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## Determining trigger values of suspended sediment for behavioral changes in a coral reef fish

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## ABSTRACT

Sediment from land use increases water turbidity and threatens the health of inshore coral reefs. This study performed experiments with a damselfish, *Pomacentrus moluccensis*, in four sediment treatments, control (0 mg l<sup>-1</sup>), 10 mg l<sup>-1</sup> (~1.7 NTU), 20 mg l<sup>-1</sup> (~3.3 NTU) and 30 mg l<sup>-1</sup> (~5 NTU), to determine when sediment triggers a change in habitat use and movement. We reviewed the literature to assess how frequently *P. moluccensis* would experience sub-optimal sediment conditions on the reef. Preference for live coral declined from 49.4% to 23.3% and movement between habitats declined from 2.1 to 0.4 times between 20 mg l<sup>-1</sup> and 30 mg l<sup>-1</sup>, suggesting a sediment threshold for behavioral changes. Inshore areas of the Great Barrier Reef, *P. moluccensis* may encounter sub-optimal conditions between 8% and 53% of the time. Changes in these vital processes may have long-term effects on the persistence of populations, particularly as habitat loss on coral reefs increases.

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### 1. Introduction

Habitat degradation is attributable to a range of anthropogenic sources and is a major threat to coastal marine environments worldwide, leading to a loss of biodiversity (e.g. Diaz and Rosenberg, 2008; Lotze et al., 2006; Tilman et al., 2001). As agricultural practices and coastal development have increased on land, coastal marine systems are receiving elevated levels of sediment that threatens the health of the species present in these zones (Brodie et al., 2012; Cloern, 2001; Lotze et al., 2006). Among these shallow marine environments, coral reefs are especially sensitive to increased sediment and turbidity (Brodie et al., 2012; Fabricius, 2005; Furnas, 2003). In the Great Barrier Reef (GBR) region of eastern Australia, the world's largest system of coral reefs, many reefs have been classified as being at high risk from sediment causing significant impacts to the existing marine communities (Devlin et al., 2003). This elevated risk is due to a fivefold increase in suspended sediment loads from rivers since European settlement (Furnas, 2003; Kroon et al., 2012), which has led to elevated turbidity on the GBR (Fabricius et al., 2012).

The effects of sediment on coral health has been widely documented, with elevated turbidity being shown to increase mucous

production (Telesnicki and Goldberg, 1995), reduce calcification and tissue growth (Anthony and Fabricius, 2000; Rogers, 1979), and alter the biodiversity and depth range of coral communities (Fabricius, 2005; Fabricius et al., 2005). Several studies have also shown that fish abundance, biomass and species diversity are lower at inshore sites and sites highly impacted by sediment compared to offshore or low impacted sites (Fabricius et al., 2005; Letourneur et al., 1998; Mallela et al., 2007). However, these are correlative studies that do not distinguish between indirect and direct effects of suspended sediment on coral reef fishes. Direct effects of suspended sediment on coral reef fishes may compound the indirect effects of habitat loss, leading to further changes in population dynamics. Recent research has shown that increased turbidity impairs habitat choice and foraging success of coral reef fishes through a reduction in their ability to distinguish visual and chemical cues (Wenger et al., 2011, 2012). Continued quantitative evaluation of the interaction between sediment and coral reef fishes is crucial to increase our understanding of how changing water quality directly affects coral reef fishes.

One of the central interactions that drive the distributions of organisms on coral reefs is the relationship between coral reef fishes and their habitat, because most species of coral reef fishes exhibit strong habitat preferences at settlement (Jones et al., 2004; McCormick et al., 2010; Öhman et al., 1998). Indeed, many show a preference for live coral at settlement even though they do not need the habitat once adult, and declines in the abundance and diversity of coral reef fishes have been linked to an indirect effect of habitat loss (Jones et al., 2004; Wilson et al., 2006). As

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coral reefs are spatially heterogeneous with live coral exhibiting a naturally patchy distribution (Ebeling and Hixon, 1991), fishes use a range of sensory modes such as smell, taste and visual stimuli to make habitat choice decisions (e.g. Lecchini et al., 2005; McCormick et al., 2010; Munday et al., 2009; Sweatman, 1983). Once settled, fish continue to use sensory cues to gain information about their environment (Kroon, 2005; Odling-Smee and Braithwaite, 2003). Though many coral reef fishes tend to be closely associated with a particular habitat, it is common that a fish's home range will include a broad array of habitat patches in order to exploit more resources (Lewis, 1997). Many juvenile fishes also undergo substantial movements after their initial settlement (e.g. McCormick and Makey, 1997). Any change in environmental conditions that restricts the movement of coral reef fish has the potential to reduce growth, condition and survivorship (Coker et al., 2012; Gaillard et al., 2010; Odling-Smee and Braithwaite, 2003). Though suspended sediment is known to impair habitat selection at settlement (Wenger et al., 2011), it is unclear whether this reduction in visibility could also change patterns of habitat use.

When trying to assess how environmental change affects coral reef fishes, it is important to determine when a specific environmental attribute reaches the point where it is producing a response (Briske et al., 2006; Groffman et al., 2006). Previous work has shown a definitive change in behavior at suspended sediment levels of  $45 \text{ mg l}^{-1}$  ( $\sim 7$  NTU) and above (Wenger et al., 2011, 2012), but it is not known at what point this behavioral change actually occurs. Our aim was to investigate the influence of suspended sediment on habitat selection and movement in a juvenile damselfish, *Pomacentrus moluccensis*. This species was chosen because it is located throughout the entire GBR, both on inshore and outer reefs (AIMS long-term monitoring data). It is found predominately on live coral and has exhibited declines in abundance associated with live coral loss (Bellwood et al., 2006; Syms and Jones, 2000), meaning that it has the potential to be both indirectly and directly affected by suspended sediment. We performed habitat choice experiments over a spectrum of suspended sediment treatments to determine when suspended sediment provoked a change in habitat choice and movement of juveniles. The sediment treatments ranged from clear water through to levels where physiological stress occurs in corals (5 NTU; Cooper et al., 2008). We then used two-channel choice flumes to clarify the sensory cues that were being affected. The study tested the prediction that, based on a reduction in settlement success due to sediment (Wenger et al., 2011), increased turbidity would also restrict movement between corals. Finally, we compared the concentrations of suspended sediment that elicited a response to observed patterns of suspended sediment recorded on reefs in the GBR where *P. moluccensis* lives. This enabled an examination of the frequency that *P. moluccensis* would be likely to experience sub-optimal concentrations of suspended sediment.

