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Nocturnal and diurnal feeding by Galaxias auratus, a lentic galaxiid fish

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2	Nocturnal and diurnal feeding by Galaxias auratus, a lentic
3	galaxiid fish
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1 Extended summary

2	1.	We examined the diel feeding pattern, gastric evacuation and daily ration of a
3		lentic, threatened Tasmanian galaxiid fish, Galaxias auratus. Analysis of
4		stomach contents and consumption estimates based on collections of fish
5		every 3 h over three 24-h periods in summer 2002/2003 revealed an unusual
6		pattern where feeding always occurred during both the day and night, with no
7		obvious peaks. No evidence of size-based temporal partitioning of feeding was
8		found, suggesting that this consistent feeding pattern was representative of the
9		population at this time, and not simply a result of different sized fish feeding at
10		different times.
11	2.	We estimated the gastric evacuation rate of G. auratus in a laboratory
12		experiment, using the two most important prey taxa and at the temperatures
13		recorded in the field during fish collections. The emptying of the stomach was
14		best described by an exponential model, with rate parameters (R) of 0.104 and
15		0.081 for the evacuation of the amphipod, Austrochiltonia australis, and the
16		cladoceran, Daphnia carinata, at water temperatures of 11.5 °C and 16.5 °C
17		respectively.
18	3.	Daily ration of <i>G. auratus</i> in summer was estimated to be approximately 3%
19		(dry body weight) using the models of Elliot & Persson and Eggers, which is
20		similar, but slightly lower than daily ration estimates reported for other similar
21		sized fishes.
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1 Abstract

2	We examined the diel feeding pattern, gastric evacuation and daily ration of a lentic,
3	endemic Tasmanian galaxiid fish, Galaxias auratus. Analysis of stomach contents and
4	consumption estimates based on collections of fish every 3 h over three 24-h periods
5	in summer 2002/2003 revealed that feeding always occurred during both the day and
6	night, with no obvious peaks. We also estimated the gastric evacuation rate of G .
7	auratus in a laboratory experiment using the two prey species found to be dominant in
8	stomachs of field sampled fish. The relationship was best described by an exponential
9	model, with rate parameters (R) of 0.104 and 0.081 for the evacuation of the
10	amphipod, Austrochiltonia australis, and the cladoceran, Daphnia carinata, at water
11	temperatures of 11.5 °C and 16.5 °C respectively. Daily ration of G. auratus in
12	summer was estimated to be approximately 3% (dry body weight) using the models of
13	Elliot & Persson and Eggers. Galaxias auratus appears to be unusual in that its
14	feeding pattern cannot be classified as nocturnal, diurnal or crepuscular, but its gastric
15	evacuation and daily ration estimates are still similar to other comparable Northern
16	Hemisphere freshwater fishes.
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1 Introduction

2	Whether they are nocturnal, diurnal or crepuscular, most fishes exhibit a distinct diel
3	pattern in feeding (Fraser et al. 1993; Brännäs & Alanärä 1997; Fraser & Metcalfe
4	1997). The potential causes of such patterns are complicated and may include factors
5	such as prey availability (Glova et al. 1987), predation risk (Metcalfe et al. 1999),
6	potential for intra- or interspecific competition (Keast & Welsh 1968), capabilities of
7	each fish species, (e.g. dependence on vision for locating prey: Forrester et al. 1994;
8	Kreivi et al. 1999), or a range of seasonal effects, (e.g. temperature and day length:
9	Riehle & Griffith 1993; Fraser et al. 1995). Many of these are also interdependent.
10	Studying the diel feeding pattern of a fish species can thus suggest a lot about its
11	ecology, and provides the foundation for estimating the amount of food it consumes
12	daily.
13	
14	
15	There are some cases where the feeding of a fish species has both diurnal and
16	nocturnal peaks (e.g. rock bass, Ambloplites rupestris; Keast & Welsh 1968). For
17	fishes that occur in high densities (or when food is limited) this may be caused by
18	temporal partitioning of feeding: in order to reduce the effects of intraspecific
19	competition, some individuals feed nocturnally and some diurnally (Brännäs &
20	Alanärä 1997). This partitioning may be size-structured and brought about by social
21	interactions, where only the larger, more dominant individuals feed at the most
22	preferred time of day ('preferred' in terms of the trade-off between optimising
23	foraging efficiency and avoiding predators sensu Lima & Dill 1990).
24	

