

Influence of habitat degradation on fish replenishment

M. I. McCormick · J. A. Y. Moore ·
P. L. Munday

Received: 9 December 2009 / Accepted: 17 March 2010
© Springer-Verlag 2010

Abstract Temperature-induced coral bleaching is a major threat to the biodiversity of coral reef ecosystems. While reductions in species diversity and abundance of fish communities have been documented following coral bleaching, the mechanisms that underlie these changes are poorly understood. The present study examined the impacts of coral bleaching on the early life-history processes of coral reef fishes. Daily monitoring of fish settlement patterns found that ten times as many fish settled to healthy coral than sub-lethally bleached coral. Species diversity of settling fishes was least on bleached coral and greatest on dead coral, with healthy coral having intermediate levels of diversity. Laboratory experiments using light-trap caught juveniles showed that different damselfish species chose among healthy, bleached and dead coral habitats using different combinations of visual and olfactory cues. The live coral specialist, *Pomacentrus moluccensis*, preferred live coral and avoided bleached and dead coral, using mostly visual cues to inform their habitat choice. The habitat generalist, *Pomacentrus amboinensis*, also preferred live coral and avoided bleached and dead coral but selected these habitats using both visual and olfactory cues. Trials with another habitat generalist, *Dischistodus* sp., suggested that vision played a significant role. A 20 days field experiment that manipulated densities of *P. moluccensis* on healthy and bleached coral heads found an influence of fish density on juvenile weight and growth, but no significant influence of habitat quality. These results suggests that coral bleaching

will affect settlement patterns and species distributions by influencing the visual and olfactory cues that reef fish larvae use to make settlement choices. Furthermore, increased fish density within the remaining healthy coral habitats could play an important role in influencing population dynamics.

Keywords Coral bleaching · Settlement patterns · Climate change · Coral reef fish · Vision · Olfaction

Introduction

How an organism interacts with its environment can have a profound effect on its life history, with documented effects on individual growth (Munday 2001; Blondel et al. 2006), body condition (Berumen et al. 2005), reproductive output (Conradt et al. 1999; Morris and Davidson 2000) and probability of survival (Paradis 1995; Burton et al. 2006). Global climate change is predicted to increase the occurrence of habitat modifying disturbances (e.g., Easterling et al. 2000; Dale et al. 2001; Travis 2003). The resulting fragmentation, degradation and loss of habitats from such disturbances are expected to compromise individual performance, reduce population sizes and, in extreme cases, result in local or even global extinctions (Hughes 2000; Williams et al. 2003; Munday 2004; Shoo et al. 2005; Parmesan 2006). Understanding the mechanisms by which an organism is affected by habitat degradation is critical to predicting the impact of disturbance on biological communities.

Coral reefs are particularly vulnerable to anthropogenic climate change, and major changes in the composition of reef habitats are predicted to occur within the next 50 years as a result of thermally induced coral bleaching (Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Water temperatures 1–2°C above the long-term summer average induce

Communicated by Environment Editor Prof. Rob van Woesik

M. I. McCormick (✉) · J. A. Y. Moore · P. L. Munday
School of Marine and Tropical Biology, James Cook University,
Townsville, QLD 4811, Australia
e-mail: mark.mccormick@jcu.edu.au

bleaching in many coral species (Hoegh-Guldberg 1999; Marshall and Baird 2000) and can lead to death. Since corals are a key component of the reef benthos, changes in their relative abundances are predicted to affect many other coral reef organisms, especially those species that depend on corals for food, shelter or breeding sites (Munday et al. 2008; Pratchett et al. 2008).

For coral reef fishes, a key life-history transition occurs when larvae complete their pelagic larval stage and settle to the reef where they become part of the benthic population. After their initial association with reef substrata (i.e., settlement), some species undergo a series of rapid migrations between habitats in close proximity over a number of days (McCormick and Makey 1997). The mortality rate during this transition between larval and juvenile phases is extremely high (Almany and Webster 2006); therefore, the selection of a suitable habitat may be vital for survival and future success. Habitat characteristics have been shown to have significant effects on juvenile growth and survival (Caley and St. John 1996; Beukers and Jones 1998; Munday 2001; Almany 2004; McCormick 2009). Furthermore, many species of fish have been found to settle to hard coral habitats and use these as nursery areas (Jones et al. 2004). As the composition of coral reef habitat changes due to global warming, so too will the chemical and visual cues emitted by these habitats that might be used by fish larvae to identify appropriate settlement habitat.

Fishes can use olfaction (Sweetman 1988; Atema et al. 2002; Lecchini et al. 2005b; Gerlach et al. 2007; Dixon et al. 2008, 2010), vision (Booth 1992; Leis and Carson-Ewart 1999) and sound (Egner and Mann 2005; Simpson et al. 2005; Wright et al. 2005) to select habitats at a range of spatial scales. While most demersal fishes settle on moonless nights (Dufour and Galzin 1993; Milicich and Doherty 1994), the patterns of settlement established by the following morning will be an unknown function of their initial habitat choice, post-settlement redistribution and differential mortality. Visual cues were tested in the present study as vision is a dominant sense used by fishes for habitat discrimination and species recognition (McFarland 1991; Lecchini et al. 2005a), and it is likely to be used by settling fish as soon as light becomes sufficient to allow visual discrimination. Currently, it is unclear how the sensory cues used in habitat selection may change as corals transition from healthy through to bleached and finally dead coral.

The costs and benefits of settling to different habitat types can also interact with the density of individuals living in those habitats (Rosenzweig 1991). If hard coral habitats become less abundant, it might be expected that the remaining coral patches will experience higher densities of resident fishes. Enhanced interaction rates within these habitat patches could then lead to a reallocation of energy among key activities such as foraging, maintenance of

social networks and anti-predator behaviours (Jones and McCormick 2002). While many studies have now shown that tropical fish assemblages change in abundance with habitat disturbance (e.g., Booth and Beretta 2002; Jones et al. 2004; Garpe et al. 2006; Wilson et al. 2006; Graham et al. 2007; Pratchett et al. 2008), the mechanism responsible for these changes is poorly understood.