## 2. Methods

### 2.1. Study species

Juvenile *P. moluccensis* ( $16.9 \pm 0.2$ , mean standard length  $\pm$  SE) were used in habitat movement trials to determine the changes in habitat preference and home range use in increasing concentrations of suspended sediment. Additional *P. moluccensis* juveniles ( $18.3 \pm 0.5$ ) were collected to test the effect of bentonite on chemoreception. The fishes were collected from coral reefs in the lagoon at Lizard Island in February 2011 from live coral using a diluted clove oil solution and a hand-net. The collection reefs experience very low levels of turbidity on average ( $0.8 \pm 0.02$ , Wenger, unpublished data). All fishes were held in 15 L tanks (10 per tank) with filtered aerated seawater and fed *Artemia* nauplii twice a day for

48 h prior to experiments. This time frame was determined based on how quickly the fishes began to swim and eat normally.

### 2.2. Experiment 1: Habitat choice in increasing levels of suspended sediment

To determine threshold levels of suspended sediment that begin to impair coral reef fishes, we conducted a controlled laboratory experiment on Lizard Island on the northern Great Barrier Reef, Australia ( $14^{\circ}40' \text{ S}$ ;  $145^{\circ}28' \text{ E}$ ). *Pocillopora damicornis*, a complex branching coral used by many coral-dwelling fishes for habitat (e.g. Feary et al., 2007), was chosen for this habitat choice experiment. Three habitat types were used: live coral, partially dead coral ( $\sim 25\%$  live coral cover), and dead coral (covered by some benthic invertebrates and algae), all of which were structurally intact (Feary et al., 2007). Ten colonies of each habitat type were collected from the Lizard Island lagoon using a hammer and chisel. All colonies were 24 cm in diameter. None of the coral colonies showed any sign of stress throughout the experiment. When trials were not being run, all coral colonies were held in tanks with clear, filtered aerated seawater.

The settlement trials were run in 285 L circular tanks supplied with filtered aerated seawater. Each tank contained one of each of the three different habitat types. The coral heads were placed in a triangle, with the inner edge of each habitat equidistant from each other (42 cm). The outer edge of each habitat was 10 cm from the tank walls. Between each trial, the tanks were emptied, cleaned, and randomly assigned a sediment level. The coral heads were also haphazardly rearranged to different tanks between each trial to ensure that settlement was based on habitat type and not location of the coral heads, direction of sunlight or other outside stimuli.

The habitat choice of each individual tested was recorded in four levels of suspended sediment: control ( $0 \text{ mg l}^{-1}$ ),  $10 \text{ mg l}^{-1}$  ( $\sim 1.7$  NTU),  $20 \text{ mg l}^{-1}$  ( $\sim 3.3$  NTU) and  $30 \text{ mg l}^{-1}$  ( $\sim 5$  NTU). These levels of suspended sediment were chosen based on the target level set for the GBR of 2.4 NTU (this is the adjusted value from De'ath and Fabricius (2008) using the calibration of  $\text{mg l}^{-1}$  to NTU proposed by Larcombe et al. (1995) and ecological stress that occurs in corals at 5 NTU (Cooper et al., 2008)). Twenty individual *P. moluccensis* were tested in 20 independent trials for each level of suspended sediment ( $n = 80$  for entire experiment). A commercially available clay (Australian Bentonite) used in previous turbidity experiments (e.g. Van de Meutter et al., 2005; Wenger et al., 2012, 2011) was used as the sediment. Muddy sediments and clays are common constituents of sediment on the inshore GBR (Carter et al., 1993; McCulloch et al., 2003). Additionally, the particle size of bentonite is in the same size class as particles found in suspension in the GBR (Devlin et al., 2012; Wenger, unpublished data). Before each trial, the water was turned off in the experimental tanks so that no sediment could leave the tanks during the trials. Then, a set amount of sediment was manually dissolved to avoid clumping into a fixed volume of water in the tanks. The water was cycled through each tank from a sump with an external pump. This ensured constant water movement, allowing the sediment to remain in suspension. Once the water was uniformly turbid ( $\sim 10$  min), one fish was placed into a clear Perspex box in the center of each tank. After a 3-min acclimation period, the box was removed and the fish was allowed to choose a habitat. Although it is generally thought that coral reef fishes settle at night, it has been noted that in many damselfish species, including *P. moluccensis*, diurnal settlement represents a substantial portion of observed settlement patterns (e.g. Leis and Carson-Ewart, 2002). Consequently, trials were run throughout the day. This allowed for the use of both visual and chemosensory cues for settlement choice. The habitat choice of each fish was recorded every 10 min for

90 min. Choice was defined as any individual within 5 cm of a coral head.

### 2.3. Experiment 2: Effect of bentonite on chemoreception

Since recent work has suggested that chemical cues from suspended sediment from inshore reefs can actually impair habitat selection in *P. moluccensis* (Wenger et al., 2011), we wanted to determine if bentonite also impaired the ability of *P. moluccensis* to distinguish between healthy live coral and dead coral using chemoreception. Colonies of live and dead *P. damicornis* were collected from the fringing reef and placed in separate 75 L aquaria containing seawater collected >100 m away from any coral reefs. Seawater was enriched with live coral cues, dead coral cues, and bentonite (1000 mg l<sup>-1</sup>). The bentonite and the coral colonies were soaked in individual bins for 24 h, allowing sufficient time for the corals and the sediment to release their chemical signatures into the water. The soaking time was determined by the time it took for the sediment to settle out of suspension. The sediment-enriched water was not used until the sediment had completely settled to the bottom, so that only clear water without suspended sediment was used during the trials. To create mixed water (i.e. live coral and sediment), equal parts of live coral enriched water and sediment-enriched water were added together.

