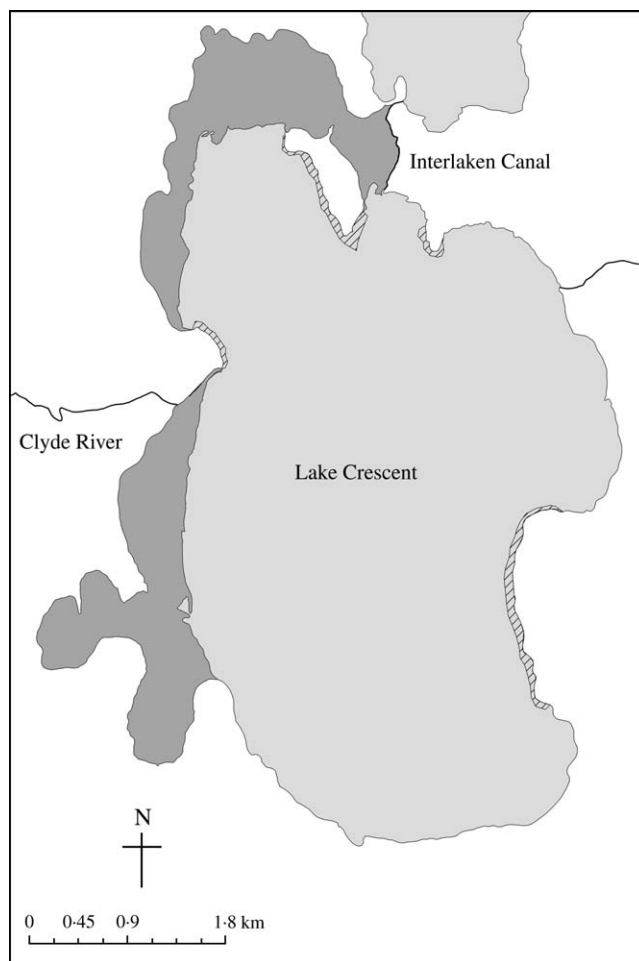


FIG. 5. Littoral areas of rocky substratum (▨) in Lake Crescent surveyed during March 2002. Lake perimeters are at full supply levels. Wetland areas are depicted by dark shading.

of spent fish is positively related to the rate of lake level changes. Although the rate of change in temperature (*temp20*) was also positively related to the proportion of fish spawned (average parameter estimate = 0.1140), it was less important ($w_+ = 0.644$) than *level20*. Overall, Lake Sorell had slightly greater proportions of spent fish across all sampling occasions than Lake Crescent (average parameter estimate = 0.0383). The inclusion of the *lake:level20* interaction in the sub-set of competitive models (Table II) suggested differential responses between the populations to changes in lake level. This is consistent with the known differences in available habitats between the two lakes: Sorell has an abundance of suitable rocky spawning areas even at low levels, whereas these habitats are more limited in Lake Crescent and not available until levels rise above 802.20 m AHD.

