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# Predator Recognition and Responses in the endangered Macquarie perch (*Macquaria australasica*)

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## KEYWORDS

*anti-predator behaviour, invasive species, Murray River cod, redfin, spangled perch*

## ABSTRACT

*Macquarie perch, Macquaria australasica, is an endangered species endemic to southern Australia whose distribution is highly fragmented and continues to decline. Key threatening processes include habitat destruction, dams and weirs, overfishing and interactions with introduced species. Here, we examined the responses of small and large Macquarie perch to two native predators and to the introduced redfin perch, Perca fluviatilis. Our results showed that Macquarie perch generally avoided large-bodied native predators but was attracted to small-bodied native predators. Responses to large and small redfin perch lay between these two extremes, suggesting that the Macquarie perch does treat these foreign fish as potential threats. Macquarie perch relied on both visual and chemical cues to identify predators, although its response tended to be stronger when exposed to visual cues. The results suggest that Macquarie perch has the capacity to recognise and respond to invasive species in a threat-sensitive manner, which has positive implications for the conservation management of the species.*

## **Introduction**

Macquarie perch, *Macquaria australasica* Cuvier 1830, has suffered a significant decrease in distribution and abundance over the past century and is listed as endangered (Ingram *et al.* 2000). It is protected at the state and federal levels in Australia (*Environment Protection and Biodiversity Conservation Act 1999*) and internationally (IUCN 2013). The species current distribution is highly fragmented and encompasses cool headwater streams of the Murray, Murrumbidgee, Mitta Mitta, Goulburn and Lachlan rivers on the western side of the Great Dividing Range and Hawkesbury–Nepean and Shoalhaven Rivers on the eastern side of the range (Lintermans 2007). Some of the populations such as that in the Yarra River are the result of translocations outside of the species historical range, whereas the Goulburn population is a translocation within its historical range (Lintermans 2007). Molecular studies have indicated that the species comprises three isolated, evolutionary significant units that require separate management

attention and may be discrete enough to warrant splitting the species (Faulks *et al.* 2010). It is likely, however, that the 'species' in the Kangaroo River is already extinct.

The Macquarie perch is a medium-sized, long lived fish (>26 years; Cadwallader, and Rogan 1977). Western fish are relatively large (commonly ~25 cm but up to 45 cm standard length, SL), whereas eastern fish seldom reach 18 cm. The western fish were highly prized by anglers because of their fighting ability and firm white flesh. Although it has high fecundity, adult recruitment levels are very low (Gray *et al.* 2000). Thus, the species is highly vulnerable to environmental perturbation. For example, the recent prolonged drought is thought to have decimated a translocated population (Lintermans 2013). Early attempts to rear and breed the fish in captivity, with a view to establishing a restocking program proved difficult, largely owing to the difficulty of getting fish to breed (Gray *et al.* 2000). There are several key threatening processes responsible for the decline of the species, including catchment-scale anthropogenic impacts (Ingram *et al.* 2000). Of these impacts, arguably blockage to river passage via the construction of dams, weirs and road crossings is the most significant because it not only causes population fragmentation but also limits migration within the stream during the spawning season. Other significant threats include the introduction of alien fish species (Rowe *et al.* 2008).

Australia has a long history of introduced fish species and these have had a wide ranging impact on native fishes (Lintermans 2004; Harris 2013). Some of the more direct impacts include predation, competition and the introduction and transport of diseases. For example, *Gambusia holbrooki*, is well known for its aggressive nature and it not only attacks native fish and crustaceans causing death or displacement, but it also competes for food (Keller and Brown 2008; Bool *et al.* 2011). The Murray–Darling Basin is a particularly good example of how prevalent invasive fish are in Australia; ~43% of the individuals present are non-native, equating to 68% of the total biomass (Davies *et al.* 2010). Several alien pest fish species were deliberately introduced to Australia. In the case of *Gambusia*, populations were spread around the country in an ill-informed bid to control mosquitos. Other fish, such as trout and redfin perch, were introduced by acclimatisation societies who saw little angling value in native Australian species (Lintermans 2004). Stocking of trout started in 1852 and still occurs to this day despite the fact that they have been implicated in the demise of several native fish species (e.g. galaxids; McDowall 2006).

Redfin perch was the second species introduced to Australia and is a significant management conundrum (Weatherley 1977). In Victoria, it is a prized angling species, whereas in New South Wales (NSW), Australian Capital Territory and Western Australia it is a recognised pest species (Morgan *et al.* 2003). Redfin perch is native to Europe and is a medium-bodied species (reaching 50 cm) renowned for its aggressiveness. It is this quality that makes it a great angling species; however, it also has the potential to decimate native fish and invertebrate populations. Introduced in 1862 (Weatherly 1977), it is now present in most river systems in southern Australia and continues to invade new habitats. In 2006, redfin perch were found in the upper reaches of the Lachlan and Abercrombie Rivers and further populations were discovered in the Macquarie River catchment in 2008 (NSW Fisheries Database). These discoveries are significant because they represent some of the last remaining natural populations of the endangered Macquarie perch. Despite the fact that redfin perch have been present in Australian waters for a substantial length of time, there have been no direct scientific observations of their interaction with native fishes (Rowe *et al.* 2008). Most of the negative impacts are implied from their aggressive nature and broad diet or based on anecdotal evidence (Cadwallader and Rogan 1977; Hutchison 1991; Pen and Potter 1992; Morgan *et al.* 2003).