The response of individual fish to chemical cues was tested in a 2-channel choice flume chamber (13 cm × 4 cm, L × W). The water from the two different sources was gravity fed from buckets, through tubes and into flow meters (Dwyer Instruments, USA) that set the flow at 100 mL min<sup>-1</sup> per channel, which was maintained throughout all trials, and then into the flume chamber (Dixon et al., 2008; Gerlach et al., 2007). The flume chamber was partitioned along half its length to enable laminar flow. The water was not recirculated. Prior to the start of each trial, dye tests using food coloring were conducted to ensure that both channels exhibited laminar water flow. During each trial, an individual fish was placed into the center of the downstream end of the flume. They were allowed an acclimation period of 2 min. At the end of the acclimation period, the position of the fish on each side of the chamber was recorded every 5 s for a 2-min period. After the 2-min trial period, the sides of the water sources were switched, to control for potential side preferences not associated with the chemical cues. During the side switch, the fish were allowed a 1-min rest period and then allowed another 2-min acclimation period before the choice trial was repeated. Each trial was run in the absence of any visual stimuli from the source of the chemical cues.

### 2.4. Risk assessment of inshore coral reefs

A review of the literature was performed to determine regions where turbidity data recorded in the GBR aligned with *P. moluccensis* data collected during fish monitoring on inshore areas (AIMS long-term monitoring Program; D. Williamson, unpublished data). This assessment was conducted in order to determine the frequency with which *P. moluccensis* would be experiencing sub-optimal conditions. Based on the overlap of data, we determined that the most relevant studies came from the inshore area off the coast of Townsville, Australia (Table 1). We extracted data from the literature about the frequency with which turbidity exceeded 5 NTU (the high level of sediment in this study; Table 1). In Larcombe et al. (1995), a calibration was made between mg l<sup>-1</sup> and turbidity in the study region, which they determined to be ~1:1. The results of the study are reported in mg l<sup>-1</sup> and we used their calibration to convert the results into NTU. The data presented represents all of the studies in the GBR where both turbidity data and *P. moluccensis* presence data are available. Data is reported in NTU because the NTU: mg l<sup>-1</sup> conversion was not available for all studies.

### 2.5. Data analysis

The location of individuals at each time interval in each treatment was pooled to determine a percentage of time that the fish associated with a particular habitat throughout the trial. A chi-squared goodness of fit was used to test whether the three habitats were chosen in equal frequency. Randomization based one-way ANOVAs with a Tukey's HSD post hoc analysis were also used to explore: (i) if there was a significant difference in habitat choice within each sediment treatment, (ii) whether there was a difference in time spent associating with each habitat type between treatments (iii) whether there was a difference in movement of *P. moluccensis* between habitat types in the different treatments, (iv) whether there was a difference in the proportion of individuals who initially settled on partially dead and dead coral and (v) whether the individuals in the different treatments that initially chose partially dead and dead coral were able to move to live coral. For the chemosensory trials, the data from before and after the side switch were pooled. The few individuals that displayed clear side preferences during their trial were excluded from any analysis. A distribution-free randomization test was performed to see whether the mean proportion of time the fishes spent in a particular water stream differed from random.

## 3. Results

### 3.1. Experiment 1: Habitat choice in increasing levels of suspended sediment

*P. moluccensis* in all treatments showed unequal frequency in which they associated with one of the three habitat types according to the chi-squared goodness of fit test (Table 2). *P. moluccensis* preferred live coral in the control, low, and medium treatments, associating with it 61.1 ± 8.3%, 51.6 ± 8.6%, and 49.4 ± 8.4% of the time, respectively (Fig. 1). In the high sediment treatment, *P. moluccensis* preferred partially dead coral over the other habitats, spending 45.5 ± 9.9% of the time associating with it and only spent 23.3 ± 8.9% of the time associating with live coral (Fig. 1). However, when a one-way ANOVA was performed, the association with partially dead coral in the high sediment treatment was not significant, due to the high variance in the choices made (ANOVA,  $p > 0.05$ ). Therefore, in the control, low, and medium sediment treatments, *P. moluccensis* significantly chose live coral, whereas in the high sediment treatment, no significant choice was actually made. When the habitat choice for each treatment was compared to the habitat choice in the other treatments, the fish in the control treatment spent significantly more time associating with live coral than the fish in the high sediment treatment (ANOVA,  $F_{3,76} = 2.79$ ,  $p = 0.04$ ). However, there was not a significant difference in time spent on live coral between the control, low and medium sediment treatments or between the low, medium and high sediment treatments (Tukey's HSD,  $p > 0.5$ ). This is possibly because the association of fish with live coral declined as suspended sediment concentration increased, though this trend was non-significant (Fig. 1). There were no significant differences between any of the treatments in time spent associating with partially dead and dead coral (ANOVA,  $p > 0.05$ ).

*P. moluccensis* showed a clear relationship between habitat movement and sediment treatment. Overall, *P. moluccensis* moved around 2.1 ± 0.5 times in the control, 2.7 ± 0.6 times in the low sediment treatment, 2.1 ± 0.4 times in the medium treatment, and 0.4 ± 0.2 times in the high sediment treatment (Fig. 2a). There was no difference in movement among the fish in the control, low, and medium treatments (Tukey's HSD,  $p > 0.5$ ), however, there was a significant difference in movement between fish in

**Table 1**  
The percentage of time that turbidity conditions exceeded 5 NTU in various locations around Magnetic Island, together with the duration of the study and whether *Pomacentrus moluccensis* was recorded in visual transects at each location. Magnetic Island is an inshore island in the middle of the GBR surrounded by fringing reefs.

Location	5 NTU exceeded (%)	Length of study	Time of year	Reference	<i>P. moluccensis</i> present
Magnetic Island 1	53	4 Months	January–April	Larcombe et al. (1995)	Yes
Magnetic Island 2	48	4 Months	January–April	Larcombe et al. (1995)	No data
Magnetic Island 3	38	4 Months	January–April	Larcombe et al. (1995)	Yes
Magnetic Island 4	33	4 Months	January–April	Larcombe et al. (1995)	Yes
Magnetic Island 5	37	4 Months	January–April	Larcombe et al. (1995)	Yes
Magnetic Island 6	38	4 Months	January–April	Larcombe et al. (1995)	Yes
Middle Reef	10.1	61 Days	April–May	Browne et al. (2012)	Yes
Horseshoe Bay	8.8	2 Years	Continuous	Cooper et al. (2008)	No data
Geoffrey Bay	8.0	4 Years	Continuous	Schaffelke et al. (2011)	Yes

**Table 2**  
Propensity of *Pomacentrus moluccensis* to have an uneven settlement distribution among three settlement habitats in a choice experiment.

