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Invasive predator influences habitat preferences in a freshwater fish

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Abstract Invasive species are an important contributor to global biodiversity loss. This is particularly true in freshwater ecosystems, where introduced species have contributed to native fish extinctions, altered native fish communities and modified aquatic ecosystem structure and function. Native species can potentially mitigate the impact of invasive predators and competitors by altering their behaviour, for example by reducing activity such as foraging or by increasing their use of shelter. This study investigated interactions between an introduced salmonid, the rainbow trout (*Oncorhynchus mykiss*), and a native fish, the riffle galaxiid (*Galaxias arcanus*), that currently co-inhabit streams in parts of south-eastern Australia. We used three separate sets of behavioural experiments to test whether riffle galaxiids avoided trout under different substrate conditions. We hypothesised that habitat selection in the presence of a predator could be an important factor in facilitating galaxiid and trout co-existence. We found that interactions between the two fish differed depending on substrate. Galaxiids avoided trout when only sand substrate was available, but did not avoid trout when cobble substrate was available. The complex structure of cobbles may afford riffle galaxiids protection from trout, thereby facilitating their current existence in trout-inhabited streams.

Keywords Galaxiid · Habitat selection · Introduced species · Predator-prey interactions · Salmonid

Introduction

Introduced species are an important contributor to biodiversity loss, habitat alteration and economic cost worldwide (Vitousek et al. 1997; Lowe et al. 2000; Fausch et al. 2001; O'Dowd et al. 2003; Drees and Lard 2006). Freshwater environments, in particular, have been adversely affected by the introduction of exotic species (Achieng 1990; Findlay et al. 2000; Dudgeon et al. 2006; Linde et al. 2008). Invasive fish have been implicated in extinctions of native fauna (Miller et al. 1989), changes in habitat occupancy and behaviour (McIntosh et al. 1992; Edge et al. 1993; Reebs 1999). as well as broader community and ecosystem impacts (reviewed in Dudgeon et al. 2006; Weber and Brown 2009).

After worldwide introductions, salmonids (predominantly brown trout, *Salmo trutta* and rainbow trout, *Oncorhynchus mykiss*) have had well-described negative effects on native fish communities (McDowall 2003; Jackson et al. 2004; McDowall 2006; Correa et al. 2012; Correa and Hendry 2012; Lindegren et al. 2012). Many large salmonids are aggressive and highly competitive for habitat and food (McDowall 2006). Fish communities in both southern Australia and New

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Zealand are relatively species poor in regards to large, piscivorous native fish (Townsend and Crowl 1991; McDowall 2006). Consequently, it has been suggested that smaller native fish may not have developed sufficient defence or escape mechanisms (e.g., through learning or as an evolved response) to counter the presence of these novel (i.e. introduced) predators (Townsend and Crowl 1991; Townsend 1996; Wong and Candlin, 2015).

One important group of fishes, the galaxiids (Galaxiidae), appears to be especially vulnerable to predation and competition from introduced salmonids (Glova et al. 1992; Closs and Lake 1996; McIntosh 2000; Glova 2003). Several studies have documented the decline and fragmentation of galaxiid populations across much of the Southern Hemisphere since the introduction of salmonids (Townsend and Crowl 1991; Habit et al. 2010; Young et al. 2010; Correa et al. 2012; Correa and Hendry 2012; Lindegren et al. 2012). Trout, like galaxiids, are mainly opportunistic invertebrate feeders, and therefore, may compete directly with galaxiids for food and habitat (McIntosh et al. 1992). In addition, larger trout also present a significant predation threat to galaxiids (McIntosh 2000). Behavioural experiments have demonstrated that brown trout (*Salmo trutta*) can significantly alter patterns of habitat occupancy of some fish species, such as *Galaxias auratus* (Baker et al. 2003; Atkinson et al. 2004; Vehanen and Hamari 2004; Stuart-Smith et al. 2008).

