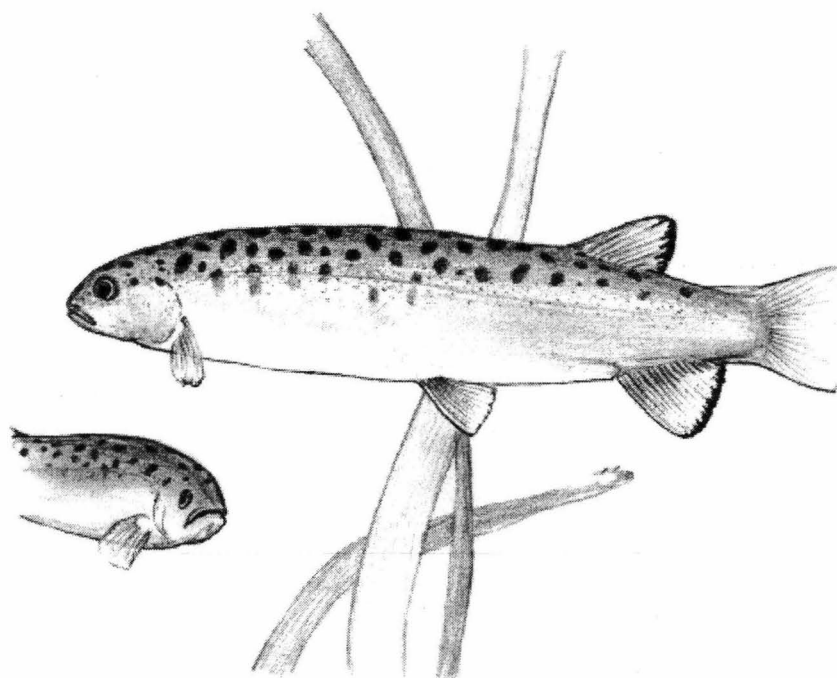

**The importance of complex habitats for the predator-
prey interaction between a threatened galaxiid fish and
an introduced salmonid**

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Submitted in fulfillment of the requirements for the
Degree of Doctor of Philosophy

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Declaration

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text of this thesis.

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Abstract

Theoretically, there are a number of ways in which predator and prey can co-exist, including temporal and spatial partitioning and the presence and use of refuge habitats by prey. Whilst these factors have been shown to promote co-existence in well-studied, co-evolved predator and prey pairs, there has been a lack of applied research into how predator-prey theory fits when predators are introduced species. Understanding the mechanisms behind the success, or lack of, by native species when predators have been introduced, thus requires knowledge of whether the same factors promote co-existence, and contexts in which predation pressure is likely to be greatest on native species.

This thesis examines the interactions of *Galaxias auratus*, a threatened galaxiid species that has shown unusual resilience to the predation pressure imposed by the introduced brown trout, in order to gain insight into the mechanisms that have assisted it in co-existing with an introduced piscivore that has adversely impacted other galaxiid populations. There has been a substantial reduction in the availability of complex habitats in the entire natural range of this species, prompting an investigation into the likely importance of these habitats in facilitating the co-existence of this unnatural predator-prey pair.

An initial study on the feeding of *G. auratus* in the wild revealed it to be an efficient forager that feeds constantly, both day and night. This occurred whilst it appeared to undertake a diel shift in habitat use, and its daily ration was still comparable to other well-studied freshwater fishes, despite it using complex

habitats for some of this time. A laboratory experiment was conducted to examine this apparent diel switch between habitats, and test whether *G. auratus* behaviourally altered this pattern when predation risk was high. This confirmed that *G. auratus* uses complex habitats (macrophytes and rocks) during the day and open water during the night, but reduces its use of open water significantly when brown trout are near and predation risk is high.

In order to determine whether this habitat use pattern and response to the predation risk imposed by brown trout was likely to promote co-existence of these species, two experiments were run to assess the potential foraging costs usually associated with using complex habitats, and the benefits to using such habitats in terms of reducing predation risk. The foraging of *G. auratus* was found not to be significantly reduced in complex habitats, but the risk of predation was substantially reduced. These results imply that the behaviour of *G. auratus* is “adaptive” and is likely to have contributed to its success with brown trout. These findings also suggest, however, that if the availability of macrophytes was severely reduced for this species, as is likely to continue in the future, the importance of predation pressure in determining the outcome of its interaction with trout is likely to substantially increase.

The implications for other native species are that the importance of predation by introduced species is context-dependent, and that conservation must focus on maintaining contexts in which predation pressure is likely to be lessened. This includes conservation of important habitats that may mediate interactions between introduced predators and native prey.

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Preface

This PhD thesis is made up of four data chapters that have been published in international journals. Thus, the formatting of each chapter is slightly different, following the requirements of each particular journal. To improve the readability and appearance of the thesis, I have removed the author addresses, keywords and acknowledgements from each paper, but have retained the remainder, including reference lists, as submitted to each journal in the final accepted version. I am first author on all four papers, and my two supervisors, Dr Leon Barmuta and Associate Professor Rob White, are co-authors. My wife, Jemina Stuart-Smith, is also a co-author on two (Chapters 4 and 5) as she assisted in a substantial component of field and laboratory work for these.

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Stuart-Smith RD, Stuart-Smith JF, White RWG, Barmuta LA (2007). The impact of an introduced predator on a threatened galaxiid is reduced by the availability of complex habitats. *Freshwater Biology*. Online publication, DOI: 10.1111/j.1365-2427.2007.01787.x

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Chapter 1: Introduction

Understanding how predator and prey can co-exist formed much of the early and major theoretical developments in community and population ecology (Solomon 1949; Holling 1965). Early studies, including those by Rosenzweig and MacArthur (1963) and Sih (1987), established that habitat heterogeneity and, in particular, the presence of refuge habitats, promotes system stability. Whilst this theory has been thoroughly discussed in the literature (e.g. McNair 1986; Chesson and Rosenzweig 1991), a need for further applied research in this area has been highlighted by recent reviews (Sinclair et al. 1998; Ormerod 2002). Agrawal et al. (2007) discussed context-dependence of interaction strengths and have specifically identified the need for research into situations in which interactions (e.g. between predator and prey) are likely to be most important. These requirements for research may be particularly crucial and applicable for understanding the ecology of the galaxiid fishes of the Southern Hemisphere.

The galaxiids have recently been labelled as a particularly vulnerable group of fishes due to a range of natural and anthropogenically-induced impacts (McDowall 2006), yet the ecology of many species remains poorly studied. Arguably, the most damaging impact on these small fishes has been the widespread introduction of salmonids to Southern Hemisphere fresh waters which has been linked to declines in ranges and abundances of many galaxiids (Cadwallader 1975a, 1975b; Tilzey 1976, Townsend and Crowl 1991; Flecker and Townsend 1994; Crook and Sanger 1998a, 1998b; McIntosh 2000; Baigun and Ferriz 2003; McDowall 2003). Tasmania has 16 species of galaxiids, 11 of which

are listed as threatened by the Tasmanian *Threatened Species Protection Act* 1995. Introduced salmonids have been identified as a key threat to all these species (Hardie et al. 2006).

The existing body of literature on predator-prey co-existence in freshwater fish includes some well-developed and tested theory on the influence of complex habitats, particularly with respect to the habitat use of fishes and its links with foraging efficiency and predation risk. Influential studies, such as those by Crowder and Cooper (1982), Werner et al. (1983), Werner and Hall (1988), Diehl (1988), and Persson and Eklöv (1995), have identified the importance of habitat complexity in promoting predator-prey co-existence by reducing predation risk, but usually at a cost to the prey species in foraging success and growth. Werner and Hall (1988) demonstrated that bluegill sunfish (*Lepomis macrochirus*) were faced with a trade-off between predation risk and feeding (and consequently growth) rate when they shift between open water and vegetated habitats. Predation risk and diet of juvenile perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are also strongly influenced by habitat complexity (Persson and Eklöv 1995).

These and many other similar studies have tested theory with experiments using either bluegill sunfish in America, or perch and roach in Europe (e.g. Winfield 1986; Savino and Stein 1989). These fishes evolved sympatrically with piscivorous fishes (largemouth bass, *Micropterus salmoides*, and adult perch, *Perca fluviatilis*, respectively), so their responses to predation risk from these piscivores have had the opportunity for refinement through evolutionary processes. Many galaxiids, however, evolved in isolation from aggressive, mobile

piscivorous and competitive fishes (McDowall 1990; Townsend and Crowl 1991), and their responses to introduced predators may not be as stabilizing or predictable as those observed for bluegill sunfish or juvenile perch. Reeb (1999) pointed out that a lack of appropriate predator-avoidance behaviour may occur in populations that have not been in contact with particular predators. Before the introduction of trout, birds and eels were the major predators of many galaxiids. The predation pressure exerted by these predators, however, is likely to be much less pervasive than that of the much more aggressive and mobile trout, and the evolved behavioural responses of galaxiids to these predators should clearly be different. It is not known if a habitat-dependent trade-off in foraging success and predation risk actually occurs for galaxiids that occur with trout, and whether their behavioural responses to the predation risk imposed by these introduced piscivores promote co-existence (*sensu* Mills et al., 2004).

***Galaxias auratus*: specific needs for research**

Galaxias auratus (Johnston) is a threatened galaxiid, listed as ‘rare’ under the Tasmanian *Threatened Species Protection Act 1995*, and ‘vulnerable’ under the national *Commonwealth Environment Protection and Biodiversity Conservation Act 1999* due to its restricted distribution. It is endemic to Lakes Crescent and Sorell, associated wetlands and the upper Clyde River on the Tasmanian Central Plateau. This species is unusual because, despite the introduction of brown trout (*Salmo trutta* L.) to these lakes in 1868, it has remained very abundant and occurs in higher densities than any of Tasmania’s other land-locked galaxiids (A. Uytendaal, S.A. Hardie, R.W.G. White, unpublished data).

Despite the unusually high abundance of this species, which could easily lead to complacency about its long-term security, there have been recent, substantial changes to Lakes Crescent and Sorell, including a reduction in the availability of the habitats that may have enabled *G. auratus* to co-exist with trout so far. Consistently low water levels in these lakes from the 1990s onwards, and more frequent re-suspension events coupled with algal blooms, have resulted in the loss of the once-extensive in-lake macrophyte beds in Lakes Sorell (Uytendaal 2003), and the large areas of fringing wetland habitat have remained dry or disconnected from the lakes for extended periods (Heffer 2003). The only significant areas of rocky habitat in Lake Crescent have also been dewatered several times during recent years, leaving little refuge for *G. auratus* throughout the entire lake. By contrast, rocky patches of substrate are found throughout Lake Sorell, and much of the exposed shores of this lake are occupied by this habitat. Fig. 1 shows the relationship between the water levels and the availability of the wetland macrophyte habitat in both lakes, and the rocky habitat in Lake Crescent, and Fig. 2 shows the extent of wetlands and limited stretches of rocky shoreline in Lake Crescent.

Historically, these two lakes have had contrasting limnologies, leading Cheng & Tyler (1973) to term the situation a “limnological paradox”. Lake Sorell has generally been a clear-water lake, with prominent vascular hydrophytes (i.e. macrophytes), sporadically high densities of large-bodied zooplankton (mostly *Daphnia carinata*), and infrequent algal blooms. By contrast, Lake Crescent is dominated by phytoplanktonic blooms, small-bodied zooplankton and has very limited cover of vascular hydrophytes. Since mid- to late 1990s, Lake Sorell

appears to have been oscillating between the alternative states (i.e. macrophyte-dominated “clear water” v. phytoplankton-dominated “turbid”) that have been identified in recent limnological literature (Scheffer et al. 2001; Beisner et al. 2003; Hargeby et al. 2004; Schroder et al. 2005). Continued excessive drawdown for irrigation and potable supply could very likely result in a full shift to a turbid phytoplankton-dominated state, where re-establishment of macrophyte beds would be hampered by self-stabilizing feedback mechanisms (Blindow et al. 1993).

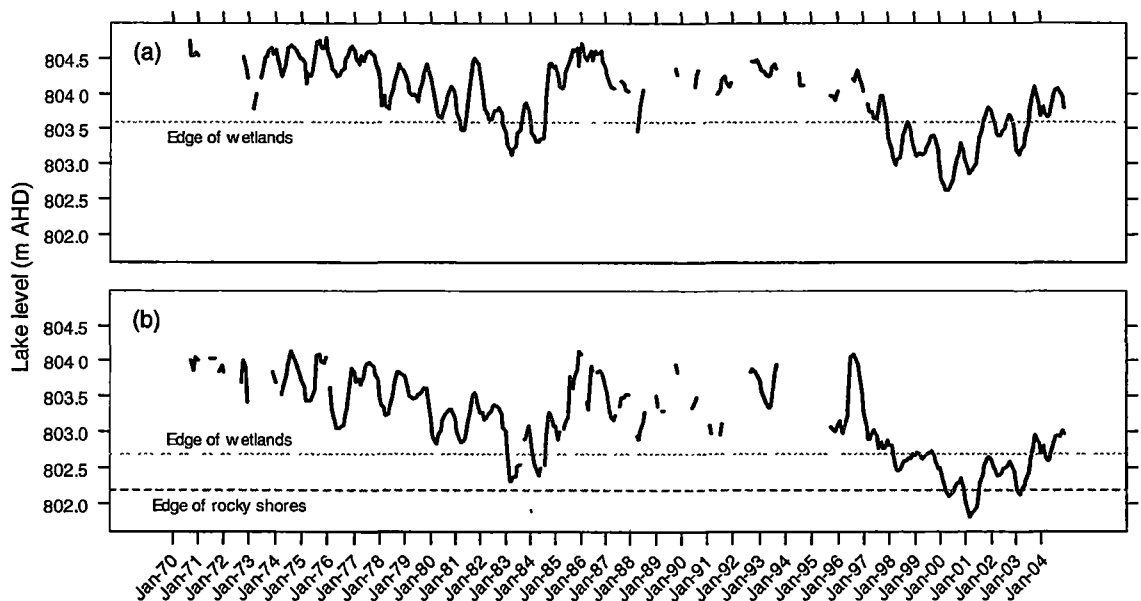


Fig. 1 Historic lake water levels (in metres above Australian Height Datum (AHD)) in Lake Sorell (a) and Lake Crescent (b). Blank regions in the solid line denote missing lake level data. Horizontal dashed lines show the levels at which the wetlands become disconnected in both lakes and the rocky shores are left dry in Lake Crescent. Figure taken from Hardie (2007).

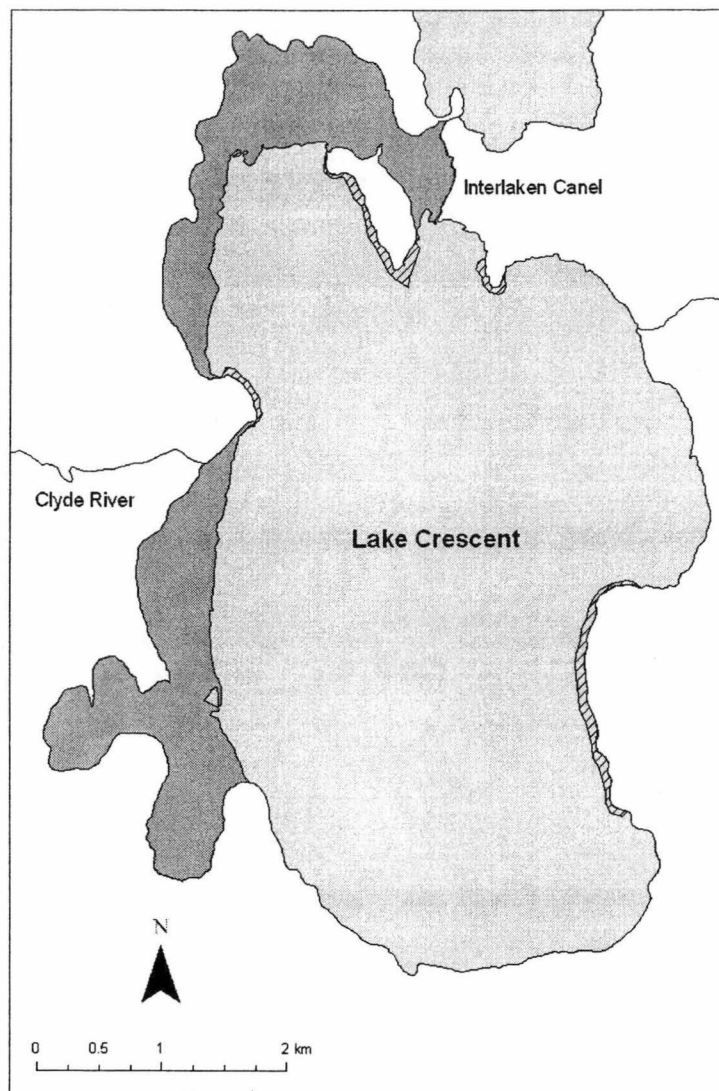


Fig. 2 Map of Lake Crescent showing extent of the wetlands (darker grey) and the limited rocky shorelines (diagonal hatching). Figure taken from Hardie (2007).

Restricting the availability of macrophyte habitats in these two lakes is likely to have a damaging effect on *G. auratus*, but, to date, there has been no research to determine the role that macrophyte habitats may play in allowing its co-existence with trout, and the likely future of this species in Lakes Crescent and Sorell if the current water level regime continues. The research reported in this thesis took advantage of the unique opportunity to explore the unexpected success of a

galaxiid that co-occurs with an introduced piscivore, whilst concurrently gaining insight into the potential future impacts of the recent habitat loss that has occurred in its entire natural range. Typically, such applied research is only conducted in cases when a native species is affected deleteriously (e.g. Swenson 1999; Labbe and Fausch 2000; Hamer et al. 2002), but this research took a novel, proactive approach, addressing research questions about a threatened species which has actually fared well, with an additional aim of providing information that will assist in understanding mechanisms that may contribute to the success, or lack of, of other species in the presence of an introduced predator.

The ecology of lacustrine galaxiids has been relatively poorly studied, and further study should contribute to an understanding their importance in temperate Southern Hemisphere lakes, as well as identifying when and what management intervention is needed. Priorities for such purposes include understanding the importance of different habitats for each species, their reproduction, and interactions with predators and prey. Work by Hardie (2007) has highlighted the importance of complex habitats for the reproduction of *G. auratus*, but no data existed on its foraging and interactions with predators in the previously extensive, but now intermittently available macrophyte habitats of Lakes Crescent and Sorell. Such data could assist in understanding its past success in co-existing with trout and the potential consequences of the recent environmental changes for its future, and have been identified as a high priority for its conservation (Hardie et al. 2004). These data may also contribute to an understanding the likely importance of complex habitats for the conservation of other lentic galaxiids.

Hardie et al. (2006) and Townsend and Crowl (1991) have suggested the likely importance of habitat loss for galaxiid conservation, and the particular physical changes that have occurred in Lakes Crescent and Sorell (low water levels, high turbidity and changes in habitat loss) have also impacted the ecology of other freshwater fishes. Pyrovetsi and Papastergiadou (1992) reported that the loss of habitat diversity, including large areas of macrophyte habitat, in Lake Kerkini in Greece resulted in declines in fish diversity and abundance. Extreme turbidity has also been shown on many occasions to affect the ecology of freshwater fish (Sweka and Hartman 2001; Richardson and Jowett 2002; Zamor and Grossman 2007). But despite many reports of the negative impacts of macrophyte loss and extreme turbidity, characteristics of the globally increasing problem of eutrophication of fresh waters, Diehl (1988) pointed out that these changes affect the ecological interactions of different species in different ways. As suggested by Agrawal et al. (2007), determining these will assist in improving our knowledge of community ecology.

