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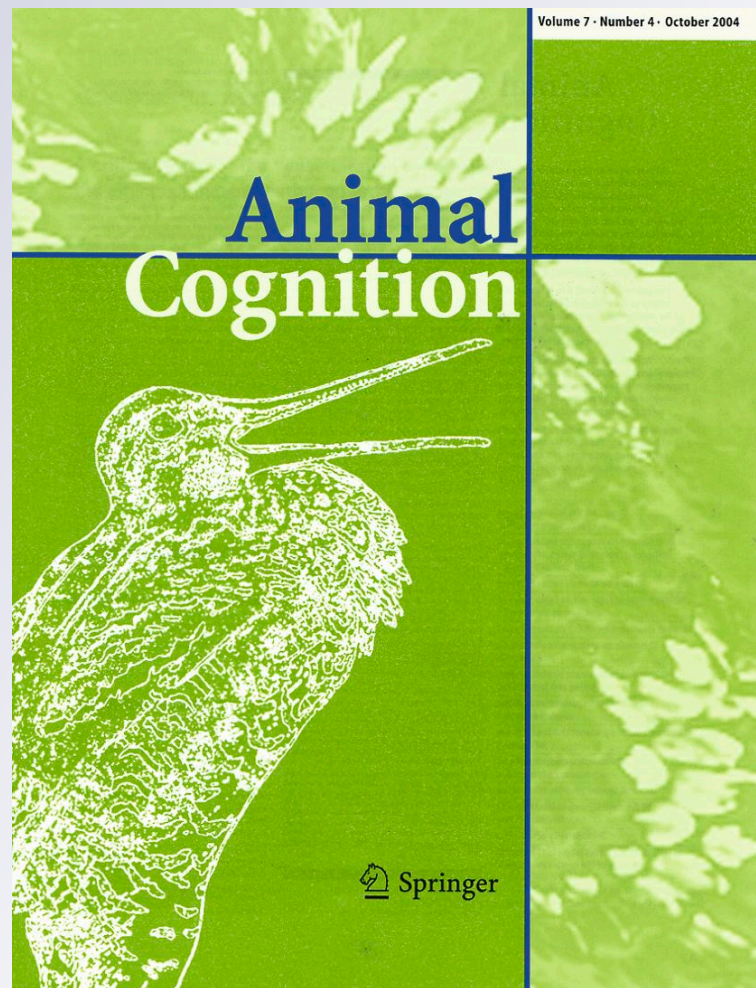
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# Social learning and acquired recognition of a predator by a marine fish

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**Abstract** Predation is known to influence the distribution of behavioural traits among prey individuals, populations and communities over both evolutionary and ecological time scales. Prey have evolved mechanisms of rapidly learning the identity of predators. Chemical cues are often used by prey to assess predation risk especially in aquatic systems where visual cues are unreliable. Social learning is a method of threat assessment common among a variety of freshwater fish taxa, which incorporates chemosensory information. Learning predator identities through social learning is beneficial to naïve individuals as it eliminates the need for direct interaction with a potential threat. Although social learning is widespread throughout the animal kingdom, no research on the use of this mechanism exists for marine species. In this study, we examined the role of social learning in predator recognition for a tropical damselfish, *Acanthochromis polyacanthus*. This species was found to not only possess and respond to conspecific chemical alarm cues, but naïve individuals were able to learn a predators' identity from experienced individuals, the process of social learning. Fish that learned to associate risk with the olfactory cue of a predator responded with the same intensity as conspecifics that were exposed to a chemical alarm cue from a conspecific skin extract.

**Keywords** Coral reef fishes · Chemical cue · Predation risk · Behavioural mechanisms · Social learning

## Introduction

Chemosensory assessment of predation risk is widespread among fish species (Brown 2003) as visual cues are often limited in aquatic systems (Ferrari et al. 2010). In some species, recognition of predators is innate (e.g. Berejikian et al. 2003; Dixon et al. 2010; Wiebe 2004), with an ability to detect predators when first encountered often crucial for survival. However, in other species, the identity of predators must be learnt (Brown 2003). Damage to the epidermis in many organisms results in the release of chemicals that upon detection elicit a fright reaction in nearby conspecific and/or heterospecific individuals (reviewed in Brown 2003). The chemicals that cause this species-specific response are termed 'chemical alarm cues' (Ferrari et al. 2007a).

