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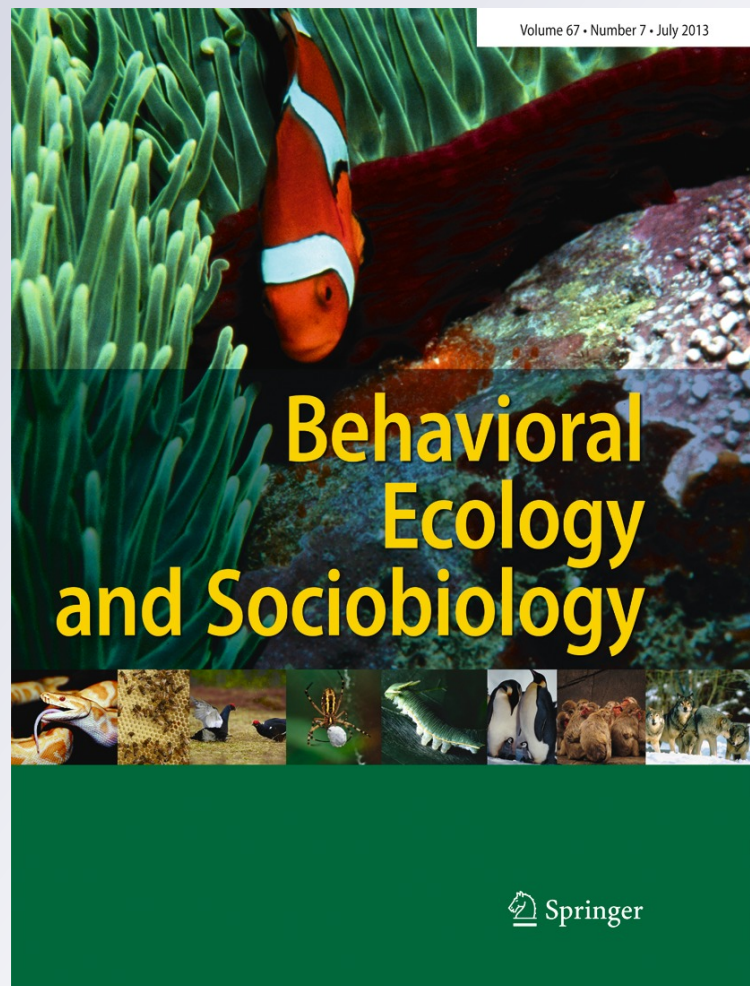
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Ontogenetic differences in chemical alarm cue production determine antipredator responses and learned predator recognition

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Abstract How individuals assess, respond and subsequently learn from alarm cues is crucial to their survival and future fitness. Yet this information is not constant through time; many individuals are exposed to different predators throughout their life as they outgrow some predators or move to habitats containing different predators. To maximise overall fitness, individuals should discriminate between different cues and respond and learn from only those that are relevant to their current ontogenetic stage. We tested whether juvenile spiny chromis, *Acanthochromis polyacanthus*, could distinguish between chemical alarm cues from conspecific donors of different ontogenetic stages and whether the cue ontogenetic stage of the cue donor affected the efficacy of learning about predators. Juveniles displayed a significant antipredator response when conditioned with juvenile chemical alarm cues paired with predator odour but failed to respond when conditioned with predator odour paired with either adult alarm cues or with saltwater. Subsequently, individuals only recognised the predator odour alone as a threat when conditioned with juvenile alarm cues. This demonstrates that prey may be highly specific in how they use information from conspecific alarm cues, selectively responding to and learning from only those cues that are relevant to their developmental stage.

