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Olfactory responses of coral-reef fishes to coral degradation and crown-of-thorns (*Acanthaster planci*)

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Abstract. Coral degradation is a major threat towards the biodiversity of coral-reef ecosystems, either through the physical effects of environmental change, or biological agents such as crown-of-thorns (*Acanthaster planci*). Coral loss is leading to significant declines in reef-fish assemblages, particularly those dependent on live coral as settlement sites. Most reef fishes use olfactory stimuli at settlement; however, their ability to detect chemical stimuli from degraded corals or *A. planci* is unknown. Here, olfactory responses of juvenile reef fishes to the presence of stressed corals and *A. planci* were tested. Juveniles of eight common coral-associated species were subjected to a series of pair-wise choice tests, where the period of time spent in two differing water sources was noted. All species demonstrated a significant attraction towards healthy coral (≥76%), avoiding cues emitted by stressed coral colonies. When given the choice between a control water (untreated reef water) and water containing chemical cues from *A. planci*, most species elicited no response. Finally, when given the choice between chemical cues derived from feeding *A. planci* or the control, all species avoided *A. planci* (≥70%). Our results indicated that juvenile reef fish are capable of distinguishing the state of coral health, but not directly from disturbance agents.

Additional keywords: Chaetodontidae, chemosensory cues, coral degradation, habitat selection, Labridae, olfaction, Pomacentridae.

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Introduction

Coral-reef ecosystems are becoming seriously degraded, as evidenced by a global decline in coral cover (Gardner *et al.* 2003; Bellwood *et al.* 2004; Feary *et al.* 2007*a*, 2007*b*). This loss has been attributed to a range of factors, including the overfishing of herbivorous species (e.g. Jackson *et al.* 2001; Mumby and Steneck 2008; Rasher *et al.* 2013), changing environmental conditions, such as increasing temperatures, turbidity and sedimentation (Fitt *et al.* 2001; Lough and van Oppen 2009; Wenger *et al.* 2012) and outbreaks of biological disturbance agents such as the devastating crown-of-thorns (COTs) starfish, *Acanthaster planci* (Kenchington and Kelleher 1992; Feary *et al.* 2007*b*; Baird *et al.* 2013). COTs are found on coral reefs throughout the Indo-Pacific, normally occurring in low densities. However, at times of outbreak, they can have a dramatic and immediately devastating effect on coral reefs, in some instances killing up to 80% of corals (e.g. Moran 1986; Baird *et al.* 2013). Coral loss, in turn, is causing significant declines in the biodiversity and abundance of reef-associated organisms such as coral-reef fishes (Jones *et al.* 2004; Munday 2004; Feary *et al.* 2007*a*, 2007*b*; Pratchett and Berumen 2008; Munday *et al.* 2009). Evaluating the severity of this threat depends on knowledge of how individuals and populations respond to different levels of coral stress or degradation. In particular, the behavioural mechanisms used by reef fishes to avoid coral degradation or circumstances that would be detrimental to their survival are poorly understood.

The effects of habitat degradation appear to be greatest for reef fish species that depend on coral for food, shelter and living space (e.g. Booth and Beretta 2002; Feary *et al.* 2007*a*; Munday *et al.* 2009). Coral degradation is known to severely affect the growth and mortality of reef-associated fishes (Munday 2001; Schlaepfer *et al.* 2002; Blondel *et al.* 2006; McCormick 2009). However, coral loss may be most critical at the time of larval settlement to the reef, when the majority of species are dependent on coral for recruitment sites (Jones *et al.* 2004). Most reef fishes demonstrate strong habitat selection at settlement, including selection for particular substrate types (Tolimieri 1995; Öhman *et al.* 1998; Holbrook and Schmitt 2002; Feary *et al.* 2007*b*). Juvenile fishes have the ability to sense and avoid degraded reefs (Lecchini *et al.* 2013, Dixson *et al.* 2014); however, their ability to avoid initial degradation processes (such as increased levels of stress, COTs or the effect of COTs consuming corals) remains uninvestigated.