The temporal coupling of a conspecific chemical alarm cue with the odour of a predator can lead to subsequent olfactory recognition of a threat from the predator's smell alone (Ferrari and Chivers 2006). However, fish do not necessarily require the coupling of these cues to learn the identity of a predator. Social animals may acquire information on predator identities through social learning, where less experienced prey individuals learn from experienced prey members within the social group (Chapman et al. 2008; Ferrari et al. 2007b, 2009; Mineka and Cook 1986, Suboski and Templeton 1989). Social learning is beneficial to naïve individuals as they are able to acquire knowledge without having to directly interact with a potential predator (Holmes and McCormick 2010; Kelley et al. 2003). Individuals that live in single-species or mixed-species aggregations are expected to benefit most from this type of learning as the suite of predator species that an individual will respond to will quickly equate to the sum of the experiences across the whole group (Mathis et al. 1996).

Social learning is widespread among a number of fish taxa (Duffy et al. 2009). A study by Suboski et al. (1990)

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demonstrated that the recognition of a synthetic chemical by naïve zebra danios (*Danio rerio*) occurs through the association of behavioural cues from experienced individuals. Social learning has also been shown in brook sticklebacks (*Culaea inconstans*) (Smith 1999) and harlequin fish (*Rasbora heteromorpha*) (Verheijen 1956), with a study by Mathis et al. (1996) demonstrating that naïve fathead minnows (*Pimephales promelas*) were able to learn a predator identity by observing the fright response of experienced conspecifics in the presence of a predator odour alone. Furthermore, this method of predator recognition allows naïve individuals to learn the intensity of the anti-predator response elicited by experienced individuals (Ferrari et al. 2005). Ferrari et al. (2005) demonstrated that the response intensity of experienced individuals was positively correlated with that exhibited by naïve individuals when tested with only predator odour.

The benefits of social learning, such as forewarning of immediate threats (short-term) and the learned recognition of unfamiliar predators (long-term) (Mathis et al. 1996), predict that social learning of predators should be common among marine species that possess a chemical alarm signalling system. Currently, no research has been undertaken into the importance of social learning in marine fishes. Coral reef fish are exposed to a diverse and unpredictable array of predators differing with every life-stage, necessitating a mechanism that facilitates the rapid learning of predator identities whilst minimising predation risk. Predation pressures are higher during the earlier or transitional life-stages of fishes (Almany and Webster 2006; McCormick and Hoey 2004), suggesting that the use of chemical alarm cues may be essential during this stage as individuals are required to learn rapidly and react appropriately to predators (Holmes and McCormick 2010).

The present study examines the role of social learning in predator recognition for the tropical damselfish, *Acanthochromis polyacanthus*. Specifically, we investigate (1) whether *A. polyacanthus* has a chemical alarm cue and (2) whether this species could transmit the recognition of a natural predator odour, black barred rock cod, *Cephalopholis boenak*, to conspecifics. A series of experiments determined whether naïve individuals could receive and respond to information from experienced individuals and whether conditioned individuals retained the fright response.

## Materials and methods

### Study species

*Acanthochromis polyacanthus* (Pomacentridae) is a reef-associated planktivore that is common in waters of the

Great Barrier Reef, Australia. It has a long embryonic stage (9–16 days), producing large well-developed hatchlings (Donelson et al. 2008; Nakazono 1993; Southgate and Kavanagh 1999) that are guarded by the breeding pair. The predatory species used in this experiment was *C. boenak* (Serranidae), a common predator of reef fishes within the habitats occupied by *A. polyacanthus* (Beukers-Stewart and Jones 2004). Freshwater swordtails, *Xiphophorus helleri*, were used as controls for the addition of skin extract as they are phylogenetically distant from *A. polyacanthus* and lack the damselfish chemical alarm cue (Lason and McCormick 2005).