Research aims

This project aimed to examine the interactions of *Galaxias auratus* with brown trout and test existing, relevant ecological theories in order to understand the ecological factors that may have contributed to its success in co-existing with trout to date, and that may make it vulnerable in future as a result of the changes in habitat availability that have occurred in Lakes Crescent and Sorell. An initial, field-based study was designed to provide fundamental foraging data including what and how much this species consumes, and when it forages in the wild (Chapter 2). This was a necessary first step to document its natural feeding habits,

and allowed hypotheses to be generated regarding its ability to forage under different conditions, and its use of different habitats. It also yielded quantitative data on daily ration and feeding rate that can be incorporated into the next iteration of limnological simulation models that were initiated by Uytendaal (2006) using the CAEDYM-DYRESIM framework, as well as allowing subsequent experiments to be designed under more natural conditions, including the use of appropriate numbers and types of prey and lighting conditions.

The direct effect of trout presence on the habitat use patterns of *G. auratus* first needed to be determined, before being able to examine if its behavioural response to brown trout is likely to promote co-existence, whether there are any associated costs, and whether the availability of different habitats was likely to alter their interaction. In Chapter 3, I examined the behavioural responses of *G. auratus* to brown trout under habitat conditions that simulated the scenarios of past and present habitat availability in Lakes Crescent and Sorell. In the other two experimental chapters (Chapters 4 and 5), I tested the resulting impacts of the behavioural responses of *G. auratus* to trout, by assessing foraging costs and predation risk in these contrasting habitats to see whether a trade-off occurs, *sensu* Werner and Hall (1988) and Persson and Eklöv (1995). In Chapter 4, I assessed potential foraging costs of an increased use of complex habitats that occurs in the presence of trout, thus examining the potential indirect effect of trout on the feeding (and likely growth) of *G. auratus*. In Chapter 5, I examined the direct outcomes of an increased use of complex habitats by *G. auratus* in terms of predation mortality to trout. I tested the predation risk of *G. auratus* to trout under the different habitat scenarios, again simulating those experienced in Lakes

Crescent and Sorell in the past, present and likely in the future. The specific aims and hypotheses tested in each experiment are given in each of the relevant chapters.

***G. auratus* and Lakes Crescent and Sorell**

Galaxias auratus is a relatively large galaxiid (max total length (TL) ~240 mm, but more commonly to 140 mm) believed to be derived from a landlocked population of *Galaxias truttaceus* (Johnson et al. 1981; Ovenden et al. 1993). It occupies a similar ecological niche to *G. truttaceus* being a generalist consumer, but adopting more of an epibenthic lifestyle (Hardie et al. 2004). Adults have been found to forage on a variety of aquatic and terrestrial invertebrates, but most often consume epibenthic crustaceans and insect larvae and plankton when available (Hardie et al. 2004). It is much more abundant in Lake Crescent than in Lake Sorell, with Hardie (2003a) recording up to 10-fold greater catches in fyke nets in Crescent than Sorell on identical sampling occasions.

Lakes Crescent and Sorell are shallow, polymictic lakes that lie on the eastern edge of the Tasmanian Central Plateau at c. 42° 5' S; 147° 10' E and are connected by a canal approximately 1 km long. Prior to the construction of this canal, these lakes were likely connected by mosaic of ill-defined channels and wetlands during high water, usually over the austral winter and spring. Lake Sorell is 804.36 m a.s.l. at full supply level (f.s.l.) and is the largest of the two with a surface area of approximately 5310 ha, a mean depth of 3.07 m and a max depth of 4.30 m (also at f.s.l.). At f.s.l, Lake Crescent is 803.8 m a.s.l. and has a surface area of approximately 2305 ha. The mean depth of Lake Crescent is only

2.30 m, and its maximum depth is 3.80 m. The water levels of both lakes, however, are manipulated by humans. Lake levels have been artificially raised a number of times since the first weirs were constructed in 1833 (Cheng and Tyler 1973; Cutler et al. 1990; Deakin 2002) and have been regulated for downstream irrigation, with additional minor allocations for town water supply. The catchment area for these lakes is relatively small compared to their surface area, with a ratio of total catchment area to lake surface area of 1.75 (Uytendaal 2003). The vulnerability of these lakes to decreases in water levels during times of drought is thus high due to the combined effects of the small catchment area and the high surface area to volume ratio of both lakes. This results in potentially large evaporative losses of water, and these losses dominate the water-balance for these lakes (Department of Primary Industries, Water and the Environment 2005). Rainfall for the area averages 699 mm per year (Uytendaal 2003).

Despite their geographic proximity, geologic, geomorphic, vegetational and climatic similarities, Lakes Crescent and Sorell have persistently different phytoplankton and zooplankton communities. Cheng and Tyler (1973) found Lake Crescent to have ten times the standing crop biomass of phytoplankton than Lake Sorell, and Burrows (1968) found copepods (*Boeckella rubra*) and cladocerans (*Bosmina hagdmani*) to dominate the zooplankton communities of Lakes Sorell and Crescent, respectively. Both lakes contain a range of fish species, both native and introduced. As well as the natural, endemic populations of *G. auratus*, the native short-finned eel (*Anguilla australis* Richardson) is present in both lakes. This species has been maintained artificially by stocking of elvers since upstream migration was blocked by the construction of Meadowbank Dam on the Derwent

River (into which the Clyde River flows) in the 1960's. Native *Galaxias maculatus* (Jenyns) has also been found in small numbers, but these are believed to have been accidentally introduced with elvers and have apparently not established a self-sustaining population (S. A. Hardie, pers. comm.). The introduced fish species found in these lakes are brown trout and rainbow trout (*Oncorhynchus mykiss* Walbaum), which were deliberately introduced for recreational fishing in 1868 and 1932, respectively, and common carp (*Cyprinus carpio* L), which were discovered in 1995. Nothing is known of potential impacts of common carp on *G. auratus*, and this was not investigated in this thesis because an extensive and successful program of eradication has been pursued by the Inland Fisheries Service since 1996, and numbers of this species were very low during this study.

Lakes Crescent and Sorell have significant wetlands which make up 17% (385 ha) and 7.8% (415 ha) of the surface areas at full supply, respectively, and are considered important habitats for a range of invertebrates, frogs, snakes, water birds and fishes (Heffer 2003). Heffer (2003) provided a comprehensive report on the nature and importance of these wetlands. Historically, Lake Sorell also supported extensive areas of submerged macrophytes (*Myriophyllum simulans*). Lake Crescent had far less extensive submerged macrophyte beds, but still possessed pockets of submerged and emergent macrophytes outside of the wetlands in the littoral zone.

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Chapter 2: Nocturnal and diurnal feeding by *Galaxias auratus*, a lentic galaxiid fish

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Abstract

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

Introduction

Whether they are nocturnal, diurnal or crepuscular, most fishes exhibit a distinct diel pattern in feeding (Fraser et al. 1993; Brännäs & Alanärä 1997; Fraser & Metcalfe 1997). The potential causes of such patterns are complicated and may include factors such as prey availability (Glova et al. 1987), predation risk (Metcalf et al. 1999), potential for intra- or interspecific competition (Keast & Welsh 1968), capabilities of each fish species, (e.g. dependence on vision for locating prey: Forrester et al. 1994; Kreivi et al. 1999), or a range of seasonal effects, (e.g. temperature and day length: Riehle & Griffith 1993; Fraser et al. 1995). Many of these are also interdependent. Studying the diel feeding pattern of a fish species can thus suggest a lot about its ecology, and provides the foundation for estimating the amount of food it consumes daily.

There are some cases where the feeding of a fish species has both diurnal and nocturnal peaks (e.g. rock bass, *Ambloplites rupestris*; Keast & Welsh 1968). For fishes that occur in high densities (or when food is limited) this may be caused by temporal partitioning of feeding: in order to reduce the effects of intraspecific competition, some individuals feed nocturnally and some diurnally (Brännäs & Alanärä 1997). This partitioning may be size-structured and brought about by social interactions, where only the larger, more dominant individuals feed at the most preferred time of day ('preferred' in terms of the trade-off between optimising foraging efficiency and avoiding predators *sensu* Lima & Dill 1990).

Members of the Galaxiidae form an important component of the native freshwater fish fauna in temperate regions of the Southern Hemisphere, yet diel feeding

patterns are unknown for most species. The lotic galaxiids of New Zealand have been the best studied in this respect, and many are nocturnal foragers (Glova & Sagar 1989a, 1989b). *Galaxias auratus* (Johnston) is a lentic Tasmanian galaxiid that it has co-existed with introduced brown trout (*Salmo trutta* Linnaeus) in Lakes Crescent and Sorell, to which it is endemic, since 1868 and still remains in very high densities. Little is known, however, of its ecology. It is believed that the activity of this species is greater at night, but its diel feeding pattern is unknown (Hardie et al. 2006). We hypothesised that *G. auratus* would also be a nocturnal forager both because of the prevailing evidence from New Zealand congeners and because the potential selective pressures imposed by brown trout (the major predator of *G. auratus*) would foster feeding in low light conditions. Thus the primary objective of this study was to examine the diel feeding pattern of this lentic galaxiid. The potential for size-based temporal partitioning of feeding was also examined in relation to the observed feeding patterns.

When the diel feeding pattern is known, daily ration (or daily food intake) can be estimated with greatest accuracy (Darnell & Meierotto 1962; Mann 1978; Madon 1998). If samples of stomach contents have been collected in the field and the nature of gastric evacuation is known, daily ration can be estimated using a number of existing models, the most commonly used being those of Elliot & Persson (1978) and Eggers (1977) (Boisclair & Marchand 1993; Specziár 2002). Despite the importance of galaxiids in temperate Southern Hemisphere freshwater systems, there are no published estimates of daily ration for any species. A secondary objective of this study was to use the diel feeding data in conjunction with an estimate of the rate of gastric evacuation to estimate daily ration.

Methods

Study species and site

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

G. auratus is listed as 'rare' under the Tasmanian *Threatened Species Protection Act 1995*, and 'vulnerable' under the national *Environment Protection and Biodiversity Conservation Act 1999* due to its restricted distribution, yet within these lakes it 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).

Diel feeding patterns

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

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 was estimated. Stomach contents were then dried ($60^\circ\text{C} > 48 \text{ h}$) and weighed (to 0.1 mg) using a Mettler AE 100 analytical balance. A sub-sample of contents from 40 stomachs was ashed ($540^\circ\text{C} > 24 \text{ h}$), and ash-free dry weight (AFDW) was estimated for the remainder of stomach contents using the relationship between AFDW and dry weight (DW) of stomach contents in the sub-sample (linear regression, $\text{AFDW} = 0.8324 \times \text{DW} + 0.0007$, $r^2 = 0.99$, $p < 0.001$, $n = 40$). To calculate the DW of whole fish minus their stomach contents, the emptied

stomachs were returned to the abdominal cavity of the fish, which were then also dried (60°C > 96 h) and weighed. For graphical purposes and use in daily ration estimation, the relative stomach contents weight (F_t) was also calculated for fish captured at each time using equation 1:

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

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

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 $\log_e(\text{fish DW})$ 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 the 9 samples were identified, Tukey's post-hoc test was used to determine which pairs of times differed. In addition to analysis of the amount of food in the stomach, estimates of consumption during each of the 3-h intervals were also used to determine the diel feeding pattern of *G. auratus*. These were based on the model of Elliot & Persson (1978) (equation 2, below).

Trellis plots, as implemented in the lattice package of R (Sarkar 2005), were used to examine whether there was any evidence of size-based temporal partitioning in

feeding. On each sample date, the fish were split into six slightly overlapping size classes (i.e. “shingles” sensu Cleveland 1994) with equal numbers of fish in each size class, and F_i was plotted against time. Any trends were visualised using a loess smoother. If size-based partitioning occurred, we expected that these plots would show different trends over time for small and large fish.

Epibenthic prey

Samples of epibenthic invertebrate prey were also taken with fish samples with the aim of detecting if diel changes in prey positioning resulted in changes in abundance of prey that may be available to the fish at different times of the day, a phenomenon well documented in lotic invertebrates (Cowan & Peckarsky 1994; McIntosh & Townsend 1994). Immediately before electrofishing each stretch of shoreline, prey were sampled using a suction sampler, with three randomly located quadrats of 576 cm² sampled in each stretch. This method samples prey from exposed surfaces of the substrate, so it probably more closely represents prey that were available to the fish than other sampling methods which sample interstitial and other sub-surface habitats (e.g. cores or grabs). Prey samples were preserved in 80% ethanol and later identified to a minimum of genus level and enumerated in the laboratory using a dissecting microscope. The densities of the amphipod, *Austrochilonia australis* on 6-7 February 2003 were estimated by sub-sampling because of the particularly large numbers of this species. Precision of estimates based on sub-sampling ranged up to $\pm 23\%$, but for most samples was approximately $\pm 15\%$.

The diet of the fish was very low in diversity, with a single prey taxon forming the bulk of stomach contents on each day (Table 1). Only the amphipod *A. australis*

and the gastropod *Austropyrgus* sp. were used in analyses as these were the most dominant epibenthic prey found in stomach contents. The densities of each in the environment at each sample time were analysed for correlation with their mean relative proportion in stomach contents of fish at those times. Densities of *A. australis* on 11-12 December 2002 were log transformed as they differed by more than an order of magnitude between times.

Gastric evacuation

The rates at which prey are evacuated from the stomach of *G. auratus* were determined under controlled laboratory conditions. Due to the dominance of *A. australis* and *Daphnia carinata* in the diets of field sampled fish on different days (Table 1), two experiments were conducted, one with each prey species. Water temperature influences the rate of gastric evacuation (Elliot 1972; Dos Santos & Jobling 1991; Andersen 1999), so as the purpose of the gastric evacuation experiments was to allow estimation of daily ration on different days, experiments were run at the mean temperatures recorded on the days on which these prey were dominant (11.5 °C for *A. australis* and 16.5 °C for *D. carinata*). Otherwise, both experiments followed the same protocol.

Table 1. Times of fish sampling, sample and fish sizes and % volume of dominant prey found in stomachs of *Galaxias auratus* sampled from Lake Crescent (11-12/12/2002 and 6-7/02/2003) and Lake Sorell (13-14/02/2003).

Date	Time	<i>n</i>	Mean TL (range)	% <i>A.</i> <i>australis</i>	% <i>D.</i> <i>carinata</i>	% <i>Austropyrgus</i>
11/12/2002	15:15	27	103 (83-123)	40.85	0	45.10
	18:15	29	104 (79-143)	93.57	0	5.63
	21:15	28	103 (81-145)	88.73	0	0
12/12/2002	00:15	27	101 (84-124)	83.71	0	5.09
	03:15	23	107 (82-166)	63.48	0	20.89
	06:15	27	106 (89-136)	83.53	0	14.46
	09:15	26	100 (80-131)	98.34	0	0.30
	12:15	26	104 (81-132)	97.44	0	0
	15:15	25	100 (82-128)	82.03	0	16.41
6/02/2003	09:15	21	91 (76-112)	25.32	73.55	0
	12:15	20	95 (85-116)	20.06	77.33	0
	15:15	21	93 (82-114)	48.34	51.01	0
	18:15	21	88 (78-101)	20.63	70.16	0
	21:15	17	89 (79-111)	8.02	91.83	0
7/02/2003	00:15	7	89 (81-100)	30.12	69.28	0
	03:15	10	95 (88-114)	28.89	71.11	0
	06:15	24	93 (84-113)	34.45	65.55	0
	09:15	28	91 (78-123)	27.21	69.36	0
13/02/2003	09:15	21	98 (87-120)	0	99.24	0
	12:15	20	99 (81-147)	2.68	97.32	0
	15:15	18	98 (86-136)	2.42	97.58	0
	18:15	20	95 (80-144)	0.26	99.48	0
	21:15	20	94 (76-117)	0.28	99.44	0.28
14/02/2003	00:15	20	97 (81-134)	10.88	83.08	0
	03:15	22	96 (78-120)	1.75	98.00	0
	06:15	24	99 (81-149)	2.36	97.41	0
	09:15	21	97 (82-130)	6.87	91.66	0

Fish were captured in Lake Crescent by electrofisher ($n = 54$, mean TL = 103 mm, range 84-144 mm) and maintained in the laboratory in two large holding tanks (approx. 350 L) for a minimum of 2 weeks to allow them to acclimate. At the beginning of a trial, they were placed in individual, food-free tanks (350 x 210 x 260 mm) for 48 h. A known number of prey was introduced and the fish were allowed to feed for 3 h. Fish were then transferred into new tanks without any

prey and the number of remaining prey was counted. The DW of prey consumed by each fish was estimated from linear regression of number and DW of each prey species (*A. australis*: $\log_e(\text{DW}) = -0.9182 + 1.0362\log_e(\text{number})$, $r^2 = 0.95$, $p < 0.001$, $n = 20$; *D. carinata*: $\log_e(\text{DW}) = -1.8949 + 0.9860\log_e(\text{number})$, $r^2 = 0.93$, $p < 0.001$, $n = 20$). Fish were killed at each of a series of pre-determined intervals after the feeding period and the fish and remaining stomach contents were dried and weighed separately, following the same procedures and equipment as for the field sampled fish.

Regression analysis was used to identify the best model to describe the evacuation of *A. australis* and *D. carinata* from the stomach of *G. auratus* and for estimation of the rate parameter R , which was required for the Elliot & Persson and Eggers models. We 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 r^2 and SE values (Elashoff et al. 1982; Bromley 1994).

Daily ration

It is widely reported that the Elliot & Persson model usually provides accurate estimates of consumption (Hayward 1991; Héroux & Magnan 1996; Specziár 2002), but it is subject to two major sources of error. The first is that as it is based on differences in mean relative stomach contents weights between sample times, and does not account for variation about these means, or when data are not normally distributed or do not satisfy parametric assumptions. Some researchers have used geometric means or medians rather than arithmetic means because of this (Amundsen & Klemetsen 1986; Parrish & Margraf 1990). The second is that

there is error associated with the measurement of the gastric evacuation rate (R), which is not accounted for. Many studies have completely neglected this.

In our study, estimates of consumption based on the Elliot & Persson model (C_i) for each 3-h interval were made using the bootstrap method, which allowed the error associated with both F_t and R to be estimated (Trudel & Boisclair 1993). Transformed (arcsine $\sqrt{\cdot}$) F_t values from each time period were sampled 5000 times with replacement and means from each were back-transformed. Each of the 5000 back-transformed means (multiplied by 100 to convert to %DW of fish) (F_t^*) was then used in the Elliot & Persson model:

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

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

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

where SE_R is the standard error of R , and RN is a normally distributed random number with a mean of 0 and a standard deviation of 1 (Trudel & Boisclair 1993). Values of R and SE_R were estimated from the non-linear regressions of gastric evacuation (i.e. of *A. australis* for 11-12 December 2002, and of *D. carinata* in

calculations for 6-7 and 13-14 February 2003). 95% confidence intervals of bootstrap estimates were calculated using Hall's basic method (Davison & Hinkley 1997). These analyses were conducted in the package "boot" (Canty & Ripley 2005) in R version 2.2.0 (R Development Core Team 2005).

Daily ration using the Elliot & Persson model is equal to the sum of C_i for each day. The bootstrap method was also employed to estimate daily ration using the Eggers model (C_{24}), with re-sampling of transformed F_t values (5000 permutations) and combining the back-transformed means (%) with appropriate R^* values in equation 4:

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

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

Results

Diel feeding pattern

Only four empty stomachs were found in 593 fish sampled, and AFDW of stomach contents were consistently high and variable. Differences in AFDW between times on any of the days sampled were not significant, with the exception

of the sample at 18:15 on 6 February 2003, in which stomach contents weights were significantly 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 time intervals revealed feeding during both day and night, but did differ significantly between some sample times, as indicated by non-overlapping confidence intervals (Fig. 1). The greatest feeding occurred between 15:15 – 18:15 and 00:15 – 03:15 on 11-12 December 2002, and 18:15 – 00:15 on 6-7 February 2003. Feeding was more consistent in Lake Sorell on 13-14 February. There were also periods in which Elliot & Persson estimates were negative. However, confidence intervals of all of these overlapped zero. These were between 15:15 – 18:15 and 00:15 – 03:15 on 6-7 February 2003, and 03:15 – 06:15 on 13-14 February 2003 (Fig. 1).

