

Habitat degradation disrupts neophobia in juvenile coral reef fish

MARK I. MCCORMICK¹, DOUGLAS P. CHIVERS², BRIDIE J. M. ALLAN¹ and MAUD C. O. FERRARI³

¹ARC Centre of Excellence for Coral Reef Studies, College of Marine and Environmental Sciences, James Cook University, Townsville, Qld 4811, Australia, ²Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 5E2, Canada,

³Department of Biomedical Sciences, WCVI, University of Saskatchewan, Saskatoon, SK S7W 5B4, Canada

Abstract

Habitat degradation not only disrupts habitat-forming species, but alters the sensory landscape within which most species must balance behavioural activities against predation risk. Rapidly developing a cautious behavioural phenotype, a condition known as neophobia, is advantageous when entering a novel risky habitat. Many aquatic organisms rely on damage-released conspecific cues (i.e. alarm cues) as an indicator of impending danger and use them to assess general risk and develop neophobia. This study tested whether settlement-stage damselfish associated with degraded coral reef habitats were able to use alarm cues as an indicator of risk and, in turn, develop a neophobic response at the end of their larval phase. Our results indicate that fish in live coral habitats that were exposed to alarm cues developed neophobia, and, *in situ*, were found to be more cautious, more closely associated with their coral shelters and survived four-times better than non-neophobic control fish. In contrast, fish that settled onto degraded coral habitats did not exhibit neophobia and consequently suffered much greater mortality on the reef, regardless of their history of exposure to alarm cues. Our results show that habitat degradation alters the efficacy of alarm cues with phenotypic and survival consequences for newly settled recruits.

Keywords: chemical alarm cues, climate change, coral degradation, coral reef fish, habitat loss, neophobia, olfactory cues, predator–prey interactions, risk assessment, survival

Received 24 April 2016 and accepted 1 June 2016

Introduction

Habitat degradation is one of the main causes of species extinction and community change globally (Lambin *et al.*, 2003; Lotze *et al.*, 2006; Spalding & Brown, 2015). Habitat degradation can be seen as a change in states between one where the provision of resources leads to an ecosystem with high complexity and species diversity, to a state where the resources do not support communities of high diversity (Doak, 1995). The drivers of degradation include land clearing and sedimentation, eutrophication and pollution, and these are compounded by the broader-scale issues of changing global weather patterns caused by increasing levels of atmospheric CO₂ (Holoak & Heath, 2016). Regardless of the causes of the change in habitat resources, habitat degradation is a gradual process that occurs on time scales relevant to both ecological (Alvarez-Filip *et al.*, 2015; Wong & Candolin, 2015) and evolutionary processes (Munday *et al.*, 2013; Santos *et al.*, 2015). Community change occurs through the loss of various resources on

scales of patchiness that slowly gets greater with time. Habitats are most dramatically affected when habitat-forming species such as large primary producers including trees, shrubs, kelps and corals change their spatial patterns (Hughes *et al.*, 2007; Filbee-Dexter & Scheibling, 2014). Then, species that rely on these must alter their patterns of resource use or migrate to compensate. It is the capacity of species to compensate for a changing resource base that determines the speed and nature of change at the community level (Colles *et al.*, 2009).

As the organisms that comprise the community in which an animal lives change, or when an animal migrates between habitats in search of limited resources, successful individuals will be those that can efficiently update the information about safe and dangerous sites. By doing so, these individuals can best balance asset-promoting behaviours, such as foraging and mating, with predator vigilance to maximize fitness. The type of information used by prey to assess risk will be determined by how well particular sensory cues penetrate the habitat, and the extent to which cues are altered by the characteristics of the habitat between their source and recipient (McCormick & Lönnstedt,

Correspondence: Mark I. McCormick, tel. +61 409371015, fax +61 747251570, e-mail: mark.mccormick@jcu.edu.au

2013). For instance, visual cues are of limited value for judging risk in dense forest, but may prove very useful in an open savannah.

In aquatic environments, olfactory cues have been shown to be a crucially important source of information on which to reliably judge risk (Chivers & Smith, 1998). Most aquatic organisms, including corals, insects, fishes and amphibians, have an innate avoidance of damage cues released from closely related or ecologically similar species (Ferrari *et al.*, 2010). These chemical alarm cues play an important role in the rapid cataloguing of predator identity through associative learning, which can then be passed onto bystanders through social learning (Crane & Ferrari, 2013). These cues pass through an aquatic environment that is already made up of a cocktail of odours emanating from each ecosystem component, comprised of both the habitats and the community that live within it. The fact that species-specific chemicals can be identified within this olfactory milieu is a testament to the sophistication of this risk assessment mechanism (Mitchell *et al.*, 2011). However, recent evidence suggests that a marine damselfish species has a limited ability to use alarm cues for risk assessment when the odour has passed over degraded coral habitat (Lönnerstedt *et al.*, 2013, 2014). Whether this response reflects a lack of detection or a lack of motivation to respond to the cues is unknown. The lack of an overt behavioural response also does not mean that the prey cannot incorporate the information into its risk decision-making algorithm (Brown & Smith, 1996).