Treatment	$\chi^2$	df	P
Control	40.02	2	<0.0001
Low (10 mg/l)	19.34	2	<0.0001
Medium (20 mg/L)	15.38	2	0.0005
High (30 mg/L)	7.94	2	0.02

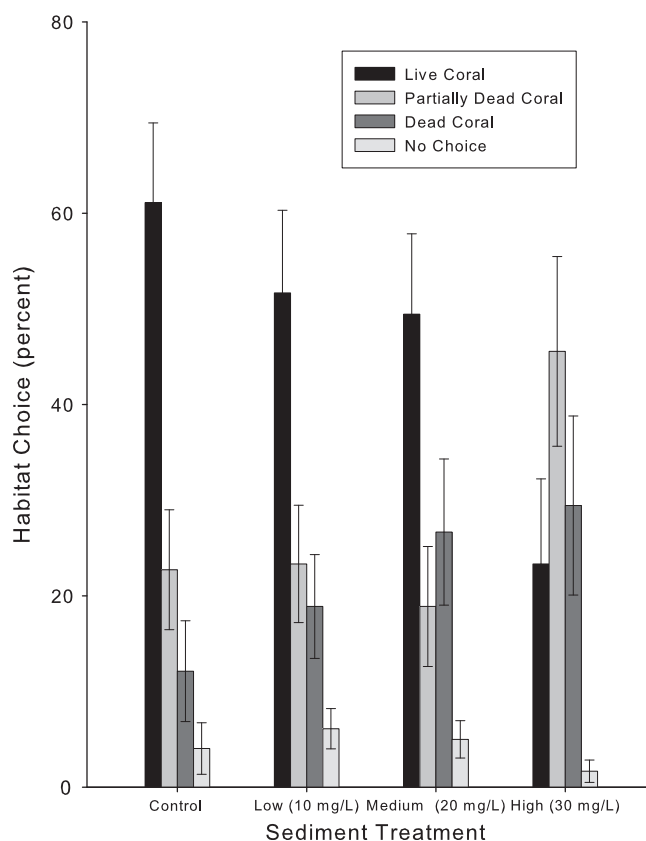
the high treatment and fish in the other treatments (ANOVA,  $F_{3,76} = 12.97$ ,  $p < 0.0001$ ). Further exploration into the movement of the fish showed that there was a significant difference in the percentage of fish that initially chose partially dead and dead coral in the different treatments (ANOVA,  $F_{3,76} = 3.12$ ,  $p = 0.033$ ). Overall, partially dead and dead coral was initially chosen 40.9%, 45%, 75%, and 75% of the time by individuals, in the control, low, medium, and high sediment treatments respectively (Fig. 2b). However, out of the fish that initially chose partially dead and dead coral, 33.3%, 22%, and 40% of the fish in the control, low, and medium treatments ended up associating primarily with live coral. In contrast, only 6.7% of the fish in the high treatment that initially associated with partially dead and dead coral ultimately moved to live coral (Fig. 2c).

### 3.2. Experiment 2: Effect of bentonite on chemoreception

When choosing between live coral in bentonite enriched water and dead coral in bentonite enriched water juvenile *P. moluccensis* significantly preferred the live coral cue over the dead coral cue (randomization test,  $p < 0.0001$ ); overall spending  $61.4 \pm 4.67\%$  associating with the live coral and bentonite cue.

### 3.3. Risk assessment of inshore coral reefs

All studies recorded turbidity values consistently above 5 NTU. The length of each study differed so we report the percent that turbidity exceeded 5 NTU only for the time of the study. Additionally, the reporting metrics were different. The data from Browne et al. (2012) and Larcombe et al. (1995) are reported as the percentage of time that each data point exceeded 5 NTU. Cooper et al. (2008) reports specific times and events when turbidity exceeded 5 NTU and only states the number of days when the values were above 5 NTU, suggesting that they were reporting the data as daily means. Schaffelke et al. (2011) reports the data as the percentage of daily means that were above 5 NTU. The length and time of the studies differs considerably (Table 1) and this affects the percentages of time that turbidity exceeded 5 NTU. Overall, the frequency that 5 NTU was exceeded ranged between 8% and 53%, with an average time of  $30.4 \pm 5.7\%$ . Presence of *P. moluccensis* overlapped with 7 out of the 9 turbidity locations, spanning the