In some areas, galaxiids have been able to persist in the presence of salmonids, potentially by exploiting habitat structure or disturbance regimes (McIntosh 2000). Many species take cover from large piscivorous fish in or around refuge structures (Persson 1993; Sih 1997; Jacobsen and Perrow 1998). However such predator avoidance behaviour often reduces foraging opportunities (Sih 1992; Krause et al. 1999). Refuge structures can vary from the simple (e.g., holes) to the more complex (e.g., vegetation, woody debris, cobbles, or larger rocks) (Caley and St John 1996; Manatunge et al. 2000). Complex habitat has been shown to affect both the behaviour and density of predators and prey (Abramsky et al. 1992). with some studies suggesting that this complexity can influence the anti-predator responses of prey (Persson and Eklöv 1995; Caley and St John 1996; Manatunge et al. 2000). For example, structurally complex habitat provides refuge for insects against spiders and, in so doing, dampens the otherwise antagonistic interaction between predator and prey (Finke and Denno 2002). Predator foraging strategy may also affect the degree to which habitat complexity can influence predator-prey interactions, as seen in both roach (*Rutilus rutilus*) and gobies (*Gymnogobius heptacanthus*) (Horinouchi et al. 2009; Martin et al. 2010). Nevertheless, for native fish species, the role that complex habitat plays in providing refuge from recently introduced piscivores remains largely unknown.

This study aims to investigate the interactions between the recently described riffle galaxiid (*Galaxias arcanus*, Raadik 2014). and an introduced salmonid, the rainbow trout (*Oncorhynchus mykiss*). Currently, both species co-inhabit several streams in south-eastern Australia. Specifically, using a series of experiments, we set out to determine whether substrate complexity affected the behavioural response of the galaxiid to the presence/absence of trout. In the first experiment, we tested the substrate preference of riffle galaxiids in the absence of trout. In the second set of experiments, we investigated whether galaxiids avoided trout when substrate type was kept uniform. Lastly, in the third set of experiments, we examined the effect of trout on the galaxiid's choice of preferred habitat. We predicted that galaxiids would have a preference for certain substrate types over others, and that this choice could potentially be impacted depending on the presence/absence of trout.

Methods

Collecting and housing

The riffle galaxiid is a small (standard body length = 70–110 mm) fish native to south-eastern Australia. The riffle galaxiid's morphology, in particular a straight ventral profile, long and low caudal peduncle and a downturned mouth suggest that it is adapted to benthic conditions in fast flowing streams (Raadik 2014). Riffle galaxiids (n = 38) were collected from the Corryong/Nariel Creeks and Cudgewa Creek, in north-eastern Victoria, Australia, using a backpack electrofisher (Smith-Root Model 600-800 V, square wave pattern). We found riffle galaxiids in shallow fast flowing riffle areas with coarse substrate material. By contrast, we did not find any riffle galaxiids in deeper pool areas. Riffle galaxiids co-existed with multiple large introduced fish species (including salmonids), which mainly inhabited sandy pools, but also riffle areas. Fish were transported from the collection site in coolers filled with stream water aerated by battery-powered pumps. In the laboratory, fish were housed in aerated stock aquaria, with a thin layer of sand and gravel substrate, containing dechlorinated tap water (100 L). Water temperature (16 °C) and pH (6.4) were kept consistent with average measurements taken from collection locations. Light was maintained on a 16:8 h day: night cycle. Galaxiids were fed ad libitum on a diet of brine shrimp (*Artemia* sp.), locally sourced aquatic macro-invertebrates and commercial fish food. Cobble (diameter ~ 0.5 cm to 2 cm) and sand (diameter < 1.5 mm) were also collected from the study site, to be used in habitat selection experiments, with the latter supplemented with additional sand (matching in grain coarseness) purchased from a local aquarium supplier. Rainbow trout (n = 4; body length = 210–250 mm) were sourced from a commercial trout farm in Buxton, Victoria, and housed individually under the same aforementioned conditions. Previous research has found that trout longer than 150 mm are capable of preying on all size classes of the common river galaxiid (*Galaxias vulgaris*) (McIntosh 2000). Therefore, the trout used in our experiment are likely to act as both a predator and competitor to riffle galaxiids in the wild. There was no possible visual contact between trout and galaxiids in their housing tanks. All fish were kept under laboratory conditions for one week before experimental trials began.