Most species are most vulnerable to predation during their early life stages and when they enter a novel habitat during a life-history transition, that is, when predator naiveté is at its highest. Thus, these individuals should have reliable and rapid methods of assessing and learning risk, a skill crucial to their survival. For aquatic organisms with complex life cycles, such as insects, amphibians and fishes, alarm cues have been found to be important in the rapid assessment of risk when entering a settlement habitat at the end of the larval phase (Lönnerstedt *et al.*, 2012). If the habitat is assessed as being of high risk, then risk-averse behaviours are promoted in response to all novel stimuli, a state that is termed neophobia (Brown *et al.*, 2013). Having a well-developed and behaviourally flexible response to predator threats is key to the survival of many organisms. As organisms move into new habitats with new and usually variable predation threats, there will be uncertainty about the reliability of public information on which to judge general risk (Dall *et al.*, 2005). Neophobia is seen as a way of reducing the risk associated with initially learning local threats. However, because responding to all unknown cues as a threat is

costly, neophobia is an inducible response and elicited by the perceived background level of risk (Brown *et al.*, 2014). The benefits of this neophobic state are many and include increased laterality (i.e. the preferential use of one side of the body) that promotes more efficient escape responses, more conservative behaviour and higher initial survival in the field (Ferrari *et al.*, 2015a). Given the importance of olfactory cues for risk assessment in aquatic organisms, it is currently unknown the extent to which the chemical cues from degraded habitats alter risk assessment and the development of neophobic behavioural types. If the chemistry from degraded coral habitats alters risk cues, it is likely to subsequently adversely affect mortality in these vulnerable juveniles.

This study examines whether degraded coral habitats affect the ability of a fish to gauge risk, develop neophobia and hence adopt a risk-averse behavioural phenotype that promotes survival when they first enter a new habitat. The study involves the manipulation of risk history in the laboratory under conditions that mimic being in a habitat dominated by live coral or degraded algal-covered dead coral and then testing them in the laboratory to see whether they have become neophobic to novel olfactory cues. We also placed them in the field, on habitat patches of live or degraded coral and quantified their natural mortality trajectories. Given the impact of coral degradation on the utility of alarm cues found by recent studies (Lönnerstedt *et al.*, 2013, 2014), we predict that the development of neophobia may be compromised in degraded habitats and this will have an impact on survival through space use and their ability to judge risk.

Materials and methods

Study species and collection

The field and laboratory studies were conducted at Lizard Island Research Station (14° 40' S, 145° 28' E) and fringing reef, on the northern Great Barrier Reef, Australia, during October–November 2015. The Ambon damselfish, *Pomacentrus amboinensis*, is a common fish within coral reef fish communities of the Indo-Pacific (especially on the Great Barrier Reef), and adults are found in highest densities in shallow areas with a mixture of sand, rubble and live hard coral (McCormick & Meekan, 2007; McCormick & Weaver, 2012). Juveniles settle from the larval phase after 15–23 days [at about 10–12 mm standard length (SL)] to a broad range of habitats including live coral (70% of settlers), dead coral (20%) and rubble (10%) (McCormick & Weaver, 2012). For this study, fish at the end of their larval stage were collected in light traps (Meekan *et al.*, 2001) at night and returned to the laboratory in 60-L tanks, sorted by species and transferred to 35-L tanks of aerated flow-through seawater. Light

traps were moored at least 30 m from the nearest reef edge. As such, the fish we caught had not yet experienced the fish community on the benthic coral reef habitat and were naive to the specific predators that awaited them upon settlement (Lönstedt *et al.*, 2012). Previous research on the Ambon damselfish has found that the newly settled fish have an innate antipredatory response to damage-released chemical cues from the skin of conspecifics both in the field and laboratory (Lönstedt *et al.*, 2013). This antipredatory response involves reduced foraging and activity, and increased shelter use, and is similar to the reaction shown in many other damselfishes (e.g. Ferrari *et al.*, 2011; Lönstedt *et al.*, 2012). To test the responses of fish to a novel predator, we used the odour of dusky dotyback, *Pseudochromis fuscus*. Dotybacks naturally prey on juvenile Ambon damselfish, but the prey fails to exhibit behavioural response to the dotyback unless they have experience (Holmes & McCormick, 2010; Feeney *et al.*, 2012). In the current study, dotyback odour was generated from two dusky dotyback (11.3–14.1 cm total length) which had been previously collected from the shallow fringing reef around Lizard Island. Dotyback were maintained in 5-L tanks with flowing seawater pumped to the Lizard Island research station straight from the back-reef lagoon and backup aeration was supplied through an airstone. The flow was stopped for 2 h prior to collection of the water that contained the dotyback odour, and the odour was used fresh.

Coral degradation manipulations

Throughout this study, we used either live healthy or dead-and-degraded *Pocillopora damicornis* (hereafter referred to as coral). It is a common bushy hard coral around the Lizard Island fringing reef and is a common nursery habitat for reef fishes. The live healthy coral and dead/degraded corals used had similar structural complexity. For the purpose of our experimental manipulation, we define a degraded habitat as *Poc. damicornis* that had been dead for approximately 3 months to 1 year, had a similar structural complexity to live coral, but was covered a variety of algae and sessile invertebrates (Fig. S1).

