

Social learning improves survivorship at a life-history transition

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Abstract During settlement, one of the main threats faced by individuals relates to their ability to detect and avoid predators. Information on predator identities can be gained either through direct experience or from the observation and/or interaction with others, a process known as social learning. In this form of predator recognition, less experienced individuals learn from experienced members within the social group, without having to directly interact with a predator. In this study, we examined the role of social learning in predator recognition in relation to the survival benefits for the damselfish, *Pomacentrus wardi*, during their settlement transition. Specifically, our experiments aimed to determine if *P. wardi* are capable of transmitting the recognition of the odour of a predator, *Pseudochromis fuscus*, to conspecifics. The experiment also examined whether there was a difference in the rate of survival between individuals that directly learnt the predator odour and those which acquired the information through social learning compared to naïve individuals. Results show that naïve *P. wardi* are able to learn a predator's identity from experienced individuals via social learning. Furthermore, survival between individuals that directly learnt the predator's identity and those that learnt through social learning did not significantly differ, with fish from both treatments surviving at least five times better than controls. These results demonstrate that experience may play a vital role in determining the outcome of predator–prey interactions,

highlighting that social learning improves the ability of prey to avoid and/or escape predation at a life-history transition.

Keywords Survival · Risk assessment · Learning · Reef fishes · Sociality

Introduction

Animals face a variety of decisions throughout their lives including: where to forage, who to mate with, where to breed and who to avoid. As such, decisions that are based on a large amount of reliable information are most likely to lead to a profitable outcome. Information can either be acquired through direct experience or through public information made available by other individuals (Valone and Templeton 2002). Public information can be acquired through signals (e.g. alarm calls, vocalisations, and chemical alarm cues) or inadvertently through observing the activities of others (Brown 2003; Valone 2007). Learning that involves the use of public information is referred to as social learning, with a wide variety of animals (e.g. birds, eutherian mammals, marsupials and fish) known to benefit from this type of information transmission (Brown and Laland 2001; Griffin 2004; Laland 2004; Manassa and McCormick 2012). One of the main threats faced by individuals during life-history or habitat transitions is the ability to detect and avoid predators. As such, any mechanism that allows for the rapid identification of predators and reinforcement of relevant stimuli is likely to be highly advantageous.

Predation risk assessment in aquatic environments often involves the use of chemical information, with a plethora of research demonstrating the use of damage-released

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chemical cues (released from skin of injured prey) as reliable indicators of predation risk (Chivers and Smith 1998; Ferrari et al. 2010). Likewise, studies have shown that, upon simultaneous detection of damage-released chemical cues and a novel chemical cue (such as the smell of a predator), prey individuals learn to associate the novel cue with risk (Wisenden 2000). This method of direct experience ensures that prey individuals identify potential predators resulting in anti-predator behaviour in future encounters (Wisenden 2000). However, this method of learning comes at a potential cost, as prey must be in the vicinity of an actively foraging predator before the initial association can be made. Therefore, given the costs associated with direct learning, it is not surprising that social learning is used in a broad range of taxa (including birds, marsupials and freshwater fishes; Brown and Laland 2001; Griffin 2004). No studies to date have demonstrated that social learning affects survival, with only two studies documenting that coral reef fish have the capacity to use this mechanism to associate predator odours with danger (Ferrari et al. 2012; Manassa and McCormick 2012).

Coral reef fishes like most marine organisms have a complex lifecycle involving a series of ecological and life-history transitions. Larvae develop in the pelagic and settle into the reef matrix following a period of weeks to months in the open ocean (Leis 2007). During this time, the suite of predators they encounter is both diverse and unpredictable (Leis 2007). Mortality during settlement is exceptionally high (>60 % in the first 48 h), highlighting the need for rapid learning and appropriate responses to ensure survival (Gosselin and Qian 1997; Almany and Webster 2006; Holmes and McCormick 2011). Few studies have investigated the importance of prey experience to the survival of coral reef fishes, with the first evidence that experience directly leads to higher survival demonstrated in a study by McCormick and Holmes (2006). A further study by Lönnstedt et al. (2012) found that, if naïve individuals were conditioned with visual, chemical or a combination of predator cues, survival was eight times greater than those with no experience. However, the link between social learning of predator identities and survival trajectories remains unknown.