1	Members of the Galaxiidae form an important component of the native freshwater fish
2	fauna in temperate regions of the Southern Hemisphere, yet diel feeding patterns are
3	unknown for most species. The lotic galaxiids of New Zealand have been the best
4	studied in this respect, and many are nocturnal foragers (Glova & Sagar 1989a,
5	1989b). Galaxias auratus (Johnston) is a lentic Tasmanian galaxiid that it has co-
6	existed with introduced brown trout (Salmo trutta Linnaeus) in Lakes Crescent and
7	Sorell, to which it is endemic, since 1868 and still remains in very high densities.
8	Little is known, however, of its ecology. It is believed that the activity of this species
9	is greater at night, but its diel feeding pattern is unknown (Hardie et al. 2006). We
10	hypothesised that G. auratus would also be a nocturnal forager both because of the
11	prevailing evidence from New Zealand congeners and because the potential selective
12	pressures imposed by brown trout (the major predator of G. auratus) would foster
13	feeding in low light conditions. Thus the primary objective of this study was to
14	examine the diel feeding pattern of this lentic galaxiid. The potential for size-based
15	temporal partitioning of feeding was also examined in relation to the observed feeding
16	patterns.
17	
18	
19	When the diel feeding pattern is known, daily ration (or daily food intake) can be
20	estimated with greatest accuracy (Darnell & Meierotto 1962; Mann 1978; Madon
21	1998). If samples of stomach contents have been collected in the field and the nature
22	of gastric evacuation is known, daily ration can be estimated using a number of
23	existing models, the most commonly used being those of Elliot & Persson (1978) and
24	Eggers (1977) (Boisclair & Marchand 1993; Specziár 2002). Despite the importance

25 of galaxiids in temperate Southern Hemisphere freshwater systems, there are no

1 published estimates of daily ration for any species. A secondary objective of this

2 study was to use the diel feeding data in conjunction with an estimate of the rate of

- 3 gastric evacuation to estimate daily ration.
- 4

5 Methods

6 Study species and site

7 Galaxias auratus is a relatively large galaxiid (max total length (TL) ~240 mm, but 8 more commonly to 140 mm), which is endemic to the interconnected Lakes Crescent 9 and Sorell on the Tasmanian Central Plateau (c. 42° 5' S; 147° 10' E). It is an 10 opportunistic feeder, with adults eating a variety of aquatic and terrestrial 11 invertebrates, but most often consuming epibenthic crustaceans and insect larvae and 12 plankton when available (Hardie et al. 2004). Brown trout are also abundant in these 13 lakes, which also contain smaller numbers of rainbow trout (Oncorhynchus mykiss 14 Walbaum), short-finned eel (Anguilla australis Richardson) and common carp 15 (Cyprinus carpio L.). The brown trout prey heavily on G. auratus, although their 16 efficiency appears to have been reduced since the mid 1990s, when both lakes became 17 highly turbid (Uytendaal 2003) and G. auratus presumably became harder to locate 18 and capture (Stuart-Smith et al. 2004). 19 20 21 G. auratus is listed as 'rare' under the Tasmanian Threatened Species Protection Act 22 1995, and 'vulnerable' under the national Environment Protection and Biodiversity

- 23 Conservation Act 1999 due to its restricted distribution, yet within these lakes it
- 24 occurs in arguably the highest densities of any of Tasmania's lentic galaxiids.

Although Lakes Crescent and Sorell are relatively large (23.1 and 51.6 km²
 respectively), they are shallow (2.3 and 3.1 m average depth, respectively), and there
 are estimated to be in excess of 2 million and 0.5 million *G. auratus* in Lakes
 Crescent and Sorell respectively (A. Uytendaal, unpublished data).

6

7 **Diel feeding patterns**

8 Galaxias auratus were captured using a backpack electrofishing unit (Smith-Root Inc. 9 model 12-B) at 3-h intervals for 24 h. A replicate sample was taken exactly 24 h from 10 the first. This was done on three occasions over summer 2002 - 2003, with two of 11 these from Lake Crescent (11-12 December 2002 and 6-7 February 2003) and one 12 from Lake Sorell (13-14 February 2003). The study was conducted in both Lakes 13 Crescent and Sorell in case the feeding pattern of G. auratus was affected by 14 differences in their own populations, or trout or prey populations between the lakes. 15 On each occasion, a suitable stretch of shoreline consisting of uniform cobble rock 16 habitat was chosen and divided into nine shorter stretches, each to be sampled once in 17 that day. Immediately after capture, the fish were killed by overdosing in benzocaine 18 (300 mg L^{-1}) , weighed, measured (TL), and preserved in 4% formalin with their 19 abdominal cavity slit open. The water temperature was measured at the time and place 20 of each sample.