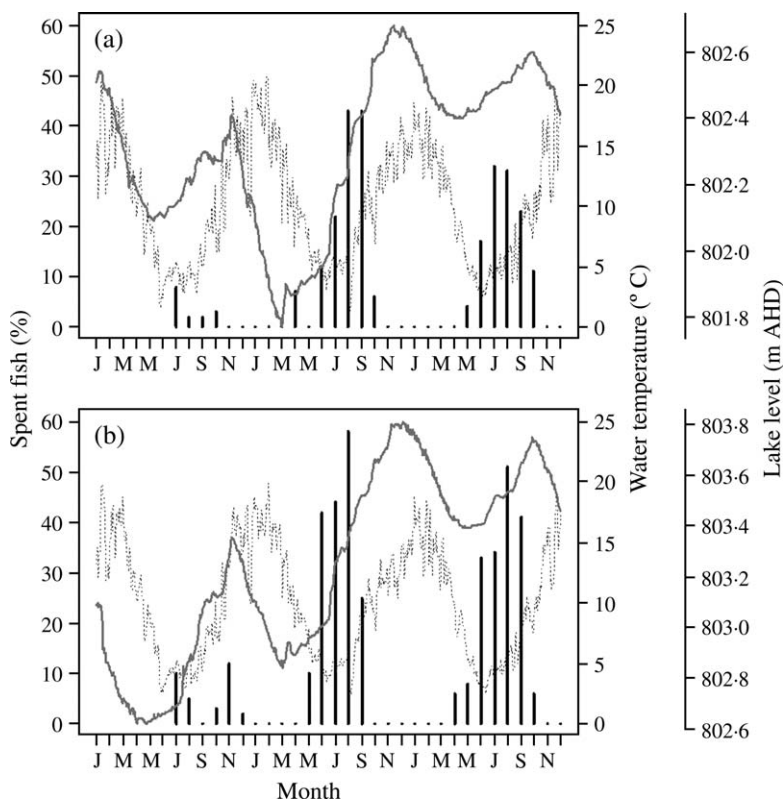


FIG. 6. Per cent of spent (stage V) *Galaxias auratus* (■) and daily mean water temperatures (.....) and water levels (—) in (a) Lake Crescent and (b) Lake Sorell between January 2000 and December 2002. Water levels are measured in metres of elevation according to the Australian Height Datum (m AHD).

DISCUSSION

SEXUAL DIMORPHISM, SEX RATIO AND MATURATION

Galaxias auratus females, compared with males, mature later and attain greater sizes, and overall appear to be more abundant. Based upon age and growth data from a related study (unpubl. data), L_F at maturity estimates (males v. females: $L_{F50} = 52$ v. 76 mm, $L_{F95} = 75$ v. 87 mm) indicate some males mature in their first year and the remainder in their second, whereas females mature in their second year. Age at maturity varies amongst galaxiid species, from short-lived *Galaxiella* spp. with predominantly annual life cycles (Pen *et al.*, 1993), to longer-lived (commonly >3 years) species such as banded kokopu *Galaxias fasciatus* Gray with males and females maturing at 2 and 4 years, respectively (Hopkins, 1979a). Similar to *G. auratus*, in both a lacustrine population of the closely related spotted galaxias *Galaxias truttaceus* (Valenciennes) on the TCP (Humphries, 1989) and a diadromous population in south-western

Australia (Morgan, 2003), some males mature in their first year and the remainder of the populations in their second.

Larger *G. auratus* were predominately females in Lakes Crescent and Sorell (*i.e.* $P_{95} = 138$ mm L_F) and sex ratios of sampled fish from both populations were strongly female biased (*c.* 2:1). Larger fish tend to be females in lacustrine (Pollard, 1971; Rowe *et al.*, 2002b), non-diadromous riverine (Bonnett, 1990; O'Connor & Koehn, 1991; Pen & Potter, 1991b) and some diadromous (McDowall, 1968; Hopkins, 1979b; Morgan, 2003) populations of *Galaxias* spp. Female-biased sex ratios have also been reported for dwarf inanga *Galaxias gracilis* McDowall (Rowe & Chisnall, 1996) and lacustrine populations of common galaxias (Pollard, 1971; Chapman *et al.*, 2006). These findings suggest that faster growth and greater longevity in females is due to either physiological differences or mechanisms which increase mortality in males at smaller sizes (*e.g.* aggressive reproductive behaviour). The testes of teleosts frequently represent a much lower proportion of the body mass than ovaries (Wootton, 1998); however, male *G. auratus* had larger gonads (*v.* body mass) than females which they maintained for longer periods. The greater reproductive investment of males may decrease their longevity (or growth) by reducing feeding rates during gonad development and spawning. Impaired locomotion at these times due to large-sized testes (*i.e.* I_G values >30) would also increase their vulnerability to predation by introduced salmonids.