Evidence suggests that in areas where Redfin perch has been introduced, Macquarie perch populations decline, or in some cases become extinct (M. Lintermans and D. Gilligan, pers. comm.; Cadwallader and Rogan 1977). The reason for this is largely unknown, but predation, competition and viral transmission

(Langdon 1989) are all likely causes, none of which has been examined experimentally. There have been urgent calls for science-based decision making so as to develop alien-species management plans within the Murray–Darling Basin (Koehn and Lintermans 2012). In response to this, we conducted controlled laboratory experiments examining staged interactions between two size classes of Macquarie perch and redfin perch. Our primary interest was whether or not Macquarie perch recognised redfin perch as a potential predator or aggressive competitor using visual or olfactory cues. By way of comparison, we also examined their response to two native predators, spangled perch (*Leiopotherapon unicolor*) and Murray cod (*Maccullochella peelii*). Thus, we collectively examined the response of large and small Macquarie perch to large and small native and introduced potential predators and/or competitors. While large Macquarie perch may not be directly vulnerable to predation from any of these species, they may be indirectly affected via aggressive interactions, resulting in injury or habitat displacement. In contrast, small Macquarie perch are certainly vulnerable to predation from Murray cod and large redfin, and are also susceptible to aggressive displacement from both small redfin and spangled perch. We had the expectation, therefore, that small individuals (<20 cm) would be more susceptible to attack than large individuals (>20 cm) and thus ought to display more caution in the presence of potential predators.

## Materials and methods

### *Fish collection & maintenance*

Adult Macquarie perch (western form) were collected by the NSW DPI Fisheries from two locations on the Abercrombie River in NSW in May, 2008 ('Millvale': 34°09'18"S, 149°56'16"E; and 'Hadley': 34°10'59"S, 149°59'38"E). These sites were chosen because they are established sampling sites of the NSW DPI's Macquarie Perch Project. Fish were captured overnight at a depth of between 0.4m and 0.7m by using fyke nets (mesh sizes 15–30 mm). No redfin perch have been recorded at these locations so all *M. australasica* were tentatively designated as redfin naïve. Nevertheless, redfin perch have been reported elsewhere in the catchment. Other species present at the time of capture included common carp *Cyprinus carpio*, gambusia *Gambusia holbrooki*, golden perch *Macquaria ambigua*, Australian smelt *Retropinna semoni* and mountain galaxias *Galaxias olidus*.

Macquarie perch were transported to NSW DPI Narrandera Fisheries Centre (NFC) in an aerated 1000-L tank. On arrival, they underwent a health condition check which included confirming that the fish had good fin condition, appropriate buoyancy control and a lack of skin lesions (only healthy fish were utilised in experiments) and then had a uniquely numbered electronic PIT tags were inserted for identification purposes. Fish were then separated into two discrete size classes which corresponded to age 1+ years (<20cm, 'small' fish) and 2+ years (>20 cm, 'large' fish). They were housed in 2500-L tanks and immediately salted at 6 ppt to prevent infections. After 5 days, the tanks were flushed and then salted at 6 ppt for a further week. During holding at NFC, the fish were fed every 2–3 days with a mixture of frozen bloodworms, earthworms and shrimp.

Twenty Macquarie perch (11 small and 9 large) were transported in oxygenated bags to Macquarie University, North Ryde, NSW, in October, 2009. One large fish died shortly after transit for unknown reasons. Fish were separately housed in 1000-L semi-natural tanks on the basis of the two size classes. Light was provided by fluorescent tubes on a 12-h light : 12-h dark photoperiod, temperature was maintained at ~18°C and pH was close to neutral. Fish were fed a mixture of earthworms, mealworms and frozen prawns every 2–3 days.