Phenotypic expression of neophobia

In fish and amphibians, short-term exposures to alarm cues (i.e. conditions mimicking a high-risk environment) have been shown to induce the neophobic phenotype described above (Brown *et al.*, 2013). We thus manipulated background level of risk to induce the expression of the neophobic phenotype. High-risk conditions were generated by exposing fish to injured conspecific cues three times a day. Low-risk condition tanks received seawater injection three times per day, to control for any disturbance. Injections occurred on a random schedule, between 07:00 and 18:00, with at least 1.5 h between successive injections. Injured conspecific cues were chosen as they represent a reliable indicator of risk, but do not provide any information regarding the source of the risk. These cues were prepared by sacrificing donor fish via cold shock and

making several vertical cuts on each side of the donors. Each donor was then rinsed with a small quantity of seawater such that when 5 mL of the solution was injected into each tank, we achieved a final concentration of two cuts L⁻¹ in the tank. This concentration is known to elicit overt antipredator responses in this species (Chivers *et al.*, 2014). Cues were prepared 3–5 minutes prior to being used to condition the fish. The risk treatment lasted for 4 days and fish were tested the following day.

Experiment 1: Effect of degraded habitat on the development of neophobia

This experiment followed a 2 × 2 design where fish were maintained in seawater flowing over either live healthy or degraded coral and exposed to high- or low-risk conditions for 4 days. The fish were then tested for their response to a novel predator odour and their behaviour was recorded.

Treatment exposure. Juvenile *P. amboinensis* were placed in groups of three fish in 5-L plastic exposure tanks that had water flowing into them from header tanks (15-L buckets) that contained a piece (~60 cm in circumference) of either live or degraded coral. The header tanks were equipped with an airstone, and fresh seawater was constantly flowing through at a rate of 1 L min⁻¹. Each header tank was plumbed to allow the overflow to fall into eight 5-L exposure tanks. Each tank thus received water at a rate of ~0.13 L min⁻¹ (one tank turnover every 40 minutes). The pieces of coral in each header tank were changed daily. Fish were randomly placed in their tanks, and the risk treatment started the following day.

The eight fish tanks from each header tank were randomly divided into four high-risk and four low-risk tanks and fish were treated for 4 days as described above. One hour after the end of the last injection, fish were moved in preparation for the testing phase.

Testing phase. Fish (~11 mm SL) were moved individually into similar 5-L plastic tanks, equipped with a sand substrate, a moulded plastic branched coral object (15 cm high) serving as shelter, and an air stone, to which was attached a 1.5-m-long injection hose. A 4 × 4 cm grid was drawn on the tank to facilitate data collection. Each test tank received flow-through water from a header tank containing live or degraded coral, as described above. The fish were left to acclimate overnight and were tested the following day.

The bioassay followed established protocols. We first introduced 2 mL of an *Artemia* solution containing ~100 *Artemia* mL⁻¹. After 3 min, we injected another 2 mL of food and started the 3-min prestimulus observation period. During that time, we recorded the number of feeding strikes of the fish (regardless whether they were successful) and the number of grid lines crossed. After this baseline observation period, we injected 15 mL of dotyback odour, followed by another 2 mL of food, and recorded the behaviour of the fish for another 3 minutes. The difference between the pre- and post-stimulus period indicates the response of the fish to the cues.

A reduction in feeding and activity is both well-established antipredator responses (Ferrari *et al.*, 2010). The observer was blind to the treatment, and the order of treatment was randomized.

Experiment 2: Influence of degradation on behaviour and survival of neophobic fishes in the field

This experiment also followed a 2×2 design where fish were maintained in water flowing from either live healthy or degraded coral and exposed to high- or low-risk conditions for 4 days. In contrast to Experiment 1, the fish were then released in the wild, and their *in situ* behaviour and survival were monitored.

Treatment exposure. This phase was nearly identical to that described in Experiment 1. One notable exception is that light-trap-caught *P. amboinensis* were tagged with one of four fluorescent elastomer tags (see Hoey & McCormick, 2006 for protocol) 4 hours after being sorted into species groups. Groups containing equal numbers of fish from each colour tag were randomly formed and placed into each of 16 tanks. Fish were subsequently kept for 4 days prior to release during which time we manipulated background environment odours (live vs. dead coral) and risk (low vs. high).

Field protocol. Fish were placed individually into 1-L, numbered plastic bags of aerated seawater and photographed against a 1-cm grid for size determination using ImageJ (U. S. National Institutes of Health, Bethesda, MD, USA, <http://imagej.nih.gov/ij/>, 1997–2016). Fish were then transported to the experimental site in their respective plastic bags in a darkened 60-L container of seawater to minimize the stress associated with transport. Fish were then released individually onto numbered patch reefs ($25 \times 20 \times 20$ cm) consisting of alternating live healthy *Poc. damicornis* or dead-and-degraded *Poc. damicornis* established 3–8 m away from the reef edge in 2–3 m of water. Fish were released in a blocked design so that treatments were interspersed down the reef edge, and fish with the same colour of tag and treatment were not adjacent. This allowed us to determine whether any migration associated with habitat type occurred in the experimental fish.