Our study investigated the role of social learning in predator recognition and the potential survival benefits for a naïve damselfish prey, *Pomacentrus wardi*. Specifically, we investigated: (1) if prey individuals were capable of transmitting the recognition of the odour of a common predator to conspecifics, and (2) whether a difference in the rate of survival occurred between individuals that directly learnt the predator odour and those which acquired the information through social learning compared to naïve individuals.

Materials and methods

The experiment was conducted at Lizard Island Research Station (14°40'S, 145°28'E) on the Great Barrier Reef, Australia, during November and December 2011. Newly settling *Pomacentrus wardi* (mean SL \pm SE: 15 \pm 0.36 mm) were collected from light traps (for design, see Meehan et al. 2001, small trap) moored overnight near the reef crest, during the summer larval recruitment pulse. Light trap-caught individuals were maintained in 32 l aerated flow-through holding tanks (density: approx. 50–100 per 32 l) at ambient temperatures (26–29 °C), under a 12:12 light:dark photoperiod. Fish were fed ad libitum twice a day with *Artemia franciscana* and Aquaculture Nutrition NRD 5/8 pellets.

Pseudochromis fuscus, a common predator of newly settled fish (Feeney et al. 2012), were collected by SCUBA using hand nets and a clove oil–ethanol–seawater solution (as an anesthetic). Individuals were maintained in separate compartments within 32 l aerated flow-through holding tanks (density: approx. 6–8 per 32 l). Individuals used to produce predator odours were fed twice daily with INVE Aquaculture Nutrition NRD G12 pellets (commercially manufactured diet); however, no feeding occurred 24 h prior to collection of predator odours.

Experiment 1: social learning

Experimental protocol

To determine if social learning of a predator odour occurred in *P. wardi*, experiments were conducted in three separate stages: (a) conditioning of a demonstrator (naïve individual) (b) pairing of the demonstrator with an observer (naïve individual); and (c) testing for an anti-predator response in the observer (Fig. 1). If the observer displayed an anti-predator response in stage c to the predator odour compared to the controls, it was seen as evidence that the fish had learnt that the predator odour represented a potential threat through social learning.

Stage a: conditioning of a demonstrator

Individuals were acclimated in the observation tanks for a period of 18 h. Prior to the initial observation period, the flow-through system was turned off, with 60 ml of tank water drawn up the stimulus injection tube and discarded to remove any stagnant water. A further 135 ml was collected and kept. Immediately prior to the initial observation period, 10 ml of live *A. franciscana* (~2,500 nauplii per tank) was injected into the tube followed by 60 ml of previously collected tank water, to flush the tube. The behaviour of the focal *P. wardi* was then recorded for 3 min. After

Stage 'a' - conditioning of a demonstrator

- Initial observation period (3 min)
- Addition of either:
 - 15 ml of damage-released chemical cue and 60 ml of predator odour (CCPO)
 - 15 ml of seawater and 60 ml of predator odour (SWPO)
- Final observation period (3 min)

Stage 'b' - pairing for social learning opportunity

- Addition of 60 ml of predator odour (PO)

Stage 'c' - testing for anti-predator response

- Initial observation period (3 min)
- Addition of either:
 - 60 ml of predator odour (PO)
 - 60 ml of seawater (SW)
- Final observation period (3 min)