Four redfin perch individuals were collected via angling on 10 April 2009 from Dunlop Dam (35°11'27.20"S, 149°00'59.99"E) by using barbless hooks. The two smaller fish were ~17 cm in length and the two larger fish were 40 cm SL. Dunlop Dam is an artificial impoundment that has been illegally

stocked with various introduced species, including redfin perch, and was chosen on the basis of the advice of local fishing experts. The four native fish, two spangled perch (~17 cm SL) and two Murray cod (~40 cm SL) were purchased from a commercial hatchery specialising in native fish (Australian Native Fish Enterprises, Kallangur, Queensland) and were transported to Macquarie University in oxygenated bags. Although these species are not found in the same locations from which the Macquarie perch were collected, they are both widely distributed in the Murray–Darling Basin. All stimulus fish were housed in 150-L semi-natural aquaria either separately or in pairs, depending on the species and individual fish size. The aquaria were furnished with gravel, rocks, woody debris and plants. Light was provided by fluorescent tubes on a 12-h light : 12-h dark photoperiod, and temperature was maintained at 22°C and pH was close to neutral. The fish were fed a mixture of commercially raised earthworms, mealworms and frozen prawns every 2–3 days. All of the fish species had adjusted to captive conditions before experimentation, as evidenced by their activity levels and foraging motivation.

#### *Chemical stimulus preparation*

To eliminate dietary cues, all fish (stimulus and subjects) were fed the same diet so that any food-related odours were unlikely to elicit a fear response. Stimulus fish were placed in species-specific, aerated tanks (120 L) for 1 week. During this period, stimulus tank water was not filtered and fish were deprived of food for 48 h before collection to avoid contaminating the samples. One litre of water from the tank was collected, passed through filter paper (6 µm) and frozen at –20°C in 40-mL aliquots for at least 24 h before testing. This method of producing and preserving predator odours has been used successfully previously (e.g. Hickman *et al.* 2004). To control for the possibility that the odour of individual stimulus fish from the same species varied, samples were mixed together in equal portions.

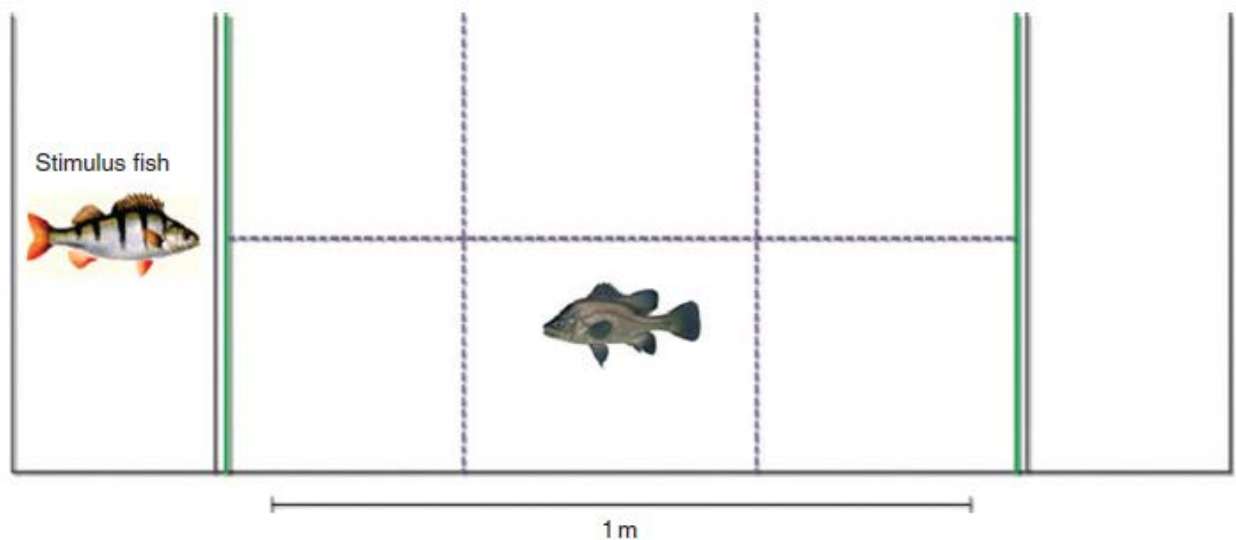
#### *Experimental apparatus*

All predator-recognition experiments were conducted using a ‘choice tank’ (2 m × 0.6 m), which consisted of a central section (1.2 m) and two smaller sections (0.4 m) on either side created by clear glass partitions (Fig. 1). Water was maintained at 60-cm depth. This allowed stimulus fish to be placed at either end to control for side biases. The tank was lit by over-head fluorescent tubes located over the small stimulus sections. Thus, the central compartment was relatively dark, which is the condition in which Macquarie perch is most active. Three sides of the tank were lined with black plastic and it rested on a custom-made, moveable stand. The clear side was visibly marked into six 40-cm long sections (three along the bottom and three along the top). The two sections adjacent to the predator stimulus were designated as the ‘inspection area’. Opaque plastic barriers were positioned adjacent to the glass barriers that could be lifted and lowered using a remote pulley system. An observer sat at a distance in a darkened room and recorded fish behaviour in real time.