Behavioural assessment. One to 3 hour after release onto the patch reefs, a single observer (MIM) assessed the behaviour and space use of the fish using a well-established behavioural protocol (e.g. McCormick, 2009). In brief, fish behaviour was assessed over a 3-minute period by an observer that was ~1.5 m away from the patch reef with the aid of a magnifying glass. Four aspects of activity and space use were assessed: (i) bite rate, (ii) total distance moved (estimated from knowing the length of each reef), (iii) maximum distance ventured (DV) from the habitat patch and (iv) boldness. Boldness was assessed using a continuous scale between 0 and 3 where 0 is hiding in hole and seldom emerging; 1 is retreating to hole when scared and taking more than 5 seconds to re-emerge, weakly or tentatively striking at food; 2 is shying to shelter of patch when scared but quickly emerging, purposeful strikes at

food; and 3 is not hiding when scared, exploring around the coral patch, and striking aggressively at food (McCormick, 2009). At the end of the 3-minute observation period, the fish was approached with a pencil and the fish's reaction and latency to emerge from shelter was taken into account in the assessment of boldness. This boldness measure has been shown to be repeatable (e.g. repeatability values of ~0.5 over a 2-hour period; White *et al.*, 2013, 2015). Three-minute behavioural assessments have previously been found to be sufficiently long to obtain a representative estimate of an individual's behaviour (McCormick & Weaver, 2012; White *et al.*, 2015). The observer was blind with regard to risk treatment.

Survival monitoring. Fish on patch reefs were monitored twice per day for 72 hours. On the rare occasion that other fishes settled to the occupied reefs, these were removed with a dip net at the time of census. These intruders were released onto the main reef, well away from the patch reefs.

Statistical analyses

Experiment 1. The two behaviours recorded (foraging and activity) were analysed together using a MANOVA to test for differences between treatments. We first tested for any behavioural difference in their baseline (prestimulus) activity and foraging levels between treatments. We then computed a proportion change in behaviour ((post/pre)/pre) and used these variables in our subsequent analyses. For both analyses, we ran a 2×2 MANOVA, testing the effect of habitat (live vs. dead coral) and risk (low vs. high) on the fish behaviour. Two-factor ANOVAS were used to determine the nature of differences found by MANOVA, and these were followed by Tukey's HSD means comparisons when necessary.

Experiment 2. To determine whether the behaviour of *P. amboinensis* in the field was different with risk (low vs. high) or habitat (live or dead coral), a 2×2 MANOVA was undertaken on the four behavioural variables (bite rate, total distance moved, maximum DV and boldness). Two-factor ANOVAS were used to determine the nature of differences found by MANOVA, and these were followed by Tukey's HSD means comparisons when necessary. Before all analyses, the assumptions of homogeneity of variance and normality were explored using residual analysis.

Results

Experiment 1: Effect of degraded habitat on the development of neophobia

Fish from different treatment groups did not differ in their prestimulus behavioural baseline (Pillai's Trace: Risk, $F_{2,35} = 2.55$, $P > 0.1$; Habitat, $F_{2,35} = 0.75$, $P > 0.4$; Risk \times Habitat: $F_{2,35} = 2.15$, $P > 0.1$). Their change in behaviour after introduction of the predator odour was affected by an interaction between risk and habitat type

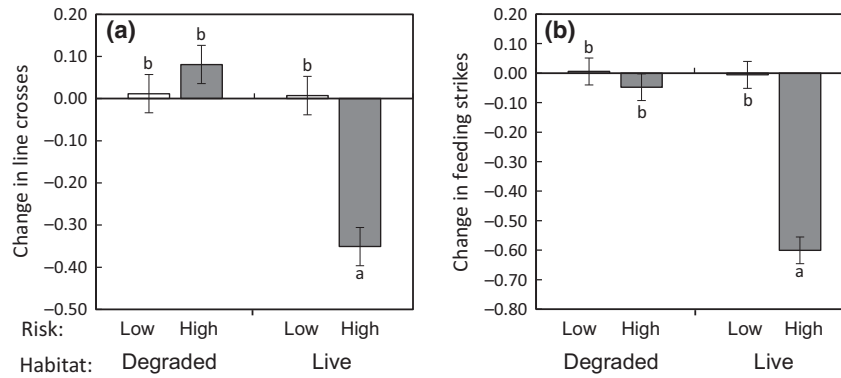


Fig. 1 Comparison of the change in activity (a, mean proportion change in line crosses \pm SE) and feeding strikes (b) after exposure to a novel predator odour for juvenile *Pomacentrus amboinensis* maintained in seawater from dead-degraded coral or live coral and under a history of low-risk (white bars) or high-risk (grey bars) for 4 days. Letters above or below error bars represent Tukey's HSD means comparison groupings. $N = 10$.

(Pillai's Trace: $F_{2,35} = 29.38$, $P < 0.0001$, Fig. 1). This interaction was evident in both variables (line crosses, $F_{1,36} = 23.92$, $P < 0.0001$; feeding rate, $F_{1,36} = 35.55$, $P < 0.0001$), which showed the same trends (Fig. 1). The low-risk fish showed no elevation of activity or feeding in response to the novel predator odour, while under a history of high risk, they showed a marked reduction in both variables, but only when maintained in seawater that had passed over live coral (Fig. 1a and b).