21

22

Stomachs were dissected from fish and contents were removed. Each prey taxon was
identified at least to genus, and the relative proportion of volume made up by each

1	was estimated. Stomach contents were then dried ($60^{\circ}C > 48$ h) and weighed (to 0.1
2	mg) using a Mettler AE 100 analytical balance. A sub-sample of contents from 40
3	stomachs was ashed (540°C > 24 h), and ash-free dry weight (AFDW) was estimated
4	for the remainder of stomach contents using the relationship between AFDW and dry
5	weight (DW) of stomach contents in the sub-sample (linear regression, AFDW =
6	$0.8324 \times DW + 0.0007$, $r^2 = 0.99$, $p < 0.001$, $n = 40$). To calculate the DW of whole
7	fish minus their stomach contents, the emptied stomachs were returned to the
8	abdominal cavity of the fish, which were then also dried ($60^{\circ}C > 96$ h) and weighed.
9	For graphical purposes and use in daily ration estimation, the relative stomach
10	contents weight (F_t) was also calculated for fish captured at each time using equation
11	1:
12	
	G

$$F_t = \frac{G_t}{D_t \times 1000}$$

15 where G_t is the weight of the stomach contents (mg DW) and D_t is the DW (g) of a 16 fish captured at time *t*.

17

18

Stomach contents AFDW were log-transformed in order to homogenise variances and compared between times of day by one-way analysis of covariance (ANCOVA) with log_e(fish DW) as the covariate. The positive relationships between transformed fish weights and stomach contents weights were similar for all times on all days, satisfying the ANCOVA assumption of homogeneity of slopes. Any differences in fish sizes are thus unlikely to effect interpretation of results. Where significant differences across

1 the 9 samples were identified, Tukey's post-hoc test was used to determine which 2 pairs of times differed. In addition to analysis of the amount of food in the stomach, 3 estimates of consumption during each of the 3-h intervals were also used to determine 4 the diel feeding pattern of G. auratus. These were based on the model of Elliot & 5 Persson (1978) (equation 2, below). 6 7 8 Trellis plots, as implemented in the lattice package of R (Sarkar 2005), were used to 9 examine whether there was any evidence of size-based temporal partitioning in 10 feeding. On each sample date, the fish were split into six slightly overlapping size 11 classes (i.e. "shingles" sensu Cleveland 1994) with equal numbers of fish in each size class, and F_t was plotted against time. Any trends were visualised using a loess 12 13 smoother. If size-based partitioning occurred, we expected that these plots would 14 show different trends over time for small and large fish. 15 16 17 **Epibenthic prey** 18 Samples of epibenthic invertebrate prey were also taken with fish samples with the 19 aim of detecting if diel changes in prey positioning resulted in changes in abundance 20 of prey that may be available to the fish at different times of the day, a phenomenon 21 well documented in lotic invertebrates (Cowan & Peckarsky 1994; McIntosh & 22 Townsend 1994). Immediately before electrofishing each stretch of shoreline, prey 23 were sampled using a suction sampler, with three randomly located quadrats of 576 24 cm² sampled in each stretch. This method samples prey from exposed surfaces of the 25 substrate, so it probably more closely represents prey that were available to the fish

1	than other sampling methods which sample interstitial and other sub-surface habitats
2	(e.g. cores or grabs). Prey samples were preserved in 80% ethanol and later identified
3	to a minimum of genus level and enumerated in the laboratory using a dissecting
4	microscope. The densities of the amphipod, Austrochiltonia australis on 6-7 February
5	2003 were estimated by sub-sampling because of the particularly large numbers of
6	this species. Precision of estimates based on sub-sampling ranged up to \pm 23%, but for
7	most samples was approximately $\pm 15\%$.
8	
9	
10	The diet of the fish was very low in diversity, with a single prey taxon forming the
11	bulk of stomach contents on each day (Table 1). Only the amphipod A. australis and
12	the gastropod Austropyrgus sp. were used in analyses as these were the most
13	dominant epibenthic prey found in stomach contents. The densities of each in the
14	environment at each sample time were analysed for correlation with their mean
15	relative proportion in stomach contents of fish at those times. Densities of A. australis
16	on 11-12 December 2002 were log transformed as they differed by more than an order
17	of magnitude between times.
18	
19	
20	Gastric evacuation
21	The rates at which prey are evacuated from the stomach of G. auratus were
22	determined under controlled laboratory conditions. Due to the dominance of A.