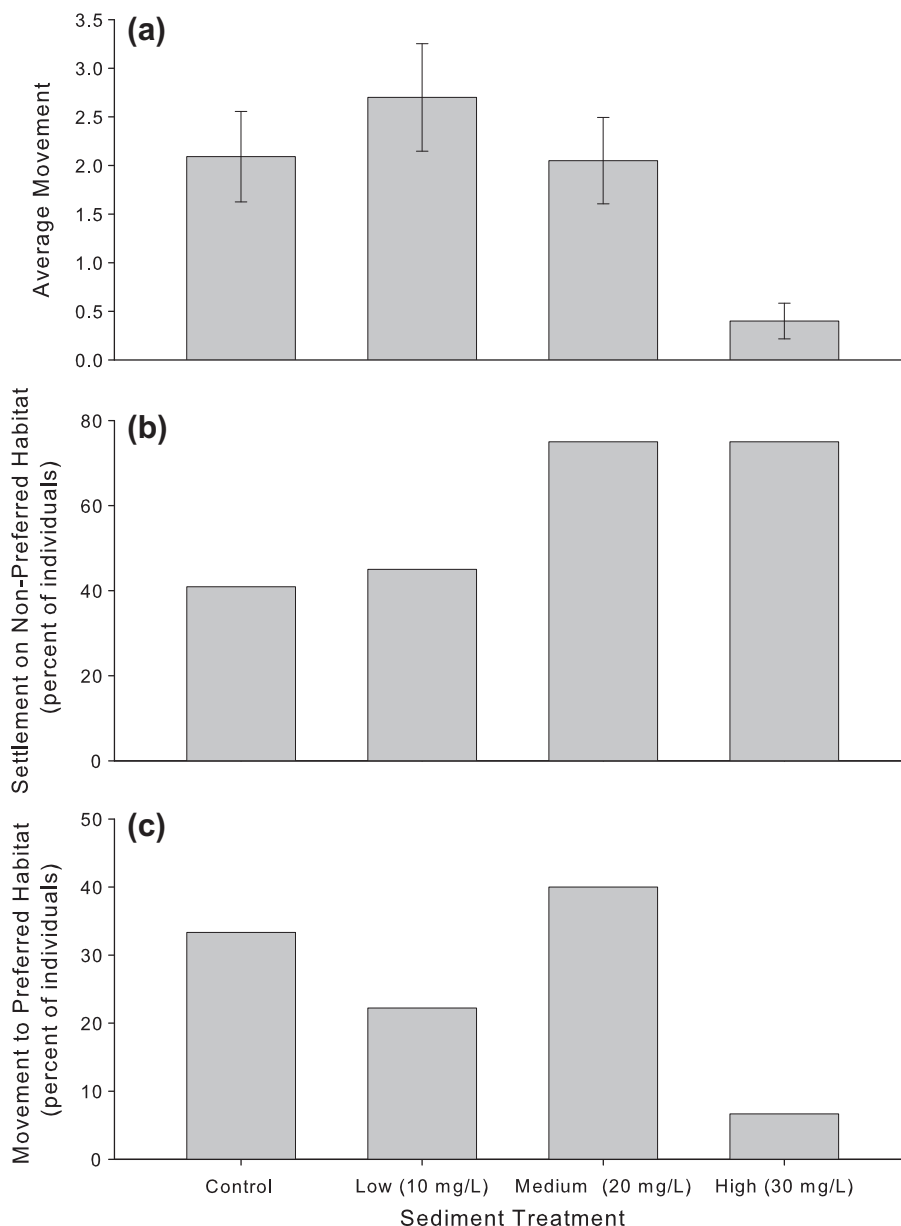


**Fig. 1.** Proportion of time ( $\pm$ SE) that *Pomacentrus moluccensis* associated with each habitat type in the four sediment treatments.

entire spectrum of turbidity data, meaning that *P. moluccensis* lives in areas that consistently see sub-optimal turbidity conditions. There was no fish survey data present for the remaining two sites so it is unclear if *P. moluccensis* is found there.

## 4. Discussion

This study demonstrates that suspended sediment can restrict the movement of a coral reef fish, *P. moluccensis*, by diminishing the visual cues used to assess the environment. The reduction in visual cues resulted in an inability to locate and migrate to live coral, the habitat type with which they primarily associate, and restricted access to the surrounding environment. The present study expands on previous studies exploring the relationship between suspended sediment and habitat choice by determining when sediment begins to impair habitat choice (Wenger et al., 2011). This study revealed that clear thresholds for sediment tolerance



**Fig. 2.** Differences between treatments of *Pomacentrus moluccensis* in: (a) movement ( $\pm$ SE) between habitat types, (b) proportion of individuals that initially settled on partially dead and dead coral and (c) proportion of individuals that successfully relocated to live coral after initially choosing partially dead or dead coral.

exists in *P. moluccensis* at around 5 NTU and that inshore reefs on the Great Barrier Reef are regularly experiencing levels of suspended sediment that create sub-optimal conditions for coral reef fishes. Annual loads of suspended sediment into the GBR have increased 5.5 times since European development in the 1860s (Kroon et al., 2012), leading to an increase in turbidity levels (Fabricius et al., 2012). The results of this study demonstrate the importance of better understanding thresholds for behavioral changes due to sediment.

*P. moluccensis* are predominately found on live coral throughout their life and new recruits are closely associated with it (McCormick and Weaver, 2012; Öhman et al., 1998). In this study, we showed that in relatively low levels of suspended sediment *P. moluccensis* had difficulty distinguishing live coral from other habitat types, resulting in reduced success in choosing appropriate habitat. These results are applicable to settling coral reef fish, as studies show that post-settlement *P. moluccensis* make habitat choices consistent with settlement aged fish (Öhman et al., 1998;

Wenger et al., 2011). Habitat specialists, such as *P. moluccensis*, may experience physiological consequences as a result of settling into sub-optimal or inappropriate habitat, such as reduced body condition or growth (Booth, 1995; Munday, 2001; Pratchett et al., 2004). Live coral dwelling fish may also experience increased predation risk when associated with degraded habitat due to increased conspicuousness and competitive interactions (Coker et al., 2009; McCormick, 2009, 2012). These small scale changes in the ability of coral reef fish to find suitable habitat may have long-term effects on the persistence of populations, particularly as habitat loss on coral reefs increases (Jones and McCormick, 2002; Wilson et al., 2006).

Coral reef fishes use a combination of sensory cues in order to maximize the likelihood of finding suitable habitat (Lecchini et al., 2005; McCormick et al., 2010; Munday et al., 2009). In this study we found that the sediment used to simulate a turbid environment did not reduce chemical cues of live coral and therefore, in this study, *P. moluccensis* would have been able to use chemical

cues to find live coral. However, the increase in sediment ultimately blocked the visual cues necessary to find live coral and the use of chemical cues alone was not able to compensate for reduced visual cues. Previous studies have shown that visual cues are important (Lecchini et al., 2005; McCormick et al., 2010) and the present study highlights how important visual cues may be for fine scale decision making, such as when trying to choose between two close habitats.

Coral reef fishes often occupy a home range or territory that they conduct normal activities within, such as foraging, territorial defense and resting (Grüss et al., 2011; Lewis, 1997). Space use by a fish species can be affected by a variety of biotic (e.g. size, gender, density, food availability, presence of competitors and predators) and abiotic (e.g. shelter availability, topography) factors, and use can be modified as resource availability and requirements change (Grüss et al., 2011; Snover, 2008). In this study, *P. moluccensis* showed reduced movement at the high sediment level, meaning that once they had chosen a habitat, they generally stayed put. The reduction in movement may have been associated with an inability to assess predation risk. Adopting anti-predator behavior can cause sacrifices in time and energy for foraging and territorial defense, which could lead to fitness consequences (Lönnerstedt and McCormick, 2011). Though one would expect that coral reef fish might be safer staying in the habitat than in moving, recent research suggests that in suspended sediment at a concentration slightly higher than the ones used in this study (45 mg l<sup>-1</sup>, ~7.5 NTU) coral reef fish can experience increased risk of predation (Wenger et al., 2013). More research is required to untangle the interactive effects of suspended sediment on trade-offs between daily activities and risk avoidance.