This study examined the impacts of coral bleaching on early life-history processes of coral reef fishes. First, the settlement preference of fishes to healthy, thermally bleached and dead corals was examined in the field. Secondly, behavioural experiments examined the sensory cues (olfaction or vision) used in the settlement choice of fishes for healthy, bleached and dead coral habitats. Lastly, the influence of coral bleaching on individual post-settlement processes was investigated. In a field-caging experiment, the interactive effects of hard coral health and conspecific density on individual growth rate and body condition of a planktivorous, coral-dwelling damselfish, *Pomacentrus moluccensis*, were examined.

Materials and methods

Study species and location

Research was conducted at Lizard Island (14°41'S, 145°27'E) on the northern Great Barrier Reef, Australia. Most of the species that settled to habitat patches that were monitored for settlement (below) were damselfishes (Pomacentridae). This family was therefore used as the focus of the study. Damselfishes are an ideal group for investigating the mechanisms responsible for differences in habitat use, since they exhibit a broad range of habitat preferences at settlement and are one of the numerically dominant families of fishes on coral reefs.

Settlement patterns

Settlement patterns of coral reef fishes to healthy, thermally bleached and dead coral colonies were investigated by daily collections of newly settled fish over a 10-day period in November 2006 coinciding with a peak in settlement that occurs around the new moon (Milicich et al. 1992). A grid of small patch reefs (~25–30 cm diameter) was constructed in shallow water approximately 5 m from the reef edge in the Lizard Island lagoon. Patch reefs were placed 5 m apart to prevent migration between coral heads. Patch reefs were constructed from colonies of the bushy hard coral *Pocillopora damicornis* in three different states: (1) live healthy colonies, (2) colonies that had been thermally bleached in aquaria and were still alive, (3) colonies of dead coral that were overgrown by a small amount of

invertebrates and algae ($n = 5/\text{colony state}$). Bleaching was induced in round 450-l aquaria where water temperature was incrementally raised over a 24- to 48-h period from ambient (26°C) to a sustained maximum of 32°C. Aquaria were constantly aerated, flow was maintained using two 1,200 l hr⁻¹ powerheads and heated with two 300-W aquarium baton heaters. After colonies were visibly bleached, water temperature was lowered to ambient incrementally over a 24-h period. The bleaching process took approximately 10 days. These colonies were transported to the field site and arranged haphazardly in the grid along with the other two coral treatments. Colonies stayed alive but remained bleached for at least 6 weeks, after which most were re-colonised by zooxanthellae.

Abundance and species richness of fish recruits were pooled across days as daily settlement rates were low. Species richness data required no transformation; however, abundance data were $\log_{10}(x + 1)$ transformed to meet statistical assumptions. Data were analysed using one-way analysis of variance (ANOVA) followed by Tukey's HSD tests to identify the nature of significant differences between treatments.

Settlement choice and sensory cues

Multiple-choice selection trials were used to test habitat preferences of juveniles at and soon after settlement and to investigate the sensory cues used in habitat selection. Three fish species were chosen to represent a range of associations with live coral: *Pomacentrus moluccensis*, which is associated with live coral (Beukers and Jones 1998), *P. amboinensis*, which inhabits rubble, dead coral and live coral patches at the base of reefs (McCormick 2009), and *Dischistodus* spp. (mostly *D. perspicillatus*), which inhabits sand and rubble patches adjacent to the reef edge (Bay et al. 2001). Settlement-stage larvae were collected overnight in light traps (see Meekan et al. 2001 for trap design) deployed over sand away from reefs. Traps were emptied just after dawn, and fishes were transferred to a flow-through aquarium system at the Lizard Island Research Station. The fishes collected in light traps were at the end of their larval phase and were assumed to have not yet encountered reef substrata. Fishes were used in selection trials within 48 h of capture, by which time they had acquired juvenile colouration.

The test arena consisted of three habitat choices and a sand control presented on a layer of beach sand that covered the bottoms of the 450-l tanks. Tanks were continuously supplied with fresh seawater and drained by a central stand-pipe (Fig. 1). Three similar sized colonies (10–15 cm diameter) of the focal coral species *Pocillopora damicornis* were randomly placed near the perimeter of the test arena: one live colony; one thermally bleached colony; and one

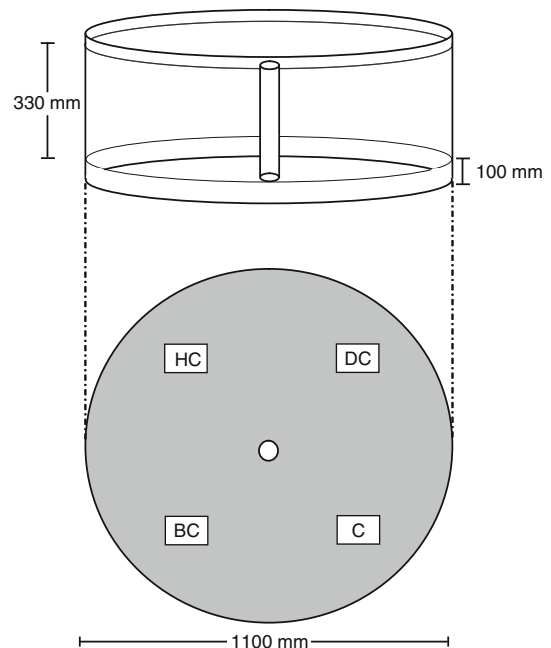


Fig. 1 Schematic diagram of experimental arena used for habitat preference and sensory cue trials. Aerial view (*bottom*) shows orientation of substrate types: healthy *Pocillopora damicornis* hard coral (HC); bleached coral (BC); dead coral (DC); blank control (C). Locations of substrate were randomised between trials. Profile view (*top*) shows central drain-pipe above 100 mm depth of sand. The water level ~ 20 mm from top of tank. Perspex containers and header tanks used in visual and olfactory cue trials are not shown

dead colony that had similar structure to the other two categories but was overgrown with algae and benthic invertebrates. Between trials, habitat choices were rotated, the sand layer stirred and the aquaria drained and refilled.