Experiment 2: Influence of degradation on behaviour and survival of neophobic fishes

There was no migration detected on any of the patch reefs. The overall behaviour of fish in the field was affected by the combination of their initial exposure to risk (i.e. high or low) and the habitat to which they were exposed (MANOVA, Habitat \times Risk, Pillai's Trace, $F_{4,82} = 0.44$, $P < 0.0001$, Fig. 2). ANOVAs indicated that

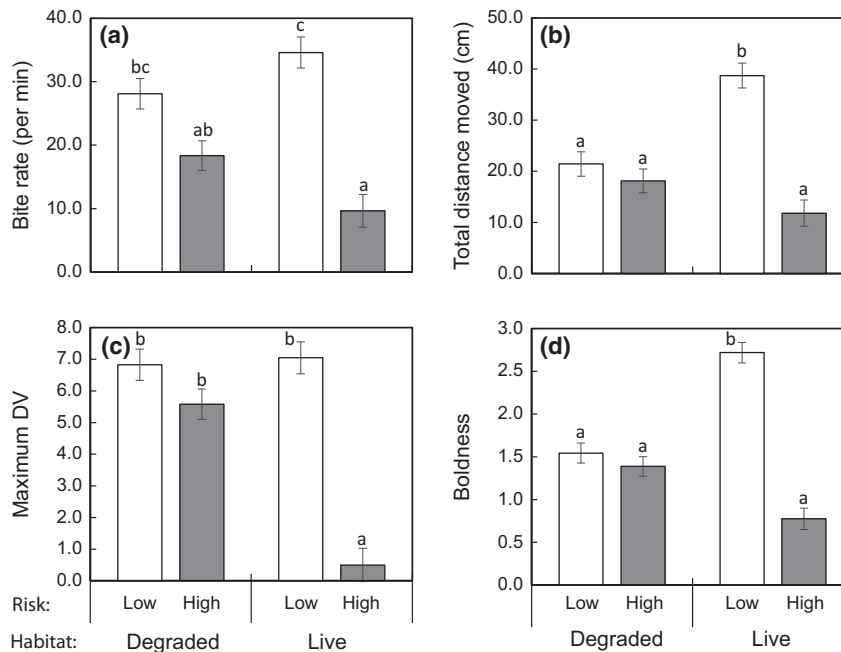


Fig. 2 Behaviour of juvenile *Pomacentrus amboinensis* that have a history of low risk (white bars) or high risk (grey bars), when placed on small isolated patch reefs comprised of either live or dead-degraded coral. (a) bite rate per minute; (b) total distance moved in 3 minutes; (c) maximum distance ventured from coral shelter; (d) boldness (continuous index between 0 and 3). Mean are given with standard errors. Letters above or below error bars represent Tukey's HSD means comparison groupings. $N = 20-24$.

there was a significant interaction for all the four recorded variables: bite rate ($F_{1,85} = 5.52$, $P < 0.021$), total distance moved ($F_{1,85} = 23.51$, $P < 0.0001$), Max DV ($F_{1,85} = 28.09$, $P < 0.0001$) and boldness ($F_{1,85} = 56.24$, $P < 0.0001$). In all cases, fish on the degraded habitat did not differ between risk categories (Tukey's HSD tests $P > 0.05$). In contrast, fish on live coral had lower values of all variables when they had been exposed to high risk during their first 4 days after settlement ($P < 0.05$, Fig. 2).

There was a significant effect of risk history and habitat on survival of *P. amboinensis* on isolated patch reefs ($\chi^2_3 = 19.53$, $P = 0.0002$; Fig. 3). Fish from the high-risk treatment living on live coral had the highest survival after 3 days, while the other three treatments had similarly low survival ($\chi^2_2 = 5.01$, $P = 0.081$).

Discussion

Chemical cues that are released from degraded coral habitats were found to dramatically affect the ability of a damselfish to be able to develop a neophobic response to risk and this resulted in an impact on behaviour and survival of newly settling fishes in the field. This is the first time that the olfactory background of a habitat has been found to affect a fundamental mechanism that is central to how naïve individuals survive in a high-risk habitat as they develop a risk management framework. Development of a risk framework in relation to the background level of risk is seen as integral to

developing cost-effective means of responding to information on risk that is of unknown reliability (Brown *et al.*, 2014; Ferrari *et al.*, 2015a,b). Hampering the development of neophobia and curtailing the use of alarm cues to inform, educate and reinforce prey about risk fundamentally alters the way prey interact with predators and reduces their likelihood of surviving.

When fish were exposed to high-risk conditions, they were conservative in their space use when placed into a natural habitat of healthy live coral. They displayed low activity and stayed close to their coral shelter. This is a typical neophobic response to novel cues for fishes that have a history of high risk (Brown *et al.*, 2014; Ferrari *et al.*, 2015b). Meanwhile, fish that were exposed to high-risk conditions in degraded coral water showed a response that was no different from fish that had a history of low-risk. Fish on degraded patches were up to eight times further away from the shelter than high-risk fish on live coral patches, but showed relatively low activity or exploratory behaviour. The combination of being away from shelter and relatively stationary resulted in these fishes sustaining four times the mortality of high-risk fish in a healthy habitat over the 3 days of monitoring. Clearly, the inability to assess risk and develop a neophobic phenotype had mortal consequences.