The use of olfactory cues in settlement-site selection is well documented (Atema *et al.* 2002; Kingsford *et al.* 2002; Dixson *et al.* 2008, 2011). Experiments involving olfactory choice flumes have shown that juveniles can respond to a variety of chemical cues, including substratum types (Dixson *et al.* 2008; Lecchini *et al.* 2005*a*, 2005*b*; Lecchini and Nakamura 2013), the presence of conspecific fishes (Sweatman 1988; Booth 1992; Booth and Wellington 1998; Lecchini and Nakamura 2013) and the presence of other fish species (Vail and McCormick 2011; Dixson *et al.* 2012). However, the degree to which fish can distinguish differences in the health of coral tissues, solely by olfaction, is not yet fully understood (Lecchini *et al.* 2013). Corals in the process of being eaten by crown-of-thorns are likely to be emitting a cocktail of chemical stimuli that may indicate the presence of a poor settlement site. Likewise, COTs themselves may have unique chemical signatures, and, in outbreak situations, it may be advantageous to avoid settling anywhere near them. However, olfactory responses of juvenile fishes to crown-of-thorns, either feeding or not feeding, have not been investigated.

Given that a major decline in the health of reef habitats has already occurred, and may reach catastrophic levels within the next 50 years (Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007; McCormick *et al.* 2010), our understanding of how fishes respond to habitat loss or agents of disturbance must be expanded quickly. To this end, the overall aim of the present study was to assess the ability of newly recruited coral-reef fish juveniles to discriminate among chemical cues from coral differing in health states and the presence of *A. planci.* Specifically, we used olfactory choice flumes to assess choices between (1) healthy and degraded coral tissue, (2) the presence and absence of COTs (non-feeding) and (3) the presence and absence of COTs (feeding). We predicted that juveniles would have the ability to chemically detect and avoid stressed corals, and the presence of COTs both when feeding, and, not feeding on corals. The study targeted eight common coral-reef fish known to be strongly associated with live coral habitats, in Kimbe Bay (Papua New Guinea), including five species of damselfish (Pomacentridae), two species of wrasse (Labridae) and one butterflyfish species (Chaetodontidae).

Materials and methods

Study location and species

The study was conducted at Kimbe Bay, Papua New Guinea (5°12.530′S, 150°22.801′E), between October 2013 and May 2014 at Mahonia Na Dari Research and Conservation Centre. The focal species for the study consisted of eight common coral specialist species, including the following: five species of damselfish (Pomacentridae), namely, *Dascyllus melanurus*, *D. reticulatus*, *Chrysiptera arnazae* (formerly *C. parasema*), *Pomacentrus moluccensis* and *P. aurifrons*; two species of wrasse (Labridae), namely, *Halichoeres melanurus* and *Labrichthys unilineatus*, and one butterflyfish (Chaetodontidae) species, *Chaetodon octofasciatus.* All eight species were used to test responses to coral health. However, because of the limited availability of the other species, only four core damselfish species, namely, *D. melanurus*, *D. reticulatus*, *C. arnazae* and *P. moluccensis*, were used throughout; hence, they were subjected to olfactory trails testing both the effect of coral health and the presence of *A. planci.*

Collection of juveniles

Newly settled juveniles ($<$2.5cm SL) were collected from small coral colonies (10 × 10cm) on areas of nearby inshore reef (2–20 m depth). Juveniles were anesthetised with clove oil and then collected with hand nets. Following their capture, fish were allowed to recover for a 2-h period before being subjected to olfactory discrimination trials. Juveniles were housed in small groups of conspecifics, in aquaria, up until this point. All fish demonstrated active swimming behaviour in the holding aquaria, indicative of recovery from the anaesthetic. Fish that were housed in aquaria for periods exceeding 12 h were fed live *Artemia* nauplii following exposure to the trials. Newly recruited juveniles were used instead of 'naïve' larvae caught in light traps, because this allowed for a greater number of samples to be collected within the period of time available.

Choice flume apparatus

The responses of juveniles to olfactory cues were tested using a two-channel choice-flume (13 × 4 cm), developed by Atema *et al.* (2002). The apparatus allows for pairwise choice experiments to be conducted, in which individual fish can move freely between water flowing from two different sources. Water from two alternate sources was gravity-fed into the choice-flume, which was partitioned along half its length. Recruits were released in the downstream end of the flume (as per Coppock *et al.* 2013), where the exploration of both water sources was possible, allowing for the selection of a preferred source. Water flow was maintained at a constant speed of 100 mL min^{-1} throughout all trials and dye tests were conducted before each trial to ensure that laminar flows were apparent.