The ability to safely move away from a habitat is not only important in terms of home range use, it also allows for fish to emigrate. In the present study, suspended sediment levels in the medium and high treatments resulted in more fish selecting partially dead and dead coral. However, once settled, a high proportion of individuals in the medium sediment treatment were able to emigrate to live coral, whereas individuals in the high sediment treatment that settled on partially dead and dead coral were much less likely to leave, possibly due to their inability to assess risk. Coral reef fish may emigrate for a number of reasons. As the needs of an individual change throughout their life, their initial habitat may no longer be suitable (Dahlgren and Eggleston, 2000). If there is a high density of conspecifics on a particular habitat that are competing for resources, the negative interactions and the fitness consequences associated with them may drive an individual to another habitat (Hixon, 1998; McCormick, 2012, 2009). To emigrate, the risk of staying has to be greater than risk associated with leaving, meaning that coral reef fish may continue to occupy sub-optimal conditions if they cannot predict the risk of predation and the presence of alternative habitats (Snover, 2008). As coral reef habitats continue to degrade, it will be increasingly important for coral reef fish to be able to initially locate suitable habitat or to move to more favorable habitat (Coker et al., 2012; McCormick, 2009). The results of the present study suggest that as suspended sediment and turbidity increase, it will be more difficult for coral reef fish to withstand habitat degradation, which could lead to changes in the community structure of reef fish populations.

To predict how environmental disturbances may affect reef communities and mitigate important impacts, it is crucial to know how organisms respond to the agents of change and the timescales on which changes occur (Groffman et al., 2006). The present study revealed that although *P. moluccensis* can tolerate low amounts of turbidity, when it reached a critical level, the performance of *P. moluccensis* markedly declined. It is clear that between the medium (3.3 NTU) and high (5 NTU) sediment treatment the sediment exceeded a level beyond which *P. moluccensis* could not properly

detect visual cues and assess risk. In each response variable measured there was a clear separation between the high sediment treatment and the lower levels of sediment. Our other studies that have examined the behavior of coral reef fish in elevated sediment have shown that there are clear sediment thresholds for changes in foraging ability and predation success (Wenger et al., 2012, 2013). However, this is the first study to show clear effects of sediment at such a low level. Since coral reef fishes will have different tolerances to sediment depending on their habitat, their range, and their functional group, it is important to further explore how sediment affects the day to day activities of fishes and the processes that regulate fish communities.

The surveys of turbidity and fish distribution presented here demonstrate that *P. moluccensis* live in areas where they are regularly exposed to turbidity levels that create sub-optimal conditions (i.e. >5 NTU). In this study, the threshold sat between the medium and high turbidity level, meaning that 5 NTU already negatively affects the fish. However, the survey results should be interpreted cautiously as the studies span different time periods and only encompass one region. The risk assessment is limited by the number of studies that have actually monitored turbidity and inshore reef fish populations. These areas are difficult to work in and thus only a small amount of information on inshore reefs actually exists. The lack of information about these reefs represents a critical knowledge gap. In addition, the impact of river plumes in the GBR has extended 20–30 km further offshore since European development (Wooldridge et al., 2006), meaning that coral reefs not previously exposed to flood plumes will be affected. A more comprehensive assessment of inshore reefs, including a longer time frame for turbidity monitoring and fish population evaluations is necessary to elucidate the full extent of the effects of suspended sediment on coral reef fish populations.

It is possible that different populations might have different responses to turbidity, depending on natural turbidity regimes where they are found. Ljunggren and Sandström (2007) found that species in high turbidity environments had better foraging ability than species found primarily in low turbidity environments. On the other hand, the rapidly fluctuating nature of turbidity events may make it difficult for different populations to adapt to increased turbidity, as has been seen with certain coral species (Anthony and Hoegh-Guldberg, 2003; Larcombe et al., 1995). More work is needed to explore how populations in these high turbidity areas are faring and whether or not the *P. moluccensis* used in our experimental studies that were collected from clear water reefs have different tolerance thresholds to individuals that have lived their settled lives on turbid reefs.

The high level of sediment in this experiment exceeded the trigger value set for suspended sediment in the GBR (De'ath and Fabricius, 2008; GBRMPA, 2009), so it is reasonable that *P. moluccensis* exhibited behavioral changes at this level. However, the surveys of turbidity clearly show that suspended sediment regularly exceeds the suspended sediment trigger point. The suspended sediment trigger point set by the Great Barrier Reef Marine Park Authority is actually an annual mean (2.0 mg l<sup>-1</sup>) with a slight adjustment during the wet season (2.4 mg l<sup>-1</sup>) (De'ath and Fabricius, 2008; GBRMPA, 2009). Unfortunately, there is not a conversion listed to convert this value into NTU, but based on the relationship that Larcombe et al. (1995) used to convert mg l<sup>-1</sup> to NTU, the GBRMPA target values would be 2.0 NTU and 2.4 NTU. Setting the threshold as an annual mean makes it possible for important small scale ecological changes to occur without being detected. During the wet season in Australia, suspended sediment levels can reach extreme concentrations, reaching up to 300 mg l<sup>-1</sup>. The wet season corresponds with a high fish recruitment season on the Great Barrier Reef (Brodie et al., 2007; McCormick, 2003) meaning that newly settled fish on turbid coral reefs would be experiencing

sub-optimal conditions early in life. Habitat choice at this stage is crucial for survival as newly settled coral reef fish experience over 50% mortality within the first 2 days of being on the reef (Almany and Webster, 2006). If suspended sediment drives reduced habitat choice, as this study suggests, then significant changes in populations may occur on a time scale of hours not years. Turbidity events occur year round and are increasing, meaning that turbidity is becoming a chronic condition on coral reefs (Fabricius et al., 2012). It is likely that during each turbidity event, coral reef fishes will be affected, and these small scale interactions may add up to become larger issues. More research is necessary to refine suspended sediment thresholds so that they take into consideration how short term turbidity events modify coral reef fish populations.

In conclusion, this study provides clear evidence that relatively low levels of suspended sediment can impair the ability of *P. moluccensis* to successfully find optimal habitat and move around the surrounding environment. Furthermore, there was a clear sediment threshold for behavioral changes, and this turbidity is currently reached relatively frequently on inshore reefs of the GBR. This study illustrates the need to fully understand the influence of suspended sediment on coral reef fish behavior if we are to better ascertain how coral reef fishes are affected by increasing sediment loads. Given the compounding effects of multiple pollutants that are also common inshore (Brodie et al., 2012), it is important to explore the coupled interaction between sediment and other contaminants. This is the first study to attempt to identify coral reefs where fishes may be experiencing sub-optimal conditions and it has important implications for water quality management on coral reefs. Small scale ecological changes can have large impacts on cohort success (Houde, 1987) and so increased suspended sediment has the potential to significantly reduce the resilience of reef fish communities on inshore coral reefs, particularly through its effects on the vulnerable juvenile life stages of fishes.

