

## Suspended sediment alters predator–prey interactions between two coral reef fishes

A. S. Wenger · M. I. McCormick · I. M. McLeod · G. P. Jones

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**Abstract** Sediment derived from agriculture and development increases water turbidity and threatens the health of inshore coral reefs. In this study, we examined whether suspended sediment could change predation patterns through a reduction in visual cues. We measured survivorship of newly settled *Chromis tripteronalis* exposed to *Pseudochromis fuscus*, a common predator of juvenile damselfishes, in aquaria with one of four turbidity levels. Increased turbidity led to a nonlinear response in predation patterns. Predator-induced mortality was ~50 % in the control and low turbidity level, but exhibited a substantial increase in the medium level. In the highest turbidity level, predation rates declined to the level seen in the control. These results suggest an imbalance in how the predator and prey cope with turbidity. A turbidity-induced change to the outcome of predator–prey interactions represents a major change to the fundamental processes that regulate fish assemblages.

**Keywords** Turbidity · Sediment thresholds · Damselfish · Predation

### Introduction

Elevated sediment loading into marine environments increases water turbidity and poses a threat to the health of coral reefs worldwide, with increased turbidity being associated with declines in the abundance of fish and coral and shifts in species distributions on impacted reefs (Brodie et al. 2012). Coral reef fishes rely heavily on visual cues for basic functions such as foraging and predator avoidance (Hobson 1979; Goatley and Bellwood 2009). Impacts that have chronic negative effects on the visual environment may be detrimental to these important activities. Recent research has shown that high levels of turbidity can impair habitat choice and foraging success of planktivorous coral reef fishes through a reduced ability to detect visual cues (Wenger et al. 2011, 2012). However, the impact of increased turbidity on predator–prey interactions on coral reefs has received little attention. Fish generally rely on visual and chemical cues to detect predators (Ferrari et al. 2010). Anything that reduces their detection of one or both of these cues will affect how the prey and predator perceive each other and therefore the outcome of the predatory encounter (Lima and Steury 2005). Research suggests that in the absence of visual cues, fish respond more strongly to chemical cues of predators (e.g., Hartman and Abrahams 2000); for instance, Leahy et al. (2011) found that *Acanthochromis polyacanthus*, a planktivorous coral reef fish, moved around more cautiously in turbid water when predator chemical cues were present. However, the impact of increasing turbidity on actual predation rates between coral reef fishes has not been investigated.

The interactions between predators and prey are strongly impacted by environmental conditions; for instance, for foraging planktivorous fishes, mild turbidity in freshwater lakes and subtropical estuaries appears to enhance prey

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A. S. Wenger (✉) · M. I. McCormick · I. M. McLeod · G. P. Jones  
School of Marine and Tropical Biology, ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia  
e-mail: amelia.wenger@my.jcu.edu.au

A. S. Wenger  
Catchment to Reef Research Group, TropWATER,  
James Cook University, Townsville, QLD 4811, Australia

contrast with its background, making it easier for the predator to see them (e.g., Gregory and Northcote 1993; Utne 1997; Utne-Palm 1999; Rowe and Dean 1998). However, at higher levels of turbidity, foraging success declines, generating a nonlinear relationship between foraging success and turbidity (Utne-Palm 2002).

In contrast, piscivores appear to be much more sensitive to increasing turbidity because they tend to detect prey from farther away. The increased encounter distance intensifies the reduction in light intensity and contrast degradation created by suspended sediment (Fiksen et al. 2002). Several studies have shown a linear/exponential decline in foraging success of a piscivore with increasing turbidity (e.g., Hect and Van de Lingen 1992; Reid et al. 1999; De Robertis et al. 2003). In this case, prey may use high levels of turbidity as shelter from predation, thereby increasing survival (Utne-Palm 2002). However, Gregory and Levings (1996) found that turbidity had no effect on the predation of juvenile salmonids by *Oncorhynchus clarkii clarkii*, a cutthroat trout species, so the prey species were unable to use turbid areas as shelter. Regardless of whether studies showed changes in fish–zooplankton or fish–fish predator–prey interactions, there was always a threshold level of turbidity that elicited a behavioral change. Because coral reefs are receiving increased loads of suspended sediment (Kroon et al. 2012), it is critical to better understand how turbidity influences important ecological processes such as predator–prey interactions and when these behavioral changes are likely to occur.

This study experimentally examined the predation rates of *Pseudochromis fuscus*, a common piscivore, on juvenile *Chromis atripectoralis* (Pomacentridae), a planktivorous damselfish in four turbidity levels in order to determine when turbidity provoked a behavioral response. We predicted that *P. fuscus* would exhibit similar patterns as freshwater predators and would therefore show reduced predation as turbidity increased.