Differential space use on live and degraded coral has been previously documented and has been interpreted as the different coral states modifying the balance of cues used to assess risk. McCormick (2009) found that

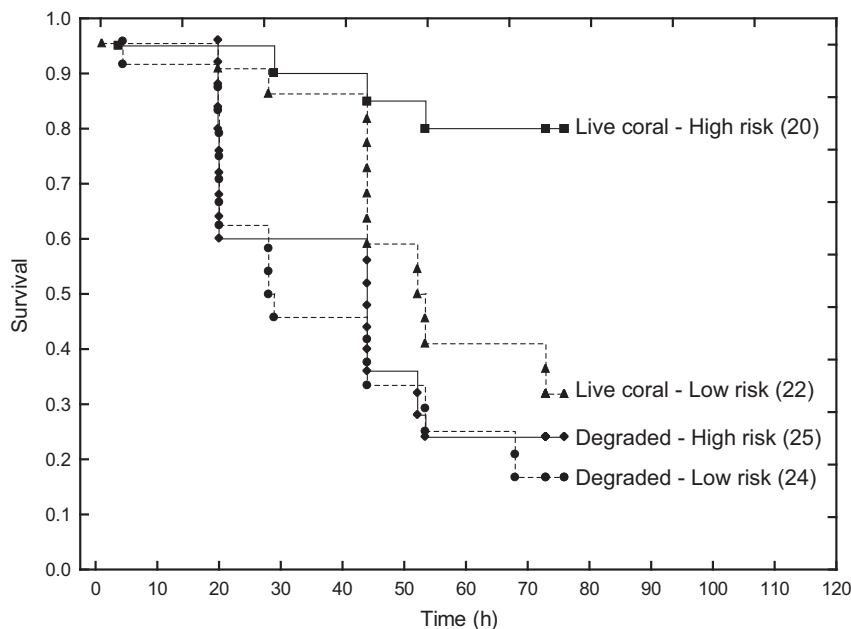


Fig. 3 Survival of juvenile *Pomacentrus amboinensis* that have a history of high or low risk and were placed on either live or dead-degraded coral patches. N in brackets.

juvenile *P. amboinensis* were located further away from bleached and degraded coral than live coral and suggested that this may be due to the noxious cues from degrading habitat pushing individuals further away from the shelter. Olfactory cues are a crucial source of information with which to inform their activities, particularly for site-attached organisms, providing information on foraging opportunities (DeBose & Paul, 2014), available mates (Oliveira & Gonçalves, 2008), stressful encounters (Manassa *et al.*, 2013) and successful or attempted predation events (Lönstedt & McCormick, 2015). By moving further away from degraded habitats, fish may be attempting to extract themselves from the boundary layer of the coral and enable themselves to receive unmodified olfactory information.

The breakdown of the risk-labelling process is likely due to the inability to perceive the conspecific alarm cues that represent a reliable indicator of threat in the immediate vicinity. Lönstedt *et al.* (2013) found that only a small amount of seawater that had passed over degraded habitat was capable of reducing the response of *P. amboinensis* to chemical alarm cues to a level where they would no longer perform a detectable antipredator response. However, it is still unclear whether water from degraded habitats actually modifies, and by doing so deactivates the alarm cue, or whether the chemistry from the degraded habitat acts as an olfactory receptor antagonist or inhibits the receptors, effectively blocking the ligand binding site (e.g. Oka *et al.*, 2004). If the alarm cue alteration is environmental, then the cue utility will be restored if the fish is capable of migrating to a nearby healthy habitat, though sadly, many juvenile fishes have a very small home range and show little propensity to move from their settlement site even when higher quality habitat is nearby (McCormick, 2009). If the alteration to the response to the alarm cue in degraded habitats resides at the site of the olfactory receptors, then responsiveness may still be restored, but this may take longer to occur. Obviously further study is required to clarify the mechanism underlying the habitat-related alteration of the behavioural response to chemical alarm cues.

How long it takes for a live coral patch to degrade to a state where it affects fishes through this olfactory mechanism is unknown. Many of the sources of habitat change in coral reefs happen quickly with respect to the lives of fishes, often within days to weeks, with the most common disturbance agents being storms, Crown of Thorns starfish (*Acanthaster planci*) feeding episodes, thermal bleaching and coral disease (De'ath *et al.*, 2012). Within the context of the present study and similar previous small-scale experiments (e.g. Lönstedt *et al.*, 2013, 2014), the progression from live coral to the dead-degraded coral used in the current study is

estimated at 3 months to a year. Because the components of the degraded coral community that modify the chemical alarm cues of *P. amboinensis* are yet to be characterized, it is currently unknown how quickly the alarm cue-modifying effect will develop after coral death and this awaits further study.

Other mechanisms are available for learning the identity of predators and updating risk information. Studies that have manipulated environmental conditions to reduce or negate the effectiveness of one sensory mode have found that animals upregulate the use of other sensory modes to compensate, in keeping with the sensory compensation hypothesis (Hartman & Abrahams, 2000). Leahy *et al.* (2011) manipulated the amount of suspended sediment in water and found that fish increased their reliance on chemical information when vision was obscured. Similar findings have also been shown with increases of topographic complexity (McCormick & Lönstedt, 2013) or in response to a lack of visual cues at night (Leduc *et al.*, 2010). Thus, relying more on visual (or mechanical) cues to learn threats is a viable alternative that will still allow associative learning, particularly through social learning (Crane & Ferrari, 2013). If some species, like *P. amboinensis*, are affected by the chemistry of degraded habitats, while other residents within the habitat are not adversely affected, then public information will prove a potent means by which those affected can compensate for the loss of an important source of information.

