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Reef fishes innately distinguish predators based on olfactory cues associated with recent prey items rather than individual species

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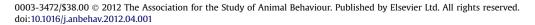
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Keywords: Amphiprion percula anemonefish chemical ecology coral reef fish diet larvae olfaction predation An individual's ability to identify and respond accurately to a predator greatly affects its probability of survival. Chemosensory cues are an important mechanism for predator detection in aquatic environments. Whether fish are aware of the risks posed by distinct fish species, or whether a common chemosensory cue distinguishes predatory fishes, is unknown. One possibility is that fish distinguish predatory fishes based on their diet. To test this, we manipulated the diet of three nominally nonpiscivorous species and examined behavioural responses of juvenile anemonefish, Amphiprion percula, to chemical cues of nonpredators fed a diet rich in fish product. In pairwise choice trials, naïve A. percula showed indifference to chemosensory cues from nonpiscivorous fishes fed their usual diet, but significantly avoided chemical cues from piscivorous and nonpiscivorous fishes fed a diet containing fish product. These results indicate that A. percula larvae innately distinguish between piscivorous and nonpiscivorous fishes based on chemosensory cues in the diet. To test for an effect of piscivorous diet in nature, we constructed patch reefs that emitted scents of dietary cues in natural concentrations. Patches that emitted scent of a piscivorous diet received on average 22% less settlement than control patches or than patches that emitted scent of an herbivore or invertivore. Chemosensory detection of recent prey provides a robust cue to assess predation risk associated with a diverse range of fishes (especially during settlement) and may be reinforced through additional sensory (e.g. visual) and learned recognition of individual species consistently associated with these distinctive chemosensory cues.

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Early detection and avoidance of predators greatly enhances individual survival. Consequently, a range of morphological and behavioural adaptations have evolved to help individuals identify potential predators (Blanchard & Blanchard 1989; Kats & Dill 1998; Apfelbach et al. 2005; Kindermann et al. 2009). Many taxa innately recognize potential predators (fishes: Hawkins et al. 2004; Dixson et al. 2010; Vail & McCormick 2011; crustaceans: Wahle 1992; reptiles: Amo et al. 2005; Balderas-Valdivia & Ramírez-Baustista 2005; birds: Goth 2004; rodents: Apfelbach et al. 2005; primates: Brown et al. 1992). This innate predator recognition is even maintained in laboratory strains of rats and mice that have not been exposed to selection pressure from predators for several hundred generations (Blanchard & Blanchard 1990; Wallace & Rosen 2000; Yang et al. 2004; Fendt 2006). Innate recognition of potential predators is highly advantageous, particularly when organisms are young or are transitioning to new environments. However, it is unclear what cues are used to detect predation risk associated with each new species encountered, especially given the large number of species that may be encountered in highly diverse ecosystems such as tropical rainforests and coral reefs.

Visual and chemosensory cues are important in the recognition of potential predators, but their relative importance appears to differ between terrestrial and aquatic environments. Although birds rely heavily on visual cues to recognize potential predators, experimental studies have shown that birds respond to subtle behavioural traits to distinguish potential predators rather than distinguishing specific species of predators. Most notably, birds respond in a consistent fashion (producing alarm calls and aggressive behaviour) to known predators and model species that mimic predators (Curio 1975; Veen et al. 2000). Chemosensory cues are also important for terrestrial prey species that can identify predator-rich areas based on territorial markings (Dickman & Doncaster 1984; Dickman 1992; Kats & Dill 1998; Stapley 2003; Labra & Niemeyer 2004; Amo et al. 2005; Apfelbach et al. 2005). Predator-naïve, laboratory-reared rats show innate chemical predator recognition by performing species-specific defence behaviours in response to urine samples of feline and canid







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predators, but not in response to urine of herbivorous nonpredators (Fendt 2006). Both visual and chemosensory predator recognition studies document the ability of naïve animals to generalize risk, responding not to specific organisms but to a dietary component or a physical attribute indicative of a threat.

In the aquatic environment, chemosensory cues produced by predators are thought to be the most useful mechanism of predator detection (Wisenden 2000a, b: Chivers & Mirza 2001: Kellev & Magurran 2003). The role of predator diet in predator detection has been well studied in freshwater systems, with the majority of studies demonstrating the importance of predator diet with naïve prey organisms responding to chemical cues from (1) a predator fed a conspecific or sympatric species compared to an unfed predator (Jachner 1997), (2) a predator fed a distantly related prey species (Gelowitz et al. 1993; Mathis & Smith 1993; Brown et al. 1995a,b, 1996; Jones & Paszkowski 1997; Brown & Cowan 2000; Brown & Dreier 2002), or (3) a predator fed a completely novel diet, such as earthworms or insects, when testing a fish or tadpole's recognition ability (Chivers et al. 1996; Laurila et al. 1997). However, in some cases, prey may respond to lingering chemical alarm cues from ingested prey in the faecal matter of the predator, and, thus, generalization of predators is limited because recognition of alarm cues requires learning and tends to be species specific (Brown et al. 1995a,b; Mirza & Chivers 2003). Although these studies provide important findings on the relationship between predator recognition and diet, an important next step is to use a diet that does not contain a chemical alarm cue and to use a species that is not normally considered a predator. The ability to manipulate the diet of a nonpredator, causing naïve organisms to recognize a nonpredator as a predator, would experimentally demonstrate the importance of dietary components in predator recognition, removing the potential effects of chemical alarm cues as well as the predator itself.