Keywords Predator recognition · Learning · Ontogeny · Threat sensitivity · Coral reefs · Fish

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Introduction

Despite the potential costs associated with encountering predators, learning through experience is critical for many prey species in the development of antipredator strategies. Learned, as opposed to innate, predator recognition endows individuals with the flexibility to adjust responses to match perceived levels of risk as they change through time and space (Lima and Dill 1990; Ferrari et al. 2005). In aquatic environments, chemical alarm cues (released by mechanical damage to the skin during a predation event) serve as a warning about the presence of a predator to local conspecifics and facilitate learnt predator recognition (Chivers and Smith 1998), and their detection significantly enhances survival during predation events (Lönnstedt et al. 2012; Manassa and McCormick 2012). Using chemical alarm cues, prey may gain recognition of predators through associative learning, when they see or smell a novel predator paired with a chemical alarm cue following a predation event (Chivers and Smith 1998). On the next encounter with the predator, prey are able to recognise the predator as a threat in the absence of an alarm cue. Additionally, the concentration of alarm cues during a conditioning event has been shown to determine the level threat associated with the predator during subsequent encounters (Ferrari et al. 2006), allowing prey to match the intensity of their antipredator response with the level of threat (Helfman 1989). Such threat-sensitive responses are critical to balance the inherent costs of antipredator behaviours with those that promote an individual's fitness (Helfman 1989; Lima and Bednekoff 1999).

While threat-sensitive learning has been demonstrated with respect to the concentration of alarm cues released during predation events, there is little understanding of how the developmental characteristics of the captured prey

affects how conspecifics nearby learn about predators. Threat-sensitive learning should not only depend on the concentration of the alarm cue but also on the reliability or relevance of the indicator of risk (Blumstein and Daniel 2004; Blumstein et al. 2004). Prey are exposed to a myriad of cues relating to potential predation risks, yet not all of these cues are relevant or represent an equal level of risk to the individual at any given time. For example, prey are exposed to a variety of gape-limited predators, which display size-specific selection in prey choice, with large predators targeting larger prey (Holmes and McCormick 2010). The relevance of different cues will not only change between conspecifics and heterospecifics (Dalesman et al. 2007) but will likely change throughout development, coinciding with ontogenetic shifts in habitat use and exposure to different groups of predators (Sih et al. 2000). Under such circumstances, prey should preferentially respond to and learn from the alarm cues released by individuals that will provide the most relevant information regarding which predators are a risk to their current developmental stage, e.g. similar sized conspecifics. As such, individuals should learn about predators using chemical alarm cues from different developmental stages in a similar way as they do chemical alarm cues of different concentrations, thus displaying specific responses to alarm cues from individuals at different developmental stages.

Indeed, several studies have demonstrated that responses to chemical alarm cues from both conspecifics and heterospecifics change throughout development, to account for changes in information relevant to balancing risk against other fitness-related activities (Brown et al. 2002; Golub and Brown 2003; Marcus and Brown 2003; Mirza and Chivers 2003; Golub et al. 2005). While research suggests that ontogeny influences responses to chemical alarm cues, evidence is mixed as to whether individuals preferentially respond to cues from conspecifics of a similar developmental stage. For example, brook charr, *Salvelinus fontinalis*, shows a clear threat-sensitive response to alarm cues from different developmental stages, as juvenile brook charr responded to cues from individuals of a similar size with a greater intensity than to cues from larger individuals (Mirza and Chivers 2002). However, other studies have shown that individuals respond with a similar intensity to alarm cues irrespective of developmental stages (Golub and Brown 2003; Brown et al. 2004; Carreau-Green et al. 2008). Many of these studies have been conducted in systems where most predators target all developmental stages of their prey. It seems that the variability in how prey respond to cues from different ontogenetic stages may depend on the complexity of the predator community to which they are exposed.

Little is known about the effects of ontogeny on responses to alarm cues and how individuals learn to recognise predators in complex environments such coral reefs.