### Fish collection and maintenance

Breeding pairs of *A. polyacanthus* were collected in June 2005 and July 2005 from Bramble reef (146°41'E, 18°25'S) and Pelorus Island (146°29'E, 18°32'S) using barrier nets, hand nets and a clove oil-alcohol solution (GBRMPA Permit G03/3871.1). *C. boenak* were collected in Pioneer Bay at Orpheus Island (146°20'E, 18°35'S), Great Barrier Reef, Australia, using similar methods (GBRMPA Permit G03/3871.1). Fishes were transported to the James Cook University Marine and Aquaculture Research Facility Unit where they were maintained in aerated 70-l aquaria (*A. polyacanthus*) with flowing saltwater (27.4–28.2 °C). After breeding occurred, hatched juveniles (between 22 and 41 days after hatching) were placed into separate 70-l aquaria in mixed broods of twenty. Offspring were fed commercial fish pellets (INVE Aquaculture Nutrition NRD 2/4 Pellets) daily (~0.055 g per juvenile). Swordtails were obtained commercially and maintained in dechlorinated fresh water at approximately 22.5 °C and fed commercial marine fish flakes and live brine shrimp (*Artemia franciscana*) daily.

### Observation tanks

Experiments and behavioural observations were undertaken in 15-l aquaria with an air stone at the back corner of each tank. An additional piece of plastic tubing, for stimulus injection, was attached to the airline with the end fixed 1 cm above the air stone. Trials showed that dye injected through the stimulus tube took 12-s to disperse throughout the tank. Aquaria had a 2 cm deep substratum of aquarium gravel and a shelter consisting of terrestrial larval rock (9 cm high and 9 cm wide at the highest point) located at the opposite corner to the air stone. Each tank was surrounded on three sides by black plastic to avoid test fish observing adjacent tanks. A random individual, between 165 and 187 days old [mean standard length (SL) ± SE: 48.75 ± 5.25 mm], was selected for each trial with no individual used more than once.

## Stimulus preparation

Skin extracts from *A. polyacanthus* (mean SL  $\pm$  SE: 48.75  $\pm$  5.25 mm) and *X. helleri* (swordtails, as controls) (mean SL  $\pm$  SE: 42.43  $\pm$  1.65 mm) were prepared. Specimens were euthanised by a quick blow to the head and then placed in a clean disposable petri dish, with 25 superficial cuts to the skin (minor flesh damage) made on each side using a clean scalpel blade. Specimens were then rinsed in 15 ml of saltwater, previously obtained from each test tank. In order to remove any solid matter, each 15 ml of stimulus water was filtered through filter paper (125 mm diameter) prior to being drawn up into a syringe, with extracts used within 20 min of preparation.

Predator odours were collected in such a way that they were free of possible *A. polyacanthus* chemical alarm cues. This involved *C. boenak* (mean SL  $\pm$  SE: 170.25  $\pm$  11.40 mm) being fed a 5-day regime: no food on day 1, an individual *X. helleri* on days 2 and 3, no food on days 4 or 5. Individuals were transferred to a clean 15-l tank on day 4, and after 24 h, 60 ml of tank water was collected to be used as an experimental stimulus (water used within 20 min of collection).

## Behaviour of study species

Known anti-predator behaviour in damselfish consists of an increase in shelter use and hence a decrease in the use of vertical and horizontal spaces (Holmes and McCormick 2010). The observation tanks were divided into three equal vertical areas (i.e. bottom, middle and top) and four equal horizontal areas (1–4 increasing from shelter to injection tubing). The use of space was quantified by allocating indices to each area of the tank, both vertically and horizontally.

The location of the individual's body within the tank was recorded at 15-s intervals during both pre- and post-stimulus periods by one observer from behind a blind. The mean difference between the pre- and post-stimulus periods for both horizontal distance from shelter and vertical height above the bottom was calculated. From this information, an index of the relative distance from shelter was determined using Pythagoras' theorem. This index was then examined with ANOVAs, followed by Tukey's HSD means comparison tests when appropriate. Residual analysis was used to examine the assumptions of normality and homogeneity of variance, which were satisfied.