Although feeding occurred during both the day and night, this was not the result of different sized fish feeding at different times, i.e. there was no evidence of any size-based differences or temporal partitioning of feeding. Visual inspection of the trellis plots of relative stomach contents weights from different size classes of fish (Fig. A1) revealed no differences in trends over the day on any of the sampling dates. There were also no significant differences in the size (TL) of fish captured at each time on any day (ANOVA: 11-12 December: $F_{8, 229} = 0.641, p = 0.743$; 6-7 February: $F_{8, 160} = 1.680, p = 0.107$; 13-14 February: $F_{8, 177} = 0.312, p = 0.961$).

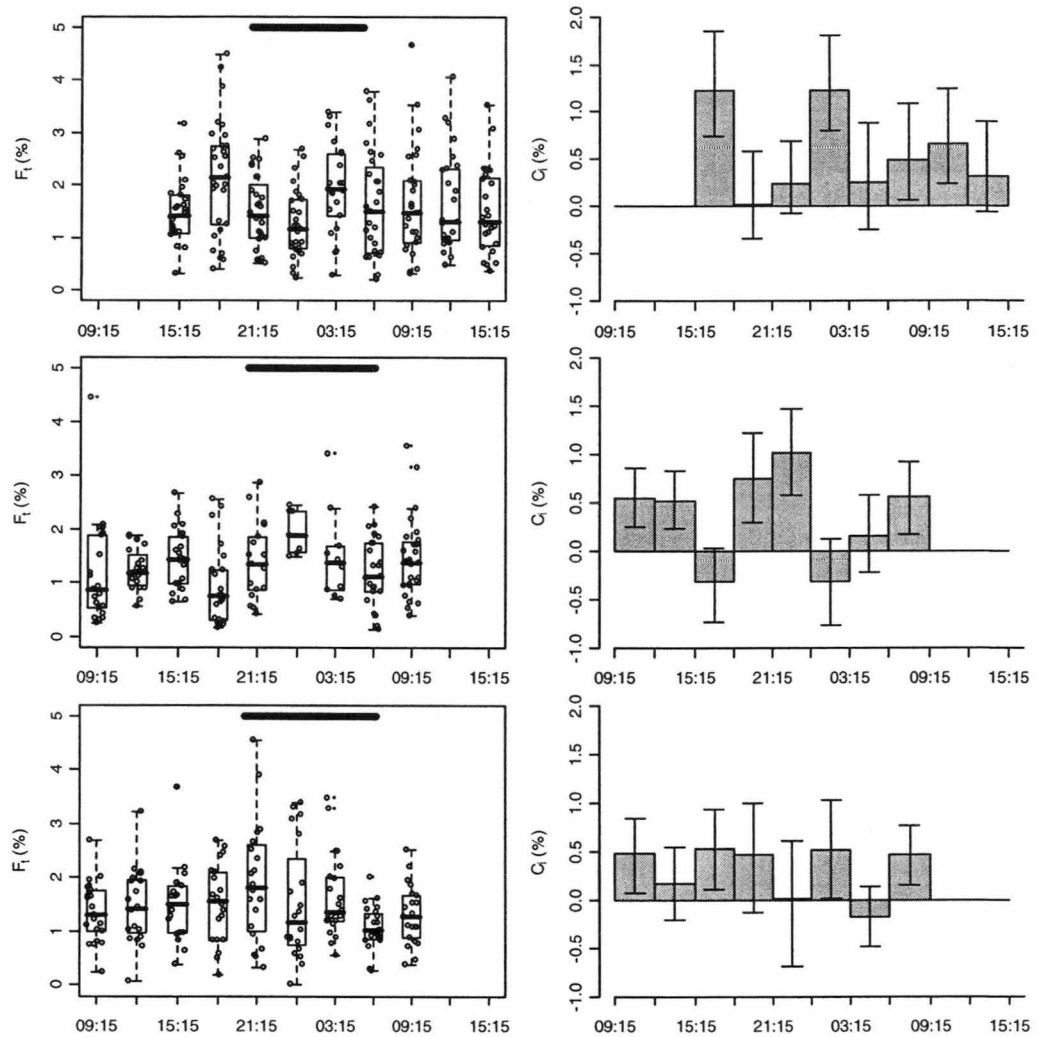


Fig. 1. Diel patterns in relative stomach contents weights (F_t , left column) and corresponding Elliot & Persson three-hourly consumption estimates (C_t , right column) for *Galaxias auratus* sampled from Lake Crescent on 11-12 December 2002 (top), 6-7 February 2003 (middle) and from Lake Sorell on 13-14 February 2003 (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.

Epibenthic prey

Austrochiltonia australis dominated both stomach contents and epibenthic prey samples on 11-12 December 2002. There was a strong, positive linear relationship between the proportion of *A. australis* in stomachs of *G. auratus* and its densities in environmental samples on this day (Pearson correlation coefficient, $r = 0.76$), with peaks early in the night and early in the day (Fig. 2). There were no

correlations between stomach contents and the densities of *Austropyrgus* sp. on this day despite the fact that this species increased in proportion in stomach contents late in the day and late in the night. There were no correlations between stomach contents and the densities of either prey on the 6-7 and 13-14 February 2003 (all $|r| < 0.13$).

Gastric evacuation

The evacuation of both *A. australis* and *D. carinata* from the stomach of *G. auratus* followed a curvilinear decay with time (Fig. 3). A simple exponential model yielded the greatest r^2 and smallest SE for both prey species (equation 5):

$$(5) \quad M_t = M_0 e^{-Rt}$$

where M_t is the amount of prey remaining in the stomach at time t (mg DW) and M_0 is the initial meal size (mg DW).

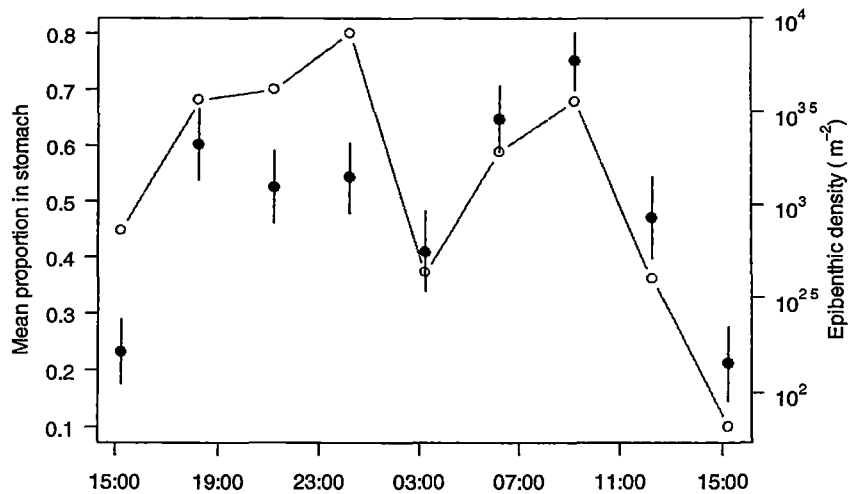


Fig. 2. Density of *Austrochiltonia australis* in samples of epibenthic prey (open circles) and the mean (\pm SE) proportion by volume of stomach contents made up by this prey in *Galaxias auratus* (closed circles) on 11-12 December 2002. No significant correlations were found between prey density and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

Daily ration

Daily ration estimates ranged from 2.2 % DW ($0.43 \text{ g} \cdot 100\text{g wet wt}^{-1} \cdot \text{day}^{-1}$, Eggers model, 6-7 February 2003) to 3.9 % ($0.76 \text{ g} \cdot 100\text{g wet wt}^{-1} \cdot \text{day}^{-1}$, Eggers model, 11-12 December 2002)(Fig. 4), with the overall mean close to 3%. This equates to around 118 amphipods (*A. australis*) or 406 *Daphnia carinata* for a fish of the average sampled size (1.87 g DW, 98 mm TL). Eggers and Elliot & Persson estimates differed by almost 1% on 6-7 February 2003, but this was not statistically significant, and estimates on other days were more similar. Elliot & Persson estimates were almost identical for all three days. Although not statistically significant, the highest estimates were on 11-12 December 2002, despite the water temperature being considerably cooler on this day (mean 11.5°C as opposed to mean 16.5°C on the other two days).

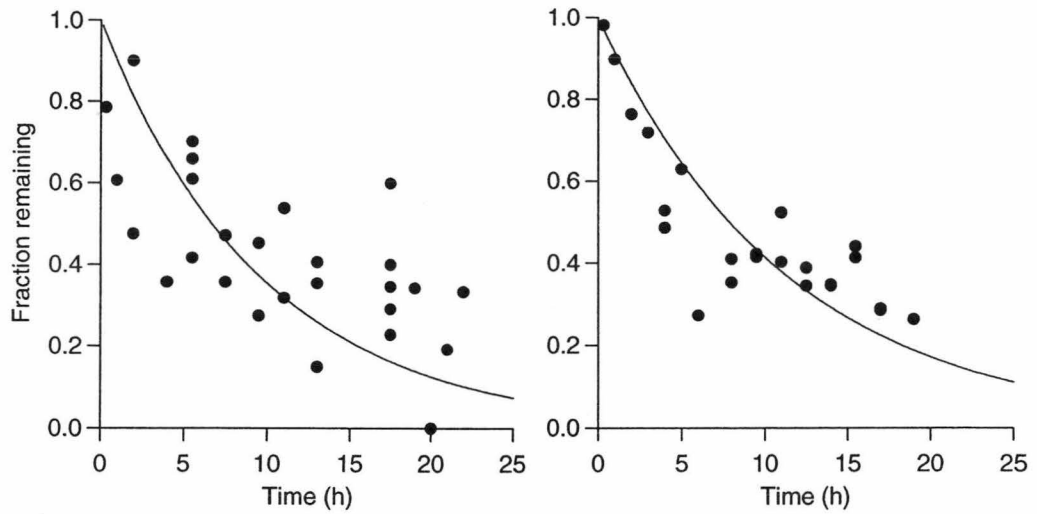


Fig. 3. Evacuation of *Austrochiltonia australis* (left) and *Daphnia carinata* (right) from the stomach of *Galaxias auratus* at 11.5 °C and 16.5 °C, respectively. Circles represent the fraction (by DW) of the original meal remaining in the stomach at each time. The rate parameter, R (\pm its asymptotic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

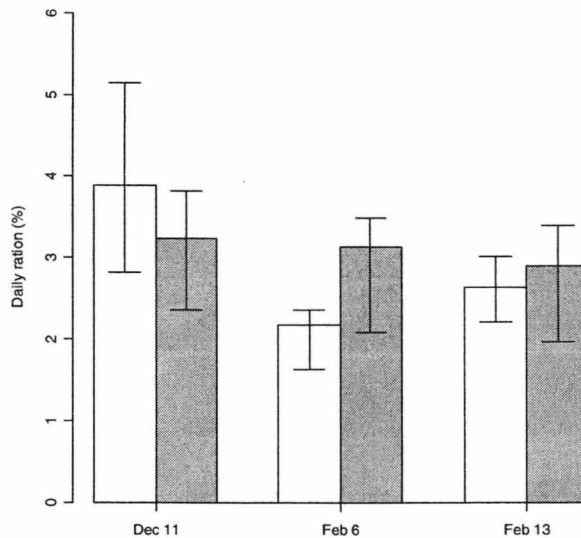


Fig. 4. Daily ration estimates (%DW) (and 95% CI) for *Galaxias auratus* on the three days sampled using the Eggers (1977) model (unshaded bars) and the Elliot & Persson (1978) model (shaded bars).

Discussion

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

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 intervals in which consumption is low and not continuous. By keeping the sampling interval short (≤ 3 h, Elliot & Persson 1978; Cortés, 1997), and because the diet was “fine-grained” (large numbers of small food particles, Cochran & Adelman 1982), the likelihood of violating this assumption was minimised. However, this assumption may still be violated when fish are feeding close to satiation (Elliot & Persson 1978; Cochran & Adelman 1982; Persson

1983). As there were very few empty stomachs found in *G. auratus* and stomach contents weights were consistently high, it is possible that they were feeding close to satiation, and therefore, in an inconsistent manner. Elliot & Persson (1978) experimentally tested the effects of violating this assumption and found that even in extreme cases (a fish feeding for only 20 min every 3 h) their model still provided good estimates of actual consumption when the interval was 3 h, but that when there were differences between estimates and actual consumption, the estimates were normally slightly lower than actual consumption. Thus, even if the assumption of continuous feeding was not satisfied in our study, the resulting estimates are unlikely to differ considerably from the real consumption of *G. auratus*; but if at all, they may be slight underestimates. This may help explain those estimates that were low (some negative but with 95% CI overlapping zero).

Feeding of *G. auratus* was consistent and was not significantly greater during night, day or twilight periods. Although this pattern has occasionally been seen in other species (e.g. coho salmon, *Oncorhynchus kisutch*: Ruggerone 1989, and brook charr, *Salvelinus fontinalis*: Héroux & Magnan 1996) it is unusual amongst fish (Fraser et al. 1993; Fraser & Metcalfe 1997). Although McIntosh & Townsend (1995) found that *Galaxias vulgaris* (the common river galaxias) foraged both nocturnally and diurnally, most galaxiid species have been reported to be nocturnal foragers (Cadwallader 1975; Glova & Sagar 1989a, 1989b; McDowall 1990) and there is evidence that activity and movement of this species is also greater at night. Diel surveys of *G. auratus* in a recently translocated population in a trout-free, clear-water dam (Hardie et al. 2006) have suggested that *G. auratus* spends more time in the cover of complex habitats such as macrophytes during the day, and then moves about in search of food at night. This

was supported by preliminary electrofishing for this study, which indicated that numbers of *G. auratus* in areas of uniform silt substrate were low throughout the day but increased at night. Interestingly, McIntosh & Townsend (1995) recorded this type of activity/habitat use pattern for *G. vulgaris* even though this species also feeds during the day. They found that *G. vulgaris* spent most of the daylight hours in cover, emerging only to capture prey, but actively moved about in search of food during the night.

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

Another reason that we hypothesised that *G. auratus* would show a nocturnal peak in foraging is because the risk of predation by brown trout is also likely to differ during the diel cycle. Brown trout are primarily visual predators; although they are capable of nocturnal foraging, they present the greatest predation threat from dawn through to dusk (Allan 1978; Ringler 1979). Brown trout were introduced

into Lakes Crescent and Sorell in 1868 and it is possible that they have provided a selective pressure for *G. auratus* to forage nocturnally. While this study cannot determine whether brown trout influence habitat use by *G. auratus*, it does appear, however, that threat of predation by brown trout has not resulted in a nocturnally biased feeding pattern by *G. auratus*.

Diel patterns in prey availability are also known to influence feeding patterns of fishes, and have been implicated in causing the nocturnal peaks in the feeding of other galaxiids (Glova & Sagar 1989a, 1989b). Prey availability in our study was consistently high throughout the day and night and we suggest that it did not influence the feeding pattern of *G. auratus*. The evidence for this includes the presence of very 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 observation of very large, dense swarms of *Daphnia carinata* during all fish sampling periods on the 6-7 and 13-14 February 2003. Unfortunately *Daphnia carinata* were not quantitatively sampled as a part of this study due to the absence of planktonic prey in the diet of *G. auratus* in preliminary samples and the added logistical considerations of attempting to quantitatively and efficiently sample an invertebrate with such a patchy distribution.

Feeding during both day and night may be caused by intraspecific interactions. Size is the most commonly recorded determinant of social structure in fishes (Danylchuk & Tonn 2001; Whiteman & Cote 2004), and size-based resource partitioning has been reported in other galaxiids (Whitehead et al. 2002; David & Stoffels 2003). Although we could not test explicitly for differences in feeding

patterns of individuals in this study because we did not sample the same individual fish at each time of day, there was no evidence of size-based differences in feeding when we examined the amount of food in the stomach throughout the day in different sized individuals within the range of sizes sampled.

The gastric evacuation rates and daily ration estimates of *G. auratus* are slightly lower than, but still similar to other similar sized lentic fishes from studies undertaken in the Northern Hemisphere (Persson 1982; Boisclair & Leggett 1988). Interestingly, even though consumption by *G. auratus* may be a little less than other planktivorous fish (e.g. dace, *Phoxinus eos* x *P. neogaeus*: Trudel & Boisclair 1993; Gauthier & Boisclair 1997), adult *G. auratus* may still consume around 400 *Daphnia carinata* per day. *Daphnia carinata* are relatively large zooplankters (up to 6 mm), and are probably the dominant algal grazers in Lakes Crescent and Sorell (Uytendaal 2003). Thus the predation pressure exerted by such high densities of *G. auratus* on *D. carinata* may possibly have a strong influence on algal biomass in these lakes. There has been a growing number of studies that have demonstrated such abilities of fishes to exert top down control on lower trophic levels through trophic cascades (He & Wright 1992; Karjalainen et al. 1999; Zambrano et al. 2001). This study has not only provided an unusual example of a fish that feeds throughout both night and day, but has also provided empirical data on the predatory capabilities of a galaxiid fish, which offer insight into their role as predators in Southern Hemisphere freshwater systems.

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Appendix

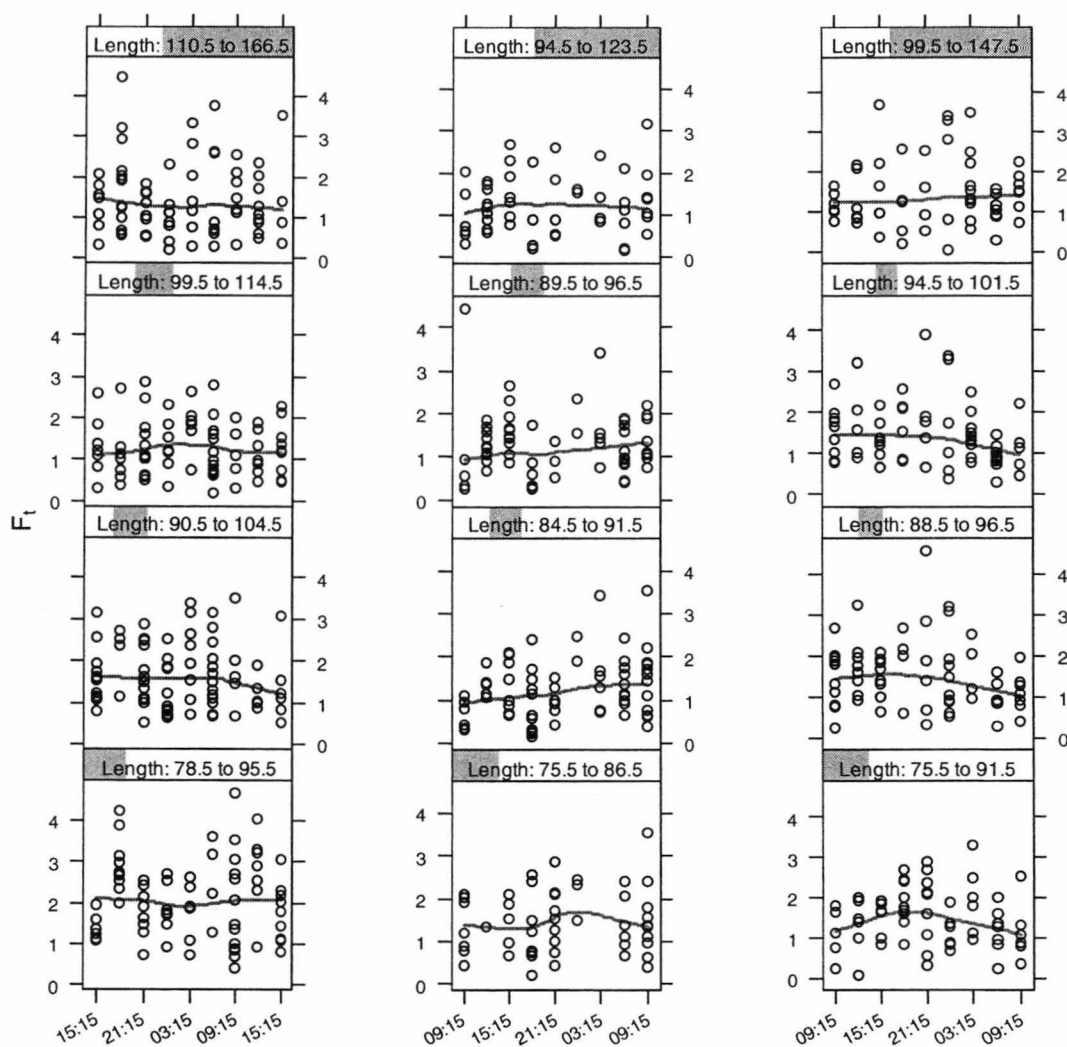


Fig A1. Trellis plots of relative stomach contents weights (F_t) of different size classes of fish (TL in mm) on 11-12 December 2002 (left column), 6-7 February, 2003 (middle column) and 13-14 February 2003 (right column) with a loess smoother superposed (gray line) to assist in visualizing any trends. 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 the sizes specified in each title strip. The shading in the title strip of each panel provides a graphical key to the size range of fish included in each panel.