The diversity of predator communities in coral reefs is exceedingly high (Bellwood and Hughes 2001), and prey fish are targeted by an ever changing community of predators throughout development (Holmes and McCormick 2010). Consequently, prey fish are under a strong selective pressure to be highly selective when learning about predators. Recently, Lönnstedt and McCormick (2011) found that the response of juvenile damselfish, *Pomacentrus amboinensis*, to conspecific chemical alarm cues diminished with increasing size of the donor individual and juveniles failed to respond to adult alarm cues. A lack of response may suggest that juveniles do not associate cues from adults with a predation risk and that they should not learn from such cues. However, it has been demonstrated that alarm cues that fail to elicit a behavioural response during a conditioning event may still provide relevant information about a predator, enhancing survival during encounters with the predator (Mirza and Chivers 2003), and facilitate learnt recognition of a predator (Brown and Smith 1996; Brown et al. 2001; Ferrari et al. 2005).

The aim of this study was to determine whether a common coral reef damselfish, *Acanthochromis polyacanthus*, learn about predators from conspecifics of different developmental stages in a threat-sensitive manner. The study was conducted in two experiments: firstly, we tested the antipredator responses of juvenile *A. polyacanthus* exposed to chemical alarm cues from small (juveniles) and large (adult) individuals. This enabled us to determine whether threat-sensitive responses displayed by *P. amboinensis* (Lönnstedt and McCormick 2011) occurred in other damselfishes. Secondly, we examined whether juveniles learned to recognize the predator after being conditioned with alarm cues from either juveniles or adults. We predicted that *A. polyacanthus* would learn only from chemical cues from conspecifics providing relevant information on predation risk (i.e. conspecifics at similar developmental stages). We also predicted that prey would display threat-sensitive antipredator responses when learning, thus responding more strongly to chemical alarm cues from size-matched conspecifics and more weakly to chemical alarm cues from larger individuals

Methods

Study species

The spiny chromis, *A. polyacanthus*, (family: Pomacentridae) is an abundant, widespread damselfish that is site attached and is one of the few reef fishes lacking a pelagic larval stage (Thresher 1983). Juveniles remain with parents until they reach approximately 20 mm total length (Connell 2000) and are exposed to a range of gape-limited predators, some of which target all sizes of *A. polyacanthus*.

A. polyacanthus were bred and reared from a breeding population at James Cook University MARFU aquarium facility. Both juveniles and adults were maintained in 80-l flow-through aquaria and fed daily with NRD marine food pellets (Spectrum Aquaculture). Captive breeding ensured juveniles would be naïve to the predator odours. Two dottybacks, *Pseudochromis fuscus* (Pseudochromidae; 6 and 7 cm standard length), a known predator of juvenile fishes (Feeney et al. 2012) were purchased commercially, maintained in individual 40-l aquaria and fed with the same NRD food pellets.

Stimulus preparation

Chemical alarm cues were prepared directly before the start of each conditioning trial. One juvenile per trial and one adult per four trials (a fresh section of the epidermis was damaged to produce cues for each of the four trials) were sacrificed by a blow to head (following James Cook University animal ethics permit: A1067). Twelve superficial incisions were made along each flank of the fish. To ensure the amount of cue produced per trial was consistent between juveniles and adults, a piece of plastic with a 6×3-mm rectangle cut out of it was placed over the juvenile or adult body prior to cuts being made. The fish were then rinsed with 10 ml seawater and the solution filtered to remove any particulates. A total of 30 juveniles (19.18 mm±0.22 SD) and 8 adults (67.43 mm±1.74 SD) were used to prepare the chemical alarm cues.

To make the *P. fuscus* odour, the individuals were placed in separate clean tanks containing 9 l aerated seawater, at 18:00 h each night and left overnight. Ten milliliters of water were then collected from each tank and mixed (20 ml total) prior to the start of each conditioning and predator recognition trial.