For each trial, a single recruit was placed in the downstream end of the flume and left to acclimate for 2 min. During this period, the fish was able to swim throughout the chamber. At the end of the acclimation period, the position of the fish within the chamber was recorded at 5-s intervals for the duration of 2 min. This was followed by a 1-min rest period, during which the water sources were altered, providing a control for potential chamber side preferences. Following this alteration, the entire test, including the acclimation period, was repeated. Any fish that did not swim throughout the chamber during the acclimation period were removed from the trials, because it was not deemed to have assessed the choices available. Of the 323 fish acclimated, 58 were removed before olfactory trials were conducted.

Experimental design

In each trial, recruits were given the choice between either a water source that had been treated with a specific chemical cue (stressed coral *v.* healthy coral, COT *v.* reef water, or COT and coral *v.* reef water) and a water source that had not been treated with any chemical cues (the control). Reef water collected at high tide, from the same reef as the juvenile fishes and coral colonies, was used as a base (control) water source throughout the trails and collected daily. Chemical discrimination trials were run on 15–20 individual fish of each species per treatment. No fish was used more than once.

(a) Coral health treatments

Healthy coral treatment water was prepared by soaking small live coral colonies (10 × 10 cm) in 20 L of reef water for a period

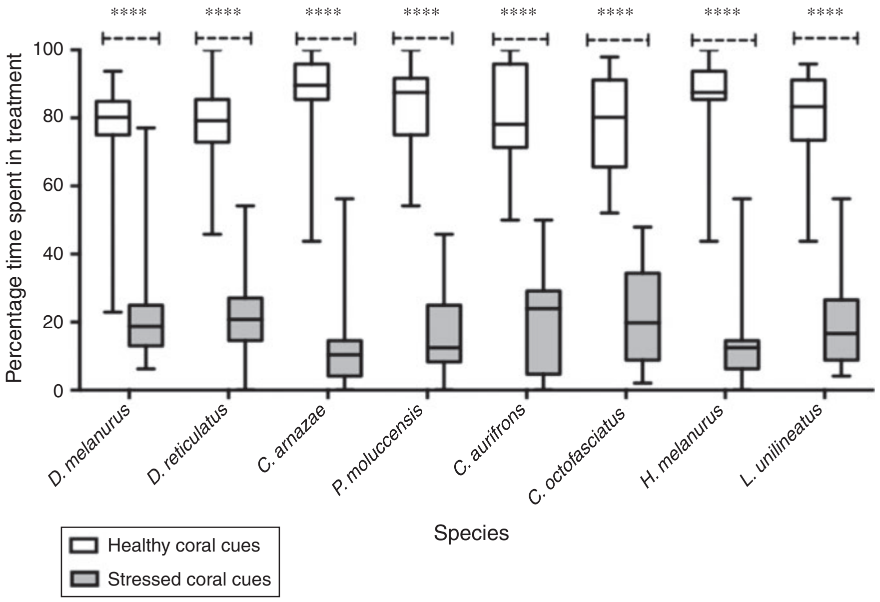

Fig. 1. Response of test species to olfactory cues, indicating alterations to coral health. Focal species were *Chaetodon octofasciatus*, *Dascyllus melanurus*, *D. reticulatus*, *Chrysiptera arnazae*, *Pomacentrus moluccensis*, *P. aurifrons*, *Halichoeres melanurus* and *Labrichthys unilineatus.* Boxes show the percentage of time that recruits spent in healthy coral cue-treated water (white boxes) *v.* in water containing cues derived from stressed coral (grey boxes). This includes the median percentage time (horizontal line), standard error (vertical rectangle) and total range (vertical line). Species are denoted on the *x*-axis. All *P*-values are significant at $P < 0.0001$.

of 2 h. Water for the stressed-coral treatment was prepared in a manner similar to that for the coral treatment. Specifically, small colonies of *Acropora* spp. (10 × 10 cm) were soaked in 20 L of reef water, with an air source for a period of 24 h. During this time, coral displayed copious mucus production, discolouration of tissue and bleaching. Excess mucous was removed from the surface of the water of the treatment before conducting the trials. This prevented any blockages from occurring within the apparatus set up. In all instances, the reef water used in producing the water treatments containing specific chemical cues was derived from the same area of reef as the juvenile fishes being tested.

