Prey experience of predation influences mortality rates at settlement in a coral reef fish, *Pomacentrus amboinensis*

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Previous exposure to predators influenced the survival immediately after settlement in a coral reef damselfish, *Pomacentrus amboinensis*. Rapid learning of antipredator behaviour may in part have driven the rapid increase in survival in the days following this critical transition.   © 2006 The Fisheries Society of the British Isles

Key words: antipredator behaviour; coral reef fish; naïvety; selective predation; settlement.

The outcome of a predator-prey encounter can be determined by prey behaviour (Chipps *et al.*, 2004). The quicker naïve prey learn to recognize predators, the better their chance of survival. Rapid learning of antipredator behaviour will be most important at ecological or life-history transitions, when organisms shift from one habitat or niche to another. Coincident with these shifts are elevated mortality rates (Booth & Brosnan, 1995; Doherty *et al.*, 2004). For demersal fishes, one of the most important and ubiquitous transitions is metamorphosis and settlement (McCormick & Makey, 1997; McCormick *et al.*, 2002).

When demersal marine fishes settle at the end of their larval phase they are immediately exposed to a novel suite of predators that have quite different attack strategies from the pelagic predators the larvae had previously encountered. The reward for fishes that make correct decisions in predator-prey encounters is survival, and selection should favour individuals that respond correctly in the presence of potential predators. Few studies have examined the importance of prey learning to survival of marine fishes, however, studies in freshwater systems emphasize the importance of learned antipredator behaviour to the outcome of predator-prey encounters (Brown, 2003; Kelley & Magurran, 2003; Kristensen & Closs, 2004). The rapid learning of antipredator behaviour may be an important

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factor driving the shape of the negative exponential survival curve that is a common feature of newly-settled reef fishes (Planes & Lecaillon, 2001; McCormick & Hoey, 2004). The present study is the first to examine how previous exposure to a predator may influence the subsequent survival of a newly-settled coral reef fish, the ambon damselfish *Pomacentrus amboinensis* Bleeker (Pomacentridae).

The ambon damselfish is common within coral reef fish communities in the Indo-Pacific. They settle to a wide variety of habitats on the northern Great Barrier Reef, but are found in highest densities associated with small reef patches at the base of shallow reefs. The most common predators of small reef fishes in this habitat are: lizardfish *Synodus variegatus* (Lacepède), moonwrasse *Thalassoma lunare* (L.), rock cod *Cephalopholis boenak* Bloch and the dottyback *Pseudochromis fuscus* Müller & Troschel (Holmes & McCormick, in press). *Pomacentrus amboinensis* has a pelagic larval duration of 15–23 days and settles at 10·3–15·1 mm standard length (L_S) (Kerrigan, 1996) and undergoes little change in body morphology associated with metamorphosis (McCormick *et al*., 2002). Once settled, *P. amboinensis* is attached to the site, making it an ideal species for both field observations and experimental manipulation.

Late-stage larval *P. amboinensis* were collected using light traps (Stobutzki & Bellwood, 1997) moored in 10–15 m of water and positioned so that the collection openings were 1 m below the surface. The light traps were set at dusk and left in place overnight before being collected at 0700 to 0730 hours the following morning. Fish collected from each trap were immediately transported to the laboratory where 50 *P. amboinensis* were randomly placed into each of two identical 60 l flow-through aquaria. Each aquarium contained a 3 cm layer of sand and coral rubble and a small dead *Pocillopora damicornis* (L.) (a bushy scleractinian) coral head. Densities of up to 65 individuals per 0·125 m^3 of patch reef have been found in the field during the recruitment season (McCormick & Hoey, 2004) and, although not strictly comparable, the conditioning-trial densities were slightly less than double natural densities. Two predatory fishes (*S. variegatus* and *P. fuscus*) known to feed on *P. amboinensis* juveniles (Martin, 1994), were placed into one of the aquaria (predator-conditioned treatment). No predators were released into the other aquarium ('naïve' treatment). Both treatments were fed an equal amount of *Artemia* sp. nauplii twice daily. Observations from other studies suggest that *S. variegatus* and *P. fuscus* feed on one or two prey per day (Sweatman, 1984; Martin, 1994), so *P. amboinensis* within the predator-conditioned treatment were probably exposed to *c*. four to eight predation events over the 2 day conditioning period. After 2 days, *P. amboinensis* were removed from the aquaria, put into a clip-seal plastic bag containing aerated sea water and measured for L_S ($\pm0\cdot1$ mm) using callipers. Fish were then placed into pairs such that both were of equal L_S ($\pm0\cdot2$ mm), but from different predator treatments (*i.e.* one 'experienced' and one 'naïve'). Individuals within a pair were tagged with either a red or black subcutaneous fluorescent elastomer tattoo using a 27-gauge hypodermic needle for the purpose of individual identification. Laboratory trials have shown that these tattoos have no influence on the growth or survival of this species (Hoey & McCormick, in press). The tag colour was randomly assigned to treatments within each pair to eliminate any bias associated with selective loss due to tag colour.

A single experimental pair of *P. amboinensis* was placed onto one of a series of small patch reefs (20 × 20 × 20 cm) located *c.* 2 m from the shallow (2–3 m) reef base and 5 m apart at each of the two lagoon study sites (Back-reef and Vicki's, *c.* 200 m apart) at Lizard Island (14° 38′ S; 145° 28′ E), northern Great Barrier Reef, Australia, during December 2003. Fish were released between 0900 and 1100 hours and shielded from predators by the diver for 5–10 min until acclimated to their surroundings. Within 30 s of release, fish were observed feeding on food items from the water column, suggesting a rapid acclimation to their new environment. Each patch reef consisted of a combination of live and dead *P. damicornis* separated by 3 m of sand, and was open to the full array of reef-based and transient predators present at each of the sites. Prior to releasing the tagged pairs, the patch reefs were cleared of all resident fishes and large invertebrates using small hand-nets.