Chapter 3: A shift in the habitat use pattern of a lentic galaxiid fish: an acute behavioural response to an introduced predator

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Abstract

Despite potentially reducing predation mortality, behavioural responses of native species to introduced predators may still have sub-lethal impacts. In video-recorded laboratory trials, we examined the effects of introduced brown trout on the short-term behaviour of a threatened, lake-dwelling galaxiid fish and confirmed a suspected diel pattern in habitat use by this species. We found that *Galaxias auratus* followed a distinct diel pattern in the use of complex habitats and open water, which was significantly altered by the presence of brown trout. In trials without the introduced predator, *G. auratus* used complex habitats (rocks or macrophytes) during the day, and open water during the night. In trials with brown trout present, *G. auratus* spent significantly less time in open water and rarely ventured out of the macrophytes. However, when given the option of using only rocky substrate or open water, which is the more common situation in the lakes to which this galaxiid is endemic, the fish reduced the amount of time they spent in the open water during the night, but still spent more time in open water than when macrophytes were available. Spending the daylight hours amongst the cover of rocks or macrophytes is most likely an adaptation to reduce the risk of

predation by visual predators, and the pattern of reduced use of open water habitats in the presence of brown trout is an acute response to the close proximity of the introduced predator. The difference in the nocturnal use of macrophytes and rocks when trout are present may be related to differences in feeding opportunities or success within these habitats.

Introduction

Animals often respond to the presence of predators by altering their use of habitats or reducing their activity (Jacobsen and Perrow 1998; Reeb 1999; Nystrom et al. 2001; Jennions et al. 2003; Marquis et al. 2004). Although predation is a fundamental component of predator-prey interactions, identifying and understanding sub-lethal effects of predators on their prey is necessary for a more complete understanding of interactions between the predator and prey (Lima 1998). In freshwater systems, introduced piscivorous fishes have impacted native species in many ways, with direct predation and competition commonly responsible for declines in abundance and reductions in the range of small native fishes (Townsend and Crowl 1991; Crowl et al. 1992; Marsh and Douglas 1997; McIntosh 2000; Jackson et al. 2004). Frequently, little is known of the sub-lethal, behavioural impacts on native species. Behavioural responses of fishes to introduced predators may take the form of short-term behavioural changes, such as shifts in habitat use in response to a nearby predator, or adaptation, for those species which survive long enough in the presence of the introduced predator for this to occur. This former response, although on a smaller temporal scale, may still impact the native species by substantially interfering with other necessary

activities such as foraging and reproduction (Edge et al. 1993; McIntosh and Townsend 1994; Jennions et al 2003).

The introduction of brown trout to southern hemisphere waters has detrimentally impacted many native species, particularly galaxiid fishes (McDowall 2006).

Whether trout indirectly affect galaxiids by modifying their habitat use is unknown. *Galaxias auratus* is a threatened galaxiid fish naturally endemic to the turbid Lakes Crescent and Sorell on the Tasmanian Central Plateau. As with other galaxiid fishes in Tasmania, this species evolved in isolation from larger predatory fishes (Hardie et al 2006b), and is vulnerable to predation by brown trout, which were introduced into Lakes Crescent and Sorell in 1868 and are now its major predator (Stuart-Smith et al 2004). Despite being found to feed during both day and night-time (Stuart-Smith et al. 2006), there is some evidence to suggest its activity and habitat use does show a diel pattern. Hardie et al. (2006a) reported that in a small "insurance" population of *G. auratus* translocated to a clear-water, trout-free farm dam reservoir, the fish were more likely to be found in open water habitats during the night, while during daylight they appeared to be generally confined to heavily vegetated macrophyte beds. The objective of the present study was to experimentally test whether the increased predation risk associated with the close proximity of brown trout resulted in a short-term shift in this suggested diel pattern in the use of complex habitats by *Galaxias auratus*, in order to more clearly understand potential impacts of trout on this threatened species.

The habitat use of *G. auratus* could not be directly observed in Lakes Crescent and Sorell due to persistent high turbidity [approximately 100 Nephelometric

turbidity units (NTU) or greater at the time of the study]. Consequently, observation of the diel pattern in the use of complex habitats by *G. auratus* and the manipulation of brown trout presence was undertaken in the laboratory. This, however, allowed us to also examine whether diel patterns in habitat use differ depending on the type of complex habitat available. The two main types of complex habitat available to *G. auratus* in Lakes Crescent and Sorell are the macrophytes in the marshes, which are only available during high water, and areas of rocky substrate. Since habitat use is often associated with a trade-off between foraging opportunities and predation risk (sensu Werner et al. 1983; Lima 1998), we hypothesized that potential differences in foraging opportunities within these two habitat types may alter the relative importance of foraging in this trade-off for *G. auratus*, and therefore its use of these habitats under high predation risk.

Materials and methods

Galaxias auratus [range 81 - 97 mm total length (TL), $n = 30$] and brown trout (204 and 231 mm TL) were collected by backpack electrofisher (Smith-Root Inc. model 12-B) in Lake Crescent and transported to the laboratory in 100 L containers with aeration from battery-operated pumps. They were held in large acrylic tanks (1100 x 650 x 400 mm) prior to beginning the experiments, with brown trout and *G. auratus* held separately but in identical conditions.

Trials were conducted in a large rectangular opaque acrylic tank (1100 x 650 x 400 mm) with half of the bottom area covered by complex habitat [either rocks (collected from Lake Crescent; diameter ranging from approximately 100 mm to 250 mm) or artificial macrophytes (at 625 stems m⁻²)] and half left bare, with a

substrate consisting of a thin layer of sand glued to the acrylic. Artificial macrophytes represented *Triglochin procerum*, an important littoral macrophyte in Lake Crescent (Heffer 2003), and were constructed from strands of buoyant nylon rope long enough to reach the water surface, tied to a base of plastic lattice. Lighting consisted of fluorescent room lighting during the day, with dawn and dusk periods created by staggered timing of the lighting that lasted for 20-min before or after the lights were all switched on or off. Day length and temperature were maintained close to the conditions in Lakes Crescent and Sorell at the time the experiments were conducted (11 h and 14°C). Trials were run in random order and the water in the experimental tank was changed between each trial to eliminate the chance of *G. auratus* detecting a predator in trials without trout due to olfactory cues remaining in the water from previous trials.

Five randomly selected *G. auratus* and one brown trout (only in trials with the predator present) were added to the experimental tank 24 h prior the beginning of each trial and all filtration was turned off. Natural prey (*Austrochiltonia australis* collected from Lake Crescent) were added to the tank 10 minutes prior to the beginning of each trial at a density of approximately 700 m⁻², and were observed distributing themselves throughout the tank. The duration of the trials was 24 h. The position of *G. auratus* was monitored using an infrared video camera (constructed in the laboratory) and an infrared light source (250 W, also constructed in the laboratory), both mounted above the tank, and a Panasonic™ time-lapse video cassette recorder (model AG-6730). As Lakes Crescent and Sorell are turbid and this may affect the behaviour of *G. auratus*, we attempted to run the trials in water as turbid as possible without interfering with our ability to

determine the location of the fish. Preliminary trials revealed that a turbidity of 30-40 NTU (measured with an Analite™ 156 high sensitivity model nephelometer) permitted excellent images using the sensitive infrared equipment during both day and night, whilst still appearing turbid to the naked eye. Videos of the trials were sampled at 15 min intervals in addition to every 2 min for 14 min before and after “dawn” and “dusk”. The number of *G. auratus* in the open water was recorded at each of these times.

To examine the diel use of complex habitats by *G. auratus* and test the effects of predator presence and habitat type on this, a 2-way factorial design was used with complex habitat type (macrophyte cover or rock cover) crossed with trout (2 levels: present or absent). Four replicate trials were run for each combination of these experimental treatments. A priori we were interested in comparing each treatment combination with macrophytes and trout absent. Although the original intent was to model the number of fish in the complex habitat (rocks or macrophytes) as a continuous covariate with autocorrelation between successive observations included in the model, inspection of the data showed a clear division between night-time and day-time activity. Because of this, we used the mean number of fish in the complex habitat in each of day and night periods as the response variable, with the mean weighted according to the number of observations in each time period. Thus time of day (i.e. a two-level, fixed factor: night vs. day) was nested within the 2-way factorial treatment design.

A multi-stratum analysis of variance model was fitted using appropriate error terms (see Quinn and Keough 2002). Overall, the habitat \times trout \times time of day

interaction was highly significant, so after first testing whether there was a difference between night and day in the reference treatment of macrophyte cover without trout, the data were then analysed in terms of Δd , the number of *G. auratus* in cover during day minus the number of *G. auratus* in cover during the night. In the absence of trout, this difference was always positive (i.e. more of the galaxiids were in the complex habitat in daylight than at night). All pairwise comparisons of Δd were carried out using Westfall's simulation procedure for simultaneous confidence intervals which is more powerful than conventional procedures for unplanned multiple comparisons (Westfall 1997). Assumptions of homoscedasticity and normality of errors were checked using standard plotting procedures (Quinn and Keough 2002), and no transformations were required prior to analysis. All analyses were conducted using R 2.3.1 (R Development Core Team 2006) and Westfall's procedure was implemented in the multcomp package (Bretz et al. 2004).

Results

Galaxias auratus showed a distinct diel pattern in its use of complex habitats (Figure A1), with significantly more fish using the complex habitats during the day than at night ($F_{1,12} = 578.1$, $P < 0.005$). In the absence of brown trout, most *G. auratus* were found in the sheltered habitats during daylight (mean no. in macrophytes: 4.4; in rocks: 4.2) and left the sheltered habitats at night (mean no. in macrophytes: 1.6; in rocks: 1.3). Overall differences in the mean number of fish found in rocks and macrophytes in the absence of trout were not significant ($t = 0.45$, $P = 0.662$).

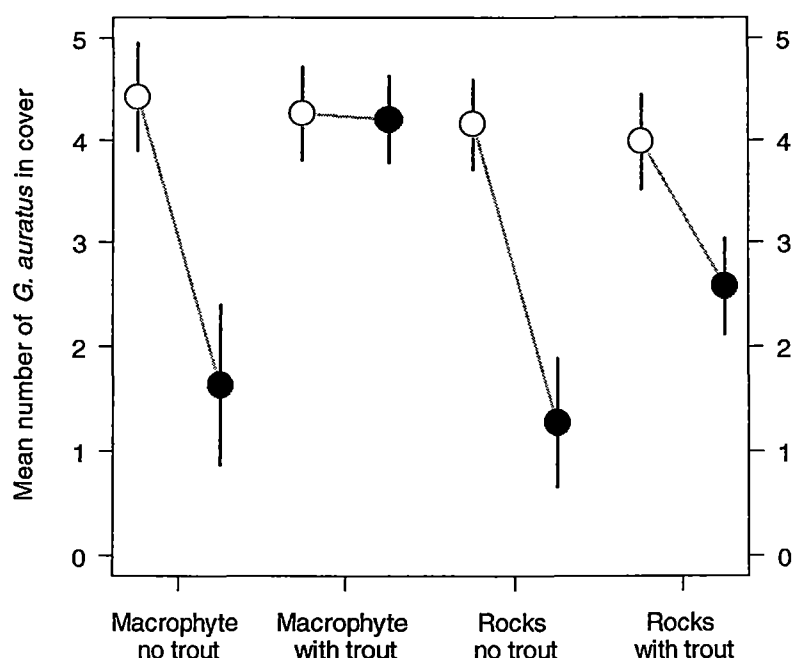


Figure 1 The mean number of *Galaxias auratus* found in cover during the day (open symbols) and night (black symbols) in each treatment combination. Day and night means within each treatment combination are joined by a grey line. Vertical lines are ± 1 standard error of the mean.

Trout affected the diel habitat use pattern of *G. auratus* by suppressing the nighttime use of open water substantially (Figure 1). This resulted in significant reductions in Δd for both complex habitat types (Table 1). The predator effect was greater when macrophytes provided cover than when rocks provided cover (Table 1). When trout were present, *G. auratus* showed a smaller difference in the use of cover between day and night (i.e. reduced Δd) much more in trials with macrophytes than in those with rocks (Figure 1). Thus, the effect of trout on *G. auratus* was essentially to reduce the magnitude of Δd and this effect was greater in macrophytes than in rocks. In all trials with trout, the trout tended to remain in

the open water much of the time, with rare excursions into the macrophytes or over the rocks.

Table 1 Pairwise comparisons of Δd values (i.e. the difference in the number of *G. auratus* in the complex habitat between day and night) between all treatment combinations. Δd_1 and Δd_2 are Δd values for the first and second named treatment combinations respectively in each row of the table. For example, the day – night difference in *G. auratus*’ use of macrophytes without trout present was greater by 2.7 (of five) fish than the day – night difference in macrophytes with trout present. Simultaneous confidence intervals for these differences are given in parentheses. *P* values are Bonferroni adjusted. MNT = macrophytes as cover and no trout, MT = macrophytes with trout, RNT = rocks as cover and no trout, and RT = rocks with trout present.

Treatment Comparison	$\Delta d_1 - \Delta d_2$	<i>t</i>	<i>P</i>
MNT - MT	2.7 (2.1, 3.3)	12.982	<0.001
MNT - RNT	-0.1 (-0.7, 0.5)	-0.448	0.969
MNT - RT	1.4 (0.8, 2.0)	6.594	<0.001
MT - RNT	-2.8 (-3.4, -2.2)	-13.430	<0.001
MT - RT	-1.3 (-2.0, -0.7)	-6.389	<0.001
RNT - RT	1.5 (0.9, 2.1)	7.041	<0.001

Discussion

The behaviour of *G. auratus* observed in this study confirms Hardie et al.’s (2006a) suggested diel pattern in the use of complex habitats. In the absence of brown trout, *G. auratus* remained concealed in the artificial macrophytes or rocks during the day, but spent far more time in open water and showed an increase in activity during the night. This pattern of behaviour is commonly observed for fishes under predation pressure from visual predators such as piscivorous fish or birds (Reebs 2002).

Although aiming to confirm this overall pattern of habitat use, the focus of this study was to test whether increased predation risk associated with the close proximity of an introduced predator affected the behaviour of *G. auratus*. We have clearly shown that the close presence of an adult brown trout results in a pronounced, acute behavioural response by *G. auratus*. In the laboratory, when trout were present, the proportion of time spent by *G. auratus* in the open water adjacent to either macrophytes or rocks was significantly reduced. Clearly the close proximity of trout, or the imminent threat of predation, largely restricted *G. auratus* to whichever complex habitat was available. Such an increase in the use of complex habitats in the presence of a predator has been observed for many animals including the house mouse (*Mus domesticus*: Dickman 1992) and numerous fishes (e.g. bluegill sunfish, *Lepomis macrochirus*: Werner et al. 1983; Eurasian perch, *Perca fluviatilis*: Persson and Eklöv 1995; Jacobsen and Berg 1998; roach, *Rutilus rutilus*: Bean and Winfield 1995; rudd, *Scardinius erythrophthalmus*: Bean and Winfield 1995; and rainwater killifish, *Lucania parva*: Jordan 2002). The modification of habitat use by *G. auratus* in this study is particularly important as it suggests that the impacts of brown trout on many galaxiids may go beyond predation and competition, with potential indirect impacts on feeding, growth and reproduction.

Predation risk and foraging success are usually highly habitat-dependent (Manatunge et al. 2000; Laegdsgaard and Johnson 2001; Fullerton and Lamberti 2006), so the behavioural response of *G. auratus* to brown trout is likely to alter its risk of predation and foraging success. The purpose of *G. auratus* response to

trout presence would likely be to reduce predation risk, and the effectiveness of this could be experimentally evaluated quite easily. It is still unclear, however, whether any reduction in foraging returns may result from the increased use of complex habitats. Werner et al. (1983) found that small bluegill sunfish, which switched from foraging in open water to the macrophyte habitat in the presence of a predator (largemouth bass, *Micropterus salmoides*), grew significantly less than bluegills feeding in the open water in the absence of the predator. Thus, it is possible that altered habitat use of *G. auratus* during times in which brown trout are near may similarly result in decreased feeding and reduced growth rates.

Obviously, an important consideration is how long the behaviour of *G. auratus* remains altered after a close encounter with brown trout. The duration of their response will clearly affect the magnitude of any negative affect of altered habitat use. Jennions et al. (2003) found that the length of the response by fiddler crabs to predation risk depended on aspects of the encounter such as proximity of the predator. More data are needed on the behavioural response of *G. auratus* to encounters with brown trout to determine the longevity of habitat use changes. Knowledge of the independent effects of habitat complexity and brown trout presence on feeding of *G. auratus* would also help give an overall impression of the sub-lethal effects of introduced brown trout on this threatened species.

The effect of trout on habitat use of *G. auratus* differed according to the type of habitat that was available. A greater use of open water during the night by *G. auratus* in trials with rocks and trout (as opposed to almost no use of open water in corresponding trials with macrophytes and trout), suggests that they may be

more willing to make themselves vulnerable to predation when this is the only complex habitat available. It is conceivable that there are differences in foraging opportunity or returns between these two habitats that may result in these observed differences. The visual field, and in addition *G. auratus*' access to interstices in which prey may hide, would be more restricted amongst rocky habitat such as that in Lakes Crescent and Sorell (and that used in our trials) than in macrophyte habitats. Experimental work on European perch (*Perca fluviatilis*) has found that their ability to forage in mussel-covered rocky habitat is limited (Dieterich et al. 2004), but that they are capable of foraging efficiently within dense stands of aquatic vegetation (Diehl 1988; Persson and Eklöv 1995). So, if foraging returns within the rocky habitat are comparatively poor, we suggest that the fish must consequently expose themselves to a greater risk of predation by actively searching for prey in the open water. Vehanen (2003) observed similar risk taking by hungry Atlantic salmon (*Salmo salar*). Conversely, foraging returns in the macrophyte habitat might be high enough to allow them to minimise predation risk by considerably reducing the amount of time they spend outside of the cover. A future experimental evaluation of *G. auratus*' ability to feed in macrophyte habitats would be essential to support this suggestion.