#### *Experimental procedure*

Macquarie perch individuals were randomly chosen from the holding tank and identified using a PIT-tag reader (Trovan GR-250, Trovan Ltd, UK). They were then introduced to the experimental tank and acclimated for 30 min. Following this, their behaviour and location were recorded in real time for 10 min before stimulus exposure and 10 min during stimulus exposure. The side of the tank in which the stimulus was introduced was alternated to adjust for side fidelity. All test subjects were exposed to stimuli from all four predators. The stimulus fish order for each subject was pseudo-randomly assigned to reduce the likelihood of order effects. All observations were recorded using the EthoLog 2.25 (Ottoni 2000). After each treatment, the Macquarie perch was returned to a separate housing tank. The choice tank was then drained, rinsed and refilled with aged, de-chlorinated tap water. Fish had a resting period of at least 1 month between experiments.

**Fig. 1. Schematic of the experimental arena (2m × 0.6 m), which consisted of a central section (1.2 m) and two smaller sections (0.4 m) separated by glass partitions. Water depth was 60 cm. Stimulus predators were placed at either end and test subjects in the centre. Predator odours were injected via airline tubing.**



#### *Experiment 1: response to visual stimulus*

Just before the test subject was placed in the test apparatus, the predator was positioned in the stimulus compartment. Following acclimation and the pre-stimulus period, the barrier was slowly removed to reveal one of the four predator fish, namely, large redfin, small redfin, spangled perch or Murray cod. The location in the tank of the focal animal was then recorded for 10 min, after which the barrier was replaced. It was expected that if the fish viewed the predator as a potential threat, they would reduce activity, increase the time spent on the bottom of the tank (a form of crypsis) and move to the far end. This behaviour might be interspersed with periods of predator inspection.

#### *Experiment 2: response to chemical stimuli*

A 25-mL syringe attached to airline tubing was used to introduce the predator odour into the central compartment of the test tank. The tubing was placed at both ends of the test tank and extended 5 cm below the water level. Immediately following the pre-stimulus period, one of the four predator odours (large redfin, small redfin, spangled perch or Murray cod) was injected into the experimental tank at a rate of  $1\text{mLs}^{-1}$ . This was then flushed with a further 25mL of aged tap water. Preliminary tests with food dye showed that when injected at this rate, the stimulus solution spread through the entire tank within 30 s. Given the rapid dispersal of odour, it is unlikely that the fish would show any change in the distribution in the tank with respect to the source location. However, if the fish perceive the odour as potentially threatening, one would expect the fish to increase their use of the bottom half of the tank and decrease their activity levels. At all stages during the experiment, the end compartments were empty and the trapdoor was lowered.

#### *Experiment 3: combined visual and chemical stimuli*

This protocol simply combined those from Experiments 1 and 2, as detailed above. Subjects were exposed to both visual and chemical stimuli from the predators. Predator odours were injected into the tank as the partition was raised to expose the predator. Our expectation was that both visual and

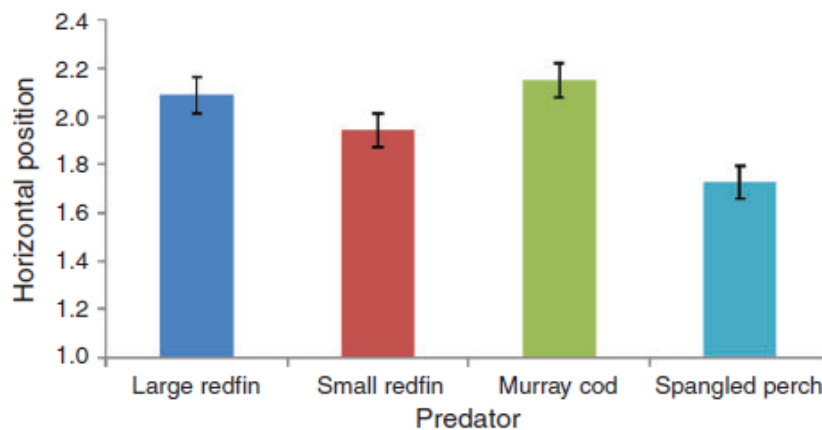
chemical cues would reinforce one another but the response would be qualitatively similar to that in Experiment 1.

### Data analysis

Given the limited number of Macquarie perch individuals for test subjects, we had to repeatedly expose the fish to multiple cues throughout the study, although each exposure was separated in time by at least 1 month. We resorted to general linear mixed models to analyse the data (Bolker *et al.* 2009), where individual ID was entered as a random factor to control for repeated observations of individuals across treatments. Our fixed variables included treatment (chemical, visual or combined cues), subject size (large or small) and predator identity (Murray cod, silver perch, large and small redfin). We conducted separate analyses on the following dependent variables: average distance to the predator compartment, time spent in the zone closest to the predator (the inspection zone; min), the time spent on the bottom of the test tank and activity level. Activity level was obtained by simply summing the number of times the fish moved between the six subsections of the central compartment (Fig. 1). Because we collected data both before exposure to predator cues and during exposure, we subtracted the former from the latter to create a change in behaviour index. Positive scores represent an increase in the behaviour during exposure and negative scores represent a decrease in behaviour when exposed to the treatment, relative to background levels.