Three selection experiments were undertaken. The first examined whether the three fish species exhibited a non-random distribution in relation to habitat type and if so which habitats were preferred. These trials were conducted overnight since research suggests that the first association of demersal fishes with reef substrata generally occurs at night (e.g., Kaufman et al. 1992). As this experiment did not separate between the potential role of olfaction versus visual cues, a second set of experiments were conducted during the day, which allowed the evaluation of settler responses to each cue independently.

In the first experiment, habitat preferences of naïve light-trap caught individuals were examined during overnight trials where one fish was released at dusk into the centre of the experimental arena, following a 30-min acclimation period in a circular PVC shelter (Fig. 1). Preference was scored as the substratum, each individual was observed associating with at first light the following morning. Associations displayed at dawn have been shown to persist throughout the day (Öhman et al. 1998). In all laboratory choice experiments, habitat preference was

analysed using a χ^2 goodness of fit test, under the expectation of an equal distribution between habitats. Binomial tests were then conducted to determine whether particular habitats obtained more fish than expected from a random distribution.

To investigate the role of vision and olfaction in discriminating among corals in different states, behavioural choice experiments were conducted where individual fish were offered live coral, bleached coral, dead overgrown coral and a blank sand patch arranged randomly around the perimeter of the tank. Individuals were released into 450-l tanks following a 10-min acclimation period and observed at 5-min intervals over the course of 1 h. Fish were observed from behind black plastic screens to negate observer influence. Individual location was scored every 2 min for 1 h, and habitat choice was assigned at the end of each trial as the habitat most frequently associated with over the course of that trial. To test the importance of visual cues in habitat selection, individuals were presented with the same three habitat choices inside sealed transparent Perspex containers in the absence of chemical signatures. A control container was filled with water only.

To determine the importance of olfactory cues in habitat selection, 4 identical moulded plastic branching coral skeletons were placed regularly around the perimeter of the tank (item no. 21505; Wardleys/TFH, Sydney; dimensions: 14 × 11.5 × 5 cm), providing shelter for the fish. Olfactory stimuli alone were introduced into the tank by gravity feeding water from external header tanks containing one of the three habitat choices. Water was directed directly onto the plastic corals at constant flow rate of 2 l min⁻¹ using plastic tubing. The experimental control was seawater gravity fed from a header tank. Frequency distributions of habitat choices were statistically analysed using χ^2 and binomial tests as previously described.

Influence of coral bleaching and juvenile density on post-settlement growth and condition

The influence of coral bleaching and settler density on early post-settlement growth and condition of the coral-dwelling damselfish *Pomacentrus moluccensis* was investigated by caging light-trap caught individuals on small patch reefs (ca. 25–30 cm diameter) constructed of either live or thermally bleached *Pocillopora damicornis* colonies at high (final densities: 8–14, mean 12) and low (all with six fish) densities for 20 days in December 2006. Five replicate colonies of live or bleached coral were established at each of the two fish densities, representing the lower and upper limits of recruit density observed on surrounding reefs during prior recruitment pulses. Galvanised wire cages (6.5-mm diameter mesh) excluded all predation and migration for the duration of the experiment. At the end of

the 20 days, all remaining fishes were collected and killed by an overdose of clove oil anaesthetic.

To assess post-settlement growth rate and body condition differences, a sample of thirty fish was taken from each treatment combination. This means all fish were used from the low-density treatments, while a random subsample of 30 fish were used from the high-density treatment. Individuals were measured for standard length (SL) and blotted wet weight before and after the removal of the sagittal otoliths prior to freeze drying for total body lipid assays. Methodology for lipid assays followed Folch et al. (1957). Briefly, freeze-dried whole fish were homogenised in 1.0 ml of distilled water per 10 mg of freeze-dried tissue. Lipids were extracted in a chloroform/methanol solution, the solvent evaporated and colour evolved by reaction with a sulphophosphovanillin complex. Lipid concentration was determined spectrophotometrically against calibration curves obtained using analytical grade cholesterol (Sigma–Aldrich Corp.) as the lipid standard.

Individual growth trajectories were estimated from otolith increment widths. Sagittal otoliths were sectioned transversely and processed for increment widths as described by Wilson and McCormick (1997). Daily increments and cumulative otolith size were determined using image analysis software (Optimas 6.5) from digitised images of the prepared otoliths captured at 200× magnification.

Body condition differences were examined using factorial ANOVA for blotted wet weight and total body lipids. For each metric, the mean value of individuals on each individual reef was analysed as a single replicate to meet the assumption of independence. Further transformation was unnecessary as all other assumptions were met. Individual otolith growth trajectories were compared between treatments using repeated measures ANOVA of daily otolith increment widths.

Results

Settlement patterns

Significant differences were found in the number of settlers ($F_{2,12} = 4.11$, $P < 0.05$) and number of species ($F_{2,12} = 5.04$, $P < 0.05$) settling among the three coral habitats. Total abundance of settlers over the 10-day study period was greatest on healthy coral (mean = 47 fish per coral head) and fewest on bleached colonies (mean = 5.4). Total abundance of recruits to dead coral was intermediate (mean = 23.6) and not significantly different from either healthy or bleached coral as determined by post hoc analyses (Fig. 2a). Species diversity, however, was significantly higher on dead coral colonies (mean = 6.6) than on bleached coral (mean = 3.2). Species diversity of recruits