This study only considered the behaviour of adult *G. auratus* during late summer. We acknowledge that habitat use of fishes often changes seasonally (David and Closs 2003), but the timing of this study was specifically chosen to coincide with when feeding is at a maximum due to increased metabolism and the needs associated with gonad development (Hardie et al. 2004). At other times of the year the relative importance of predation risk in determining habitat use may be

greater, as the importance of feeding in this trade-off may not be as great. It has also been reported that habitat use changes during ontogeny for a number of fishes (Roussel and Bardonnnet 1999; Whitehead et al. 2002; Byström et al. 2004; Imre and Boisclair 2004), and this is also the case for *G. auratus*. We only considered adult fish, from 1+, as the larvae and young juveniles of this species are wholly pelagic and do not utilize complex habitats until at least 4-5 months of age (Hardie et al. 2004). Additionally, it has been suggested that behaviour that minimizes predation risk is more evident in larger or older individuals (Clark 1994; Byström et al. 2004; Imre and Boisclair 2004), so using larger individuals was considered more appropriate for examining the behavioural response of *G. auratus* to an introduced predator.

The littoral marshes currently represent the only significant macrophyte habitat in Lakes Crescent and Sorell, making the availability of the macrophyte habitat to *G. auratus* highly dependent on water levels. The availability of rocky substrate is also water level dependent in Lake Crescent, with the lake bed mainly consisting of silt and clay at low water levels. Thus manipulation of water levels can potentially interfere with ecological interactions of *G. auratus*, and this study provides an example of how the way in which *G. auratus* reacts to introduced brown trout could be influenced by the water level through changes to habitat availability. If the water level drops so that the marshes are left dry, then *G. auratus* has only rocky habitat available, a situation in which they may potentially spend more time in open water, thus increasing their vulnerability to predation. An attempt to determine any differences in relative predation risk of *G. auratus* in both habitat types would be useful and may provide extra support to this

hypothesis, and reinforce the importance of high water levels for *G. auratus* through the effect on habitat availability.

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Appendix

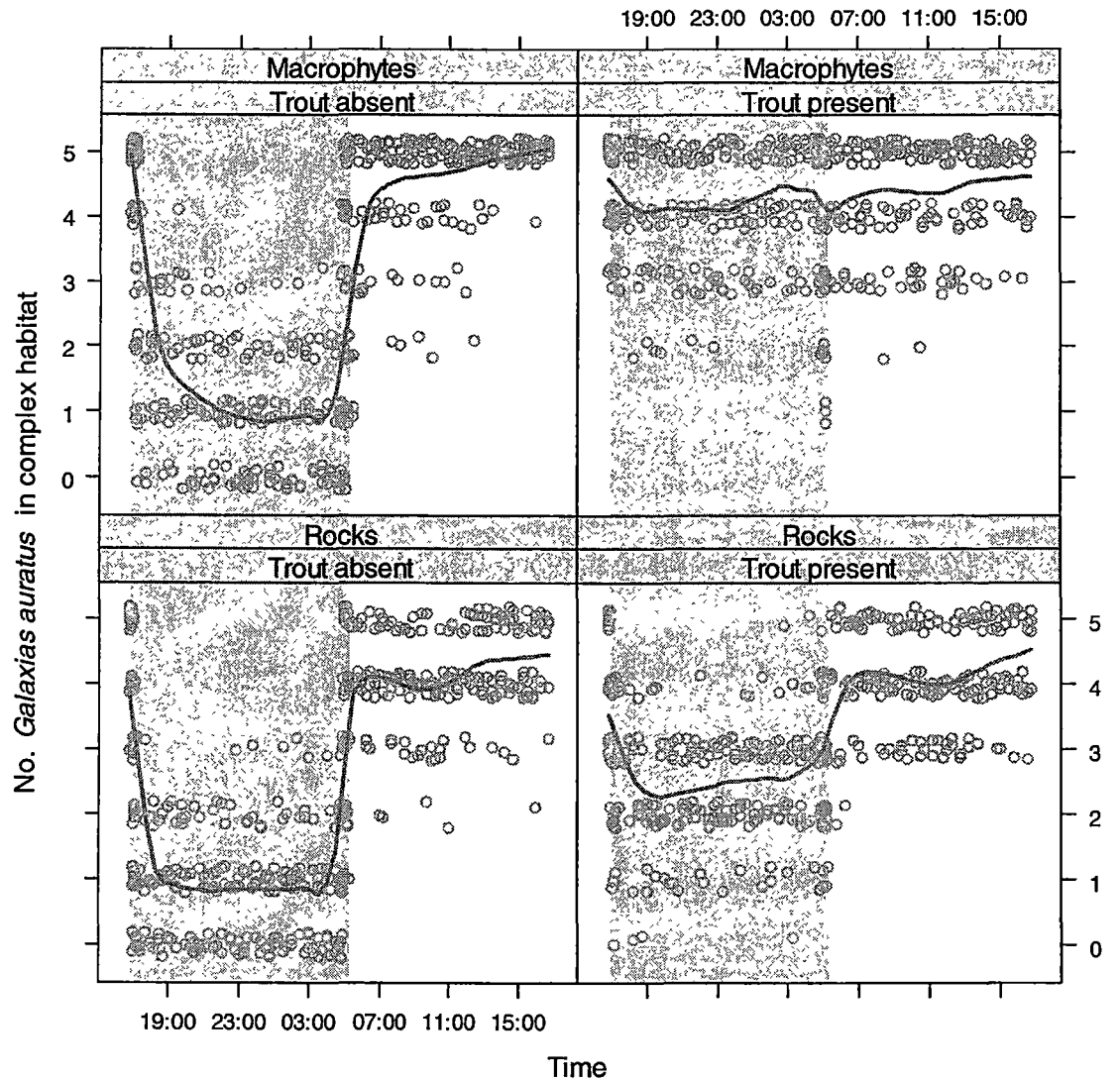


Figure A1. Number of *Galaxias auratus* in the complex habitat for each time interval observed on the video recording. Values have been jittered on the ordinate to avoid over plotting. The trend line is lowess-smoothed number of fish, and the dark vertical bar denotes hours of darkness. Note the abrupt change in the number of fish in the complex habitat around dusk and dawn in trials with trout absent.

Chapter 4: Are there foraging costs associated with the use of complex habitats by a lentic galaxiid fish?

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Abstract

The habitat used by animals plays an important role in their interactions with predators and prey. By using complex habitats such as areas of dense macrophyte cover in response to elevated predation risk, small fishes may reduce their foraging success. Because the threat of predation by introduced brown trout increases the use of complex habitats by the threatened *Galaxias auratus* (Johnston), we experimentally examined its foraging in different habitats to estimate indirect impacts of brown trout presence. The lakes in which *G. auratus* lives have recently become more turbid, so the experiment was also conducted under different turbidity levels. Laboratory feeding trials in which planktonic and epibenthic prey were simultaneously offered to *G. auratus* in the presence or absence of artificial macrophytes and at three turbidity levels (0, 50 and 100 NTU), revealed that its overall foraging success was unaffected by habitat complexity, however, in trials with artificial macrophytes, *G. auratus* consumed a greater proportion of planktonic prey than in the absence of artificial macrophytes. Neither overall foraging success nor prey selection by *G. auratus* was affected by

high turbidity, indicating that water clarity does not appear to directly negatively impact its feeding. The switch in prey types would probably not be detrimental to *G. auratus* in the long-term, and thus it appears that there is no substantial feeding cost associated with its increased use of complex habitats. It could, however, affect lower trophic levels in the lakes to which it is endemic.

Introduction

The structural complexity of habitats is an important physical characteristic of shallow lakes, and can have significant impacts on predator - prey interactions (Crowder and Cooper 1982; Gilinski 1984; Swisher *et al.* 1998; Wilhelm *et al.* 2002; Warfe and Barmuta 2004). Usually, the foraging success of fish predators decreases with increasing habitat complexity (Coull and Wells 1983; Anderson 1984; Bertolo *et al.* 1999). Thus, small fishes, which often use complex habitats such as macrophyte stands to reduce their risk of predation (Bean and Winfield 1995; Hölker *et al.* 2002; Reeb 2002), may incur a cost in terms of foraging success if their ability to effectively locate and capture prey is impaired by the physical structure of the habitat. Therefore, examining a fish's ability to forage in complex habitats is necessary to evaluate potential negative indirect effects of predators.

Galaxias auratus is a locally abundant but threatened galaxiid fish that is endemic to Lakes Crescent and Sorell, Tasmania. It is important to determine the foraging habits of *G. auratus* in structurally complex habitats, because it spends more time in these habitats when its major predator, introduced brown trout (*Salmo trutta* L.), is in close proximity (R.D. Stuart-Smith, unpublished data). An additional

potential impact on the foraging of this fish is that both the lakes in which *G. auratus* lives have become highly turbid over the past decade owing to lake levels being reduced by prolonged drought and increased abstraction for irrigation (Uytendaal 2003). The potential deleterious impacts of increased turbidity are, therefore, a clear concern for the management of this species. So, although many galaxiid species are able to feed non-visually (Bonnet *et al.* 1989; McDowall 1997; David and Closs 2003), it is also important to identify whether turbidity affects the foraging success of *G. auratus*.

Both complex habitats and high turbidity may alter the vulnerability of various prey types due to differences in contrast (De Robertis *et al.* 2003) and behaviour (Persson and Eklöv 1995; Starry *et al.* 1998). If changes in habitat complexity or turbidity result in prey switching, this can affect a fish's growth rate and possibly fecundity or survival. If prey switching is density-independent, it can be non-stabilizing and possibly lead to changes in invertebrate prey communities through selective predation (Murdoch and Bence 1987; Kornijów *et al.* 2005). Thus, identifying situations in which prey switching occurs is important for understanding whether consequences of habitat use and elevated turbidity may also extend to lower trophic levels.

The primary aim of this study was to experimentally determine whether the overall foraging success of *G. auratus* is affected by the structural complexity of macrophytes and by high turbidity. By providing its two most important prey types (epibenthic and planktonic; Stuart-Smith *et al.* 2006) in experiments, a

second aim was to assess whether prey selection by *G. auratus* is also influenced by these important physical characteristics of shallow lakes.

Materials and methods

Presently, Lakes Crescent and Sorell contain only three main habitat types which represent three different degrees of structural complexity: macrophytes (sparse littoral vegetation and dense cover in wetlands at high water levels), areas of reef (low relief bedrock and boulders smaller than 0.3 m diameter, but up to 0.5 m), and areas of barren silt, without any structure. The most structurally simple habitat, the areas of silt substrate, contains very little in the way of cover for fish or prey, yet occupies the majority of the lakebed of Lake Crescent and extensive areas of Lake Sorell and is used by *G. auratus* for feeding during the nighttime (Stuart-Smith et al. 2006). We assessed *G. auratus*' feeding ability in the most simple and the most complex habitats (the featureless silt and the macrophytes).

Two prey types were used in trials: the epibenthic amphipod, *Austrochiltonia australis* (Ceinidae), and the planktonic cladoceran, *Daphnia carinata*. These species were chosen because they have been the dominant prey items (both numerically and volumetrically) in the diet of *Galaxias auratus* in recent years (Stuart-Smith et al. 2006). They are also found in all three habitat types in Lakes Crescent and Sorell; *A. australis* has been super-abundant in Lakes Crescent and Sorell in recent years (mean densities of up to 13 300 m⁻²; Stuart-Smith et al. 2006), even over the featureless silt substrate in which they lack cover, and *D. carinata* are found in dense blooms throughout the lakes during the summer and

end up in the fringing wetlands during windy weather (Leon Barmuta, pers. comm.).

To determine the effects of habitat structural complexity and turbidity on the foraging success and prey selection of *G. auratus*, experimental tanks were set up with all combinations of two levels of habitat complexity (presence or absence of artificial macrophytes), three levels of turbidity [low = 1.32 ± 0.10 NTU (mean \pm standard error margin (SEM)), medium = 51.03 ± 1.42 NTU, and high = 97.31 ± 2.22 NTU] and presence or absence of *G. auratus*, which provided a control for natural prey mortality or inaccuracies of prey counts during the experiment. We conducted a power analysis on the portion of the design that just included *G. auratus* to determine the number of replicates needed in each treatment combination to detect an average squared interaction effect of one-quarter of the within-cell variance at $\alpha = 0.05$. Eight replicate trials of each treatment combination were used in this experiment as this was identified as sufficient (power = 0.858).

Galaxias auratus were captured from Lake Crescent ($n = 42$, mean total length (TL) = 114 mm, range = 84-142 mm) using a backpack electroshocker (Smith-Root Inc. model 12-B) and maintained in two large holding tanks (1100 x 650 x 400 mm) in the laboratory for a minimum of three weeks prior to use in trials. Prey used in trials were collected from the same lake and were sieved to ensure that similar sizes of both types (2 – 4 mm) were used in the experiment. Trials consisted of individual fish in opaque experimental tanks (350 x 210 x 260 mm). After a 48-h settling period without food, 150 (equivalent to high natural

densities) of each prey were added. Trials lasted for 3 h, as preliminary trials indicated that both this time period and the number of prey added were sufficient to allow enough consumption for analysis of selection (> 20% of prey offered; Peterson and Renaud 1989) without allowing satiation. At the conclusion of each trial, the fish were removed, measured (TL), returned to the large holding tanks and the remaining number of each prey in the experimental tanks was counted. Control trials (i.e. without fish) underwent an identical protocol.

Turbidity was manipulated by diluting or evaporating turbid water from Lake Crescent in 100 L tanks until the desired levels were obtained. Turbidity was then maintained in these large holding tanks by circulation produced by heavy aeration. Turbidity was measured with an Analite™ 156 high sensitivity model nephelometer. In the smaller experimental tanks, light aeration reduced settling of the sediment during the 48-h period prior to the beginning of the trials, but aeration was ceased immediately before prey were introduced, to eliminate current from affecting prey distributions. A second turbidity measurement was made at the end of every trial and while there was very little reduction in turbidity during the course of the trials, this measurement was used in analyses.

Artificial macrophytes simulated *Triglochin procerum*, a common macrophyte in the littoral zone of Lakes Crescent and Sorell (Heffer 2003), with stems at a density similar to that amongst an individual plant (900 stems m⁻²). They were constructed from strands of plastic packing tape bound together into small bunches and held to a suction cup by a rubber band; this allowed bunches to be separated at the end of each trial to remove and count remaining prey. Trials

without artificial macrophytes simulated areas of barren silt lakebed in Lakes Crescent and Sorell, which have no cover for fish or prey. Fluorescent lighting was maintained in the laboratory with a fixed photoperiod. As previous work has demonstrated that *G. auratus* feeds during both night and day in the field (Stuart-Smith *et al.* 2006), but more actively searches for food during times of low light (R.D. Stuart-Smith, unpublished data), trials were conducted during the last hour before and two hours following the lighting being switched off.

The total number of prey consumed in each trial was analysed by analysis of covariance (ANCOVA). To test for inaccuracies in counts between experimental treatments, a one-way ANCOVA with habitat structural complexity as a fixed factor and the measured turbidity in the trials as a continuous covariate was conducted on the number of prey not recovered in each trial in only those trials without fish (controls). Then, in the trials that included a fish, another one-way ANCOVA was used to analyse differences in total prey consumption between trials with and without artificial macrophytes, with both fish TL and the measured turbidity as covariates.

Prey selection by *G. auratus* was examined using the Chesson-Manly index (α_{CM} , Chesson 1983), which accounts for prey depletion (Manly 1985; Turnbull and Barmuta 2002). Values of α_{CM} were calculated for *Daphnia carinata* (values for *Austrochiltonia australis* are simply the complement) and were used as the dependent variable in the same combination of analyses as was used for the total prey consumption.

Results

From observations in preliminary trials, *Galaxias auratus* appeared to feed naturally in the experimental setup. In open water, they swam slowly above the substrate and actively searched for prey. Short swimming bursts were made to consume detected prey. This meant that they took prey both from the water column and from near the surfaces of the aquaria when prey that were disturbed by the fish's movement tried to escape. In artificial macrophytes, *G. auratus* adopted more of an ambush strategy, generally remaining stationary and lunging only after detecting moving prey.

Counts of remaining prey were reliable and independent of experimental treatment, with only $2.97 \pm 0.16\%$ (mean \pm SEM) of 300 prey not recovered at the end of each of the control trials (habitat complexity: $F_{1,44} = 0.88$, $P = 0.35$; turbidity: $F_{1,42} = 0.38$, $P = 0.54$; habitat complexity \times turbidity: $F_{1,44} = 0.30$, $P = 0.59$). Thus the omission of controls in further analyses was justified.

In the analysis of overall foraging success of *G. auratus*, the homogeneity of slopes assumption was satisfied ($F_{4,40} = 0.65$, $P = 0.63$, combined covariate interactions) and a reduced model was fitted without covariate interaction terms (Table 1). Neither the habitat structural complexity nor the turbidity level affected the *G. auratus*' overall foraging success. The total number of prey eaten in each 3-h trial ranged from 78.5 ± 6.9 (mean \pm SEM) in the medium turbidity level without artificial macrophytes to 107.5 ± 26.0 in the low turbidity level without macrophytes (Fig. 1). There was no effect of fish size on the number of prey consumed (Table 1).

Table 1. One-way ANCOVA of the effects of habitat complexity, turbidity and fish size on the overall foraging success of *Galaxias auratus* in feeding trials (insignificant covariate interactions were omitted for this analysis).

	MS	df	<i>F</i>	<i>P</i>
Habitat complexity	7.932	1	0.003	0.956
Turbidity	324.999	1	0.124	0.726
Fish TL	4413.598	1	1.689	0.201
Error	2613.431	44		

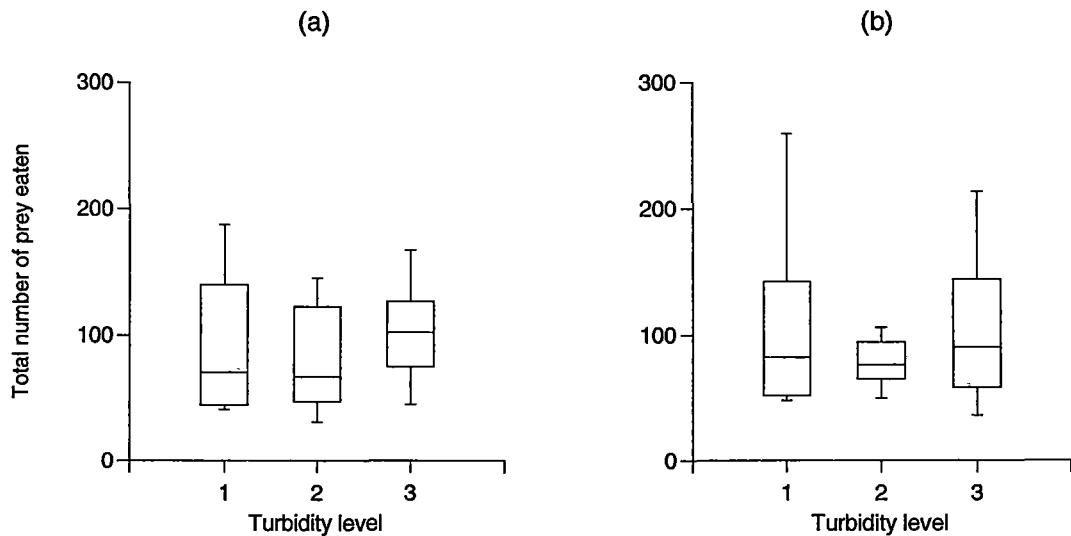


Fig. 1. Box and whisker plots showing overall foraging success of *Galaxias auratus* in feeding trials with artificial macrophytes (a) and trials without artificial macrophytes (b), and at different turbidity levels (1 = 1.32 ± 0.10 NTU (mean \pm SEM), 2 = 51.03 ± 1.42 NTU, and 3 = 97.31 ± 2.22 NTU).