While the change in behaviour index is a statistically robust method of examining the data, it does not allow us to visualise (or indeed examine) the general responses to the treatments. To help with this, we also examined the data using repeated-measures ANOVA but we violated the assumption of independence by assuming that the data collected in each of the three experiments were independent (they were separated by more than a month). Data were checked for normality before analysis using normal probability plots and Anderson–Darling normality tests. *Post hoc* tests were conducted using Fisher's l.s.d.

**Fig. 2.** The mean ( $\pm$  s.e.) horizontal position of Macquarie perch relative to the predator compartment. Values of 1 are the closest to, and values of 3 are the furthest from the predator compartment.



## Results

### Mean distance to predator compartment

When analysing the average distance to the predator compartment, our mixed model found a highly significant effect of treatment ( $F_{2,189} = 8.781$ ,  $P < 0.001$ ). When exposed to the predators with visual cues

only, the test subjects approached the predator, whereas no such change in behaviour was observed in the other treatments. *Post hoc* analysis revealed that the change in average distance to the predator compartment during the visual treatment was significantly smaller than during the chemical and combined treatments (Fishers' I.s.d.:  $P < 0.001$  in both cases). No other main effects or interactions were detected.

The repeated-measures analysis found a main effect of predator type ( $F_{3,204} = 3.901$ ,  $P = 0.008$ ). Our test subjects tended to maintain the greatest distance from the large redfin perch and Murray cod and the least distance from the spangled perch (Fig. 2). We also detected a significant change in behaviour from before exposure to during exposure ( $F_{2,204} = 7.778$ ,  $P = 0.006$ ), but this was primarily driven by the response during the visual treatment (time  $\times$  treatment interaction:  $F_{2,204} = 9.219$ ,  $P = 0.001$ ) where fish tended to approach the predator as indicated by the mixed model.

#### *Time spent in the inspection zone*

Given the results above, it is hardly surprising that the mixed model also found a significant effect of treatment on the time spent in the inspection zone ( $F_{2,189} = 8.388$ ,  $P < 0.001$ ). Fish significantly increased their time in the inspection zone during the visual treatment. There were no other significant effects.

The repeated-measures analysis found a main effect of predator identity ( $F_{3,204} = 3.4$ ,  $P = 0.019$ ), which mirrored the mean distance data. Fish spent more time inspecting the spangled perch and the least time inspecting the large redfin perch and Murray cod. We also revealed a significant time  $\times$  treatment interaction ( $F_{2,204} = 8.764$ ,  $P < 0.001$ ), which supports the mixed model result. Fish spend significantly more time in the inspection zone while the predator was present.

#### *Time spent on the bottom of the test tank*

The general linear mixed model found a significant interaction between the size of the Macquarie perch and the type of predator ( $F_{3,187} = 4.878$ ,  $P = 0.003$ ) as well as a significant effect of fish identity ( $F_{18,189} = 2.068$ ,  $P = 0.008$ ), suggesting that each fish had very specific individual responses to the treatments. Small Macquarie perch tended to increase the amount of time spent on the bottom when exposed to a Murray cod and spangled perch (both native predators) and showed no change in response to redfin perch. In contrast, large Macquarie perch tended to increase their time on the bottom in response to the redfin perch (particularly large redfin perch) but decrease it in response to the spangled perch (Fig. 3). There were no other significant main effects or interactions.

The repeated-measures analysis found a main effect of treatment ( $F_{2,204} = 14.253$ ,  $P < 0.001$ ) and predator type ( $F_{3,204} = 3.042$ ,  $P = 0.03$ ). Fish spent significantly more time on the bottom in response to the visual treatment than to other treatments (I.s.d.:  $P < 0.001$  in both cases). They also spent the most time on the bottom in response to spangled perch, followed by Murray cod, large redfin perch and small redfin perch (Fig. 4). There was a significant increase in the time spent on the bottom when the trapdoor opened and the Macquarie perch individuals were exposed to the predators ( $F_{1,204} = 4.380$ ,  $P = 0.037$ ) and a significant three-way interaction between time, Macquarie perch size and the type of predator ( $F_{3,204} = 4.289$ ,  $P = 0.006$ ), as suggested by the mixed model.