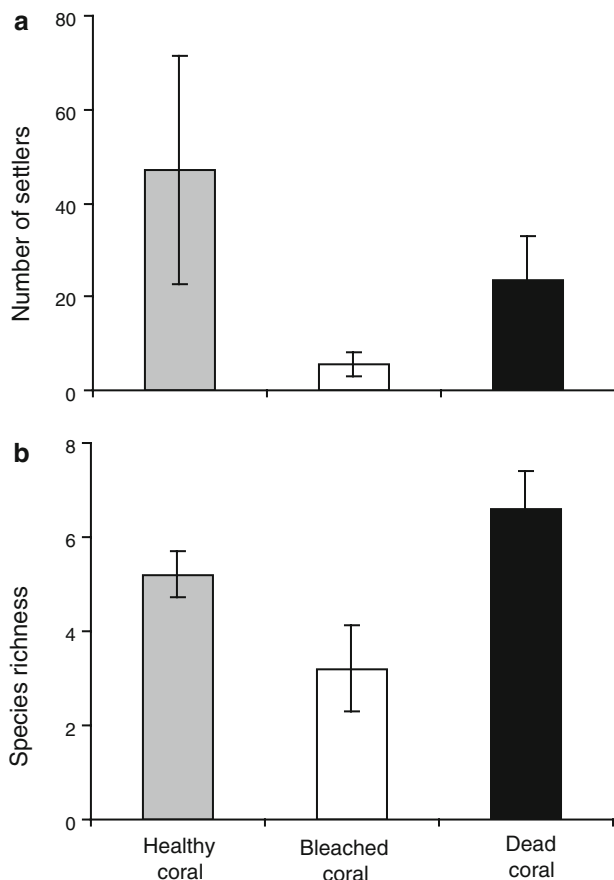


Fig. 2 Fish settlement to three habitat types: healthy *Pocillopora damicornis* hard coral; thermally bleached by live coral; and dead coral. **a** Mean number of recruits per habitat type and **b** mean number of species per habitat type, collected over 10-day sampling period. Error bars are standard errors

to live coral was intermediate (mean = 5.2) and not significantly different to species diversity on dead or bleached colonies (Fig. 2b).

Settlement choice experiments

When allowed both olfactory and visual cues in overnight trials, both *Pomacentrus* species exhibited non-random habitat use in the laboratory, with a strong preference for healthy coral (Fig 3a, *P. moluccensis* $\chi^2_{df\ 3} = 16.000$, $P = 0.001$, $n = 12$, binomial test $P < 0.01$; Fig. 3b, *P. amboinensis* $\chi^2_{df\ 3} = 28.667$, $P < 0.001$, $n = 12$, binomial test $P < 0.01$). Bleached, dead coral and sand were selected infrequently, with *P. amboinensis* choosing bleached coral and sand less than expected by random at the 0.05 level (binomial test, $P = 0.03$). Habitat use of *Dischistodus* spp. was overall not significantly different from random ($\chi^2_{df\ 3} = 4.667$, $P = 0.198$, $n = 12$) and was distributed among the habitats more evenly than the other species (Fig. 3c). Binomial tests indicated more fish than expected

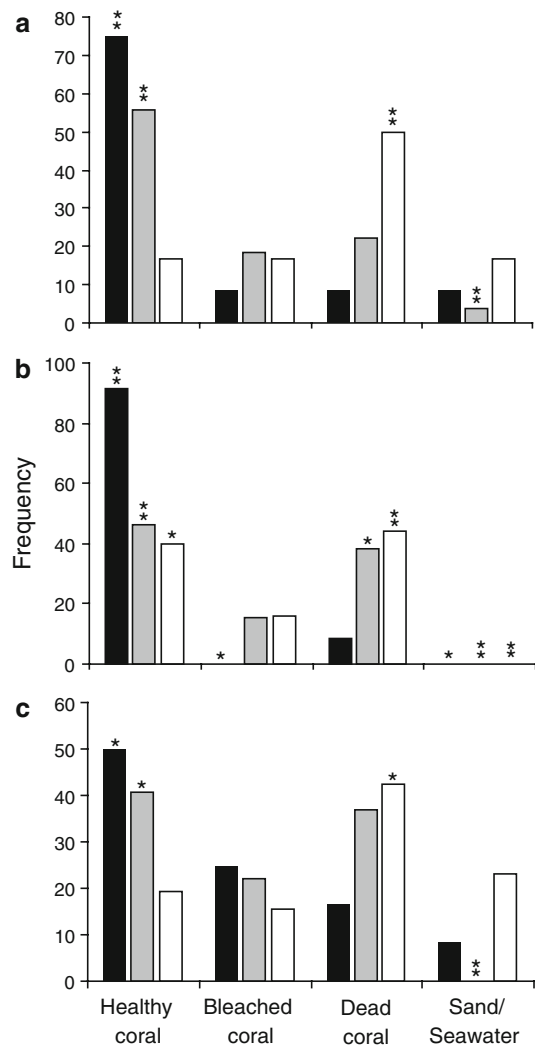


Fig. 3 Frequency (%) of habitat types selected by juveniles of three damselfishes during laboratory habitat preference experiments: **a** *Pomacentrus moluccensis*, **b** *P. amboinensis* and **c** *Dischistodus* sp.. Habitat choices offered were healthy *Pocillopora damicornis* hard coral, thermally bleached coral, dead coral and a control (sand or seawater). Fish were allowed to use all senses (black bars; trial run overnight), the visual sense (grey bars; diurnal trials) or olfaction alone to inform their choices (clear bars; diurnal trials with cues released over model corals). Sample sizes by species and sense are: *P. moluccensis* 12 (all senses), 27 (visual), 30 (olfaction); *P. amboinensis* 12, 26, 25; *Dischistodus* 12, 27, 26. Stars indicate significant differences from a random distribution (binomial tests): * $P < 0.05$; ** $P \leq 0.01$

at the 0.05 level were found only on healthy coral (binomial test, $P = 0.04$). The sand patch control was selected only twice from 36 independent trials.

Habitat choice by *P. moluccensis* significantly differed from random in visual ($\chi^2_{df\ 3} = 15.5$, $P < 0.01$) and olfactory cue trials ($\chi^2_{df\ 3} = 14.0$, $P < 0.01$). Using visual cues alone, healthy coral was chosen by 15 of 27 individuals (binomial test, $P = 0.0005$), whilst bleached and dead coral heads were selected by five and six individuals,

respectively, as the secondary habitat choice and did not differ from the frequency of occurrence predicted from a random distribution (binomial test, $P > 0.14$; Fig. 3a). Only one individual chose the sand control in visual cue trials, which was significantly less than expected from random (binomial test, $P < 0.004$). In olfactory cue trials, individuals did not discriminate between the smell of bleached coral, healthy coral and the seawater control, choosing each water source with the same frequency as expected from a random distribution (binomial tests, $P > 0.1$). However, olfactory cues from dead colonies attracted *P. moluccensis* (binomial test, $P = 0.002$), with 15 of 30 individuals choosing dead coral over the three other choices (Fig. 3a).