GONADAL CYCLE AND SPAWNING

This study shows that whilst the peak investment period in the gonadal cycle of *G. auratus* is similar to that of lacustrine populations of *G. truttaceus* (Humphries, 1989) and *G. maculatus* (Pollard, 1971) in south-eastern Australia, spawning occurs mostly during winter. Both sexes of *G. auratus* begin to develop gonad mass when daylength is near its maximum and the rate of development is rapid between January and May (mean I_G values increase from <7 to >13 in both sexes), when daylength and water temperature decline. Development during this time would allow fish to utilize the relatively short periods of warmer water temperatures (*i.e.* $>10^\circ$ C) in these highland lakes and their probable increases in food resources. Similarly to lacustrine *G. truttaceus* of the TCP (Humphries, 1989), male *G. auratus* develop gonad mass and reach ripe condition earlier than females (some running-ripe in late February) indicating that females dictate when spawning occurs. By April, many males and females are ripe and some spawning activity was recorded in both populations, but most fish spawn 2–4 months later during winter. Whilst this delay would give first-year males further time to mature, allowing them to contribute to spawning, it is likely to be associated with a wait for suitable environmental conditions.

Whilst *G. auratus* in these neighbouring lakes had extended winter-based spawning periods, peaks in spawning activity occurred earlier in Lake Sorell than in Lake Crescent during both 2001 and 2002. Multiple regression modelling indicated that rises in water levels over the 20 days prior to monthly sampling was the most important factor in predicting the occurrence of spent fish in both lakes. Therefore, these temporal variations in spawning are likely to be

associated with the differing hydrological regimes of the lakes (e.g. levels rise earlier in Lake Sorell). Change in water temperature was not an important spawning cue with spawning periods encompassing a large range of temperatures (1.4–9.7° C); however, further finer-scale temporal sampling would be needed to evaluate its importance.

The winter spawning of *G. auratus* is unusual for a non-diadromous galaxiid. Selective pressures in freshwater teleost populations usually ensure that spawning occurs at times that provide subsequent optimal conditions (i.e. abundant food resources and favourable temperatures) for larvae during their first growing season (Wootton, 1998). The two life-history strategies of galaxiids illustrate this pattern; generally, diadromous galaxiid populations spawn in late autumn to early winter, whilst non-diadromous populations in lotic and lentic waters spawn in late winter to early summer (Humphries, 1989; Pen & Potter, 1991a). These strategies allow larvae and juveniles to encounter conditions that are advantageous to their growth and survival in their respective estuarine and marine and freshwater nursery habitats. Other lacustrine galaxiid populations on the TCP follow the usual pattern of non-diadromous galaxiids with *G. truttaceus* (Humphries, 1989) and Great Lake paragalaxias *Paragalaxias eleotroides* McDowall & Fulton (Fulton, 1982) spawning in spring and Shannon paragalaxias *Paragalaxias dissimilis* (Regan) in summer (Fulton, 1982). Whilst *G. auratus* larvae occur in the water column during winter, the peak hatching period is early to mid-spring (unpubl. data). *Galaxias auratus* appear to respond to different spawning stimuli (i.e. rising water levels) to those of other galaxiids on the TCP, which lengthens incubation of their eggs. Their overall life cycle, however, follows the usual pattern of a non-diadromous lacustrine galaxiid.

FECUNDITY AND SPAWNING SITE

Egg size and fecundity of galaxiids vary both between and within species which follow either diadromous or non-diadromous life-history strategies (Pen & Potter, 1991a). Generally, fecundity is related to body size (Humphries, 1989) with smaller sized species (commonly <80 mm L_F) having fewer eggs (commonly <1000), whilst larger sized galaxiids (particularly those which are diadromous or have close diadromous ancestry) are more fecund (c. 1000–20 000 eggs). The results of this study indicate that the fecundity (71–181 mm L_F fish had from 619 to 14 478 eggs) and egg size (c. 1.5 mm diameter) of *G. auratus* are consistent with values for diadromous and lacustrine stocks of the closely related *G. truttaceus* in Tasmania (Humphries, 1989) and also show similarities to other larger-sized species such as *G. fasciatus* (Hopkins, 1979a) and climbing galaxias *Galaxias brevipinnis* Günther (O'Connor & Koehn, 1998). Some other galaxiids in Tasmania that have much lower fecundity have also had their distributions severely reduced by introduced salmonids [e.g. Swan galaxias *Galaxias fontanus* Fulton (Crook & Sanger, 1998a) and Clarence galaxias *Galaxias johnstoni* Scott (Crook & Sanger, 1998b)]. Therefore, the relatively high fecundity of *G. auratus* may have contributed to this species coexistence with introduced salmonids for over a century despite heavy predation (Stuart-Smith *et al.*, 2004).