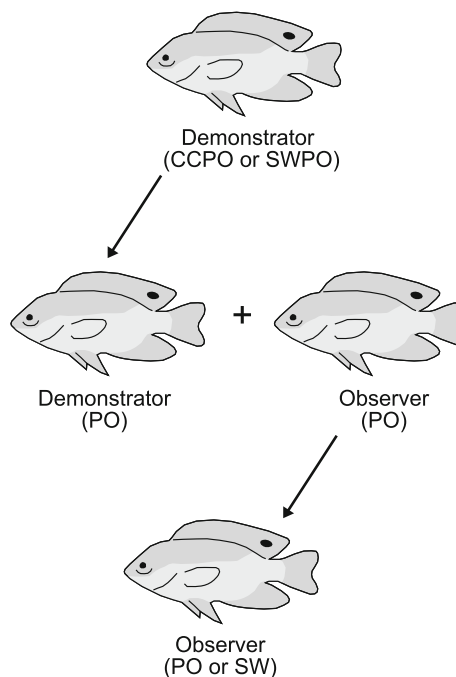


Fig. 1 Flow chart illustrating the three-stage experimental design to test the importance of social learning for newly settled *Pomacentrus wardi* (see Table 1 for a description of treatment codes)

Table 1 Grouping, treatment code, description of cue combinations and cue abbreviations for seven treatments in the study (see Fig. 1 for experimental design)

Grouping	Treatment code	Cue combination	Cue abbreviation
Demonstrator conditioning stage	C1	Damage-released chemical cue and predator odour	CCPO
	C2	Seawater and predator odour; conditioning stage control	SWPO
Observer testing stage for anti-predator response	C3	Predator odour stimulus following conditioning with C1 individual	CCPO + PO + PO
	C4	Predator odour stimulus following conditioning with C2 individual	SWPO + PO + PO
	C5	Seawater stimulus following conditioning with C1 individual	CCPO + PO + SW
	C6	Seawater stimulus following conditioning with C2 individual	SWPO + PO + SW
Control	C7	No conditioning, control	CC

initial observations, one of two treatments [(a solution of 15 ml of the damage-released chemical cue and 60 ml of predator odour (*P. fuscus*) (C1) or a solution of 15 ml of the seawater and 60 ml of predator odour (*P. fuscus*) (C2)] (Table 1) was injected into the tank, along with a further 10 ml of live *A. franciscana*. Following this, 60 ml of previously collected tank water was injected, to ensure all the cue was flushed through. This was followed by a final 3 min observation period, with 30 replicates undertaken for each treatment.

Stage b: pairing for social learning opportunity

Immediately following the final observation period, the individual from stage a (demonstrator) was dipped in clean

seawater then transferred to another observation tank housing a naïve individual (observer) (acclimated for 18 h). To distinguish between the individuals, the observer was tagged with a coloured elastomer injected under the skin behind the dorsal fin. This tagging does not influence the behaviour or survivorship of juvenile damselfishes (Holmes and McCormick 2009). The two individuals were then acclimated in the tank for 2 h before experiments commenced. After the acclimation period, the flow-through system was turned off and 60 ml of tank water was drawn up the stimulus injection tube and discarded, with a further 60 ml collected and kept. A 60 ml aliquot of predator odour along with 10 ml of live *A. franciscana* was injected into the tank followed by 60 ml of previously collected tank water.

Stage c: testing for anti-predator response

Immediately following stage b, the observer was rinsed in clean seawater then transferred to an empty observation tank and acclimated for 2 h before observations commenced. After the acclimation period, the flow-through system was turned off and 60 ml of tank water was drawn up the stimulus injection tube and discarded with a further 120 ml collected and kept. Immediately prior to the initial observation period 10 ml of *A. franciscana* was injected into the tube followed by 60 ml of previously collected tank water, to flush the tube. The behaviour of the focal *P. wardi* was then recorded for 3 min. After initial observations, one of two treatments (60 ml of predator odour or 60 ml of seawater) (C3 to C6) (Table 1) was injected into the tank, along with a further 10 ml of live *A. franciscana*. Following this, 60 ml of previously collected tank water was used to flush through the tube. This was followed by a final 3 min observation period, with 15 replicates undertaken for each treatment crossed with each treatment in stage a (see Fig. 1). This resulted in a total of four cue combinations (C3 to C6) (refer Table 1).