## Materials and methods

This experiment was conducted on Lizard Island on the Great Barrier Reef, Australia (14°40'S, 145°28' E), in February 2011. Newly settled *C. atripectoralis* (15–20 mm SL) were selected as the prey due to their high abundance on tropical reefs. *Pseudochromis fuscus* (75–80 mm), a common predator of juvenile damselfishes (Feeney et al. 2012), was chosen as the predator. All fishes were collected using diluted clove oil and hand nets and were held in aquaria with artificial habitat and filtered aerated seawater for 48 h prior to experiments, during which *C. atripectoralis* and *P. fuscus* were fed newly hatched *Artemia* sp. and frozen squid, respectively.

The effects of turbidity on the predation of *C. atripectoralis* were examined by adjusting suspended sediment levels in aquaria to four concentrations: (1) control (0 mg L<sup>-1</sup>), (2) low (30 mg L<sup>-1</sup>), (3) medium (45 mg L<sup>-1</sup>), and (4) high (60 mg L<sup>-1</sup>). Australian bentonite was used as sediment to reflect the muddy sediments and clays common on the inshore GBR (McCulloch et al. 2003). The turbidity levels were selected to encompass the range found on coral reefs worldwide (Wenger et al. 2012). These levels of suspended sediment represent natural variability that can occur on inshore coral reefs (e.g., Larcombe et al. 1995; Ogston et al. 2004). Predation experiments were performed in eight 45-L (50 × 30 × 30 cm) tanks, from 7 a.m. to 7 p.m. in a temperature-controlled laboratory (29 °C) with artificial light. Each tank was fed by a submersible pump (1,000 L h<sup>-1</sup>) placed in an external 10-L aerated sump. Each sump also contained a disturbance pump (1,000 L h<sup>-1</sup>) to create uniform turbidity throughout each trial. Each tank had a coral head (10 cm) of *Pocillopora damicornis*, a branching coral used by many coral-dwelling fish as habitat (Feary et al. 2007), to provide shelter for *C. atripectoralis*. The coral heads were suspended off the bottom of the tank to ensure that no sediment could settle around them. A small piece of PVC pipe was also placed into each tank as habitat for the *P. fuscus*.

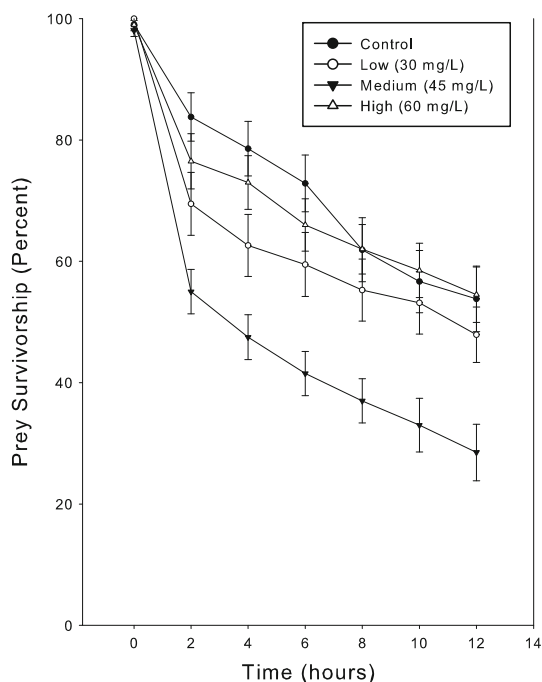
At the start of each trial, tanks were randomly assigned to one of the four turbidity levels. Ten *C. atripectoralis* were selected haphazardly from the holding tank and placed in each of the eight experimental tanks. Once all *C. atripectoralis* were in the tanks, they were fed *Artemia* sp. ad libitum. The *C. atripectoralis* were given 8 h to acclimate before the start of the experiment. This acclimation time was based on acclimation times used in a previous study on species of the same genus (Feary et al. 2007). The *P. fuscus* were starved for 12 h prior to the experiment to ensure that they would actively hunt for food. At the start of each predation trial, one naïve *P. fuscus* was randomly assigned to each tank. A barrier was put in prior to the addition of the *P. fuscus* to separate the prey and the predator. The *P. fuscus* was given 30 min to acclimate before the barrier was carefully removed. Surviving *C. atripectoralis* was counted every 2 h over a 12-h period. A total of 20 predation trials were run for each turbidity level. A randomization-based one-way ANOVA with Tukey's HSD post hoc analysis was performed in MATLAB 7.13 to determine whether there were significant differences in predation between turbidity treatments after 2 h and at the end of each trial.