23 australis and Daphnia carinata in the diets of field sampled fish on different days

- 24 (Table 1), two experiments were conducted, one with each prey species. Water
- 25 temperature influences the rate of gastric evacuation (Elliot 1972; Dos Santos &

1	Jobling 1991; Andersen 1999), so as the purpose of the gastric evacuation
2	experiments was to allow estimation of daily ration on different days, experiments
3	were run at the mean temperatures recorded on the days on which these prey were
4	dominant (11.5 °C for A. australis and 16.5 °C for D. carinata). Otherwise, both
5	experiments followed the same protocol.
6	
7	
8	Fish were captured in Lake Crescent by electrofisher ($n = 54$, mean TL = 103 mm,
9	range 84-144 mm) and maintained in the laboratory in two large holding tanks
10	(approx. 350 L) for a minimum of 2 weeks to allow them to acclimate. At the
11	beginning of a trial, they were placed in individual, food-free tanks (350 x 210 x 260
12	mm) for 48 h. A known number of prey was introduced and the fish were allowed to
13	feed for 3 h. Fish were then transferred into new tanks without any prey and the
14	number of remaining prey was counted. The DW of prey consumed by each fish was
15	estimated from linear regression of number and DW of each prey species (A.
16	<i>australis</i> : $\log_e(DW) = -0.9182 + 1.0362\log_e(number)$, $r^2 = 0.95$, $p < 0.001$, $n = 20$; D.
17	<i>carinata</i> : $\log_{e}(DW) = -1.8949 + 0.9860\log_{e}(number)$, $r^{2} = 0.93$, $p < 0.001$, $n = 20$).
18	Fish were killed at each of a series of pre-determined intervals after the feeding period
19	and the fish and remaining stomach contents were dried and weighed separately,
20	following the same procedures and equipment as for the field sampled fish.
21	
22	
23	Regression analysis was used to identify the best model to describe the evacuation of
24	A. australis and D. carinata from the stomach of G. auratus and for estimation of the

25 rate parameter *R*, which was required for the Elliot & Persson and Eggers models. We

1 used non-linear regression, rather than linear regression on transformed variables, so 2 that the best model could be chosen and comparisons could be made based on r^2 and 3 SE values (Elashoff et al. 1982; Bromley 1994).

4

5

6 **Daily ration**

7 It is widely reported that the Elliot & Persson model usually provides accurate 8 estimates of consumption (Hayward 1991; Héroux & Magnan 1996; Specziár 2002), 9 but it is subject to two major sources of error. The first is that as it is based on 10 differences in mean relative stomach contents weights between sample times, and 11 does not account for variation about these means, or when data are not normally 12 distributed or do not satisfy parametric assumptions. Some researchers have used 13 geometric means or medians rather than arithmetic means because of this (Amundsen 14 & Klemetsen 1986; Parrish & Margraf 1990). The second is that there is error 15 associated with the measurement of the gastric evacuation rate (R), which is not 16 accounted for. Many studies have completely neglected this. 17 18 19 In our study, estimates of consumption based on the Elliot & Persson model (C_i) for 20 each 3-h interval were made using the bootstrap method, which allowed the error 21 associated with both F_t and R to be estimated (Trudel & Boisclair 1993). Transformed (arcsine $\sqrt{}$) F_t values from each time period were sampled 5000 times with 22 23 replacement and means from each were back-transformed. Each of the 5000 backtransformed means (multiplied by 100 to convert to %DW of fish) (F_t^*) was then used 24

25 in the Elliot & Persson model:

2 (2)
$$C_i^* = \frac{(F_{(t+1)}^* - F_t^* e^{-R^*t})R^*t}{1 - e^{-R^*t}}$$

4 where C_i is the mean of the 5000 C_i^* estimates the consumption during the interval *i* 5 (always 3 h in this study) expressed as %DW of fish, F_t^* and $F_{(t+1)}^*$ are mean back-6 transformed relative stomach contents weights (%) at two successive sampling times, 7 and R^* is a bootstrap estimate of the evacuation rate. Values of R^* were generated 8 using equation 3:

9

10 (3)
$$R^* = R + (SE_R \times RN)$$

11

where SE_R is the standard error of *R*, and RN is a normally distributed random number 12 13 with a mean of 0 and a standard deviation of 1 (Trudel & Boisclair 1993). Values of R 14 and SE_R were estimated from the non-linear regressions of gastric evacuation (i.e. of 15 A. australis for 11-12 December 2002, and of D. carinata in calculations for 6-7 and 16 13-14 February 2003). 95% confidence intervals of bootstrap estimates were 17 calculated using Hall's basic method (Davison & Hinkley 1997). These analyses were 18 conducted in the package "boot" (Canty & Ripley 2005) in R version 2.2.0 (R 19 Development Core Team 2005). 20 21 22 Daily ration using the Elliot & Persson model is equal to the sum of C_i for each day.