Observation tanks

Experiments were undertaken in observation tanks (height 17 cm, length 27 cm, width 17 cm) with an air stone placed at the back corner of each tank. An additional piece of plastic tubing, for cue injection, was attached to the airline with the end fixed approximately 1 cm above the air stone. Trials with dye showed that it took 12 s for the dye to disperse through the tank. Aquaria had a 2-cm-deep substratum of sand and a shelter consisting of coral rubble 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. Individual *P. wardi* (mean SL \pm SE: 15 \pm 0.36 mm) were placed in the observation tanks 18 h prior to experimentation.

Stimulus preparation

Damage-released chemical cues were prepared according to the protocol from McCormick and Manassa (2008), with a total of 30 *P. wardi* (mean SL \pm SE: 15 \pm 0.36 mm) (1 individual per 15 ml of seawater) sacrificed. Specimens were euthanised by a quick blow to the head, with 10 superficial (minor flesh damage) cuts made to the skin with a clean razor blade. Cue donors were then rinsed in 15 ml of seawater, previously obtained from each test tank. Following this, the 15 ml of damage-released chemical cue was filtered prior to use, with the cues used no longer than 20 min after preparation.

Predator odours were collected in such a way that they were free of possible *P. wardi* damage-released chemical cues. This involved *P. fuscus* (up to 72.4 mm SL) being fed a diet of Aquaculture Nutrition NRD G12 pellets which are manufactured commercially and known to contain no trace elements of chemical cues. The flow-through aquaria system was turned off 2 h prior to experimentation to ensure the predator odours collected just prior to the experiment were concentrated within the holding tanks.

Quantification of behaviour

The behavioural responses of the demonstrators and observers were quantified by recording the frequency of two behaviours: the number of feeding strikes (measures foraging levels) and the number of line crosses (measures activity levels). Known anti-predator behaviour of damselfish includes decreases in both foraging and overall activity levels (Holmes and McCormick 2010; Manassa and McCormick 2012). The observation tanks were divided into four equal vertical areas and six equal horizontal areas (grid of 4.7 \times 4.2 cm rectangles), with every line crossed by the fish recorded. The number of feeding strikes was recorded regardless of success, with the controls in each experiment not expected to show any changes between initial and final observation periods for the variables measured.

Experiment 2: survival

Focal individual *P. wardi* from five cue combinations (C1 to C4 and C7) used in Experiment 1 (refer to Table 1) were tested for survival differences over 48 h periods. Individuals exposed to a seawater stimulus (C5 and C6) following conditioning were not tested as it was unclear if social learning had occurred. Individuals were acclimated in a cylindrical standing pipe (height 50 cm, diameter 20 cm) within 300 l observation tanks (height 33 cm, diameter 110 cm) for 1 h along with 1 l of predator odour. Tanks had a 2-cm-deep substratum of sand and two shelters consisting of coral rubble located at either sides of the tank. Prior to experimentation, the flow through system was turned off and remained so for the duration of the experiment. Following the acclimation period, focal individuals were released from the chamber and allowed to acclimate for a further 30 min period. An individual *P. fuscus* (predator) was then placed into the centre of the observation tank. The study required a total of 55 individual *P. fuscus*, with a total of 22 replicates per treatment (each individual predator was randomized and used twice).

Focal individuals were released from the chamber within the observation tanks between 0830 and 1100 hours. Survival of the *P. wardi* individuals was monitored hourly for the first 12 h. Following this, survival was recorded at

24 h, 36 h and a final 48 h. The trial was terminated after a 48 h period with the number of surviving *P. wardi* individuals recorded.

Statistical analysis

The difference in the total counts of feeding strikes and line crosses between the initial and final 3 min observation periods were compared among the two conditioning stage combinations (C1 and C2) (Table 1) with one-way ANOVAs. One-way ANOVAs were then used to examine the difference in total counts of feeding strikes and line crosses between the initial and final 3 min observation periods among the four testing stage combinations (C3 to C6) (Table 1). Tukey's HSD means comparison tests were used to determine the nature of the significant differences. Residual analysis found that the assumptions of normality and homogeneity of variance were satisfied.