Observation tanks

All observations were conducted in 9-l aquaria (30×20×15 cm) containing a 2-cm layer of gravel, a small terracotta pot (5 cm diameter) at one end and an airstone with an injection tube placed at the opposite end. The injection tube allowed food and alarm cues to be introduced into the aquarium with minimal disturbance. A 6×3 grid was drawn (horizontal×vertical) onto the front of each tank, and the tanks were surrounded by black plastic curtains, with a small observation hole cut into the front curtain, to visually isolate the fish from conspecifics and the observer.

Experimental overview

The study was conducted in two experiments. In the first experiment, the ‘conditioning trials’, we exposed juveniles

to predator odour paired with either a juvenile chemical alarm cue, adult chemical alarm cue or saltwater. Behavioural observations during these trials allowed us to record responses to the different alarm cues and a saltwater control. The following day, we conducted the second experiment, the ‘predator recognition trials’. Juveniles that had been exposed to one of the three conditioning treatments were exposed to either predator odour or a saltwater control. During this experiment, we tested if the different conditioning regimes facilitated learned recognition of the predator odour.

Behavioural observations

Individual juveniles were acclimated to the observation tanks for 1 day prior to the experiment starting. The conditioning and predator recognition trials were conducted using the following protocol: an initial feeding period, a pre-stimulus observation period and then a post-stimulus observation period. Fish were fed 20 ml of freshly hatched *Artemia* (250 individuals per ml) 1 h prior to the start of each trial, to ensure fish were well fed prior to the start of the trials. The flow through system was then turned off. Four minutes before the start of the observations, 3 ml of *Artemia* were injected into the tank followed by 15 ml seawater (to flush all the *Artemia* through the injection tube), in order to establish a consistent feeding rate and avoid individuals becoming satiated during the trials. At the start of the pre-stimulus observation period, a further 2 ml of *Artemia* followed by 15 ml seawater were injected into the tank. The focal fish was then observed for the 4-min pre-stimulus observation. Directly following this, 2 ml of *Artemia*, flushed with 15 ml of seawater, were injected and then a randomly assigned stimulus was injected into the tank followed by 15 ml of seawater. The fish was then observed again for 4 min during the post-stimulus observations. For conditioning trials, the stimulus consisted of 20 ml of predator odour paired with 10 ml of juvenile chemical alarm cue, adult chemical alarm cue or saltwater. For the recognition trials, the stimulus consisted of 20 ml of predator odour or 20 ml of saltwater. At the end of each conditioning trial, the fish were left to condition to the stimuli for 20 min before the flow-through system was turned back on to flush the odours from the tanks, ready for the recognition trials the following day. A total of 90 juveniles were placed into one of the three conditioning regimes and tested for their response to either predator odour or saltwater, in a standard 3×6 crossed design ($n=14-17$ individuals per treatment).

During the observation periods, two behaviours were measured: feeding strikes and line crosses. Feeding strikes were defined as any attempted strike at food irrespective of success. Line crosses (proxy for activity) were defined as every time the entire body of the fish

crossed a grid line. Reductions in feeding strikes and reduction in line crosses are both well established proxies for antipredator behaviours (increased vigilance and reduced conspicuousness, respectively) and are known to provide reliable and accurate results across a range of species (Ferrari et al. 2010).

Statistical analysis

Changes in behavioural counts (feeding strikes and line crosses) from the pre-stimulus baseline (post - pre) were used as the raw data for the statistical analysis. A one-factor multivariate analysis of variance (MANOVA) was used to test for the behavioural responses to odours (juvenile alarm cue vs. adult alarm cues vs. saltwater) during conditioning. Significant effects were investigated using ANOVA's and Tukey's HSD means comparisons. To test for learnt predator recognition, the effect of conditioning with chemical alarm cues from conspecifics at different ontogenetic stages (juvenile alarm cue vs. adult alarm cue vs. saltwater) and test odour (predator odour vs. saltwater) on behavioural responses was conducted using a two-factor MANOVA. Again, significant effects were investigated using ANOVA's and Tukey's HSD means comparisons. Residual analysis revealed all data were normal and homoscedastic.