The present study, and that of Ferrari *et al.* (2015a,b), has shown that the capacity to develop neophobia leads to a marked survival advantage. Moreover, neophobia has been shown to provide a survival advantage that is independent and additive to that of learnt information about common predators (Ferrari *et al.*, 2015b). This finding highlights that the significant survival advantage which neophobia provides cannot necessarily be wholly compensated for with an alternative learning strategy. Neophobia will be most important at life-history bottlenecks, such as the habitat transition and physiological remodelling associated with metamorphosis and settlement in animals with complex life histories (Wilbur, 1980; McCormick, 1999; Nilsson *et al.*, 2007). Changes in physiology and structure of sensory systems are coincident with the necessity to rapidly catalogue the identity of new threats and it is at this time of high risk that neophobia will prove most beneficial.

Our study shows that the loss of neophobia through the modified efficacy of chemical alarm cues has repercussions for the survival of fishes settling or migrating into degraded habitats. We are yet to determine how widespread this effect may be, but there is currently no reason to believe that the target species is very different from the other hundreds of species that comprise

complex coral reef fish assemblages. Interestingly, the focal species survives in dead-coral-dominated areas of the reef (McCormick & Weaver, 2012), and this proffers questions regarding the mechanisms used by survivors to balance risk, whether they can overcome the issues associated with alarm cue identification as they acclimate to the new habitat, or whether parental effects may enable progeny from fishes that breed within degraded habitats to be better able to adjust to the modified chemical environment.

Acknowledgements

We should like to thank all the staff at the Lizard Island Research Station, and all the students and volunteers who helped with the light traps and fish sorting.

Ethics statement

All work carried herein was in accordance with the James Cook University Animal Ethics guidelines (JCU Animal Ethics approvals A2005 and A2080, collection permit G12/35117.1).

Funding statement

Funding was provided by an Australian Research Council Centre of Excellence for Coral Reef Studies (EI140100117).

References

- Alvarez-Filip L, Paddock MJ, Ben C, Robertson DR, Cote IM (2015) Simplification of Caribbean reef-fish assemblages over decades of coral reef degradation. *PLoS One*, **10**, e0126004.
- Brown GE, Smith RJF (1996) Foraging trade-offs in fathead minnows (*Pimephales promelas*, Osteichthyes, Cyprinidae): acquired predator recognition in the absence of an alarm response. *Ethology*, **102**, 776–785.
- Brown GE, Ferrari MCO, Elvidge CK, Ramnarine I, Chivers DP (2013) Phenotypically plastic neophobia: a response to variable predation risk. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 20122712.
- Brown GE, Chivers DP, Elvidge CK, Jackson CD, Ferrari MCO (2014) Background level of risk determines the intensity of predator neophobia in juvenile convict cichlids. *Behavioral Ecology and Sociobiology*, **68**, 127–133.
- Chivers DP, Smith RJF (1998) Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. *Ecoscience*, **5**, 338–352.
- Chivers DP, Ramasamy RA, McCormick MI, Watson SA, Siebeck UE, Ferrari MCO (2014) Temporal dynamics of risk assessment in a changing world. *Science of the Total Environment*, **500**, 332–338.
- Colles A, Liow LH, Prinzing A (2009) Are specialists at risk under environmental change? Neoeological, paleoecological and phylogenetic approaches. *Ecology Letters*, **12**, 849–863.
- Crane AL, Ferrari MCO (2013) Social learning of predation risk: a review and prospectus. In: *Social Learning Theory: Phylogenetic Considerations Across Animal, Plant, and Microbial Taxa* (ed. Clark KB), pp. 53–82. Nova Science Publisher, New York.
- Dall S, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, **20**, 187–193.
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 17995–17999.
- DeBose JL, Paul VJ (2014) Chemical signatures of multi-species foraging aggregations are attractive to fish. *Marine Ecology Progress Series*, **498**, 243–248.
- Doak DF (1995) Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology*, **9**, 1370–1379.
- Feeney WE, Lönnstedt OM, Bosiger YJ, Martin J, Jones GP, Rowe RJ, McCormick MI (2012) High rate of prey consumption in a small predatory fish on coral reefs. *Coral Reefs*, **31**, 909–918.
- Ferrari MCO, Wisenden BD, Chivers DP (2010) Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Canadian Journal of Zoology*, **88**, 698–724.
- Ferrari MCO, Dixon DL, Munday PL, McCormick MI, Meekan MG, Sih A, Chivers DP (2011) Intrageneric variation in tolerance of coral reef fishes to ocean acidification: implications for climate change projections on marine communities. *Global Change Biology*, **17**, 2980–2986.
- Ferrari MCO, McCormick MI, Meekan MG, Chivers DP (2015a) Background level of risk and the survival of predator-naïve prey: can neophobia compensate for predator naivety in juvenile coral reef fishes? *Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20142197.
- Ferrari MCO, McCormick MI, Bridie JM *et al.* (2015b) Living in a risky world: the onset and ontogeny of an integrated antipredator phenotype in a coral reef fish. *Scientific Reports*, **5**, 15537.
- Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, **495**, 1–25.
- Hartman EJ, Abrahams MV (2000) Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proceedings of the Royal Society of London B: Biological Sciences*, **267**, 571–575.
- Hoey AS, McCormick MI (2006) Effects of subcutaneous fluorescent tags on the growth and survival of a newly settled coral reef fish, *Pomacentrus amboinensis* (Pomacentridae). *Proceedings of the 10th International Coral Reefs Symposium*. Japanese Coral Reef Society, Tokyo, Japan, 420–425.
- Holmes T, McCormick MI (2010) Size-selectivity of predatory reef fish on juvenile prey. *Marine Ecology Progress Series*, **399**, 273–283.
- Holyoak M, Heath SK (2016) The integration of climate change, spatial dynamics, and habitat fragmentation: a conceptual overview. *Integrative Zoology*, **11**, 40–59.
- Hughes TP, Rodrigues MJ, Bellwood DR *et al.* (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360–365.
- Lambin EF, Geist HJ, Lepers E (2003) Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources*, **28**, 205–241.
- Leahy SM, McCormick MI, Mitchell M, Ferrari MCO (2011) To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biology Letters*, **7**, 811–813.
- Leduc AOHC, Kim J-W, Macnaughton CJ, Brown GE (2010) Sensory complement model helps to predict diel alarm response patterns in juvenile Atlantic salmon (*Salmo salar*) under natural conditions. *Canadian Journal of Zoology*, **88**, 398–403.
- Lönnstedt OM, McCormick MI (2015) Damsel in distress: captured damselfish prey emit chemical cues that attract secondary predators and improve escape chances. *Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20152038.
- Lönnstedt OM, McCormick MI, Meekan MG, Ferrari MCO, Chivers DP (2012) Learn and live: the role of predator experience in influencing prey behaviour and survival. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 2091–2098.
- Lönnstedt OM, McCormick MI, Chivers DP (2013) Degraded coral disrupts innate antipredator responses of fish. *Ecology and Evolution*, **3**, 38–47.
- Lönnstedt OM, McCormick MI, Chivers DP, Ferrari MCO (2014) Habitat degradation is threatening reef replenishment by making fish fearless. *Journal of Animal Ecology*, **83**, 1178–1185.
- Lotze HK, Lenihan HS, Bourque BJ *et al.* (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, **312**, 1806–1809.
- Manassa RP, McCormick MI, Chivers DP, Ferrari MCO (2013) Social learning of predators in the dark: understanding the role of visual, chemical and mechanical information. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 20130720.
- McCormick MI (1999) Delayed metamorphosis of a tropical reef fish (*Acanthurus triostegus*): a field experiment. *Marine Ecology Progress Series*, **176**, 25–38.
- McCormick MI (2009) Behaviourally mediated phenotypic selection in a disturbed coral reef environment. *PLoS One*, **4**, e7096.
- McCormick MI, Lönnstedt OM (2013) Degrading habitats and the effect of topographic complexity on risk assessment. *Ecology and Evolution*, **3**, 4221–4229.
- McCormick MI, Meekan MG (2007) Social facilitation of selective mortality. *Ecology*, **88**, 1562–1570.
- McCormick MI, Weaver C (2012) It pays to be pushy: intracohort interference competition between two reef fishes. *PLoS One*, **7**, e42590.