Multi-sample survival analysis using a Cox's proportional hazard model compared the survival of fish in the five cue combinations (C1 to C4 and C7) through the 48 h census period. Survival curves were calculated and plotted using the Kaplan–Meier product-limit method (Kaplan and Meier 1958). The Kaplan–Meier method uses a non-parametric estimator of survival that incorporates incomplete observations, such as those cases in this study where trials were ended before the 48 h period had concluded. Differences in survival between individuals from the conditioning stage treatment (C1) and the testing stage treatment (C3) were compared using a Cox *F* statistic.

Results

Social learning

The behavioural response of the demonstrators (*Pomacentrus wardi*) to the conditioning stage treatment (C1) and the conditioning stage control (C2) was examined (Table 1). There was a significant decrease in both feeding strikes ($F_{1,58} = 191.607$, $P < 0.001$; Fig. 2) and line crosses ($F_{1,58} = 27.495$, $P < 0.001$; Fig. 2) when the damage-released cue was injected (C1) compared to the control (C2).

The behavioural response of the observers (*P. wardi*) to the four cue combinations was examined (C3 to C6) (Table 1). There was a significant difference in both feeding strikes ($F_{3,56} = 35.315$, $P < 0.001$; Fig. 3) and line crosses ($F_{3,56} = 11.542$, $P < 0.001$; Fig. 3) between the initial and final observation periods among the four cue combinations. Tukey's HSD means comparison tests highlighted a reduction in both feeding strikes and line crosses in response to the testing stage treatment (C3), compared to the other three cue combinations (C4 to C6; Table 1; Fig. 3) suggest-

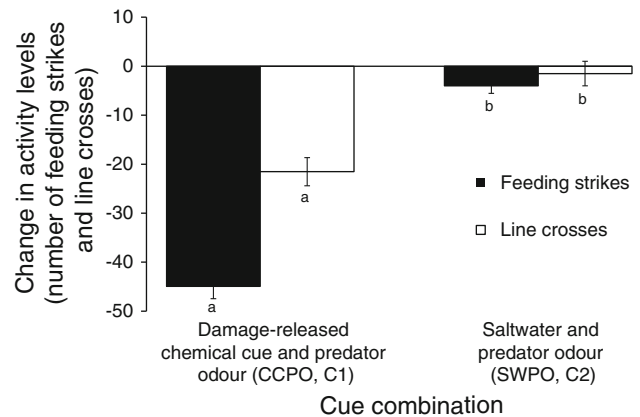


Fig. 2 Demonstrator conditioning: change in feeding strikes (foraging level) and line crosses (activity level) by *Pomacentrus wardi* between initial and final observation periods for treated fish (C1) exposed to a solution of damage-released chemical cues and predator odour (CCPO) or control fish (C2) exposed to a solution of seawater and predator odour (SWPO), mean \pm SE, $n = 15$ per treatment. Letters below the bars represent Tukey's HSD groupings of means (see Table 1 for a description of treatment codes)

ing that fish had learnt that the predator odour represented a threat through social learning.

Survival

There was a significant difference in survival among the five cue combinations (Chi-square = 50.783, $df = 4$, $P < 0.001$; Fig. 4). Survival was highest for individuals from the conditioning stage treatment (C1) (63 % surviving more than 44 h), with the lowest survival for individuals from the testing stage treatment with conditioning control (C4) (31 % surviving more than 1 h). There was no significant difference between individuals from the conditioning stage treatment (C1) and those from the testing stage treatment (C3) (Cox's *F*-Test, $F_{24,34} = 1.682$, $P = 0.081$; Fig. 4).