Results

The one-factor MANOVA revealed that there was a significant effect of odour type on behavioural response during the conditioning trials ($F_{4, 168}=28.89, p<0.0001$). Univariate results showed that there was a significant effect on feeding strikes ($F_{2, 85}=66.74, p<0.0001$) and line crosses ($F_{2, 85}=4.69, p=0.0117$). Individuals significantly reduced the number in feeding strikes and line crosses in response to chemical alarm cues from juveniles but not to other cues (Fig. 1).

The two-factor MANOVA showed there was a significant interaction between the conditioning treatment and the testing odour (MANOVA, $F_{4, 162}=13.35, p<0.0001$). This interaction was driven by differences in foraging rate (ANOVA, $F_{2, 82}=30.75, p<0.0001$, Table 1). Individuals conditioned with predator odour paired with juvenile alarm cue and tested for their response to predator odour significantly reduced their foraging rate compared to all other treatment combinations, including those conditioned with predator odour and adult alarm cue (Fig. 2). There was no significant difference in response to any conditioning-by-testing combination for line crosses (Table 1), although the data showed similar patterns to those seen for feeding strikes.

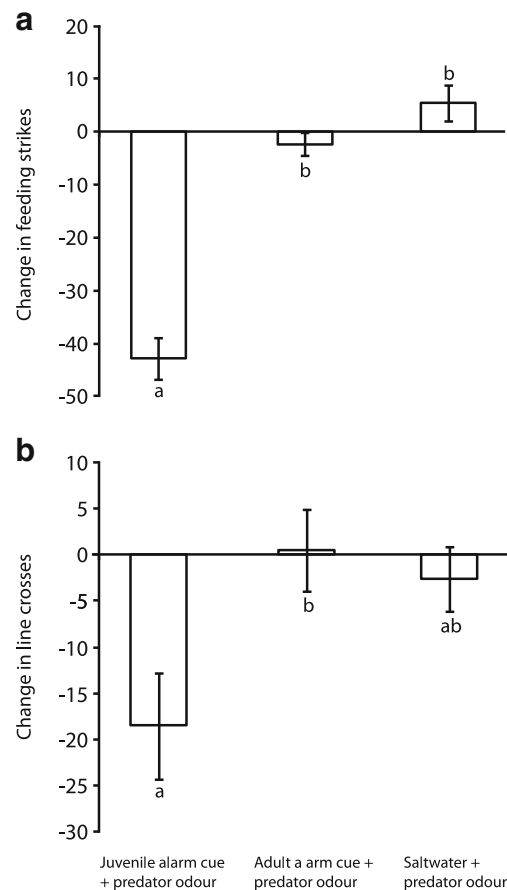


Fig. 1 Mean change (\pm SE) in **a** feeding strikes and **b** line crosses by juvenile *A. polyacanthus* in response to exposure to predator odour paired with either juvenile chemical alarm cues, adult chemical alarm cues or saltwater. Letters below bars indicate Tukey's HSD comparison groupings ($p<0.05$)

Discussion

Our results demonstrate that juvenile *A. polyacanthus* are able to discriminate between the chemical alarm cues of different ontogenetic stage conspecifics and use these cues to learn to respond to predators that are a threat to their current ontogenetic stage. During the conditioning phase, juvenile *A. polyacanthus* displayed distinct antipredator responses (reductions in feeding strikes and activity) when exposed to juvenile chemical alarm cues, but they did not respond to chemical alarm cues from adults. Subsequently, individuals learned to fear the predator odour alone following conditioning using juvenile alarm cues but failed to recognise the predator when conditioned with alarm cues from adults. These results support previous studies demonstrating that prey have the capacity to distinguish between chemical alarm cues originating from conspecifics of different developmental stages and respond to them in a threat-sensitive manner (Mirza and Chivers 2002; Lönnstedt and McCormick 2011). Additionally, to our knowledge, this is