23 The bootstrap method was also employed to estimate daily ration using the Eggers

model (C₂₄), with re-sampling of transformed F_t values (5000 permutations) and
combining the back-transformed means (%) with appropriate R^{*} values in equation 4:

4 (4)
$$C_{24} = F^* \times R^* \times 24$$

5

6 where C_{24} is the daily ration expressed as %DW of fish, and F^* is the mean of all F_t^* 7 for that day. The correction method of Eggers (1979) was not used as F_t values did 8 not differ significantly between replicate samples at the same time 24 h apart on any 9 day (ANOVA: 11-12 December: $F_{1,50} = 0.001$, p = 0.971; 6-7 February: $F_{1,47} = 1.279$, 10 p = 0.264; 13-14 February: $F_{1,40} = 0.098$, p = 0.756). 11

12

13 **Results**

14 **Diel feeding pattern**

15 Only four empty stomachs were found in 593 fish sampled, and AFDW of stomach 16 contents were consistently high and variable. Differences in AFDW between times on 17 any of the days sampled were not significant, with the exception of the sample at 18 18:15 on 6 February 2003, in which stomach contents weights were significantly 19 lower than samples at 12:15, 15:15, and 00:15, 03:15 and at 09:15 on the following day (ANCOVA: $F_{8,159} = 2.153$, p = 0.034). Estimates of consumption in each of the 20 21 time intervals revealed feeding during both day and night, but did differ significantly 22 between some sample times, as indicated by non-overlapping confidence intervals 23 (Fig. 1). The greatest feeding occurred between 15:15 - 18:15 and 00:15 - 03:15 on 24 11-12 December 2002, and 18:15 – 00:15 on 6-7 February 2003. Feeding was more

1	consistent in Lake Sorell on 13-14 February. There were also periods in which Elliot
2	& Persson estimates were negative. However, confidence intervals of all of these
3	overlapped zero. These were between $15:15 - 18:15$ and $00:15 - 03:15$ on 6-7
4	February 2003, and 03:15 – 06:15 on 13-14 February 2003 (Fig. 1).
5	
6	
7	Although feeding occurred during both the day and night, this was not the result of
8	different sized fish feeding at different times, i.e. there was no evidence of any size-
9	based differences or temporal partitioning of feeding. Visual inspection of the trellis
10	plots of relative stomach contents weights from different size classes of fish (Fig. A1)
11	revealed no differences in trends over the day on any of the sampling dates. There
12	were also no significant differences in the size (TL) of fish captured at each time on
13	any day (ANOVA: 11-12 December: $F_{8, 229} = 0.641$, $p = 0.743$; 6-7 February: $F_{8, 160} =$
14	1.680, $p = 0.107$; 13-14 February: $F_{8, 177} = 0.312$, $p = 0.961$).
15	

Epibenthic prey

18Austrochiltonia australis dominated both stomach contents and epibenthic prey19samples on 11-12 December 2002. There was a strong, positive linear relationship20between the proportion of A. australis in stomachs of G. auratus and its densities in21environmental samples on this day (Pearson correlation coefficient, r = 0.76), with22peaks early in the night and early in the day (Fig. 2). There were no correlations23between stomach contents and the densities of Austropyrgus sp. on this day despite24the fact that this species increased in proportion in stomach contents late in the day

1	and late in the night. There were no correlations between stomach contents and the
2	densities of either prey on the 6-7 and 13-14 February 2003 (all $ r < 0.13$).
3	
4	
5	Gastric evacuation
6	The evacuation of both A. australis and D. carinata from the stomach of G. auratus
7	followed a curvilinear decay with time (Fig. 3). A simple exponential model yielded
8	the greatest r^2 and smallest SE for both prey species (equation 5):
9	
10	$(5) M_t = M_0 e^{-Rt}$
11	
12	where M_t is the amount of prey remaining in the stomach at time t (mg DW) and M_0 is
13	the initial meal size (mg DW).
14	
15	
16	Daily ration
17	Daily ration estimates ranged from 2.2 % DW (0.43 g·100g wet wt ⁻¹ ·day ⁻¹ , Eggers
18	model, 6-7 February 2003) to 3.9 % (0.76 g \cdot 100g wet wt ⁻¹ ·day ⁻¹ , Eggers model, 11-12
19	December 2002)(Fig. 4), with the overall mean close to 3%. This equates to around
20	118 amphipods (A. australis) or 406 Daphnia carinata for a fish of the average
21	sampled size (1.87 g DW, 98 mm TL). Eggers and Elliot & Persson estimates differed
22	by almost 1% on 6-7 February 2003, but this was not statistically significant, and
23	estimates on other days were more similar. Elliot & Persson estimates were almost
24	identical for all three days. Although not statistically significant, the highest estimates

1 were on 11-12 December 2002, despite the water temperature being considerably

2 cooler on this day (mean 11.5°C as opposed to mean 16.5°C on the other two days).