Patterns of habitat selection for *P. amboinensis* were similar in the visual and olfactory cues trials (Fig. 3b) and significantly differed from a random distribution (visual: $\chi^2_{df\ 3} = 14.0$, $P < 0.01$; olfactory: $\chi^2_{df\ 3} = 12.9$, $P < 0.01$). In both trials, healthy and dead corals were chosen more often than expected from random (binomial tests, $P \leq 0.05$), while the controls (sand and seawater) were chosen less than expected from random (binomial tests, $P < 0.001$). The number of *P. amboinensis* choosing bleached coral did not differ from random in either visual or olfactory trials (binomial test, $P > 0.1$; Fig. 3b).

Patterns of habitat selection by *Dischistodus* spp. during the visual trials were similar to those observed for *P. amboinensis* and significantly differed from random (Fig. 3c, $\chi^2_{df\ 3} = 12.9$, $P < 0.01$). Healthy coral was chosen with similar frequency (11 of 27 individuals) to dead coral (10 of 27), though only healthy coral was chosen significantly more than expected by random (binomial test, $P = 0.03$). Only six fish chose bleached coral (binomial test, $P = 0.171$) while sand was significantly avoided (binomial test, $P < 0.001$). Similar to the results from the olfactory cue trials for *P. moluccensis*, *Dischistodus* sp. chose olfactory cues from healthy and bleached corals as frequently as the background seawater control and these choices did not differ from a random distribution (binomial tests, $P > 0.1$; Fig. 3c). Olfactory cues from dead coral were detected by 11 of 26 individuals and differed significantly from a random distribution (binomial test, $P = 0.024$), although the overall distribution of choices among the four habitats was not significant ($\chi^2_{df\ 3} = 4.5$, $P > 0.05$).

Influence of coral bleaching and juvenile density on post-settlement growth and condition

Pomacentrus moluccensis juveniles stocked at high density were on average heavier than those stocked at low density after 20 days on the experimental reefs ($F_{1,16} = 6.605$, $P < 0.05$) (Fig. 4a). In contrast, there was no effect of

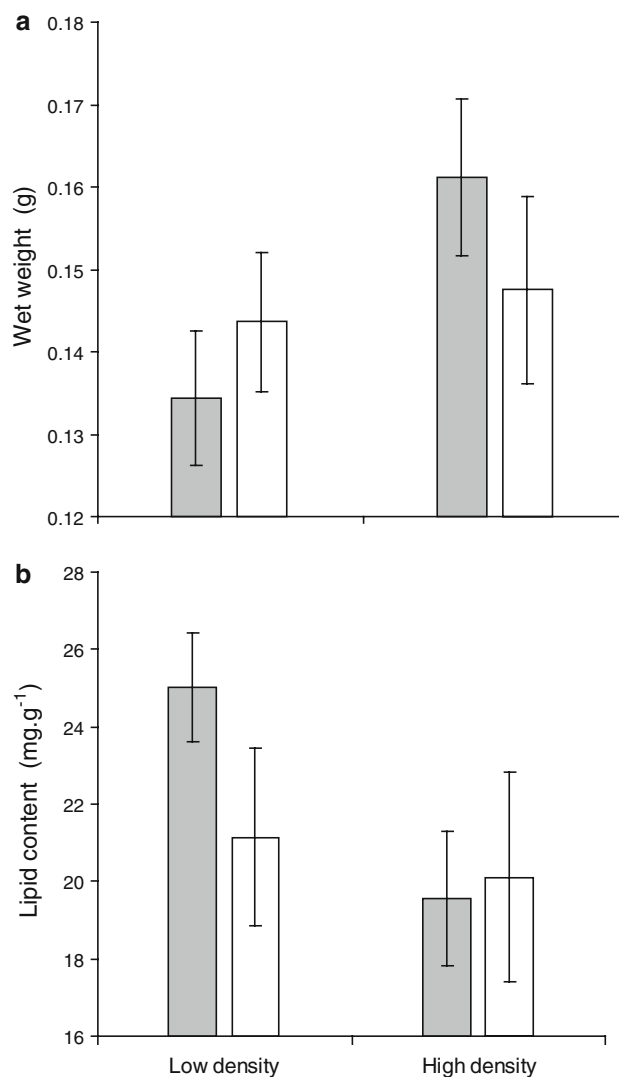


Fig. 4 The influence of fish density [low (6 fish/coral colony), high (12 fish/coral colony)] and habitat (healthy coral—grey bars; thermally bleached coral—white bars) on the wet weight and total lipid content of *Pomacentrus moluccensis* caged on habitats for 20 days. $n = 5$ fish per treatment combination. Error bars are standard errors

coral condition (healthy versus bleached) on the average weight of juveniles. Individuals stocked at low density on healthy coral contained on average 25% more total body lipids than fish from either of the three other treatment levels, although this result was not statistically significant by ANOVA (Fig. 4b). Fish at high density also had significantly larger mean otolith increment widths indicating that high density promoted growth rate ($F_{1,16} = 7.256$, $P < 0.05$). This divergence in growth rate was observed towards the end of the experiment, with a significant interaction between time and density, indicating that density effects on growth were accrued over time (repeated measures ANOVA: $F_{20,320} = 1.719$, $P < 0.05$) (Fig. 5). A