Experimental procedure

Experimental trials were conducted over eight weeks, in a large shallow opaque 'choice' tank (L × W × D = 122 cm × 51.5 cm × 21.5 cm. Water depth = 15 cm. Figure 1) between 08:00 and 16:00 h. The rear of the tank was designated as a neutral zone (containing no substrate) and delineated from the front by a laterally placed strip of tape. The front half was divided longitudinally by an opaque plastic partition (length = 60 cm), providing the focal galaxiid with an option between two different habitat choice zones on either side of the partition. In our second group of experiments one rainbow trout was placed in the experiment tank inside a smaller transparent (to allow visual contact) container in one of the two choice zones, an empty identical container was also placed in the other choice zone. Trout containers had holes drilled in the sides to facilitate water flow, thus allowing any chemical cues to move between the trout container and experiment tank. Powerheads (water pumps) were placed to

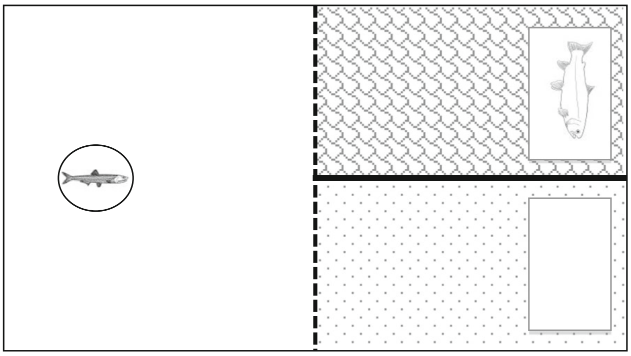

Fig. 1 Diagram of the experimental set up. Focal fish (*shown on left*) were initially placed into the experimental tank in a clear cylinder. The fish was then given a choice of two habitat areas partitioned by an opaque barrier, in which trout (*shown on right*) may have been absent or present. The *dashed line* separates the neutral zone (*left*) and the choice zone (*right*)

generate a current moving from the end of the choice zone towards the galaxiid, ensuring that olfactory cues from the predator reached the experimental fish. Powerheads and containers were present in every trial, regardless of whether trout were used or not.

Habitat selection experiments

Do galaxiids display a preference for substrate type?

Firstly, a dichotomous choice experiment was conducted to investigate the substrate preference of the riffle galaxiid in the absence of trout. Riffle galaxiids were tested individually in the choice tank, each galaxiid was initial placed inside a clear plastic cylinder (diameter = 120 mm), open at both ends, and left to acclimate for 5 minutes in the neutral zone. Following the acclimation period, the cylinder was gently lifted, thereby allowing the focal galaxiid to move freely around the tank for 10 minutes. Riffle galaxiids were offered the choice of associating with either cobble substrate in one choice zone or sand substrate in the other. The amount of time spent in each of the two choice zones was recorded, with galaxiids able to move between the neutral zone and choice zones. The side of the partition that each substrate was on was initially randomised and then alternated with each trial.

Do galaxiids actively avoid trout?

Secondly, using the same set-up described above, we carried out a separate set of experiments to investigate whether galaxiids avoided trout when substrate was kept uniform across the two choice zones. To do this, a trout was placed in one of the choice zones while the other remained trout-free. Here, we had two treatments using either sand or cobble substrates as follows: (1) trout-free sand substrate versus trout-occupied sand substrate; and (2) trout-free cobble substrate versus trout-occupied cobble substrate.

Does trout presence influence galaxiid substrate choice?

Lastly, to investigate whether riffle galaxiids avoided trout when substrate differed between the two choice zones, we conducted a third set of experiments with the following choice zones: (1) trout-free sand substrate versus trout-occupied cobble substrate; and (2) trout-free cobble substrate versus trout-occupied sand substrate.

Each galaxiid was tested only once per experiment ($n = 38$ per experiment). Importantly, we tested individuals across multiple experiments to account for constraints on behaviour, with each individual given at least a one-week rest period between experiments to minimize any potential carry over effects (Bell 2013).

Statistical analysis

All statistical analyses were carried out using the statistical program R (R core development team 2013). All data was checked for normality and heterogeneity of variances prior to analyses. For each experiment, the absolute amount of time spent in either habitat zone was recorded and then compared using paired t-tests.

Results

In each experiment every galaxiid moved from the neutral zone into at least one of the choice zones.

Do galaxiids display a preference for substrate type?