- 3
- 4

5 **Discussion**

6 Both analysis of stomach contents weights and the estimation of consumption using 7 the Elliot & Persson model show that there were no significant peaks in feeding by G. 8 *auratus* and that they fed rather consistently during both night and day on all the dates 9 sampled and in both lakes. Thus, the hypothesis that they feed primarily at night was 10 not supported by our findings. Feeding appeared to be more consistent throughout the 11 24 hr day in fish sampled from Lake Sorell, but this does not alter the conclusions of 12 the study, with G. auratus still observed feeding during day, night and twilight 13 periods. Although the variability in stomach contents weights was high, this is 14 characteristic of fish feeding (Jenkins & Green 1977; Grant & Kott 1999; Hartman 15 2000), and, in the context of other similar studies, these data were remarkably free of 16 the problems emphasised by Amundsen & Klemetsen (1986): weights of stomach 17 contents were not skewed, nor were there many empty stomachs. Our sample sizes 18 were also comparable to, or larger than most similar studies (e.g. Brodeur & Pearcy 19 1987; Johnson & Dropkin 1995; Madon 1998).

20

21

One of the assumptions of the Elliot & Persson model is that feeding is continuous during each 3-h interval (Elliot & Persson 1978). Failure to satisfy this assumption can lead to errors in estimates of consumption and possibly negative estimates during

1	intervals in which consumption is low and not continuous. By keeping the sampling
2	interval short (\leq 3 h, Elliot & Persson 1978; Cortés, 1997), and because the diet was
3	"fine-grained" (large numbers of small food particles, Cochran & Adelman 1982), the
4	likelihood of violating this assumption was minimised. However, this assumption may
5	still be violated when fish are feeding close to satiation (Elliot & Persson 1978;
6	Cochran & Adelman 1982; Persson 1983). As there were very few empty stomachs
7	found in G. auratus and stomach contents weights were consistently high, it is
8	possible that they were feeding close to satiation, and therefore, in an inconsistent
9	manner. Elliot & Persson (1978) experimentally tested the effects of violating this
10	assumption and found that even in extreme cases (a fish feeding for only 20 min every
11	3 h) their model still provided good estimates of actual consumption when the interval
12	was 3 h, but that when there were differences between estimates and actual
13	consumption, the estimates were normally slightly lower than actual consumption.
14	Thus, even if the assumption of continuous feeding was not satisfied in our study, the
15	resulting estimates are unlikely to differ considerably from the real consumption of G .
16	auratus; but if at all, they may be slight underestimates. This may help explain those
17	estimates that were low (some negative but with 95% CI overlapping zero).
18	
19	
20	Feeding of G. auratus was consistent and was not significantly greater during night,
21	day or twilight periods. Although this pattern has occasionally been seen in other
22	species (e.g. coho salmon, Oncorhynchus kisutch: Ruggerone 1989, and brook charr,
23	Salvelinus fontinalis: Héroux & Magnan 1996) it is unusual amongst fish (Fraser et al.
24	1993; Fraser & Metcalfe 1997). Although McIntosh & Townsend (1995) found that
25	Galaxias vulgaris (the common river galaxias) foraged both nocturnally and diurnally,