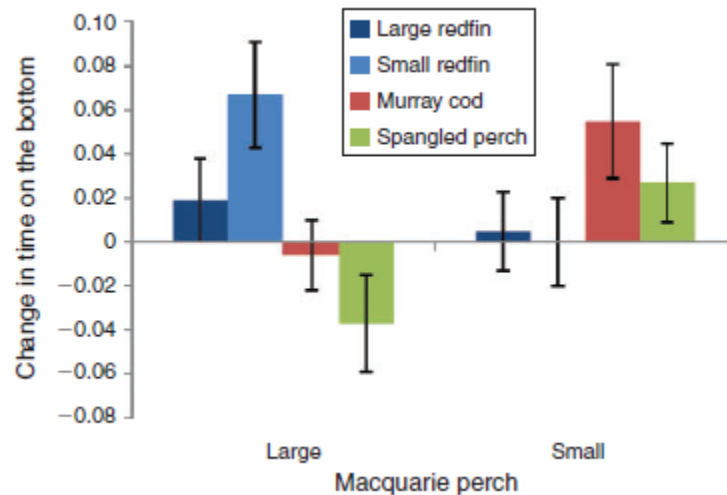
#### *Activity*

Analysis of the activity levels showed no effect of treatment, Macquarie perch size or any interactions. The lack of a significant interaction between predator and treatment suggests the response was similar irrespective of whether the exposure was to chemical or visual cues. However, there was a highly significant effect of predator identity ( $F_{3,119} = 3.326$ ,  $P = 0.022$ ). In general, Macquarie perch increased their activity when exposed to the spangled perch, reduced their activity when exposed to a large Murray

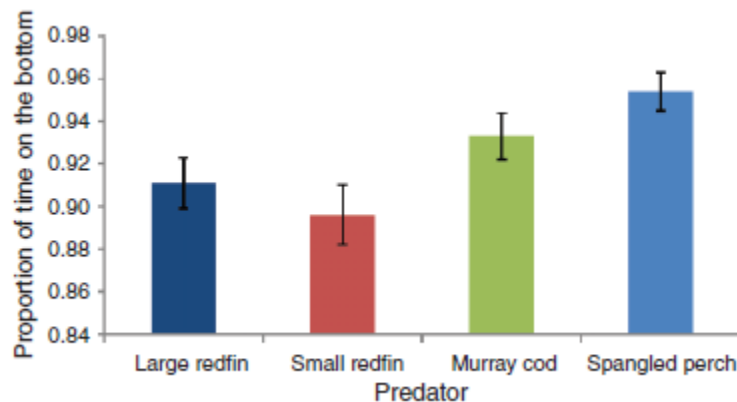


cod and small redfin perch, and showed no change in activity when exposed to the large redfin perch (Fig. 5). *Post hoc* tests (Fishers l.s.d.) showed that the change in activity in response to spangled perch was significantly greater than the response to Murray cod and small redfin perch ( $P = 0.013$  and  $0.022$  respectively), with that to large redfin perch being intermediate and not significantly different from any other treatment. There was also an effect of fish identity ( $F_{17,119} = 2.056$ ,  $P = 0.013$ ), suggesting that responses were highly individualistic.

**Fig. 3.** The mean ( $\pm$  s.e.) change in the proportion of time large and small Macquarie perch spent on the bottom of the test tank during exposure to predators. Negative values represent a decrease in time spent on the bottom and positive values represent an increase in time spent on the bottom from background levels.



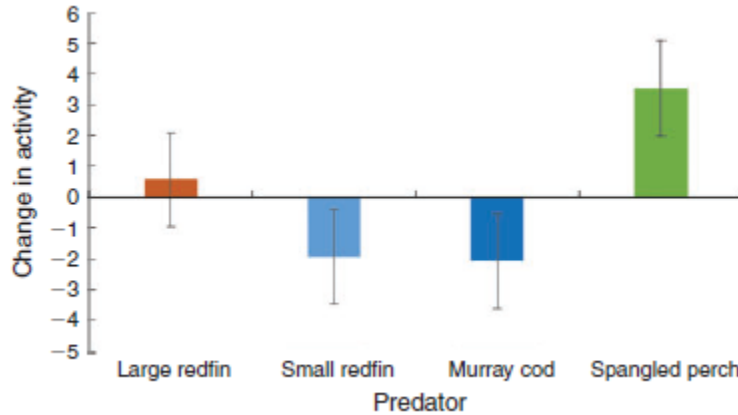
**Fig. 4.** The mean ( $\pm$  s.e.) proportion of time Macquarie perch spent on the bottom of the test arena when exposed to four different predators.