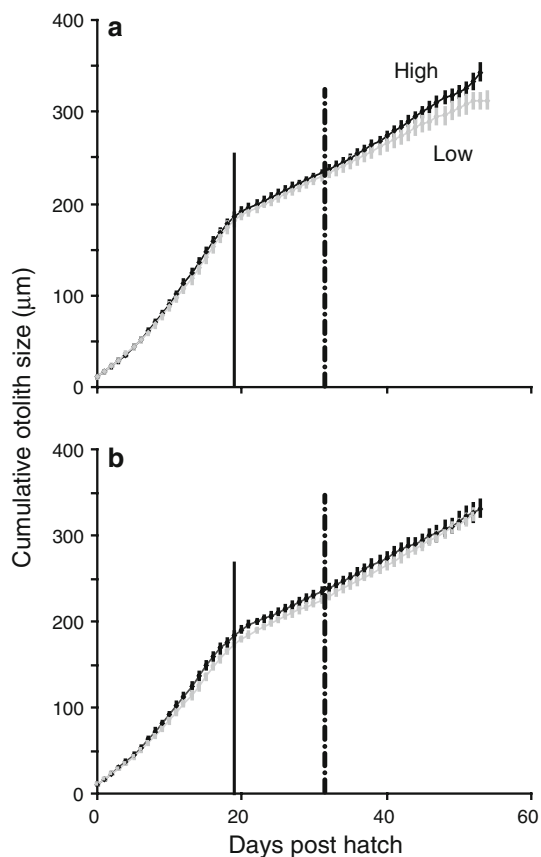


Fig. 5 Sagittal otolith growth trajectories from individuals at high and low density on **a** healthy coral, and **b** thermally bleached coral colonies. *Unbroken line* indicates light-trap catch date (and settlement), while the *dashed line* represents day individuals were placed onto experimental habitat patches. $n = 5$ per treatment combination

weak, non-significant interaction was also apparent with individuals from high-density healthy coral patches growing fastest relative to individuals from the other treatment combinations (Fig. 5).

Discussion

As disturbance events become increasingly frequent on coral reefs, it is likely that sensory cues that were once reliable indicators of habitat quality will become less dependable, thereby ‘trapping’ animals in sub-optimal habitats (Schlaepfer et al. 2002; McCormick 2009; Munday et al. 2009). For coral reef fishes, selecting a suitable habitat at the end of the larval stage is critical to post-settlement survival and success. The present study showed that habitat choice was mediated by sensory mechanisms, which enable individuals to discriminate between habitat patches in different biological condition (i.e., healthy, bleached or dead coral). Settlement-stage larvae of three damselfish species preferred live coral habitat over

bleached or dead coral habitat. Naturally occurring settlement of larval fishes was higher on healthy coral patches compared with bleached coral, and laboratory experiments showed that visual and olfactory cues are important for larvae to distinguish healthy corals from bleached and dead corals, although the relative importance of these cues appears to vary among species. While predictions are that fish may cluster in the remnant patches of live coral after bleaching with negative effects, experiments found that the planktivorous fish targeted for study grew faster when in higher density suggesting at least a short-term advantage to aggregation on remnant coral patches. This study suggests that changes in coral health may strongly impact fish communities through the modified recruitment of fishes that target live coral and that density-dependent processes may play an important role in influencing the dynamics on remnant patches of live coral.

Scleractinian corals are critical settlement habitat for many coral reef fishes, but most of these are not strictly coral dependent as adults (Jones et al. 2004; Wilson et al. 2006; Pratchett et al. 2008). In the present study, patches of healthy coral received nearly ten times the number of recruits as colonies that were sub-lethally bleached, underscoring the importance of coral condition to recruitment processes. This comparison was not confounded by differences in topography of the habitats, but rather simply a change in the tissue health and the cues emitted (Strychar and Sammarco 2009). Rising sea surface temperatures are likely to cause more severe and frequent coral bleaching events in the future (Hoegh-Guldberg 1999; Sheppard 2003). As fish replenishment often coincides with peaks in water temperature during summer months (Milicich et al. 1992), it is likely that larvae will increasingly encounter bleached corals at settlement. This could lead to increased settlement to patches of live coral compared with nearby bleached coral.

The daily census undertaken during the present study makes it unlikely that observed settlement patterns were due to differences in habitat-related mortality levels. While differences in mortality on corals of differing health have been found for another damselfish within one day of settlement (McCormick 2009), Bonin et al. (2009) found no difference in mortality trajectories of *P. moluccensis* in Papua New Guinea (PNG) between healthy and bleached coral over a 4-week period. Mortality on dead coral was significantly lower, but only 4 weeks after settlement. The more likely explanation is that naturally settling larvae actively selected live coral patches and avoided bleached coral patches. This was supported by the laboratory choice trials where the three damselfish species either settled onto bleached coral in accordance with its occurrence or significantly avoided the habitat.

Pomacentrus moluccensis and *P. amboinensis* exhibited a strong preference for live coral and avoided bleached

coral in the habitat choice trials. *Dischistodus* sp. exhibited more even use of the alternative habitats but still preferred live coral over bleached and dead coral. This suggests that there are significant benefits for all these species to associating with live coral and avoiding bleached coral. Whilst life-history consequences of occupying sub-optimal habitats are relatively well documented in terrestrial systems, for example in snakes and lizards (Huey 1991; Webb et al. 2009), birds (Petit and Petit 1996; Wilkin et al. 2009) and mammals (Conradt et al. 1999; Morris and Davidson 2000; Couturier et al. 2009), few studies assess the within-species costs of association with different habitats for coral reef fishes (but see Munday 2001). Settlement to sub-optimal habitats may affect growth (Munday 2001), body condition (Pratchett et al. 2004; Berumen et al. 2005) and survival (Munday 2001; Feary et al. 2009) of juvenile reef fishes. In the current study, we did not detect significant effects of coral condition on the growth rate or body condition of *P. moluccensis* that had been transplanted to bleached corals, even though this species avoided bleached coral in the preference experiment. The absence of strong effect of coral bleaching on growth and body condition may be related to the planktivorous diet of this species. Individuals might potentially be exposed to a greater risk of predation when feeding near bleached corals (Coker et al. 2009; McCormick 2009), but bleaching is unlikely to hinder their ability to feed in the water column.