## Experiment 1: Response to conspecific skin extracts

Prior to experimentation, each *A. polyacanthus* juvenile was acclimated in the observation tanks for a period of 5 days, with each tank receiving 30 ml of *A. franciscana* daily (~1 individual per ml of tank water). Prior to each

trial, 60 ml of tank water was drawn up the stimulus injection tube and discarded to remove any residue from previous trials. Following this, a further 75 ml was collected and kept. A pre-stimulus period of 10 min was then conducted. Afterwards, 15 ml of a stimulus (either conspecific skin extract, *X. helleri* skin extract or saltwater) was injected into the tank, followed by 60 ml of previously collected tank water to ensure that the injection tube was empty. A post-stimulus period of 10 min was then undertaken, with a total of 20 replicates for each stimulus. If a significant difference between the response of *A. polyacanthus* to conspecific skin extract and the controls occurred, it was concluded that *A. polyacanthus* possess a chemical alarm cue.

## Experiment 2a: Social learning and acquired recognition of a predator odour (control experiments)

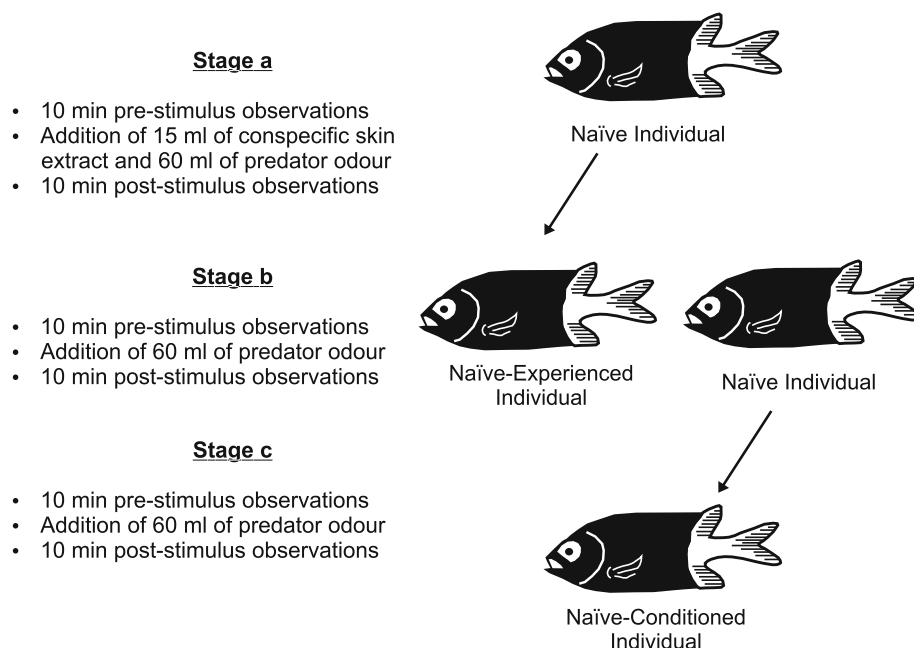
Initially, a series of control trials were undertaken to determine whether naïve *A. polyacanthus* have an innate recognition to the chemical cues of *C. boenak*. *A. polyacanthus* were acclimated to the observation tanks for 2 days. Prior to each trial, 60 ml of tank water was drawn up the stimulus injection tube and discarded to remove any stagnant water. Following this, a further 60 ml was collected and kept. After the pre-stimulus observation period, 60 ml of predator odour was injected into the tank followed by 60 ml of previously collected tank water. Post-stimulus observations were then conducted, with 20 replicates undertaken. If no significant difference between the response of *A. polyacanthus* to saltwater and the response to predator odour was observed, it was concluded that there was no innate recognition of *C. boenak*.

## Experiment 2b: Social learning and acquired recognition of a predator odour

To determine whether social learning of a predator odour occurred in *A. polyacanthus*, experiments were conducted in three separate stages: (a) conditioning of a naïve *A. polyacanthus* to a predator by temporal coupling of the smell of a predator with a conspecific chemical alarm cue; (b) exposure of a second naïve conspecific to the response of the individual conditioned in 'a' to a predator odour alone; and (c) testing for an anti-predator response of the individual conditioned in 'b' to a predator odour alone (Fig. 1). If the individual in stage 'c' responds to the predator odour with an anti-predator response, then this was evidence that the second fish has learnt that the predator odour represented a potential threat through social learning.