Glova & Sagar 1989a, 1989b; McDowall 1990) and there is evidence that active movement of this species is also greater at night. Diel surveys of <i>G. auratus</i> in recently translocated population in a trout-free, clear-water dam (Hardie et al. 2 have suggested that <i>G. auratus</i> spends more time in the cover of complex habit such as macrophytes during the day, and then moves about in search of food at This was supported by preliminary electrofishing for this study, which indicate numbers of <i>G. auratus</i> in areas of uniform silt substrate were low throughout th but increased at night. Interestingly, McIntosh & Townsend (1995) recorded th of activity/habitat use pattern for <i>G. vulgaris</i> even though this species also feed during the day. They found that <i>G. vulgaris</i> spent most of the daylight hours in emerging only to capture prey, but actively moved about in search of food durin night.	1	most galaxiid species have been reported to be nocturnal foragers (Cadwallader 1975;
movement of this species is also greater at night. Diel surveys of <i>G. auratus</i> in recently translocated population in a trout-free, clear-water dam (Hardie et al. 2 have suggested that <i>G. auratus</i> spends more time in the cover of complex habit such as macrophytes during the day, and then moves about in search of food at This was supported by preliminary electrofishing for this study, which indicate numbers of <i>G. auratus</i> in areas of uniform silt substrate were low throughout th but increased at night. Interestingly, McIntosh & Townsend (1995) recorded th of activity/habitat use pattern for <i>G. vulgaris</i> even though this species also feed during the day. They found that <i>G. vulgaris</i> spent most of the daylight hours in emerging only to capture prey, but actively moved about in search of food durin night.	2	Glova & Sagar 1989a, 1989b; McDowall 1990) and there is evidence that activity and
4 recently translocated population in a trout-free, clear-water dam (Hardie et al. 2 5 have suggested that <i>G. auratus</i> spends more time in the cover of complex habit 6 such as macrophytes during the day, and then moves about in search of food at 7 This was supported by preliminary electrofishing for this study, which indicate 8 numbers of <i>G. auratus</i> in areas of uniform silt substrate were low throughout th 9 but increased at night. Interestingly, McIntosh & Townsend (1995) recorded th 10 of activity/habitat use pattern for <i>G. vulgaris</i> even though this species also feed 11 during the day. They found that <i>G. vulgaris</i> spent most of the daylight hours in 12 emerging only to capture prey, but actively moved about in search of food duri 13 night.	3	movement of this species is also greater at night. Diel surveys of G. auratus in a
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7 This was supported by preliminary electrofishing for this study, which indicate 8 numbers of <i>G. auratus</i> in areas of uniform silt substrate were low throughout th 9 but increased at night. Interestingly, McIntosh & Townsend (1995) recorded th 10 of activity/habitat use pattern for <i>G. vulgaris</i> even though this species also feed 11 during the day. They found that <i>G. vulgaris</i> spent most of the daylight hours in 12 emerging only to capture prey, but actively moved about in search of food duri 13 night.	6	such as macrophytes during the day, and then moves about in search of food at night.
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of activity/habitat use pattern for <i>G. vulgaris</i> even though this species also feed during the day. They found that <i>G. vulgaris</i> spent most of the daylight hours in emerging only to capture prey, but actively moved about in search of food duri night.	9	but increased at night. Interestingly, McIntosh & Townsend (1995) recorded this type
during the day. They found that <i>G. vulgaris</i> spent most of the daylight hours in emerging only to capture prey, but actively moved about in search of food duri night.	10	of activity/habitat use pattern for G. vulgaris even though this species also feeds
12 emerging only to capture prey, but actively moved about in search of food duri13 night.	11	during the day. They found that G. vulgaris spent most of the daylight hours in cover,
13 night.	12	emerging only to capture prey, but actively moved about in search of food during the
	13	night.

15

16 Although further research is needed to establish whether the proposed diel activity/ 17 habitat use pattern of G. auratus persists in the presence of brown trout, it appears that 18 like G. vulgaris, G. auratus still captures prey during times in which it uses complex 19 habitats. This may be due either to a change in feeding strategy from ambush or sit-20 and-wait foraging from the edge of complex habitats during the day, to actively 21 searching for prey at night, or to the ability to search for, and capture prey amongst 22 the complex habitat. The latter may be realistic in habitats such as macrophytes, 23 because the ability to feed at night suggests that this species is capable of locating and 24 capturing prey using non-visual stimuli, which would also be advantageous in habitats

that reduce or break up the visual field. This ability also suggests that the current high
 turbidity of Lakes Crescent and Sorell may not negatively affect their feeding ability.
 3

- 4

5 Another reason that we hypothesised that G. auratus would show a nocturnal peak in 6 foraging is because the risk of predation by brown trout is also likely to differ during 7 the diel cycle. Brown trout are primarily visual predators; although they are capable of 8 nocturnal foraging, they present the greatest predation threat from dawn through to 9 dusk (Allan 1978; Ringler 1979). Brown trout were introduced into Lakes Crescent 10 and Sorell in 1868 and it is possible that they have provided a selective pressure for G. 11 *auratus* to forage nocturnally. While this study cannot determine whether brown trout 12 influence habitat use by G. auratus, it does appear, however, that threat of predation 13 by brown trout has not resulted in a nocturnally biased feeding pattern by G. auratus. 14

15

16 Diel patterns in prey availability are also known to influence feeding patterns of 17 fishes, and have been implicated in causing the nocturnal peaks in the feeding of other 18 galaxiids (Glova & Sagar 1989a, 1989b). Prey availability in our study was 19 consistently high throughout the day and night and we suggest that it did not influence 20 the feeding pattern of G. auratus. The evidence for this includes the presence of very 21 few empty stomachs, very high densities of sampled epibenthic invertebrates (the mean density of A. australis was 13 300 m⁻² and Austropyrgus sp., 264 m⁻²), and the 22 23 observation of very large, dense swarms of Daphnia carinata during all fish sampling 24 periods on the 6-7 and 13-14 February 2003. Unfortunately Daphnia carinata were 25 not quantitatively sampled as a part of this study due to the absence of planktonic prey

1 in the diet of *G. auratus* in preliminary samples and the added logistical

2 considerations of attempting to quantitatively and efficiently sample an invertebrate3 with such a patchy distribution.