The present results suggest that the cost of inhabiting bleached coral may only be realised for *P. moluccensis* if the coral dies. A recent study found one of two planktivorous damselfishes at a PNG location, showed significantly lower growth on dead coral patches after 4 weeks (Feary et al. 2009). Bonin et al. (2009) showed that mortality of *P. moluccensis* increased dramatically on corals that had died through bleaching compared with live and bleached (but live) corals in a study that followed the fate of newly settled recruits of *P. moluccensis* in Papua New Guinea. This suggests that the benefits of behavioural avoidance of bleached coral may relate more to cost of inhabiting corals that are ultimately likely to die than it is to the cost of living on bleached coral per se.

The three damselfish species examined in the present study exhibited a preference for live coral over bleached and dead coral in the habitat selection trials. Vision appeared to play a major role in habitat selection, with all species still selecting live coral most frequently when olfactory cues were excluded. In fact, selection of live coral by *P. moluccensis* was even stronger than usual when olfactory cues were absent. Furthermore, in the absence of visual cues, all three species chose dead coral in much greater frequency. This suggests that there is an attraction to olfactory cues from dead corals, but that vision often overrides this attraction when all sensory cues are

available. In a field examination of the habitat preferences of *Chromis viridis*, Lecchini et al. (2005b) found that olfactory signals were important at greater distances than were visual cues, which operated at short distance of <0.75 m. Both studies stress the importance of olfaction for habitat attraction, but that visual may modulate the final habitat choice. As the majority of reef fishes are not reliant on live corals as a nutritional resource (Cole et al. 2008), further work is urgently needed to understand the nature of the benefits live coral confers to coral reef fishes.

Density-dependent competition for habitats may increase if bleaching or other disturbances increase the small-scale patchiness of live coral resources in a habitat (Garpe et al. 2006; Pratchett et al. 2008). The present study suggests that for juvenile *P. moluccensis*, the allocation of energy to growth or storage (i.e., lipids) was density dependent. Increasing densities may have a positive effect on growth, possibly as a result of the general advantages of group living, such as reduced per capita vigilance and increased foraging efficiency (Krause and Ruxton 2002), which can lead to enhanced per capita survival. This finding is opposite to a manipulation of the density of juvenile *P. amboinensis* which found that a tripling of density reduced fish growth (Jones 1987) due to enhanced aggression. In the present study, increased intraspecific competition may also be the incentive to grow fast at the expense of storage to outgrow competitors, thereby attaining a size advantage. While increased density may be an advantage at the juvenile stage, competition generally intensifies as animals become larger and place more demands on their limited or finite resource base (in this case shelter and food) (Jones 1987). A longer study is required to examine the impact of bleaching through these potentially lagged effects.

The frequency and magnitude of coral bleaching and other disturbance events (e.g., cyclones) on coral reefs are predicted to increase markedly over the next 50 years (Hoegh-Guldberg et al. 2007). However, the likely consequence for coral reef fish communities is still not fully understood (Pratchett et al. 2008). We suggest that recovery and resilience of fish populations following major coral bleaching episodes may in part depend on the flexibility of individuals in choosing settlement habitat. As relative abundance of preferred habitats changes, there is a strong possibility that individuals will be forced to choose between alternate, less preferred habitats. In turn, this may increase the magnitude of competition for these alternate habitats. Interspecific competition, in particular, may be of increasing importance in shaping fish communities if certain species possess a competitive advantage when competing for newly abundant habitat. Obviously, more work is needed on the link between coral reef fishes and their dependence of specific habitats, in particular the

consequences of use and occupation of non-preferred habitats where sub-lethal stressors may greatly impact individual performance. A more detailed understanding of the link between habitat selection, individual growth and condition and subsequent survival in changing habitats is urgently required in the face of a changing habitat landscape.

Acknowledgements We are grateful to J. Maddams, C. Villa-Corta Rath, J. Scannell, T. Holmes who assisted with the field work. Two anonymous reviewers and R. van Woosik provided useful comments that improved the manuscript. Funding was provided by the ARC Centre of Excellence for Coral Reef Studies. We thank the staff at the Lizard Island Research Stations for logistic support. Research was undertaken under an Animal Ethics approval from JCU.