## Results and discussion

Increasing turbidity led to significant changes in predation patterns exhibited by *P. fuscus* throughout the experiment

(ANOVA,  $F_{3,76} = 6.32$ ,  $p < 0.001$ ). The relationship between turbidity and predation was nonlinear, with highest prey mortality in the medium turbidity level, in which the *P. fuscus* consumed  $70.8 \pm 4.7\%$  (mean  $\pm$  SE) of the *C. atripectoralis* (Tukey's HSD,  $p = 0.002$ ). In the control and low turbidity treatments, *P. fuscus* consumed  $45.8 \pm 5.4\%$  and  $52.1 \pm 4.6\%$  of the *C. atripectoralis*, respectively. Though predation rates were high in the medium treatment, they actually declined in the high turbidity treatment and the *P. fuscus* only consumed  $44.9 \pm 4.6\%$  of the *C. atripectoralis* (Fig. 1). There were no significant differences in predation rates among the control, low, and high turbidity treatments (Tukey's HSD,  $p > 0.5$ ).

The nonlinear relationship observed contradicts previous studies examining piscivory and turbidity (Hect and Van de Lingen 1992; Reid et al. 1999; De Robertis et al. 2003) and reflects the patterns more often seen in studies on planktivory and turbidity (Utne-Palm 2002). The results of this experiment demonstrate that suspended sediment can have a marked effect on the interactions between a predatory coral reef fish and its prey. Predator-prey interactions are critical in shaping the demography and community structure of coral reef fishes (Hixon 1991; Holmes and McCormick 2010) and this research shows that suspended sediment can lead to significant changes in mortality rates for juveniles that are already extremely vulnerable to predation (Almany and Webster 2006). The



**Fig. 1** Differences over time in survival ( $\pm$ SE) of *C. atripectoralis* among four sediment treatments

high and selective pressure at this life stage means that relatively small changes in mortality rates can lead to large differences in the number of prey individuals that reach maturity.

In this study, the medium level of turbidity was advantageous for *P. fuscus*, establishing that increased turbidity can confer some benefit to coral reef predators. Turbidity at the medium level may have enhanced the contrast between the prey and its background, allowing the predator to better visualize the prey (Utne-Palm 2002). This result is surprising as previous studies indicate that piscivores are more sensitive to turbidity than planktivores (Fiksen et al. 2002; De Robertis et al. 2003). The current study is the first one to show that up to a threshold, a piscivore's ability to visualize prey may be positively affected by suspended sediment.

*Pseudochromis fuscus* has relatively large eyes that enable it to detect prey in low light conditions in which it may be difficult for the prey species to detect the predator (Goatley and Bellwood 2009). Recent studies have shown that at  $45 \text{ mg l}^{-1}$  (the medium level of sediment in this study), *Pomacentrus amboinensis* and *P. moluccensis* lose their ability to detect suitable habitat at settlement (Wenger et al. 2011). Additionally, at  $45 \text{ mg l}^{-1}$ , *A. polyacanthus* (Pomacentridae) shows decreased foraging efficiency and reduced growth rates (Wenger et al. 2012). The results of this study and previous studies imply that  $45 \text{ mg l}^{-1}$  may be a threshold for visual cues in prey species. Miner and Stein (1996) observed that the reactive distance of the prey, *Lepomis macrochirus* (bluegill), to the predator, *Micropterus salmoides* (largemouth Bass), decreased exponentially in turbidity, suggesting that a reduction in the ability of *C. atripectoralis* to detect and escape *P. fuscus* may have led to an increase in predation at the medium level of sediment.

Predation is one of the main drivers of mortality in newly settled coral reef fish (Hixon 1991; Almany and Webster 2006; McCormick and Meekan 2007). Small differences in juvenile mortality rates can translate into major differences in adult population size (Jones 1990, 1991; Caley et al. 1996). The sediment-induced increase in mortality of the magnitude described here could lead to a substantial reduction in the numbers of fish surviving to reproductive age. Sediment and turbidity have been shown to change fish community structures in other aquatic ecosystems, such as freshwater lakes (Swenson 1978) and subtropical estuaries (Cyrus and Blaber 1992). This study shows that a moderate amount of suspended sediment can drive changes in predator-prey interactions that significantly impact prey.

In all the turbidity levels, *P. fuscus* was the most successful at capturing prey within the first 2 h of the trial, consuming  $15.4\% \pm 3.9\%$ ,  $30.5 \pm 5.2\%$ ,  $43.8 \pm 3.8\%$ , and  $22.7 \pm 4.5\%$  of *C. atripectoralis* in the control, low,