Table 1 Effects of conditioning with chemical alarm cues from conspecifics at different ontogenetic stages or saltwater and test odour on behavioural responses (feeding strikes and line crosses) of juvenile *Acanthochromis polyacanthus*

Source of variation	Feeding strikes			Line crosses		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Conditioning	2, 82	19.732	<0.0001	2, 82	1.949	0.149
Test odour	1, 82	22.564	<0.0001	1, 82	0.151	0.699
Conditioning × test odour	2, 82	30.748	<0.0001	2, 82	0.771	0.466

the first study to demonstrate that the use of chemical alarm cues in predator learning is dependent on the ontogenetic stage of the individual from which chemical alarm cues originate.

Ontogeny clearly plays an important role in risk assessment as individuals need to alter antipredator responses to account for the variable nature of risk as it changes throughout their lifetime. Ontogenetic shifts in response to predation cues with development have been demonstrated for a number of fish species (Brown et al. 2001, 2002; Mirza and Chivers 2003;

Harvey and Brown 2004). Here, we found that ontogeny had a significant effect on responses to conspecific alarm cues in juvenile *A. polyacanthus*. Juveniles displayed antipredator responses when exposed to alarm cues from similar sized individuals but failed to respond to alarm cues originating from larger individuals. Size-dependent responses to chemical alarm cues have previously been demonstrated for freshwater brook char, *S. fontinalis*, (Mirza and Chivers 2002) and coral reef fish, *P. amboinensis* (Lönnstedt and McCormick 2011), with juveniles of both species displaying a stronger response to alarm cues of similar sized individuals than to alarm cues of larger individuals. Both *A. polyacanthus* and *P. amboinensis* completely failed to respond to the cues from larger individuals, unlike brook char who still responded to adult cues but with a reduced intensity compared to cues from similar sized individuals (Mirza and Chivers 2002). Additionally, several species of cichlid responded equally to conspecific chemical alarm cues irrespective of size (Golub and Brown 2003; Mirza and Chivers 2003; Brown et al. 2004; Golub et al. 2005). Although the limited number of species which have been investigated so far prevents making broad generalizations, it appears that freshwater species use alarm cues from all developmental stages, while reef fishes are more selective, responding to only individuals of a similar size. Whether such results arise from species specific responses to the predator communities found within their respective environments is an intriguing possibility that requires further investigation.

Juveniles that failed to respond to alarm cues from adults during the conditioning phase subsequently failed to learn to recognise the predator *P. fuscus* as a threat, whereas those conditioned with juvenile alarm cues responded to *P. fuscus* as a predator. These findings match studies investigating threat-sensitive predator recognition, where the concentration of alarm cue used during conditioning determined the intensity of the response to the predator odour alone (Ferrari et al. 2006; Ferrari and Chivers 2009). However, studies have demonstrated that individuals exposed to chemical alarm cue concentrations that fail to elicit a behavioural response may still learn to recognise a predator (Brown and Smith 1996; Brown et al. 2001; Ferrari et al. 2005). Fathead minnows exposed to the predator odour paired with concentrations of chemical alarm cues weak enough that they failed to elicit an observable