Deposition of eggs in shallow marginal habitats is common amongst galaxiids which occupy both lotic (O'Connor & Koehn, 1991, 1998; Allibone & Townsend, 1997; Moore *et al.*, 1999; Charteris *et al.*, 2003) and lentic (Pollard, 1971; Fulton, 1982; Humphries, 1989) environments. *Galaxias auratus* spawned demersal adhesive eggs over cobble substrata in littoral areas. Whilst spawning behaviour was not observed, the dispersed arrangement of eggs at spawning sites indicates that spawning takes place midwater and eggs settle onto the substratum rather than being laid in defined nests. The occurrence of eggs on a stem of aquatic vegetation on a single occasion in Lake Sorell and on submerged vegetation in an off-stream agricultural water storage containing a refuge population of this species (unpubl. obs.) suggest that *G. auratus* will use aquatic vegetation when available. The occurrence of spawned eggs on fyke nets (Hardie *et al.*, 2005) also shows flexibility in spawning site selection and perhaps the primarily requirement for surfaces to which eggs can adhere. Other *Galaxias* spp. also spawn on rocks (O'Connor & Koehn, 1991; Allibone & Townsend, 1997; Moore *et al.*, 1999) and submerged vegetation (Pollard, 1971; Humphries, 1989; Charteris *et al.*, 2003).

INFLUENCE OF LAKE HYDROLOGY

Hydrological variables are important in the reproduction of some galaxiids. For example, high flows in rivers (Pen & Potter, 1991a; O'Connor & Koehn, 1998; Charteris *et al.*, 2003) or inflowing tributaries of lakes (Pollard, 1971) have been associated with the time of spawning. This study suggests that lake hydrology strongly influences the reproductive cycle of *G. auratus* by possibly providing a stimulus for spawning and controlling the availability of spawning habitat. Because of relatively low water levels, the quantity of suitable spawning habitat for *G. auratus* was much less in Lake Crescent than in Lake Sorell and its availability there was significantly influenced by water level fluctuations. Some teleost species delay spawning until suitable spawning substratum is available (Lam, 1983; Jobling, 1995). This appeared to occur in Lake Crescent during 2001, when spawning occurred 2–3 months later than in Lake Sorell, during which time almost no spawning habitat was submerged (*i.e.* levels were <802.20 m AHD). The timing and magnitude of rises in water level may be important for successful recruitment of this species as delays could cause the uncoupling of larval emergence and availability of suitable food resources (Cushing, 1990), resulting in slower growth in later spawned fish (Ludsin & DeVries, 1997; Pine *et al.*, 2000). Based on this information, the production of the Lake Crescent population is likely to be significantly constrained by limited availability of spawning habitat during periods of relatively low water levels.

Management options for these and other shallow lakes on the TCP are limited to manipulation of water-level regimes, and this study provides evidence that seasonal hydrological cycles (*i.e.* rises during late autumn and winter) and a base 'environmental level' of 802.20 m AHD in Lake Crescent during autumn are critical to *G. auratus* populations. Compared with interactions with exotic species [*e.g.* predation by salmonids (Stuart-Smith *et al.*, 2004; Hardie *et al.*, 2005)], stressors associated with lake hydrology have previously been overlooked as threats to *G. auratus*. Future changes in lacustrine hydrological

regimes of the TCP caused by climatic trends, episodic droughts and increased hydroelectric and agricultural demands are likely to pose serious threats to galaxiids in this region. Detailed bathymetries coupled with mapping littoral habitats have been useful in linking fish biology and hydrological changes elsewhere (Rowe *et al.*, 2002a). This is a prominent information gap for the TCP that urgently needs to be filled before more sophisticated risk analyses can be attempted for this region's galaxiid fauna.

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