Discussion

An individual's probability of survival is greatly influenced by their ability to recognise and respond to predation threats (e.g. Lönnstedt et al. 2012). Responses to irrelevant information can be costly; therefore reliable information on the local environment and its predators is essential. The results of this study demonstrate that naïve *Pomacentrus wardi* are capable of transmitting the recognition of a predator odour to conspecifics through the process of social learning. Interestingly, the results reveal that the survival trajectories between directly-experienced individuals and those who 'learnt' the information through social learning

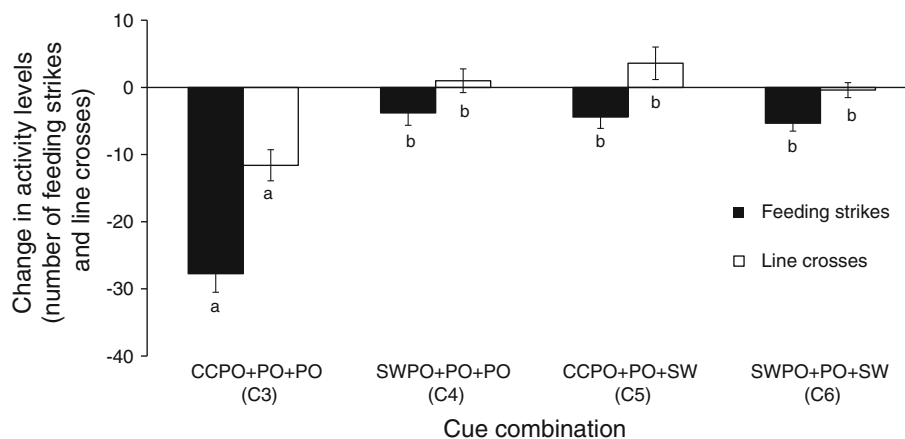


Fig. 3 Observer testing stage for anti-predator response: change in feeding strikes and line crosses by *Pomacentrus wardi* between initial and final observation periods for fish exposed to predator odour or seawater stimulus following conditioning with either a predator-expe-

rienced demonstrator (CCPO, C3 and C5) or a non-experienced demonstrator (SWPO, C4 and C6). Data are mean \pm SE, $n = 15$ per treatment. See Table 1 for a description of treatment codes. Letters below the bars represent Tukey's HSD groupings of means

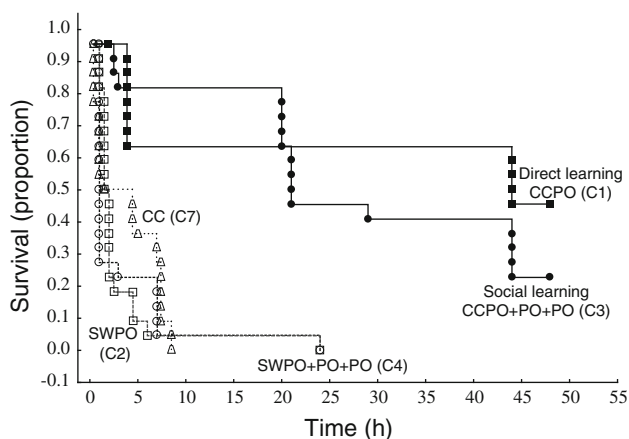


Fig. 4 Observer survival: survival trajectories (Kaplan–Meier plot) of individuals exposed to either: (1) a solution of damage-released chemical cue and predator odour (direct learning; CCPO, C1), (2) a solution of seawater and predator odour (SWPO, C2), (3) predator odour following conditioning with a predator experienced demonstrator (social learning; CCPO + PO + PO, C3), (4) predator odour following conditioning with a non-experienced demonstrator (SWPO + PO + PO, C4), (5) control individuals (no conditioning CC, C7). The time variable represents hours from trials starting between 0830 and 1100 hours, $n = 22$ per treatment. Note: individuals exposed to a seawater stimulus following conditioning (C5 and C6) were not tested as it was unclear if social learning had occurred

did not significantly differ. This suggests that social learning was a rapid and highly effective means of acquiring predator recognition.

This study demonstrates the use of social learning as a mechanism of acquiring predator identities and is similar to the findings by Manassa and McCormick (2012) and Ferrari et al. (2012) for other fish species, highlighting the widespread function of this mechanism amongst coral reef damselfish. As coral reef fishes are exposed to intense

predation pressures during early and transitional life-stages (McCormick and Hoey 2004; Almany and Webster 2006; McCormick and Holmes 2006), a mechanism which allows for the rapid spread of information throughout a community, without the costs associated with direct learning, would be beneficial (Kelley et al. 2003; Holmes and McCormick 2010). Learning from experienced individuals also allows for fine-tuning of anti-predator behaviours, eliminating responses to non-threatening species (Brown et al. 2006). Coral reefs are complex ecosystems containing a high diversity of species within most guilds or tropic groups, with species living in close proximity to one another. This is exactly the sort of system one would expect a large reliance on public information to inform activity patterns of individuals.