Turbidity did not significantly affect prey selection, but the presence of artificial macrophytes did (Table 2). *G. auratus* selected the planktonic *D. carinata* in trials with artificial macrophytes and *A. australis* in trials without artificial macrophytes (Fig. 2). Prey selectivity was apparently not influenced by fish size; however, diagnostic plots (i.e. Cook's D vs. Leverage; Quinn and Keough 2002) showed one strongly influential fish which, when omitted, resulted in better diagnostics

and a significant interaction between habitat complexity and fish TL ($F_{1,41} = 6.31$, $P = 0.016$). This effect was such that the value of α_{CM} increased with fish size in the simple habitat only, indicating that smaller fish in these trials consumed proportionally more *A. australis* than the larger fish (Fig 3). While it is possible that, with more replicates, this pattern would become more robust to the presence of the influential datum, there was no *a priori* reason to exclude the fish with high influence, and all covariate interactions were insignificant when included ($F_{4,40} = 1.95$, $P = 0.12$). We concluded, therefore, that there might be a weak tendency for preference for *Daphnia* to increase with fish length, but only in simple habitats.

Table 2. One-way ANCOVA of the effects of habitat complexity, turbidity and fish size on prey selection by *Galaxias auratus* in feeding trials (insignificant covariate interactions were omitted for this analysis).

	MS	df	<i>F</i>	<i>P</i>
Habitat complexity	1.820	1	56.79	<0.001
Turbidity	0.035	1	1.08	0.30
Fish TL	0.014	1	0.43	0.51
Error	0.032	44		

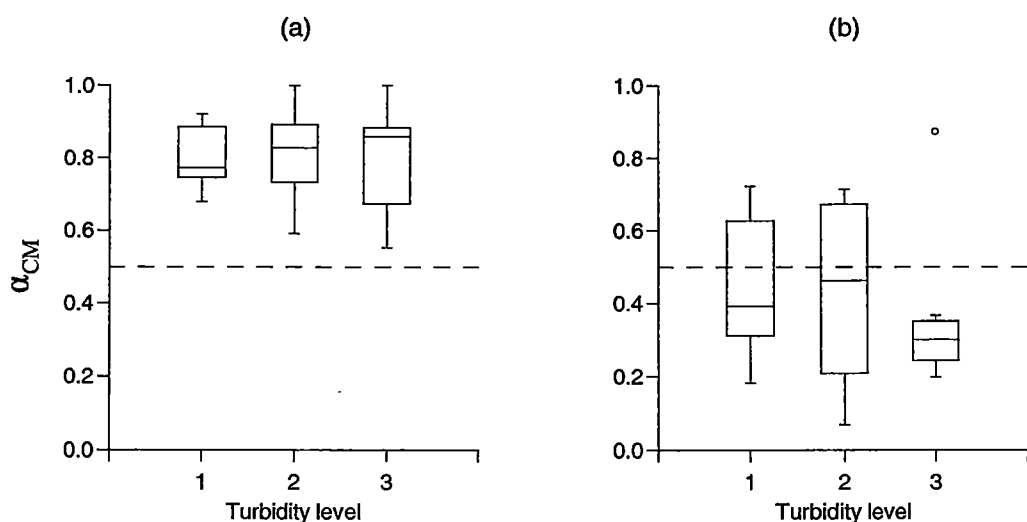


Fig. 2. Box and whisker plots showing prey selection by *Galaxias auratus* in feeding trials with artificial macrophytes (a) and trials without artificial macrophytes (b), and at different turbidity levels (levels same as in Fig. 1). The Chesson-Manly index (α_{CM}) was calculated for *Daphnia carinata* so values greater than 0.5 indicate preference, or greater selection for this prey, and values less than 0.5 indicate preference for the amphipod, *Austrochiltonia australis*. The lone data point not encompassed by the whisker in the high turbidity level in plot (b) is an outlier.

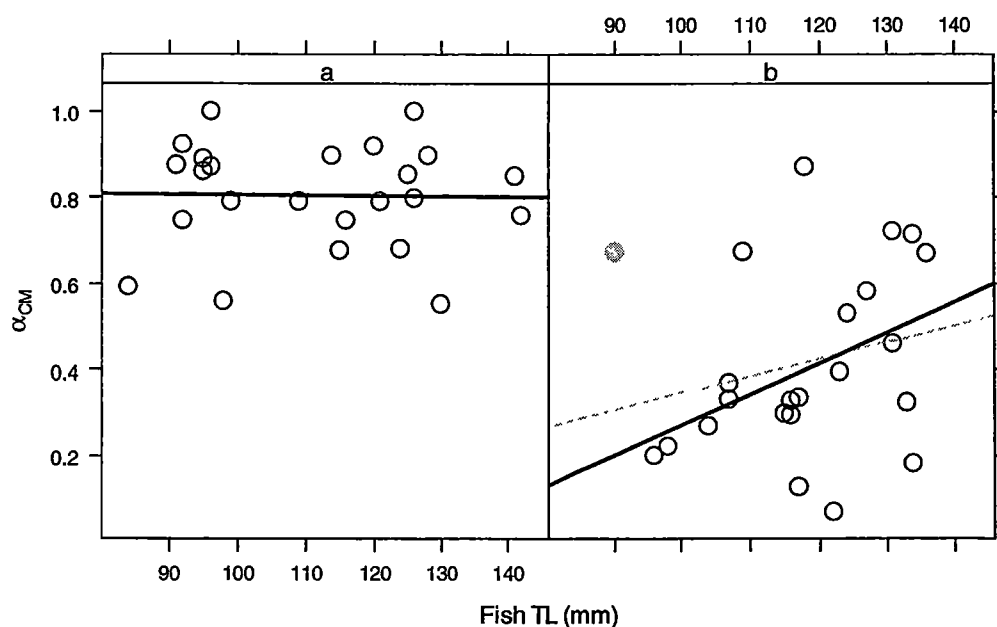


Fig. 3. Plots of prey selection (α_{CM}) versus fish TL in feeding trials with artificial macrophytes (a) and trials without artificial macrophytes (b), with regression lines superimposed. In the simple habitat (b) the broken grey regression line includes the influential observation indicated by the solid grey symbol.

Discussion

The results suggest that the use of structurally complex habitats, such as areas of dense macrophyte cover, by *G. auratus* may not reduce its foraging success. This is a significant finding as the threat of predation by introduced brown trout has been shown to dramatically increase the use of macrophyte habitats by this threatened species (Stuart-Smith *et al.* in review) and Hardie *et al.* (2006) have found that this species confines itself to macrophyte beds during the daytime in a trout-free insurance population in a small, artificial water storage. While we tentatively conclude that this fish is not deleteriously affected in terms of its foraging by living in macrophytes, by contrast, most research on other fishes has found that the structure of dense macrophytes reduces foraging success. For example, Diehl (1988) found the capture rates of bream (*Abramis brama*) and roach (*Rutilus rutilus*) were considerably reduced in artificial vegetation, and the results of Manatunge *et al.* (2000) were similar for *Pseudorasbora parva*. There are some species, however, that are capable of foraging effectively in macrophyte habitats. Winfield (1986) and Persson and Eklöv (1995) found European perch (*Perca fluviatilis*) to maintain prey capture rates with increasing habitat structure (macrophytes). We speculate that European perch and *G. auratus* are able to locate and capture prey in such habitats by using multiple cues including visual and non-visual stimuli.

Most studies on fish foraging in complex habitats, such as those of Diehl (1988) and Manatunge *et al.* (2000) have used only one prey type, eliminating the potential for the fish to switch to prey that is more easily located or captured in the complex habitat. Whether the apparent reduction in the feeding efficiency of these

species in complex habitats can be compensated for by switching to other prey taxa in the wild is unknown. Persson and Eklöv (1995) noted that the overall foraging success of juvenile European perch did not appear to be reduced when it was forced to use macrophytes, because its reduced consumption of planktonic prey was balanced by increased consumption of epiphytic macroinvertebrate prey. Similarly, in our study *G. auratus* was able to feed in macrophytes by switching from an epibenthic macroinvertebrate to a planktonic prey.

Apart from differences in relative abundances, habitat-dependent prey switching can often be the result of prey appearance or behaviour altering their vulnerability in different habitats. Savino and Stein (1989) suggested that the way in which prey use the structure to avoid predators plays a major role in determining foraging costs associated with the use of complex habitats by a predator. We propose that this was important in the pattern we observed, and that *G. auratus* was probably consuming more *Daphnia* in the trials with artificial macrophytes because the *Daphnia* were not able to use the smaller spaces between the macrophytes in which *A. australis* hid to their advantage. Starry et al. (1998) also found that freshwater amphipods were good at seeking refuge amongst the interstitial spaces of a complex habitat in the presence of a fish predator. *Daphnia*, however, would be more vulnerable to the sit and wait strategy that *G. auratus* appears to use in cover. McIntosh & Townsend (1995) described that *Galaxias vulgaris* took more prey from the water column when feeding in cover, but captured more prey that were disturbed from the bottom when actively moving about and feeding away from cover. Our results indicate that *G. auratus* feeds in a similar way to *G. vulgaris*, but that the switch in feeding methods associated with

the use of cover or open water results in different prey being eaten due to the different behaviours of the prey.

The reason for the weak pattern observed with smaller fish consuming proportionally more epibenthic prey than larger fish in the trials without artificial macrophytes is unknown. It is possible that it may reflect a slightly different foraging strategy by smaller fish or different physical capabilities. By swimming closer to the bottom smaller fish may disturb and locate more epibenthic prey, perhaps also encountering less planktonic prey at the same time. Our casual observations from preliminary trials could not detect this as the sides of the aquaria were opaque and observations were made from above. It is also possible that the smaller fish were physically more capable of extracting epibenthic prey that sought refuge in corners of the aquaria than larger fish due to a smaller head size. However, the same pattern was not observed in the trials with artificial macrophytes. In addition, from observations in preliminary trials it appeared that most of the amphipods that were consumed were actually taken whilst moving above the substrate, usually after being disturbed by the fish's movement. Small head size would be no advantage for such a feeding strategy. The possibility that the position in the water column differed for foraging fish of different sizes is more likely to explain the observed pattern, but further observational work would be required to identify whether this occurs.

Whether habitat-dependent prey switching has the potential to have a negative impact on *G. auratus* over time depends on prey diversity and availability in Lakes Crescent and Sorell and the nutritional value of the prey taxa being

consumed. Differences in prey availability between habitats are unlikely to negatively impact *G. auratus* as prey abundance and diversity is high in the macrophyte habitat of the littoral wetlands of these lakes (Hardie 2003), and *A. australis* has been super-abundant in all habitats, including areas of silt substrate (mean densities of up to 13 300 m⁻²; Stuart-Smith et al. 2006). While the energy content of amphipods and cladocerans are often similar to each other, with reported values of 3.6 – 6.9 cal g⁻¹ dry weight (DW) for freshwater amphipods (Bajchorov and Semenchenko 1977; Driver 1981; Bortkevitch *et al.* 1984), and 4.2 – 5.0 cal g⁻¹ DW for various *Daphnia* species (Wissing and Hasler 1971), the biomass of *A. australis* is greater than *Daphnia carinata* per individual (regressions of number and DW: *A. australis*: $\log_e(\text{DW}) = -0.9182 + 1.0362\log_e(\text{number})$, $r^2 = 0.95$, $p < 0.001$, $n = 20$; *D. carinata*: $\log_e(\text{DW}) = -1.8949 + 0.9860\log_e(\text{number})$, $r^2 = 0.93$, $p < 0.001$, $n = 20$; Stuart-Smith *et al.* 2006). Thus, *G. auratus* would need to consume more *Daphnia* than *A. australis* to receive the same energy gain. While we found no evidence for this in our experiment, stomach contents data from field caught fish suggest that this may occur in the wild, with no differences observed in the DW of stomach contents of fish that had consumed only *Daphnia* from those that had consumed only *A. australis* (Stuart-Smith *et al.* 2006). In light of data from field caught fish and the greater diversity and abundance of alternative prey in the macrophyte habitat in Lakes Crescent and Sorell, we suggest that the prey switching observed in our experiment is unlikely to negatively impact *G. auratus* in the long term.

Our experiment indicated that the feeding of *G. auratus* was not reduced by high turbidity. Whilst the feeding of many fishes has been found to be negatively

affected by high turbidity (e.g. bluegill sunfish, *Lepomis macrochirus*, Gardner 1981; rainbow trout, *Oncorhynchus mykiss*, Barrett 1992; brook trout, *Salvelinus fontinalis*, Sweka and Hartman 2001), results of the few studies to have examined the abilities of galaxiid fishes to feed in turbid water vary (Rowe and Dean 1998; Rowe *et al.* 2002). The nocturnal habits of many galaxiids (Glova and Sagar 1989a, 1989b; Whitehead *et al.* 2002; David and Closs 2003) and the well-developed mechano-sensory system (McDowall 1990) including an additional “accessory” lateral line in many species, including *G. auratus* (McDowall 1997), suggest that many fishes within this family do not rely solely on vision for locating prey and are likely to be capable of feeding in turbid water. From a study which examined the structure of the retina of various galaxiid species, Ali *et al.* (1990) suggested that *G. auratus* was probably adapted to a crepuscular existence. However, considering that *G. auratus* was capable of foraging equally as well in 100 NTU as in clear water with prey selection unaffected, which implies that it is efficient at using non-visual cues for feeding, it appears that it is also well adapted to a nocturnal existence.

We have shown that the current high turbidity of lakes Crescent and Sorell should not directly negatively affect the feeding of *G. auratus* (although it may well have indirectly impacted *G. auratus* through changes to prey communities), and it is even possible that high turbidity may benefit *G. auratus* by reducing the risk of it being preyed on by trout. A reduction in the number of *G. auratus* in brown trout stomachs was observed during years of increasing turbidity in Lakes Crescent and Sorell (Stuart-Smith *et al.* 2004) and it would be expected that the foraging success of brown trout would be reduced by the high turbidity due to its

predominant reliance on vision for feeding (Allan 1978; Ringler 1979; Glova *et al.* 1992; Heggenes *et al.* 1993). Rowe *et al.* (2003) also suggested that high turbidity might favour the survival of Koaro (*Galaxias brevipinnis*) in some New Zealand lakes by reducing predation pressure from trout.

Galaxias auratus appears to be a very capable forager of pelagic and epibenthic prey in turbid conditions and amongst dense macrophyte stands. The apparent habitat-dependent prey switching does not necessarily imply that the increased use of complex habitats in response to brown trout is directly having a negative impact on this species. The degree to which complex habitats reduce predation risk for *G. auratus* under field conditions is unknown, but will also be an important factor in determining the overall outcome of the modified habitat use by this species and thus requires further study. The observed prey switching is significant for the ecology of Lakes Crescent and Sorell, however, because the impact of *G. auratus* on prey populations is habitat-dependent, and brown trout may also be having indirect effects on invertebrate prey communities by modifying its habitat use.

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Chapter 5: The impact of an introduced predator on a threatened galaxiid fish is reduced by the availability of complex habitats

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Summary

1. The availability of complex habitats such as macrophytes may be vital in determining the outcomes of interactions between introduced predators and native prey. Introduced brown trout (*Salmo trutta*) have impacted numerous small native freshwater fishes in the southern hemisphere, but the potential role of complex habitats in determining the direct outcomes of brown trout – native fish interactions has not been experimentally evaluated.
2. An in-lake enclosure experiment was used to evaluate the importance of structurally complex habitats in affecting the direct impacts of brown trout on a threatened galaxiid fish. Five *Galaxias auratus* and a single brown trout were added to enclosures containing one of three different habitat types (artificial macrophytes, rocks, and bare silt substrate). The experiment also had control enclosures without brown trout. Habitat-dependence of predation risk was assessed by analysis of *G. auratus* losses to predation, and stomach contents of remaining fish were analysed to

determine if brown trout directly affect the feeding of *G. auratus* and whether this is also habitat-dependent.

3. Predation risk of *G. auratus* differed significantly between habitat types, with the highest mortality in enclosures with only bare silt substrate and the lowest in enclosures containing artificial macrophytes. This result highlights the importance of availability of complex habitats for trout – native fish interactions and suggests that increasing habitat degradation and loss in fresh waters may exacerbate the direct impacts of introduced predators.
4. Stomach contents analyses were restricted to fish in enclosures with artificial macrophytes and rocks, as most fish were consumed in enclosures with brown trout and only bare silt substrate. These analyses suggest that brown trout do not directly affect the feeding of *G. auratus* in complex habitats, but it is still unknown whether its feeding is reduced if complex habitats are unavailable.

Introduction

Of the many impacts introduced species have on native species, predation has the most direct and readily detectable effects. Declines in numerous freshwater fishes have been linked to predation by introduced species (Crown, Townsend & McIntosh, 1992; Marsh & Douglas, 1997; McIntosh, 2000; Jackson *et al.*, 2004; McDowall, 2006), but the factors that influence the interaction between introduced predator and prey are often complicated and not well understood. The availability of structurally complex habitats and the pattern of usage of these by native species, as well as predator and prey densities (Jones *et al.*, 1995;

Beauchamp *et al.*, 1999; Zambrano, Scheffer & Martinez-Ramos, 2001), feeding and activity patterns (Beauchamp *et al.*, 1999), and the availability and behaviour of other prey species (Schwartz, 2002; Woodward & Hildrew, 2002) can ultimately influence predation mortality of native species to introduced predators. Structurally complex habitats such as macrophyte beds, if available, may provide refuge for native species by interfering with the foraging of an exotic predator.

The direct impacts of introduced predators on native species may not only include predation, but also decreased feeding activity and consequently growth rates, and these impacts may also be determined by the habitat types used by the native species. Introduced predators can affect the feeding of native species directly by instigating increased vigilance and escape responses in the native species, potentially reducing feeding motivation and time (Van Buskirk & Yurewicz, 1998; Foam *et al.*, 2005; Sunardi, Asaeda & Manatunge, 2005). This may be habitat-dependent, with native species possibly able to feed more freely within the perceived safety of complex habitats, provided they can still locate and capture prey in these environments (Diehl, 1988; Manatunge, Asaeda & Priyadarshana, 2000).

As well as those associated with introduced species, additional impacts on native species result from habitat degradation and loss, which are increasingly occurring globally due to anthropogenic impacts such as water level manipulation and severe eutrophication (Riis & Sand-Jensen, 2001). Macrophyte beds are particularly vulnerable to such impacts, with loss of littoral wetlands and in-lake macrophyte beds common in lakes that are used as water supplies for town water,

irrigation, or hydroelectricity (Pyrovetsi & Papastergiadou, 1992; Hellsten *et al.*, 1996) and a switch to phytoplankton-dominated primary production also increasingly evident in shallow lakes world-wide (Hilt *et al.*, 2006). Such changes are of particular concern due to the importance of habitat type in influencing predator-prey interactions. The interactive effects of introduced predators and the reduction or loss of complex habitats like macrophyte beds may be critically detrimental for threatened species, with a potential side effect of anthropogenic (and some natural) disturbances being that the impacts of introduced predators may be exacerbated.

The galaxioids are a group of fishes that have recently been labeled as particularly at risk, and have suffered severely from introductions of exotic species (McDowall, 2006). Little is known, however, of present ecological factors that influence their vulnerability to exotic species. Much of the existing research on these fishes has been undertaken in lotic systems, and there is a need for research on the ecology of lacustrine species, for which habitat diversity may be greater and habitat type has greater potential to interact with the impacts of introduced species (Wissinger, McIntosh & Greig, 2006).