References

- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- Almany GR, Webster MS (2006) The predation gauntlet: post-settlement mortality in reef fishes. *Coral Reefs* 25:9–22
- Atema J, Kingsford MJ, Gerlach G (2002) Larval reef fish could use odour for detection, retention and orientation to reefs. *Mar Ecol Prog Ser* 241:151–160
- Bay LK, Jones GP, McCormick MI (2001) Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. *Coral Reefs* 20:289–298
- Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Mar Ecol Prog Ser* 287:217–227
- Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- Blondel J, Thomas DW, Charmantier A, Perret P, Bourgault P, Lambrechts MM (2006) A thirty-year study of phenotypic and genetic variation of blue tits in Mediterranean habitat mosaics. *BioSci* 56:661–673
- Bonin MC, Munday PL, McCormick MI, Srinivasan M, Jones GP (2009) Recruitment and persistence of coral-dwelling fishes is resilient to bleaching but not mortality of host corals. *Mar Ecol Prog Ser* 394:215–222
- Booth DJ (1992) Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. *J Exp Mar Biol Ecol* 155:85–104
- Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. *Mar Ecol Prog Ser* 245:205–212
- Burton NHK, Rehfish MM, Clark NA, Dodd SG (2006) Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *J Appl Ecol* 43:464–473
- Caley MJ, St. John J (1996) Refuge availability structures assemblages of tropical reef fishes. *J Anim Ecol* 65:414–428
- Coker DJ, Pratchett MS, Munday PL (2009) Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behav Ecol*. doi:10.1093/beheco/arp113
- Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish Fish* 9:286–307
- Conradt L, Clutton-Brock TH, Guinness FE (1999) The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia* 120:218–224
- Couturier S, Cote SD, Otto RD, Weladji RB, Huot J (2009) Variation in calf body mass in migratory caribou: the role of habitat, climate, and movements. *J Mammal* 90:442–452
- Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001) Climate change and forest disturbance. *Bioscience* 51:723–734
- Dixon DL, Jones GP, Munday PL, Planes S, Pratchett MS, Srinivasan M, Syms C, Thorrold SR (2008) Coral reef fish smell leaves to find island homes. *Proc R Soc B* 275:2831–2839
- Dixon DL, Munday PL, Jones GP (2010) Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol Lett*. doi: 10.1111/j.1461-0248.2009.01400.x
- Dufour V, Galzin R (1993) Colonization patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. *Mar Ecol Prog Ser* 102:143–152
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: Observations, modeling, and impacts. *Science* 289:2068–2074
- Egner SA, Mann D (2005) Auditory sensitivity of sergeant major damselfish *Abudefduf saxatilis* from post-settlement juvenile to adult. *Mar Ecol Prog Ser* 285:213–222
- Feary DA, McCormick MI, Jones GP (2009) Growth of reef fishes in response to live coral cover. *J Exp Mar Biol Ecol* 373:45–49
- Folch AJ, Less M, Sloan-Stanley GH (1957) A simple method for isolation and purification of total lipids from animal tissues. *J Biol Chem* 226:497–509
- Garpe KC, Yahya SAS, Lindahl U, Öhman MC (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar Ecol Prog Ser* 315:237–247
- Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. *Proc Natl Acad Sci USA* 104:858–863
- Graham NAJ, Wilson SK, Jennings S, Polunin NV, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv Biol* 21:1291–1300
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioioulos ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Huey RB (1991) Physiological consequences of habitat selection. *Am Nat* 37:S91–S115
- Hughes L (2000) Biological consequences of global warming: is the signal already. *Trends Ecol Evol* 15:56–61
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Jones GP (1987) Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68:1534–1547
- Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale PF (ed) *Coral reef fishes— dynamics and diversity in a complex ecosystem*. Academic Press, London, pp 221–238
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Kaufman L, Ebersole J, Beets J, McIvor CC (1992) A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Environ Biol Fishes* 34:109–118

- Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, New York
- Lecchini D, Planes S, Galzin R (2005a) Experimental assessment of sensory modalities of coral-reef fish larvae in the recognition of their settlement habitat. *Behav Ecol Sociobiol* 58:18–26
- Lecchini D, Shima JS, Banaigs B, Galzin R (2005b) Larval sensory abilities and mechanisms of habitat selection of a coral reef fish during settlement. *Oecologia* 143:326–334
- Leis JM, Carson-Ewart BM (1999) In situ swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the coral trout *Plectropomas leopardus* (Pisces: Serranidae). *Mar Biol* 134:51–64
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155–163
- McCormick MI (2009) Behaviourally mediated phenotypic selection in a disturbed coral reef environment. *PLoS One* 4:e7096
- McCormick MI, Makey LJ (1997) Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. *Mar Ecol Prog Ser* 153:247–257
- McFarland WN (1991) The visual world of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, pp 16–38
- 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
- Milicich MJ, Doherty PJ (1994) Larval supply of coral reef fish populations: magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. *Mar Ecol Prog Ser* 110:121–134
- Milicich MJ, Meekan MG, Doherty PJ (1992) Larval supply: a good predictor of the recruitment of three species of reef fish (Pomacentridae). *Mar Ecol Prog Ser* 86:153–166
- Morris DW, Davidson DL (2000) Optimally foraging mice match patch use with habitat differences in fitness. *Ecology* 81:2061–2066
- Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* 128:585–593
- Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biol* 10:1642–1647
- Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. *Fish Fish* 9:261–285
- Munday PL, Dixon DL, Donelson JM, Jones GP, Pratchett MS, Devitsina GV, Døving KB (2009) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc Nat Acad Sci USA* 106:1848–1852
- Öhman MC, Munday PL, Jones GP, Caley MJ (1998) Settlement strategies and distribution patterns of coral-reef fishes. *J Exp Mar Biol Ecol* 225:219–238
- Paradis E (1995) Survival, immigration and habitat quality in the Mediterranean Pine Vole. *J Anim Ecol* 64:579–591
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669
- Petit LJ, Petit DR (1996) Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell-Lucas models. *Ecol Monogr* 66:367–387
- Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs* 23:352–356
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes - ecological and economic consequences. *Oceanogr Mar Biol Annu Rev* 46:251–296
- Rosenzweig ML (1991) Habitat selection and population interactions: the search for mechanism. *Am Nat* 137:S5–S28
- Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. *Trends Ecol Evol* 17:474–480
- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* 425:294–297
- Shoo LP, Williams SE, Hero J-M (2005) Climate warming and the rainforest birds of the Australian wet tropics: Using abundance data as a sensitive predictor of change in total population size. *Biol Conserv* 125:335–343
- Simpson SD, Meekan MG, Montgomery JC, McCauley R, Jeffs A (2005) Homeward bound. *Science* 308:221
- Strychar KB, Sammarco PW (2009) Exaptation in corals to high seawater temperatures: Low concentrations of apoptotic and necrotic cells in host coral tissue under bleaching conditions. *J Exp Mar Biol Ecol* 369:31–42
- Sweatman H (1988) Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *J Exp Mar Biol Ecol* 124:163–174
- Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc R Soc Lond B Biol Sci* 270:467–473
- Webb JK, Pringle RM, Shine R (2009) Intraguild predation, thermoregulation, and microhabitat selection by snakes. *Behav Ecol* 20:271–277
- Wilkin TA, Gosler AG, Garant D, Reynolds SJ, Sheldon BC (2009) Calcium effects on life-history traits in a wild population of the great tit (*Parus major*): analysis of long-term data at several spatial scales. *Oecologia* 159:463–472
- Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc R Soc Lond B Biol Sci* 270:1887–1892
- Wilson DT, McCormick MI (1997) Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. *Mar Ecol Prog Ser* 153:259–271
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biol* 12:2220–2234
- Wright KJ, Higgs DM, Belanger AJ, Leis JM (2005) Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces: Pomacentridae). *Mar Biol* 147:1425–1434