Prior to the start of the experiment, individual *A. polyacanthus* were acclimated to the observation tanks for 2 days. Stage 'a' of the experiment involved the exposure of single randomly selected naïve *A. polyacanthus* to a

**Fig. 1** Flow chart illustrating the three-stage experimental design



solution of 15 ml of the conspecific skin extract and 60 ml of predator odour injected through the stimulus tube, followed by 60 ml of previously collected tank water (to flush the stimuli into the tank). Behaviour was recorded during both pre- and post-stimulus periods.

Stage 'b' of the experiment required that immediately following stage 'a', the now experienced individual was rinsed in clean saltwater and then transferred to another observation tank housing a naïve individual (acclimated for 2 days), which was either 5 mm smaller or larger than the conditioned fish to enable the individual identification. The two individuals were then acclimated in the tank for 2 h before observations commenced. After the acclimation period, 60 ml of tank water was drawn up the stimulus injection tube and discarded and a further 60 ml collected and kept. After a 10 min pre-stimulus period, 60 ml of predator odour was injected through the tank stimulus tube followed by 60 ml of previously collected tank water. Post-stimulus observations were then undertaken for 10 min on both individuals ( $n = 20$  replicates).

Stage 'c' of the experiment required that immediately following stage 'b', the naïve individual from that stage was rinsed in clean saltwater and then transferred to an empty observation tank and acclimated for 2 h before observations commenced. After the acclimation period, 60 ml of tank water was drawn up the stimulus injection tube and discarded and a further 60 ml collected and kept. After the 10 min pre-stimulus period, a 60 ml filtered aliquot of predator odour was injected followed by 60 ml of previously collected tank water. Post-stimulus observations were then undertaken for 10 min ( $n = 20$  replicates).

A series of controls ( $n = 20$  replicates) were undertaken to ensure the integrity of the experimental design. These tri-

als replaced the 15 ml of the conspecific skin extract (injected in stage 'a') and 60 ml of predator odour (injected in stages 'a', 'b' and 'c') with 60 ml of saltwater.

## Results

### Response of *A. polyacanthus* to conspecific skin extracts

The behavioural response of *A. polyacanthus* to three test stimuli was examined: response to conspecific skin extract (treatment), response to *X. helleri* skin extract (control) and response to saltwater (control). *A. polyacanthus* were found to decrease their distance from shelter when the conspecific skin extract was injected (Fig. 2;  $F_{2,57} = 12.579$ ,  $P < 0.001$ ) compared to the two control stimuli. There was no change in behaviour in response to the *X. helleri* skin extract or saltwater controls ( $P = 0.607$ , Fig. 2).

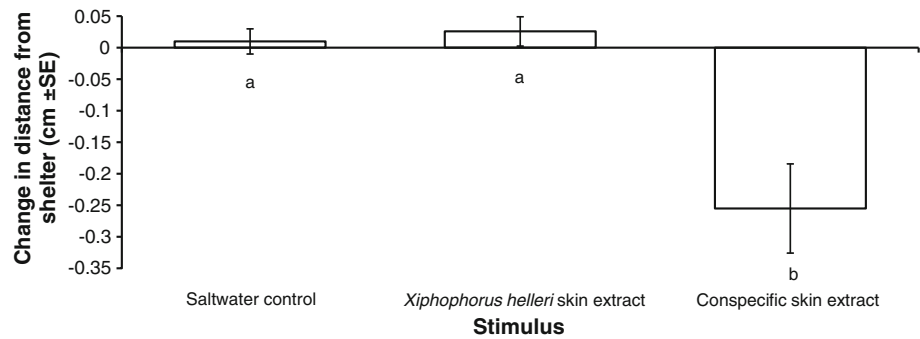
### Response of *A. polyacanthus* to odour of *C. boenak*

The behavioural response of *A. polyacanthus* to the odour of *C. boenak* was examined and compared to the response elicited to saltwater (Experiment 1), with no significant differences in distance from shelter observed (Figs. 2, 3;  $F_{1,38} = 0.469$ ,  $P = 0.498$ ).