(b) Acanthaster planci *treatments*

Water from *Acanthaster planci* treatment (non-feeding) was prepared by soaking a single small crown of thorns starfish (≤30cm) in 50 L of reef water, with an air source for a period of 24 h. Treatment water where the starfish was allowed to feed was prepared in a manner akin to that of the non-feeding *Acanthaster* water. A single small crown-of-thorns starfish (≤30cm) and small *Acropora* spp. coral colony (10 × 10 cm) were soaked in 50 L of reef water, with an air source, for a period of 24 h. *Acropora digitifera* was used in coral treatments throughout, because Coppock *et al.* (2013) noted limited preferences towards individual branching coral species.

Statistical analysis

Kolmogorov–Smirnov (K–S) tests were used to compare the total proportion of time that individual recruits spent in different streams of water (*sensu*: Munday *et al.* 2009; Dixson *et al.* 2010). The time spent in treatment water was recorded for each individual by summing the number of 5-s intervals a fish spent in the treatment water over the total 4-min period (maximum count: 48). The median was calculated from the 15–20 replicate trials for each comparison. The null hypothesis was that the presence of chemical cues would provoke a limited response; thus, a uniform distribution would occur between the two water sources. Where observed and expected distributions differed significantly, a preference for a particular water source could be stated. Thus, before statistical analysis, it was hypothesised that no significant differences would arise between (1) the presence of healthy coral cues *v.* those derived from stressed coral colonies, (2) between a control water (untreated reef water) and chemical cues emitted by a non-feeding COT, and (3) between a control water (untreated reef water) and the presence of chemical cues, indicating the presence of a feeding COT.

Results

Coral health treatments

All species exhibited a dramatic avoidance of water from stressed coral treatments, preferring, instead, to spend the majority of each trial in water from the healthy coral treatment (on average, ≥76% of time was spent in healthy coral water; Fig. 1). This pattern was consistent across all the species tested.

Acanthaster planci *treatments*

Acanthaster planci *treatment (non-feeding)*

Three of the four species tested (*D. melanurus*, *D. reticulatus* and *P. moluccensis*) showed no preference or avoidance reaction

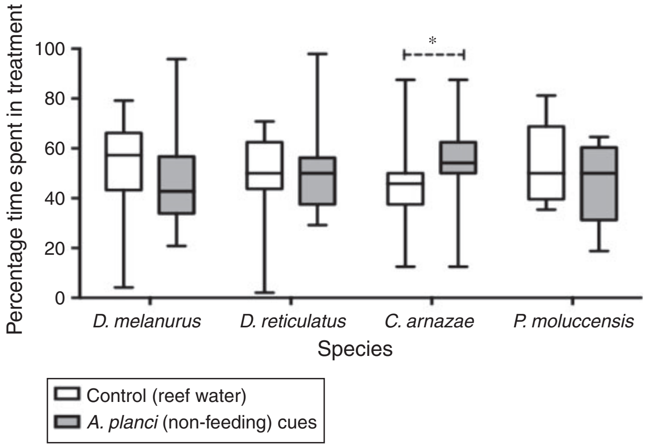

Fig. 2. Response of *Dascyllus melanurus*, *D. reticulatus*, *Chrysiptera arnazae* and *Pomacentrus moluccensis* to olfactory cues from the presence of *Acanthaster planci* (non-feeding). Boxes show the percentage of time that recruits spent in reef water containing no specific olfactory cue (control) (white boxes) *v.* in water containing cues derived from *A. planci* (non-feeding) (grey boxes). This includes the median percentage time (horizontal line), standard error (vertical rectangle) and total range (vertical line). Species are denoted on the *x*-axis. *P*-values are significant at *, $P < 0.05$.