In the absence of trout, riffle galaxiids ($n = 38$) spent significantly more time associating with cobble substrate than sand substrate ($t_{36} = 6.1$, $p < 0.001$; Fig. 2).

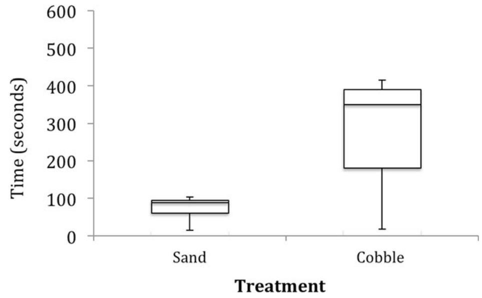

Fig. 2 Riffle galaxiid substrate preference. Time (seconds) spent associating with either sand (mean ± se = 88, 15.84) or cobble (mean ± se = 350, 73.1) substrate in the absence of trout. Central *horizontal lines* within the boxes indicate means. Whiskers indicate minimum and maximum values

Do galaxiids actively avoid trout?

When substrate was kept uniform in the two choice zones, we found that, on sand substrate, riffle galaxiids spent significantly more time within the trout-free choice zone ($t_{36} = 5.12$, $p < 0.001$; Fig. 3a). However, on cobble substrate, riffle galaxiids demonstrated no significant preference for either the trout-free or trout-occupied choice zones ($t_{36} = 0.05$, $p = 0.96$; Fig. 3b).

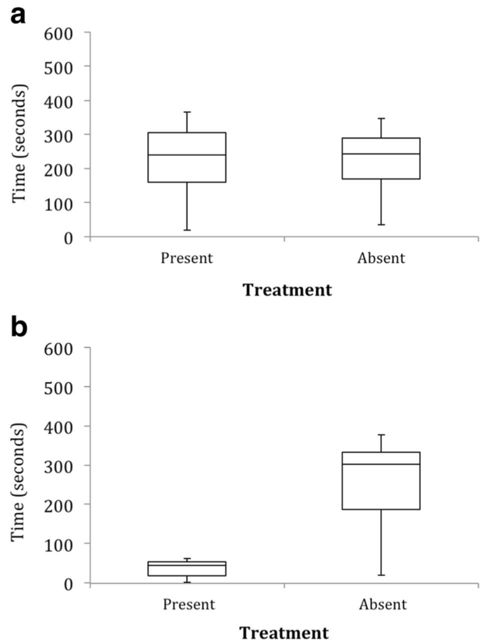

Fig. 3 Riffle galaxiid substrate preference (seconds spent in choice zone) when choice was between **a** trout present (mean ± se = 240, 59.12) versus trout absent (mean ± se = 243, 54.01) on sand substrate, and **b** trout present (mean ± se = 45, 11.28) versus trout absent on cobble (mean ± se = 302, 64.29) substrate. Central *horizontal lines* within the boxes indicate means. Whiskers indicate minimum and maximum values

Does trout presence influence galaxiid substrate choice?

When offered the choice between trout-free cobble substrate over trout-occupied sand substrate, we found that riffle galaxiids spent significantly more time associating with the former (t_{36} = 6.99, p < 0.001; Fig. 4a). However, when presented with a choice between trout-occupied cobble substrate over trout-occupied sand substrate, riffle galaxiids showed no clear preference for either substrate choice (t_{36} = 0.59, p = 0.56; Fig. 4b).

Discussion

In the absence of trout, we found a significant preference for cobble substrate versus sand substrate. However, riffle galaxiids altered their behavioural responses depending on the nature of the underlying substrate. In sand substrate, the galaxiids consistently and significantly avoided the introduced fish cue. However, with cobble substrate, the fish seemed willing to tolerate the presence of the introduced trout. This suggests that the type of underlying substrate mediates the behaviour of