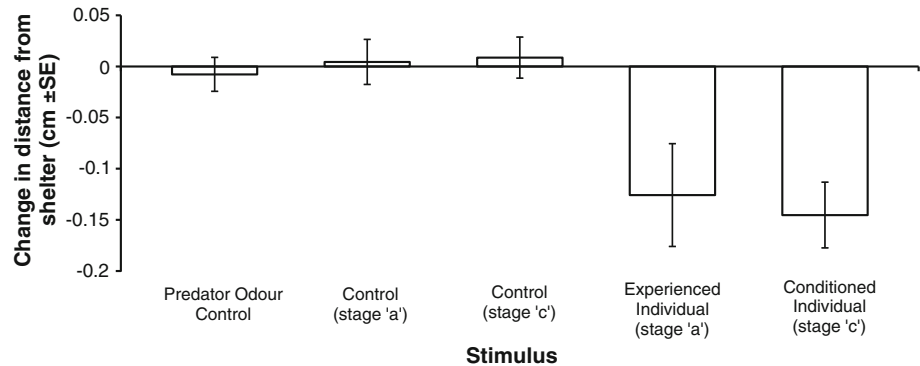
### Social learning in *A. polyacanthus*

No significant differences in distance from shelter between the control individual in stage 'a' and the control individual in stage 'c' were observed (Fig. 3;  $F_{1,38} = 0.020$ ,  $P = 0.888$ ). Likewise, no significant difference between the

**Fig. 2** Mean change ( $\pm$ SE) in distance from shelter by *A. polyacanthus* between 10 min pre- and post-stimulus periods, for fish exposed to; saltwater control, *X. helleri* skin extract or conspecific skin extract. Letters above or below the bars represent Tukey's HSD groupings of means



**Fig. 3** Mean change ( $\pm$ SE) in distance from shelter by *A. polyacanthus* between 10 min pre- and post-stimulus periods, for fish exposed to; predator odour control, saltwater control (stage 'a'), saltwater control (stage 'c'), conspecific skin extract and predator odour (experienced individual stage 'a') or predator odour (conditioned individual stage 'c')



experienced individual in stage 'a' (exposed to the conspecific skin extract and predator odour) and conditioned individual in stage 'c' (observed the conditioned fish during exposure to predator odour) occurred (Fig. 3;  $F_{1,38} = 0.107$ ,  $P = 0.745$ ).

In keeping with the predictions of social learning, there was a difference in tank use between conditioned individuals in stage 'c' and fish that were exposed to predator odour alone (Fig. 3;  $F_{1,38} = 14.458$ ,  $P < 0.001$ ), with conditioned individuals decreasing their distance from shelter when tested. Differences were also seen between the conditioned individuals in stage 'c' and the control fish in stage 'c' (Fig. 3;  $F_{1,38} = 16.493$ ,  $P < 0.001$ ).

The response of conditioned individuals in stage 'c' was compared to the response elicited to the pure conspecific skin extract (Experiment 1), with no significant differences in distance from shelter observed (Figs. 2, 3;  $F_{1,38} = 1.994$ ,  $P = 0.166$ ).

## Discussion

This study highlights the importance of olfactory cues for predator recognition in a complex reef environment. The tropical fish species studied, *A. polyacanthus*, was found to possess and respond to conspecific chemical alarm cues, with naïve individuals able to socially learn the identity of a predator from experienced individuals. This is the first documentation on a coral reef fish to demonstrate the

importance of social learning for predator recognition, highlighting the speed with which information on the identity and activities of a predator could be transmitted through a local prey population.

The retreat towards shelter displayed by juvenile *A. polyacanthus* in response to chemicals from injured conspecifics demonstrates that this species possesses a chemical alarm cue. This response appears to be typical anti-predator behaviour exhibited by damselfish, with previous studies on two species (*Pomacentrus moluccensis* and *Pomacentrus amboinensis*) demonstrating similar responses (Holmes and McCormick 2010). The behaviour of *A. polyacanthus* to its chemical alarm cue was not a generalised response to the cue of an injured fish as no reaction was exhibited to the skin extracts of a phylogenetically distant fish (*X. helleri*).