medium, and high treatments, respectively (Fig. 1). Although these results may be partially due to the hunger levels of the *P. fuscus*, it is important to note that the predator was successful in finding the prey immediately, meaning that it adjusted to the turbidity conditions quickly. There was a significant difference in predation among treatments after 2 h (ANOVA,  $F_{3,74} = 6.32$ ,  $p = 0.002$ ), with the *P. fuscus* in the medium treatment consuming significantly more prey than either the control treatment (Tukey's HSD,  $p < 0.0001$ ) or the high treatment (Tukey's HSD,  $p = 0.0009$ ). Although overall the predation rates in the low turbidity treatment were significantly lower than in the medium turbidity treatment, predation rates between the low and medium treatments after 2 h were not significantly different (Tukey's HSD,  $p > 0.5$ ). The pulsed nature of turbidity conditions means that coral reef fishes may only be exposed to high levels of turbidity for a short period of time (Larcombe et al. 1995) and predators may be able to capitalize on these conditions before the prey species has time to adapt. Rapidly fluctuating turbidity conditions have been shown to limit the ability of coral species to successfully acclimate to increased sediment (Anthony and Hoegh-Guldberg 2003). More research is necessary in order to fully assess acclimation abilities of predator and prey species in fluctuating turbidity conditions.

Prey species use a combination of chemical and visual cues to assess risk; however, when one of the senses is limited, fishes can compensate for this reduction in information by relying more on another (Hartman and Abrahams 2000). Interestingly, the predation rates in the turbidity treatments seem to level off after 2 h and show a similar linear decline between treatments (Fig. 1). Though  $45 \text{ mg l}^{-1}$  may be a threshold for visual cues, it seems that there may be an increased reliance on chemical cues by *C. atripectoralis*. Previous studies have shown that coral reef fishes can learn predator chemical cues when in conjunction with conspecific chemical alarm cues (Ferrari et al. 2010). Additionally, recent studies show an increased use of chemical cues (Hartman and Abrahams 2000) and reduced activity (Leahy et al. 2011) when no visual cues of the predator are present. Once individuals had been captured by *P. fuscus* in the treatments and chemical alarm cues had been released, the *C. atripectoralis* may have learned the predator cue and modified their behavior. More research on the different responses of the predator and prey to sensory cues in increasing levels of sediment is necessary to elucidate the exact causes for changing predation rates.

In the high level of turbidity used in this experiment, predation rates returned to rates seen in the control and low levels of turbidity. Because *P. fuscus* feed on relatively large, mobile prey, they may not have evolved to perceive fine detail (Hobson 1979; Goatley et al. 2010). The increase in survival rate of *C. atripectoralis* from the medium to the high level of

sediment may indicate that the turbidity reached a level where it was impacting the visual information of the predator. This threshold level of turbidity most likely inhibited predation due to the degradation of the contrast between the prey and its background (Utne-Palm 2002; Horodysky et al. 2010). *P. fuscus* naturally feeds on recently settled fishes and small benthic invertebrates and in periods of no fish recruitment they predate overwhelmingly (99.4 %) on invertebrates (Feeney et al. 2012). In periods of high turbidity that hindered the ability of *P. fuscus* to capture fishes, they could potentially focus foraging efforts on the substrate to compensate for reduced consumption of fishes. The constraints of a tank experiment did not allow for an examination of the complex dynamics of coral reef communities and the multiple predator–prey interactions that may exist. More research is necessary to disentangle all of the effects that turbidity may have on trophodynamics.

This experiment used coral reef fishes that were adapted to the relatively clear water around Lizard Island. It is likely that different populations will have different responses to turbidity, depending on natural turbidity regimes where they are found. Indeed, Ljunggren and Sandström (2007) showed that species living in areas of high turbidity are better at foraging in turbidity than species found primarily in low turbidity environments. Additionally, Bisson and Bilby (1982) showed that previous experience in turbid conditions can increase the threshold turbidity level required to elicit behavioral changes in fishes. More work is needed to explore whether similar responses to turbidity would exist in populations on naturally turbid reefs.

This is a preliminary study on the effects of suspended sediment on predator–prey interactions between two coral reef fishes, and the mechanisms identified above that may be causing the changes in predation rates are still largely hypothetical. Unfortunately, one of the limitations of this experiment is that the turbid conditions limited the ability of the researchers to observe behavioral changes. Behavioral studies that do not rely on visual observation are needed to clarify the underlying mechanisms that led to the shifts in the predator–prey interactions in different levels of turbidity.

In conclusion, this study provides clear evidence that suspended sediment can influence predator–prey interactions between two coral reef fishes. Moderate sediment levels favored the predator, leading to enhanced predation rates. However, when sediment increased further, predation was reduced. This study provides the first indication that as suspended sediment increases, coral reef fish community interactions are altered. As development and urbanization become more prevalent, coral reefs will be subjected to greater loads of suspended sediment (Brodie et al. 2012). With an increasing amount of fine sediment flowing onto the reef that will be available for resuspension, reef fish will be exposed to higher turbidity year round (Fabricius

et al. 2012). The results of this study highlight the importance of examining the effects of suspended sediment on fish species from a range of functional groups to better understand how small-scale ecological processes are altered by increasing suspended sediment.

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