- 4
- 5

6 Feeding during both day and night may be caused by intraspecific interactions. Size is 7 the most commonly recorded determinant of social structure in fishes (Danylchuk & 8 Tonn 2001; Whiteman & Cote 2004), and size-based resource partitioning has been 9 reported in other galaxiids (Whitehead et al. 2002; David & Stoffels 2003). Although 10 we could not test explicitly for differences in feeding patterns of individuals in this 11 study because we did not sample the same individual fish at each time of day, there 12 was no evidence of size-based differences in feeding when we examined the amount 13 of food in the stomach throughout the day in different sized individuals within the 14 range of sizes sampled.

- 15
- 16

17 The gastric evacuation rates and daily ration estimates of G. auratus are slightly lower 18 than, but still similar to other similar sized lentic fishes from studies undertaken in the 19 Northern Hemisphere (Persson 1982; Boisclair & Leggett 1988). Interestingly, even 20 though consumption by G. auratus may be a little less than other planktivorous fish 21 (e.g. dace, *Phoxinus eos x P. neogaeus*: Trudel & Boisclair 1993; Gauthier & 22 Boisclair 1997), adult G. auratus may still consume around 400 Daphnia carinata per 23 day. Daphnia carinata are relatively large zooplankters (up to 6 mm), and are 24 probably the dominant algal grazers in Lakes Crescent and Sorell (Uytendaal 2003). 25 Thus the predation pressure exerted by such high densities of G. auratus on D.

1	carinata may possibly have a strong influence on algal biomass in these lakes. There
2	has been a growing number of studies that have demonstrated such abilities of fishes
3	to exert top down control on lower trophic levels through trophic cascades (He &
4	Wright 1992; Karjalainen et al. 1999; Zambrano et al. 2001). This study has not only
5	provided an unusual example of a fish that feeds throughout both night and day, but
6	has also provided empirical data on the predatory capabilities of a galaxiid fish, which
7	offer insight into their role as predators in Southern Hemisphere freshwater systems.
8	

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1 Figure captions

2 Fig. 1. Diel patterns in relative stomach contents weights (F_t , left column) and

corresponding Elliot & Persson three-hourly consumption estimates (*C_i*, right column)
for *Galaxias auratus* sampled from Lake Crescent on 11-12 December 2002 (top), 6-7
February (middle) and from Lake Sorell on 13-14 February (bottom) 2003. Relative
stomach contents weights are plotted as box-and-whisker plots with raw data overlaid
as open circles. Consumption estimates are bootstrap estimates of means + 95%
confidence intervals. Horizontal black bars represent hours of darkness.



10

Fig. 2. Density of *Austrochiltonia australis* in samples of epibenthic prey (open
 circles) and the mean (± SE) proportion by volume of stomach contents made up by
 this prey in *Galaxias auratus* (closed circles) on 11-12 December 2002. No significant
 correlations were found between prey density and stomach contents on any of the
 other days sampled.



Fig. 3. Evacuation of *Austrochiltonia australis* (left) and *Daphnia carinata* (right) from the stomach of *Galaxias auratus* at 11.5 °C and 16.5 °C, respectively. Circles represent the fraction (by DW) of the original meal remaining in the stomach at each time. The rate parameter, R (± its asymptotic standard error), for the evacuation of A. *australis* = 0.1044 ± 0.0158 and the r^2 = 0.8096. For the evacuation of D. *carinata*, R(± its asymptotic standard error) = 0.0805 ± 0.0052 and r^2 = 0.8277.



- Fig. 4. Daily ration estimates (%DW) (and 95% CI) for Galaxias auratus on the three
- days sampled using the Eggers (1977) model (unshaded bars) and the Elliot & Persson



(1978) model (shaded bars).

1 Appendix





Fig A1. Trellis plots of relative stomach contents weights (*F_t*) of different size classes
of fish (TL in mm) on 11-12 December 2002 (left column), 6-7 February, 2003
(middle column) and 13-14 February 2003 (right column) with a loess smoother
superposed (gray line) to assist in visualizing any trends. Each panel has an equal
number of fish, and the lengths of the fish included in each panel increase from
bottom to top with a slight overlap in the fish included in each panel as indicated by

- 1 the sizes specified in each title strip. The shading in the title strip of each panel
- 2 provides a graphical key to the size range of fish included in each panel.