For most marine organisms, periods of extreme predation risk occur at critical life-history transitions, such as when larvae attempt to settle to benthic habitat at the completion of their pelagic larval phase (Caley et al. 1996; Almany & Webster 2006). For example, Almany & Webster (2006) found that 55.7% of newly settled recruits across 24 species of fish were consumed within the first 2 days after settlement. Given the high predation pressure experienced during early life stages, strong selection for innate predator recognition would be expected. Indeed, several species of coral reef fish show innate predator recognition. Dixson et al. (2010) showed that both newly hatched larvae (less than 24 h old) and settlement-stage larvae of anemonefish, Amphiprion percula, are able to recognize and distinguish between chemosensory cues of predatory and nonpredatory fish species (Dixson et al. 2010). Vail & McCormick (2011) also demonstrated innate predator recognition in settlement-stage damselfishes, using patch reefs manipulated to release a predator scent. Patch reefs that released predator scent received significantly fewer recruits than patch reefs that released no predator chemical cues (Vail & McCormick 2011). However, it is unknown which chemical cues account for this innate recognition of specific predators. It is unlikely that these fishes are innately aware of all species that do or do not pose a significant predation risk. Rather, there is probably a specific cue that distinguishes piscivorous and nonpiscivorous fishes.

Here, using a novel experimental design, we tested whether predator diet affects innate recognition of predators by naïve larvae of the anemonefish *A. percula*. We hypothesized that larval fish would respond to the chemical cues produced by fish fed a piscivorous diet, and, as a result, would avoid the scents of any species consuming a fish-based diet, even if that species was not naturally a piscivore. Therefore, we experimentally manipulated the diet of three nonpredators (two herbivorous species and one invertivore) to contain a large fraction of fish product. We used two artificial fish-based diets derived from nonreef species that had been either previously frozen, or dried and stored at room temperature, and thus, that lacked chemical alarm cues of *A. percula* (Smith 1989); therefore, only the piscivorous diet was experimentally tested in our study. We then tested the behavioural responses of naïve A. percula larvae to the chemosensory cues of each nonpredator species when it was fed a natural diet (algae or invertebrates) or the fish-based diet. We compared these responses to the behavioural responses of larvae exposed to the chemosensory cues of two predator species that had been fed either the artificial diet rich in fish product or a natural diet of fish larvae. To examine the effects of natural concentrations of dietary cues on settlement behaviour of reef fish larvae, we conducted a field experiment to determine whether damselfishes would avoid reef patches manipulated to emit the scent of a piscivorous diet.

METHODS

Laboratory Experiment

A two-channel choice chamber $(13 \times 4 \text{ cm})$, developed by Gerlach et al. (2007), was used to assess the ability of larval coral reef fish to recognize and respond to chemosensory cues of adult coral reef fish species fed different diets. A single larval fish was released at the downstream end of the chamber, where it was free to move to either side or swim towards the preferred water source. Using the protocols outlined in Gerlach et al. (2007), a constant gravity-driven flow of 100 ml/min per channel was maintained throughout all trials using flow meters. Each fish was given a 2 min acclimation period; fish that did not swim during this time were discarded (less than 1% for all trials). The acclimation period was followed by a 2 min testing period where the position of the fish (right or left side of the chamber) was recorded at 5 s intervals. A 1 min rest period followed during which we exchanged the water sources from one side to the other to ensure that no side preference was being displayed. Initial dye tests revealed that the 1 min rest period was adequate for cues to be flushed from the chamber at the given flow rate. Dye tests were also conducted at each water change to ensure that the two flow channels showed parallel water flow, with no area of turbulence or eddy. Tests were then repeated, including the acclimation period. The pairwise choice experiments allowed fish to choose freely between water flowing from two sources. We conducted laboratory trials on settlement-stage A. percula larvae (11 days posthatching) to test behavioural responses of predator-naïve larvae to nine sources of chemosensory cues, all compared against untreated sea water: (1) untreated sea water, blank control trial; (2) Cephalopholis argus (a natural predator) fed an artificial fish-based diet (Frozen Marine Dinners, Fish Fuel Co. Pty Ltd, Thebarton, S.A.); (3) Pseudochromis fuscus (a natural predator) fed an artificial fish-based diet (NRD pellets, dry diet developed for marine fish, INVE Aquaculture, Salt Lake City, UT, U.S.A.); (4) Acanthurus pyroferus (a natural nonpredator) fed algae; (5) A. pyroferus fed an artificial fish-based diet (NRD pellets); (6) Rhinecanthus lunula (a natural nonpredator) fed an invertebrate diet; (7) R. lunula fed an artificial fish-based diet (NRD pellets); (8) Signus coralinus (a natural nonpredator) fed algae; and (9) S. coralinus fed an artificial fish-based diet (NRD pellets).

Chemosensory testing

Laboratory experiments were conducted at James Cook University's experimental aquarium facility during November 2008–March 2009. All larvae used in the experiment were Download English Version:

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