We investigated habitat-dependence of predation risk of a threatened, lentic galaxiid fish to an introduced predator in field enclosures. The use of complex habitats, particularly macrophytes, by *Galaxias auratus* (Johnston) increases substantially in the presence of introduced brown trout (*Salmo trutta* L.) (Stuart-Smith, White & Barmuta, 2007a), so we hypothesized that use of these habitats is likely to decrease its risk of predation to this introduced predator. The availability

of macrophyte habitats to this galaxiid has been reduced in recent times, yet the importance of macrophytes for its interactions with trout has not yet been demonstrated. In a previous experiment, we have shown that the feeding ability of *G. auratus* is not compromised in structurally complex habitats (Stuart-Smith, Stuart-Smith, White & Barmuta, 2007b) and, in this way, brown trout are not indirectly influencing the feeding success of this small fish. However, a secondary objective of this study was to examine how brown trout might directly influence *G. auratus*' feeding and whether this influence differs depending on the habitat type occupied by *G. auratus*.

Materials and methods

Study species and site

Galaxias auratus is a relatively large galaxiid (max total length, TL ~240 mm, but more commonly to 140 mm), which is endemic to the interconnected Lakes Crescent and Sorell on the Tasmanian Central Plateau (c. 42° 5' S; 147° 10' E) and is listed as 'rare' under the Tasmanian *Threatened Species Protection Act* 1995, and 'vulnerable' under the national *Commonwealth Environment Protection and Biodiversity Conservation Act* 1999 due to restricted distribution. It is an opportunistic forager, with adults eating a variety of aquatic and terrestrial invertebrates, but most often consuming epibenthic crustaceans, insect larvae and plankton when available (Hardie, Barmuta & White, 2004; Stuart-Smith, Barmuta & White, 2006). Brown trout were introduced into Lakes Crescent and Sorell in 1868 as a recreational fishing target and are now the major predator of *G. auratus* (Stuart-Smith, Richardson & White, 2004). The lakes also contain smaller

numbers of rainbow trout (*Oncorhynchus mykiss* Walbaum), short-finned eel (*Anguilla australis* Richardson) and European carp (*Cyprinus carpio* L.).

Lakes Crescent and Sorell have experienced significant physical changes during the last decade. Low rainfall and abstraction for irrigation (both lakes have been artificially raised since the 1830's and have been regulated for downstream irrigation purposes) have resulted in prolonged low water levels and a substantial increase in turbidity. The resulting changes to habitat availability for *G. auratus* have included the almost complete loss of once extensive in-lake macrophyte beds, and the recent water level regime has left the extensive littoral wetlands of the lakes dewatered for extended periods. Habitat mapping has revealed that not only is the macrophyte habitat now largely confined to the shallow wetlands, but that in Lake Crescent, the rock substrate is also restricted to the littoral zone (Hardie, 2003). So at low water levels in this lake, both the macrophyte and rocky habitat become unavailable, leaving much of the lakebed barren silt. The recent shift in availability of the wetland macrophyte habitat and rocky substrate, as indicated by the lake levels below which they are left dry or disconnected from the lakes, is shown in Fig. 1. It is suspected that the lost in-lake macrophyte beds and the now typically unavailable macrophyte habitats in the wetlands were important for the ecology of *G. auratus*, including potentially mediating their interactions with brown trout, but no research has been undertaken to examine this.

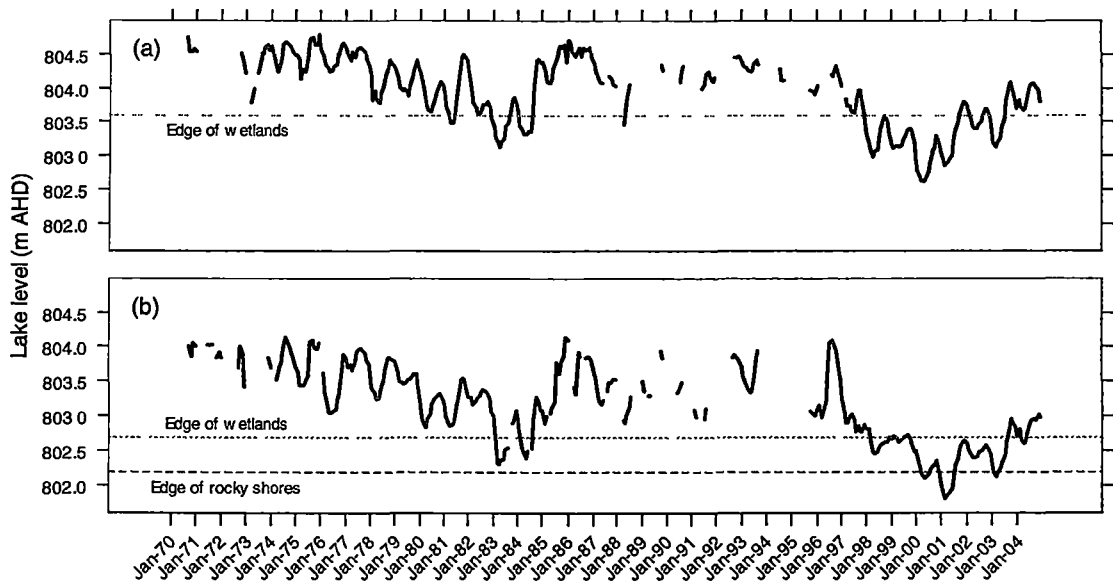


Fig. 1 Historic lake levels in Lake Sorell (a) and Lake Crescent (b), and the levels at which the wetlands become disconnected in both lakes and the rocky shores are left dry in Lake Crescent (Figure prepared by S. Hardie, unpub data).

Experimental design and set-up

A field enclosure experiment using a randomized complete block design was used to test whether habitat type affects predation mortality of *G. auratus* to brown trout and possible effects of brown trout on foraging by *G. auratus*. Three habitat types representing the major habitats present in Lakes Crescent and Sorell (two artificial habitats representing cobble rock substrate and macrophytes, and natural bare silt) were crossed with the presence and absence of trout (controls). Each combination was replicated twice in each block (time was a blocking factor), with the experiment replicated three times in January and February 2005.

Twelve cylindrical enclosures constructed from 6 mm knotless “honeycomb” mesh, supported by three hoops (one each at the bottom and top and one in the middle made from 12 mm PVC conduit) were fastened in place using four star pickets on silt substrate in a sheltered bay in Lake Crescent in water depth of approximately 0.9 m. Dimensions were 1.75 m diameter, 1.20 m height and a volume of 2165 L (at a water depth of 0.9 m). Artificial macrophytes were constructed from lengths of buoyant nylon rope tied to a base of plastic lattice (800 x 800 mm) at a density of 625 stems m⁻², with a structure similar to an important littoral macrophyte in Lake Crescent, *Triglochin procerum* (Heffer, 2003).

A feature of the structure of cobble rock substrate in Lakes Crescent and Sorell that we considered important is the variable size of interstices such that there are refuges for *G. auratus* from adult brown trout and refuges for invertebrate prey from *G. auratus*. We represented this in a replicable manner using 800 x 800 mm sheets of Laserlite[®] (corrugated plastic) (Bayer AG, Leverkusen, Germany), glued on top of each other (seven layers) in a consistent manner to achieve a range of interstitial sizes (none accessible to adult brown trout). The four replicates of each of these two artificial habitat types were randomly allocated to enclosures (one per enclosure, occupying approximately 30% of the bottom area of the enclosure) and left submerged in Lake Crescent for four weeks before commencement of the experiment to allow colonization by natural prey populations. The remaining four enclosures were designated as silt substrate and were left bare.

Five *G. auratus* (overall mean TL = 86 mm, range 67 – 122 mm) were added to each enclosure 24-h prior to the commencement of each block to allow them to become accustomed to the conditions before the trials started. One adult trout was also added to appropriate enclosures the next day (overall mean TL = 441 mm, range 355 – 530 mm). The density of *G. auratus* used was comparable to that observed in littoral areas of Lake Crescent (R.D. Stuart-Smith, unpublished data); however the trout density was higher in the experiment due to the constraints of an enclosure experiment. All *G. auratus* were captured by backpack electrofisher (Smith-Root Inc. model 12-B, Vancouver, WA, U.S.A.) and were weighed (to nearest 0.01g) and measured (to nearest mm) before being stocked in enclosures. The whole process from fish capture to stocking was never more than 90-min. Brown trout were captured in Fyke nets set overnight and were introduced immediately after collection.

After 4 days, all *G. auratus* were removed, measured and weighed again and immediately killed by anaesthetic overdose (benzocaine 300 mg L⁻¹). In the laboratory, stomachs were dissected from fish and both fish and stomach contents were dried separately (60°C > 96-h and > 48-h, respectively) and weighed. Relative stomach contents weight (*F*) was calculated for each fish using equation 1:

$$(1) \quad F = \frac{G}{D \times 1000}$$

where *G* is its stomach contents weight (mg DW) and *D* is its DW (g).

Analyses

Mortality data were analysed by two-way ANCOVA with habitat type and date (block effect) as independent variables, brown trout TL as a covariate, and the number of *G. auratus* eaten by the trout as the dependent variable. Enclosures not containing trout were excluded from this analysis, as there was no mortality in the absence of brown trout. As it has been shown that *G. auratus* feeds throughout the day without any significant peaks in stomach contents weights (Stuart-Smith *et al.*, 2006), stomach contents of fish at the end of the trials were used as a point sample indication of feeding. Unfortunately, stomach contents data were unbalanced due to fish lost to predation in enclosures with brown trout, with very few fish remaining in enclosures without the artificial macrophytes or rocks (i.e. those designated “silt”). Consequently, data from enclosures with the silt habitat type were omitted and remaining data were \log_e transformed and analysed by 3-way ANOVA with predator presence (trout present or absent), habitat type (rock or macrophyte) and block as fixed factors and $\log_e F$ as the dependent variable. For both sets of analyses, Tukey’s post hoc test was used to determine which treatment combinations differed from each other when significant effects were found.

Results

Habitat type had a significant effect on predation mortality of *G. auratus*, but no differences occurred due to the size of the trout or the date the experiment was run on (block effect). There was also no significant interaction among experimental treatments (Table 1). The greatest loss of *G. auratus* to predation by brown trout was in enclosures with only silt habitat (i.e. no complex habitat available. Fig. 2).

Enclosures containing artificial rock substrate had the next greatest predation mortality, but this was not significantly less than those enclosures with silt. Enclosures containing artificial macrophytes had the least predation mortality, which was significantly less than both other habitats. The effect of the date (block effect) was not significant.

There were also no statistically significant differences in stomach fullness of *G. auratus* between enclosures containing trout and those without, or between enclosures with artificial macrophytes or rocks (Table 2). More importantly, there was no significant interaction between the effects of trout presence and habitat type on the stomach fullness of *G. auratus* (Fig. 3). The only significant term was the interaction between trout presence and the date (block effect), which indicated that there was an effect of trout on the stomach fullness of *G. auratus*, but this only occurred in the first block of replicates (Fig. 4). On this occasion, the mean relative stomach contents weight of *G. auratus* in enclosures without trout was more than double that of *G. auratus* in enclosures with trout.

Table 1 Two-way ANCOVA of the effects of habitat type, date (block effect) and brown trout TL (covariate) on the predation mortality of *Galaxias auratus* in enclosures.

	MS	df	<i>F</i>	<i>P</i>
Habitat	17.102	2	14.530	0.002
Date	0.155	2	0.132	0.878
Habitat × Date	0.414	4	0.352	0.836
Trout TL	0.084	1	0.071	0.797
Error	1.056	8		

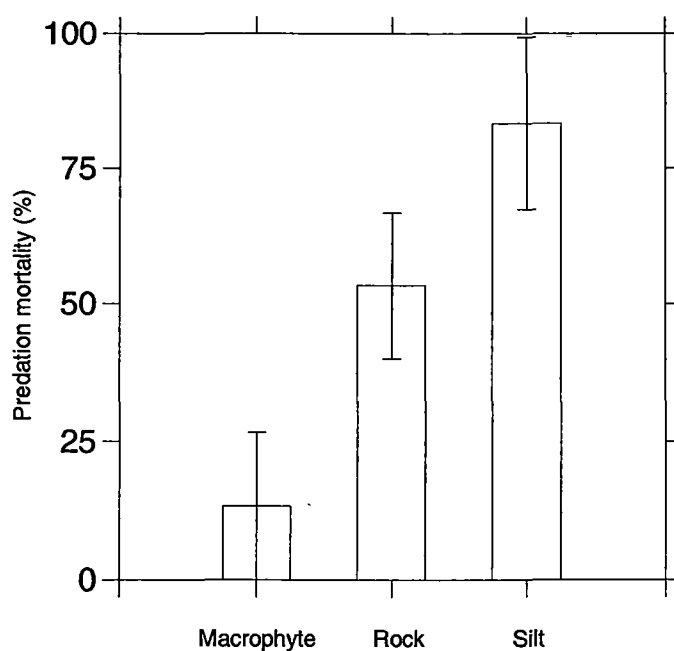


Fig. 2 Mean predation mortality (\pm 95% CL) of *Galaxias auratus* to brown trout in enclosures containing different habitat types. Enclosures containing macrophytes were significantly different from those with rocks or silt.

Table 2 Three-way ANOVA of the effects of trout, habitat type and date (block effect) on the relative stomach contents weights of *Galaxias auratus* from enclosures.

	MS	df	F	P
Trout	0.426	1	0.702	0.404
Habitat*	0.266	1	0.439	0.509
Date	0.068	2	0.112	0.894
Trout \times Habitat	0.003	1	0.005	0.944
Trout \times Date	2.622	2	4.324	0.016
Habitat \times Date	0.090	2	0.149	0.862
Trout \times Habitat \times Date	0.579	2	0.955	0.389
Error	0.606	87		

*Due to insufficient sample sizes in enclosures with silt habitat, only macrophyte

and rock habitats were analysed

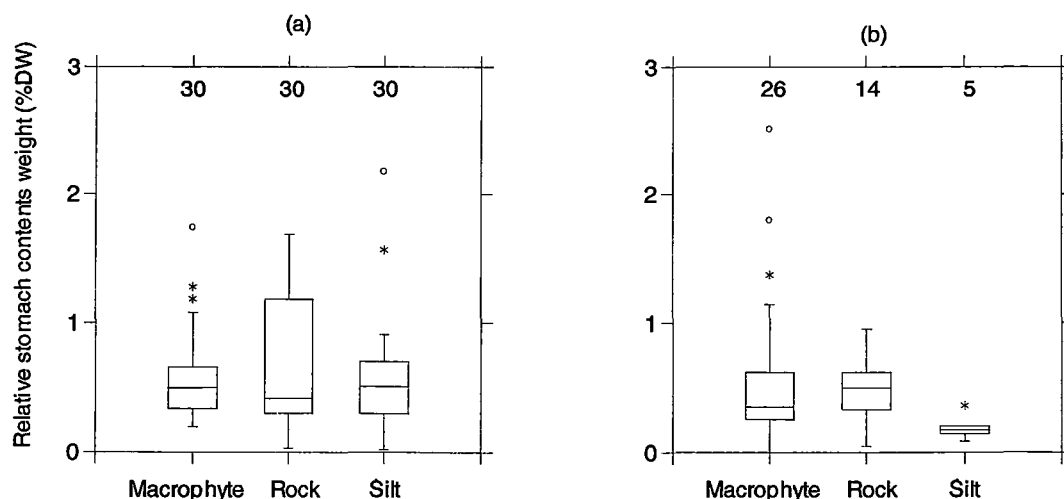


Fig. 3 Box and whisker plots of relative stomach contents weights of *Galaxias auratus* from enclosures containing different habitat types (a) without trout, and (b) with trout. Symbols outside whiskers represent outliers, and corresponding sample sizes are given above each box. Note that enclosures with only silt substrate were excluded from the analysis due to the small sample size.

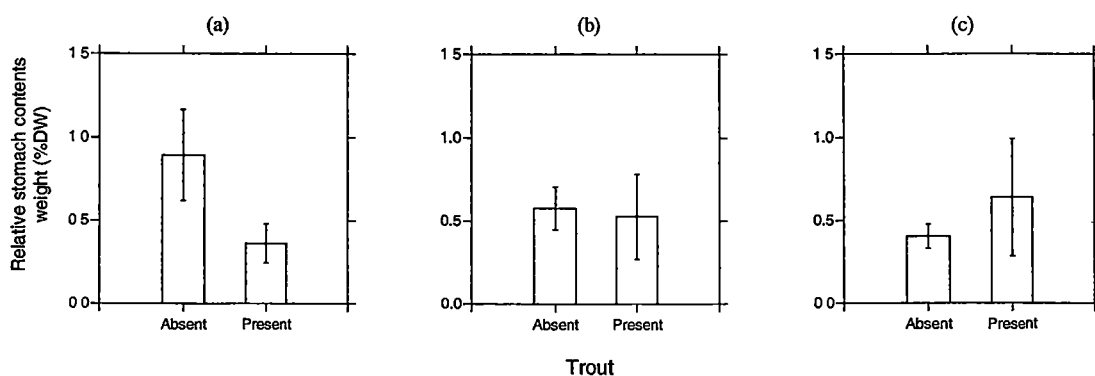


Fig. 4 Mean relative stomach contents weights (\pm 95% CL) of *Galaxias auratus* from enclosures with and without brown trout from (a) block 1 (12 – 15 January 2005), (b) block 2 (30 January – 2 February 2005), and (c) block 3 (7 – 10 February 2005). The only significant difference was in block 1.

Discussion

The field enclosure experiment clearly demonstrated that the risk of predation by brown trout is dependent on the habitat type available to *Galaxias auratus*. The availability of structurally complex habitats such as artificial macrophytes, and to a lesser extent the artificial rocky substrate considerably reduced predation mortality of *G. auratus*, whereas predation mortality was very high when no refuge habitat was available. Studies on other fishes have shown predation risk to be reduced in a range of complex habitat types including vegetated areas (Savino & Stein, 1989; Stunz & Minello, 2001; Snickars, Sandström & Mattila, 2004) and areas of rock or coral (Almany, 2004), and predation risk to be high in open habitats (Stunz & Minello, 2001; Belanger & Corkum, 2003). Complex habitats often reduce predation risk because they interfere with location and capture of prey by the predator (Heck & Thoman, 1981; Dionne & Folt, 1991) and provide areas of shelter for the prey that are inaccessible to the predator (e.g. holes in a coral reef; Almany, 2004).

Predation risk was lower in the artificial macrophytes than the artificial rocky substrate, despite the fact that the brown trout could potentially penetrate all areas of the macrophytes, while the rocky substrate contained interstices that provided complete refuge for *G. auratus*. This difference in predation risk between these two habitats is probably related to the way in which *G. auratus* uses them. The diel pattern of habitat use by *G. auratus* has been found to differ between these habitats (see Stuart-Smith *et al.*, 2007a), with almost exclusive use of macrophytes throughout both the day and night in the presence of brown trout. When only rocky substrate is available, however, *G. auratus* emerges from the

cover during the night and spends time in open water adjacent to the rocks, a pattern evident in the absence of the introduced predator. The structure of macrophytes often significantly interferes with foraging success of piscivorous fish (Savino & Stein, 1989; Persson & Eklöv, 1995) and the observed protection of *G. auratus* afforded by this habitat could be expected when *G. auratus* occupies this habitat during both day and night. Despite gaining complete refuge from predation when using rocky habitat, however, still using open water during the night leaves it relatively more vulnerable to predation during this period. Although brown trout are visual predators and pose a greater predation threat from dawn through to dusk (Allan, 1978; Ringler, 1979; Glova, Sagar & Näslund, 1992), they are still capable of feeding during the night (Heggenes *et al.*, 1993). The potential reasons for the differences in diel use of these two habitats are discussed by Stuart-Smith *et al.* (2007a). It is likely, however, that this habitat-dependent behaviour of *G. auratus* may be a determining factor in the observed habitat-dependent differences in predation risk. It appears therefore, that predation risk of *G. auratus* to brown trout in Lakes Crescent and Sorell may be influenced both by habitat availability and its patterns of use of these habitats. This highlights that the impacts of introduced species may not only be altered by the availability of certain habitat types for native species, but that the manner in which these habitats are used as refuge and for foraging is also particularly important.