This is the first study for any species to show that survival was strongly influenced by social learning and demonstrated that survival was the same regardless of whether the information on predator identity was learnt directly, or through experience with others. Earlier work on *P. wardi* has shown that, regardless of the information type (visual and/or olfactory), direct experience significantly increased the likelihood of survival in the natural environment (Lönnstedt et al. 2012). Studies which have examined the functional importance of social information in freshwater fishes have compared the survival of experienced and non-experienced individuals during staged encounters with predators (Griffin 2004). All studies demonstrated a similar result, highlighting the higher survival rates of fish that had direct experience with predators in both laboratory and field studies (Griffin 2004). Along with these, a study conducted by Webster and Laland (2008) examined the difference in the use of information, gained either directly or publically, to individuals during varying levels of predation risk. They

demonstrated that, when information is too costly to acquire or use personally, individual minnows (*Phoxinus phoxinus*) rely more heavily on the information from others (Webster and Laland 2008). Therefore, in conjunction with the results of the present study, one would predict that individuals should increase their use of public information when the costs of obtaining or using direct experience are high (e.g. increased predation levels during critical life-history stages).

Demersal marine fishes typically follow a Type III mortality curve following settlement, with the majority of individuals dying within the first 5 days (Hixon 1991; Caley 1998; Planes and Lecaillon 2001; McCormick and Hoey 2004). This curve is likely driven by two factors: selection of individuals with preferred traits by predators, and the learning of anti-predator behaviours by prey increasing their ability to avoid consumption (Lönnerstedt et al. 2012). The relative importance of these factors on the shape of the mortality trajectory is unknown. However, it is very likely that fish which have survived a week on the reef will have experienced predation attempts or will have witnessed strikes at neighbours. Individuals that settle after the first recruitment pulse of the replenishment season will therefore settle into a predator-aware community possibly enhancing their chances of survival through social learning. It is currently unclear whether this temporal survival advantage occurs in natural populations due to the multiple factors that confound such temporal comparisons of per capita mortality (e.g. density dependence, variable size/social structures, temperature, etc.).

Prior experience of potential predators significantly influences the survival of juvenile reef fish during the critical life-history transition from the pelagic environment to a benthic reef-associated lifestyle. The ability of individuals to associate a novel cue with risk and then pass this information onto others, through the process of social learning, allows for the rapid spread of information throughout a community. Given the survival advantages observed in this study, social learning is likely to benefit a number of marine fish species, especially during the first few days following settlement. However, given the complexity of coral reef ecosystems, field studies are recommended to ensure the patterns of behaviour and survivorship observed in this study translate into the natural environment. As the type of predator and the level of predation fluctuate with life-stage and environmental conditions, prey are required to continuously learn new predator identities, whilst modifying their response to those that are no longer important. Therefore, social learning is likely to play a vital role throughout an individual's life, as it allows for the continued updating of information on the identity of relevant predators, whilst maximising survival.