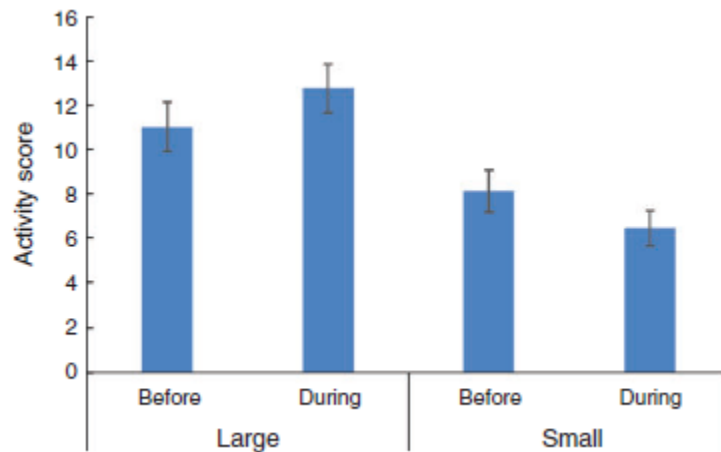
The repeated-measures analysis revealed similar results, showing main effects of treatment ( $F_{1,136} = 5.008$ ,  $P = 0.0269$ ) and Macquarie perch size ( $F_{1,136} = 16.538$ ,  $P < 0.001$ ). Macquarie perch were generally less active during the visual treatment and small Macquarie perch were less active than large Macquarie perch. There was a significant interaction between predator identity and time (before as after predator exposure) ( $F_{3,136} = 2.938$ ,  $P = 0.036$ ) and a significant interaction between Macquarie perch size and time ( $F_{1,136} = 4.994$ ,  $P = 0.028$ ). Small Macquarie perch tended to reduce activity when exposed to

the predator, whereas large Macquarie perch tended to increase their activity (Fig. 6). When exposed to large redfin perch, Macquarie perch showed little change in activity levels; they reduced their activity levels in response to Murray Cod and small redfin perch, and increased them in response to spangled perch. *Post hoc* tests (Fisher's l.s.d.) suggested that the change in behaviour was significant only in response to the spangled perch ( $P = 0.05$ ).

**Fig. 5.** Mean ( $\pm$ s.e.) change in activity levels when Macquarie perch were exposed to four predators. Negative values represent a decrease in activity and positive values represent an increase in activity from background levels.



**Fig. 6.** Mean ( $\pm$  s.e.) level of activity by large and small Macquarie perch before and during exposure to predators.



## Discussion

Our results indicated that Macquarie perch primarily relied on vision when responding to predatory cues. Interestingly, however, the levels of activity did not vary depending on cue type, suggesting that the detection of predator odours can also result in anti-predator responses. When Macquarie perch visually detected a predator, the general response was to increase activity, decrease the distance to the predator and spend more time inspecting it than was the background level of these activities. They also tend to spend more time on the bottom of the tank, presumably with a view to increasing crypsis during inspection visits (Godin and Davis 1995; Kelley and Brown 2011). Freezing in this manner is a typical

anti-predator response in several species, but is most often displayed by predator-naïve populations (Templeton and Shriner 2004). These general responses, however, were modified principally by the type of predator the Macquarie perch were exposed to. Spangled perch, although relatively small, are highly active and in response to this the Macquarie perch tended to show the most pronounced effects as describe above. In contrast, in response to the Murray cod, which is only moderately active but is a large, natural predator, Macquarie perch tended to decrease their activity levels, stayed further away, spent very little time in the inspection zone and were higher above the substrate. These contrasting responses to the native predators are likely to represent alternative ends of the predator-avoidance spectrum, with spangled perch generally attracting the Macquarie perch and the Murray cod causing avoidance. Such responses are typical of threat-sensitive behaviour towards predators (Lima and Dill 1990; Helfman and Winkelman 1997) and suggest that the spangled perch represented a relatively low threat and the Murray cod a relatively high threat. Previous research has shown similar responses to potential predators by naïve fishes. Predator naïve rainbowfish was highly attracted to an active predator but ignored a passive predator, whereas predator sympatric rainbowfish avoided both active and passive predators (Brown and Warburton 1999). The responses to the introduced predators, small and large redfin perch, seemed to lie somewhere between these two extremes. The large redfin perch invoked no change in activity, the fish spending an intermediate amount of time off the bottom, inspected little and generally maintained their distance, being a response perhaps most similar to avoidance. In response to small redfin perch, in contrast, Macquarie perch decreased activity levels, spent the most time off the bottom, maintained an intermediate distance and spent only a moderate amount of time in the inspection area. This latter response seems to be intermediate in nature, suggesting that Macquarie perch viewed the small redfin as a moderate threat.