- Meekan MG, Wilson SG, Halford A, Retzel A (2001) A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. *Marine Biology*, **139**, 373–381.
- Mitchell M, McCormick MI, Ferrari MCO, Chivers DP (2011) Coral reef fish rapidly learn to identify multiple unknown predators upon recruitment to the reef. *PLoS One*, **6**, e15764.
- Munday PL, Warner RR, Monro K, Pandolfi JM, Marshall DJ (2013) Predicting evolutionary responses to climate change in the sea. *Ecology Letters*, **16**, 1488–1500.
- Nilsson GE, Ostlund-Nilsson S, Penfold R, Grutter AS (2007) From record performance to hypoxia tolerance: respiratory transition in damselfish larvae settling on a coral reef. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 79–85.
- Oka Y, Nakamura A, Watanabe H, Touhara K (2004) An odorant derivative as an antagonist for an olfactory receptor. *Chemical Senses*, **29**, 815–822.
- Oliveira RF, Gonçalves DM (2008) Hormones and social behaviour of teleost fish. In: *Fish Behaviour* (eds Magnhagen C, Braithwaite VA, Forsgren E, Kapoor BG), pp. 61–150. CRC Press, Boca Raton.
- Santos ME, Berger CS, Refki PN, Khila A (2015) Integrating evo-devo with ecology for a better understanding of phenotypic evolution. *Briefings in Functional Genomics*, **14**, 384–395.
- Spalding MD, Brown BE (2015) Warm-water coral reefs and climate change. *Science*, **350**, 769–771.
- White JR, Meekan MG, McCormick MI, Ferrari MCO (2013) A comparison of measures of boldness and their relationships to survival in young fish. *PLoS One*, **8**, 268900.
- White JR, Meekan MG, McCormick MI (2015) Individual consistency in the behaviors of newly-settled reef fish. *PeerJ*, **3**, e961.
- Wilbur HM (1980) Complex life cycles. *Annual Review of Ecology and Systematics*, **11**, 67–93.
- Wong BB, Candolin U (2015) Behavioral responses to changing environments. *Behavioral Ecology*, **26**, 665–673.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. An area of shallow reef damaged by cyclones Ita (April 2014, Cat 3) and Nathan (March 2015, Cat 5) showing degraded coral.

Figure S2. (a) Area of healthy reef with good coverage of live hard coral; (b) adjacent area of degrading coral with a high percentage of dead, algal-covered coral.