Although the results of the stomach contents analysis did not provide clear evidence of a direct impact of brown trout on the feeding of *G. auratus*, we suggest that there may have been a habitat-dependent effect of trout on the feeding of *G. auratus*, but that our experiment was not able to clearly identify this.

Not detecting an effect was possibly an artefact of our experimental design, as we were unable to test for reduced feeding in enclosures with only bare silt substrate due to the low sample sizes that resulted from the higher predation mortality in these enclosures. Relative stomach contents weights of the few *G. auratus* that were remaining in these enclosures were very low, whereas the values from *G. auratus* in enclosures containing artificial macrophytes and rocks were similar to those found in fish sampled from Lakes Crescent and Sorell at a similar time of year (Stuart-Smith *et al.* 2006). It would be expected considering such high predation risk that all *G. auratus* in enclosures without artificial macrophytes or rocks would need to spend more time evading trout and would need to be constantly alert, thus affording less foraging time. Numerous studies have shown that high predation risk usually results in reduced foraging time and success, and consequently reduced growth over longer periods (Milinski & Heller, 1978; Van Buskirk & Yurewicz, 1998; Foam *et al.*, 2005; Sunardi *et al.*, 2005). When all habitat types were considered together, we did observe an effect of trout in one of the blocks (12 – 15 January 2005), but this was restricted to this one occasion.

Whilst an examination of the effects of trout on *G. auratus*' feeding was a secondary objective of this study, the reduced sample sizes due to predation mortality were a weakness in the design of the experiment. A similar experiment, but with a mesh partition separating the trout from *G. auratus* in the enclosures to eliminate predation mortality, similar to that used by Persson & Eklöv (1995), would be needed to confirm the direct effect of brown trout on the feeding of *G. auratus* and properly test whether this is habitat-dependent.

The direct impacts of brown trout appear to depend on the habitats available to *G. auratus*. This experiment has clearly demonstrated that predation risk is habitat-dependent, and whilst more experimentation is needed to test the effects of brown trout on *G. auratus*' feeding, there is some evidence (albeit very small) to suggest that this may also be habitat-dependent. The potential for these complex habitats to influence interactions between *G. auratus* and brown trout in a way that likely reduces the direct impacts of this introduced species suggests that complex habitat availability may have been an historically important factor for the ecology of *G. auratus* post-trout introduction, and may be a very important factor in determining impacts of introduced species on other galaxiids.

Galaxioid fishes have been identified as a highly vulnerable group of fishes (McDowall, 2006). This is in part due to the widespread introduction of predatory salmonids in the southern hemisphere and the fact that many galaxioid fishes evolved in isolation from larger piscivorous fishes. This study has provided direct evidence that complex habitats can significantly reduce the impacts of introduced salmonids on this group of fishes. In previous work we have shown that *G. auratus* can forage efficiently within macrophytes (Stuart-Smith *et al.*, 2007b), and the extent to which complex habitats benefit other species' interactions with introduced salmonids will also depend on their own foraging capabilities within these habitats. Whilst there is a clear need for further research in this area, conservation of this group of fishes must also focus on maintaining habitat diversity and conserving complex habitats such as macrophyte beds.

Considering the strong link between water levels and habitat availability in Lakes Crescent and Sorell, low water levels due to abstraction for irrigation may be indirectly detrimental to the threatened *Galaxias auratus* by increasing their vulnerability to predation by trout. There are also links between habitat availability and water levels in other lakes that are managed for town water or hydroelectricity, and similar, but more long-term, habitat loss is also occurring globally due to severe eutrophication and pollution (Hellsten *et al.*, 1996; Wolter *et al.*, 2000; Hilt *et al.*, 2006). By clearly demonstrating the importance of complex habitats in reducing the impact of an introduced species on a threatened species and a link between water levels and the availability of complex habitats in this system, this study suggests that human-induced disturbances such as water level manipulation and associated habitat loss may also impact other threatened species by altering the outcomes of their interactions with predators.

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Chapter 6: General discussion

Studying the mechanisms by which predators and prey can co-exist has long been a central aspect of ecological research, with niche partitioning, low prey densities and behavioural or morphological adaptation often identified as key components to predator-prey co-existence (Solomon 1949; Holling 1965). Also linked to behavioural adaptation, the use of complex habitats by prey as refuge is another mechanism that can promote co-existence of predator and prey (McNair 1986; Sih 1987; Dudgeon 1996). This, however, often results in trade-offs for the prey, such as foraging costs associated with using a habitat in which feeding may be retarded, and possibly increased competition with other sheltering prey.

A need for more research on the role of predation in applied issues has recently been emphasized (Sinclair et al. 1998; Ormerod 2002). The impact of introduced predators is one area that requires research, as the successful co-existence of native prey and introduced predators has not been common (Arthington 1991; Rowe 1993; Clavero and García-Berthou 2005). Foundational studies, such as those by Rosenzweig and MacArthur (1963) and Sih (1987) suggest that the availability of prey refuges promotes co-existence (i.e. it is stabilizing). This assumes adaptive responses by prey via co-evolution with their predator, and that the costs of using such refugial habitats are small. Yet when predators are introduced species that have usually arrived through anthropogenic avenues, there has often been little evolutionary time for native prey to adapt to the new situation, and thus, their responses may not necessarily be adaptive.

This has possibly been the case with many galaxiid fishes, which have been forced into co-habitation with salmonids, from which they apparently diverged some time in the Mesozoic, as a result of the widespread introduction of trout in the Southern Hemisphere during the 19th and 20th centuries (McDowall 1969; Fink 1984; McDowall 1990). With little evolutionary armor to protect them from the larger and aggressive salmonids, they are highly vulnerable to being out-competed and consumed, and many species have suffered considerably (McDowall 2006). However, *G. auratus* is one species that has fared well, despite the consistent abundance (and all evidence suggests also predation pressure) of brown trout (and rainbow trout) in their entire natural range for over 130 years. So, the questions of just how it has done this, and what the likelihood is of other species also showing similar resilience, beg to be asked. Research on the reproductive biology of *G. auratus* has revealed it to be similar to the more numerous and fecund diadromous galaxiid species (e.g. *G. maculatus*, Hardie 2007), which may have played an important role in its success and persistently high abundance. But according to theory, low abundance rather than high abundance of a prey species usually makes co-existence with its predator more likely (Sinclair et al. 1998; Holling 1965). This thesis was the first to address the predator-prey interactions of *G. auratus*, and potential mechanisms that may have facilitated its successful co-existence with brown trout.

Being a lacustrine galaxiid, with historical access to extensive areas of macrophyte cover and rocky substrate, the potential for *G. auratus* to have behaviourally responded to trout by choosing the safest habitat type may have substantially contributed to this success. The study reported in this thesis was

designed to answer whether it does respond in this way, but also whether a trade-off between predation risk and foraging success occurs, thus reducing the effectiveness of this behavioural response.

Although competitive interactions with juvenile brown trout and other *G. auratus* individuals, which were beyond the scope of this study, will also contribute to determining its habitat use, this research has clearly demonstrated that the habitat use pattern shown by *G. auratus* and its response to the presence of trout, significantly reduce its predation risk. In addition, the potential foraging costs often associated with such behaviour (Werner and Hall 1988; Persson and Eklöv 1995) appear to be minimized by it being an unusually efficient forager. These observations suggest adaptive behaviour, despite *G. auratus* only spending a relatively short period of time, in evolutionary terms (139 years, or approximately 35 generations), in the presence of brown trout. Its behaviour appears to promote co-existence with brown trout, provided that macrophyte habitats are available. In this way, the results of these experiments support both the theory that the behavioural selection of appropriate habitats can promote co-existence of predator and prey, and the idea emphasized by Agrawal et al. (2007), that the strength of predator – prey interactions is likely to differ in different contexts.

A fundamental difference between what I observed for *G. auratus* and what has been widely reported in the literature for other species (Werner and Hall 1988; Diehl and Eklöv 1995; Persson and Eklöv 1995; Gliwicz et al. 2006), is that a significant trade-off between predation risk and foraging returns does not appear to occur for *G. auratus* when it has the option of using macrophytes for cover. As

I reported in Chapters 2 and 4, *G. auratus* is an unusually efficient forager, feeding throughout day and night, in open water and amongst macrophytes, and its foraging abilities allow it to use complex habitats at minimal cost. This may be a very important characteristic of this species that has assisted in its atypical co-existence with brown trout to date. There is still potential that a trade-off occurs if *G. auratus* has only rocky habitat available, however, but more research is needed to determine this (see section on need for further research at the end of the discussion).

The behavioural traits of *G. auratus* (i.e. the diel periodicity in habitat use and the shift in response to predation risk) that appear to have contributed to its success appear adaptive. The shift in habitat use in response to nearby trout is likely the result of behavioural plasticity, and was the focus of the discussion in Chapter 3, but the consistent diel pattern in habitat use may either be the result of rapid adaptation (to trout), a learnt response, or possibly an inherited trait. As discussed in other chapters, a diel switch in habitats has also been observed for other freshwater fishes (Roussel and Bardonnnet 1999; Bremset 2000; Reeb 2002; David and Closs 2003) and is believed to be the result of adaptation to diel patterns in food availability and predation risk, amongst other things. But how long does it take for such adaptations to develop when a new predator is introduced? There is strong evidence of zooplankton and macroinvertebrate species showing adaptive behaviour (and morphological changes) after spending only a relatively short time with a novel predator (Flecker 1992; Fisk et al. 2007; Latta et al. 2007), but these animals have shorter generation times than *G. auratus*. What little is known from studies on fish have shown a degree of

behavioural and phenotypic plasticity in a short time frame, but of a magnitude less than due to natural variation (Holopainen et al. 1997; Reebbs 2002). The time frames discussed in these studies, however, is considerably shorter than the time *G. auratus* has been with trout, so the possibility of its behaviour being a result of adaptation to trout should not be discounted.

Despite being a typical adaptation to visual predators (Reebbs 2002), the diurnal use of complex habitats by *G. auratus* is unlikely to be an adaptation to its natural predators (birds and eels). The predation pressure exerted by birds (e.g. herons) would likely be greatest amongst the shallow macrophyte habitats during the day, while that of eels (which are largely non-visual predators: Sagar et al. 2005) would be distributed throughout all habitats during the night. So the observed diel periodicity in habitat use of *G. auratus* would place it in the worst places at the worst times with respect to its natural predators.

It is remotely possible that the “adaptive” behaviour of *G. auratus* is a result of learning. Reebbs (1999) suggested, however, that while time-place learning in fish is possible based on food, daily habitat shifts in fish that may be rooted in minimizing predation risk are most likely not a direct result of learning, but are probably innate. If this were true, then the behaviour shown by *G. auratus* may have been phylogenetically inherited. *G. auratus* was likely derived from a landlocked population of *G. truttaceus* (Ovenden et al. 1993). There are no published records of the diel habitat use of *G. truttaceus* populations, but this species, like *G. auratus*, possesses an additional, accessory lateral line, which is a physical adaptation to nocturnal activity (McDowall 1997). It has also been reported to

forage nocturnally (Williams 1975), so it is very possible that *G. truttaceus* shows a similar habitat use pattern, and that the behaviour of *G. auratus* has been retained since diverging from their common ancestral stock.

Interestingly, lacustrine populations of *G. truttaceus* in Tasmania (which are mostly also on the Central Plateau) have also been reasonably successful in co-existing with brown trout. It must be noted, however, that its densities in these lakes are nowhere near as great as those of *G. auratus* in Lakes Crescent and Sorell (A. Uytendaal, S.A. Hardie, R.W.G. White, University of Tasmania, unpublished data), and trout densities are lower than have been traditionally recorded in Lake Sorell (T. Farrell, Inland Fisheries Service Tasmania unpublished data). An examination of the habitat use patterns and responses of *G. truttaceus*, and other closely related galaxiids, to brown trout may provide some valuable insight into whether the success of *G. auratus*, and the extreme vulnerability of other galaxiid species, is related to the phylogeny of this group. This may greatly assist conservation of this group of fishes by identifying members that may be particularly susceptible to predation by introduced salmonids.

Conservation of *Galaxias auratus*

The direct and indirect impacts of brown trout on *G. auratus* and the ability of *G. auratus* to minimize these is very important for understanding the historical success of this species. Its future success is very much dependent on the effects of the substantial changes that have occurred in its natural environment and the interactive effects of these with those of brown trout.

Impacts of brown trout

Mills et al. (2004) suggested that multiple negative interactions should be examined to assess the likely outcome (co-existence or extinction) of interactions between introduced and native species. Whilst many potentially negative interactions between *G. auratus* and brown trout were beyond the scope of this thesis and still require research, the collective experiments presented here have found the following:

- Predation is a clear threat, but this appears to be effectively countered by a combination of a diel pattern in habitat use by *G. auratus* that minimizes its risk and a short-term increase in its use of complex habitats when trout are near. The effects of prolonged exposure of *G. auratus* to higher densities of brown trout, however, are unknown.
- No evidence was found for a habitat-related indirect impact of brown trout on the feeding of *G. auratus*. More data are needed for *G. auratus* using rocky habitat, and to determine longer-term effects of habitat-dependent prey switching and whether this mechanism occurs in the wild.
- Only circumstantial evidence was found for a direct impact of brown trout presence on the feeding of *G. auratus*, and it is likely that this may only occur in extremely low water levels in Lake Crescent when neither macrophytes nor rocks are available (see Chapter 5).

Thus, predation was the biggest observed impact of brown trout, and the extent of this was reduced by a behavioural modification by *G. auratus* (a shift in its diel pattern in the use of complex habitats), as discussed above. However, the potential

for *G. auratus* to benefit from this (i.e. for it to promote co-existence with trout) is highly dependent on the availability of macrophytes. Agrawal et al. (2007) highlighted the need for empirical evidence on context-dependence of interaction strengths for a better understanding of community ecology. This research has provided such evidence, suggesting that the importance of predation on *G. auratus* populations depends on the availability of macrophyte habitats. This is an important observation given that the availability of these habitats is currently restricted and is likely to remain that way in future (see below), potentially increasing the importance of trout predation in the ecology of Lakes Crescent and Sorell.

Effects of habitat degradation and loss on Galaxias auratus

Despite the ability of *G. auratus* to minimise predation risk to an introduced species that has negatively impacted other galaxiid populations (McDowall 1990; Townsend and Crowl 1991; McIntosh 2000; McDowall 2006), its future is uncertain because of the recent changes that have occurred to its entire natural range. The loss or unavailability of macrophyte habitats (both in-lake macrophyte beds and the littoral wetlands) appears to be of far greater concern than the episodes of elevated turbidity, the impact of which is possibly limited to inducing physiological stress during periods of extreme turbidity (S.A. Hardie, unpublished data). The macrophyte habitats in the extensive wetlands of both Lakes Crescent and Sorell, and previously abundant in the main basins of Lake Sorell and patches of the Lake Crescent littoral zone, have likely played a large role in facilitating the successful co-existence of *G. auratus* and brown trout, as discussed above. No data are available on macrophyte habitat availability prior to the first artificial

raising of the water level, and so no conclusions can be made as to the importance of this habitat type for *G. auratus* prior to European settlement. However, this thesis has identified that macrophytes appear to be vital to its ecology after European interference, and it is unclear whether the littoral vegetation will be able to adjust to the lower lake levels likely to prevail if the current dry conditions and increased demands for human abstraction continue. Importantly, modelling by Uytendaal (2006) has established that at sustained low levels, much of the bed of Lake Crescent is susceptible to elevated shear stress, which would be unfavourable for emergent or submerged vascular plants.

Habitat conservation is an important conservation tool for freshwater fishes (Maitland and Lyle 1992; Dudgeon 1999; Dudgeon 2005; Hardie et al. 2006), and must be considered of great importance for the future of *G. auratus*. Because of the critical influence of water levels on the availability of wetland macrophyte habitat and suitable spawning habitats (Hardie 2007), and for the future re-establishment of in-lake macrophyte beds, management of water levels is probably the single most important aspect to conserving this unique species.

Given the prediction of lower rainfall in this area due to climate change (Bureau of Meteorology, Australia: <http://www.bom.gov.au/>; G.P. Harris, pers. Comm.), and the associated increase in the need for abstraction for irrigation, the littoral wetlands may be inundated even less frequently than during the past decade. Consistently low water levels may also force Lake Sorell into a stable phytoplankton-dominated state, in which re-establishment of macrophyte beds will become even less likely. Thus, unless water levels are managed with the

conservation of *G. auratus* in mind, the situation may worsen for this species with macrophyte habitats possibly being completely eliminated. This situation would leave *G. auratus* without suitable habitat in which they may minimize the impact of brown trout, and extremely low levels would also leave it without suitable spawning habitat in Lake Crescent (Hardie 2007). On the other hand, reducing or eliminating water abstraction may assist maintenance of water levels during dry spells. Whilst possibly keeping the wetlands more frequently inundated and connected to the main lakes, higher water levels may also minimize resuspension events (Uytendaal 2006), providing better opportunities for improved water clarity and the re-establishment of in-lake macrophyte beds.

Needs for further research

There are areas of the biology of *G. auratus* that require further research to allow a better understanding of its ecology and its likely success in the future. Experimental evaluation of the foraging ability of *G. auratus* in the rocky habitat typical of Lake Sorell and the shallow exposed areas of Lake Crescent would greatly assist in both understanding potential impacts of a continuation of the current water level regime as well as its diel habitat use patterns in the presence of trout (as identified in Chapter 3). The effect of trout on the growth of *G. auratus* is also likely to be dependent on the availability of complex habitats, but this project was not able to identify this due to the design of the experiment in Chapter 5 and the sensitivity of *G. auratus* to abrasion on the enclosure mesh over longer periods of time. It would be possible to set up an experiment similar to that in Chapter 5, but with a mesh partition eliminating the potential for predation by trout in the enclosures, and using larger enclosures. Larger enclosures would reduce the

number of times individuals contacted the mesh, thus reducing damage to their slime coat (and consequently death or reduced growth over longer periods), but some more well-planned pilot studies may need to be conducted to reassure bioethical and wildlife authorities that minimal harm would occur to fish under such conditions. The sociopolitical constraints of researching listed, threatened species are real and need to be addressed directly in future research proposals.

Potential further impacts of brown trout on *G. auratus* that were not explored in this thesis also require further study. These include the potential for both inter- and intra-specific competition to occur as a result of increased use of complex habitats by *G. auratus* in the presence of brown trout, and the effect of turbidity on predation by brown trout. If juvenile trout are also using macrophyte and rocky habitats to reduce their own predation risk, then this increases the likelihood of inter-specific interference or exploitative competitive interactions.

Finally, the impact of the introduced common carp on the ecology of *G. auratus* should be investigated. Whilst carp numbers are currently low (D. Jarvis, Inland Fisheries Service Tasmania), complete eradication is certainly not guaranteed, and it is possible that carp may impact this species, or potentially other species if further introductions occur in future. The impacts of this other alien species on galaxiids are unknown, and efforts to understand whether it competes significantly for food or space, consumes or disturbs the eggs of *G. auratus* once laid must be amongst the priorities for such research.

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