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## References

- Almany, G.R., Webster, M.S., 2006. The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* 25, 19–22.
- Anthony, K.R.N., Fabricius, K.E., 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *J. Exp. Mar. Biol. Ecol.* 252, 221–253.
- Anthony, K.R., Hoegh-Guldberg, O., 2003. Kinetics of photoacclimation in corals. *Oecologia* 134, 23–31.
- Bellwood, D.R., Hoey, A.S., Ackerman, J.L., Depczynski, M., 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biol.* 12, 1587–1594.
- Booth, D.J., 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* 76, 91–106.
- Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecol. Manage.* 59, 225–236.
- Brodie, J., De'ath, G., Devlin, M., Furnas, M., Wright, M., 2007. Spatial and temporal patterns of near-surface chlorophyll *a* in the Great Barrier Reef lagoon. *Mar. Freshwater Res.* 58, 342–353.
- Brodie, J.E., Kroon, F.J., Schaffelke, B., Wolanski, E.C., Lewis, S.E., Devlin, M.J., Bohnet, I.C., Bainbridge, Z.T., Waterhouse, J., Davis, A.M., 2012. Terrestrial pollutant runoff to the Great Barrier Reef: an update of issues, priorities and management responses. *Mar. Pollut. Bull.* 65, 81–100.
- Browne, N.K., Smithers, S.G., Perry, C.T., 2012. Spatial and temporal variations in turbidity on two inshore turbid reefs on the Great Barrier Reef, Australia. *Coral Reefs*. <http://dx.doi.org/10.1007/s00338-012-0965-1>.

- Carter, R.M., Johnson, D.P., Hooper, K.G., 1993. Episodic post-glacial sea-level rise and the sedimentary evolution of a tropical embayment (Cleveland Bay, Great Barrier Reef shelf, Australia). *Aust. J. Earth Sci.* 40, 229–255.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210, 223–253.
- Coker, D.J., Pratchett, M.S., Munday, P.L., 2009. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behav. Ecol.* 20, 1204–1210.
- Coker, D.J., Pratchett, M.S., Munday, P.L., 2012. Influence of coral bleaching, coral mortality and conspecific aggression on movement and distribution of coral-dwelling fish. *J. Exp. Mar. Biol. Ecol.* 414–415, 62–68.
- Cooper, T.E., Ridd, P.V., Ulstrup, K.E., Humphrey, C., Slivkoff, M., Fabricius, K.E., 2008. Temporal dynamics in coral bioindicators for water quality on coastal coral reefs of the Great Barrier Reef. *Mar. Freshwater Res.* 59, 703–716.
- Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81, 2227–2240.
- De'ath, G., Fabricius, K.E., 2008. Water quality of the Great Barrier Reef: distributions, effects on reef biota and trigger values for the protection of ecosystem health. Final Report to the Great Barrier Reef Marine Park Authority. Australian Institute of Marine Science, Townsville, Australia.
- Devlin, M., Brodie, J., Waterhouse, J., Mitchell, A., Audas, D., Haynes, D., 2003. Exposure of Great Barrier Reef inner-shelf reefs to river-borne contaminants: protecting the Values of Rivers, Wetlands and the Reef. In: 2nd National Conference on Aquatic Environments: Sustaining our Aquatic Environments – Implementing Solutions, 20–23 November 2001, Townsville, Australia.
- Devlin, M.J., Wenger, A.S., Waterhouse, J., Alvarez-Romero, J., Abbot, B., Bainbridge, Z.T., Lewis, S.E., 2012. Reef rescue marine monitoring program: flood plume monitoring annual report. Incorporating Results from the Extreme Weather Incident Response program, Flood Plume Monitoring. Report Number 11/12.
- Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321, 26–29.
- Dixon, D.L., Jones, G.P., Munday, P.L., Planes, S., Pratchett, M.S., Srinivasan, M., Syms, C., Thorrold, S.R., 2008. Coral reef fish smell leaves to find island homes. *Proc. R. Soc. B.* 275, 2831–2839.
- Ebeling, A.W., Hixon, M.A., 1991. Tropical and temperate reef fishes: comparison of community structures. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 509–563.
- Fabricius, K., De'ath, G., McCook, L., Turak, E., Williams, D.M.C.B., 2005. Changes in algal, coral, and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar. Pollut. Bull.* 51, 384–398.
- Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50, 125–146.
- Fabricius, K.E., De'ath, G., Humphrey, C., Zagorski, I., Schaffelke, B., 2012. Intra-annual variation in turbidity in response to terrestrial runoff on near-shore coral reefs of the Great Barrier Reef. *Estuar Coast. Shelf Sci.*, <<http://dx.doi.org/10.1016/j.ecss.2012.03.010>>.
- Feary, D.A., Almany, G.R., Jones, G.P., McCormick, M.I., 2007. Coral degradation and the structure of tropical reef fish communities. *Mar. Ecol. Prog. Ser.* 333, 243–248.
- Furnas, M., 2003. Catchments and Corals: Terrestrial Runoff To The Great Barrier Reef. Australian Institute of Marine Science, Townsville, Australia.
- Gaillard, J., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van-Moorter, B., 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Phil. Trans. R. Soc. B* 365, 2255–2265.
- Gerlach, G., Atema, J., Kingsford, M.J., Black, K.P., Miller-Sims, V., 2007. Smelling home can prevent dispersal of reef fish larvae. *Proc. Nat. Acad. Sci.* 104, 858–863.
- Great Barrier Reef Marine Park Authority, 2009. Water Quality Guidelines for the Great Barrier Reef Marine Park. Great Barrier Reef Marine Park Authority, Townsville, Australia.
- Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., Poff, N.L., Rejeski, D.W., Reynolds, J.F., Turner, M.G., Weathers, K.C., Weins, J., 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* 9, 1–13.
- Grüss, A., Kaplan, D.M., Guénette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.* 144, 692–702.
- Hixon, M., 1998. Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Austral. Ecol.* 23, 192–201.
- Houde, E.D., 1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2, 17–29.
- Jones, G.P., McCormick, M.I., 2002. Numerical and energetic processes in the ecology of coral reef fishes. In: Sale, P.F. (Ed.), *Coral Reef Fishes: Dynamics and Diversity in A Complex Ecosystem*. Academic Press, San Diego, pp. 221–238.
- Jones, G., McCormick, M., Srinivasan, M., Eagle, J.V., 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc. Nat. Acad. Sci.* 101, 8251–8253.
- Kroon, F.J., 2005. Behavioural avoidance of acidified water by juveniles of four commercial fish and prawn species with migratory life stages. *Mar. Ecol. Prog. Ser.* 285, 193–204.
- Kroon, F.J., Kuhnert, P.M., Henderson, B.L., Wilkinson, S.N., Kinsey-Henderson, A., Abbott, B., Brodie, J.E., Turner, R.D.R., 2012. River loads of suspended solids, nitrogen, phosphorous and herbicides delivered to the Great Barrier Reef lagoon. *Mar. Pollut. Bull.* 65, 167–181.
- Larcombe, P., Ridd, P.V., Prytz, A., Wilson, B., 1995. Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. *Coral Reefs* 14, 163–171.