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References

- Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* 25:19–22. doi:10.1007/s00338-005-0044-y
- Brown GE (2003) Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish Fish* 4:227–234. doi:10.1046/j.1467-2979.2003.00132.x
- Brown C, Laland K (2001) Social learning and life skills training for hatchery reared fish. *J Fish Biol* 59:471–493. doi:10.1111/j.1095-8649.2001.tb02354.x
- Brown C, Laland K, Krause J (2006) Fish cognition and behaviour. In: Brown C, Laland K, Krause J (eds) *Fish cognition and behaviour*. Blackwell, Oxford, pp 1–8
- Caley MJ (1998) Age-specific mortality rates in reef fishes: evidence and implications. *Aust J Ecol* 23:241–245. doi:10.1111/j.1442-9993.1998.tb00726.x
- Chivers DP, Smith RJF (1998) Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. *Ecoscience* 5(3):338–352
- Feeney WE, Lönnerstedt OM, Bosiger Y, 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(3):909–918. doi:10.1007/s00338-012-0894-z
- Ferrari MCO, Wisenden BD, Chivers DP (2010) Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Can J Zool* 88:698–724. doi:10.1139/Z10-029
- Ferrari MCO, Manassa RP, Dixson DL, Munday PL, McCormick MI, Meekan MG, Sih A, Chivers DP (2012) Effects of ocean acidification on learning in coral reef fishes. *PLoS ONE* 7(2):e31478. doi:10.1371/journal.pone.0031478
- Gosselin LA, Qian P (1997) Juvenile mortality in benthic marine invertebrates. *Mar Ecol Prog Ser* 146:265–282
- Griffin AS (2004) Social learning about predators: a review and prospectus. *Learn Behav* 32(1):131–140
- Hixon MA (1991) Predation as a process structuring coral-reef fish communities. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic, San Diego, pp 475–508
- Holmes TH, McCormick MI (2009) Influence of prey body characteristics and performance on predator selection. *Oecologia* 159:401–413. doi:10.1007/s00442-008-1220-x
- Holmes TH, McCormick MI (2010) Smell, learn and live: the role of chemical alarm cues in predator learning during early life history in a marine fish. *Behav Process* 83:299–305. doi:10.1016/j.beproc.2010.01.013
- Holmes TH, McCormick MI (2011) Response across a gradient: behavioural reactions of newly settled fish to predation cues. *Anim Behav* 81:543–550. doi:10.1016/j.anbehav.2010.11.019
- Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *Am Stat Assoc* 53:457–481
- Kelley JL, Evans JP, Ramnarine IW, Magurran AE (2003) Back to school: can antipredator behaviour in guppies be enhanced through social learning? *Anim Behav* 65:655–662
- Laland KN (2004) Social learning strategies. *Learn Behav* 32(1):4–14
- Leis JM (2007) Behaviour as input for modeling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny,

- physiology and phylogeny meet hydrography. *Mar Ecol Prog Ser* 347:185–193
- Lönstedt OM, McCormick MI, Meekan MG, Ferrari MCO, Chivers DP (2012) Learn and live: predator experience and feeding history determines prey behaviour and survival. *Proc R Soc Lond B*. doi:10.1098/rspb.2011.2516
- Manassa RP, McCormick MI (2012) Social learning and acquired recognition of a predator by a marine fish. *Anim Cogn*. doi:10.1007/s10071-012-0484-z
- McCormick MI, Hoey AS (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. *Oikos* 106:225–242. doi:10.1111/j.0030-1299.2004.13131.x
- McCormick MI, Holmes TH (2006) Prey experience of predation influences mortality rates at settlement in a coral reef fish, *Pomacentrus amboinensis*. *J Fish Biol* 68:969–974. doi:10.1111/j.0022-1112.2006.00982.x
- McCormick MI, Manassa RP (2008) Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs* 27:105–113. doi:10.1007/s00338-007-0296-9
- 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. *Mar Biol* 139:373–381
- Planes S, Lecaillon G (2001) Caging experiment to examine mortality during metamorphosis of coral reef fish larvae. *Coral Reefs* 20:211–220. doi:10.1007/s003380100161
- Valone TJ (2007) From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behav Ecol Sociobiol* 62(1):1–14. doi:10.1007/s00265-007-0439-6
- Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond B* 357:1549–1557. doi:10.1098/rstb.2002.1064
- Webster MM, Laland KN (2008) Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proc R Soc Lond B* 275(1653):2869–2876. doi:10.1098/rspb.2008.0817
- Wisenden BD (2000) Olfactory assessment of predation risk in the aquatic environment. *Philos Trans R Soc Lond B* 355:1205–1208. doi:10.1098/rstb.2000.06681471-2970