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

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1 **Extended summary**

1 **Abstract**

1 **Introduction**

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*. 42º 5' S; 147º 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.

1 Although Lakes Crescent and Sorell are relatively large (23.1 and 51.6 km² 2 respectively), they are shallow (2.3 and 3.1 m average depth, respectively), and there 3 are estimated to be in excess of 2 million and 0.5 million *G. auratus* in Lakes 4 Crescent and Sorell respectively (A. Uytendaal, unpublished data). 5

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

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23 Stomachs were dissected from fish and contents were removed. Each prey taxon was 24 identified at least to genus, and the relative proportion of volume made up by each

$$
13 \qquad (1) \qquad \qquad F_t = \frac{G_t}{D_t \times 1000}
$$

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

19 Stomach contents AFDW were log-transformed in order to homogenise variances and 20 compared between times of day by one-way analysis of covariance (ANCOVA) with 21 loge(fish DW) as the covariate. The positive relationships between transformed fish 22 weights and stomach contents weights were similar for all times on all days, satisfying 23 the ANCOVA assumption of homogeneity of slopes. Any differences in fish sizes are 24 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 12 class, and *Ft* was plotted against time. Any trends were visualised using a loess 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

- 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 &

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 that the best model could be chosen and comparisons could be made based on $r²$ 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 (*Ci*) 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 22 (arcsine $\sqrt{F_t}$ values from each time period were sampled 5000 times with 23 replacement and means from each were back-transformed. Each of the 5000 back-24 transformed means (multiplied by 100 to convert to %DW of fish) (F_t^*) was then used

25 in the Elliot & Persson model:

$$
1 \\
$$

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

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

12 where SE_R is the standard error of R , and RN is a normally distributed random number 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

1 model (C_{24}) , with re-sampling of transformed F_t values (5000 permutations) and 2 combining the back-transformed means $(\%)$ with appropriate R^* values in equation 4: 3

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 20 day (ANCOVA: $F_{8, 159} = 2.153$, $p = 0.034$). Estimates of consumption in each of the 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

17 **Epibenthic prey**

18 *Austrochiltonia australis* dominated both stomach contents and epibenthic prey 19 samples on 11-12 December 2002. There was a strong, positive linear relationship 20 between the proportion of *A. australis* in stomachs of *G. auratus* and its densities in 21 environmental samples on this day (Pearson correlation coefficient, *r* = 0.76), with 22 peaks early in the night and early in the day (Fig. 2). There were no correlations 23 between stomach contents and the densities of *Austropyrgus* sp. on this day despite 24 the fact that this species increased in proportion in stomach contents late in the day

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).

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- 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

22 One of the assumptions of the Elliot $&$ Persson model is that feeding is continuous 23 during each 3-h interval (Elliot $&$ Persson 1978). Failure to satisfy this assumption 24 can lead to errors in estimates of consumption and possibly negative estimates during

1 most galaxiid species have been reported to be nocturnal foragers (Cadwallader 1975; 2 Glova & Sagar 1989a, 1989b; McDowall 1990) and there is evidence that activity and 3 movement of this species is also greater at night. Diel surveys of *G. auratus* in a 4 recently translocated population in a trout-free, clear-water dam (Hardie et al. 2006) 5 have suggested that *G. auratus* spends more time in the cover of complex habitats 6 such as macrophytes during the day, and then moves about in search of food at night. 7 This was supported by preliminary electrofishing for this study, which indicated that 8 numbers of *G. auratus* in areas of uniform silt substrate were low throughout the day 9 but increased at night. Interestingly, McIntosh & Townsend (1995) recorded this type 10 of activity/habitat use pattern for *G. vulgaris* even though this species also feeds 11 during the day. They found that *G. vulgaris* spent most of the daylight hours in cover, 12 emerging only to capture prey, but actively moved about in search of food during the 13 night.

14

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

1 that reduce or break up the visual field. This ability also suggests that the current high 2 turbidity of Lakes Crescent and Sorell may not negatively affect their feeding ability. 3

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- 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 22 mean density of *A. australis* was 13 300 m⁻² and *Austropyrgus* sp., 264 m⁻²), and the 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 invertebrate 3 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.*

10 **Acknowledgements**

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1 **References**

1 **Figure captions**

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

3 corresponding Elliot & Persson three-hourly consumption estimates (*Ci*, right column) 4 for *Galaxias auratus* sampled from Lake Crescent on 11-12 December 2002 (top), 6-7 5 February (middle) and from Lake Sorell on 13-14 February (bottom) 2003. Relative 6 stomach contents weights are plotted as box-and-whisker plots with raw data overlaid 7 as open circles. Consumption estimates are bootstrap estimates of means + 95%

8 confidence intervals. Horizontal black bars represent hours of darkness.

1 Fig. 2. Density of *Austrochiltonia australis* in samples of epibenthic prey (open 2 circles) and the mean $(\pm \text{ SE})$ proportion by volume of stomach contents made up by 3 this prey in *Galaxias auratus* (closed circles) on 11-12 December 2002. No significant 4 correlations were found between prey density and stomach contents on any of the 5 other days sampled.

1 Fig. 3. Evacuation of *Austrochiltonia australis* (left) and *Daphnia carinata* (right) 2 from the stomach of *Galaxias auratus* at 11.5 °C and 16.5 °C, respectively. Circles 3 represent the fraction (by DW) of the original meal remaining in the stomach at each 4 time. The rate parameter, *R* (± its asymptotic standard error), for the evacuation of *A.* 5 australis = 0.1044 ± 0.0158 and the $r^2 = 0.8096$. For the evacuation of *D. carinata*, *R* 6 (\pm its asymptotic standard error) = 0.0805 ± 0.0052 and $r^2 = 0.8277$.

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

3 (1978) model (shaded bars).

Appendix

4 Fig A1. Trellis plots of relative stomach contents weights (*Ft*) of different size classes 5 of fish (TL in mm) on 11-12 December 2002 (left column), 6-7 February, 2003 6 (middle column) and 13-14 February 2003 (right column) with a loess smoother 7 superposed (gray line) to assist in visualizing any trends. Each panel has an equal 8 number of fish, and the lengths of the fish included in each panel increase from 9 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.