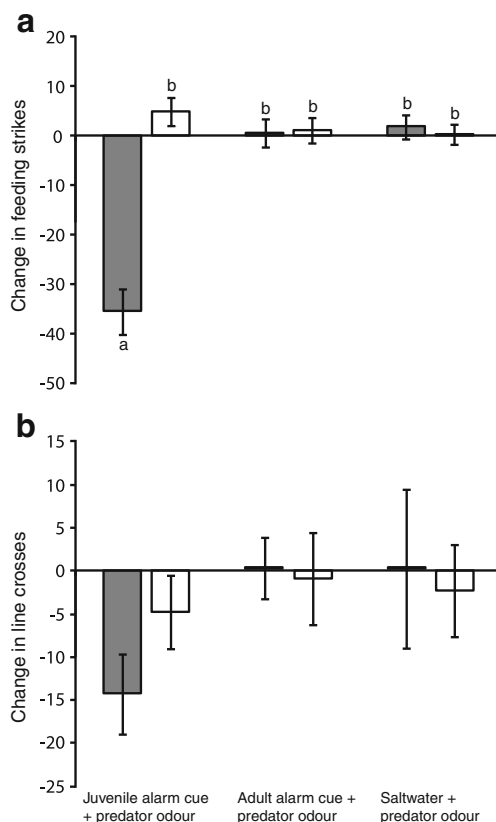


Fig. 2 Mean change (\pm SE) in **a** feeding strikes and **b** line crosses by juvenile *A. polyacanthus* in response to either predator odour (shaded bars) or saltwater (open bars) after being conditioned with predator odour paired with either juvenile chemical alarm cues, adult chemical alarm cues or saltwater. Letters below bars indicate Tukey's HSD comparison groupings ($p < 0.05$)

behavioural response during the conditioning phase, recognised the predator odour when tested at a later time (Brown et al. 2001). However, even weaker concentrations failed to facilitate learned recognition of the predator (Brown et al. 2001). It seems likely that chemical alarm cues from adults act in a similar way to very weak concentrations of chemical alarm cue. It is important to note, however, that the mechanisms that result in the threat-sensitive learning, using either alarm cue concentration or alarm cues from different developmental stages, are possibly not the same. Studies where alarm cues of different concentrations have been used to teach fishes about predators have used cues produced from size-matched individuals (Ferrari et al. 2005) or synthetic cues (Brown et al. 2001). Threat-sensitive responses should therefore be based on perceived changes in the magnitude of risk associated with the concentration of an alarm cue that represents a given level of reliability regarding predation risks. Conversely, threat-sensitive responses to alarm cues from different developmental stages might result from the preys' perception of the relevance of that specific cue to their current developmental stage, or their ability to recognise cues from different stages.

The relevance of information concerning the activity of predators on other developmental stages to a prey individual will depend on the abundance and diversity of the predator community to which prey are exposed. Specifically, the ratio of predators shared by both developmental stages compared to the number of predators specific to each ontogenetic stage. In freshwater systems, where predator diversity is low and predators target all sizes of a prey population, responding to alarm cues irrespective of who they originate from will enhance their chances of survival. In coral reef systems, prey are subjected to intense predation pressure from a highly diverse predator community that changes throughout their development; as predators that target both small and large prey are relatively rare compared to gape-limited predators that target specific size ranges of prey. Consequently, predation events on larger conspecifics may not accurately predict the predation risk for juveniles. Responding to predation risk is selectively advantageous only when it produces higher fitness than ignoring predation risk (Nonacs and Blumstein 2010). Given the need to grow rapidly to escape the extremely high levels of predation experienced following settlement (Almany and Webster 2006), the cost of responding to cues from larger conspecifics may be high and may promote a selective response to alarm cues only from conspecifics of similar size.

This study demonstrates that prey are selective in how they utilise information on predation risk from their environment, responding to and learning only from cues that are relevant to them at that particular time. In environments where prey are exposed to diverse assemblage of predators, many of whom only target specific size ranges of fish, individuals must be

selective with regard to which alarm cues they use to learn about relevant predation risks. Clearly threat-sensitive responses play an important role in optimising antipredator responses, having been demonstrated for alarm cue concentration (Brown et al. 2001; Ferrari et al. 2005), heterospecific alarm cues (Dalesman et al. 2007) and through ontogeny. By responding selectively to cues that are relevant to the specific predation risk they experience prey are expected to enhance their chances of surviving to reproduce.

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Ethical standards This research complies with current laws of Australia and was undertaken with approval of the James Cook University animal ethics committee (permit: A1067) and according to the University's animal ethics guidelines.

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