- Lecchini, D., Planes, S., Galzin, R., 2005. Experimental assessment of sensory modalities of coral-reef fish larvae in the recognition of their settlement habitat. *Behav. Ecol. Sociobiol.* 58, 18–26.
- Leis, J.M., Carson-Ewart, B.M., 2002. In situ settlement behaviour damselfish (Pomacentridae) larvae. *J. Fish Biol.* 61, 325–346.
- Letourneur, Y., Kulbicki, M., Labrosse, P., 1998. Spatial structure of commercial reef fish communities along a terrestrial runoff gradient in the northern lagoon of New Caledonia. *Environ. Biol. Fish.* 51, 141–159.
- Lewis, A.R., 1997. Recruitment and post-recruit immigration affect the local population size of coral reef fishes. *Coral Reefs* 16, 139–149.
- Lönnerstedt, O.M., McCormick, M.I., 2011. Growth history and intrinsic factors influence risk assessment at a critical life transition for a fish. *Coral Reefs* 30, 805–812.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312, 1806–1809.
- Ljunggren, L., Sandström, A., 2007. Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. *J. Fish Biol.* 70, 1319–1334.
- Mallela, J., Roberts, C., Harrod, C., Goldspink, C.R., 2007. Distributional patterns and community structure of Caribbean coral reef fishes within a river-impacted bay. *J. Fish Biol.* 70, 523–537.
- McCormick, M.I., 2012. Lethal effects of habitat degradation on fishes through changing competitive advantage. *Proc. R. Soc. London B.* <http://dx.doi.org/10.1098/rspb.2012.0854>.
- McCormick, M.I., 2009. Behaviourally mediated phenotypic selection in a disturbed Coral Reef environment. *PLoS ONE* 4, e7096.
- McCormick, M.I., 2003. Consumption of coral propagules after mass spawning enhances larval quality of damselfish through maternal effects. *Oecologia* 136, 37–45.
- McCormick, M.I., Weaver, C., 2012. It pays to be pushy: intracohort interference competition between two reef fishes. *PLoS ONE* 7, e42590.
- McCormick, M.I., Makey, L.J., 1997. Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. *Mar. Ecol. Prog. Ser.* 153, 247–257.
- McCormick, M.I., Moore, J.A.Y., Munday, P.L., 2010. Influence of habitat degradation on fish replenishment. *Coral Reefs* 29, 537–546.
- McCulloch, M., Fallon, S.R., Wyndham, T., Hendy, E., Lough, J., Barnes, D., 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421, 727–730.
- Munday, P.L., 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* 128, 585–593.
- Munday, P.L., Dixon, D.L., Donelson, J.M., Jones, G.P., Pratchett, M.S., Devitsina, G.V., Doving, K.B., 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Nat. Acad. Sci.* 106, 1848–1852.
- Odling-Smee, L., Braithwaite, V.A., 2003. The role of learning in fish orientation. *Fish. Fish.* 4, 235–246.
- Öhman, M.C., Munday, P.L., Jones, G.P., Caley, M.J., 1998. Settlement strategies and distribution patterns of coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 225, 219–238.
- Pratchett, M.S., Wilson, S.K., Berumen, M.L., McCormick, M.I., 2004. Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs* 23, 352–356.
- Rogers, C.S., 1979. The effect of shading on coral reef structure and function. *J. Exp. Mar. Biol. Ecol.* 41, 269–288.
- Schaffelke, B., Carleton, J., Doyle, J., Furnas, M., Gunn, K., Skuza, M., Wright, M., Zagorskis, I., 2011. Reef Rescue Marine Monitoring Program, Final Report of AIMS Activities 2010/11 – Inshore Water Quality Monitoring. Report for the Great Barrier Reef Marine Park Authority. Australian Institute of Marine Science, Townsville, Australia.
- Snover, M.L., 2008. Ontogenetic habitat shifts in marine organisms: influencing factors and the impact of climate variability. *Bull. Mar. Sci.* 83, 53–67.
- Sweatman, H.P.A., 1983. Influence of conspecifics on choice settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. *Mar. Biol.* 75, 225–229.
- Syms, C., Jones, G.P., 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81, 2714–2729.
- Telesnicki, G.J., Goldberg, W.M., 1995. Effects of turbidity on the photosynthesis and respiration of two south Florida reef coral species. *Bull. Mar. Sci.* 57, 527–539.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Van de Meutter, F., Meester, L.D., Stoks, R., 2005. Water turbidity affects predator-prey interactions in a fish damselfly system. *Oecologia* 144, 327–336.
- Wenger, A.S., Johansen, J.L., Jones, G.P., 2011. Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. *Coral Reefs* 30, 879–887.
- Wenger, A.S., Johansen, J.L., Jones, G.P., 2012. Increasing suspended sediment reduces foraging, growth and condition of a planktivorous damselfish. *J. Exp. Mar. Biol. Ecol.* 428, 43–48.
- Wenger, A.S., McCormick, M., McLeod, I.M., Jones, G.P., 2013. Suspended sediment alters predator-prey interactions between two coral reef fishes. *Coral Reefs*. <http://dx.doi.org/10.1007/s00338-012-0991-z>.
- Wilson, S.K., Graham, N.A., Pratchett, M.S., Jones, G.P., Polunin, N.V., 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biol.* 12, 2220–2234.
- Wooldridge, S., Brodie, J., Furnas, M., 2006. Exposure of inner-shelf reefs to nutrient enriched runoff entering the Great Barrier Reef lagoon: post-European changes and the design of water quality targets. *Mar. Pollut. Bull.* 52, 1467–1479.