Survival of each of the *P. amboinensis* pairs was monitored three times per day (morning, mid-day and evening) by visual census. Each replicate trial ended when one (or both) of the tagged fish were found to be missing from a patch, at which point the subsequent survivor was recorded and the surrounding reef area was searched to determine whether the missing individual had simply emigrated. Since experience of predators can be attained rapidly, if a result had not occurred within 36 h, the *P. amboinensis* pair was removed and the trial was abandoned. Trials where both individuals were found to be missing were discarded from the replicate group, since the objective was to determine the order in which prey were removed. Twenty-five successful trials were conducted at the Back-reef study site and 24 at the Vicki's site. Final counts of naïve and predator-conditioned survivors at each of the sites were compared using a χ^2 goodness of fit test (incorporating Yates' correction for d.f. $= 1$). Fisher's exact test was used to compare survivor counts between sites.

Overall, fish that had experienced benthic predators before their release in the field survived in 44% more trials than fish of a similar size that had no experience with reef based predators. Interestingly, this trend was largely driven by results from the Back-reef site, where 61% more fish that had experienced predators prior to the trial survived (χ^2, d.f. $= 1$, $P < 0.05$; Fig. 1). There was no significant difference in survivor counts at Vicki's site (χ^2, d.f. $= 1$, $P > 0.05$), however, there was a trend for experienced individuals to have a higher probability of survival than naïve individuals (Fig. 1). There was no difference in the trend among sites (Fisher's exact test, $P = 0.159$).

The present study provides the first evidence to indicate that prey experience may be important in determining the outcome of predator-prey interactions immediately after settlement in a coral reef fish. The field experiment suggested that experience gained by individuals while in close proximity to predation events enhanced their ability to avoid or escape predation and directly lead to higher survival.

The mechanism underlying improved survival chances after direct or indirect experience with a predator probably involves the use of chemical alarm signals to facilitate rapid learning of predator identities. A recent study found that juvenile *P. amboinensis* responded to chemicals from injured conspecifics by displaying antipredator behaviours (Larson, 2003). Moreover, a further study showed that a tropical goby, *Asterropteryx semipunctatus* Rüppell, learnt to recognize a novel
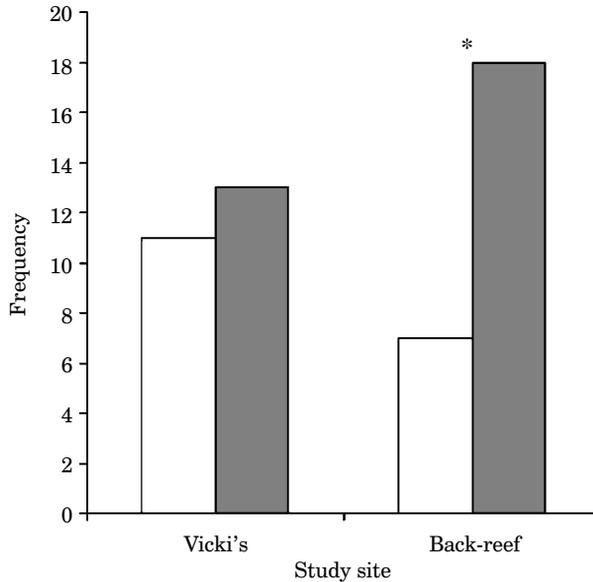
FIG. 1. Frequency of survival of predator-conditioned (■) and naïve (□) recently-settled *Pomacentrus amboinensis* from paired field trials conducted at two lagoon study sites (Vicki's, $n = 24$ trials; Back-reef, $n = 25$ trials). *, significant difference between survivor counts ($P < 0.05$).

chemical cue (such as that emitted by a predator) and associate it with danger after a single simultaneous exposure to the novel cue and a conspecific alarm signal (Larson & McCormick, 2005). These findings suggest that the predator-conditioned fish in the present experiment would have learnt to associate the two common predators used in the experiment with danger, and their mere presence would be likely to elicit an antipredator response. Differences in the magnitude of the effect of predator conditioning between the two study sites may be due to site differences in the number of lizardfish and dottybacks in the vicinity of the experimental fish.

Rapid learning of antipredator behaviour may in part drive the dramatic increase in survival in the days following this critical transition. Recent studies have shown that many demersal fishes show type III mortality trajectories after settlement (Webster, 2002; Doherty *et al.*, 2004). While for *P. amboinensis* 50% of individuals die within 5 days of the settlement event, only 6% die in the following 4 days (McCormick & Hoey, 2004). The shapes of these mortality trajectories are likely to be driven by two mechanisms. Firstly, individuals with disadvantageous traits (*e.g.* low burst speed) may be selectively lost. As the number of these preferred fish diminish, predators have to switch to prey that are harder to catch. Secondly, prey may simply rapidly learn antipredator strategies and become harder for predators to catch. The ability of fish in the naïve treatment to rapidly learn the identity of predators once on the reef may have lead to an underestimation of the importance of learnt avoidance strategies in the present study. These two mechanisms are unlikely to be mutually exclusive. Recent research on *P. amboinensis* has shown that mortality immediately after settlement can be strongly selective for body traits such as size, late-larval

growth, body condition (Fulton's K) and total lipid content (Hoey & McCormick, 2004; McCormick & Hoey, 2004; Holmes & McCormick, in press). Further studies are required to determine how prior predator experience interacts with prey body traits to determine which individuals survive the initially high levels of mortality after settlement.

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