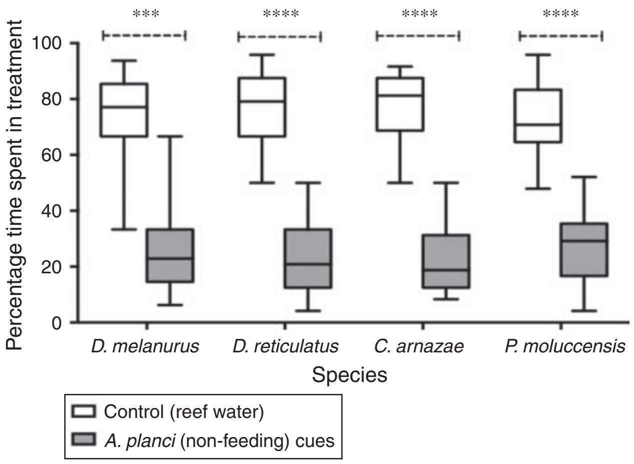

Fig. 3. Response of *Dascyllus melanurus*, *D. reticulatus*, *Chrysiptera arnazae* and *Pomacentrus moluccensis* to olfactory cues from the presence of *Acanthaster planci* (feeding). Boxes show the percentage of time that recruits spent in reef water containing no specific olfactory cue (control) (white boxes) *v.* in water containing cues derived from *A. planci* (feeding) (grey boxes). This includes the median percentage time (horizontal line), standard error (vertical rectangle) and total range (vertical line). Species are denoted on the *x*-axis. *P*-values are significant at: ***, $P < 0.001$; ****, $P < 0.0001$.

towards the presence of chemical cues emitted from *A. planci* in isolation (Fig. 2). That is, they spent approximately equal time in waters containing COT chemical cues (but not coral) and the base (control) water, which lacked specific chemical cues. One species, *C. arnazae*, showed a slight but significant preference for the treatment water containing *A. planci* chemical cues over the base (control) water (54 *v.* 46%, K–S = 0. 53, $P < 0.05$).

Acanthaster planci *treatment (feeding)*

When pair-wise choice tests were run to examine any response towards the presence of chemical cues from feeding *A. planci*, all species demonstrated a significant avoidance (Fig. 3). The majority of each trial, therefore, was spent in the reef water that lacked specific chemical cues (control) (70%). The strongest reactions in this instance were exhibited by *D. reticulatus* and *C. arnazae*, where 79% of the trial period was spent in the reef water with no associated cues. This level of avoidance was close to that observed in the stressed coral treatment.

Discussion

The present study is the first to investigate whether the chemosensory system of juvenile reef fishes aids choices between not only, healthy and stressed coral colonies, but also in the avoidance of the most destructive agent of disturbance on coral reefs, namely, the crown-of-thorns. Our results supported the hypothesis that habitat-quality cues are critical in determining settlement patterns in many coral-reef fish species. When exposed to pairwise olfactory choice trials, all species demonstrated a strong preference for water sourced from live healthy corals, as opposed to the water derived from corals under stressed conditions. Similarly, when exposed to the scent of coral tissue that was being consumed by *A. planci*, the same strong response was apparent. Settlers spent upward of 70% of the trial period choosing to associate with the reef-water treatment that did not contain the *A. planci* feeding cue. However, most juvenile fishes exhibited no detectable avoidance of *A. planci* individuals that were not feeding. Overall, our findings suggested that a coral stress signal needs to be elicited before fishes exhibit an olfactory response. Once present, juveniles will immediately elicit strong avoidance behaviour. However, a COT alone is not considered a threat.