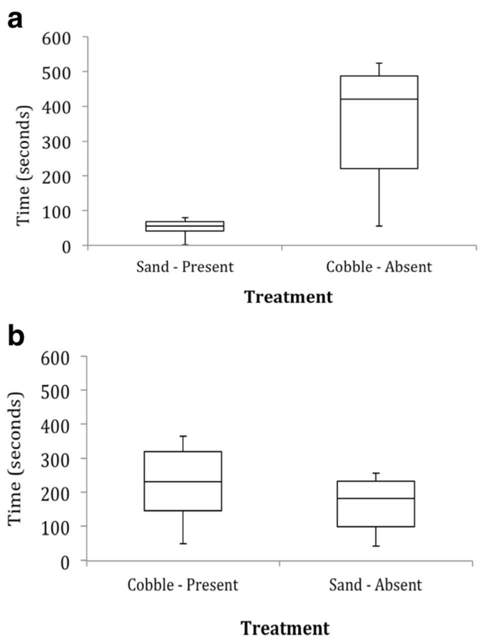

Fig. 4 Riffle galaxiid substrate preference (seconds spent in choice zone) when choice was between **a** trout present (mean ± se = 56, 13.35) on sand substrate versus trout absent (mean ± se = 412, 86.83) on cobble substrate, and **b** trout present (mean ± se = 230, 53.52) on cobble substrate versus trout absent (mean ± se = 182, 46.21) on sand substrate. Central *horizontal lines* within the boxes indicate means. Whiskers indicate minimum and maximum values

riffle galaxiids in the presence of trout. Alternatively, trout may have been less visible in more complex substrate and therefore galaxiids may not have perceived the same level of risk. In this respect, cobbles most likely offer riffle galaxiids refugia by allowing them to hide in interstitial spaces (which would also confer foraging benefits through a high abundance of benthic invertebrates; sensu Flecker and David Allan 1984; Barmuta 1990; Glova et al. 1992; Webster and Hart 2004).

Apart from their role as predators, trout have also been hypothesised to out compete galaxiids for food and habitat (McIntosh 2000). This is because trout are generally mid-drift opportunist, whereas most galaxiids typically must venture from the bottom into the water column to feed (McIntosh 2000). Such differences would give trout a competitive advantage (Allibone and McIntosh 1999). This could be pertinent for riffle galaxiids when feeding on drift invertebrates, given that they appear to readily associate with trout in cobble habitat, potentially exposing them to resource competition by trout. However, this interpretation should be treated cautiously, as direct physical contact between trout and galaxiids was prevented in our experiment.

Despite the evidence linking the decline of galaxiids with the introduction of trout (Crowl et al. 1992; Closs and Lake 1996; Lintermans 2000). in some areas riffle galaxiids and trout (both brown and rainbow) are, for now, coexisting in close proximity (W. Sowersby, unpublished data). Complex habitats may be allowing galaxiids to shelter and survive in the presence of larger predators (Stuart-Smith et al. 2007). The risk of predation by trout is therefore likely to depend on galaxiid habitat selection and the availability of complex habitat. For example Stuart-Smith et al. (2007) found that, in experimental trials, *G. auratus* survived in enclosures despite the presence of brown trout when structurally complex habitat was available (i.e. in the presence of macrophytes, rocks). By contrast, *G. auratus* suffered greater predation losses in homogeneous substrate, such as sand (i.e. silt) (Stuart-Smith et al. 2007). Similarly, in the wild, the riffle galaxiids' preference for complex cobble substrate may offer protection and shelter from trout aggression and help lead to their current coexistence.

Adjacent land use activities are likely to have substantial consequences for the interactions between native fish and introduced predators. Rivers and creeks have been extensively altered by human disturbance regimes such as agriculture, riparian clearance, channelling and the drainage of floodplains (Allan 2004). These anthropogenic changes have resulted in a reduction in overall structural complexity and ecosystem function (Stevens and Cummins 1999; Allan 2004). For example, creek habitats adjacent to disturbed sites are often inundated with sand and silt (Allan 2004). The loss of riparian vegetation, in particular, is linked to a decrease in substrate complexity, with sand and silt replacing tree roots, pebbles and cobbles (Stevens and Cummins 1999). The clearance of riparian vegetation is widespread in our study system, with potential management implications for the continued persistence of riffle galaxiids in trout-occupied areas.

In conclusion, we found evidence of habitat preferences in riffle galaxiids that may facilitate their coexistence with trout. Galaxiid fishes constitute a major component of Australasia's freshwater fish fauna. Introduced salmonids, in this regard, represent a threat, with well-documented declines reported in a number of galaxiid species following salmonid introductions. The negative impact of introduced salmonids on native fish species has serious consequences for fish conservation and, as a result, warrants further empirical attention.

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