When all other things are equal, one would expect small fish to be more cautious of large predators than larger fish because they are more vulnerable to attack (Persson *et al.* 1996; Kelley and Brown 2011). Both the time spent on the bottom of the tank and the level of activity varied depending on the size of the Macquarie perch. The change in the amount of time Macquarie perch spent off the bottom depended both on the size of the Macquarie perch and the identity of the predator. Small Macquarie perch showed an increase in the time near the substrate in response to both native predators and no change in response to redfin perch. This suggests that they were not attempting to hide from the native predators despite the contrasting responses in all other variables. It may well be that, being of similar sizes, the small fish were attracted to the spangled perch and viewed it more as a conspecific than a potential threat. Alternatively, they may simply have been attracted to the novelty (Brown and Warburton 1999). While the distribution of spangled perch overlaps the Macquarie perch, it is unlikely that our population has come into to contact with them in recent history. Small Macquarie perch sensibly maintained a safe distance from the Murray cod and at this distance they felt safe enough to spend more time higher in the water column. Perhaps the activity of the large predator stimulated them to move up in the water column to view the predator from a safe distance. In contrast, large Macquarie perch increased the amount of time on the bottom to redfin perch of both sizes, moved higher in the water column when exposed to spangled perch and showed no response to Murray cod. The response to the spangled perch makes sense; large Macquarie perch are simply attracted to the highly active fish that likely poses no danger to them. However, one wonders why we did not observe a similar response to small redfin perch. It might well be that the redfin perch is less active and more difficult to see and for this reason the large Macquarie perch were a little more reluctant to approach. Large Macquarie perch showed relatively conservative responses to large redfin perch while maintaining a respectable distance.

With respect to the levels of activity, small Macquarie perch tended to be less active than larger Macquarie perch generally, even in the absence of any direct threat. Most interestingly, however, small Macquarie perch tended to decrease their activity further when exposed to the predators, whereas large

Macquarie perch tended to increase their activity levels. This makes some sense, given that even the small predators (spangled perch and small redfin perch) were the same size as the small Macquarie perch and thus presented a threat or, at the very least, a high-level potential for aggressive competition. In contrast, the large Macquarie perch became more animated, particularly in response to the smaller predators and especially the spangled perch.

When taken together, we can see a general pattern emerging that suggests that Macquarie perch responds to invasive redfin perch in a highly dynamic way and one that would be difficult to predict *a priori* but seems to be threat sensitive in nature (Lima and Dill 1990). The response is modified by the size (and presumably the vulnerability) of the Macquarie perch and the size and identity of the predator. In response to the size of the potential predator, Macquarie perch showed a reasonably conservative avoidance of large redfin perch but only intermediate responses to small redfin perch. Threat perception with respect to their own size alters behaviour only in subtle ways in relation to their activity levels and how they use the water column. Similarly, ornate rainbowfish, *Rhadinocentrus ornatus*, has showed higher levels of aggression and activity in the presence of gambusia. Moreover, populations that have lived in sympatry with gambusia for multiple generations have showed evidence of niche and character shifts that seem to enhance their ability to live along-side this aggressive invasive species (Keller and Brown 2008). Such repeated negative interactions with invasive species have resulted in reduced feeding, growth and reproduction in native fish (Howe *et al.* 1997).

In terms of the management implications of these findings, they look somewhat encouraging in that Macquarie perch are not entirely naive when it comes to responding to novel threats. There is, however, a distinct possibility that these fish have already had contact with redfin perch and thus altered their behaviour as a response (i.e. learning; Brown *et al.* 2011). Although no redfin perch were sampled at either of the sites at the time of collection, they have been reported in the catchment. Given the migratory nature of Macquarie perch, it is likely that they move within the catchment (Cadwallader and Rogan 1977), a behaviour that increases the likelihood of meeting a redfin perch at some juncture. However, it is possible that the Macquarie perch are naive with respect to redfin perch and are simply generalising about the potential threat redfin perch might present (Brown and Warburton 1997; Ferrari *et al.* 2008). Large body size and activity levels are two fundamental cues that might determine threat levels (Csanyi 1985; Brown and Warburton 1997), but fish might also rely on overall body shape and facial features such as the shape of the mouth and the presence of large eyes (Karplus *et al.* 1982). Redfin perch have the typical perch body form and are not unlike golden perch and other native predators that persist at the collection site. Further studies will need to be conducted to determine whether Macquarie perch is capable of generalisation; however, such learning is reasonably wide-spread among vertebrates (Griffin *et al.* 2001; Stankowich and Coss 2007) including fish (Ferrari *et al.* 2008) and thus represents a very likely possibility.

Although we have largely concentrated on the response to potential competitors and predators in the present study, we did so using relatively large, experienced fish. Even the juvenile fish in this study were multi-year fish (1+ year of age). There is a wholly practical reason for this and that is that 0+ Macquarie perch are notoriously difficult to sample in the wild. Ideally, one would work with young of the year fish which are highly vulnerable to predation. Attempts to rear this species in captivity have not been successful, but if such efforts were to work, they would provide an opportunity to study the development of anti-predator behaviour in the very early life-history stages of this endangered species. It is quite apparent that direct observations between native and invasive species provide a wealth of knowledge that can be directly applied to management plans. Moreover, greater understanding of the development of antipredator behaviour in this species could considerably boost efforts to establish new populations from hatchery stocks by providing life-skills training (Brown and Day 2002). Future studies could examine

direct competitive interactions between Macquarie perch and invasive fish species, including responses such as shifts in micro-habitat use via competitive exclusion or resource partitioning (Arthington and Marshall 1999; Morgan *et al.* 2003; Harris 2013).

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