For coral-reef fishes, there is a strong selective advantage for being able to select suitable habitat at the end of the larval stage because this is critical to post-settlement survival and success (Schlaepfer *et al.* 2002; Munday *et al.* 2009 McCormick 2009; McCormick *et al.* 2010). Settling on to healthy habitat can be advantageous for individual growth (Munday 2001; Blondel *et al.* 2006), body condition (Berumen *et al.* 2005) and reproductive output (Conradt *et al.* 1999; Morris and Davidson 2000). Our results are consistent with those by McCormick *et al.* (2010), who demonstrated that two species of settlement-stage damselfish preferentially select for live coral colonies (over bleached or dead), through a combination of visual and olfactory cues (*P. moluccensis*, *P. ambionensis*). Similarly, Lecchini *et al.* (2013) also demonstrated that several species of reef fish (e.g. families Pomacentridae, Acanthuridae and Aulstomidae) showed a distinct preference for water from areas dominated by coral, over those dominated by algae. Furthermore, these results both corroborate and expand on the results of our previous study Coppock *et al.* (2013), which demonstrated both preferences towards water treated with live coral, and avoidances towards water treated with degraded coral, when both were tested against reef water with no specific chemical cues. It is clear that reef fishes are very responsive to chemical cues coming from the corals themselves.

Acanthaster planci is clearly a specialised coral predator that grazes extensively on live coral cover (Yamaguchi and Braham 1974), frequently causing significant coral mortality and adding to the degradation of coral-reef environments (Goldberg and Wilkinson 2004; Pratchett *et al.* 2009). For fish species with strong or obligate association with live coral colonies, it might be considered advantageous for them to be able to detect the predators of their coral hosts and predict potential degradation in advance. However, when recruits were exposed to the *A. planci* treatment water, where the starfish was unable to feed, in most instances, little or no reaction was apparent. This suggests that the association between COTs and damaged coral is not frequent enough, either in evolutionary or ecological time scales, to represent a significant problem at settlement. The slight preference of *C. arnazae* to the presence of COTs has no obvious explanation.

The fact that this avoidance of *A. planci* only occurred when a live coral colony was present in the treatment water implies that it is the response of the coral to predation that the recruits are responding to, and not the presence of the starfish *per se*. Indeed, when predation was apparent in these treatments, the coral in question was seen to secrete large volumes of mucus. Chemically sensing nearby death is a powerful determinant of individual behaviour. Although this phenomenon is usually observed in relation to the death of a conspecific, the ‘smell’ of death comes in multiple forms, each of which has both direct and indirect effects on behaviour (Peacor and Werner 2001; Trussell *et al.* 2004; Byrnes *et al.* 2006; Long *et al.* 2007; Hay 2009). This may be particularly important where a species is reliant on its coral host for its own survival. Thus, where the coral is producing defensive responses in reply to being predated on, this is likely to act as a deterrent for settlement.

Although it is acknowledged that waters from the stressed-coral and feeding-*A. planci* treatments are particularly potent, and, as such, the avoidance reactions particularly strong, the use of chemical cues in avoiding habitats that would be disadvantageous to future survival and fitness is still demonstrated. The question now remains to understand the degree at which this becomes detectable, so as to establish at what concentration coral degradation would be damaging to successful recruitment.

Previous studies have shown evidence of rapid ontogenetic change in morphology and behaviour at or soon after the point of settlement (Leis and Yerman 2012). Thus, preferences for coral species may differ depending on whether juveniles are tested before or after settlement (Danilowicz 1996). Because all our focal individuals had already settled, patterns of choice may not necessarily reflect choices that were made at settlement. However, almost all studies that have compared settlement choices in pre-settlement larvae and post-settlement juveniles have found identical patterns, regardless of ontogenetic phase (e.g. Öhman *et al.* 1998; Dixson *et al.* 2008). For these species, therefore, it may be possible to infer settlement choices in pre-settlement larvae through olfactory trials carried out on post-settlement juveniles, and drawing conclusions in this manner is not incorrect. Likewise, because the majority of juveniles used throughout the trials were collected from live, healthy coral colonies, there is the potential that exposure to this chemical signal might influence the results seen in the choice flume. Ideally, future research needs to focus on the use of larval recruits, to avoid this influencing the results.

In conclusion, the results of the study corroborated the importance of olfactory cues in directing recruits away from inappropriate habitats, and towards areas of live coral, thus helping avoid areas of degraded coral that would be detrimental to their fitness. Clearly, the presence of *A. planci* in the absence of coral is not perceived as a threat. However, at times of outbreak, when predation on corals is high, juveniles are likely to show strong avoidance to affected areas. If settlers fail to find suitable habitat, widespread recruitment failure is likely to occur, with long-term consequences for a wide variety of coral-associated fishes.

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