The present study also demonstrated that naïve *A. polyacanthus* have the ability to recognise and respond to predators by learning through social interactions with experienced members of the social group. When a naïve fish was placed into a tank with an experienced individual, the naïve fish was given the opportunity to observe and thus possibly 'learn' how to respond to a predator odour. Later, when tested alone, the naïve fish exhibited a fright reaction similar to that of the experienced individual in the previous stage, indicating that learning through social enhancement had occurred. What is also of interest is that the response of the naïve fish in stage 'c' to the predator odour was not significantly different to that elicited to the pure conspecific chemical alarm cue.

This study is the first to demonstrate social learning as a mechanism of acquiring predator identities in a marine organism and is similar to the findings from research on freshwater fishes including *Phoxinus phoxinus* (European minnows), *P. promelas* (fathead minnows), *D. rerio* (zebra danios), *Poecilia reticulata* (guppies), *Oncorhynchus tshawytscha* (chinook salmon), *Oncorhynchus mykiss* (rainbow trout) and *Gasterosteus aculeatus* (three-spined sticklebacks) (reviewed by Brown and Laland 2001). It is well known that anti-predator behaviour in freshwater fishes is acquired largely through learning (Brown and Laland 2001), with encounters throughout life assisting the development of anti-predator skills (Laland et al. 2003). Olfactory learning mechanisms enable fish to augment or modify their innate response to predators and fine-tune their responses to local conditions. Brown and Laland (2001) suggest that animals which use social learning as a means of predator recognition are capable of acquiring these skills rapidly.

It is known that some species of prey require only a single exposure to their conspecific alarm substance coupled with the visual or chemical cue of a predator, for the stimulus to be labelled as a threat (Brown 2003; Ferrari et al. 2005; Holmes and McCormick 2010; McCormick and Manassa 2007). After a single exposure to an olfactory cue, long-lasting changes in anti-predator behaviour result (Brown 2003), with evidence suggesting that behaviour acquired through social learning allows for a more appropriate and effective response to develop (Hoare and Krause 2003). Social learning allows for a rapid spread of anti-predator behaviour among fishes within visual contact of one another (Suboski et al. 1990), as naïve individuals are capable of 'learning' from conspecifics without having to endanger themselves directly. It may therefore be expected that social learning of predator identity or activity should be commonplace among fish species as large risks are associated with eyewitness learning (Brown and Laland 2003).

The two novel findings from this study—*A. polyacanthus* possess a chemical alarm signalling system and social learning is used as a method of predator recognition in marine systems—support the idea that social learning is a widespread method for acquiring information about predation events in aquatic ecosystems (Shettleworth 2010). As visual information is often limited by turbidity and/or topography on coral reefs, social learning provides individuals with an energetically inexpensive and 'safe' tool for predator recognition. As many species of coral reef fish live social and communal lifestyles, it is expected that they could benefit greatly from this method of predator recognition, as it would allow continuous updates and reinforcement of current predation events within the immediate area. A recent study conducted on a newly settled (after the

initial pelagic larval stage) damselfish *P. amboinensis* demonstrated that previous exposure to predators enhanced their probability of avoidance and escape, directly increasing survival (McCormick and Holmes 2006). Social learning is likely to propagate through entire populations rapidly, with a previous study conducted by Chivers and Smith (1995), demonstrating that predator information can be transmitted through populations, resulting in a predator-aware community.

The levels of predation fluctuate with life-stage and environmental conditions; therefore, prey are required to continuously learn new predator identities and modify the risk rating of those that no longer represent a threat. Coral reefs are complex ecosystems with a number of chemical alarm cues and predator odours present at any one time. Under these conditions, it would be challenging for individuals to determine which information to respond to and which to ignore. As such, field studies that examine the use of social learning as a method of learning predator identities are difficult due to the necessity for individuals to be naïve to predator odours initially. Along with this, higher than normal concentrations of chemical cues are often used in laboratory studies to ensure the recognition of predator odours.

A study conducted in freshwater systems on fathead minnows showed that fish rely on the most recent information when adjusting the intensity of their anti-predator response (Ferrari and Chivers 2006). However, as there are distinct differences between freshwater and coral reef environments, further assessment into the chemosensory learning mechanisms of marine species is required. Studies should focus on the importance of social learning, the conditions under which it is considered beneficial for an individual to use this form of predator assessment, and how individuals reinforce important information whilst forgetting information that is no longer relevant to the assessment of risk.

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